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QUAIN'S

ELEMENTS OF ANATOMY

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IN FOUR VOLUMES

VOL. III.

NEUROLOGY

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PREFACE TO VOLUME III

THE third volume of Quain's Anatomy (Eleventh Edition) is devoted to the description of the Structure of the Nervous System, including the Organs of Special Sense. The macroscopic anatomy has been undertaken by Professor Symington, the microscopic anatomy by Professor Schäfer. The volume has been issued in two parts, the first of which, including the general structure and mode of development of the elements of the nervous system, and the structure of the central nervous system, appeared in September 1908; the second, dealing with the peripheral nervous system and sense organs, in September 1909. A considerable portion of the work has been rewritten, and a large number of the illustrations are new, many having been prepared expressly for this edition. Others are due to the courtesy of various authors and publishers, who have given permission for the reproduction of illustrations from books and journals written or published by them. The authorship of each is indicated under its title, but the editors desire especially to acknowledge their indebtedness to Professor Ramón Cajal, who was good enough to lend many of his original drawings for reproduction in this book, and whose work on the Structure of the Nervous System has been consulted throughout in the account of the microscopic structure of the brain and cord. Special acknowledgment is also due to the text-books of Edinger, van Gehuchten, and Llewellys Barker, to the important monographs on the Brain and on the Organ of Hearing by Professor G. Retzius, to various articles in the 'Biological Investigations' of the same author, and to the articles by Leber, H. Virchow, Greeff, and others, in the second edition of Græfe-Saemisch 'Handbuch der Augenheilkunde.' The Editors have to thank Dr. Lindsay Johnson for permission to reproduce the coloured plate showing the ophthalmoscopic appearance of the retina which is inserted opposite page 226, and Mr. L. Laurance for the use of the block of fig. 162.

Most of the new figures illustrating the macroscopic anatomy of the brain and sense organs have been drawn by Mr. S. A. Sewell; those illustrating the microscopic anatomy have been drawn or photographed by Mr. Richard Muir.

The index has been prepared by Dr. T. W. P. Lawrence.

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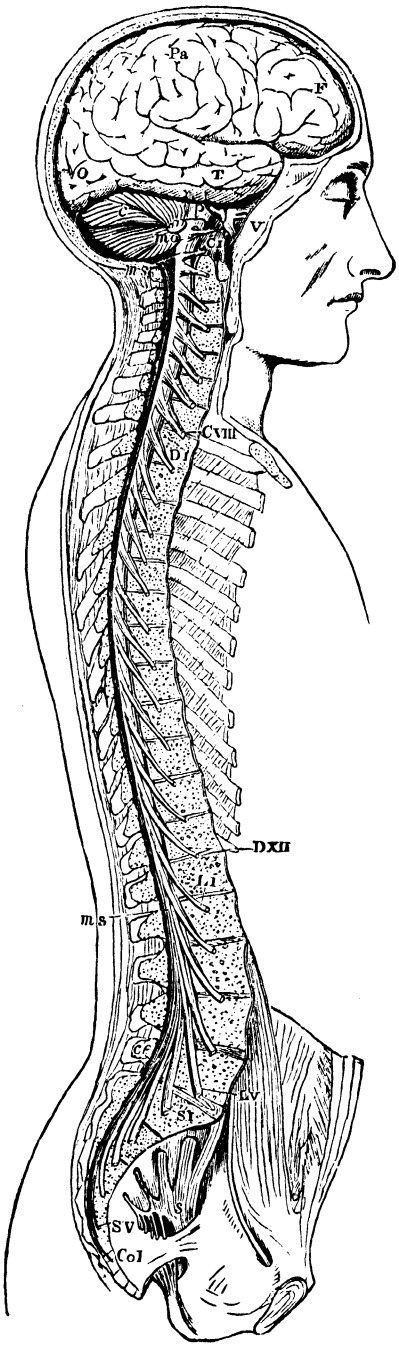
NEUROLOGY.

THE GENERAL STRUCTURE AND MODE OF DEVELOPMENT OF THE NERVOUS SYSTEM.

THE nervous system is essentially constituted of nerve-cells and their processes. The processes are termed axons and dendrons or dendrites. Nerve-fibres are always axons of nerve-cells. The nervous substance proper is supported partly by connective tissue which brings its vascular supply, partly by a tissue peculiar to the nervous system termed neuroglia, consisting of special cells and fibres, which have an ectodermic origin in common with the nerve-cells. The nucleated bodies of the nerve-cells are contained in the grey matter of the nerve-centres and in the ganglia: their nerve-fibre processes form the white matter of the nerve-centres as well as the nerves, which are distributed to all parts of the body.

Anatomically the nervous system is usually described as consisting of two parts—viz. the cerebrospinal system and the sympathetic system. The **cerebrospinal system** (fig. 1) comprises the spinal cord and the various divisions of the brain, together with the nerves which pass to and from the brain and spinal cord, and also the ganglia upon the roots of certain of these nerves (cerebrospinal ganglia). The spinal cord and brain constitute the *central nervous system* or *cerebrospinal axis*. The main divisions of the brain are from below upwards: (1) The *hind-brain*, comprising the *spinal bulb* or *medulla oblongata* (which is in direct continuation with the spinal cord), the *pons*, and the *cerebellum*; (2) the *mid-brain*, comprising the *pedunculi cerebri* and the *corpora quadrigemina*; (3) the *fore-brain*, including the *thalami*, the *corpora striata*, and the *cerebral hemispheres*.

The **sympathetic system** (fig. 2) forms a chain of nerves and ganglia in front of the vertebral column which is connected with the thoracic and lumbar regions of the spinal cord (first thoracic to third lumbar segment) by fine nervous cords, the so-called *white rami*. From the sympathetic chain nerves pass to blood-vessels and viscera, and connected with these are other ganglia belonging to the same system. From the ganglia of the chain also other fine cords, the *grey rami*, pass to be distributed to all the spinal nerves, and along with these to the vessels, hair-muscles, and glands of the skin. The white rami are composed of very fine medullated fibres, which arise from cells in the lateral part of the grey matter of the spinal cord and are passing to the sympathetic ganglia, in one of which, either a ganglion of the chain or a more peripherally placed ganglion, they end. But, besides these white fibres which pass to the sympathetic, there are other nerves, similarly constituted of fine medullated fibres,



which emerge along with certain of the cerebral nerves—viz. the third, seventh, ninth, tenth, and eleventh—and yet others which emerge along with the ventral roots of the second and third sacral nerves. These do not proceed to join the sympathetic chain, but pass more directly to the visceral and vascular systems, to end in small ganglia near the periphery. But in their mode of origin and in the parts to which they are distributed, the fibres in question, which constitute the *cranial* and *sacral splanchnic systems* of Gaskell, closely resemble the thoracic and lumbar splanchnic nerve-fibres which pass to the sympathetic chain. They are therefore grouped by physiologists along with the sympathetic nerves and ganglia, and are distinguished by Langley under the term *parasympathetic nerves* ; while to the whole system of sympathetic and parasympathetic nerve-fibres and ganglia the same author has given the name of **autonomic nervous system.**

The nerves of the autonomic system differ from those of the cerebrospinal system in being formed of much finer fibres, and further in the fact that those fibres which arise in the ganglia proper to this system as a general rule lack the medullary sheath which gives to ordinary nerves their white appearance; so that these *sympathetic nerve-fibres*, which are proceeding to their distribution in the tissues, have a greyish colour (*non-medullated fibres, fibres of Remak*). The sympathetic (autonomic) ganglia differ from those of the cerebrospinal system in being situated not on nerve-roots but more peripherally; their cells also are different—each one usually

FIG. 1.—VIEW OF THE CEREBROSPINAL AXIS. (After Bourgery.) $\frac{1}{8}$.

The right half of the cranium and trunk of the body has been removed by a vertical section; the membranes of the right side of the brain and spinal cord have been cleared away, and the roots and first part of the fifth and twelfth cerebral nerves, and of all the spinal nerves of the right side, have been dissected out and laid separately on the wall of the skull and on the several vertebræ opposite to the place of their natural exit from the craniospinal cavity.

F, Pa, T, O, frontal, parietal, temporal, and occipital lobes of cerebrum; C, cerebellum; P, pons; *m o*, placed behind medulla oblongata; *m s*, *m s*, point to the upper and lower extremities of the medulla spinalis ; *c e*, on the last lumbar vertebral spine, marks the cauda equina; V, the three principal branches of the nervus trigeminus; C I, the suboccipital or first cervical nerve; C VIII, the eighth or lowest cervical nerve; D I, the first thoracic nerve; D XII, the last thoracic; L I, the first lumbar nerve; L V, the last lumbar; S I, the first sacral nerve; S V, the fifth; Co I, the coccygeal nerve; *s*, the left sacral plexus.

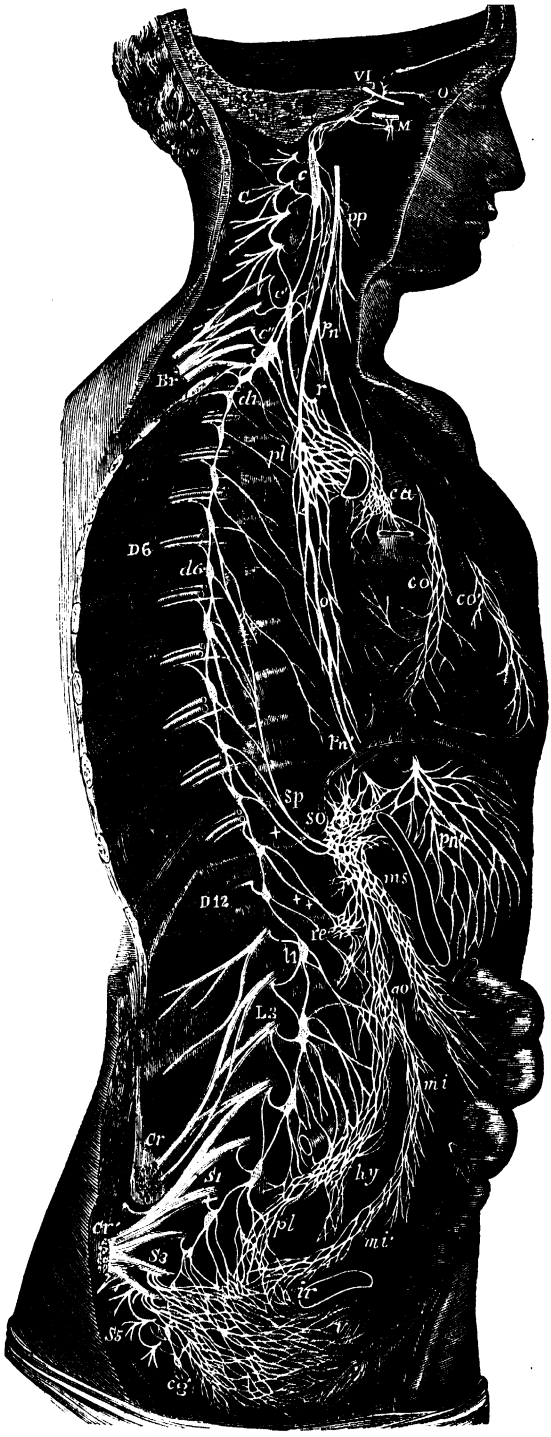


FIG. 2. — DIAGRAMMATIC VIEW OF THE SYMPATHETIC CORD OF THE RIGHT SIDE, SHOWING ITS CONNEXIONS WITH THE PRINCIPAL CEREBROSPINAL NERVES AND THE MAIN PRE-AORTIC PLEXUSES. ½.

Cerebrospinal nerves.—VI, a portion of the sixth cerebral nerve as it passes through the cavernous sinus, receiving two twigs from the carotid plexus of the sympathetic nerve; O, ciliary ganglion, connected by a twig with the cavernous plexus; M, connexion of the sphenopalatine ganglion by the large deep petrosal nerve with the carotid plexus; C, cervical plexus; Br, brachial plexus; D 6, sixth thoracic nerve; D 12, twelfth; L 3, third lumbar nerve; S 1, first sacral nerve; S 3, third; S 5, fifth; Cr, femoral nerve; Cr′, sciatic; *pn*, pneumogastric (vagus) nerve in the lower part of the neck; *r*, its recurrent branch, winding round the subclavian artery.

Sympathetic cord.—*c*, superior cervical ganglion; *c′*, middle; *c″*, inferior; from each of these ganglia cardiac nerves (all deep on this side) are seen descending to the cardiac plexus; *d* 1, placed immediately below the first thoracic sympathetic ganglion; *d* 6, is opposite the sixth; *l* 1, first lumbar ganglion; *c g*, the terminal or coccygeal ganglion.

Pre-aortic and visceral plexuses.—*pp*, pharyngeal plexus; *pl*, posterior pulmonary plexus, spreading from the vagus on the back of the right bronchus; *ca*, on the aorta, the cardiac plexus, towards which, in addition to the cardiac nerves from the three cervical sympathetic ganglia, other branches are seen descending from the vagus and recurrent nerves; *co*, right or posterior, and *co′*, left or anterior coronary plexus; *o*, œsophageal plexus in long meshes on the gullet; *sp*, great splanchnic nerve; +, small splanchnic; + +, smallest splanchnic; the first and second of these are shown joining *so*, the cœliac plexus; the third descending to *re*, the renal plexus; connecting branches between the cœliac plexus and the vagus nerves are also represented; *pn′*, above the place where the right vagus passes to the posterior surface of the stomach; *pn″*, the left vagus, distributed on the anterior surface of the fundus of the organ; from the cœliac plexus large branches are seen surrounding the arteries of the cœliac axis, and descending to *ms*, the superior mesenteric plexus; opposite to this is an indication of the suprarenal plexus; below *re* (the renal plexus), the spermatic plexus is also indicated; *ao*, on the front of the aorta, marks the aortic plexus, formed by nerves descending from the cœliac and superior mesenteric plexuses and from the lumbar ganglia; *mi*, the inferior mesenteric plexus, surrounding the corresponding artery; *hy*, hypogastric plexus, placed between the common iliac arteries, connected above with the aortic plexus, receiving nerves from the lower lumbar ganglia, and dividing below into the right and left pelvic or inferior hypogastric plexuses; *pl*, right pelvic plexus; from this the nerves descending are joined by those from the plexus on the superior hæmorrhoidal vessels, *mi′*, by sympathetic nerves from the sacral ganglia, and by numerous visceral nerves from the third and fourth sacral spinal nerves, and there are thus formed the rectal, vesical, and other plexuses, which ramify upon the viscera from behind forwards, and from below upwards, as towards *ir*, and *v*, the rectum and bladder.

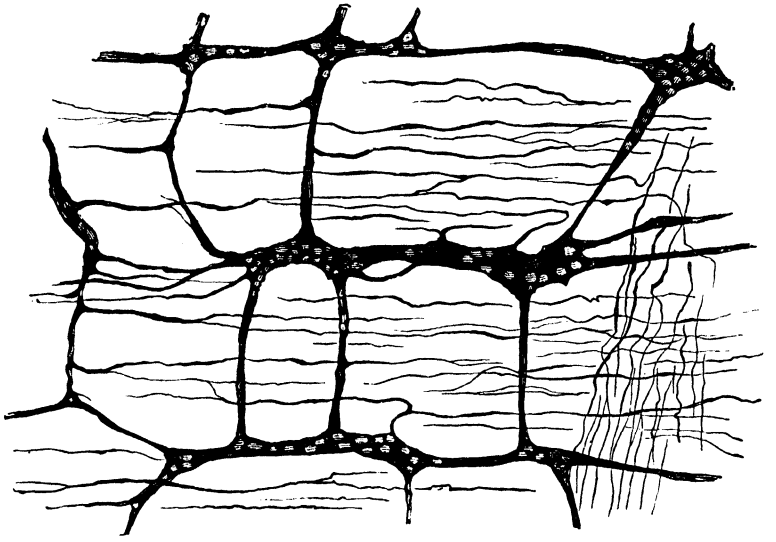


FIG. 3.—PLEXUS OF AUERBACH BETWEEN THE TWO LAYERS OF THE MUSCULAR COAT OF THE INTESTINE. Chloride of gold preparation. (Cadiat.)

giving off but a single nerve-fibre process—and this, as already stated, commonly remains non-medullated; whereas the cells of the typical cerebrospinal ganglia give off two nerve-fibre processes, each of which becomes a medullated nerve-fibre. But although in anatomical descriptions it is customary to speak of the sympathetic (autonomic) system as distinct from the cerebrospinal system, the fine medullated nerve-fibres which constitute its proximal part, and which terminate in its ganglia, are derived from cells in the grey matter of the spinal cord and of the lower parts of the brain, so that it can in no true sense of the word be reckoned an independent system of nerves and ganglia.

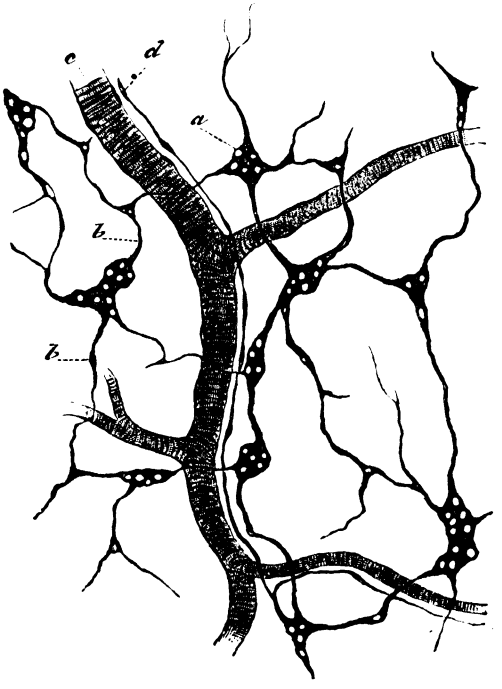


FIG. 4.—PLEXUS OF MEISSNER, FROM THE SUBMUCOUS LAYER OF THE INTESTINE. Chloride of gold preparation. (Cadiat.)

a, ganglion; *b*, *b*, cords of plexus; *c*, a small blood-vessel.

The gangliated plexuses which occur in the wall of the alimentary canal (plexus of Auerbach of the muscular coat, plexus of Meissner of the submucous coat, and end-plexus of the mucous membrane)—to which may perhaps be added the intrinsic nerve-plexuses of the heart and blood-vessels—seem to have a greater degree of independence than those of the sympathetic or autonomic system

generally; for the latter are directly controlled from the central nervous system, whereas the former are believed to act as independent nerve-centres for maintaining the movements, and possibly the secretions, of the viscera to which they are distributed. Although commonly regarded as a part of the sympathetic system, it is for some reasons convenient to describe these gangliated plexuses in a separate category.

The **cerebrospinal centre** (brain and spinal cord) is composed of grey and white matter, varying in relative amount and arrangement in its several parts. Thus in the cerebral hemispheres and cerebellum there is a cortical

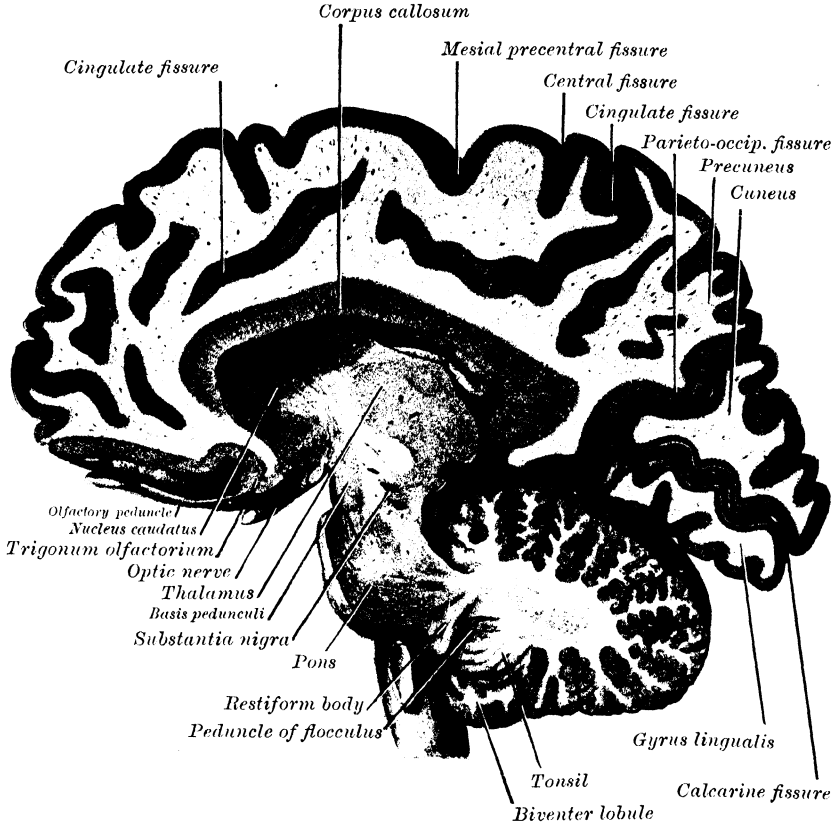


FIG. 5.—SAGITTAL SECTION OF LEFT HALF OF BRAIN, ABOUT ¾ OF AN INCH FROM MESIAL PLANE, VIEWED FROM THE OUTER ASPECT. (J. Symington.)

layer of grey matter and a central white mass (fig. 5), which contains at certain places islands or 'nuclei' of grey matter, while in the spinal cord (fig. 6) the white matter occupies the periphery and the grey matter is confined to the more central parts. If we trace the spinal cord upwards towards the brain, we find at first an arrangement which is precisely similar to that of the cord, but presently, as grey matter accumulates in larger amount, it comes at places to the surface. Running along the middle of the grey matter of the cord is a fine tube, the *central canal of the cord*; it is lined by ciliated epithelium. Above, this canal gradually expands in the upper and posterior

part of the medulla oblongata into a similarly lined cavity, the *fourth ventricle* of the brain; this is continued at the back of the pons, where it again gradually narrows, into the *cerebral aqueduct* (*aqueduct of Sylvius*), a passage passing through the mid-brain to open out in front into another expansion, the *third ventricle*. Lastly, from each side of the third ventricle, at its most anterior part, is another large expansion of these ciliated cavities, which extends into each cerebral hemisphere and is known as the *lateral ventricle*.

The morphological significance of these ciliated cavities within the vertebrate central nervous system is obscure, but Gaskell (in a series of papers published in the 'Journal of Anatomy and Physiology') has brought forward a strong body of evidence in support of the view that they represent the dorsally situated alimentary canal of the invertebrate, the walls of which have been invaded by the adjacent nervous elements, while a new alimentary system has become evolved on the ventral aspect of the body.

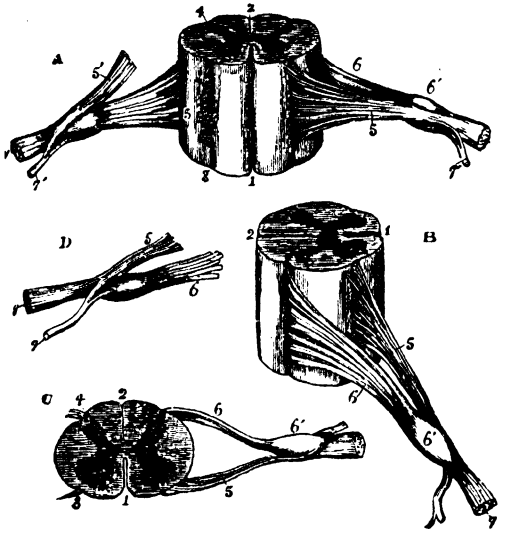


FIG. 6.—DIFFERENT VIEWS OF A PORTION OF THE SPINAL CORD FROM THE CERVICAL REGION WITH THE ROOTS OF THE NERVES. Slightly enlarged. (Allen Thomson.)

In A, the ventral surface of the specimen is shown, the ventral nerve-root of the right side having been divided; in B, a view from the side is given; in C, the upper surface is shown; in D, the nerve-roots and ganglion are shown from below. 1, the ventral median fissure; 2, dorsal median fissure; 3, ventro-lateral impression, over which the bundles of the ventral nerve-root are seen to spread (this impression is too distinct in the figure); 4, dorso-lateral groove into which the bundles of the dorsal root are seen to sink; 5, ventral root; 5′, in A, the ventral root divided and turned upwards; 6, the dorsal root, the fibres of which pass through the ganglion, 6′; 7, the united or compound nerve; 7′, the dorsal primary branch, seen in A and D to be derived in part from the ventral and in part from the dorsal root.

The **cerebrospinal nerves** are typically attached in pairs by two sets of roots—dorsal and ventral—to the cerebrospinal axis. This type is preserved in the spinal nerves (fig. 6), but is obscured in many of the cerebral nerves. A ganglion is situated upon the dorsal (posterior) root of each spinal nerve, and it is from the nerve-cells of these ganglia that the fibres of the dorsal roots all take origin. These fibres emerge from the ganglia at both their proximal and distal ends. From the proximal extremity of each ganglion they course centrally to enter the dorsal column of the spinal cord, passing thence into the grey matter, where they finally end by arborising among its cells (or eventually among corresponding cells in the grey matter of the medulla oblongata). From the distal extremity of the ganglion fibres pass towards the periphery, mingling with the fibres of the ventral root (which do not traverse the ganglion), and forming along with these the mixed spinal nerve. These peripherally directed fibres of the dorsal roots end in the integument and in other parts endowed with sensation, by some kind of terminal arborescence, either localised or diffuse; in the former case the ending is contained in a special end-organ, in the latter the branchings of the axis-cylinder extend between the elements—such as the epidermis-cells—of the tissue to which the nerve is distributed.

The fibres of the dorsal or posterior roots are traceable through the ganglia. In some fishes they traverse bipolar cells, but in man, as in most vertebrates, they are connected laterally—by a fibre which joins them at a T-shaped junction—with the ganglion-cells, which are then unipolar. A corresponding arrangement obtains with the afferent fibres of the cerebral nerves, which also arise from unipolar cells in ganglia upon the nerve-roots exactly as do the dorsal root-fibres of the spinal nerves. But the cells in the ganglia of the eighth cerebral nerve are bipolar in all animals. This is the primitive type, and is found in all cases in the early embryo, but becomes obscured in most nerves as development advances (see pp. 9, 10).

The fibres of the ventral or anterior roots do not pass through ganglia. The cells from which they emanate are situated in the part of the grey matter of the cord ventro-lateral to the central canal, and in corresponding situations in the central grey matter of the medulla oblongata, pons, and mid-

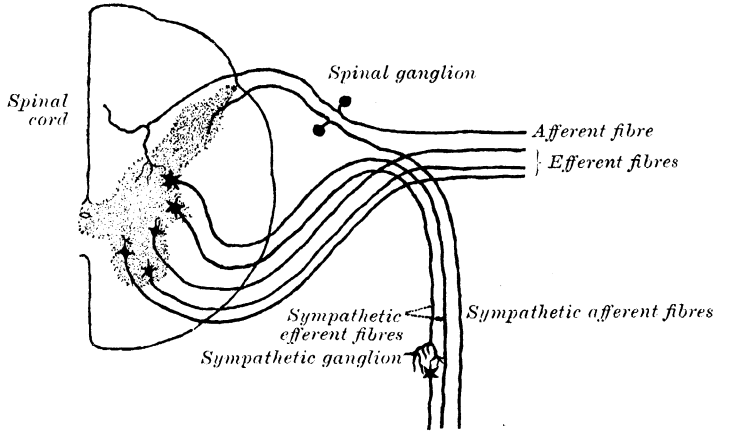


FIG. 7.—PLAN OF CONSTRUCTION OF A TYPICAL SPINAL NERVE. (G. D. Thane.)

brain. The axons of these cells acquire a medullary sheath near their origin from the cell-body and a nucleated sheath on leaving the nerve-centre. Beyond the ganglia upon the posterior roots they become commingled with the fibres of those roots to form the mixed nerves, along which they are conveyed to be distributed in the skeletal muscles, ending here in terminal arborisations of the axon within the so-called ' end-plates.'

Some of the ventral roots contain a number of fine medullated fibres, which take origin from the intermedio-lateral cell-column of the spinal cord, and, in the case of certain of the cerebral nerves, from corresponding cells in the medulla oblongata. These fine medullated fibres, which, as Gaskell showed, are, in the spinal cord, found almost exclusively in the thoracic region (from the first or second thoracic to the second lumbar segment, reappearing in the anterior roots of the second and third sacral nerves), represent an outflow from the cerebrospinal to the autonomic system.

DEVELOPMENT OF THE CEREBROSPINAL NERVOUS SYSTEM.[1]

The nervous system begins to be developed very early in embryonic life as a thickening of the ectoderm occupying the middle line of the blastoderm in front of the primitive streak. This thickening is accompanied by a depression of the general surface, which takes the form of a longitudinal groove known as the *neural groove* (fig. 8). The neural groove, which soon expands in front to form the cerebral vesicles from which the several parts of the brain (see pp. 12, 13) are eventually formed, gradually deepens (fig. 9), and as it deepens its lips approach one another and ultimately unite along the mid-dorsal line

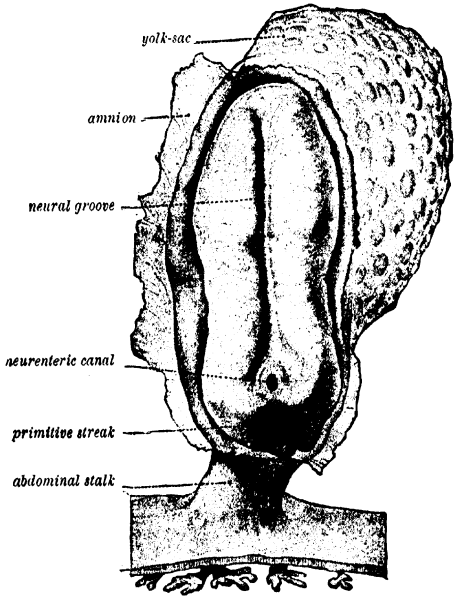


FIG. 8.—SURFACE VIEW OF EARLY HUMAN EMBRYO, 2 MM. IN LENGTH. (After Graf v. Spee.) × 30 diameters.

The amnion is opened, and on the blastoderm are seen the primitive streak, the dorsal opening of the neurenteric canal, and the neural groove.

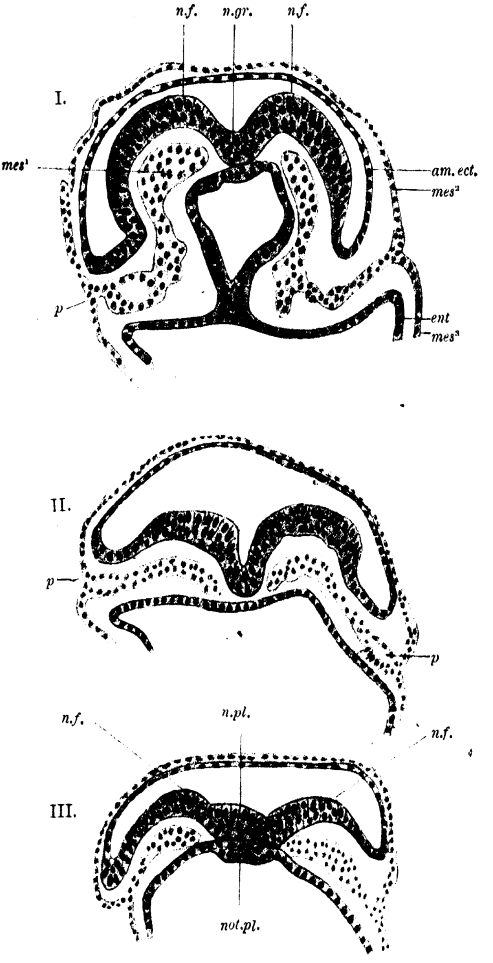


FIG. 9.—TRANSVERSE SECTIONS OF THE HUMAN EMBRYO OF 2 MM. REPRESENTED IN FIG. 8. (After Graf v. Spee.)

In I., which is most anterior, the fore-gut is separated off from the yolk-sac. *n.gr.*, neural groove; *n.f.*, neural folds; *n.pl.* (in III.), neural plate; *mes*¹, intra-embryonic mesoderm; *p*, pericardial cœlom; *am.ect.*, amniotic ectoderm; *mes*², amniotic mesoderm; *ent*, entoderm of yolk-sac; *mes*⁵, mesoderm of yolk-sac; *not.pl.* (in III.), notochord-plate.

(figs. 10, 11), so that the open groove is converted into a closed canal—the *neural canal*—lined with the thickened neural ectoderm above mentioned. As the closure of the groove is taking place there is seen on each side of it, just at

[1] A more complete account of the development of the nervous system will be found in the volume on Embryology.

the place where the neural ectoderm is continued laterally into the general ectoderm, a small outgrowth of ectodermal cells, known as the *neural crest* (fig. 11).[1] At regular intervals along this neural crest, corresponding to the

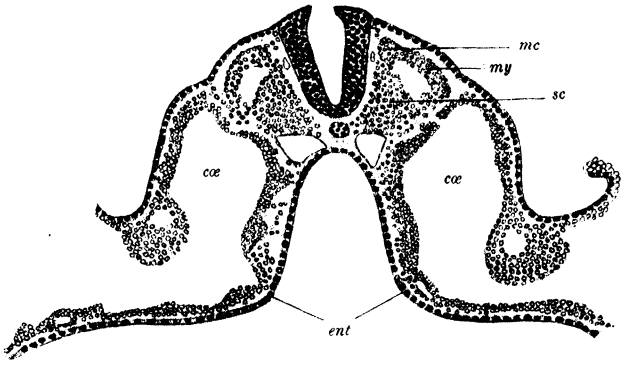


FIG. 10.—TRANSVERSE SECTION OF A HUMAN EMBRYO OF 2·4 MM. (T. H. Bryce.)

ent, entoderm of yolk-sac; the lines indicate the points of the splanchnopleuric layers which will come together to cut off the gut from the cavity of the yolk-sac; *my*, outer wall of mesodermic segment; *mc*, the part of its wall which forms the muscle-plate; *sc*, sclerotome; *cœ*, cœlom.

situation of the subsequent spinal and of some of the cerebral nerves, the outgrowth is more marked, and buds out prominently into the adjacent mesoderm; presently it becomes detached and lies on the dorso-lateral aspect of the neural canal. This detached bud of the neural crest is the blastema from which the corresponding spinal ganglion and posterior nerve-root are eventually developed. The interganglionic portions of the neural crest disappear.

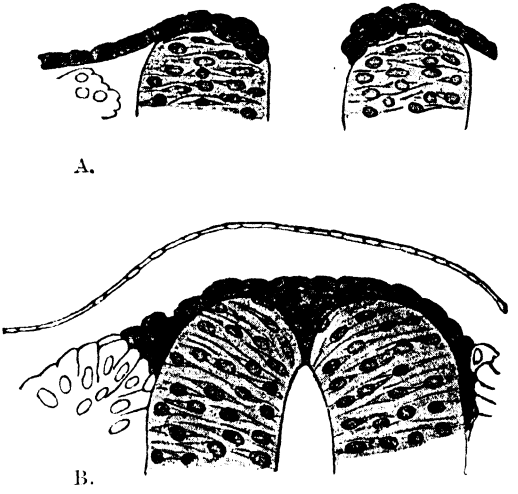


FIG. 11.—CLOSURE OF NEURAL CANAL OF HUMAN EMBRYO, SHOWING THE CELLS OF THE NEURAL CREST BECOMING SEPARATED TO FORM THE GERMS OF THE SPINAL GANGLIA. (Lenhossék.)

A, canal still open; B, canal closed.

The cells of the buds in question (*neuroblasts of the cerebrospinal ganglia*) become the cells of the cerebral and spinal ganglia. Processes grow out from them at opposite poles (fig. 12*, *d*; fig. 13, E), and these processes become the axons of the dorsal (afferent) root-fibres—one growing centralwards into the wall of the neural canal and ramifying there among its cells, the other growing distalwards and forming the axon of one of the peripheral sensory nerve-fibres. The ganglion-cells are thus at first bipolar (fig. 13), with the axon of a nerve-fibre growing out from either pole, and they retain this condition in some of the cerebrospinal ganglia in man—*e.g.* those upon the eighth nerve. But in most of the cerebral

[1] F. M. Balfour, Phil. Trans. 1876; A. M. Marshall, Jour. Anat. and Phys. 1877.

and spinal sensory nerves in man and nearly all vertebrates the bipolar cells of the ganglion become converted into unipolar cells by a gradual shifting of the origin of the two axons (fig. 14) until these come to arise from the same point in the cell-body, which grows out at this point in the form of a single fibre, furnishing the two axons with a common stem, with a bifurcation a certain distance from the cell-body. From the bifurcation the one branch or fork is formed by the central axon, the other by the peripheral, so that the sensory nerve now appears to traverse the ganglion as a single fibre, with a lateral branch connecting it with the cell-body out of which it originally grew as two fibres.

While the sensory nerve-fibres are thus forming external to the neural canal, other neuroblasts are being formed by cell-division in its walls. The cells thus differentiated are at first rounded (fig. 12 A), subsequently becoming bipolar, having two processes—one ependymal, the other axonal (fig. 12, B). The ependymal process atrophies, but the axons tend in the ventro-lateral direction and seek the surface of the cord, whence many of them emerge and grow into the adjacent mesoderm: here they meet and mingle with the peripheral fibres

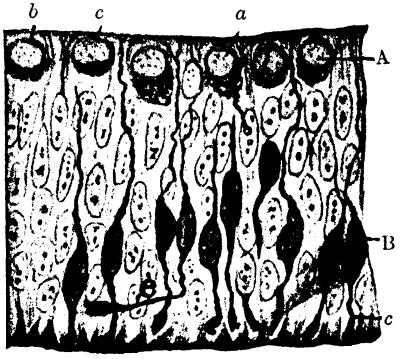


FIG. 12.—SECTION OF WALL OF NEURAL TUBE (FIRST CEREBRAL VESICLE) OF CHICK OF THREE AND A-HALF DAYS. (Cajal.)

A, germinal layer containing rounded neuroblasts, *a*, *b*, *c* (these already possess fibrils); B, bipolar neuroblasts; *c*, enlarged growing end of axon; *e*, an axon growing tangentially.

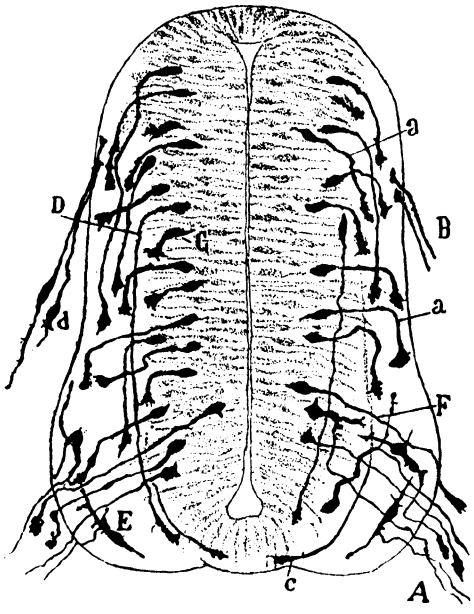


FIG. 12*.—CHICK-EMBRYO OF THE THIRD DAY. Golgi method. (Cajal.)

A, ventral root-fibres; B, dorsal root-fibres; C, a neuroblast beginning to bud out; D, a neuroblast with long fibre passing towards ventral commissure; E, a motor neuroblast with axon and dendrons; F, a motor neuroblast with axon only: the axon is expanded at the growing end; *a*, *a*, neuroblasts with axons growing into the lateral column; *c*, growing end of axon of a commissural fibre; *d*, a cell of the spinal ganglion.

which have grown from the sensory neuroblasts of the ganglia (fig. 13). The neuroblasts, from which these axons have grown, send out other processes into the adjoining grey matter; these are, however, not axons of nerve-fibres, but dendrons, and ramify for the most part in the vicinity of the cell-body. Some of the neuroblasts in the wall of the neural canal give off axons which do not join the nerve-roots, but remain within the canal and become fibres of one or other of the white columns which are eventually formed peripherally to the grey matter (fig. 12). Other ectoderm-cells of the neural canal (*spongioblasts* of His) are developed into the sustentacular elements of the nervous system—which are known as the neuroglia cells and fibres—and others remain *in situ*, at the inner

surface of the neural cavities, forming the epithelium which lines the central canal and cerebral vesicles (*ependymal epithelium*).[1]

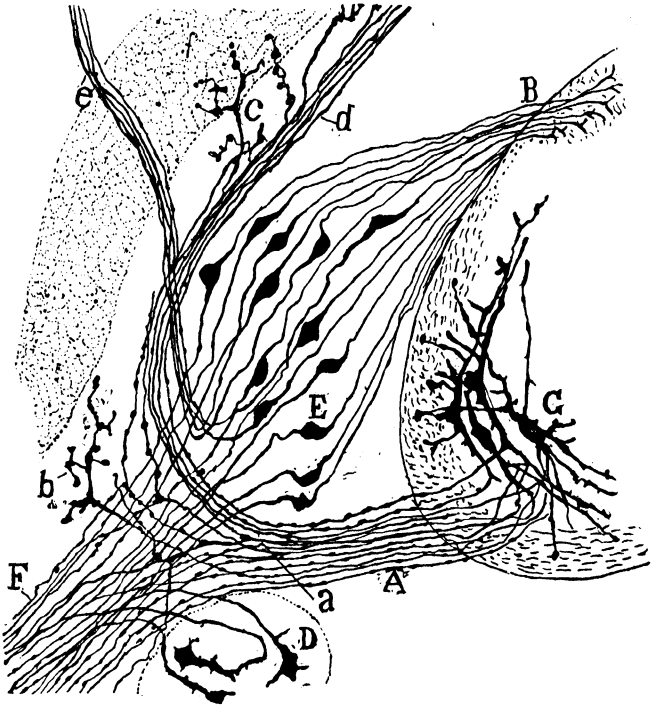


FIG. 13.—CHICK-EMBRYO OF THE FIFTH DAY. (Cajal.)

A, ventral root; B, dorsal root; C, motor nerve-cells; D, sympathetic ganglion-cells; E, spinal ganglion-cells still bipolar; F, mixed nerve; *b*, *c*, *d*, motor nerve-fibres passing to and ramifying in *f*, developing dorsal muscles; *e*, a sensory nerve-trunk

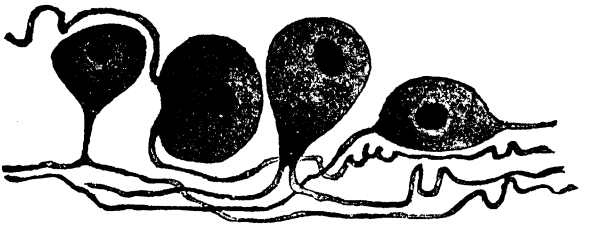


FIG. 14.—SPINAL GANGLION-CELLS SHOWING TRANSITIONS FROM BIPOLAR TO UNIPOLAR CONDITION. (Holmgren.)

The axon-processes of the neuroblasts are always at first non-medullated. The growing end generally exhibits an enlargement (*incremental cone*, Cajal; fig. 15): this is seen even before the axon-processes have emerged from the

[1] W. His, Archiv f. Anat. u. Physiol. 1879 and 1887, and Sächs. Abhandl. 1886 and 1889; Kölliker, Handb. d. Gewebelehre, Bd. ii. 1893. For details of the histogenesis of nerve and neuroglia cells, see Cajal, Anat. Anz. 1890; Testura del sistema nervioso, Madrid, 1899; Anat. Anz. xxx. 1907, and xxxi. 1908; v. Lenhossék, Feinere Bau d. Nervensystems, 1895; Held, Neurol. Centr. 1905; Besta, Riv. sper. d. fren. xxx. 1904; Bardeen, Amer. Jour. Anat. ii. 1902; Hardesty, *ibid.* and iii. 1904; Retzius, Biol. Unters. 1892, 1893, 1894, &c.; Carpenter and Main, Anat. Anz. xxxi. 1907. On the myelination of nerve-fibres, see Flechsig, Leitungsbahnen, 1876; Bechterew, Leitungsbahnen, 1894; Westphal, Arch. f. Psych. xxix. 1897; Hardesty, Amer. Jour. Anat. iv. 1905.

neural canal (fig. 12); it also occurs at the growing end in fibres which are undergoing regeneration after section (fig. 62).[1]

The part of the axon-process which is outside the central nervous system becomes invested by a membranous nucleated sheath (*sheath of Schwann* or *neurolemma*), the exact origin of which is uncertain, although it is commonly believed to be formed from mesoderm-cells which surround the axon and become elongated and wrapped round it.[2] This sheath is not formed upon the nerve-fibres within the central nervous system; and it may be added, no mesoderm-cells are at first, nor indeed for a considerable time, included within the wall of the neural canal. On the other hand, the medullary or myelin sheath of the nerve-fibres, which is developed comparatively late, and even at the time of birth is still lacking in some tracts of nerve-fibres within the nerve-centres, is formed independently of the agency of external cells, being to all appearance a direct product of the axon itself.[3] It begins to be apparent near the cell-body and may generally be traced along the whole course of the nerve, with the exception of the finest terminal ramifications; it is also continued over all collateral processes given off from the axon.

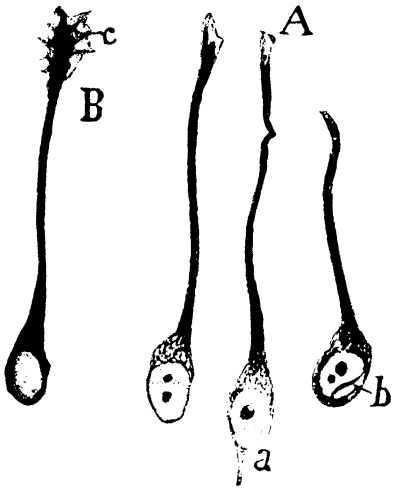


FIG. 15.—NEUROBLASTS FROM THE SPINAL CORD OF A THIRD-DAY CHICK-EMBRYO. (Cajal.)

A, three neuroblasts, stained by Cajal's reduced-silver method, showing a network of neuro-fibrils in the cell-body; *a*, a bipolar cell. B, a neuroblast stained by the method of Golgi, showing the incremental cone, *c*.

Two other views which have been taken of the mode of formation of nerve-fibres may here be briefly mentioned. According to one, which was originally promulgated by F. M. Balfour[4] and has been recently supported by O. Schultze,[5] groups of cells grow out from the neural ectoderm and from the blastema of the dorsal root-ganglion respectively, and become linked longitudinally into syncytia, the future nerve-fibres being laid down within these. According to the other view, which was originally taken by Hensen and which has been adopted in a modified form by Sedgwick and Graham Kerr, the nerve-fibres are formed within syncytial connexions between cells of the embryonic nervous system and cells at the periphery. Both these views, however, are difficult to reconcile with many established facts regarding the growth and structure of nerve cells and fibres.

Formation of the several parts of the cerebrospinal system.—The central nervous system takes at first, as we have already seen, the form of a simple groove on the dorsal aspect of the blastoderm. This groove is expanded anteriorly, and when the neural canal is closed the expansion forms the primitive brain. By this time the expansion is no longer simple, but has become elongated and pinched-in at the sides at two places, so that there are now three *primary cerebral vesicles* (fore-brain, mid-brain, and hind-brain), the last-named being continued backwards into the remainder of the neural canal, which is to form the spinal cord. These three primary cerebral vesicles are soon increased in number by a partial division of the foremost and

[1] According to the observations of Harrison in the tadpole, the incremental cone exhibits during life amœboid movements (Proc. Soc. Exp. Biol. iv. 1907).

[2] According to Lenhossék, these cells (*sheath-cells*) are derived from the neural ectoderm of the ganglion-rudiment. Cf. also Froriep, Verh. d. anat. Gesellsch., Anat. Anz. xxvii. 1905; and Kohn, *ibid.*

[3] Gurwitsch, Arch. f. Anat. 1900. [4] Phil. Trans. 1895. [5] Arch. f. mikr. Anat. Bd. lxvi. 1905.

hindmost. In this way a series of five *secondary cerebral vesicles* is produced, from which the several parts of the encephalon are ultimately formed. The first of these (which is really the anterior part of the first primary vesicle—prosencephalon) develops a hollow outgrowth on each side, which ultimately becomes very large and thick-walled, and gives origin to the corresponding *cerebral hemisphere*; its cavity becomes the *lateral ventricle*. The second vesicle (posterior part of the first primary vesicle—diencephalon) is also connected with a hollow outgrowth on each side, which becomes transformed into the *retina and optic nerve* of the corresponding eye. This *primary optic vesicle* begins to show itself very early—in fact, before the first primary cerebral vesicle is divided into two, and in some animals, including man, even before its hollow closes up to form a vesicle. The original cavity of the first primary cerebral vesicle forms the *third ventricle* of the brain, and the walls become developed into the *thalami* and other structures related to that ventricle. The third secondary vesicle (second primary vesicle—mesencephalon, mid-brain) forms the *corpora quadrigemina* and *pedunculi cerebri*; its cavity is the *aqueductus cerebri* [*Sylvii*]. The fourth secondary vesicle (epencephalon) and the fifth secondary vesicle (metencephalon), which are formed by division of the third primary cerebral vesicle, form respectively the *pons* (with the *cerebellum*) and the *medulla oblongata*; their common cavity becomes the *fourth ventricle*. The several parts of the encephalon are developed by growth and thickening of the ectodermic tissue which forms the walls of the vesicles; the histogenetic changes are similar to those which have been already described for the spinal cord.

The **autonomic system**,[1] as already explained, is not an independent system of nerves and ganglia, but is connected with and has been derived from the cerebrospinal system. It is composed of a large number of ganglia, which receive the terminations of fine medullated nerve-fibres derived from cells in the lateral part of the grey matter of the spinal cord; these fibres pass out by some of the ventral nerve-roots. The ganglia, on the other hand, send out towards the periphery fibres, which are generally non-medullated, derived from their own ganglion-cells, to terminate chiefly among the tissues of the viscera and blood-vessels.

The main part or trunk of the sympathetic consists of a chain of ganglia which are united by short, sometimes double, nervous cords. This chain lies on each side and in front of the vertebral column. In the thoracic, lumbar, and sacral regions the ganglia are equal in number to the nerve-roots, but in the neck there are only three ganglia (inferior, middle, and superior); in many animals only two. The connexions with the spinal cord form the *white rami communicantes*, which occur from the first thoracic nerve to the second or third lumbar nerve in man; in the dog, to the third and fourth; in the cat, to the fourth and fifth; and in the rabbit, to the fifth lumbar, and rarely to the sixth.

Similar bundles of fine fibres pass off from the second and third sacral (third and fourth sacral in rabbit) and from some of the cerebral nerves, and are distributed to viscera and blood-vessels without joining the sympathetic chain; these are homologous with sympathetic fibres, but have a different mode of distribution: as already stated, they are grouped together with the sympathetic proper under the term 'autonomic' nerves. These nerves all agree in the fact that they take origin from the cerebrospinal system as very fine

[1] See on the autonomic nervous system, Langley, article 'Sympathetic' in Schäfer's Text-book of Physiology, 1900; also Address to Neurol. Soc. in Brain xxvi. 1903, Journ. Physiol. xxxi. 1903, and Ergebnisse der Physiol. ii. 1903, where literature will be found.

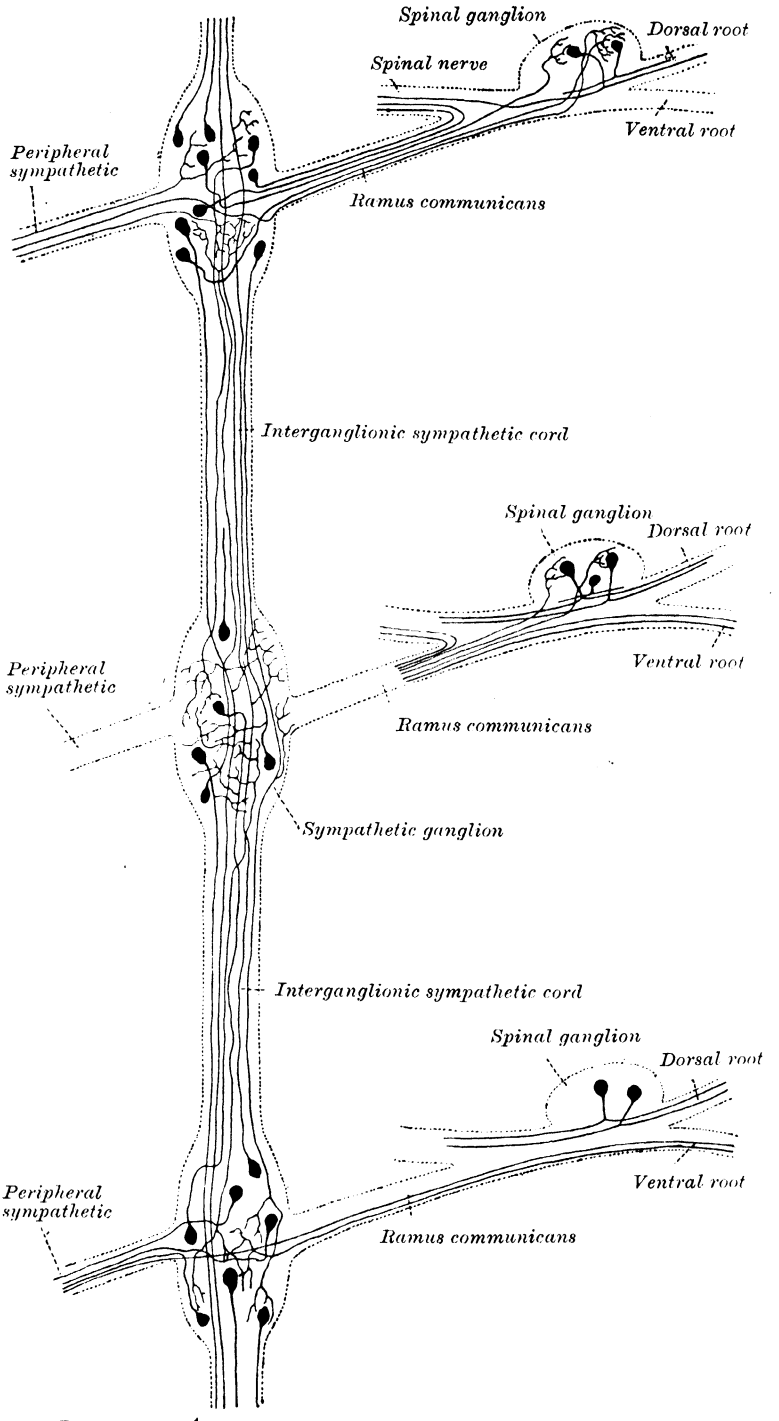


FIG. 16.—DIAGRAM OF THE SYMPATHETIC CHAIN AND ITS RELATION TO THE NERVE-ROOTS AND SPINAL GANGLIA. (Van Gehuchten.)

In the lowest of the three rami communicantes represented only fine white efferent fibres are shown; in the other two, both white fibres emanating from the cord by the ventral roots and grey fibres emanating from cells of the sympathetic ganglia are included. Some of the grey fibres are shown arborising among the cells of the spinal ganglia.

medullated fibres (Gaskell), that they pass, as *pre-ganglionic fibres* (Langley), into a sympathetic ganglion and there form synaptic connexion with its cells; while from these cells other fibres (*post-ganglionic* of Langley) proceed to be distributed to involuntary muscle of the blood-vessels, of the viscera, and of the hairs, and to the epithelium of glandular structures.

A pre-ganglionic fibre may pass through one or more ganglia before reaching that in which it terminates, and may give off collaterals to those through which it passes. In birds the post-ganglionic fibres are medullated. A post-ganglionic fibre is never distributed to another sympathetic ganglion, but passes direct to the tissue supplied (Langley).

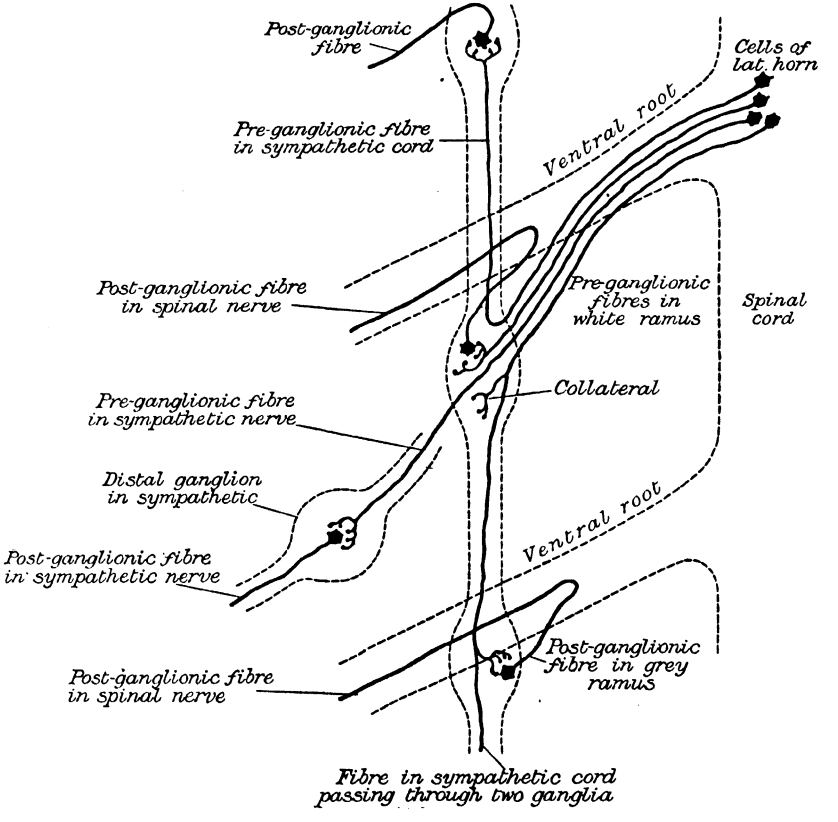


FIG. 17.—DIAGRAM OF SYMPATHETIC.

The fine medullated fibres form the only true communication between the cerebrospinal centre and the autonomic system, and in fact those of the thoracico-lumbar outflow give origin, as just stated, to the main sympathetic nerves. Passing to the ganglia of the sympathetic chain, many of them terminate among the cells of those ganglia (fig. 17), whilst new non-medullated fibres issue from the cells and pass by the grey rami to the spinal nerves, in which they are conducted to their destination; others pass through the ganglia of the chain without joining the nerve-cells, and are continued towards their peripheral distribution in offsets from the chain as fine medullated fibres; these lose their medullary sheath in the more distal ganglia.

The proportion of fine medullated nerve-fibres which the roots of the cerebro-spinal nerves contain may be taken as a direct indication of the extent to which they feed the sympathetic system.[1] This is at least true for the region of the thoracico-lumbar outflow of vascular and visceral nerves. All the ventral roots in this region contain a large number of fine medullated fibres which leave the root in a bundle and pass directly to the sympathetic chain forming the *white ramus communicans* between the spinal root and the sympathetic. The so-called

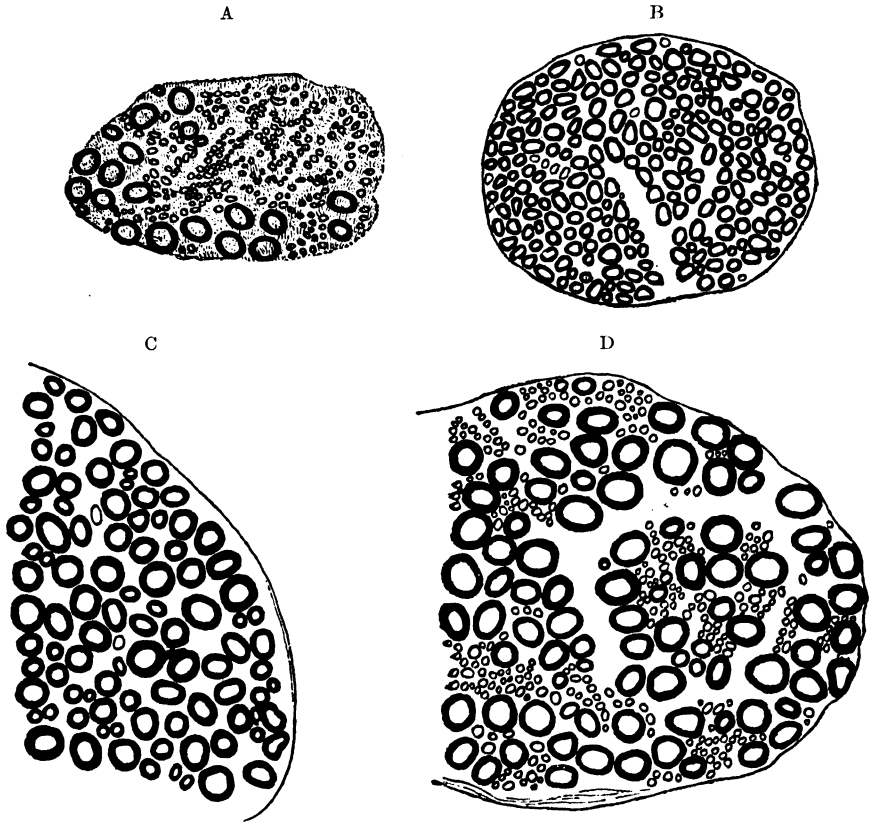


FIG. 18.—SECTIONS ACROSS PARTS OF THE ROOTS OF VARIOUS NERVES OF THE DOG, TO SHOW THE VARIATIONS IN SIZE OF THEIR CONSTITUENT FIBRES. (Gaskell.)

(The nerves were stained with osmic acid, and the sections are all drawn to one scale.)

A, from one of the upper roots of the accessory.
B, a rootlet of the hypoglossal.
C, from the first cervical ventral root.
D, from the second thoracic ventral root.

'grey ramus communicans' is in all cases merely a branch from the sympathetic to the spinal nerves. A section, therefore, through one of these ventral roots taken before the white ramus leaves it shows a large number of fine medullated fibres intermingled with the ordinary large fibres of the root, and contrasts forcibly with a section across one of the ventral roots of other regions where there is no sympathetic outflow, and therefore no white ramus communicans, and few, if any, fine medullated fibres. (Compare, in fig. 18, A with B, and

[1] Gaskell, Jour. Physiol. vii. 1886.

C with D.) The autonomic nerve-fibres leave the cerebrospinal nervous system in four regions—viz. (1) mid-brain, by third nerve to iris and ciliary muscles; (2) medulla oblongata, by seventh, ninth, tenth, and eleventh nerves; (3) thoracic and lumbar regions of cord; (4) sacral region.

The sympathetic contains a certain number of *afferent* nerve-fibres. These are medullated and rather larger than the efferent fibres just described. They

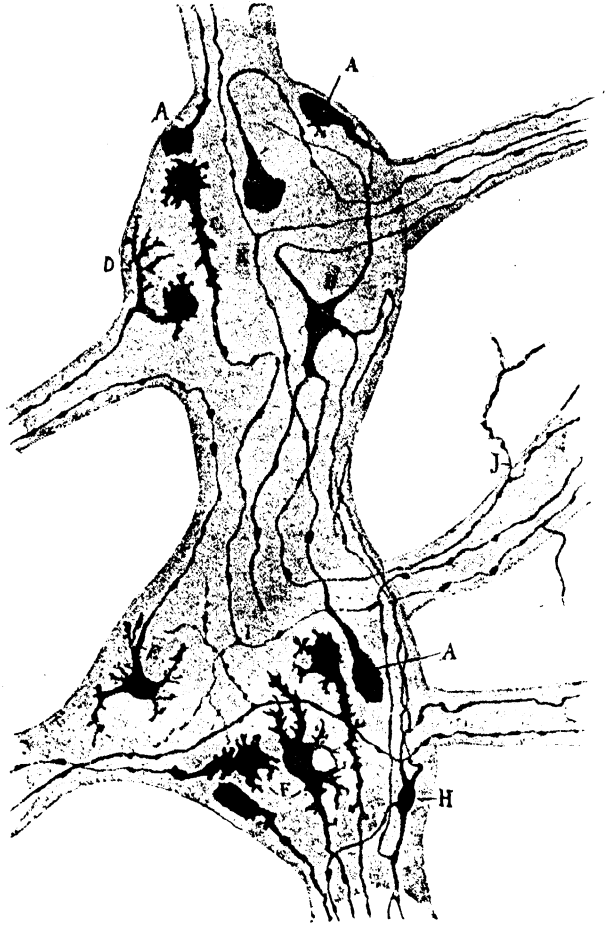


FIG. 19.—GANGLIA OF AUERBACH'S PLEXUS FROM INTESTINE OF RABBIT, ONE MONTH OLD. Methylene-blue method. (Cajal after Villa.)
A, unipolar cells; B, H, cells with several long radiating processes; C, D, E, F, cells with short dendrons as well as an axon; I, cell-axon giving off collaterals.

appear to be derived from and connected with certain cells of the spinal ganglia (autonomic root-cells), the proximal axons of which are continued along with the other fibres of the dorsal (posterior) roots into the spinal cord (see fig. 7).

The sympathetic ganglia are usually stated to be derived from the blastema of the spinal ganglia, groups of cells (*sympathetic neuroblasts*) becoming detached from the spinal ganglia and passing towards the periphery along the course of what will afterwards be the rami communicantes. Cajal, however,

considers it probable that the groups of cells in question arise from the ectoderm of the neural canal, and represent emigrated motor neuroblasts.[1] By further subdivision and outgrowth along the peripheral branches the several ganglia (proximal and distal) of the sympathetic become ultimately formed from these cell-groups. The neuroblasts of the embryonic sympathetic ganglia send their nerve-fibre processes towards the periphery; these generally remain non-medullated. They are, further, always efferent in character, possess numerous dendrons, and never exhibit a bipolar character; in these particulars they resemble the motor rather than the sensory root-cells. The sympathetic blastema is characterised by the tendency which it exhibits to produce chromophil-cells, like those found in the suprarenal medulla.[2]

The enteric nerves and ganglia belong, as already stated, to the special part of the sympathetic system which is concerned with the movements of the alimentary canal. They form in the main two gangliated plexuses of non-medullated fibres which occur in the alimentary tube from the œsophagus to the extremity of the rectum, between the layers of the muscular coat and in the sub-mucous coat respectively. The plexus which lies in the muscular coat, termed the *plexus myentericus* or *plexus of Auerbach* (figs. 3, 19), has numerous groups of small nerve-cells united by comparatively thick nerve-strands, whilst the *plexus submucosæ* or *plexus of Meissner* (figs. 4, 20) has fewer and smaller cell-groups and finer connecting cords. The cells of both plexuses are multipolar and small in size, and the axons, which are non-medullated throughout, appear to be distributed to the adjacent plain muscular tissue of the muscular coat, and to that of the tunica muscularis mucosæ. From the plexus of Meissner some fibres also pass into the mucous membrane proper (see below), and even reach the lining epithelium. Many of the cells, especially those of Meissner's plexus, are said to have one kind of process only, resembling dendrons.[3] The plexuses are connected with one another here and there by intervening nerve-fibres, and they also receive nerve-fibres from the sympathetic and in some parts from other sources (vagus, sacral nerves); but whether these actually end in the ganglia or are continued past them directly to the muscular tissue has not been ascertained. It seems clear, however, that these ganglia possess the faculty of independent activity, since it has been shown by R. Magnus [4] that if a part of the muscular coat be stripped away from the rest of the intestine and immersed in oxygenated Ringer's solution, the rhythmic contractions which are characteristic of the musculature proceed unabated for hours if a portion of the plexus myentericus remains attached to the strip, but immediately cease when the plexus is entirely detached. These gangliated plexuses therefore constitute a system of nerve cells and fibres which is essentially independent of the cerebro-spinal system, although probably capable of being influenced by the latter through autonomic nerves.

End-cells and end-plexuses.—Another plexus of nerve-fibres with nerve-cells of small size at the nodes of the plexus has been described in the mucous membrane of the intestine, in the villi, and in other situations (Drasch).[5] This plexus appears, in the intestine, to be connected with offsets from the plexus of Meissner, and must in that place be reckoned as a part of the same system. The fine nervous filaments which come off from it are in part distributed to the muscular fibres of the villi; some appear to pass toward the lining epithelium of the

[1] Anat. Anz. xxxi. 1908. F. M. Balfour, (*op. cit.*) held a somewhat similar view.
[2] H. Stilling, Anat. Anz. 1899, p. 229.
[3] La Villa, Riv. trimestr. iii. 1898.
[4] Arch. f. d. ges. Physiol. 1905.
[5] Wiener Sitzungsb. 1880. See also Cajal, Nuevos applicaciones del método de Golgi, 1889; Los ganglios y plexos nerviosos del intestino, 1895; Berkeley, Anat. Anz. 1898; Cajal and Sala, Terminación de los nervios, &c. 1891; G. Retzius, Biol. Unters. 1892; Dogiel, Anat. Anz. x. 1895.

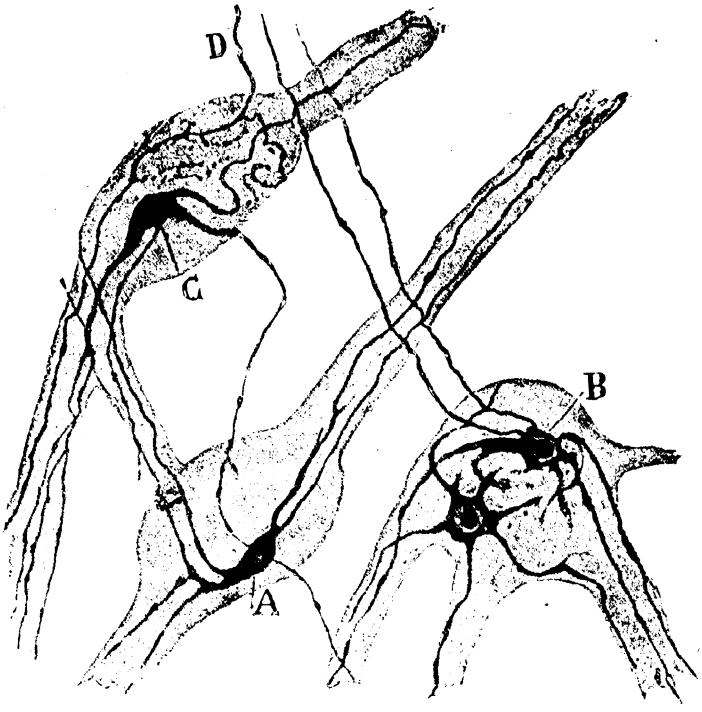


FIG. 20.—GANGLIA OF MEISSNER'S PLEXUS. Methylene-blue method. (Cajal.)
A, B, C, cells with several long radiating processes; D, a fibre traversing one of the ganglia and giving off collaterals to it.

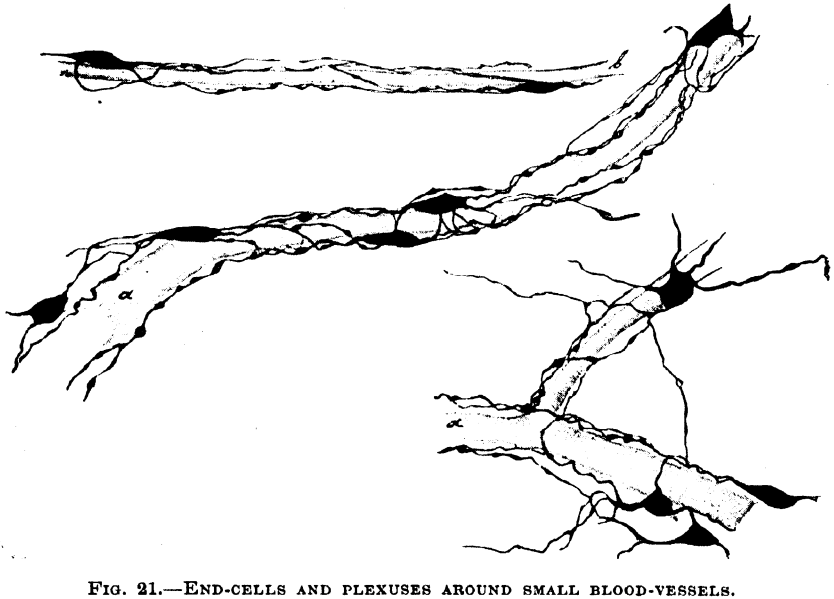


FIG. 21.—END-CELLS AND PLEXUSES AROUND SMALL BLOOD-VESSELS.
Methylene-blue method. (Dogiel.)

intestine. A plexus of like character may be demonstrated in connexion with nerve-endings in the heart and in blood-vessels, as well as in various glandular organs.

The cells and fibres of these plexuses have been thought to be of connective-tissue nature (Kölliker), and, indeed, no differentiation of their processes into axons and dendrons can be seen. But since, as Cajal has demonstrated, they exhibit neuro-fibrils when appropriately stained, since further they stain by the Golgi and Ehrlich methods, which connective-tissue cells do not, it would appear that they are to be regarded as truly nervous in nature, although less differentiated than ordinary nerve-cells. These 'end-cells' have only been shown to occur in organs which receive their nerve-supply from the sympathetic, or at any rate from autonomic nerves; they appear, therefore, to belong exclusively to the autonomic system.

THE STRUCTURAL ELEMENTS OF THE NERVOUS SYSTEM.

The nervous system is composed of three special kinds of cell—viz. (1) the true functional elements or *nerve-cells*, which give origin to the *nerve-fibres*;

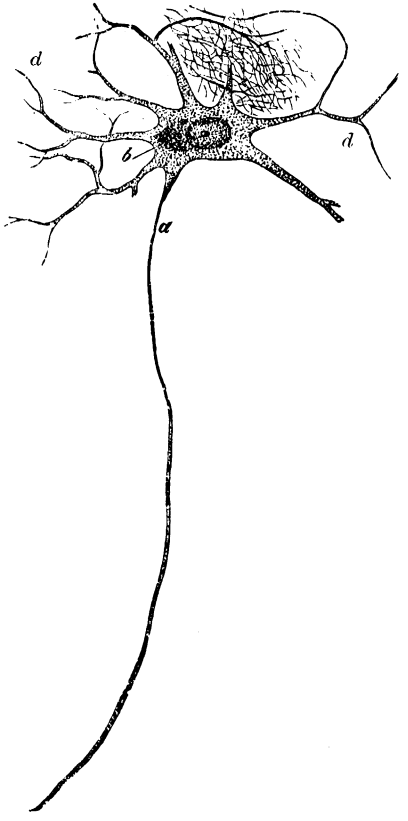


FIG. 22A.—RAMIFIED NERVE-CELL FROM VENTRAL HORN OF SPINAL CORD OF MAN. (From Gerlach.)

a, axis-cylinder process; *b*, cell-body with nucleus and clump of pigment-granules; *d*, *d*, dendrons.

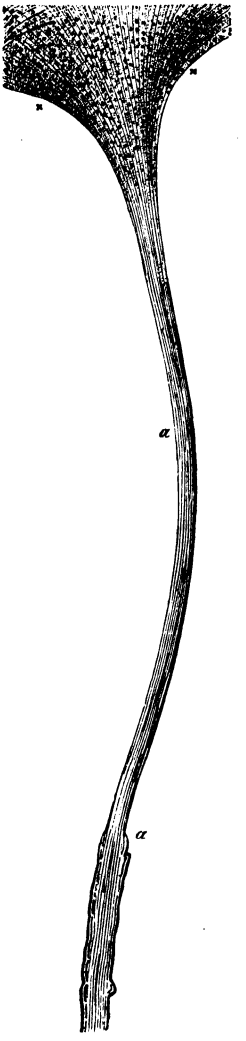


FIG. 22B.—AXIS-CYLINDER PROCESS OF A NERVE-CELL. (M. Schultze.)

×, ×, Portion of nerve-cell from spinal cord of ox, with axis-cylinder process, *a*, coming off from it and acquiring at *a'* a medullary sheath. Highly magnified.

(2) *neuroglia-cells*, giving rise to neuroglia-fibres which serve for the support of the proper nervous matter; (3) *ependyma-cells*, which are epithelium-cells, usually ciliated, lining the cavities of the central canal of the cord and ventricles of the

brain, and in parts prolonged into fibres which, like the neuroglia-fibres, subserve a sustentacular function.

Nerve-cells.—A nerve-cell when fully developed always consists of a nucleated cell-body (*perikaryon* or *soma*) and a process (*axon*), which becomes the axis-cylinder of a nerve-fibre (Deiters).[1] It may also have other processes (*dendrons* or *dendrites*) which do not become axis-cylinders, but terminate by arborising near the cell-body (fig. 22A). The whole nerve-cell, consisting of nucleated cell-body, axon (or axons), and dendrons (when present), is frequently spoken of as a *nervous unit* or *neurone*, and the term 'nerve-cell' is then often employed to designate the nucleated cell-body alone.

The 'neurone-theory' of Waldeyer[2] (which was mainly founded upon the embryological investigations of His and the histological researches of Cajal) supposes that every neurone or unit is morphologically distinct from every other one, and that connexion between the neurones is brought about by contiguity merely, and not by continuity of nerve-substance. It is based partly upon the facts of development and partly upon the circumstance that, with the Golgi method of staining, the individual nerve-cells, with all their processes, appear always absolutely distinct, and show no sign of continuity with other cells. It is further supported by the fact that degenerative and other changes which are produced experimentally, or as the result of disease, are generally confined absolutely to particular neurones or groups of neurones, without exhibiting any immediate tendency to spread to other cells, however close the anatomical and physiological relations between them may appear to be. According to this theory, the nervous impulses are propagated from one cell or neurone to the next, by virtue of the fact that there is contact without continuity between the successive elements. They are regarded as being linked together to form *neurone-chains*; the contact being effected either by the axon of one nerve-cell ramifying over the body of the next element of the chain (figs. 23, 24), or by the arborescent axon of the one interlacing with the arborescent dendrons of the next (figs. 25, 26, and figs. 72, 73). To this kind of connexion, whether by contact or by interlacement, the term 'synapse' (neuro-synapse) has been applied (M. Foster).

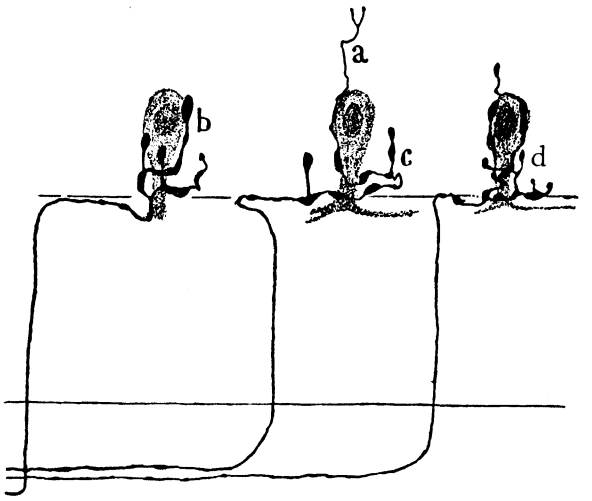


FIG. 23.—THREE CENTRIFUGAL FIBRES OF THE RETINA OF A BIRD WHICH ARISE FROM CELLS WITHIN THE BRAIN AND FORM SYNAPTIC ENDINGS (*a*, *b*, *c*, *d*) AROUND THE CELL-BODIES OF NERVE-CELLS WITHIN THE RETINA. (Cajal.)

Although the neurone-theory has been very widely accepted, especially by pathologists, on the ground of the ready explanation which it offers of many phenomena which on any continuity theory are difficult to understand, it has of late years been seriously challenged,[3] largely on the ground that it is possible to show direct continuity of fibrils from cell to cell in the nervous system of certain Invertebrata. And since similar fibrils occur in the nerves and nerve-cells of Vertebrata,[4] it is believed that there may be a similar continuity in this case also; in fact,

[1] Untersuch. ii. Gehirn u. Rückenmark, 1865.

[2] Ueber einige neuere Forschungen im Gebiete der Anatomie des Centralnervensystems, 1891. For modern developments, see Barker, Nervous System, 1899, and Cajal, Anat. Anz. xxx. 1907, and xxxii. 1908.

[3] Apáthy, Mittheilung. a. d. zool. Station zu Neapel, 1897, Bd. xii.: Anat. Anz. 1907. See also Held, Neurol. Centr. 1905; Anat. Anz. xxx. 1907; and Nissl, Die Neuron-theorie, &c. 1903.

[4] M. Schultze, Stricker's Histology, 1871; G. Mann, Verhandl. d. anat. Ges. 1898; Mönkeberg und Bethe, Arch. f. mikr. Anat. vol. xliv. 1899; Bethe, Nervensystem, 1903; Cajal, Riv. trimestr. 1905; Held, Arch. f. Anat. 1905.

some observers state that such continuity can be shown to exist. But whether this is or is not the case, it cannot be denied that from the point of view of nutrition each nucleated cell-body exerts an immediate influence over its own cell-processes alone; that is to say,

FIG. 24.—SYNAPTIC RAMIFICATIONS OF AXON OF ONE NERVE-CELL, B, AROUND THE CELL-BODIES OF OTHER CELLS, A. From the cerebellum of the rat. (Cajal.)

a, *b*, *c*, ramifying axon; *d*, dendrons.

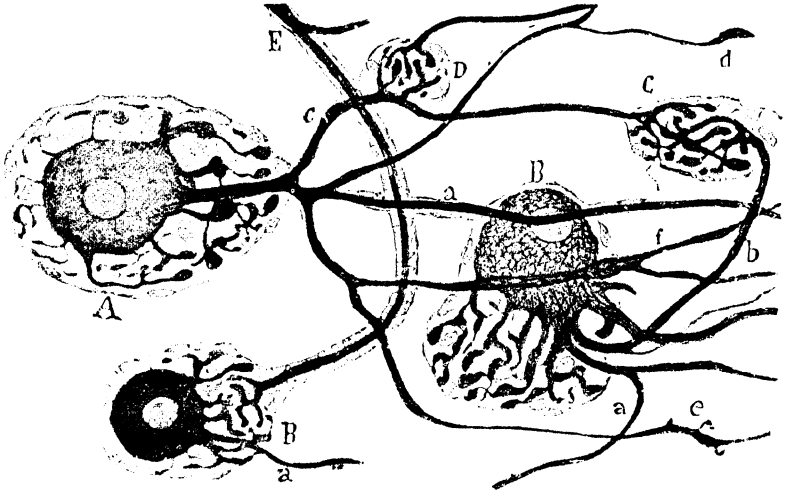


FIG. 25.—SYNAPTIC CONNEXIONS OF SYMPATHETIC CELLS FROM THE SUPERIOR CERVICAL GANGLION OF MAN. (Cajal.)

A, B, cells with intra- and extra-capsular processes. C, D, synapses between processes outside the cell-capsules; E, a fibre, which is itself surrounded by a fine spirally wound fibril, passing to a cell and forming a synapse with the cell-processes within the capsule. *a*, *a*, axons; *b*, *c*, *d*, *e*, *f*, extra-capsular dendrons.

each cell is, trophically speaking, a distinct unit, and in this sense, at any rate, the neurone-theory may be regarded as established, even should the doctrine of discontinuity, so far as the neuro-fibrils are concerned, be disproved. And it appears equally true, in spite of statements which have from time to time been made to the contrary, that each so-called 'neurone' is developmentally a distinct entity, formed from a single neuroblast: it is, indeed, this fact which explains the trophic influence which has just been alluded to.

Structure of the nerve-cell.—Every nerve-cell consists, as has been already mentioned, of a nucleated enlargement—the nerve-cell-body (*nerve-cell proper* of some authors)—and of one or more processes. If there is only one process, this is an axon and becomes the axis-cylinder of a medullated nerve-fibre, or forms the bulk of a non-medullated fibre. If two processes, both may be axons, as with the cells of the spinal ganglia. Generally, however, there is one axon and one or more dendrons, the latter ramifying almost immediately and usually ending not far from the cell-body. The axon may come off either directly from the cell-body or from a dendron.

While it is universally conceded that the axon of the cell is a conductor of nerve-impulses, the view has been taken that the dendrons or protoplasmic processes are merely for purposes of nutrition, serving the office of roots to the cell-body. This view was upheld by no less an authority than Golgi, the eminent anatomist of Pavia, who regarded all connexion between the nerve-cells as taking place between axons and their collaterals, the ultimate branches of which he supposed to terminate in a fine nervous network in the grey substance.[1] The existence of such a network had been previously conjectured by Gerlach.[2] But the conducting function of the dendrons was put beyond a doubt by the discovery—made originally by Cajal,[3] and since abundantly confirmed — (1) that the branchings of the axons do not end in a network, but have free terminations, and (2) that the axons of one nerve-cell form close contact-connexions (synapses) with the dendrons of another, of such a nature that conduction can only take place through the dendrons towards the cell-body and axon, and away from the dendrons and cell-body by way of the axon and its collaterals. This constitutes the so-called 'law of conduction' or 'of dynamic polarisation' within the neurone (fig. 26).[4] The spinal ganglion-cells offer, however, an important exception to this general law, for in them the peripheral process, which is unquestionably an axon, habitually conducts impressions towards the cell-body.

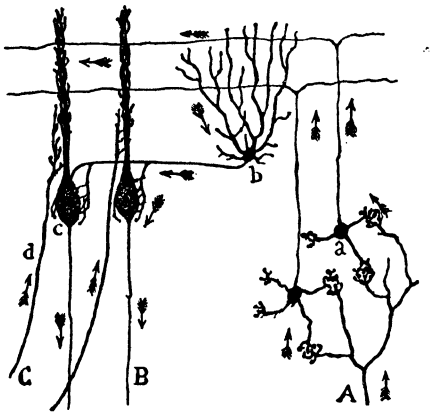


FIG. 26.—TO ILLUSTRATE THE SO-CALLED LAW OF CONDUCTION IN THE CEREBELLAR NEURONES. (Cajal.)

A, an afferent (moss-) fibre conveying impulses to the dendrons of *a*, the granule-cells. The axons of these pass them on to the dendrons of *b*, a basket-cell. The axon of the basket-cell again conveys impulses from its cell-body to the cell-bodies of the cells of Purkinje, *c*, and by the axons of these, B, impulses are conveyed away towards the white substance. C, another afferent fibre passing at *d* to the dendrons of the Purkinje cells, and carrying impulses from some other source. From the dendrons they may be supposed to pass to the cell-bodies and then away by the axons. The arrows indicate the course taken by the nerve-impulses, which is seen in every case to be towards the cell-body in the dendrons and away from the cell-body in the axons.

Many cells have long axons which terminate by arborisations at a distance from the cell-body (fig. 27 A). Others are provided with short axons which ramify in the grey matter near the cell-body (fig. 27 B). These form distinct types (types i. and ii. of Golgi) which may be termed the *long-axoned* and *short-axoned* cells respectively. The cells of type i. effect communication between the central nervous system

[1] Golgi's first observations, made by the well-known method discovered by him, were published in the Gazetta medica lombarda in 1873. A further important contribution to this subject appeared in 1886 under the title 'Sulla fina anatomia degli organi centrali del sistema nervoso.' These and other articles on the same subject were collected and republished in German in 1894 under the title 'Untersuchungen ü. d. fein. Bau d. centr. u. periph. Nervensystems.'

[2] Stricker's Handbook of Histology, 1871. It is represented in fig. 22A.

[3] Riv. trimestr. micrograph. 1888 and 1889.

[4] Cajal, Riv. trimestr. 1897. This hypothesis applies, of course, only to nervous impulses set up naturally, and not as the result of artificial excitation of the fibres.

and the periphery, and between parts of the nervous system which are distant from one another. Those of type ii. effect communications between adjoining

FIG. 27B.—A SHORT-AXONED CELL FROM THE CEREBRAL CORTEX. Golgi method. (Cajal.)
a, *a'*, *a''*, axon and its ramifications; *d*, *d*, *d*, dendrons.

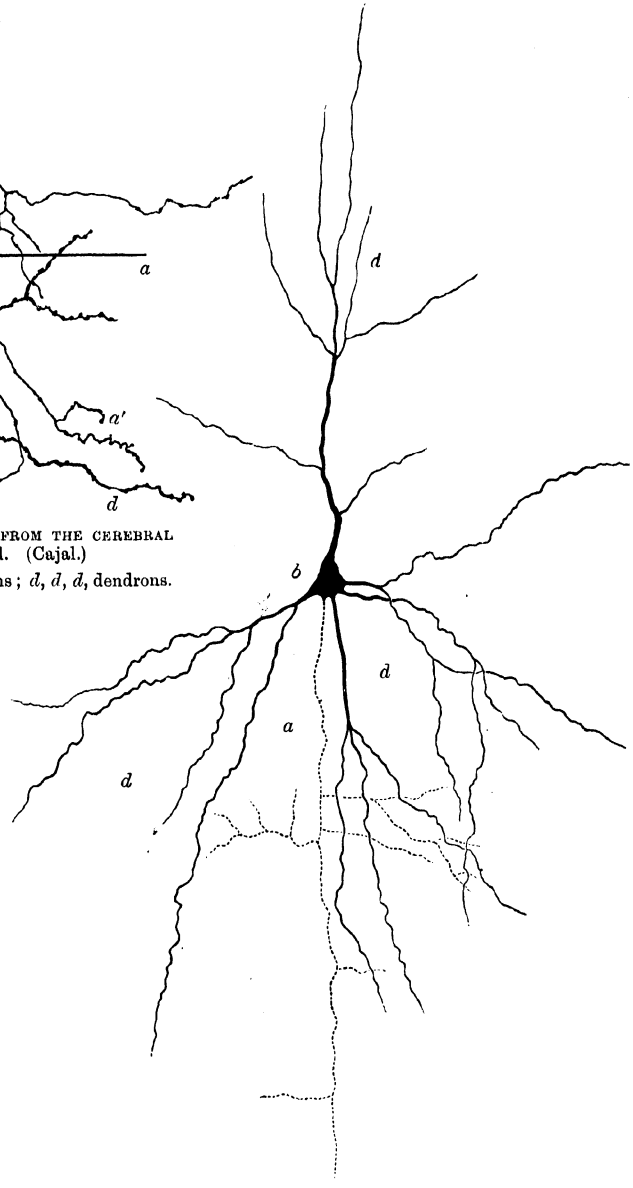


FIG. 27A.—A LONG-AXONED NERVE-CELL FROM THE CEREBRAL CORTEX. (Golgi.)
a, axis-cylinder process with collaterals; *d*, *d*, dendrons; *b*, body of cell.

nerve-cells, the action of which is thus 'associated' together. Probably all grades of transition exist between the two types, although in most cases the differences are easily recognisable. As a general rule, the longer and larger the axon the larger the cell-body from which it arises: hence a vast difference is found in the size of nerve-cells, in general correspondence with the very varying length of the nerve-fibres which spring from them. This relation between size of cell-body and size and length of axon is, however, not without exceptions.

The body of a nerve-cell always contains a characteristically large spherical nucleus with a very distinct nucleolus and membrane, but the chromatin network

of the nucleus is delicate or may not be discernible. Like other cells, the nerve-cell contains a centrosome (Lenhossék, Lewis), but it is not always easy of demonstration.

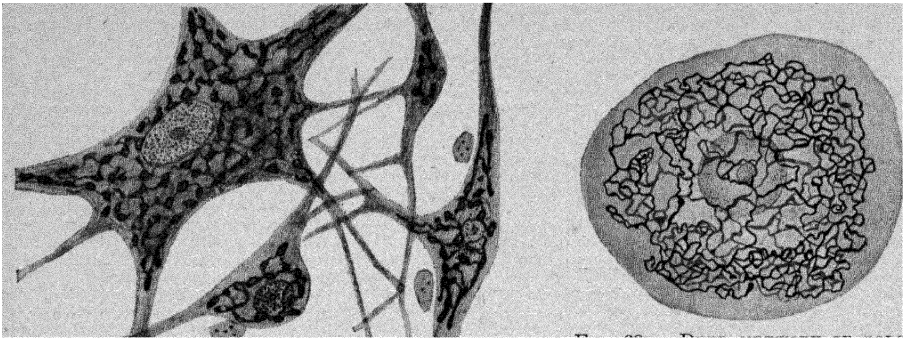


FIG. 28A.—DEEP NETWORK OF GOLGI WITHIN CELLS OF THE SPINAL CORD. (Cajal.)

FIG. 28B.—DEEP NETWORK OF GOLGI WITHIN CELL FROM SPINAL GANGLION. (Golgi.)

In the protoplasm of some nerve-cells an irregular network of fine canaliculi (fig. 28 A and B) has been described by Golgi[1] and others; according to Holmgren this is occupied by processes of extraneous cells (*trophospongium*). By other methods a fine superficial network (fig. 29) may be demonstrated on the surface of many nerve-cells; whether this is related to the neuro-fibrils or whether it is of neuroglial origin is uncertain.

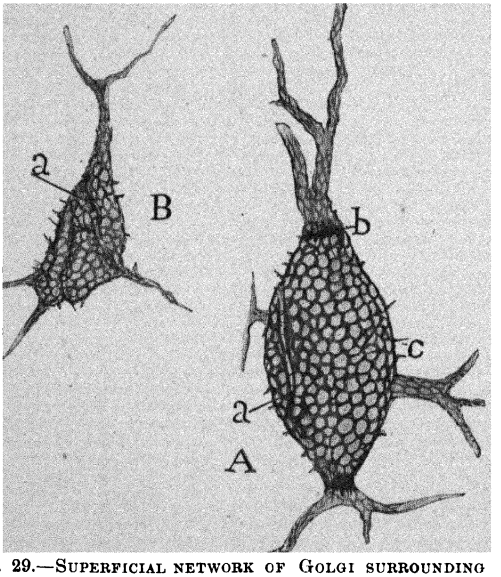


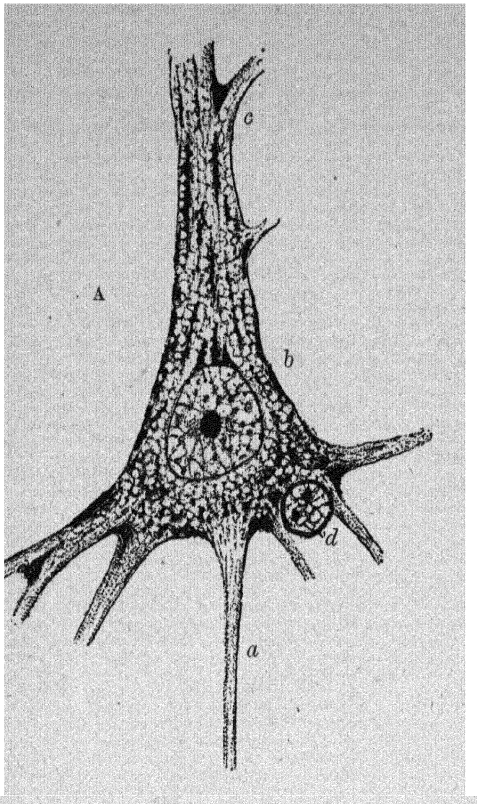
FIG. 29.—SUPERFICIAL NETWORK OF GOLGI SURROUNDING TWO CELLS FROM THE CEREBRAL CORTEX OF THE CAT. Ehrlich's method. (Cajal.)

A, large cell; B, small cell. *a*, *a*, folds in the network; *b*, a ring-like condensation of the network at the poles of the larger cell; *c*, spinous projections from the surface.

The cytoplasm of many nerve-cells contains small angular patches of a proteid material (*neuro-chromatin*) which stains deeply with basic dyes (figs. 30, 31), apparently owing to the presence of nucleo-protein. These also contain a small amount of iron (Macallum). The angular patches were first fully described and their importance recognised by Nissl[2]—hence the name *Nissl granules* applied to them. They undergo changes with alterations in activity of the nerve-cell, becoming built up during rest and broken down during activity (fatigue-effect; fig. 31). The breaking-down process is known as *chromatolysis*, and is brought about by various agencies besides fatigue, such as the action of certain drugs and the effect of diseased

[1] First in spinal ganglion cells; subsequently in the cortical cells and elsewhere. (Verh. d. anat. Gesellsch. 1901).

[2] Tagebl. d. Naturforscherversamml. zu Strassburg, 1884; Centr. f. Nervenh. u. Psych. v. 1894. The granules had been previously seen by other observers, but their functional significance had not been recognised.



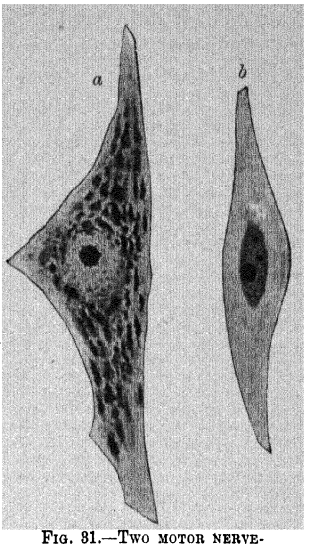


FIG. 31.—TWO MOTOR NERVE-CELLS FROM THE DOG.

a, normal; *b*, after a period of prolonged activity. (Photographed from preparations by Dr. Gustav Mann.)

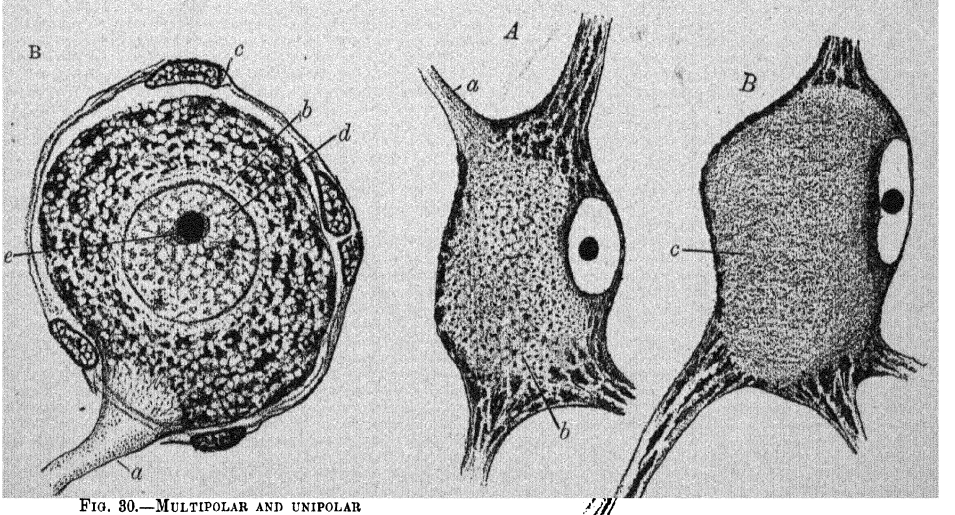


FIG. 30.—MULTIPOLAR AND UNIPOLAR TYPES OF NERVE-CELL.

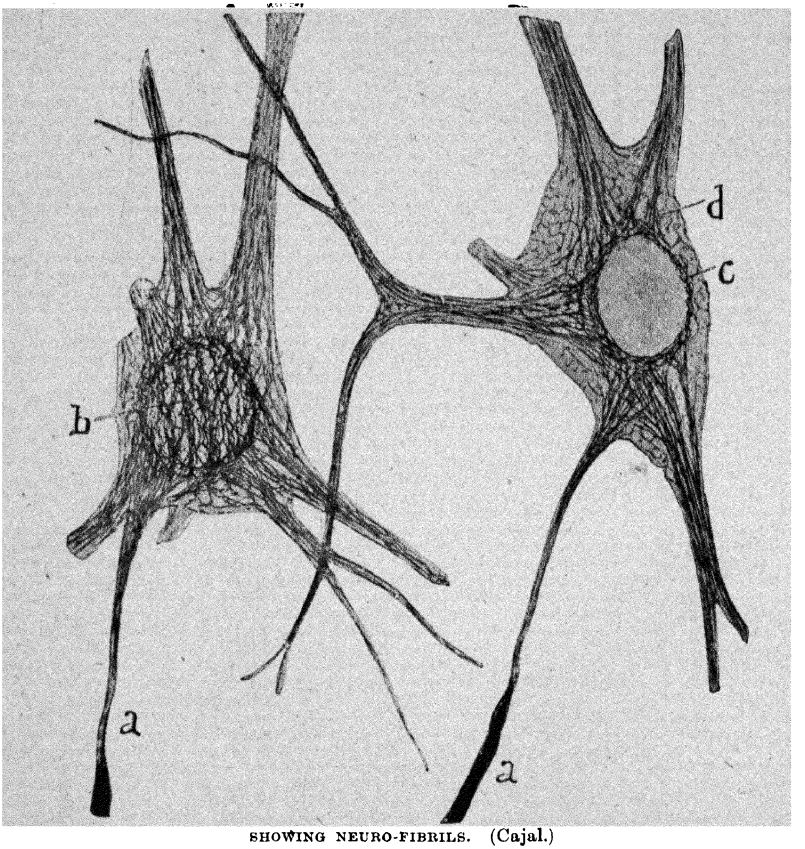
A, large pyramidal cell of cerebral cortex, human. Nissl method. (Cajal.) *a*, axon; *b*, cell-body; *c*, apical dendron; *d*, placed between two of the basal dendrons, points to the nucleus of a neuroglia-cell.

B, unipolar cell from spinal ganglion of rabbit. Nissl method. (Cajal.) *a*, axon; *b*, circumnuclear zone, poor in granules; *c*, capsule; *d*, network within nucleus; *e*, nucleolus.

FIG. 32.—TWO MOTOR CELLS FROM THE RABBIT'S SPINAL CORD, WHICH SHOW CHROMATOLYSIS AS THE RESULT OF SECTION (FIFTEEN DAYS PREVIOUSLY) OF THE NERVE-FIBRES WHICH ARISE FROM THEM. (Cajal.)

In A the chromatolysis is rather less advanced than in B. In both the nucleus has moved to the periphery, and the cell-substance (*b* and *c*) is swollen. *a*, axon-process of A.

conditions of the nervous system, or of the body generally. Most strikingly is this change of the neuro-chromatin effected if the axon of the nerve-cell be cut in any part of its course (*axonal reaction*). A few days after such a lesion the Nissl granules begin to alter and break down, and may ultimately disappear; the cytoplasm becomes swollen, and the nucleus assumes a peripheral position (fig. 32). In most cases the Nissl granules are built up again after a time. But sometimes this is not the case, and in these instances the cytoplasm undergoes ultimate atrophy.[1] Some nerve-cells are altogether destitute of Nissl bodies, but they are rarely absent from the larger type of cell. In these they also occur in



SHOWING NEURO-FIBRILS. (Cajal.)

a, axon; *b*, *c*, *d*, various parts of the intracellular plexus of fibrils.

the dendrons, but never in the axon nor in the part of the cytoplasm from which the axon issues.

Nerve-cells occasionally contain clumps of brown or black pigment lying near the nucleus.[2] Where many cells in any part of the nervous system are thus pigmented, a characteristically dark appearance is presented by the grey matter, as in the so-called *locus niger*.

[1] For the literature of this subject, see Barker, Nervous System, 1899; Cajal, Textura del sistema nervioso, 1899; Schäfer, article 'Nerve-cell' in Text-book of Physiology, 1900; and Van Gehuchten, Bull. de l'Acad. roy. de Belgique, 1897, and Anatomie du système nerveux, 1907. Chromatolysis may also occur in motor nerve-cells as the result of cutting corresponding sensory neurones (Warrington, Journ. Physiol. xxiii. xxiv. xxv. and xxx., 1897 to 1904; and Bräunig, Arch. f. Anat. u. Phys. 1903)

[2] On the pigment in nerve-cells, see Obersteiner, Arbeiten a. d. neurol. Instit. Wien, x. 1903.

A constant characteristic of the cell-body is the fact that it is traversed by fibrils (*neuro-fibrils*) which are continuous through the cytoplasm from one

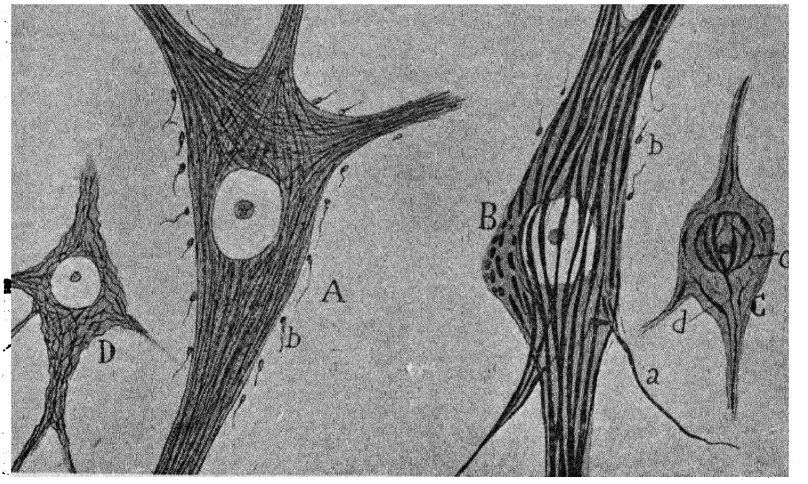


FIG. 34.—NERVE-CELLS OF LIZARD: A AND D DURING ACTIVITY, B AND C DURING HIBERNATION. (Cajal and Tello.)

a (in B), axon; *b*, *b* (in A and B), knob-like endings of extraneous fibrils; *c*, *d* (in C), superficial and deep fibril networks.

process into another (fig. 33). They form a network within the cell-body, and may also intercommunicate as they run in the nerve-fibres.[1] They are said (Cajal, Tello) to vary in size with the functional activity of the cells, being larger and coarser in hibernating animals than in the same animals when awakened (fig. 34). These fibrils are believed to be the proper conducting elements of the nervous system; but this is by no means certain, and indeed the view has been expressed by Cajal that it is the *neuroplasm* of the fibre (in which the fibrils are imbedded) which is the true conducting part of the neurone. They are traceable along the axis-cylinders of the nerve-fibres, which issue from the cells, and into the arborisations by which these axis-cylinders end, whether in motor or sensory organs. They also pass into the dendrons, and, as has already been stated, some authorities believe that they are continued from one neurone into another.

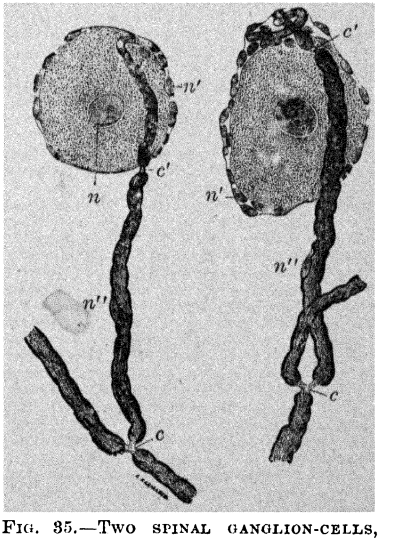


FIG. 35.—TWO SPINAL GANGLION-CELLS, SHOWING BIFURCATION OF THEIR NERVE-FIBRE PROCESSES. (Ranvier.)

n, nucleus of one of the cells; *n'*, nuclei of capsules; *n''*, nuclei of Schwann's sheath; *c*, *c*, *c'*, *c'*, constrictions of Ranvier.

The cell-processes are either *dendrons* or *axons*. The former are absent in certain cells — *e.g.* most of those of the spinal ganglia, and must therefore be regarded as

[1] Cajal, Trabajos del lab. 1903 and 1907, and Textura del sist. nerv. 1904; Donaggio, in Gaz. med. ital. 1903, and Riv. sper. d. fren. xxx. 1904; also in Rev. of Neurol. 1905; Tello, in Trabajos d. lab. d.

of subordinate importance: the latter are always present except in the cells of Drasch at the terminations of sympathetic nerves (see p. 18). Some authors

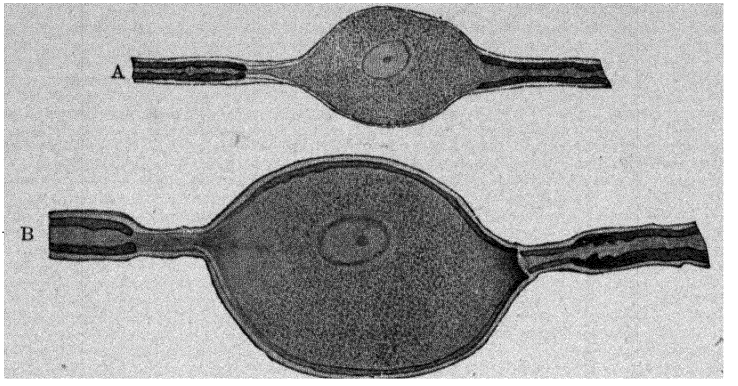


FIG. 36.—TWO BIPOLAR GANGLION-CELLS (FISH). (Holmgren.)
In B the medullary sheath is continued as a thin layer over the cell-body.

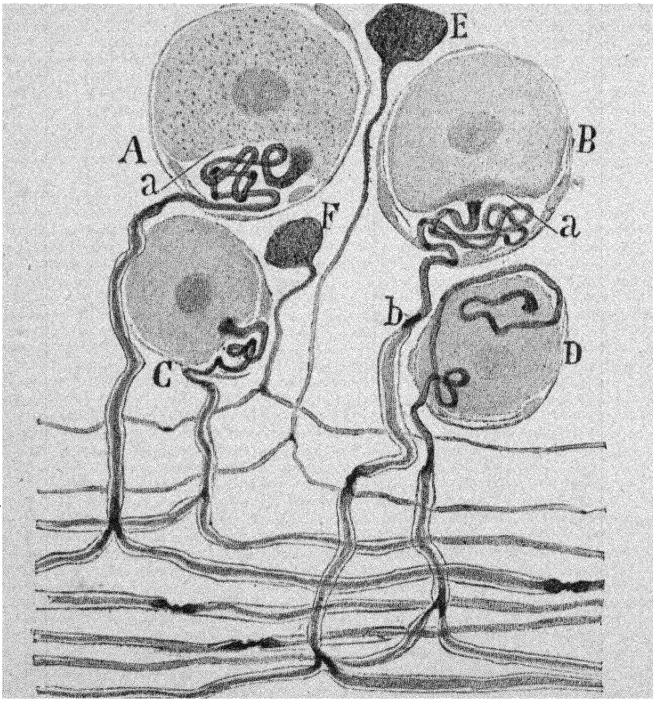


FIG. 37.—TYPES OF CEREBROSPINAL GANGLION-CELLS FROM VAGUS GANGLION OF CAT. Methylene-blue method. (Cajal.)

A, B, large clear cells with axon commencing in a convolution; C, D, smaller clear cells with less convoluted axon-process; E, F, small dark cells without convolutions of axon.

consider the peripherally directed nerve-fibre of the dorsal roots to represent a dendron on account of the fact that the nerve-impulses traverse it cellulipetally.

investig. biol. 1904; Vincenzi, Anat. Anz. xxviii. 1906; Rossi, Névraxe, vi. 1904; H. Vogt, Monatschr. f. Psych. ii. 1902; E. S. London, Arch. f. mikr. Anat. lxvi. 1903; Schiefferdecker, Arch. f. mikr. Anat lxvii.; also the works by Apáthy, Bethe, and Held referred to on page 22.

But we know of no other instance of a dendron being invested with a myelin sheath; in this and in all other structural points this fibre resembles an axon.

Some of the cells of the spinal and of the sympathetic ganglia are furnished with short processes terminating with an enlargement either within the capsule which encloses the cell, or in the interstitial substance of the ganglion (Huber, Cajal).

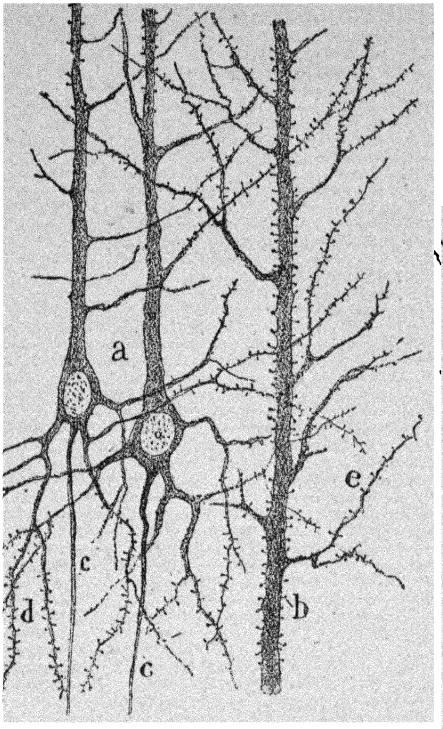


FIG. 38.—CELLS OF CEREBRAL CORTEX, SHOWING 'SPINES' ON DENDRONS. Methylene-blue method. (Cajal.)

a, cell-bodies; *b*, apical dendron of a large deeply seated cell, showing spines; *c*, *c*, axons; *d*, dendron-branches, with spines.

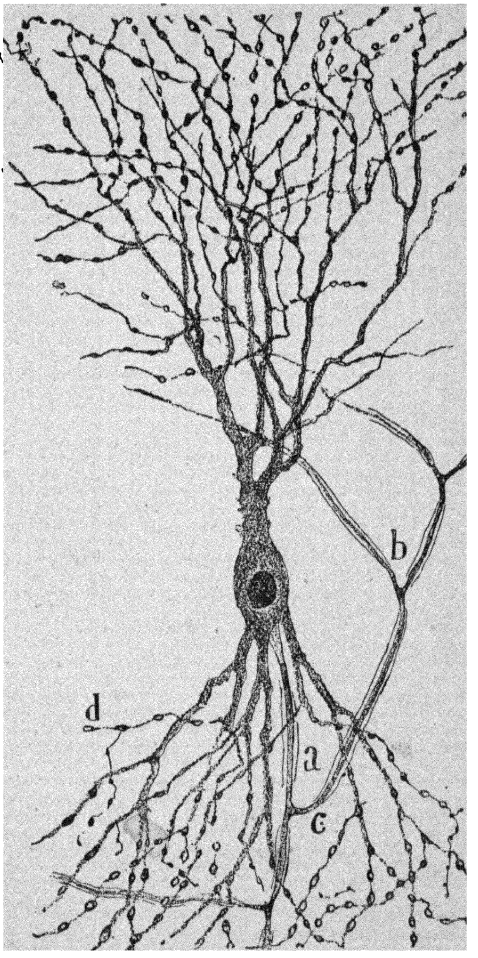


FIG. 39. — CELL FROM CEREBRAL CORTEX, SHOWING VARICOSITIES ON ITS DENDRONS AND NOT SPINES. Methylene-blue method. (Cajal.)

a, axon; *b*, *c*, a branching collateral (both this and the main axon show a medullary sheath); *d*, varicose dendrons.

These may either represent dendrons or abortive axons. In the sympathetic ganglia the dendrons are observed to form synapses with processes from other nerve-cells, or from the same cell (fig. 25).

Each nerve-cell usually has a single axon, but there are sometimes two or even three. In the absence of dendrons the cell-bodies are usually spheroidal, with one process (*unipolar*) — as in the spinal ganglia of mammals (figs. 30, 35, 37), and in the superior motor nucleus of the fifth cerebral nerve; or fusiform, with two processes (*bipolar*) — as in the spinal ganglia of some fishes (fig. 36) and in the cochlear and vestibular ganglia of all vertebrates. But when dendrons are present the cell-body is usually irregularly angular in shape, and having several processes is termed *multipolar*

(figs. 22A, 30A, 38, 39). Such cells may be stellate, or pyramidal, or flask-shaped, or may present every conceivable irregularity. The dendrons are sometimes very extensive and closely interlaced (fig. 39), sometimes scanty and widely separated. The dendrons of some cells are provided with minute lateral projections coming off close together along their whole length [1]: these have been named 'spines' (fig. 38). Others have numerous varicosities (fig. 39), best marked when the spines are deficient: this may be the result of a post-mortem change.

The part of the cell-body from which the axon springs is always devoid of Nissl bodies, and presents therefore a clearer appearance than the rest (*cone of origin*; fig. 30, *a*).

The axon differs from the dendrons (1) in its clearer appearance, due to the absence of Nissl bodies; (2) in its generally smaller and more uniform size,

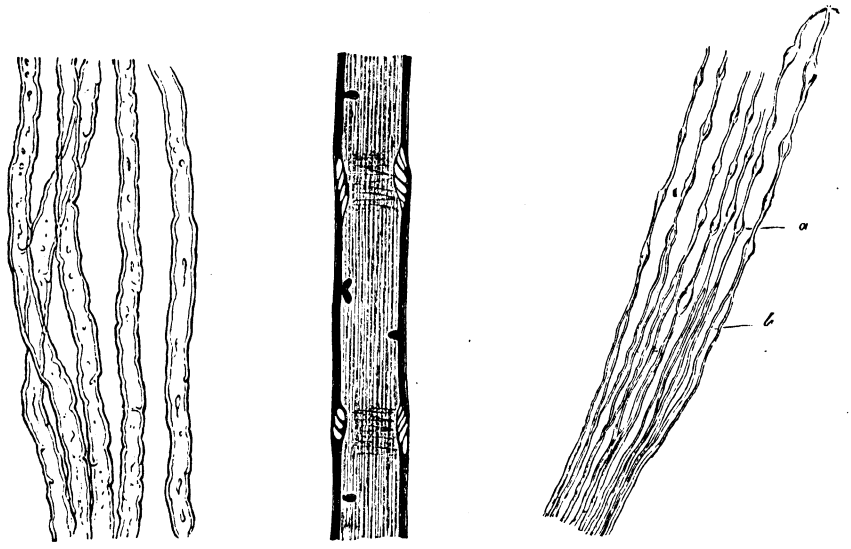


FIG. 40.—WHITE OR MEDULLATED NERVE-FIBRES, SHOWING THE SINUOUS OUTLINE AND DOUBLE CONTOURS. (After Bidder and Volkmann.)

FIG. 41.—A SMALL PART OF A MEDULLATED FIBRE HIGHLY MAGNIFIED. (E. A. Schäfer.)

The fibre looks in optical section like a tube—hence the term 'tubular,' formerly applied to these fibres. Two partial breaches of continuity are seen in the medullary sheath, which at these places exhibits a tendency to split into laminæ. The primitive sheath is here and there apparent outside the medullary sheath, and the delicate striæ which are visible in the middle of the fibre indicate the fibrillated axis-cylinder.

FIG. 42.—FINE VARICOSE MEDULLATED FIBRES FROM THE ROOT OF A SPINAL NERVE. (From Valentin.)

whereas the dendrons almost always become finer as they proceed farther from the cell; (3) in its manner of branching. It does not as a rule arborise near the cell-body as the dendrons do, but it may give off here and there, both near the body of the cell and elsewhere in its course, fine lateral branches (figs. 37, 39); these are known as *collaterals*: like the axon itself, they are generally medullated.

Nerve-fibres.—In the cells of the cerebrospinal system the axon always becomes surrounded, soon after leaving the cytoplasm, by a medullary sheath, composed of 'myelin,' a material containing, amongst other substances, lecithin and cholesterin in considerable amount, and therefore staining black with osmic acid (figs. 47, 48, 50). In this way a *medullated nerve-fibre* is formed. The whole

[1] Cajal, La Cellule, 1891.

of the white substance of the cord and brain is constituted by nerve-fibres of this character, composed mainly of the axons of the nerve-cells, each covered by a sheath of myelin (*medullated sheath, white substance of Schwann*) (figs. 40 to 43). All nerve-fibres which leave or enter the cerebrospinal axis by the nerve-roots (peripheral nerve-fibres) acquire, besides this, an external sheath, the *nucleated sheath of*

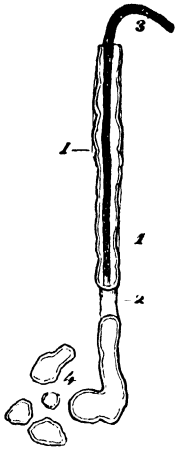


FIG. 43.

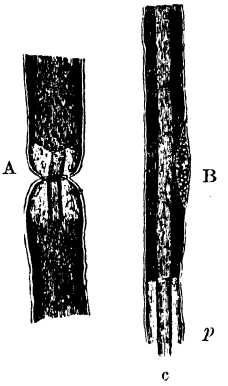


FIG. 44.

FIG. 45.

FIG. 43.—DIAGRAM to show the parts of a medullated fibre—viz. 1, 1, *neurolemma* or *primitive sheath* enclosing the doubly contoured *white substance* or *medullary sheath*. 2, a part where the white substance is interrupted, the outer sheath remaining. 3, *axis-cylinder* projecting beyond the broken end of the fibre. 4, drops of myelin escaped from the medullary sheath.

FIG. 44.—TWO PORTIONS OF MEDULLATED NERVE-FIBRES AFTER TREATMENT WITH OSMIC ACID, SHOWING THE AXIS-CYLINDER AND THE MEDULLARY AND PRIMITIVE SHEATHS. (Key and Retzius.)

A. Node of Ranvier. B. Middle of an internode with nucleus.

c, axis-cylinder, projecting at the broken end; *p*, neurolemma, within which the medullary sheath, which is stained dark by the osmic acid, is somewhat retracted.

FIG. 45.—PART OF AN AXIS-CYLINDER, HIGHLY MAGNIFIED, SHOWING FINE VARICOSE FIBRILS WITHIN IT. (Max Schultze.)

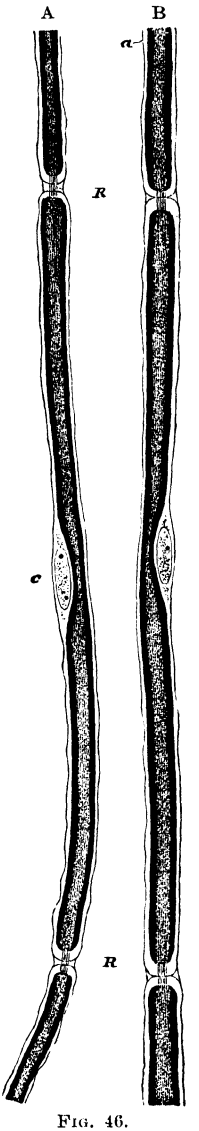


FIG. 46.

FIG. 46.—PORTIONS OF TWO NERVE-FIBRES STAINED WITH OSMIC ACID (FROM A YOUNG RABBIT). × 425 diameters. Somewhat diagrammatic.

R, R, nodes of Ranvier, with axis-cylinder passing through; *a*, neurolemma of the nerve; *c*, opposite the middle of the segment, indicates the nucleus and protoplasm lying between the neurolemma and the medullary sheath. In A the nodes are wider, and the intersegmental substance (constricting band) more apparent than in B. (From a drawing by J. E. Neale.)

FIG. 47.—TRANSVERSE AND LONGITUDINAL SECTION OF MEDULLATED NERVE-FIBRE OF FROG (OSMIC ACID AND ACID FUCHSINE). (After Biedermann.)

The longitudinal section shows one node of Ranvier and two of Lantermann's clefts. The fibrillar structure of the axis-cylinder is shown in both longitudinal and transverse section.

Schwann or *neurolemma*,[1] which consists of a fine but tough homogeneous membrane containing nuclei at regular intervals upon its inner surface.

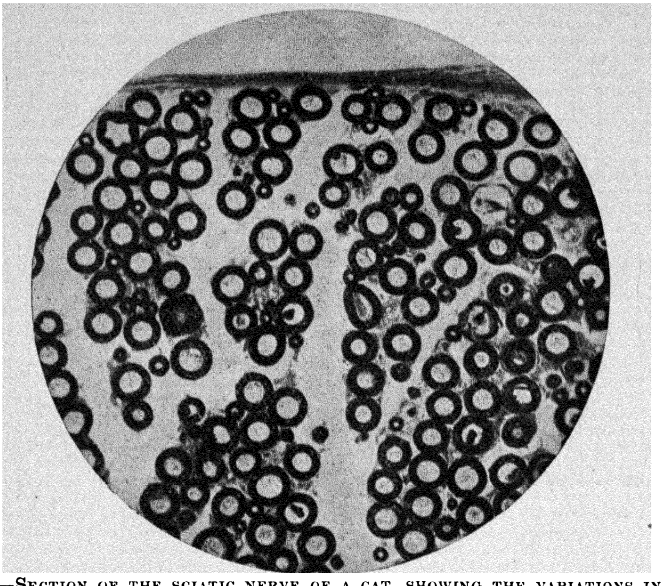


FIG. 48.—SECTION OF THE SCIATIC NERVE OF A CAT, SHOWING THE VARIATIONS IN SIZE OF ITS CONSTITUENT FIBRES. Magnified 300 diameters. The nerve was fixed with osmic acid.

Further, at regular intervals between the situations where its nuclei are found the sheath of Schwann dips in towards the axis-cylinder and thus

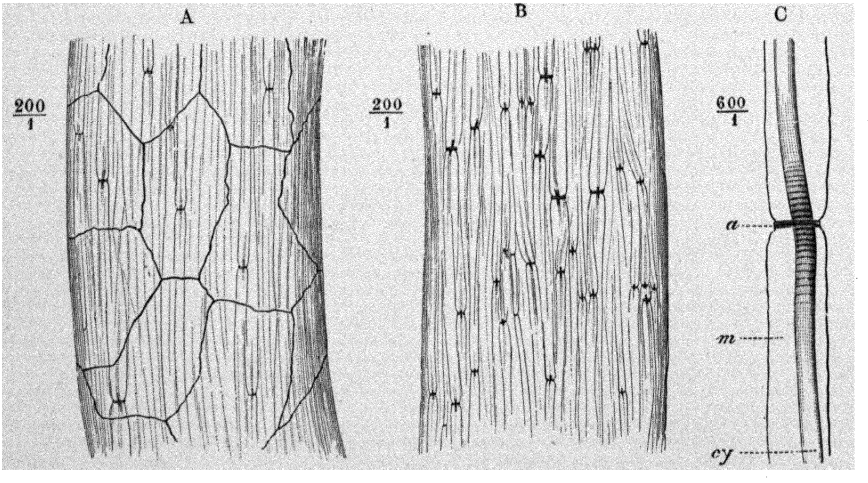


FIG. 49.—NERVES STAINED WITH SILVER NITRATE. (Ranvier.)

In A, the epithelial-like layer of flattened cells belonging to the sheath of Henle is stained. In B, the cross-like markings at the nodes are exhibited. In C, a single fibre is shown more highly magnified, with Fromann's transverse markings of the axis-cylinder. *a*, constricting band; *m*, medullary sheath; *cy*, axis-cylinder.

cuts up the medullary sheath of the peripheral nerve-fibres into a series of segments of equal length. The places where the medullary sheath is

[1] Often spelt *neurilemma*, a name which was originally given to the funicular sheath of a nerve (see p. 87). The Greek prefix is, however, invariably *νευρο-* in words compounded from *νεῦρον*.

thus interrupted are termed the *nodes* or *constrictions of Ranvier*; at each of these the sheath of Schwann forms a ring-like band which immediately invests the axis-cylinder (figs. 44, 46, 47): this is the *constricting band of Ranvier*. The band stains with silver nitrate, which at the constriction also penetrates to and stains the axis-cylinder, an appearance of small crosses being thus produced (fig. 49). By these constrictions the medullary sheath of the peripheral nerves is interrupted at regular intervals of about one millimetre,

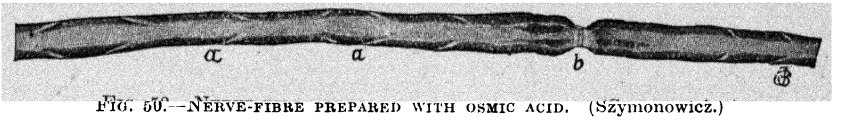


FIG. 50.—NERVE-FIBRE PREPARED WITH OSMIC ACID. (Szymonowicz.)
b, constriction of Ranvier. The intervals between the medullary segments appear as clear oblique lines, *a*, *a*.

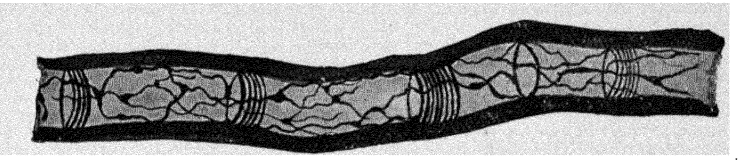


FIG. 51.—SPIRAL AND RETICULAR FIBRILS IN THE SHEATH OF A NERVE-FIBRE. (Golgi.)

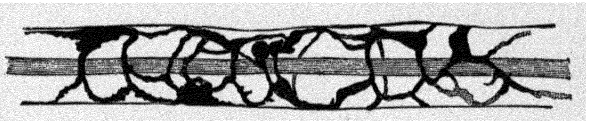


FIG. 52.—RETICULAR APPEARANCE IN THE MEDULLARY SHEATH OF A NERVE-FIBRE FROM THE GUINEA-PIG. (Gedoelst.)

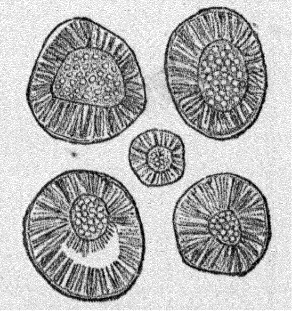


FIG. 53.—SECTION ACROSS FIVE NERVE-FIBRES. Magnified 1,000 diameters. (E. A. Schäfer.)

The nerve was hardened in picric acid and stained with picro-carmine. The radial striation of the medullary sheath is very apparent. In one fibre the rays are broken by shrinkage of the axis-cylinder. The fibrils of the axis-cylinder appear tubular. (From a photograph.)

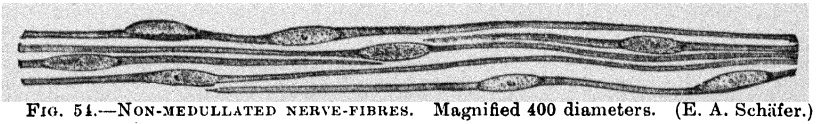


FIG. 54.—NON-MEDULLATED NERVE-FIBRES. Magnified 400 diameters. (E. A. Schäfer.)

and the axon or axis-cylinder containing the neuro-fibrils is the only part of the nerve-fibre which is continuous throughout its whole length. Certain other more frequent interruptions are apparent in teased-out nerve-fibres in the course of the medullary sheath. These take the form of oblique clefts running through its thickness and subdividing it into a number of *segments* (Lantermann) of very variable number and length (fig. 50). Another appearance which is sometimes observed in the medullary sheath after the action of alcohol and certain other

reagents is that of a *reticulum* extending through its thickness (figs. 51, 52). Picric acid, on the other hand, produces the effect of radial striations extending between

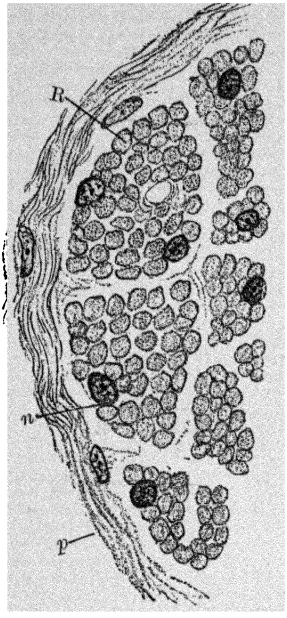


FIG. 55.—SECTION OF A VISCERAL NERVE OF THE OX. Highly magnified. (Cajal.)

R, fibre of Remak; *n*, nucleus; *p*, perineurium.

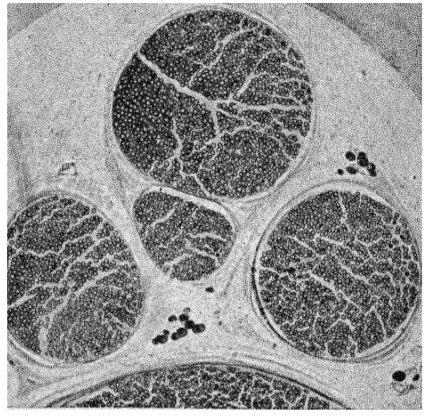


FIG. 56.—SECTION OF PART OF A NERVE-TRUNK FIXED WITH OSMIC ACID. From a photograph. Magnified 40 diameters.

Three small funiculi and a small part of a larger funiculus are shown. The fat-cells in the epineurium are stained black by the osmic acid.

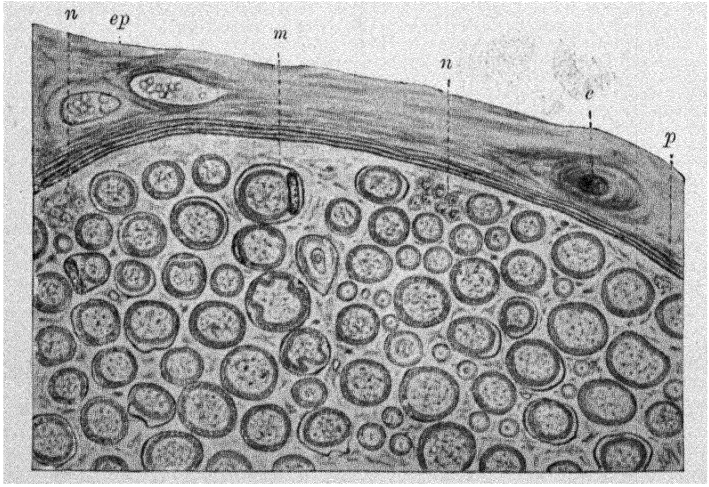


FIG. 57.—SECTION OF PART OF A FUNICULUS OF THE SCIATIC NERVE OF A CAT FIXED WITH FLEMMING'S SOLUTION. Magnified 400 diameters. (E. A. Schäfer.)

ep, epineurium with blood-vessels; *e*, section of an end-bulb; *p*, perineurium; *m*, medullated fibre cut at the level of a nucleus; *n*, *n*, bundles of non-medullated fibres.

the axis-cylinder and the neurolemma (fig. 53). All these three appearances are probably artefacts.

In the nerve-fibres within the brain and spinal cord a nucleated sheath is absent, the fibre being composed of axis-cylinder and medullary sheath only. There are consequently no constrictions of Ranvier, nor are segments of Lantermann observable. The nerve-fibres which emanate from the ganglia of the sympathetic system differ from those just described in not (as a general rule) possessing a medullary sheath. They have in man a greyish appearance, and are known as the *grey* or *non-medullated fibres* or *fibres of Remak* (figs. 54, 55). Nuclei occur upon them at frequent intervals. These may belong to a sheath, but if such a sheath exists it is far more delicate and difficult to demonstrate than the nucleated sheath of the medullated fibre. Besides these nuclei, the fibre is composed of axis-cylinder only, this being, as usual, fibrillated. The grey fibres also occur, in variable number, in ordinary nerves intermingled with the white fibres, but they have entered these nerves from sympathetic ganglia.

The autonomic fibres are, in the first instance, derived from nerve-cells in the spinal cord and lower part of the brain. They are fine medullated fibres, having exactly the same structure as the medullated fibres already described. They always, sooner or later, end in a ganglion, where they lose their medullary sheath, and their axis-cylinders break up into terminal ramifications around the ganglion-cells. From the latter the fibres of Remak emerge.

There are thus four kinds of nerve-fibre—viz.: 1. The *non-medullated autonomic fibre* (post-ganglionic fibre of Langley), which takes origin in a cell belonging to a sympathetic ganglion. 2. The *fine medullated fibre* (pre-ganglionic fibre of Langley), which also belongs to the autonomic system, but takes origin in a cell of the spinal cord or of the lower part of the brain. 3. The *medullated fibre of the white matter of the brain and spinal cord*, which possesses a medullary sheath, but no nucleated sheath of Schwann. 4. The *medullated fibre of the peripheral nerves and nerve-roots*, which consists of axis-cylinder, medullary sheath, and nucleated sheath.

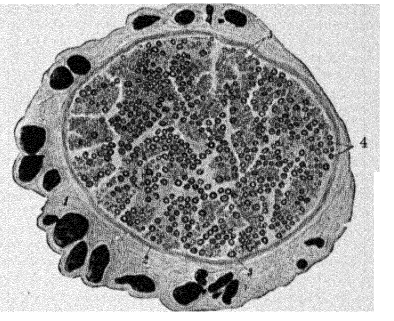


FIG. 58.—SECTION OF THE THORACIC SYMPATHETIC CORD OF THE CAT. Osmic preparation. (Fischer.)

The nerve is composed in almost equal parts of fine medullated fibres (3, 4) derived from the thoracic anterior roots, and grey fibres (5) derived from the sympathetic ganglion-cells. The dark bodies in the epineurium (1) are fat-cells; (2) perineurium.

The nerves which are met with in dissecting the body are always formed of one or more rounded bundles (*funiculi*) of nerve-fibres held together by connective tissue (fig. 56). This connective tissue forms, in the first instance, a lamellated sheath around the funiculus termed the *funicular sheath* or *perineurium* (fig. 57).[1] Within the perineurium and between the individual nerve-fibres of a funiculus is a more delicate connective tissue composed of fibres running parallel with the nerve-fibres and with many interspersed connective-tissue cells. This forms the *endoneurium* of Key and Retzius. Lastly, outside the perineurium is a loose adventitious sheath of areolar tissue which serves to connect the nerve-bundle with other funiculi to form a nerve-trunk, and also to bind the nerve down in its course between the other tissues amongst which it passes: this adventitious sheath is termed the *epineurium*. In it are conveyed the blood-vessels which are destined for the supply of the nerve, and which send off capillaries, relatively few in number, to the interior of the funiculi. The epineurium also contains a certain number of nerve-fibres which are destined to end in the sheath of

[1] Key and Retzius, Studien in der Anatomie des Nervensystems, 1876.

the nerve in end-bulbs. The peripheral nerves owe their toughness to the connective-tissue sheaths.

Degeneration and regeneration of nerve-fibres.—When a nerve-fibre is cut off from the nucleated cell-body from which it has grown, and with which it always remains connected during life, the part which is severed from the cell-body undergoes a change, which was first signalised by A. Waller in 1850. The medullary sheath—if a medullated nerve—breaks up into globular or granular particles of fatty substance (fig. 59, A, B, C), which stain intensely

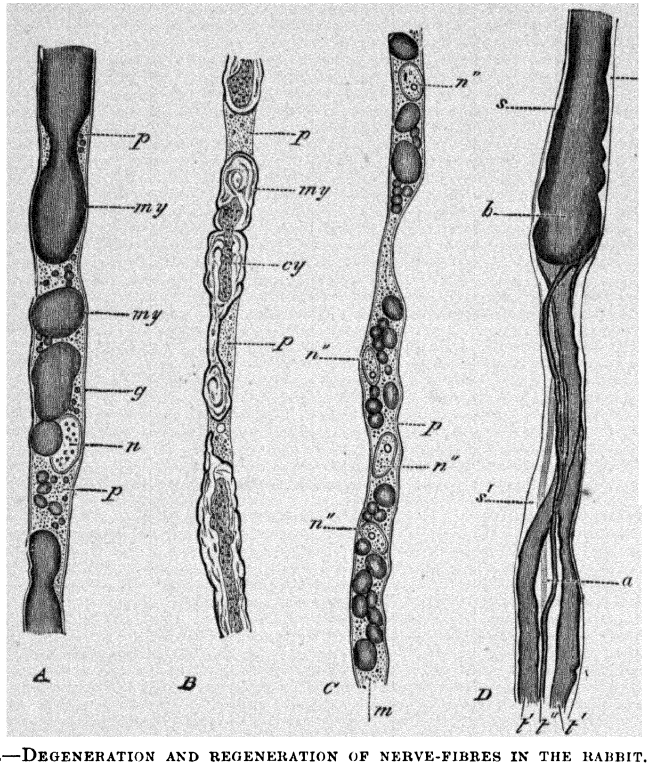


FIG. 59.—DEGENERATION AND REGENERATION OF NERVE-FIBRES IN THE RABBIT. (Ranvier.)

A, part of a nerve-fibre in which degeneration has commenced in consequence of the section, fifty hours previously, of the trunk of the nerve higher up; *my*, medullary sheath becoming broken up into drops of myelin; *p*, granular protoplasmic substance which is replacing the myelin; *n*, nucleus; *g*, neurolemma. *B*, another fibre in which degeneration is proceeding, the nerve having been cut four days previously; *p*, as before; *cy*, axis-cylinder partly broken up, and the pieces enclosed in portions of myelin, *my*. *C*, more advanced stage of degeneration, the medullary sheath having almost disappeared, and being replaced by protoplasm, *p*, in which, besides drops of fatty substance, *m*, are numerous nuclei, *n''*, which have resulted from the division of the single nucleus of the internode. *D*, commencing regeneration of a nerve-fibre. Several small fibres, *t'*, *t''*, have sprouted from the somewhat bulbous cut end, *b*, of the original fibre, *t*; *a*, an axis-cylinder which has not yet acquired its medullary sheath; *s*, *s'*, neurolemma of the original fibre. *A*, *C*, and *D* are from osmic preparations; *B*, from an alcohol and carmine preparation.

with osmic acid, even after the previous action of salts of chromic acid (Marchi). This change begins in about forty-eight hours, and it is accompanied by proliferation of the nuclei of Schwann's sheath (in the peripheral nerves), and is followed by a breaking down of the axis-cylinder, so that the nerve is now no longer able to conduct nerve-impulses if stimulated. Ultimately the degenerative process of the severed fibres proceeds to complete disappearance of these structures, except that the neurolemmal sheaths remain enclosed by the connective tissue of the nerve and filled with what appears to be a mass of

nucleated protoplasm. The fatty granules disappear in the course of a few months: they seem to be removed largely by the agency of leucocytes. The part of the nerve-fibre still connected with the cell-body does not undergo Wallerian degeneration—at least primarily. But it may sometimes occur when the cell-bodies have undergone Nissl degeneration (see p. 28) and ultimate atrophy. Under these circumstances the destruction of the cell-body may tend, secondarily, to Wallerian degeneration of this part of the fibre (Van Gehuchten).

Regeneration is effected—like the original formation of the nerve-fibres—by an outgrowth from the axis-cylinders of the fibres of the central stump of the

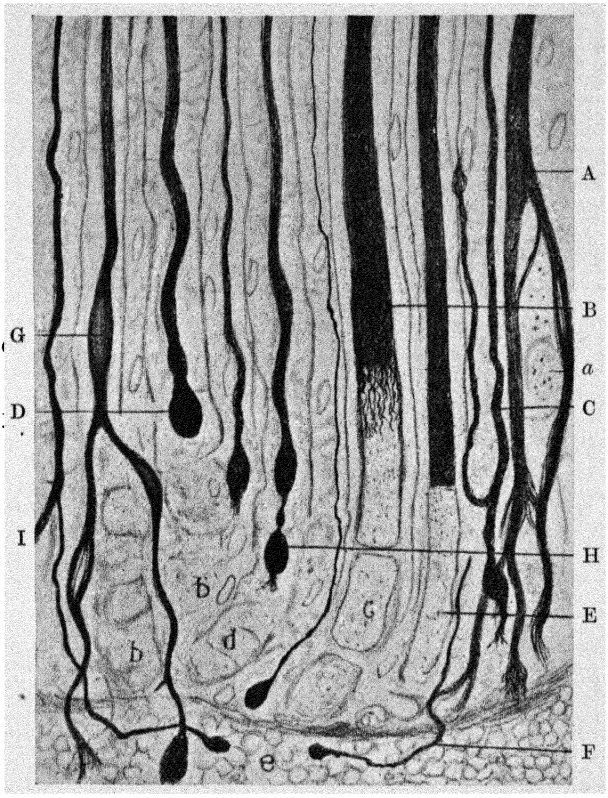
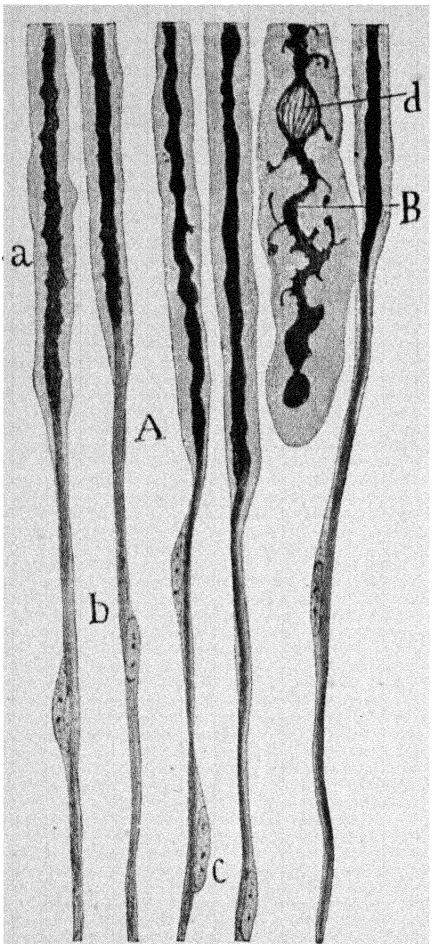


FIG. 60.—FIBRES FROM CENTRAL END OF SCIATIC NERVE OF RABBIT, CUT THIRTY-SIX HOURS BEFORE DEATH. (Cajal.)

A, an axon with fibrillation and vacuolisation, *a*; B, metamorphosed axon; C, axon giving off a retrograde branch; D, H, axons with end-enlargements; G, preterminal enlargement; E, empty sheath; F, growing end of fine axon (perhaps a fibre of Remak); another similar fibre is coming off from I; both are seen passing into *e*, which represents coagulated blood; *b*, *c*, *d*, injured and necrosed ends of nerve-fibres.

cut nerve (fig. 59, *D*; fig. 60). Exactly how soon this outgrowth may begin has not been determined. In any case, the time occupied in complete restoration of the nerve varies according to the ease or difficulty with which the process of growth, which takes place along the course of the old nerve-sheaths in the peripheral part (fig. 62), occurs. If the central and peripheral ends are brought into close juxtaposition, reparation is easier and occupies a shorter time; if, on the other hand, a piece of nerve is actually cut out, so that a space—which becomes filled by scar-tissue—separates the cut ends, a much longer time is

occupied by the growing ends of the fibres in finding their way to the peripheral sheaths. The guiding force appears to be a kind of chemiotaxis, and the attraction is strong enough to enable some fibres to find their way to the peripheral part of the nerve, even if the central stump is turned away and fixed among the adjacent tissues or to the skin.[1] Each fibre of the central stump gives rise not to one outgrowth only,



DAYS BEFORE DEATH. (Cajal.)

A, fibres showing downgrowth of axis-cylinders (*b*) which are invested by flattened nucleated cells; *a*, intact part still myelinated. B, a fibre, the axis-cylinder of which has not grown down with the rest, but which shows various degenerative appearances, such as buds from the axis-cylinder and, at *d*, a separation of the fibrils.

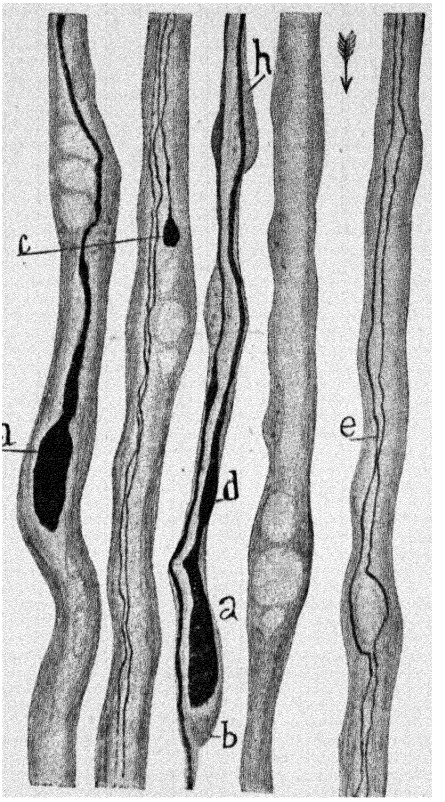


FIG. 62.—FROM THE PERIPHERAL END OF A NERVE CUT SEVENTY-EIGHT DAYS BEFORE DEATH. (Cajal.)

a, *c*, enlarged growing ends of axis-cylinder sprouts which have grown down from the central cut end into the old sheaths of the cut nerve-fibres (myelin drops are still visible within the sheaths). The middle fibres (*h*) are interstitial (not in old sheaths); they show a new formation of a nucleated sheath. The fibre *d* has an enlarged end, *a*, with sheath *b*; *e*, very fine fibres within an old sheath; to the left of it, an old sheath without nerve-fibres.

but to two, three, or more; but of these probably only one becomes functional—that, namely, which happens to find the path which leads to the peripheral organ with which the fibre was originally connected: the other offshoots no doubt eventually disappear.

[1] Cajal, Trabajos, &c. 1905 and 1907. See further on this subject, Bikeles and Francke, Neur. Centr. xxii. 1905; Head and Ham, Journ. Physiol. 1905; Ludlum, Abstr. in Review of Neurology, 1905; Mott, Halliburton, and Edmunds, Proc. Roy. Soc. 1906. The more recent papers on this subject will be found referred to in these articles.

Some observers have described the appearance of fibrils in the peripheral cut parts of the degenerated nerves, which they have interpreted as an indication that the regeneration occurs peripherally, and that the axis-cylinders growing out from the central stump join up with fibres which are already re-formed in the peripheral part.[1] There is, however, strong evidence against this view of regeneration of nerve. Although it is not denied that some kind of differentiation may occur at the periphery, by the linear arrangement of the cells which are to produce the nucleated sheaths of the new nerve-fibres, there appears to be no reason to doubt that the actual regeneration, so far as the axis-cylinder is concerned, is entirely produced by the sprout from the central stump. This would also account for the lapse of time—usually some weeks—which ensues before restoration of function begins to show itself. Cases where such restoration has been recorded as occurring very early are probably to be interpreted as due either to an overlap of nerve-terminations at the periphery—an uncut nerve partly supplying the same area as the one cut—or to an ingrowth from adjacent uncut nerves into the area supplied by the cut and degenerated nerve-fibres, and even into and along their sheaths.[2] Sometimes the more deeply lying structures have not been involved in the deprivation of nerve-supply; and the excitation of these has thus led to the erroneous supposition that a rapid regeneration of the cut nerve-fibres has taken place.

Regeneration of the myelin, or rather the formation of myelin on the newly growing axis-cylinders, begins nearest to the central stump and proceeds from above down, as with its original formation in the embryo (p. 12).

Regeneration does not occur within the central nervous system, or at most in a very incomplete manner. This fact may be associated with the circumstance that the fibres within the spinal cord and brain have no nucleated sheath of Schwann, and the conducting path which the cells of this sheath form in the peripheral nerves for the outgrowing axis-cylinders is therefore absent.

If two nerves—both afferent or both efferent—be cut and the central end of the one be joined to the peripheral end of the other, and *vice versâ*, the regenerating fibres which sprout from the central end grow along the path which is thus offered to them, and a kind of crossed regeneration is thereby established. Even if the function subserved by the nerves is entirely different, this result nevertheless takes place. Thus, in Langley's experiments[3] the fibres of the central end of the cut vagus were caused to regenerate along the track offered by the peripheral end of the cut cervical sympathetic, with the result that, after a certain lapse of time, excitation of the vagus-trunk produced all the symptoms which are usually got by exciting the cervical sympathetic. Synapses must therefore have become formed between the regenerating vagus-fibres and the cells in the superior cervical ganglia of the sympathetic, from which cells the fibres which pass to blood-vessels, hair-muscles, gland-cells, and iris-musculature emanate.

[1] This view has been advocated by Ballance and Stewart, Bethe, and others on histological and experimental grounds, and by Braus from a developmental standpoint. With regard to the results of Braus (formation of nerves in transplanted limbs in tadpoles), it has been shown by Harrison that they are susceptible of a different interpretation. Cf. also W. H. Lewis, Amer. Jour. of Anatomy, 1907.

[2] Langley and Anderson, Jour. of Physiol. xxix.

[3] Jour. Physiol. xxiii. 1898; and article 'Sympathetic' in Schäfer's Text-book of Physiology, 1900. See also Langley and Anderson (Jour. Physiol. xxxi. 1904), who even got growth-union of the motor fibres of the fifth cervical nerve with the cervical sympathetic. On the other hand, the peripheral parts of two cut nerves can, if joined, never be got to conduct—*i.e.* they exhibit no functional regeneration; nor can an afferent nerve be made to join with an efferent (*ibid.* xxix.) Cf. also W. A. Osborne, Proc. Phys. Soc. Jour. Phys. 1908.

Modes of termination of nerve-fibres.—Nerve-fibres vary in the manner in which they end, but there is one general principle which underlies

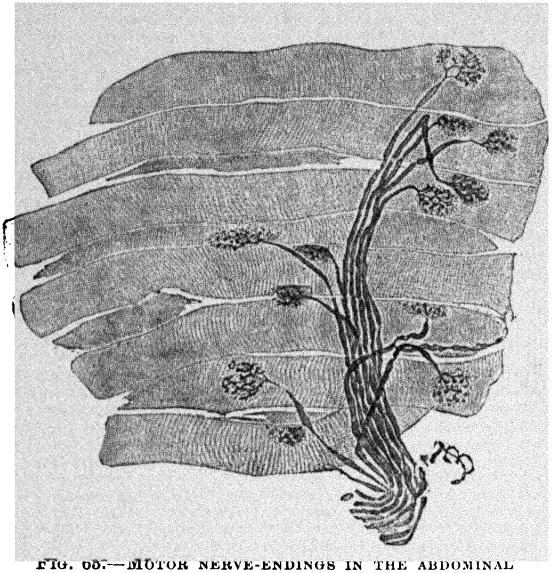


FIG. 63.—MOTOR NERVE-ENDINGS IN THE ABDOMINAL MUSCLES OF A RAT. Gold preparation. Magnified 170 diameters. (Szymonowicz.)

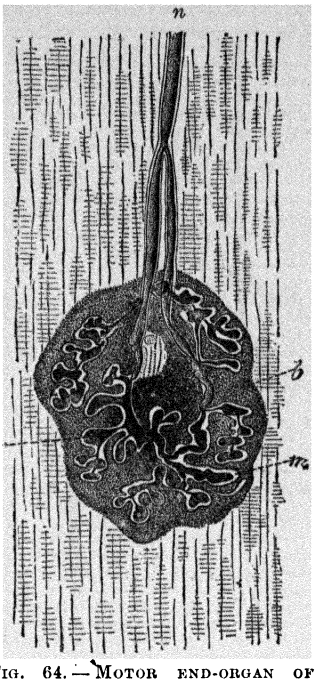


FIG. 64.—MOTOR END-ORGAN OF A LIZARD. Gold preparation. (Kühne.)

n, nerve-fibre dividing as it approaches the end-organ; *r*, ramification of axis-cylinder upon, *b*, granular bed or sole of the end-organ; *m*, clear substance surrounding the ramifications of the axis-cylinder.

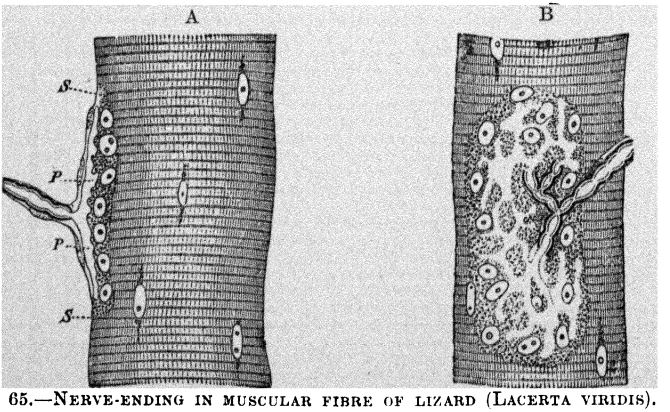


FIG. 65.—NERVE-ENDING IN MUSCULAR FIBRE OF LIZARD (LACERTA VIRIDIS). (Kühne.)

A, end-plate seen edgeways; B, from the surface; *s*, *s*, sarcolemma; *p*, *p*, expansion of axis-cylinder. In B the expansion of the axis-cylinder appears as a clear network branching from the divisions of the medullated fibres.

all the different modes of termination. The medullary and nucleated sheaths of the fibres always cease to be visible towards the point of termination, and

the actual ending is confined to the axon or axis-cylinder, which usually breaks up into a tuft of ramifying fibrils. This is the case whether the fibre ends peripherally in other tissues or centrally within the grey matter of the nervous system: in the latter case the arborisation either surrounds and comes in contact with the body of another nerve-cell, or interlaces with the ramification of the dendrons of other cells (synaptic endings, neuro-synapses).

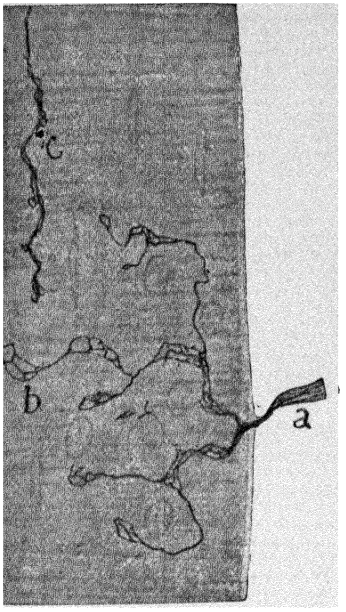


FIG. 66.—ENDING OF MOTOR NERVES IN RABBIT'S MUSCLE. Reduced silver method. (Cajal.)

a, axis-cylinder of entering nerve; *b*, *c*, parts of terminal ramification showing network of neuro-fibrils.

Motor nerve-endings.—Motor nerve-fibres arise either from the axons of nerve-cells in the anterior and lateral horns of the spinal cord and in corresponding situations in the lower parts of the brain, or, in the case of vaso-motor, viscero-motor, and other efferent fibres of the sympathetic system, from the axons of the sympathetic ganglion-cells. The *motor fibres to voluntary muscles* are always large medullated fibres, which pass in an undivided form to the muscles where they are to end, but branch within them once, twice, or several times, so that by these branchings a single nerve-fibre may pass to several muscle-fibres (fig. 63). As each branch arrives at the muscle-fibre in connexion with which it is to terminate, it is still invested by neurolemma and medullary sheath (fig. 65), and even by a thin prolongation of perineurium and endoneurium (*sheath of Henle*). At the junction with the muscle-fibre the medullary sheath ends abruptly, and the neurolemma and sheath of Henle end by becoming continued, as the *telolemma*, into and over the sarcolemma of the muscle. The axon, on the other hand, passes within the sarcolemma and forms a (usually close, sometimes more open) ramification upon the surface of the striated substance of the muscle (fig. 64): this ramification, which exhibits a network of neuro-fibrils (fig. 66),

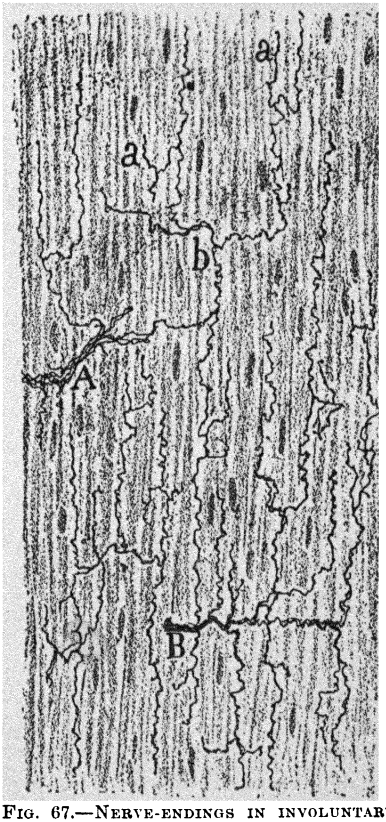


FIG. 67.—NERVE-ENDINGS IN INVOLUNTARY MUSCLE; INTESTINE OF GUINEA-PIG. (Cajal.)

A, B, larger branches of nerve; *a*, *b*, terminal ramifications.

is known as the *end-plate.* It is imbedded in a nucleated protoplasmic layer of sarcoplasm, which is termed the *sole* or *bed* of the end-plate.

The *motor fibres to involuntary muscles* are always small non-medullated fibres. They ramify between the individual muscle-cells of the plain muscular tissue (fig. 67), having sometimes slight knob-like enlargements at their termination, but show nothing corresponding to the end-plate of the voluntary motor-nerve.[1] A similar mode of nerve-ending occurs in connexion with cardiac muscle (fig. 68).

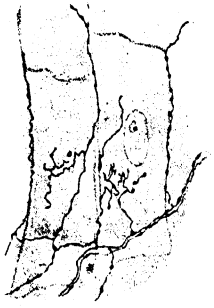


FIG. 68.—ENDING OF NERVE-FIBRES IN CARDIAC MUSCLE. (Smirnow.)

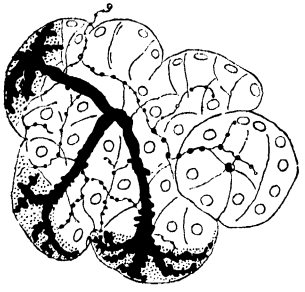


FIG. 69.—TERMINAL NERVE-FIBRILS IN AN ALVEOLUS OF THE SUBMAXILLARY GLAND OF THE DOG. Chromate of silver method. (G. Retzius.)

The extension of the lumen into the crescents of Gianuzzi is also shown.

Other efferent fibres of the autonomic system (*e.g.* inhibitory, secretory, trophic fibres) end by ramifying between the tissue-elements (gland-cells, &c.) to which they are distributed (fig. 69); they run everywhere in contact with the cells of the tissue, but do not, it is believed, pass actually into the interior of the cells.

Sensory nerve-endings.—All sensory nerves of vertebrates take origin in cerebrospinal ganglion-cells, except those of the retina and olfactory mucous membrane, which originate from cells within the peripheral organ. In some invertebrates all sensory nerves take origin from cells at the periphery, and this must be regarded as their primitive mode of origin.

Those which so originate (at the periphery) pass away from these peripheral sensory nerve-cells as axons, which course towards the grey matter of the nerve-centre. In this grey matter they end by arborising between and around other nerve-cells of the central nervous system. Such a typical mode of origin and termination of sensory nerve-fibres is met with in annelids—*e.g.* in the earthworm.

In the vertebrate retina the peripheral sensory nerve-cells are the so-called rod-and-cone cells, the axons of which ramify amongst and form synapses with the dendrons of other retinal nerve-cells—the bipolars. The axons of these again form synapses with yet other retinal cells—the ganglion-cells of the retina—and the axons of the ganglion-cells become the axis-cylinders of the optic nerve-fibres, which terminate by ramifying within the grey matter of the thalamus and corpora quadrigemina. But the retina itself is, as we have seen, developed as a protrusion of the central nervous system. In the vertebrate olfactory organ the primitive condition, such as is found in the general

[1] According to F. B. Hofmann (Arch. f. mikr. Anat. lxx. 1907), the endings of the fibrils are not free, but form loops and end-networks.

sensory nerves of the earthworm, is retained. The peripheral nerve-cells (olfactory cells) which lie between the ordinary epithelium-cells of the olfactory

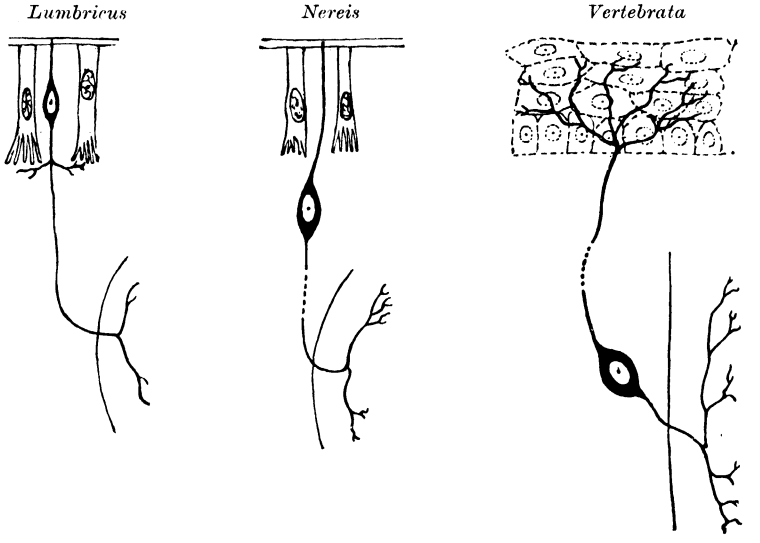


FIG. 70.—DIAGRAMS SHOWING THE RELATIVE POSITION OF THE SENSORY CELL IN LUMBRICUS, NEREIS, AND VERTEBRATA. (After G. Retzius.)

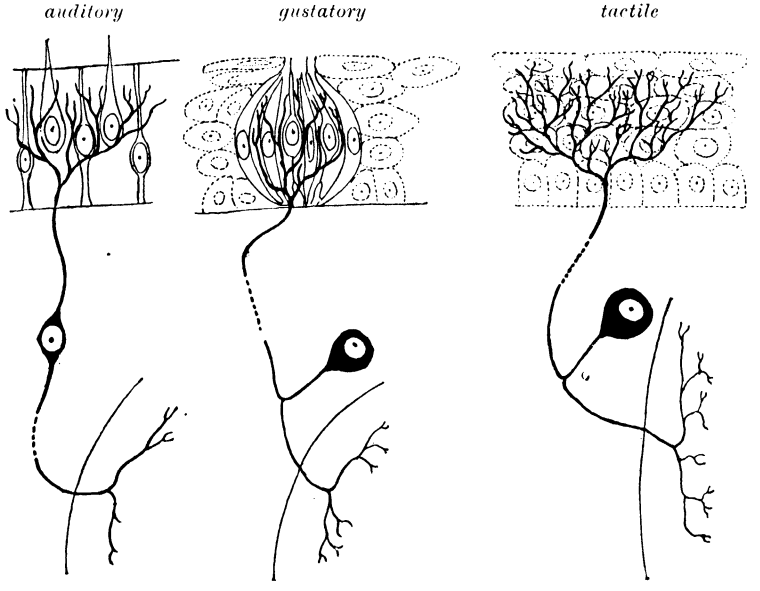


FIG. 71.—DIAGRAM SHOWING THE MODE OF TERMINATION OF SENSORY NERVE-FIBRES IN THE AUDITORY, GUSTATORY, AND TACTILE STRUCTURES OF VERTEBRATA. (After G. Retzius.)

membrane send their axons to form the fine non-medullated fibres of the olfactory nerves, which pass through the cribriform plate of the ethmoid to enter the olfactory lobe (olfactory bulb). In this they ramify and form synapses with the dendrons of its nerve-cells.

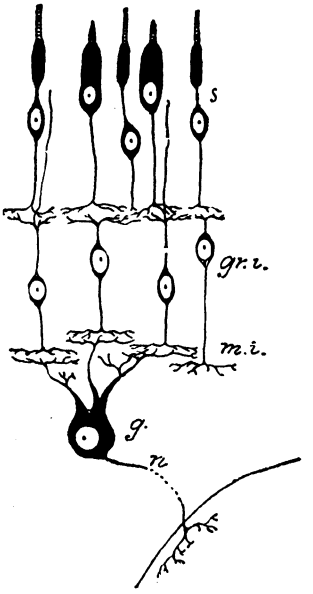


FIG. 72.—DIAGRAM OF THE CONNEXIONS OF THE RETINAL ELEMENTS. (After G. Retzius.)

s, sensory nerve-cells; *gr.i.*, inner granules; *m.i.*, inner molecular layer; *g.*, ganglion-cell; *n*, its nerve-fibre process ramifying in the nerve-centre.

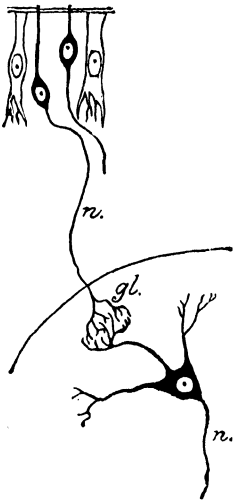


FIG. 73.—DIAGRAM OF THE ARRANGEMENT OF THE SENSORY NERVE-FIBRES IN THE OLFACTORY ORGAN AND BULB. (After G. Retzius.)

n., nerve-fibre coming off from sensory nerve cell; *gl.*, synapse within olfactory glomerulus; *n.*, nerve-cell and nerve of olfactory bulb of brain.

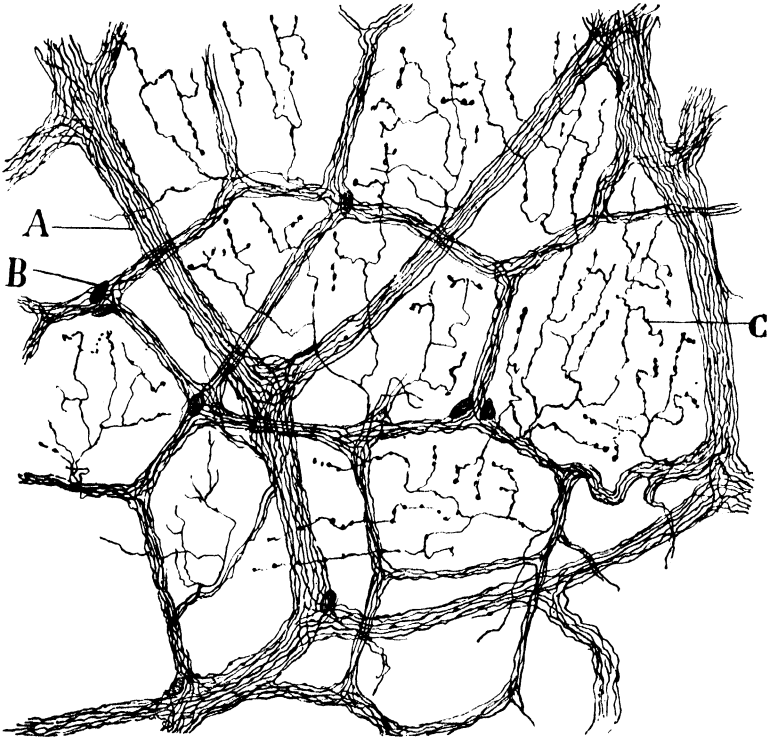


FIG. 74.—PLEXUS OF NERVE-FIBRES IN THE RABBIT'S CORNEA. Methylene blue. (Cajal.)
A, trabecula of primary plexus; B, secondary plexus; C, intra-epithelial fibrils.

The usual mode of origin of the sensory fibres in vertebrates is from the cells of the cerebrospinal ganglia (spinal ganglia, semilunar [Gasserian] ganglion, cochlear and vestibular ganglia, ganglia of the facial, glossopharyngeal, and vagus). These cells are all primitively bipolar, with two axons coming off

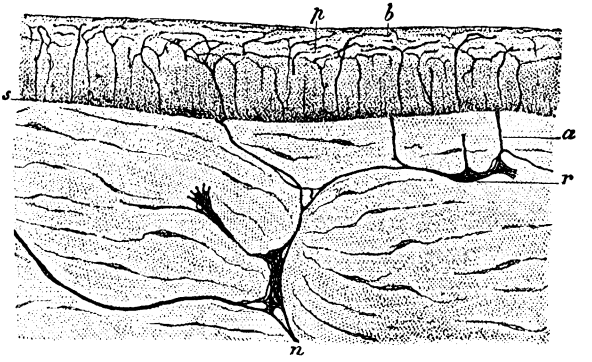


FIG. 75.—VERTICAL SECTION OF CORNEA STAINED WITH CHLORIDE OF GOLD. (Ranvier.)
n, *r*, primary plexus in connective tissue of cornea; *a*, branch passing to sub-epithelial plexus, *s*; *p*, intra-epithelial plexus; *b*, terminations of fibrils.

from opposite poles of the cell-body, but in the case of the spinal ganglia and the ganglia in the roots of the fifth, seventh, ninth, and tenth nerves they become secondarily unipolar (see p. 9); nevertheless the single process divides and its branches pass respectively centrally and peripherally. The termination of the central axon or posterior root-fibre is by ramification in the grey matter of the cord and brain, where it forms synapses with nerve-cells there situated. The peripheral axons form the axis-cylinders of the sensory nerves and pass without division to near their terminations. Here they invariably branch, and form plexuses (fig. 74), often ending in a fine ramification between the elements of the sensory surface, as with the fibres which terminate between the deeper cells of the epidermis and other stratified epithelia (fig. 75), such as the epithelium of the conjunctiva, and with those which end amongst the auditory and gustatory cells in their respective organs (fig. 71). But a more common mode of ending of sensory nerve-fibres is in the so-called *terminal sense-organs*. These take the form of enlargements of the connective tissue of the nerve, and are known according to their structure —which varies greatly in complexity—by different names, such as end-bulbs (figs. 76 to 80), tactile corpuscles (fig. 81), Pacinian bodies (fig. 82), corpuscles of Herbst and Grandry (in birds; figs. 83, 84), &c. A description of each of these will be found in the histological part of this work. It is sufficient here

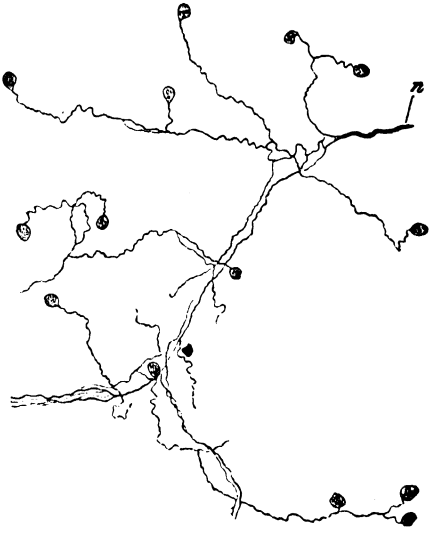


FIG. 76.—END-BULBS AT THE TERMINATIONS OF NERVES IN THE HUMAN CONJUNCTIVA, AS SEEN WITH A LENS. (Longworth.)

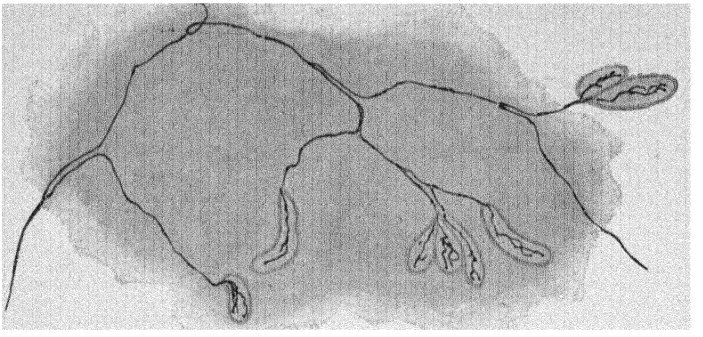


FIG. 77.—A MEDULLATED FIBRE TERMINATING IN SEVERAL END-BULBS IN THE HUMAN PERITONEUM. Low power. Methylene-blue preparation. (Dogiel.)

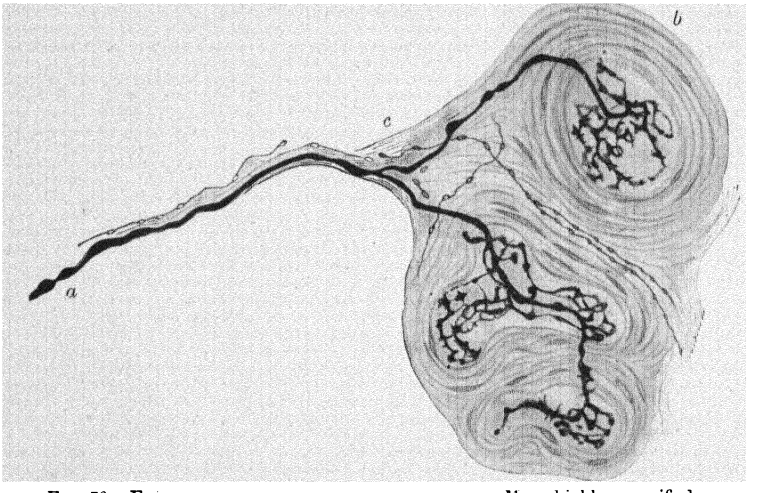
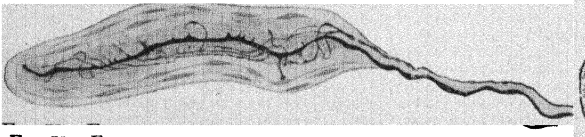


FIG. 78.—END-BULBS FROM THE HUMAN PERITONEUM. More highly magnified. Methylene-blue preparation. (Dogiel.)

a, medullated fibre; *b*, nucleated lamellated capsule of end-bulb; *c*, non-medullated fibres, possibly destined for the capillaries which surround the end-bulbs.



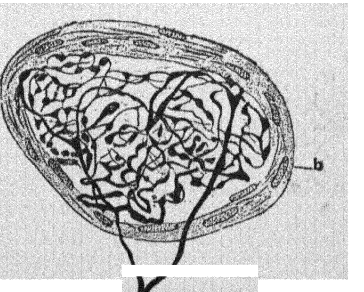


FIG. 79.—END-BULB FROM THE CENTRAL TENDON OF THE DIAPHRAGM OF THE DOG. Showing, besides the main medullated fibre terminating by an arborescence within the core, a second very fine medullated fibre, forming a more delicate arborescence around the ending of the main fibre in the outer part of the core. Methylene-blue preparation. (Dogiel.)

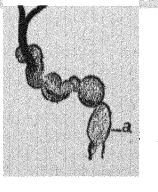


FIG. 80.—END-BULB FROM THE GLANS PENIS, SHOWING ENDING OF AXIS-CYLINDER. Methylene-blue preparation. (Dogiel.)

a, medullated nerve-fibre; *b*, sheath of end-bulb.

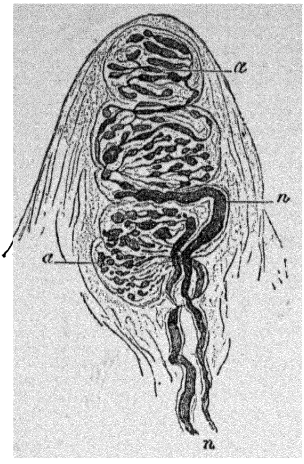


FIG. 81.—TACTILE CORPUSCLE WITHIN A PAPILLA OF THE SKIN OF THE HAND, STAINED WITH CHLORIDE OF GOLD. (Ranvier.)

n, two nerve-fibres passing to the corpuscle; *a*, *a*, varicose ramifications of the axis-cylinders within the corpuscle.

FIG. 82. — MAGNIFIED VIEW OF A PACINIAN BODY FROM THE CAT'S MESENTERY. (Ranvier.)

n, stalk of corpuscle with nerve-fibre, enclosed in sheath of Henle, passing to the corpuscle; *n'*, its continuation through the core, *m*, as axis-cylinder only; *a*, its terminal arborisation; *c*, *d*, sections of epithelioid cells of tunics, often mistaken for the tunics themselves; *f*, channel through the tunics which expands into the core of the corpuscle.

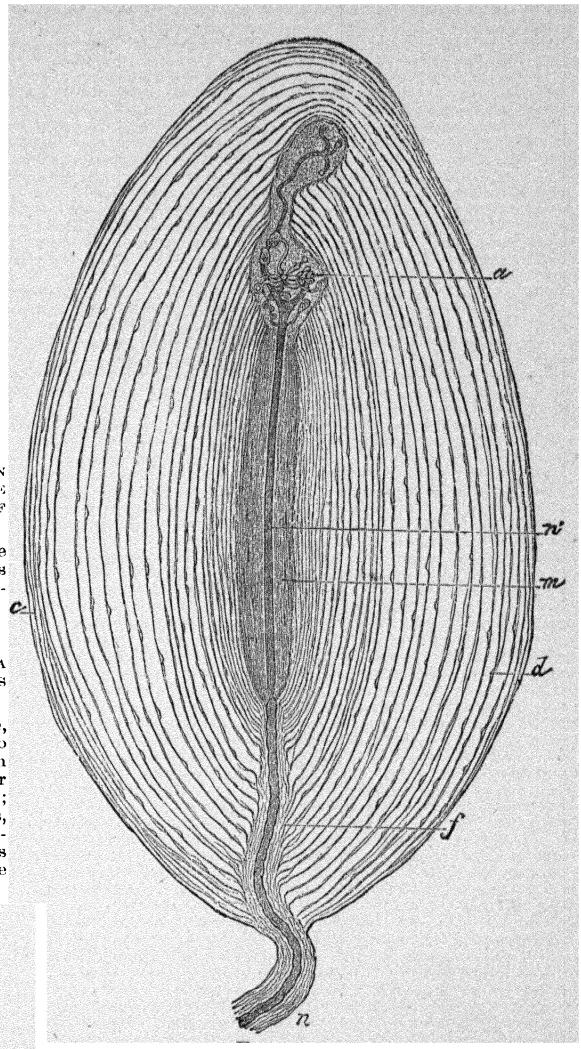


FIG. 82.

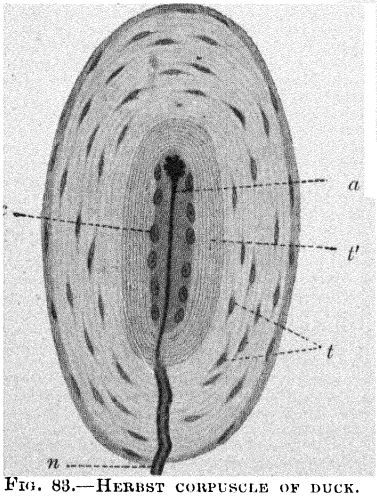


FIG. 83.—HERBST CORPUSCLE OF DUCK. (Sobotta.) × 380 diameters.

n, medullated nerve-fibre; *a*, its axis-cylinder, terminating in an enlargement at end of core; *c*, nuclei of cells of core; *t*, nuclei of cells of outer tunics; *t'*, inner tunics.

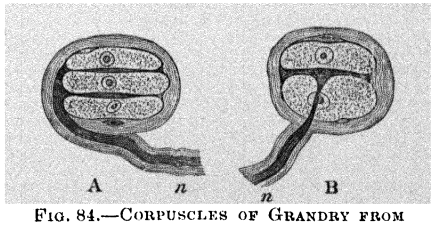
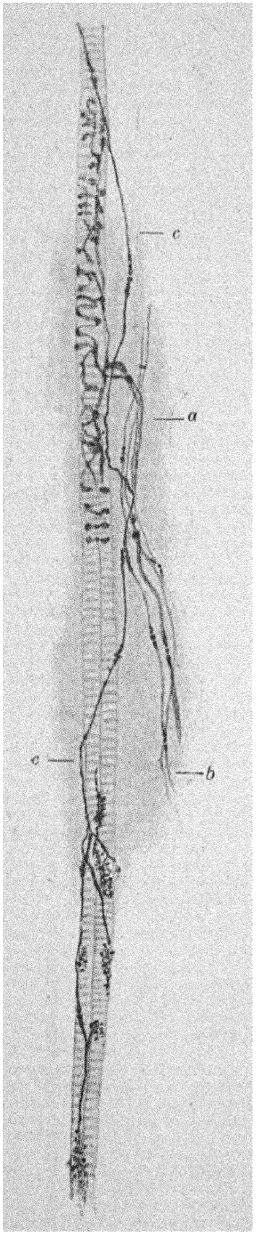


FIG. 84.—CORPUSCLES OF GRANDRY FROM THE DUCK'S TONGUE. (Izquierdo.)

A, composed of three cells, with two interposed discs, into which the axis-cylinder of the nerve, *n*, is observed to pass; in B there is but one tactile disc enclosed between two tactile cells.

to say that in every case the terminal organ is formed by an expansion of the perineural sheath; which may remain simple as in the end-bulbs, or may develop many layers of connective tissue, giving it a lamellated appearance as in the Pacinian corpuscles and in the Herbst corpuscles. Within



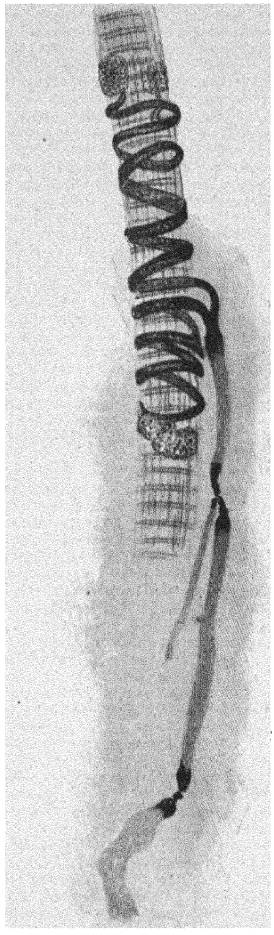


FIG. 85.—NERVE-ENDINGS UPON THE INTRAFUSAL MUSCLE-FIBRES OF A MUSCLE-SPINDLE OF THE RABBIT. Moderately magnified. Methylene-blue preparation. (Dogiel.)

a, large medullated fibre coming off from 'spindle' nerve and passing to end in an annulo-spiral termination on and between the intrafusal fibres; *b*, fine medullated fibre coming off from the same stem and dividing. Its branches, *c*, pass towards the ends of the muscle-fibres and terminate in a number of small localised arborisations, like end-plates.

FIG. 86.—AN ANNULO-SPIRAL ENDING OF INTRAFUSAL FIBRE. Highly magnified. Methylene-blue preparation. (Dogiel.)

this expansion of the perineural sheath is a *core* formed by the endoneurium, and consisting mainly of the endoneural cells. Into the core the axon penetrates, and finally ends by ramifying amongst the cells of the core, either throughout its substance as in the end-bulbs and tactile corpuscles,

or at its extremity as in the Pacinian corpuscles. In all cases the medullary sheath and neurolemma cease on the entry of the nerve-fibre into the core.

Sensory fibres of muscles and tendons.—The sensory fibres of voluntary muscles and of their tendons, which arise like other sensory fibres from the

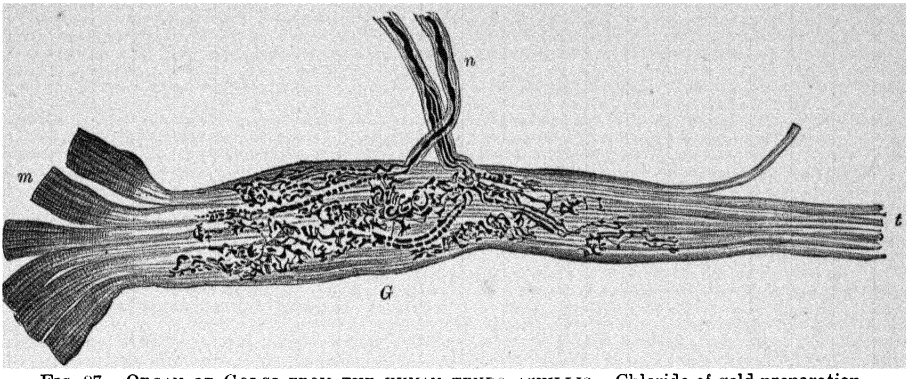


FIG. 87.—ORGAN OF GOLGI FROM THE HUMAN TENDO ACHILLIS. Chloride of gold preparation. (Ciaccio.)

m, muscular fibres; *t*, tendon-bundles; *G*, Golgi's organ; *n*, two nerve-fibres passing to it.

spinal ganglion-cells, exhibit certain peculiarities in their method of termination within the tissue. As they pass to their ending they are collected into small bundles of two or three medullated fibres. These, in the voluntary muscles, are conveyed to peculiar organs termed *muscle-spindles*, each of which consists of a small

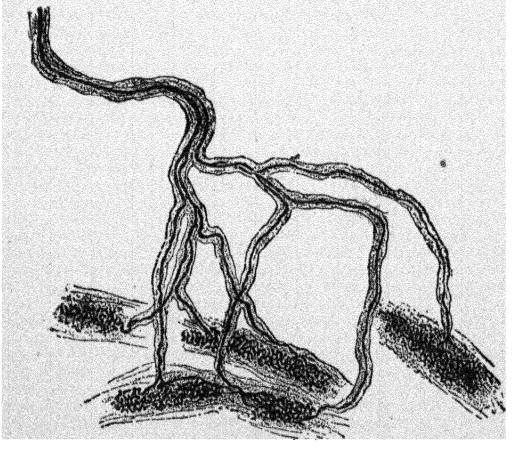


FIG. 88.—A NERVE-FIBRE IS SHOWN DIVIDING INTO SEVEN SECONDARY FIBRES TO WHICH ARE ATTACHED FIVE ORGANS OF RUFFINI. (Barker, after Ruffini.)

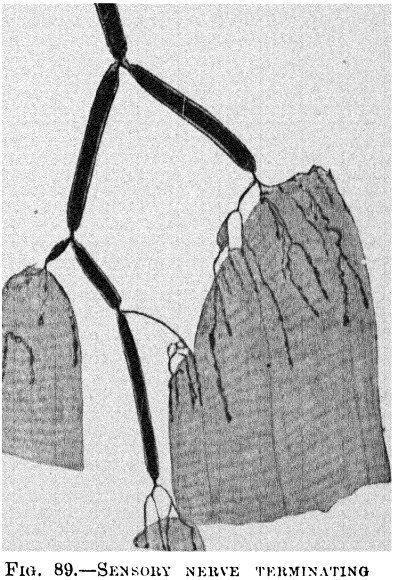


FIG. 89.—SENSORY NERVE TERMINATING IN ARBORISATIONS AROUND THE ENDS OF MUSCLE-FIBRES. (Cecchercelli.)

bundle of fine striated muscle-fibres enclosed within a loose connective-tissue sheath. The nerve-fibres pass between the muscle-fibres of the spindle and the axis-cylinders, ramify among them, winding between and over the muscle-fibres in a contorted manner, and finally terminating amongst them with free ends

(figs. 85, 86). In the case of the tendons the mode of ending is somewhat similar. Here the nerve-fibres, two or three in number, pass to the tendon near its junction with the muscle, and penetrate between the tendon-bundles within a confined area, the axons ramifying and passing between and around the individual tendon-bundles much in the same way as do the intrafusal nerve-fibres of the muscle-spindle. These localised terminations of nerve-fibres in tendons are known as *organs of Golgi* (fig. 87). Other very similarly constructed terminal organs occur in the subcutaneous connective tissue of certain parts: these are termed *organs of Ruffini* (fig. 88).

There are also a certain number of sensory nerve-fibres which end at the junctions of the muscle-fibres with the tendon, and which there arborise over the ends of the muscle-fibres (Ceccherelli; fig. 89).

Intra-central nerve-fibres; internuncial and intrinsic neurones.—Nerve-fibres are generally classified from the physiological standpoint as *afferent* and *efferent*—*i.e.* those which serve to conduct impulses towards and away from the central nervous system respectively. But many nerve-cells, and their axons, are purely intra-central, conveying impressions from one nerve-cell to another within the nerve-centre. Some of these can be distinguished, according to the situation of the cell-body and the consequent direction of the axon, as *ascending fibres* (cell-bodies in the lower parts of the cerebrospinal axis, axons passing and conducting upwards), and *descending fibres* (cell-bodies in the higher parts of the cerebrospinal axis, axons passing and conducting downwards). In other cases the axon divides, one branch passing upwards and the other downwards; and in others, the direction taken by the axon may be transverse to the cerebrospinal axis or altogether irregular.

With regard to the origin and termination of intra-central nerves there is no essential difference between these and the origin and termination of nerves which pass partly or wholly out from the nerve-centre. In every case the axon arises from the cell-body of one nerve-cell, and ends, after a shorter or longer course, by ramifying either over the body of another nerve-cell or by interlacing with the dendrons of another cell or cells. Very rarely there are two or more axons; almost invariably there is but one axon and several dendrons to each cell. The size of the cell-body exhibits a wide margin of variation, corresponding probably in the main with the size and length of the axon. Some parts of the grey matter are characterised by the presence of a large number of very small cells, which give a characteristic appearance to a stained section of the part. These small cells are commonly known as 'granules,' but in spite of their small size they exhibit all the parts and characters of nerve-cells, having a comparatively short axon and a more or less complex system of dendrons. On the other hand, in other parts of the grey matter cells are found which are large enough to be visible without the aid of the microscope. Some of the largest are found in the so-called motor region of the cerebral cortex; their axons are traceable down to the grey matter of the cord near the cells from which the motor nerves to the voluntary muscles emanate. Other large cells occur in the grey cortex of the cerebellum in the form of the cells of Purkinje. Between these and the minute cells known as 'granules,' every size of nerve-cell is met with in different parts of the grey matter.[1]

[1] The single nerve which passes on either side to the electric organ of Malapterurus emerges from a nerve-cell of, comparatively speaking, gigantic size, measuring as much as 0·2 mm. across. In this cell the protoplasm is penetrated by capillary blood-vessels. The largest nerve-cells in man are about 0·135 mm. in diameter: the smallest about 0·004 mm. (Kölliker).

Methods of tracing the paths and sources of origin of nerve-fibres. — *Method of Waller.* — It was noticed by A. Waller [1] that when a peripheral nerve is cut the parts of the fibres which are distal to the section undergo a peculiar change, which is termed, after its discoverer, *Wallerian degeneration.* The change consists of a breaking down of the white substance of the medullary sheath into globules of fatty substance; this is accompanied by alterations in and eventual disappearance of the axis-cylinder. Waller further found that when the nerve-roots are cut near the cord the fibres of the ventral roots degenerate peripherally to the section, those of the dorsal roots centrally to the section, and also within the cord, while the parts of the dorsal roots in connexion with the ganglia remain intact. In other words, the part of a nerve-fibre which is still in continuity with the nucleated body of the nerve-cell remains normal, while the part which is cut off from the body of the cell undergoes degeneration. A section or injury of any part of the central nervous system leads to similar changes in nerve-fibres or tracts of fibres, those parts of the fibres which the injury cuts off from their nerve-cell bodies becoming degenerated along their whole length. Similarly, removal of grey matter causes degeneration along all the fibres which arise from the removed cells.

Further, in certain diseases of the nervous system, particular cells and cell-groups are affected, others remaining normal, and the affection in such cases involves not only the cell-body, but all the cell-processes—in fact, the entire neurone. This observation affords a valuable method of tracing nerve-fibres within the cerebrospinal system, since the nerve-fibres arising from such cells undergo Wallerian degeneration to their most remote extremities.

When the cell-bodies are above the seat of injury, the degeneration occurs only below the injury, and is termed 'descending'; when the cell-bodies are below the seat of injury, the degeneration occurs only above this, and is termed 'ascending.'

Method of Marchi. — Marchi,[2] working in Golgi's laboratory, described a method of staining such degenerated fibres distinctively—viz. by placing portions of the tissue first in potassium-bichromate solution for a few days and then in a solution containing potassium bichromate and osmic acid. By this means it is possible to trace even single degenerated fibres amongst a mass of normal fibres.

Method of Weigert. — Another method of showing degenerated fibres — that of Weigert[3]—depends upon the fact that, under certain circumstances, degenerated fibres remain unstained by hæmatoxylin, whilst the normal fibres are stained. This method is of value only when a number of the degenerated fibres are massed together.

Method of Flechsig. — All nerve-fibres and tracts of fibres do not complete their development at the same time, and especially some undergo myelination earlier, others later. Flechsig[4] took advantage of this fact to trace the course of tracts of fibres within the central nervous system, and he was the first to show by this method that the white columns of the spinal cord can be mapped out into a number of areas, the fibres within which undergo myelination at different times, and are therefore probably different in origin and in function. If myelination occurs early, the tracts of myelinated fibres can, by appropriate staining—as, *e.g.*, by Weigert's process—be traced among those which are still non-myelinated. On the other hand, those which myelinate late are seen in sections of the nervous system of more advanced embryos as distinct tracts of

[1] Phil. Trans. 1850. [2] Riv. sper. d. fren. 1885. [3] Fortschr. d. Medizin, 1884.
[4] Leitungsbahnen, 1876.

greyish-looking fibres lying among the white fibres which have already undergone myelination; the pyramidal tracts can be thus seen in the spinal cord of the new-born infant. The method has, however, its limitations, and may lead to false conclusions, for a fibre, or a set of fibres belonging to the same system, does not undergo myelination simultaneously along its whole length, but the process starts, as a rule, in the part nearest the cell-body and extends from here along the fibre. Hence a tract of fibres may be myelinated at one part and remain for a long time unmyelinated at a distant part, and this may then erroneously be regarded as belonging to a distinct tract.

Method of Nissl.—When the axon of a nerve-cell is cut through in any part of its course, not only does the peripheral part of the fibre undergo the Wallerian degeneration, but a change occurs in the nucleated cell-body itself, which gradually undergoes the process known as chromatolysis (disintegration and disappearance of the Nissl bodies). This change shows itself later than the degeneration of the peripheral fibre, for, whereas the Wallerian degeneration begins in mammals within two or three days after injury to a nerve, the chromatolytic process within the nerve-cells does not show itself until some ten or twelve days later, and is not completed until about three weeks after the injury; it may then be followed by gradual recovery. This change in the nerve cell-body which results from severance of the axon was noticed by Nissl, and is employed for tracing the connexion of nerve-fibres with the cell-bodies from which they take origin.

While the above statement regarding Nissl degeneration is, on the whole, true, it is not without exception. Thus sometimes it is found that the mere section of a motor nerve is not followed by degeneration of all the cells of the centre or nucleus from which the nerve originates, and it is not understood why some escape. Moreover, the extent of the degeneration varies greatly in different cases. But the most important exception is found in connexion with the dorsal roots. These, as is known, take origin from the cells of the spinal ganglia, each of which gives off an axon which becomes a medullated sensory nerve-fibre, and bifurcating within the ganglion one branch passes to end peripherally, and one centrally to terminate in the grey matter of the central nervous system. It is found that section of the peripheral branches is followed by Nissl degeneration of the ganglion-cells, but that if the central branches only are cut the cells are unaffected.

In conformity with this, Anderson[1] has found that section of the peripheral branches in young animals checks the development of the ganglia, but that section of the central processes does not do so, although the central processes may atrophy back to the ganglion.

Method of Gudden.—This consists in the removal (preferably in very young animals) of a part of the nervous system, or of an organ the functions of which are carried on through the nervous system, and the determination of the parts which undergo atrophy or which fail to develop in consequence of the prolonged disuse of the part. Thus removal of an eyeball in a young animal is found to produce lack of complete development in several parts of the brain, all of which may be looked upon as in some way connected with the visual function.

Allied to this method is the determination of correlated parts of the nervous system, which may be obtained by the study of the comparative anatomy of the brain. Thus in animals such as the mole, in which the sense of vision is defective, certain parts of the brain show a lack of development, whilst others, which are concerned in the appreciation of impressions received through other and highly developed senses (such as the auditory), show a corresponding advance in development.

Neuroglia.—The neuroglia forms the sustentacular tissue proper to the nervous system. It is formed of cells (*neuroglia-cells, glia-cells*) with fibrils in

[1] Journ. Physiol. xxviii. 1902.

continuity with them.[1] The glia-cells have numerous offsets which interlace with those of neighbouring cells, penetrating between and amongst the nerve-cells and nerve-fibres, and affording them support, besides serving somewhat to isolate them one from another. The fibrils pass through the cell-body and are continued into its offsets: this can be clearly seen in isolated cells (fig. 90). There are three distinct kinds of glia-cells (fig. 91). The one kind (*fibrillar cells* of Andriezen, *spider-cells*, *a*) has very numerous fine unbranched fibrillar offsets radiating in every direction from the cell-body. Another kind (*protoplasmic cells* of Andriezen, *arborescent cells*, *b*) is provided with branched and relatively short offsets, and is found chiefly, if not exclusively, in the grey

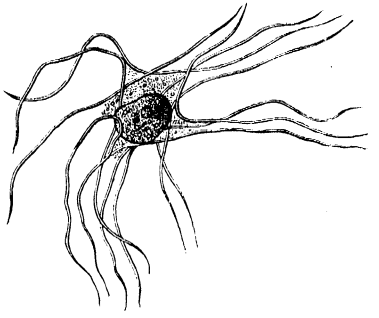


FIG. 90.—A NEUROGLIA-CELL, ISOLATED IN 33 PER CENT. ALCOHOL. (Ranvier.)

matter. One process is frequently closely attached to the wall of a blood-vessel or to the surface of the pia mater. A third kind of glia-cell (*c*) takes the form of a rounded or irregular cell-body with three or four sub-parallel processes, which may be varicose or be set with minute spines passing vertically to the pia mater and attached to it. These are seen in the grey matter of the cerebellum. Similar cells occur as the fibres of Müller in the retina. Both Andriezen and Hatai describe the glia-cells as different in origin, some being ectodermic, others (the branched) mesodermic (mesenchymic), but this is not established. All that we positively

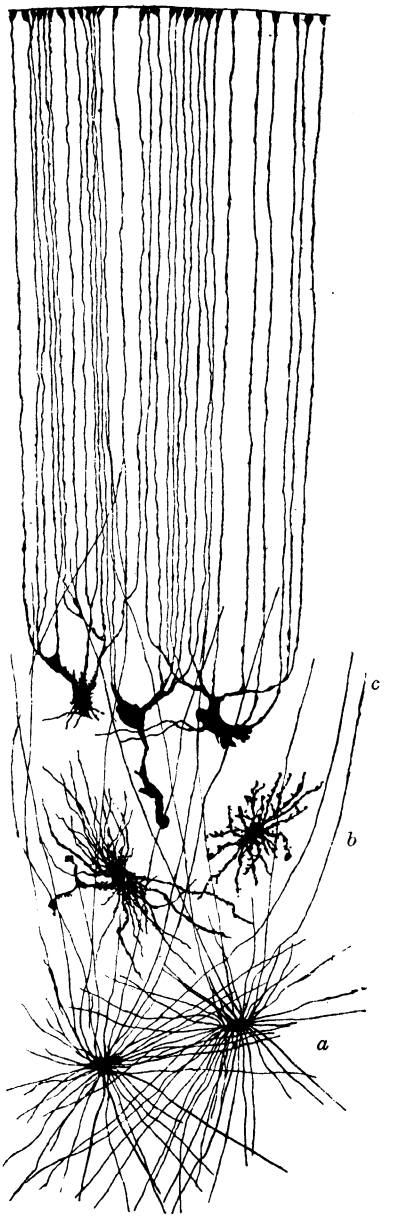


FIG. 91.—NEUROGLIA-CELLS OF CEREBELLUM. Golgi method. (G. Retzius.)

a, spider-cells; *b*, arborescent cells; *c*, ependyma-like cells.

[1] Ranvier, Arch. de Physiol. 1893; Andriezen, Brit. Med. Journ. July 1893, and Int. Monthly Journ. of Anat. and Phys. x. 1893; Retzius, Biol. Unters. v. 1893, vi. 1894; Lenhossék, Bau d. Nervensystems, 1895; Weigert, Beitr. z. Kenntniss d. norm. menschl. Neuroglia, 1895; Cajal, Riv. trim. micr. 1896, 1897; C. Huber, Amer. Journ. of Anat. i. 1901; Hatai, Journ. Comp. Neurol. xii. 1902; Rubaschin, Arch. f. mikr. Anat. lxiv. 1904.

know about the origin of the glia-cells is that they begin to make their appearance as distinct elements of the central nervous system somewhat later than the time that the neuroblasts are becoming differentiated to form nerve-cells; and that they are then seen lying amongst the rest of the cells (spongioblasts) of the neural ectoderm, and are to all appearance formed from some of these cells, or from detached and dislocated ependymal cells, which are also formed from spongioblasts. The mesenchyme, from which the processes of pia mater and blood-vessels of the brain and cord become formed, has not at this period begun to invade the neural ectoderm, and if any of the glia-cells are of mesenchymic origin it must be as the result of the later penetration of mesenchyme-cells between the ectodermic elements of the neural canal.[1]

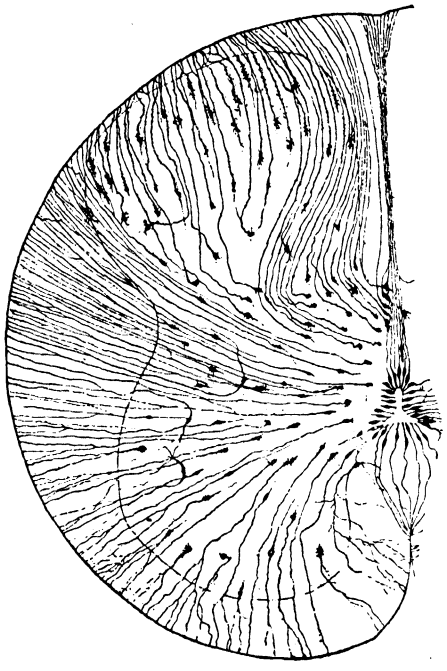


FIG. 92. — SPINAL CORD OF EMBRYO SHOWING DEVELOPMENT OF NEUROGLIA BY DETACHMENT OF EPENDYMAL CELLS. (Lenhossék.)

Ependymal epithelium. — Another sustentacular tissue of the central nervous system which is sometimes included under the term neuroglia is the *ependymal epithelium.* This is composed of the columnar ectoderm cells which form the lining of the neural canal. The fixed ends of these cells, which are branched, penetrate between the other cells of the neural epithelium and extend as far as the outer wall of the canal. Their branches, which are flattened, lie in the interstices of the neural cells proper, and form a kind of sponge-work which serves to separate and support those cells prior to the development of the neuroglia. The free ends of the ependymal cells, which are directed towards the central canal of the cord and the ventricles of the brain, acquire cilia, and, except in the human spinal cord, retain these throughout life. As the nervous tissues develop and the walls of the neural canal undergo the enormous thickening which characterises them in most parts of the central nervous system, the prolongation of the ependymal cells to the pia matral surface, which is distinct in the embryo, becomes obscured and can no longer be traced in the course of development in the higher vertebrates; but in fishes and amphibia the fibres in question may still be rendered evident, by appropriate methods of staining, extending to the external surface of the cord and brain. Immediately below the ciliated nucleated cell-bodies of the ependymal epithelium cells, the branching prolongations of these cells form a distinct greyish gelatinous-looking layer which is recognisable even with the naked eye in the ventricles of the brain and immediately around the central canal of the cord, where it forms with the cell-bodies themselves a thin stratum (substantia gelatinosa centralis) covering the true nervous substance: to this the term *ependyma* was originally applied. No blood-vessels penetrate into this layer.

[1] The development of neuroglia in the spinal cord will be subsequently referred to (see p. 74).

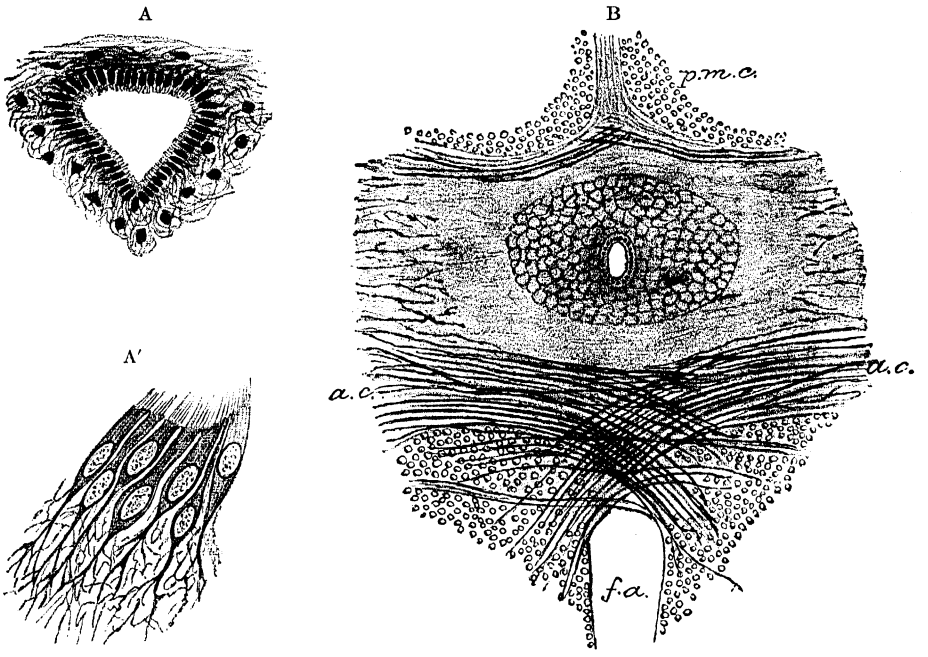


FIG. 93.—CENTRAL CANAL SHOWING ITS EPITHELIUM. (E. A. Schäfer.)

A, from a child of six. Magnified 150 diameters. A', some of the ciliated cells, highly magnified. B, section of the isthmus from the lumbar cord of an adult (æt. 33), showing the central canal in the middle surrounded by the substantia gelatinosa centralis. *f.a.*, anterior median fissure; *p.m.c.*, posterior white column; *a.c.*, anterior white commissure. Magnified 30 diameters.

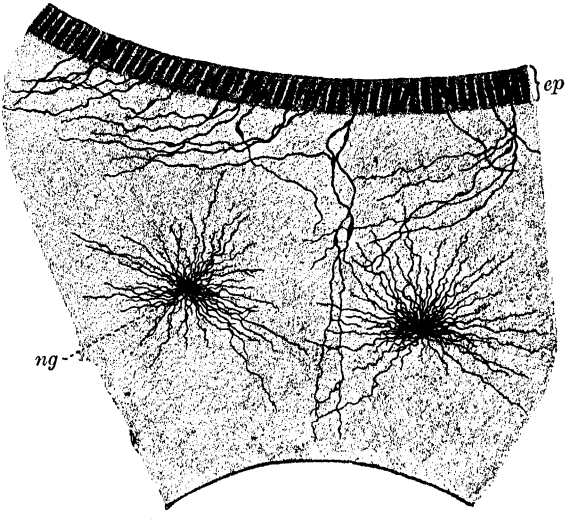


FIG. 94.—EPENDYMAL EPITHELIUM AND SUBJACENT NEUROGLIA OF THE CENTRAL CANAL NEW-BORN INFANT. Golgi method. × 120 diameters. (Sobotta.)

ep, epithelium; *ng*, neuroglia-cells.

THE CEREBROSPINAL AXIS.

The *cerebrospinal axis* is divided into the *brain* or *encephalon*, the enlarged part within the skull, and the *spinal cord* within the vertebral canal. It is symmetrical in form, consisting of a right and a left half, separated to some extent by fissures and cavities, but united by various portions of white and grey nervous substance which cross from one side to the other, and form the *commissures* of the brain and spinal cord.

The cerebrospinal axis is enveloped within the skull and vertebral canal by three connective-tissue membranes, between which are spaces occupied by a clear fluid (cerebrospinal fluid). These envelopes, which will be described later, are—(1) a firm fibrous membrane named the *dura mater*, which is placed most externally; (2) a delicate membrane called the *arachnoid*; and (3) a highly vascular membrane named the *pia mater*, which is next to, and closely invests, the surface of the brain and cord.

SPINAL CORD.

The **spinal cord** or **spinal marrow** (*medulla spinalis*) is about 18 inches (45 cm.) long, and extends from the margin of the foramen magnum of the occipital bone to about the lower part of the body of the first lumbar vertebra. Above, it is continued into the *medulla oblongata* or *spinal bulb*; below, it tapers conically and ends in a slender filament, the *filum terminale* or *central ligament* of the spinal cord.

Although the cord proper usually ends near the lower border of the body of the first lumbar vertebra, its termination is sometimes a little above or below that point, as opposite to the last thoracic or to the second lumbar vertebra.[1] The position of the lower end of the cord also varies according to the state of curvature of the vertebral column, in the flexion forwards of which the end of the cord is slightly raised. In the fœtus, at an early period, the embryonic cord occupies the whole length of the vertebral canal; but after the third month the canal and the roots of the lumbar and sacral nerves begin to grow more rapidly than the cord itself, so that at birth the lower end reaches only to the third lumbar vertebra. After birth the thoracic part of the cord lengthens proportionately more than the other parts, so that in the infant the roots of the lower thoracic nerves come off relatively higher up than at a later age (Pfitzner).[2]

The cord is enclosed in the vertebral canal within a sheath (*theca*) considerably longer and larger than itself, formed by the dura mater, and separated from the walls of the canal; the epidural space containing venous plexuses, and much loose areolar and adipose tissue (fig. 95). The cavity of the sheath between the pia mater and the dura mater is occupied by cerebrospinal fluid, and is divided by the curtain-like arachnoid into the subdural and subarachnoid spaces. Within the latter the cord, covered closely by pia mater, is suspended,

[1] For details of variations, see Ziehen, in Bardaleben's Handbuch d. Anat., Bd. iv. 1899.
[2] Morph. Jahrb. 1883.

being kept in position by a ligament on each side (ligamentum denticulatum), which fixes it at frequent intervals to its sheath, and by the roots of the spinal nerves which pass across the space from the surface of the cord towards the intervertebral foramina.

The spinal nerves come off in pairs at intervals along the cord. Each nerve is attached to the surface of the cord by two roots, one of which is anterior or ventral and non-gangliated,[1] the other is posterior or dorsal and is provided with a ganglion. The uppermost two or three nerve-roots cross

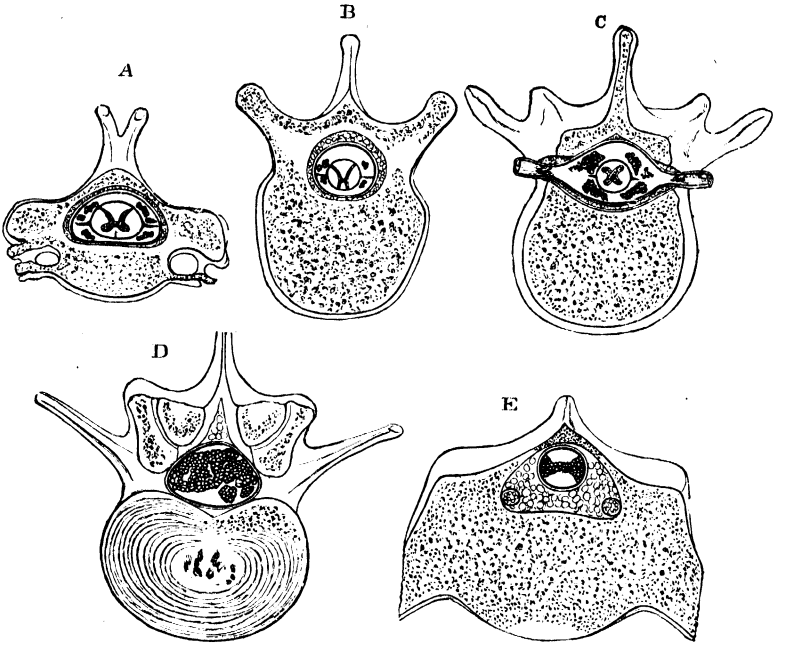


FIG. 95.—SECTIONS SHOWING THE GENERAL RELATIONS OF THE SPINAL CORD TO THE ENCLOSING THECA, AND OF THIS TO THE VERTEBRAL CANAL. (Key and Retzius.)

A, through the fifth cervical vertebra; B, through the tenth thoracic vertebra; C, through the first lumbar vertebra and the foramen of exit of the twelfth thoracic nerve-roots; D, through the disk between the second and third lumbar vertebræ; E, through the first sacral vertebra. In A, B, and C, the cord, covered by pia mater, is seen in the centre, with the ligamentum denticulatum attached to it on either side; the nerve-roots on either side form small groups which, since they pass obliquely downwards to their foramina of exit, are cut across; the dura matral sheath is separated by a considerable space from the cord, and by a quantity of loose areolar and fatty tissue from the wall of the vertebral canal. This tissue is in smaller amount in C. D and E are below the termination of the cord, and show sections of the nerve-bundles of the cauda equina within the dural sheath, which is very large in D, but comparatively small in E, the vertebral canal in the latter being largely occupied by adipose tissue. In this are seen the sections of two large veins. The arachnoid is not represented in any of these sections.

the subarachnoid and subdural spaces nearly horizontally (figs. 96 and 98), but the rest pass across with a more and more oblique downward inclination until their direction is almost vertical, and indeed the lower part of the theca below the termination of the cord (fig. 95, D, E) is occupied by the roots of the lumbar and sacral nerves, passing to the foramina between

[1] Some animals (*e.g.* cat) constantly have a few ganglion-cells interpolated among the fibres of the anterior or ventral nerve-roots of most of the spinal nerves (Schäfer, Proc. Roy. Soc. 1880). Hoch estates that in the anterior roots of the lower lumbar and sacral nerves of man, just at their junction with the cord, ganglion-cells, like those of the posterior root, are almost constantly present, lying singly or in groups, and connected with some of the issuing nerve-fibres by a T-shaped junction (Beitr. z. Kenntniss d. anat. Verhaltens d. menschl. Rückenmarkswurzeln, &c.; Heidelberg, 1891).

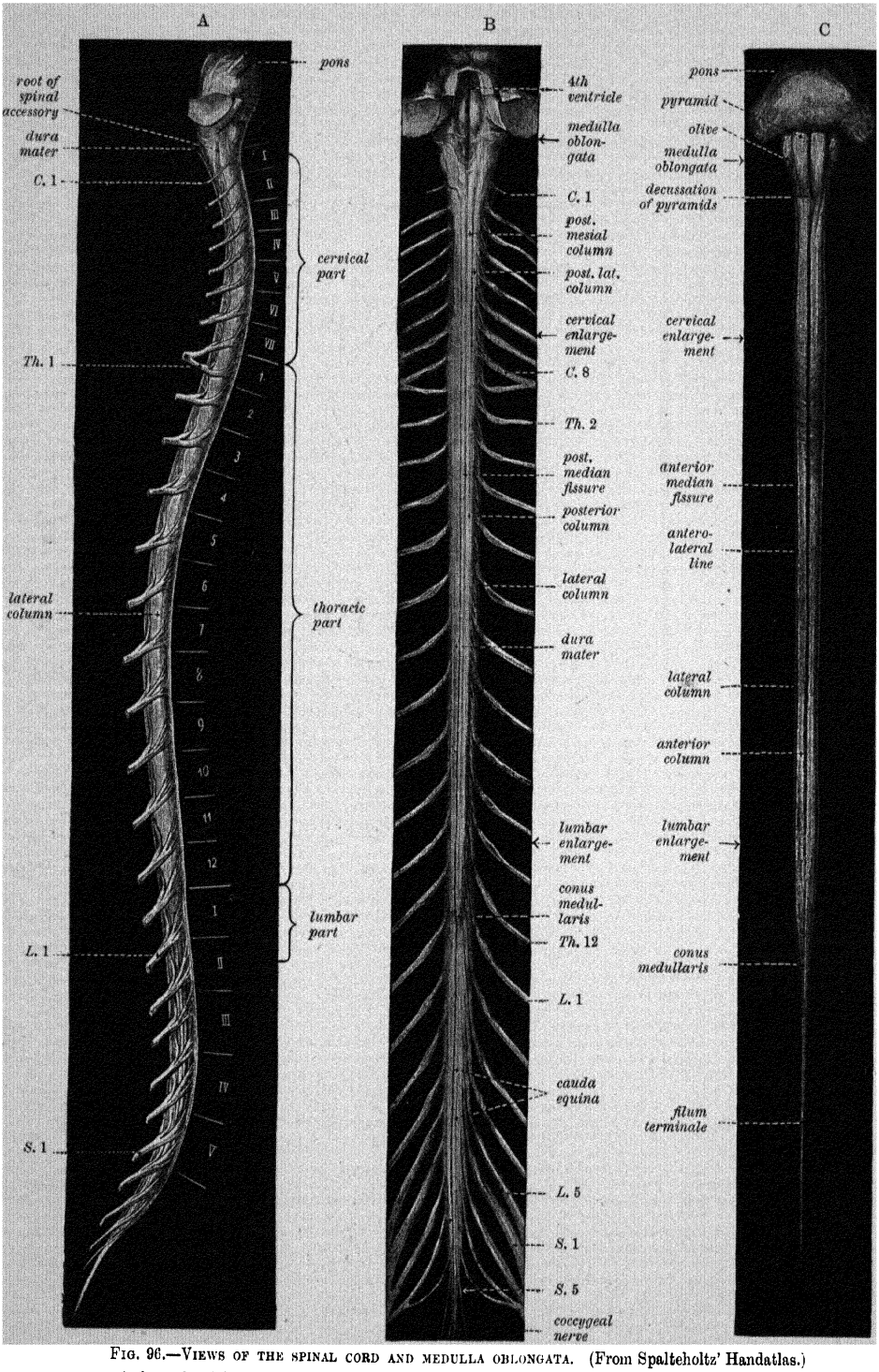


FIG. 96.—VIEWS OF THE SPINAL CORD AND MEDULLA OBLONGATA. (From Spalteholtz' Handatlas.)
A, from the right side; B, from the back; C, from the front with the nerve-roots and membranes removed.

the corresponding vertebræ. This mass of nerve-roots, which conceals the delicate filum terminale, is named the *cauda equina* (figs. 96, 98, 99).

The spinal cord does not show any indications in man of transverse segmentation by swellings opposite the spinal nerves and constrictions between them, but the portion of spinal cord corresponding to the attachment of each pair of roots is termed a 'segment.' The nerve-roots are therefore the guides to the segments of the cord, and the boundaries between these segments are represented by horizontal planes crossing the cord in the middle of the intervals between the attachment of adjacent pairs of nerve-roots.[1] The length of the spinal segments varies in different parts of the cord according to the vertical extent of the attachment of the nerve-roots and of he intervals between them. In the cervical region the segments are a little more than half an inch (13 to 15 mm.) long, and the root-bundles of successive nerves are only 1 mm. to 2 mm. apart. In the mid-thoracic region the length of the segment is about an inch (24 to 26 mm.), but they gradually diminish from this point both towards the upper and the lower ends of the thoracic part of the cord. The intervals free from attachment of nerve-roots are here nearly a quarter of an inch (5 mm.) in extent. In the lumbar and sacral portions of the cord the segments gradually diminish in length from a little more than half an inch opposite the first lumbar nerve, to not more than a sixth of an inch at the attachment of the lower sacral nerve-roots. (For further particulars as to the length of the spinal segments, consult Lüderitz, 'Ueber Wachstumsbeziehungen zwischen Rückenmark und Wirbelkanal,' Morph. Jahrb. 1884.)

The relation between the spines of the vertebræ and the places of attachment of the nerve-roots to the cord is illustrated by the appended diagram (fig. 97) from Reid, which is founded upon observations made on six adult subjects. From this it will be seen that there is a much larger amount of variation than might have been supposed.[2] This is especially the case with the thoracic nerve-roots, some of which show variations of their position of origin extending over a distance covered by as many as three spinous processes. Certain general facts can, however, be made out which are not without practical interest. Among these are the position of the second cervical nerve, opposite the arch of the atlas; that of the first thoracic nerve, opposite the sixth or seventh cervical spine; that of the

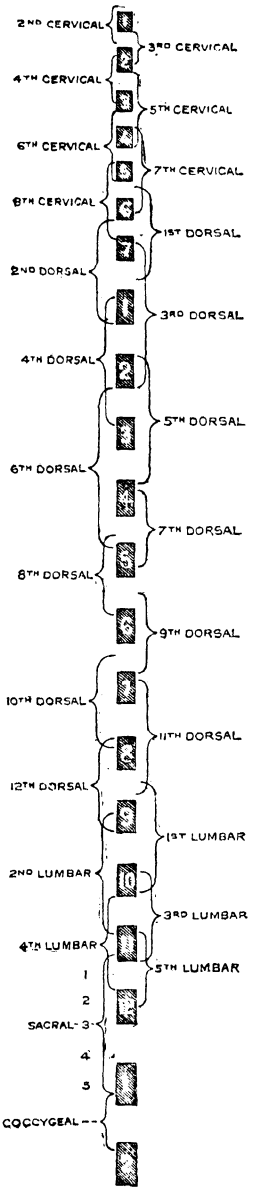
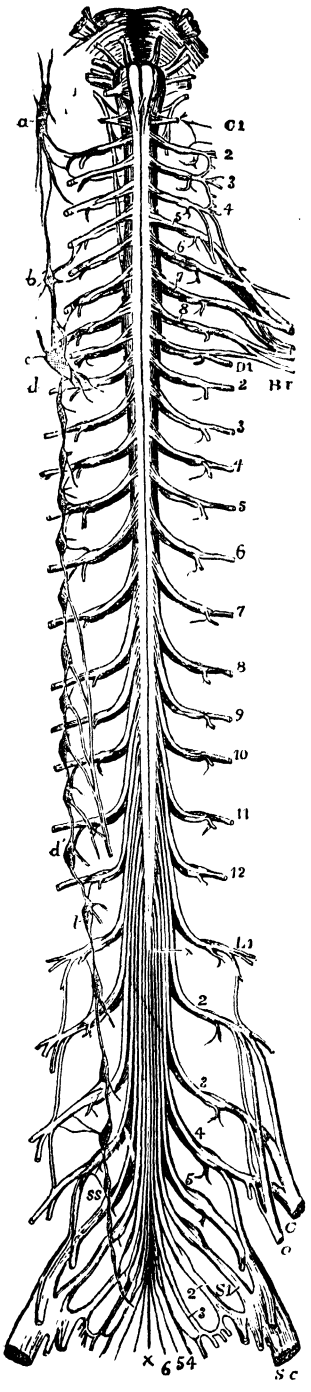


FIG. 97.—DIAGRAM SHOWING THE VARYING RELATIONS BETWEEN THE LEVELS OF THE ATTACHMENT OF THE SPINAL NERVE-ROOTS TO THE SPINAL CORD AND OF THE SPINES OF THE VERTEBRÆ. (After R. W. Reid.)

The quadrilateral areas represent the spinous processes of the vertebræ from the atlas to the second lumbar, and the levels of the spinal attachments of the various spinal nerves are indicated by brackets. (For 'dorsal' in this diagram read 'thoracic.')

[1] A. Bruce defines the limits of the spinal segments somewhat differently; he adds the interval between the lowest thread of one root and the highest of the next to the lower segment (Topographical Atlas of the Spinal Cord, 1901); while Donaldson and Davis (Journ. of Comparative Neurology, vol. xiii. 1903) regard the interval as belonging to the upper segment.

[2] Muskens (Review of Neurology, iii. 1905), from the examination of twenty-two cases, found the individual variations even greater than those given by Reid.



seventh thoracic nerve, opposite the fourth or fifth thoracic spine; and of the sacral nerves, the range of which extends from the eleventh thoracic to the first lumbar spine. The line of origin of the sacral nerves very nearly corresponds in vertical extent with the body of the first lumbar vertebra.

No doubt this variation is largely accounted for by the variations in length and obliquity of the spinous processes of the vertebræ, and accordingly we find that there is least fluctuation of relative position at the top and bottom of the series. The ventral and dorsal nerve-roots belonging to the same segment of the cord are attached practically at the same level (Reid).

The cervical enlargement about corresponds in vertical extent with the spines of the cervical vertebræ; while the lumbar enlargement corresponds with the spines of the tenth, eleventh, and twelfth thoracic, and the interval between the last-named and the first lumbar.

In section the cord is nearly circular, especially in the thoracic region, but it is somewhat flattened before and behind, so that in the whole of its extent the transverse diameter is greater than the antero-posterior. In the thoracic region it measures about 10 mm. (0·4 inch) from side to side, and about 8 mm. from before back. The cord is not, however, of uniform diameter throughout, but is swollen out in the cervical and lower thoracic regions, two enlargements being thereby produced—an upper or cervical (brachial), and a lower or lumbar (crural) (fig. 96). These enlargements are almost entirely due to an expansion in a transverse direction. Of these the cervical enlargement is of greater size and extent than the lumbar. It extends from near the upper limit of the cord to the body of the first or second thoracic vertebra; it is largest opposite the fifth or sixth cervical vertebra, where it measures from 13 to 14 mm. from side to side. The lower or lumbar

FIG. 98.—DIAGRAMMATIC VIEW FROM THE VENTRAL ASPECT OF THE SPINAL CORD AND MEDULLA OBLONGATA, INCLUDING THE ROOTS OF THE SPINAL AND SOME OF THE CEREBRAL NERVES, AND, ON ONE SIDE, THE GANGLIATED CHAIN OF THE SYMPATHETIC. ¼. (Allen Thomson.)

The spinal nerves are enumerated in order on the right side of the figure. *Br*, brachial plexus; *C*, femoral (anterior crural), *O*, obturator, and *Sc* (sciatic nerves), coming off from lumbo-sacral plexus; ×, ×, filum terminale.

a, *b*, *c*, superior, middle, and inferior cervical ganglia of the sympathetic, the last united with the first thoracic, *d*; *d'*, the eleventh thoracic ganglion; *l*, the twelfth thoracic (or first lumbar); below *s s*, the chain of sacral ganglia.

enlargement begins at the tenth thoracic vertebra, is largest opposite the twelfth (11–13 mm. across), and from this point becomes gradually smaller; its antero-posterior diameter is more nearly equal to the transverse than is the case in the cervical enlargement. Below the lumbar enlargement the cord tapers rapidly in the form of a cone (*conus medullaris*), from the apex of which the small filiform prolongation (*filum terminale*) is continued downwards.

The cervical and lumbar enlargements have an evident relation to the large size of the nerves which supply the upper and lower limbs, and which are connected with those regions of the cord. At the commencement of its development in the embryo the spinal cord is destitute of these enlargements, which, in their first appearance and subsequent progress, correspond with the growth of the limbs.

The **terminal filament** (filum terminale, central ligament) (fig. 99, *b*, *b*), about 17 to 18 cm. in length, descends in the middle line among the nerves composing the cauda equina, and, reaching the lower end of the sheath opposite to the second sacral vertebra, perforates the dura mater and, receiving an investment from it, passes on to be attached with this to the periosteum of the lower end of the sacral canal, or to the back of the coccyx. The portion within the common sheath of dura mater is sometimes termed the *filum terminale internum*; while below this sheath, where it is blended with the dura mater, it is called the *filum terminale externum* or *filum duræ matris spinalis*. It is a prolongation of the pia mater, enclosing for about half its length an enlarged continuation of the central canal of the cord (see p. 66), with a little grey matter near the upper end. Below the termination of the central canal, the filum is mainly composed of connective tissue, with blood-vessels prolonged from the anterior spinal vessels, and on either side there run in it three or four small bundles of medullated nerve-fibres, some of which have a few intermingled

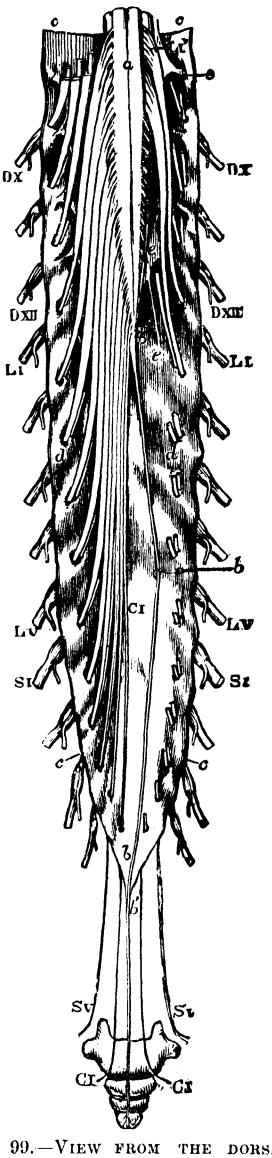


FIG. 99.—VIEW FROM THE DORSAL ASPECT OF THE LOWER END OF THE SPINAL CORD WITH THE CAUDA EQUINA AND DURAL SHEATH. ½. (Allen Thomson.)

The sheath has been opened from behind and stretched towards the sides; on the left side all the roots of the nerves are entire; on the right side both roots of the first and second lumbar nerves are entire, while the rest have been divided close to the place of their passage through the sheath. The bones of the coccyx are sketched in their natural relative position to show the place of the filum terminale and the lowest nerves.

a, placed on the dorsal median fissure at the middle of the lumbar enlargement of the cord; *b*, *b*, the terminal filament, drawn slightly aside by a hook at its middle, and descending within the dural sheath; *b'*, *b'*, its prolongation beyond the sheath and upon the back of the coccygeal bones (filum duræ matris spinalis); *c*, the dural sheath; *d*, double foramina in this for the separate passage of the ventral and dorsal (anterior and posterior) roots of each of the nerves; *e*, ligamentum denticulatum; DX and DXII, the tenth and twelfth thoracic nerves; LI and LV, the first and fifth lumbar nerves; SI and SV, the first and fifth sacral nerves; CI, the coccygeal nerve.

ganglion-cells. These nerve-bundles are regarded by Rauber as representing rudimentary coccygeal nerve-roots. They have no connexion with the coccygeal nerves proper.

The filum terminale is distinguished by its silvery hue from the nerves among which it lies.

Fissures.—The spinal cord is incompletely divided into a right and left half by two fissures which pass in from the middle of the ventral and dorsal surfaces, and penetrate through the greater part of its thickness. Of these two *median fissures* the *anterior* or *ventral* (fig. 100) is wider, and therefore more distinct than the posterior or dorsal, although it does not, in most parts, penetrate to more than one-third the thickness of the cord, while the *posterior* or *dorsal fissure* may reach more than half-way from back to front. The ventral

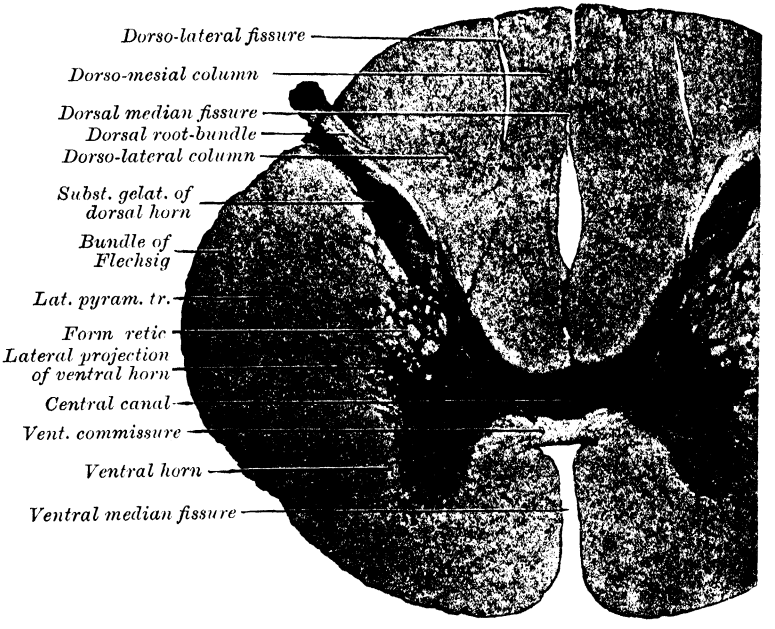


FIG. 100.—SECTION OF HUMAN SPINAL CORD FROM UPPER CERVICAL REGION. From a photograph. Magnified about 8 diameters. (E. A. Schäfer.)

contains a fold of the pia mater and also many blood-vessels, which are thus conducted to the centre of the cord. At the bottom of this fissure is a transverse connecting portion of white substance named the *anterior, ventral,* or *white commissure.*

The *posterior* or *dorsal median fissure* is not an actual fissure, for, although the lateral halves of the cord are quite separate dorsally, there is not so much a fold of the pia mater between them as merely a septum of connective tissue and blood-vessels prolonged from that membrane, which passes in nearly to the centre of the cord (*dorsal septum*). The position of the fissure is marked, especially in the lumbar enlargement and in the cervical region, by a superficial furrow. It is bounded in front by the *posterior, dorsal,* or *grey commissure.*

Besides these two median fissures, a shallow furrow is seen on each side of the cord, corresponding with the line of attachment of the dorsal roots of the spinal nerves. It is named the *dorso-lateral groove* or *sulcus.* Each

lateral half of the cord is divided superficially by the dorso-lateral groove into a dorsal and a ventro-lateral part. The attachment of the ventral roots, however, subdivides the latter into ventral and lateral portions.

A ventro-lateral sulcus has sometimes been described in the line of origin of the ventral roots of the nerves, but usually has no real existence. The fibres of these roots in fact, unlike the dorsal, do not dip into the spinal cord in one narrow line, but spread over a space of some breadth.

On the dorsal surface of the upper part of the cord there is on each side of the middle line a slightly marked longitudinal furrow (fig. 100) situated not far from the dorsal median fissure, and marking off, in the cervical region, a slender tract, the *mesio-dorsal column, funiculus gracilis*, or *column of Goll*. This sulcus, which is better marked in some individuals than in others, is termed the *dorsal intermediate furrow*. An incomplete connective-tissue septum (*dorsal intermediate septum*) extends from the furrow into the white substance of the cord. The larger remaining part of the dorsal column is termed the *latero-dorsal column, funiculus cuneatus*, or *column of Burdach*.

Weight and Dimensions of the Spinal Cord.[1]—Divested of its membranes and nerves, the spinal cord in the human subject weighs from 1 oz. to 1¾ oz. (average 30 grammes, Schwalbe).

According to Pfister[2] the spinal cord of a boy is, at all ages, both longer and heavier than that of a girl of corresponding age. The proportion of the weight of the spinal cord to that of the brain varies in both sexes in a similar manner. In the new-born the difference is greatest, and it is greater in the male than in the female. The average at birth is about 1 to 100, whereas in the adult it is 1 to 50.[3] The increase in weight of the cord from 3 to 4 grammes in the new-born to 30 grammes in the adult is most rapid during the first two years. The average length of the cord in the new-born is 14 cm.; in the adult male it is 45 cm., in the female about 41 or 42 cm.[4] The relative length to that of the body is about 3 to 10 in the new-born; by the end of the first year it has fallen to 3 to 12.

INTERNAL STRUCTURE OF THE SPINAL CORD.

Grey matter.—When the spinal cord is cut across (figs. 100, 104, 105) it is seen that the grey matter occupies the more central parts, being almost completely enclosed by the white matter. The grey matter appears in the form of two irregularly crescentic portions on either side, united across the middle line by the dorsal grey commissure before mentioned, so that its section may be compared in shape to the letter H. The concave side of each lateral crescent faces outward, and in consequence of the depth of the dorsal median fissure the commissure of grey matter joins the crescents nearer their ventral than their dorsal ends, except in the lumbar region of the cord.

The two horns or cornua of each crescent are named from their position anterior and posterior or, better, ventral and dorsal; the *anterior* or *ventral horn* is the shorter and broader, and is everywhere separated from the surface of the cord by white matter which is traversed by the bundles of the anterior (ventral) roots at the part where these leave the cord. The *posterior* or *dorsal horn* is longer and narrower, and tapers almost to a point (*apex cornu posterioris*), which closely approaches the external surface of the cord at the dorso-lateral groove, with which it is connected by a process of the superficial neuroglia which here dips in towards the horn, but is partly interrupted by a stratum of fine nerve-fibres known as the *marginal bundle* (Lissauer). The dorsal horn is slightly narrowed near its base (*cervix cornu*); from that place it gradually

[1] See on this subject, Ziehen, *loc. cit.*
[2] Neurol. Centr. xxii. 1903, pp. 757, 819.
[3] Mies, Centr. f. Nervenheilk. xvi. 1895.
[4] Ravenel, Zeitschr. f. Anat. u. Entwickel. ii. 1877.

expands into the main part of the horn (*caput cornu*), and from this it tapers in the way just noticed. Towards the apex the caput cornu has a peculiar semi-transparent aspect, an appearance due to the *substantia gelatinosa* of Rolando, which forms a kind of cap to the cornu.

The part of the grey crescent between the two horns is known as the *intermediate grey substance* (Gowers). Near the middle of the outer surface of each crescent the grey matter is less sharply marked off than elsewhere from the white matter; portions of grey matter extending into the lateral white column and uniting with one another into what in sections appears like a network enclosing portions of white substance. This is known as the *processus reticularis*; it is best marked in the cervical region (figs. 100, 104). At the dorso-lateral part of the ventral horn, immediately in front of the processus reticularis, the grey matter forms a somewhat pointed triangular projection, best marked in the upper thoracic region, which is sometimes distinguished as the *lateral horn*, but is also known as the *intermedio-lateral tract* (Lockhart Clarke) or the *intermediate process* (Gowers). Above, in the cervical region, this blends with and forms part of the enlarged ventral horn (fig. 100). This is also the case in the lumbar enlargement, but in the mid-sacral region a lateral projection again becomes distinct.

The grey crescents vary in form in different parts of the cord (see fig. 104). In the thoracic region both ventral and dorsal cornua are narrow. In the cervical and lumbar regions the ventral cornua are large and broad. The dorsal cornua are narrow in the cervical and thoracic, but very broad in the lumbar region. The grey matter is seen in a series of sections to be most abundant in the lumbar region of the cord, and least in the thoracic.

It is clear that what appear in section as irregular crescentic areas of grey matter are in reality long irregularly fluted columns, and that the commissural band uniting the convex edge of the crescents is a flattened expansion, connecting the columns along their whole length. But it is both customary and convenient to speak of the various parts of the grey matter of the cord according to their appearance in sections, although the term 'columns' is very generally applied to what appear in section as groups of nerve-cells, occurring in different parts of the grey matter, as well as to the several portions of the white matter immediately to be described.

Central canal.—Extending through the whole length of the spinal cord, in the substance of the grey commissure, there is a minute canal (fig. 100) which, in sections of the cord, is barely visible as a speck with the naked eye. It is continued above into the medulla oblongata, where it gradually approaches the dorsal surface and eventually expands into the calamus scriptorius of the fourth ventricle. It varies in shape and size in different regions. At the lower end of the cord, near the extremity of the conus medullaris, it becomes enlarged (ventriculus subterminalis), and shaped like the letter T (fig. 101), and has been described as opening on the dorsal surface of the cord; but this is normally not the case. It is continued a certain distance down the filum terminale and ends blindly. The central canal is the permanent remains of the ectodermic canal from which the spinal cord is developed. It is more distinct in the fœtus and child, and in the adult is often obliterated in places. Sometimes it is found to be duplicated for a certain distance.

FIG. 101.—SECTION OF THE SPINAL CORD NEAR THE EXTREMITY OF THE CONUS MEDULLARIS. Magnified about 6 diameters.

White matter.—The white substance of each half of the cord completely encloses the grey matter except opposite the dorsal horn. This last therefore serves to separate off a smaller *posterior* or *dorsal white column*, which is somewhat

wedge-shaped in section and is bounded internally by the dorsal median fissure, rom the rest of the white substance which forms a large *antero-lateral* or *ventro-ateral white column* (figs. 100, 104, 105). The ventro-lateral column is sometimes ,rbitrarily divided into *ventral* and *lateral* white columns, the place of passage of the bundles of the ventral nerve-roots being taken as the limit between the wo; but since these are scattered over a considerable part of the transverse ection it is clear that the limit cannot be distinctly fixed.

The white substance is traversed by imperfect septa of connective tissue prolonged inwards from the pia mater. Most of these are irregular and somewhat variable in position, with the exception of one in the cervical region extending nwards towards the grey commissure from the sulcus before described as bounding he mesio-dorsal column. This, the dorsal intermediate septum before men-ioned (p. 65), cuts off a small portion of the posterior column next to the posterior median fissure, corresponding to the projection of the mesio-dorsal column on the surface. This septum is not seen below the eighth thoracic nerve.

The lateral symmetry of the spinal cord is not always perfect. The white columns especially are found slightly to vary, the variation being generally caused by the fact that the amount of the pyramid tracts of white matter liffers somewhat on the two sides of the cord (see p. 94). More rarely, consider-able malformations are found to occur.

The accompanying curves from Donaldson and Davis,[1] who made use of four adult cords or estimating the length of the segments, but used the data given by Stilling [2] for the super-icial measurements, show the relative size of the whole cord at the level of the several segments, as well as the areas of the white and grey matter. The same facts are shown in

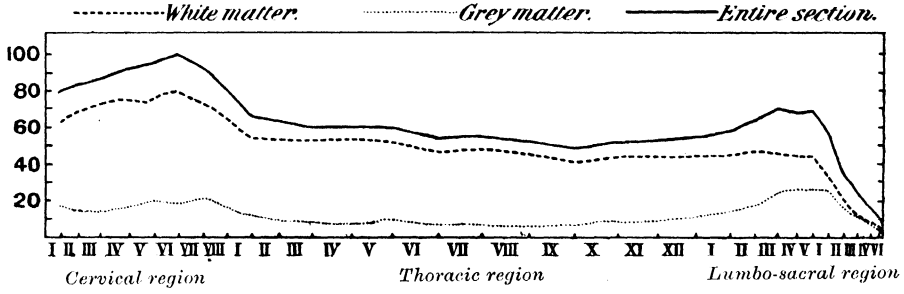


FIG. 102.—CURVES SHOWING THE SECTIONAL AREA AT DIFFERENT PARTS OF THE CORD—(1) OF THE WHOLE CORD; (2) OF THE GREY MATTER; (3) OF THE WHITE MATTER. (Donaldson and Davis.)

The ordinates show the area in square millimetres. The Roman numbers on the abscissa represent the segments: they are spaced out in accordance with their relative length.

a somewhat similar diagram by Krause and Aguesse,[3] which gives the results of the measurement of a single cord, but in which no allowance is made for the different lengths of the segments. What is most noteworthy in the result of these measurements is the rapid increase of both grey and white matter at the segments which are connected with the nerves to the limbs, and the very slight variation in area throughout the dorsal region, especially of the grey matter, although there is a slight progressive increase of the white matter. Donaldson and Davis show that the sixth cervical is the largest segment, the ninth (and tenth) thoracic the smallest. Woroschiloff's diagram (fig. 103), which is based upon Stilling's measurements of the cord of a five-year-old child, shows that the progressive increase of area of the white matter is mainly in the lateral columns, while there is a sudden increase, in the lumbar and cervical enlarge-ments, in the posterior and anterior columns.

The ventral or white commissure, like the white and grey matter generally, is proportional in size to the entering nerve-roots.

[1] Journ. Comp. Neurol. xiii. 1903. [2] Neue Untersuchungen ü. d. Bau des Rückenmarks, 1859.
[3] Anat. Anzeiger, xviii. 1900.

Characteristic features of the different regions of the cord.[1]—In the *sacro-coccygeal region* the bulk of the spinal cord is formed of grey matter which has a comparatively thin mantle of white substance surrounding it. The dorsal cornua are nearly as thick as the ventral, and the isthmus of grey matter is relatively thick; indeed, in the fifth sacral segment (see fig. 104) the dorsal horn is even larger than the ventral, and the dorsal commissure four or five times as thick as the ventral.

The terminal part of the sacro-coccygeal portion of the cord, which lies at the level of the first lumbar vertebra and gives origin to the last three pairs of sacral nerves and to the coccygeal, is known as the *conus medullaris*.[2] This receives many more dorsal than ventral root-fibres, and below the third sacral segment the large motor cells are absent from the ventral horn of grey matter, although groups of multipolar cells occur in the intermediate grey matter between the ventral and dorsal horns. Nor can the lateral pyramid tract be traced beyond the third sacral segment (Müller). As already stated, in the lower part of the conus the central canal becomes enlarged and approaches the dorsal surface.

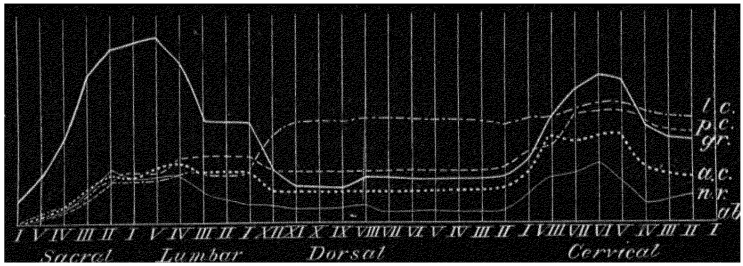


FIG. 103.—DIAGRAM SHOWING BOTH THE ABSOLUTE AND RELATIVE EXTENT OF THE GREY MATTER AND OF THE WHITE COLUMNS IN SECTIONAL AREAS OF THE CORD OF A CHILD, AS WELL AS THE SECTIONAL AREAS OF THE SEVERAL ENTERING NERVE-ROOTS. (Adapted from Ludwig and Woroschiloff.)

The sectional areas of the several entering nerve-roots (*n.r.*) as well as the extent of the grey matter (*gr.*), and of the lateral, posterior, and anterior columns of white matter (*l.c.*, *p.c.*, and *a.c.*), are represented in superposed curves, the common abscissa of which (*abs.*) is intersected at equal intervals by as many ordinates as there are pairs of spinal nerves. In the ordinates each millimetre above the abscissa represents about one square millimetre of sectional area. In this diagram the segments have been treated as if of equal length. (For 'Dorsal' read 'Thoracic.')

A lateral projection from the ventral horn is well marked in the *upper sacral region*. Both here and in the lumbar region the number of nerve-cells imbedded in the grey matter is relatively very large—a fact which is connected with the circumstance that these regions are concerned with numerous and important reflex acts as well as with the nerve-supply to the lower limbs.

In the *lumbar region* the white matter begins to predominate, owing chiefly to the accession of the large nerve-roots of the sacral and lumbar plexus, for many fibres connected with these are now running down and up the white columns of the cord. The dorsal horn and the grey matter in general is still thick, although in the uppermost part of the lumbar region it has become thinner and has more of the character which is met with in the thoracic region. The lateral projection of the ventral horn above mentioned is well marked in the fifth lumbar

[1] See on this subject, E. Bramwell, Rev. of Neur. 1906; M. and Mme. Dejerine, Rev. neur. 1906.

[2] See on the structure and relations to nerves of the conus, L. R. Müller, Deutsche Zeitschr. f. Nervenheilk. xiv. 1898, and xix. 1901; L. Minor, *ibid.* 1901; Raymond, Nouv. Iconogr. de la Salpêtrière, 1902; Sippy, Journ. of the Amer. Med. Assoc. 1902; Bálint and Benedict, Deutsch. Zeitschr. f. Nervenh. xxx. 1905.

segment. In the lumbar enlargement the grey matter receives a very considerable accession, chiefly on the ventral and lateral aspects of the ventral horn, where groups of large cells, most of which give origin to the motor nerve-fibres of the lower limb, make their appearance. At the upper part of the lumbar region the outline of the cord is beginning to be more circular, a shape which is maintained as far as the second thoracic segment.

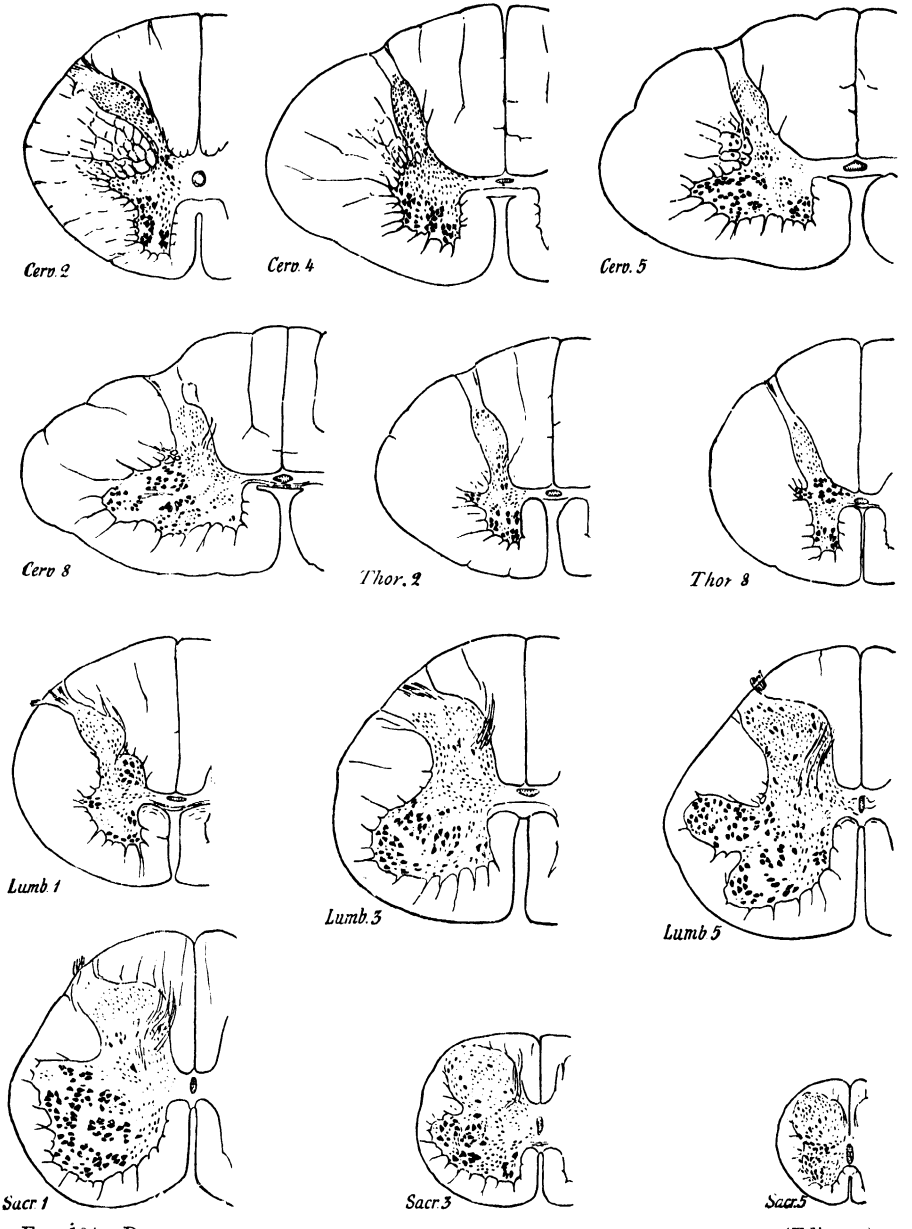


FIG. 104.—DIAGRAM OF SECTIONS OF HUMAN SPINAL CORD AT DIFFERENT LEVELS. (Edinger.)

The names refer to the origin of the corresponding nerve-roots. The relative shape and size of the cord and grey matter, the relative amounts of grey and white matter, and the principal cell-groups are shown.

In the *thoracic region* the chief characteristic is the relatively small amount of grey matter, which forms two slender crescents united by a narrow isthmus, which both here and in the cervical region is placed nearer the ventral than the dorsal aspect of the cord, whereas in the lumbar and upper sacral regions it lies near the middle of the dorso-ventral axis. The dorsal horns are very narrow and pointed. The white matter is absolutely as well as relatively greater in amount than in the lumbar region. The lateral horn forms a distinct acute prominence throughout the whole of the thoracic region. Clarke's column (see p. 83) is also to be seen near the base of the dorsal horn: it forms a distinct rounded prominence at the lower part of the thoracic region; this prominence is apparent up to the first thoracic segment. In the upper part the mesio-dorsal column begins to be marked off from the latero-dorsal.

The third to the tenth thoracic segments resemble one another so closely that they cannot be easily distinguished. The first thoracic in its general form belongs to the cervical rather than to the thoracic region, and differs markedly from the second thoracic by the lateral expansion of its ventral horn.

The *cervical region* is characterised by the fact that the cord, except at the uppermost part, is of large size and tends to be somewhat flattened dorso-ventrally. The increase in size affects both grey and white matter. The mesio-dorsal column is now sharply marked off from the latero-dorsal. Fibres of the roots of the accessory nerve may be seen passing out from the lateral aspect. A well-marked reticular formation is seen at the outer edge of the grey matter; indeed, this may be regarded as characteristic of the cervical region, and is specially well developed opposite the first and second cervical segments. From the fourth cervical segment downwards a mass of grey matter, triangular in section, is superadded laterally to the ventral horn; this extends into the first thoracic segment. The superadded part contains both many large nerve-cells and many medullated fibres, so that it becomes stained more darkly than the rest of the grey matter, both by the Nissl and the Weigert methods. The dorsal horn is but slenderly developed, contrasting with the large development of the same part in the lumbar enlargement. The part uniting the two crescents of grey matter is thin, and the central canal is flattened dorso-ventrally.

In the uppermost segments (above the cervical enlargement) the grey matter is again diminished in amount and the cord has become more nearly circular in outline, as in the thoracic region. The section has, however, the other cervical characteristics, and there is a much more strongly marked ventral commissure than in the thoracic cord. In the ventro-lateral part there is a triangular area of the white matter close to the surface which, in Weigert preparations, stains less deeply than the rest. This area corresponds with the situation of the tract of fibres known as Helweg's bundle (see p. 95). Opposite the first cervical nerve-roots the cord begins to merge into the medulla oblongata or spinal bulb, and the passage of the pyramid fibres from the pyramids on one side of the bulb to the lateral tract on the other side of the cord tends partially to obliterate the ventral median fissure and to cut up the grey crescent. In the first and second segments the substance of Rolando is very prominent and club-shaped: the descending or spinal root of the fifth nerve separates it from the surface. This root is traceable, with gradual diminution, down the upper cervical region, even below the fifth segment (Probst).

In the cervical region the nerve-roots are attached to the cord nearly at a right-angle and close together; in the other regions at an angle which is more or less oblique, the roots being directed from the cord downwards towards the intervertebral foramina.

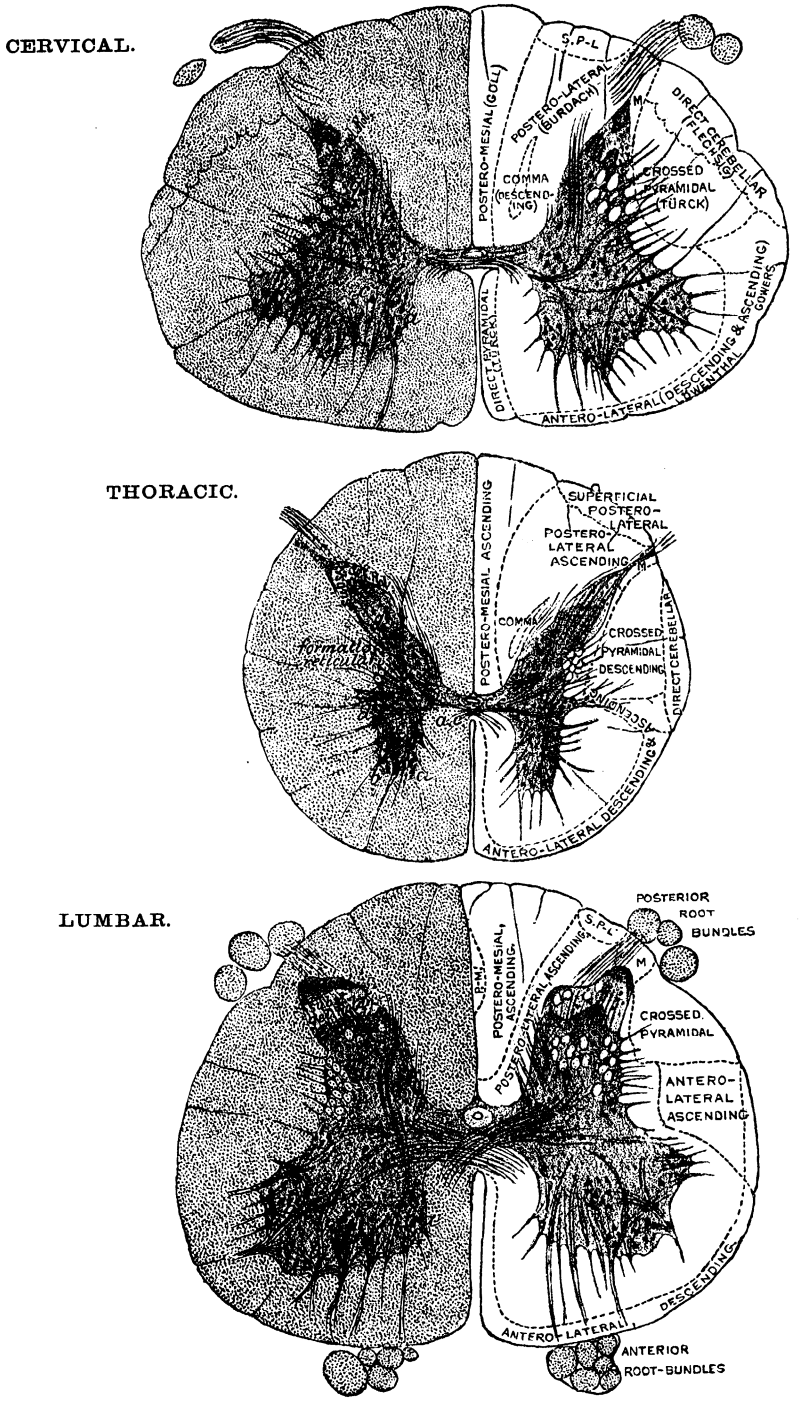


FIG. 105.—SECTIONS OF SPINAL CORD IN LOWER CERVICAL, MID-THORACIC, AND MID-LUMBAR REGIONS. (E. A. Schäfer.)

On the right side of each section conducting tracts are indicated. P.-M.' (in the lumbar region), septo-marginal tract.

Microscopic structure of the spinal cord.—The white substance of the spinal cord is almost wholly composed of longitudinally coursing medullated nerve-fibres, which in carmine-stained transverse sections of the cord (fig. 106) appear as clear rings with a stained dot—the section of the axis-cylinder—either in the middle of the ring or shifted somewhat to one side. The fibres vary much in size, and in many parts of the section larger and smaller fibres are intermixed, but some parts are characterised by containing many large fibres, others for the most part small fibres. The largest fibres are in the circumferential part of the anterior and lateral columns, the smallest in the part of the lateral column in the neighbourhood of the processus reticularis, in the marginal bundle of Lissauer near the apex of the posterior horn, and in the mesio-dorsal column. As a general rule, the larger fibres are those which have the longest paths in the cord, and these, as Sherrington has shown, tend to occupy a position nearer the periphery of the cord than fibres, belonging, it may be, to the same system, but having a shorter course.[1]

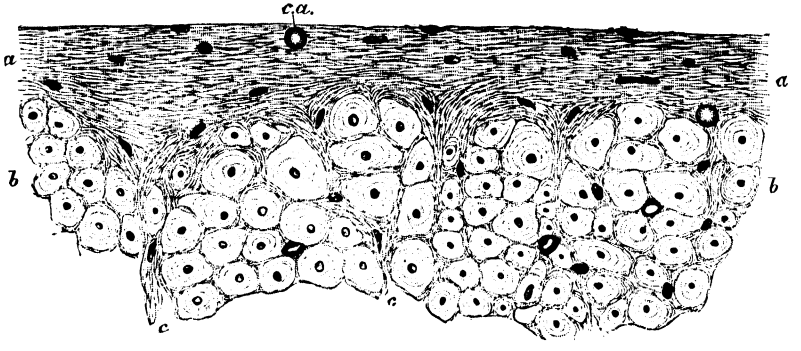


FIG. 106.—A SMALL PORTION OF A TRANSVERSE SECTION OF THE HUMAN SPINAL CORD IN THE REGION OF THE LATERAL COLUMN, TO SHOW THE SUPERFICIAL NEUROGLIA. (E. A. Schäfer.)

a, *a*, superficial neuroglia; *b*, *b*, transverse section of part of the lateral column of the cord, in which the dark points are the axis-cylinders, and the clear areas the medullary substance of the nerve-fibres. The superficial neuroglia is seen to exhibit the appearance of a fine feltwork in which numerous nuclei and one or two *corpora amylacea*, *c.a.*, are imbedded, and to extend inwards (*c*, *c*) among the nerve-fibres.

Very small fibres also occur scattered over the white substance, especially in the ventral funiculus. The white funiculi are imperfectly divided into secondary columns by incomplete septa of fibrillar connective tissue which are prolonged inwards from the inner layer of the pia mater, and convey blood-vessels to the interior of the cord.

Immediately beneath the pia mater and closely investing the cord externally is a layer of what in the fresh condition appears a homogeneous substance with nuclei imbedded in it here and there (*glial sheath, substantia gelatinosa externa*). In sections of the cord hardened in alcohol or chromic salts the substance in question is finely fibrillar (fig. 106, *a*, *a*). The layer which it forms is very thin over some parts of the surface, but comparatively thick in others, and where the pial septa pass into the cord it accompanies and invests them and their ramifications in the white substance, passing with them between the irregular bundles of nerve-fibres.[2] Not only does this subpial fibrillar substance accompany the prolongations of the connective tissue and largely assist in forming the in-

[1] Sherrington, Journ. Phys. xiv. 1893; Flatau, Zeitschr. f. Klin. Med. xxxiii. 1897; Ziehen, *op. cit.* 1899. Also Sherrington and Laslett, Journ. Phys. xxix. p. 188, 1903.

[2] For details of these glial septa, see Ziehen, *op. cit.*

complete septa above mentioned, but it extends independently amongst the individual nerve-fibres, occupying the interstices between them, and serving as a uniting medium in which they are imbedded. Hence it was named by Virchow the *neuroglia* (nerve-cement). The nuclei in it belong to branched fibrillated cells (*neuroglia-cells*) (fig. 107), which occur in considerable numbers and may be said to form the tissue; some which are more conspicuous (Deiters) appear stellate in section and are found in the larger interstices between the nerve-fibres. Along the line of origin of the dorsal roots the superficial neuroglia dips inwards towards the horn of grey matter, and expands within it to join

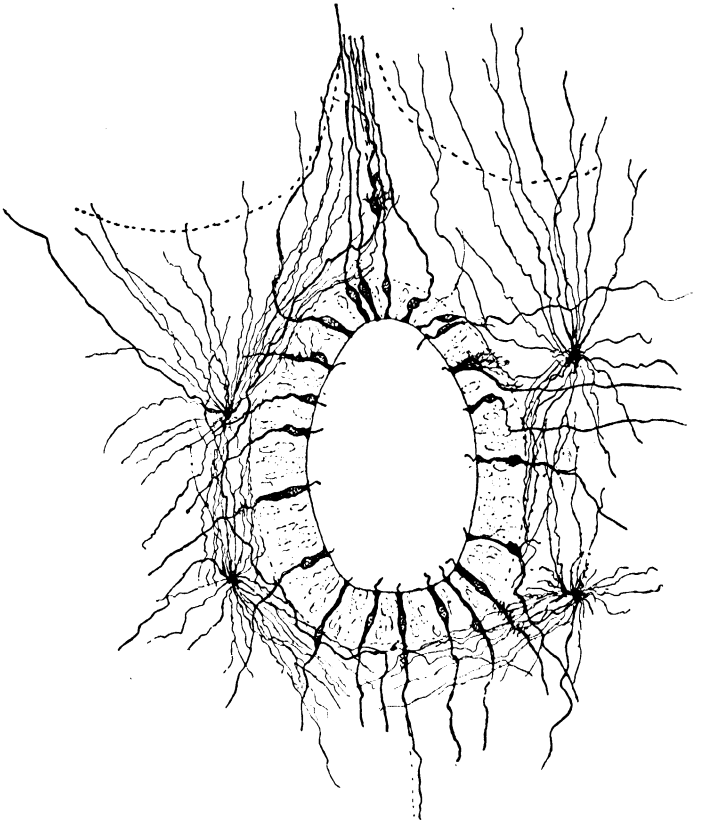


FIG. 107.—NEUROGLIA AND EPENDYMA CELLS AROUND CENTRAL CANAL OF CORD. (Lenhossék.)

the gelatinous substance of Rolando. This, as before mentioned, presents a transparent jelly-like appearance in the fresh condition, but in sections of the hardened cord it is finely fibrillar.[1] Some of the bundles of nerve-fibres of the posterior root traverse this substance, and it also contains many nerve-cells; these are mostly of small size, but some of larger dimensions are met with.

The neuroglia is prolonged into the grey matter, and pervades the latter throughout in every part; but it is here in great measure obscured by the proper nervous elements. These are, in the first place, multipolar nerve-cells, many of

[1] Kölliker (Gewebelehre, vol. ii. p. 153) found the substance of Rolando to contain numerous neuroglia-cells; but Van Gehuchten (Système Nerveux, p. 437) states that only a few neuroglia-cells are present in it, and Weigert found relatively few neuroglia-fibrils traversing it.

large size, scattered singly or occurring in groups throughout the grey substance. In connexion with these, and especially accumulated around the cells and cell-groups, is an interlacement of the finest ramifying nerve-fibrils, derived partly from the processes of nerve-cells in the grey matter and partly from the ramification of collaterals which enter the grey matter from the white columns. These and the axis-cylinder processes of the nerve-cells traverse the grey matter in all directions, coursing singly or in bundles, and confer on the grey matter a spongy appearance. Hence it is sometimes known as the *substantia spongiosa*.

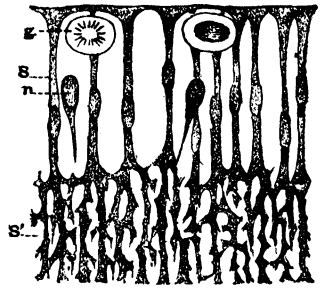


FIG. 108. — SECTION OF NEURAL EPITHELIUM OF EARLY EMBRYO. (His.)

Highly magnified view of part of a section, at the time of the first differentiation of the neuroblasts, showing *s'*, spongework formed of the outer ends of columnar epithelium cells, *s*; *g*, rounded 'germinal cells' in process of division (probably to form neuroblasts); *n*, a neuroblast.

Besides the substantia gelatinosa externa and the substantia gelatinosa Rolandi, there is another distinct area of gelatinous substance to be seen in cross-sections of the fresh cord, immediately surrounding the central canal. This, the *substantia gelatinosa* (*gliosa*, Ziehen) *centralis*, is mainly composed of neuroglia, but contains a few nerve-cells and nerve-fibres, and it is also permeated from within out by the branching processes of the (ciliated) epithelium-cells which line the central canal. To this epithelium, and to the neuroglia which underlies it both in the cord and in the ventricles of the brain, the name of *ependyma* has been applied.

The neuroglia is developed both here and in other regions of the cerebrospinal axis from the spongioblasts of His (see p. 10), which at early periods of embryonic development extend from the central canal in the middle of the grey matter to the periphery (figs. 108, 109). At subsequent periods their continuity from the central canal to the surface can no longer be recognised, although it is certain that even in the adult the cells which line the central canal and ventricles of the brain extend a long and indefinite distance into the grey matter (p. 56). It is probable that it is by transverse division of the spongioblasts, preceded by division of their nuclei, that the neuroglia-cells are originally formed. It therefore appears clear that, although nerve-cells and neuroglia-cells are functionally very different, their origin is not so dissimilar as was at one time believed to be the case. It was formerly taught that the

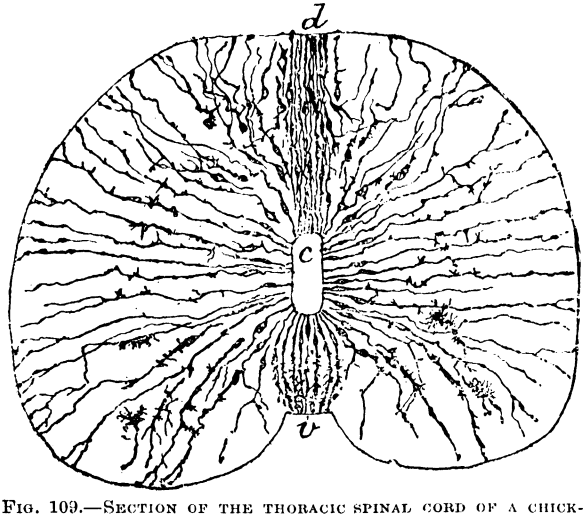


FIG. 109.—SECTION OF THE THORACIC SPINAL CORD OF A CHICK-EMBRYO OF NINE DAYS' INCUBATION. Stained by Golgi's method. (Ramón y Cajal.)

c, central canal; *v*, ventral or anterior; *d*, dorsal or posterior surface. The spongioblasts alone are stained and are seen to extend from the central canal to the periphery of the cord. Some appear to be detached and in process of conversion into neuroglia-cells.

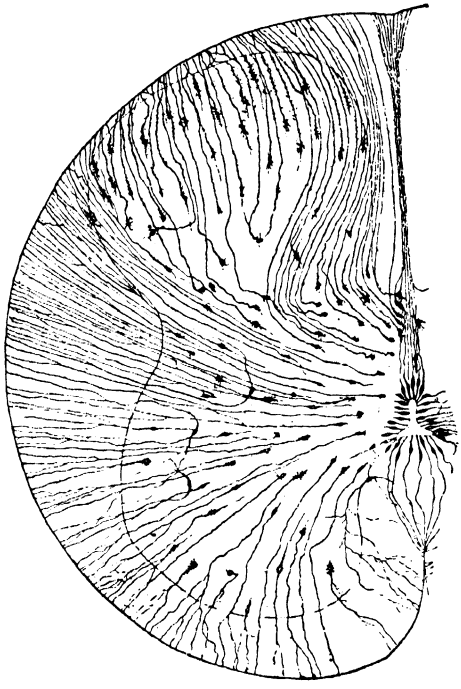


FIG. 110.—SECTION OF CORD OF EMBRYO, SHOWING SOME OF THE EPENDYMA-CELLS DETACHED AND BECOMING CONVERTED INTO NEUROGLIA-CELLS. (Lenhossék.)

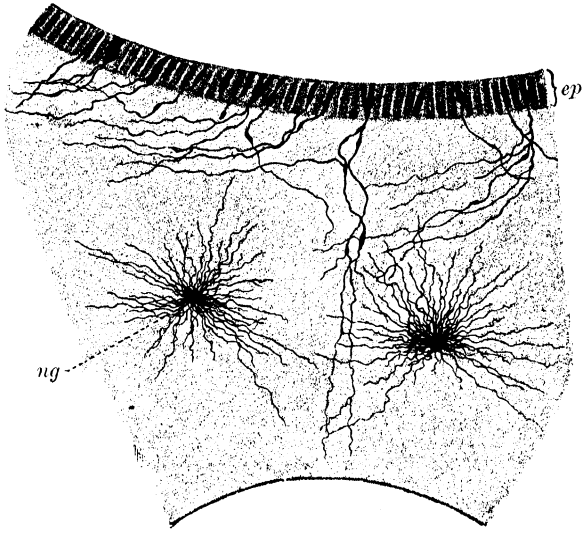


FIG. 111.—PART OF EPITHELIUM OF CENTRAL CANAL OF NEW-BORN CHILD. Stained by Golgi's method. × 120. (Sobotta.)

ep, epithelium; *ng*, neuroglia-cells in adjacent grey matter.

neuroglia is a form of connective tissue (which it resembles functionally), and it was supposed that its cells were developed from mesoderm. The researches of His have, however, shown that the spongioblasts from which the neuroglia-cells originate and the neuroblasts which give origin to the nerve-cells are both formed from the (at first undifferentiated) cells of the neural ectoderm. The investigations of Cajal upon the development of these elements in the embryo chick and mammal further indicate that the distinction into spongioblasts and neuroblasts is not a fundamental one, for cells which from their shape and position would be classed among the spongioblasts of His may alter their character, and by throwing out an axis-cylinder process become transformed into nerve-cells. But it is of course not possible for a cell which has once assumed the characters of a neuroglia-cell to become transformed into a nerve-cell, or *vice versa.*

Small concentrically striated globules, termed *corpora amylacea*, are frequently met with in the neuroglia of the cord in man (fig. 105), as well as in many of the parts of the central nervous axis. They appear to be composed of protein substance, with or without a deposit of calcareous salts, but, although long recognised, their mode of formation and their meaning are unknown.

The nerve-cells in the grey matter.—The nerve-cells of the spinal cord vary greatly in size, the larger cells of the ventral horn measuring from 50 to 135 μ, while the small cells of the substance of Rolando may not be more than 10 μ.[1] They are smaller in the fœtus and child than in the adult. All the cells met with in the spinal cord are multipolar, possessing a single axon and several dendrons. A certain number, especially in the dorsal part of the grey crescent, belong to type ii. of Golgi, having short axons ramifying in the grey matter at no great distance from the cell-body. On the other hand, the nerve-cells of the ventral horn, those of the lateral horn, and most of those of the dorsal horn belong to type i. of Golgi, and their axons pass far away from the cell-body. From some of the nerve-cells the axons pass into the ventral nerve-roots, becoming the axis-cylinders of efferent nerves (*efferent root-fibres*)[2]; from other cells the axons pass into the white matter of the same side, where they become longitudinal and pass either upwards or downwards (or, after bifurcating, both upwards and downwards) to connect the grey matter of the segment in which the cell-bodies from which they emanate lie with other neighbouring or distant segments of the cord (*homolateral association-fibres*); while from yet other cells they pass across the isthmus in the white commissure.[3] These crossing fibres have two destinations—viz. some to the grey matter of the opposite side of the cord of the same segment as that from which they originate, ending by arborescence amongst its cells (*commissural fibres*); others to the white matter of the opposite side, where they become longitudinal and pass either upwards or downwards to connect the different segments of the grey matter, as in the case of the homolateral association-fibres already mentioned. These are the *contra-lateral association-fibres.* The cells (neurones) to which these several kinds of fibres belong are distinguishable as (*a*) *intercalated* or *short-axoned cells*, (*b*) *root-cells*, (*c*) *association-cells*, and (*d*) *commissural cells.* But the last-named are obviously also association-cells, for they bring the two sides of the cord into relation.

[1] Cf. Ziehen, *op. cit.*

[2] In the chick (Cajal, Lenhossék) there are a few multipolar root-cells which send their axons into the dorsal roots: these are said by Steinach, experimenting on the frog, to pass to the intestine, but the statement is disputed by Horton Smith. They are certainly absent in adult mammals (Sherrington).

[3] Dendrons of the cells sometimes extend across the grey commissure into the grey matter of the opposite side of the cord, and others may pass into the white matter of the same side, even reaching the surface. It is by no means rare for entire cells to be found detached from the grey matter and lying in the white substance of the cord ('outlying cells,' Sherrington).

The cells which send their axons into the white matter are sometimes spoken of as the 'cells of the white columns.' Their axons give off collaterals before leaving the grey matter. In transverse sections of the cord it is seen that the nerve-cells are not equally distributed throughout the grey substance, but tend to be arranged in groups which occupy nearly the same relative position in successive sections. The groups are therefore the sections of longitudinal tracts of grey matter rich in nerve-cells, and these tracts are named the *cell-columns* of the grey matter. The longitudinal continuity of the groups can be seen in sections of the cord made parallel with its long axis and passing through the part of the grey matter where the groups occur. In such longitudinal sections it may also be observed that the cells tend, speaking generally, to be more extended longitudinally the longer the segments of the cord, as indicated by the attachment of the nerve-roots (Toldt). It may further be stated as a probable law, applicable, however, only to the cells belonging to the same cell-column, that the longer the nerve-fibre which issues from a cell, the larger is the cell. Those segments of the cord from which the longest nerve-fibres issue by the ventral roots have the largest ventral-horn cells.

The root-cells lie, for the most part, in the ventral horn, but in some regions many such cells lie in or near the lateral horn (intermedio-lateral column of Clarke) and give origin to the fine medullated fibres which occur in the thoracic and some other ventral roots ; and a few are situated even as deeply as the dorsal horn. Their axons become the axis-cylinder processes of the motor nerve-fibres. As they are leaving the grey matter they give off a few recurrent collaterals.

In some of the lower vertebrates it may be made out that there are variations in the size of the column of cells of the ventral horn in successive portions of the cord, the cells being more numerous opposite the points of entrance of the nerve-roots, the attachment of which to the cord is in them more localised than in man and higher vertebrates. In this way somewhat of a segmental formation of the column is indicated, and in some fishes and reptiles the enlargement of the group of cells and its enclosing grey matter is sufficiently marked to produce an external swelling opposite each nerve-pair. A similar segmentation is indicated in an early stage of development in all vertebrates, including man, by the fact that the cord is somewhat enlarged opposite each pair of nerve-roots.

Cell-groups of cord : ventral horn.[1]—Of the groups of efferent root-cells, the one which is most constant and contains the largest cells is found along the whole of the ventral part of the horn where the nerve-cells lie among and give off the issuing fibres of the anterior roots. This is sometimes named the *motor cell-column*, but it is more generally known as the *cell-column of the anterior* or *ventral horn*. Its cells are collected into two sub-columns—a *lateral* nearer the lateral column of white matter, and a *mesial* nearer the ventral white column ; the lateral occur only in the cervical and lumbo-sacral enlargements.

Of these sub-columns, therefore, the one which is most constant along the whole length of the cord is the *mesial* ; it is sometimes described as consisting of two sub-groups—viz. a dorso-mesial and a ventro-mesial. The nerve-fibre processes

[1] See on this subject Waldeyer, Das Gorillenrückenmark, Abh. d. k. pr. Akad. d. Wiss. z. Berlin, 1888; Kaiser, Die Functionen d. Ganglionzellen d. Halsmarkes, Haag, 1891; Collins, New York Med. Journ. lix. 1894; Van Gehuchten and De Buck, Revue neurol. 1898; Marinesco, Rev. neurol. 1898, p. 463, and 1901; also in Semaine méd. July 1904; Sano, Journ. de Neurol. 1897 and 1898, and Les Localisations &c., Brussels, 1898; also in Proc. of Anat. Congress in Anat. Anzeiger xxvii. 1905; Van Gehuchten and Nelis, Journ. de Neurol. 1899; Onuf, Journ. of Nerv. and Mental Diseases, 1899; Van Gehuchten and De Neef, Névraxe, i. 1900; De Neef, Névraxe i. and ii. 1900; Bruce, A Topographical Atlas of the Spinal Cord, 1901; Bruce and Stiles, Scottish Med. and Surg. Journ. ix. 1901; Parhon and Goldstein, Neurol. Centralbl. 1901, 1902, and 1905; Rosenberg, Neurol. Centralbl. 1902; Boissand and Bauer, Journ. de Neurol. viii. 1903 (frog); Bikeles and Francke, Deutsch. Zeitschr. f. Nervenheilk, xxiii. 1903, and xxix. 1905, pp. 171 and 180; Dr. and Mme. Parhon, Journ. de Neurol. viii. 1903; Bikeles, Neurol. Centralbl. 1904; Van Gehuchten, Système nerveux, 1906.

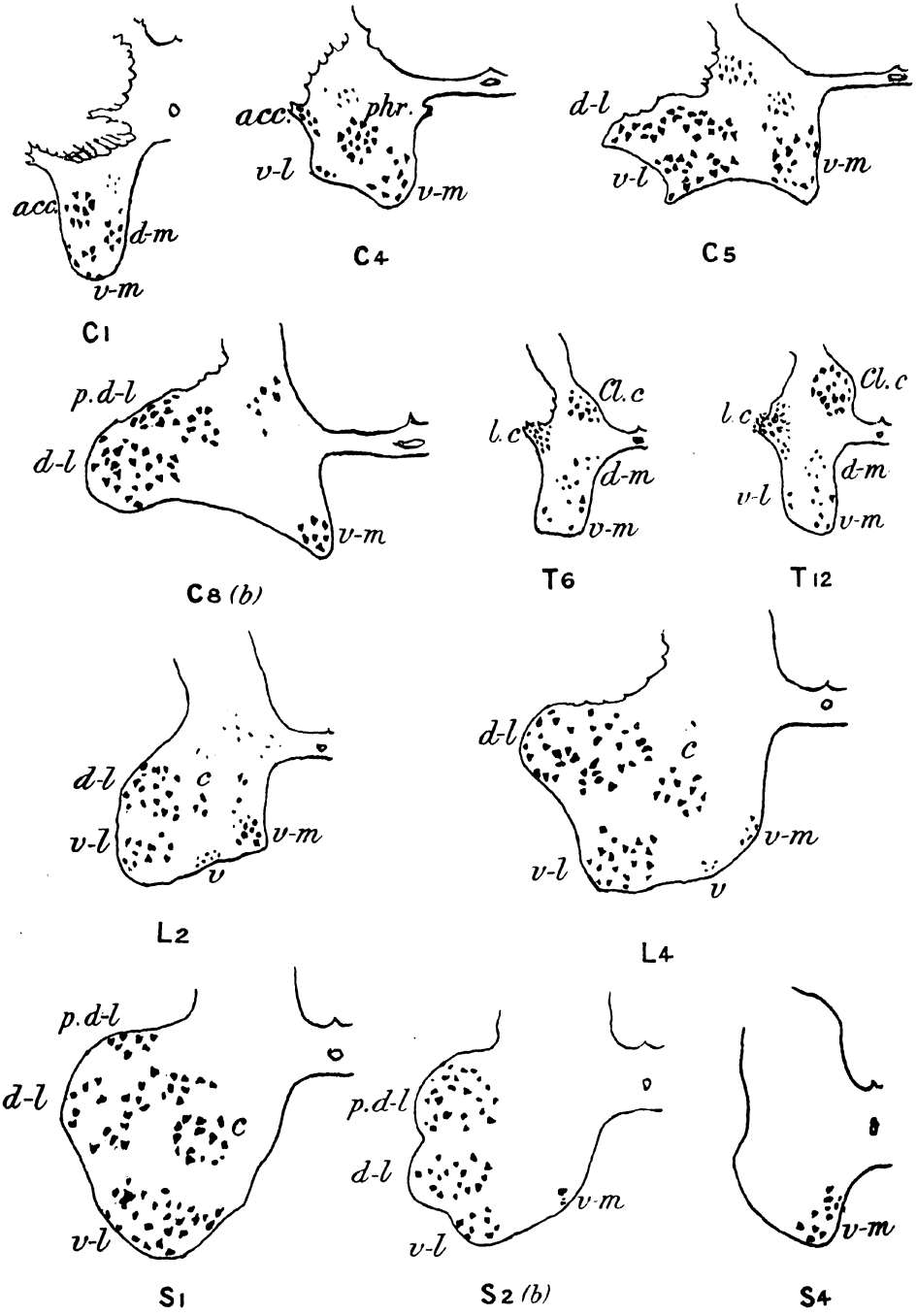


FIG. 112.—OUTLINE SKETCHES OF VENTRAL HORN OF LEFT SIDE OF CORD AT DIFFERENT LEVELS, SHOWING THE RELATIVE NUMBER AND POSITION OF THE CHIEF EFFERENT CELL-GROUPS. (After A. Bruce. Topographical Atlas of Spinal Cord.)

C 1, C 4, T 6, &c., indicate the segments—*e.g.* first cervical, fourth cervical, sixth thoracic; C 8 (*b*), lower part of eighth cervical. The following letters designate the cell-groups: *v-m*, ventro-mesial; *d-m*, dorso-mesial; *v-l*, ventro-lateral; *d-l*, dorso-lateral; *p.d-l*, post-dorso-lateral; *v*, in L 2, L 4, ventral; *c*, in L 2, L 4, S 1, central; *l.c.*, in T 6, T 12, group of lateral cornu; *acc.*, in C 1, C 4, accessorius; *phr.*, in C 4, phrenic; *Cl.c.*, in T 6, T 12, Clarke's cell-column.

of the *dorso-mesial portion* probably eventually pass into the dorsal rami of the spinal nerves to supply the dorsal musculature of the spinal column. This mesial cell-column is not represented in the fifth lumbar nor in the first and second sacral segments, nor below the fourth sacral. It shows from one to fifteen cells in a section. Its *ventro-mesial portion* is well developed in *C* 4[1] and *C* 5, and again shows an increase from *C* 8 to *L* 4. It disappears in *L* 5 and *S* 1, but is well marked in *S* 2, *S* 3, and *S* 4.

The *lateral* cell-column is mainly developed in the cervical enlargement and lumbo-sacral enlargement, and has an evident relationship to the nerve-roots of the brachial and sacral plexuses. It shows subordinate groupings, which have special connexions with the muscles of particular segments of the limbs. According to Bikeles, the cell-groups for the muscles of the proximal segments of each limb lie ventral to those for the muscles of the distal segments, and within each group the motor-cells for the dorsal muscles of a myotome lie lateral to those of the ventral muscles.

It is subdivided (Bruce) into *ventro-lateral* and *dorso-lateral sub-groups*; to which in certain parts are superadded a *post-dorso-lateral* and a *central group*.

Subdivisions of the lateral cell-column (fig. 112).—In the **cervical enlargement** of man the *ventro-lateral group* or *cell-column* begins to appear at *C* 4; at *C* 5 it forms a marked prominence at the lateral angle of the horn; at *C* 6 it is becoming displaced medianwards and is soon replaced by a new or *lower ventro-lateral cell-column*, which here becomes intercalated between it and the dorso-lateral cell-column. This new group becomes larger in *C* 7 and disappears in the lower part of *C* 8. Before disappearing it is pushed inwards by the enlarging dorso-lateral cell-column.

The *dorso-lateral cell-column* begins in the lower part of *C* 4, and enlarges rapidly, forming, along with the next described column, a considerable prominence on the lateral aspect of the horn from *C* 5 to *C* 8, where this column disappears.

A *post-dorso-lateral cell-column* begins to appear in the upper part of *C* 8, increases throughout this and the first thoracic, and then disappears.

In the **lumbo-sacral enlargement** a *ventro-lateral cell-column* begins to show itself at *L* 2 and rapidly increases in size in the succeeding segments, forming a marked projection in *L* 5; it extends as low as *S* 2, where it disappears.

The corresponding *dorso-lateral cell-column* also begins in *L* 2, is largest in *L* 5, where it forms a distinct projection, and ceases in *S* 3; but the lower limits of these two columns are difficult to define, since they tend to blend with one another below.

A *post-dorso-lateral cell-column* makes it appearance in *S* 1, increases rapidly in size in the next segment, and ceases at the lower end of *S* 3.

A *central cell-column*, which is not represented in the cervical enlargement, is seen as a very distinct group from *L* 2 to the upper part of *S* 2, attaining its maximal development at *L* 5 and *S* 1. All of the above groups show subordinate groupings.

The cells are largest in the lumbo-sacral and smallest in the dorsal region, and perhaps this difference in size is related to the size of the muscle-fibres to which their axons are supplied (Bruce. Cf., however, what is said on this subject on page 77.)

Relations of the cell-groups of the ventral horn to the limb-muscles.—In the cervical region, according to Van Gehuchten,[2] the ventro-lateral group of the horn forms a nucleus of origin of the motor fibres to the muscles of the neck. From the fourth cervical segment the cells of this group send fibres to the shoulder-muscles. From the fifth cervical segment to the first thoracic, inclusive, the considerable lateral addition to the horn is due to the appearance of an important column of cells supplying the arm-muscles; and this again shows a tendency to subdivision for the proximal and distal segments of the limb, the subdivisions for the proximal segments occupying, on the whole, somewhat higher positions in the cord than those for the distal segments. From the second thoracic to the tenth thoracic, inclusive, the extra groups of cells in the ventral horn have disappeared, and this part of the cord is almost uniform in appearance in section. But at the eleventh thoracic there is again an appearance of the ventro-lateral group of cells of the horn, forming a column of large cells extending well downwards in the lumbar region. This is the group from which the nerves to

[1] *C* 4 = fourth cervical segment. In this description the account given by A. Bruce (Topographical Atlas of the Spinal Cord, 1901) is followed.

[2] Van Gehuchten's terminology is in some respects different from that employed by Bruce.

the ilio-psoas and abdominal muscles take origin. At the upper end of the second lumbar segment another column begins to appear (dorso-lateral), soon consisting of a large mass of cells, which may itself show signs of division into two or three separate groups. These are stated to give origin to the nerves passing to the extensor muscles of the thigh.

The column in question is traceable down in the now greatly enlarged ventral horn as far as the upper border of the fifth lumbar segment, dipping as it descends somewhat more deeply into the grey matter. At about the middle of the third lumbar segment another column (central of Bruce) makes its appearance mesial to the one just described; this is also connected with the origin of nerves to certain of the thigh-muscles—viz. those supplied by the obturator nerve—the pectineus and adductor magnus. In the upper part of the fifth lumbar segment the two columns appear to become merged into a single column, which continues them as far as the lower end of the second sacral segment. From this continuation other thigh-muscles (semimembranosus, semitendinosus, and biceps) are supplied, and the column is said to show groupings corresponding respectively to the individual muscles.

At the level of the upper border of the fifth lumbar segment, and extending as far as the third sacral, two considerable columns of cells make their appearance—one ventro-lateral and the other dorso-lateral. Both produce characteristic prominences of the grey matter. Of the two the dorso-lateral is the larger, and shows signs of subdivision into subsidiary groups. These two columns appear to be connected with the fibres to the leg-muscles, the former with those to the back of the thigh, and the latter with those to the peronei and the flexors and extensors of the ankle.

Lastly, extending through the second, third, and part of the fourth sacral segments, another considerable column is seen (post-dorso-lateral of Bruce); this is connected with the origin of the nerves to the intrinsic muscles of the foot.

There thus appears to exist, according to Van Gehuchten, a rough segmental arrangement of the motor nuclei for the limb-muscles, but with a considerable amount of overlap (see below). There is little doubt that the subsidiary columns are related to separate muscles, or perhaps groups of muscles, which ordinarily act together, although the exact allocation of the subordinate columns presents considerable difficulty.

Parhon and Goldstein give the following as the relation between the segments of the lumbo-sacral cord and chief muscles of the lower limb[1]: *L* 3, *L* 4, quadriceps (from lateral group of cells), sartorius (from ventro-lateral group); *L* 3, gracilis and adductores brevis and longus (from central group); *L* 4, adductor magnus (from central group); *L* 4, *L* 5, semimembranosus (from central group), tibialis anticus (from dorsal group); *L* 5, flexors of toes (from dorsal group); *L* 5 to *S* 2, gastrocnemius (from post-central group); *S* 1, peronei (from lateral group); semitendinosus (from central group); *S* 1, *S* 2, plantar muscles (from post-dorso-lateral group).

Certain segments are characterised by the presence of special cell-groups. Thus the accessory nucleus is seen in the lateral part of the ventral horn in *C* 1; nearer the middle of the horn in *C* 2; again more laterally situated and smaller in *C* 3; it is traceable down as far as *C* 6, where it disappears. According to Bruce, the upper part of this nucleus probably supplies the muscles of the palate and larynx and the sterno-mastoid, and the lower part the trapezius.

There is a special cell-group, or short cell-column, in the cervical region, from which the fibres of the phrenic nerve arise. This group occupies the middle of the horn, and extends from the lower part of the third to the middle of the sixth cervical segment.[2]

The origin of the nerve-roots which go to form the brachial plexus is probably from the fourth cervical segment down to the lower part of the first thoracic segment, of those which go to form the lumbo-sacral plexus probably from the second lumbar to the third sacral segment.

It must be pointed out that the cell-columns which represent individual muscles and muscle-groups are, as a rule, not confined to one segment of the cord, but may extend along two or even a number of segments; there is therefore no segmental separation of the cells of origin of the efferent fibres. Nor are the segments in which the several groups occur absolutely constant, for

[1] Journ. de Neurol. 1902; Neurol. Centralbl. 1905. Also Dr. and Mme. Parhon, Journ. de Neurol. 1902 and 1903.

[2] Kohnstamm, Fortschr. d. Medizin, 1898; Sano, Journ. méd. de Bruxelles, Oct. 1898; Marinesco, Semaine médicale, Dec. 1903. Sano found the sensory fibres of the diaphragm to be connected with the third to the sixth spinal ganglion.

in some individuals both the elongated cell-groups and the fibres which emanate from them and which pass into the root-bundles and form the limb-plexuses are all shifted forwards (*prefixed*), while in other individuals they are all shifted backwards (*postfixed*); their *relative* position being always maintained. And between the extremes of prefixation and postfixation all intermediate conditions occur. The efferent roots and even the rootlets contain a mixture of fibres from the cells of the various parallel cell-columns, and innervate muscles having no functional connexion with one another. The separation of function is only found after the plexuses are passed.

Lateral cell-column; intermedio-lateral tract.—About the middle of the grey crescent, at its lateral aspect, throughout the thoracic region and extending upwards a short distance into the cervical region and downwards for two or three segments of the lumbar cord, is to be seen a well-marked group or column of moderate-sized highly chromatic cells, many of which lie in a slight projection of the grey matter, which has been termed the *lateral horn*. This group was recognised as a distinct cell-column by Lockhart Clarke, who gave it the name *intermedio-lateral tract*. The axons of its cells pass to the anterior roots and supply the fine medullated outflowing fibres of the sympathetic [1] (white rami communicantes) (Gaskell; Ziehen, however, states that these arise from the smaller cells of the ventral horn).

In the upper part of the cervical region and in the lower part of the medulla oblongata there is a similarly situated group of cells, very like those of the lateral cell-column of the thoracic cord. The grey matter in which this group lies is known in the medulla oblongata as the *lateral nucleus*.

The cells of the intermedio-lateral tract vary considerably in size (12 μ to 60 μ), and also in relative number at different segments and even in different parts of a segment (Bruce).[2] They occur from the eighth cervical to the third lumbar segment, thus corresponding with the sympathetic outflow from the cord as mapped out by Gaskell. But cells of a similar character and somewhat similarly placed occur both above (from first to fourth cervical) and below (lower sacral region) these points, although forming a less definite cell-column. In the third and fourth sacral segments they are perhaps related to the pelvic autonomic outflow. There are also cells in the adjacent part of the formatio reticularis which appear to belong to this system, and the two sets of cells have hence been distinguished by Bruce as cells of the lateral horn (apical cells) and cells of the reticularis (reticular cells). It is not, however, shown that they are of a different nature from one another. The cells of the system are in many parts very numerous, becoming especially so about the third thoracic segment. The vascular supply of the cell-column is independent of that to the motor cells of the ventral horn.

Cells of the middle part of the crescent.—There are a large number of cells scattered in the grey matter of the middle part of the crescent which are not collected into definite groups. They are most numerous in the enlargements, especially the cervical, and least numerous in the thoracic part of the cord. They contain little chromatic substance, and hence have a pale aspect as compared with the cells of the ventral horn and of the lateral cell-column, in specimens stained by Nissl's method. In the thoracic region they are most numerous near Clarke's column. They are distinguishable right into the sacral region.

Besides these scattered cells, there is a special group of moderate-sized cells which is found throughout the greater part of the cord, about the middle of the crescent, and is termed the **intermediate** or **middle nucleus** (fig. 115, B). Its cells have long dendrons, some of which run parallel with and are interlaced with collaterals from the fibres of the dorsal column. A few of these cells send their axons to the opposite side by way of the ventral commissure, but the majority are directed towards the lateral column, giving off a collateral or two on their way, and these bifurcate and become longitudinally running fibres in the region of that column which is nearest to the grey matter (Cajal).

[1] For experimental evidence, see Biedl, Wien. Klin. Woch. 1895; H. K. Anderson, Journ. Phys. xxviii. 1902; Scaffidi, Boll. accad. med. di Roma, 1902; P. T. Herring, Journ. Phys. xxix. 1903.

[2] Trans. Roy. Soc. Edin. xlv. 1906; also Bruce and M. Campbell, Rev. of Neurol. 1904.

Cells of dorsal horn.—The cells of the dorsal horn are mostly smaller than those of the ventral horn, and are not all distributed into definite groups. For purposes of description they may be arranged into—(1) those of the middle of the horn; (2) those of the base of the horn; (3) those of the gelatinous substance of Rolando; (4) those of Clarke's column; (5) those of the reticular formation; (6) those of the caput cornu; and (7) those of the grey commissure. They vary in size, the largest being found in Clarke's column and near the mesial margin of the horn: these last often have a characteristic long curved process (comet-cell, Waldeyer); even within the same group both large and small cells may be found intermixed.

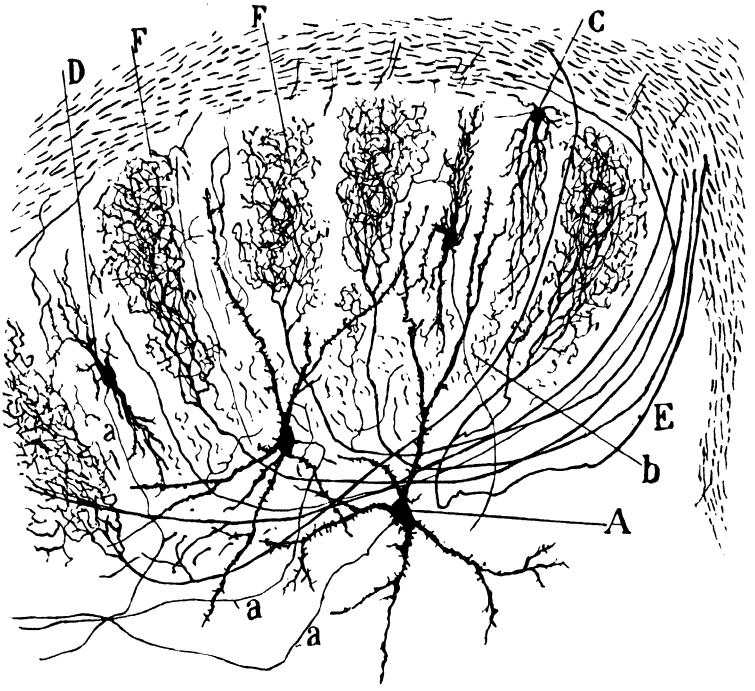


FIG. 113.—PART OF A SECTION ACROSS THE CERVICAL CORD OF A NEW-BORN KITTEN. Golgi method. (Cajal.)

A, large cells of the apex of the dorsal horn sending their axons, *a*, *a*, into the lateral column; *b*, longitudinal fibres arborising at the apex of the horn, cut across or obliquely; C, D, cells of the substance of Rolando; E, collateral fibres coming from the dorsal white column, sweeping round the substance of Rolando, and turning dorsalwards to arborise around its cells; F, their terminal arborisations.

(1) **Cells of the middle of the horn.**—These are scattered through its thickness. They vary much in form and size, but are mostly stellate or spindle-shaped. They are sometimes spoken of as the *solitary cells*. The axis-cylinder processes from these cells pass towards the ventral horn and commissure.

(2) **Cells of the base of the horn.**—These are especially numerous at its lateral aspect (in the cervical region near the *formatio reticularis*). This part of the grey matter is characterised by receiving numerous collaterals from the fibres of the pyramid tract, which here pass into the base of the dorsal horn, and some of which, in the thoracic region, traverse its thickness to enter Clarke's column on its mesial aspect. These cells belong partly to type ii. of Golgi, their short axons ending in the adjoining grey matter of the lateral and anterior horns; others

belong to type i., their axons entering the lateral column; but some pass to the ventral commissure.

(3) **Cells of the substance of Rolando.**—These are for the most part small and provided with many dendrons, which extend in a direction vertical to the surface[1] (figs. 113, 114). They are separated into groups by the passage of collaterals from the dorsal root-fibres. The destination of their axons is chiefly to the lateral column close to the dorsal horn (bundle of the dorsal horn, Cajal). Cells of considerable size lie tangentially at the margin of the substantia gelatinosa. These *marginal cells* also send their axons into the bundle of the posterior horn (fig. 114, F, G). On reaching this column the axons usually divide, one branch passing upwards, the other downwards. A few axons pass into the

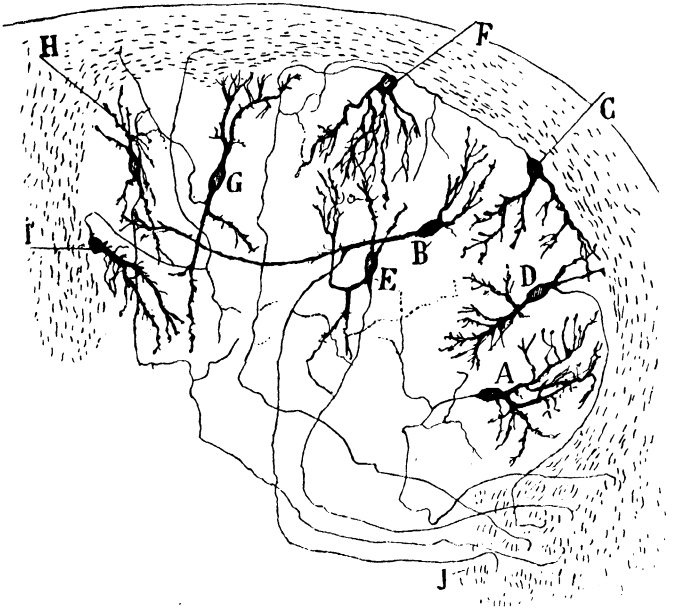


FIG. 114. — CELLS OF THE SUBSTANCE OF ROLANDO FROM THE SPINAL CORD OF THE CHICK ON THE NINETEENTH DAY OF INCUBATION. Golgi method. (Cajal.)

A, D, E, H, cells sending their axons into a bundle at the dorsal part of the lateral column; C, F, cells at the boundary of the gelatinous substance with axons passing at first tangentially to it, and then through it into the same bundle; B, transversely placed cell; G, I, cells sending their axons into the dorsal white columns.

marginal bundle of Lissauer, which lies between the substantia gelatinosa and the surface of the cord. The axons of the marginal cells frequently come off from one of the larger dendrons.

The substantia gelatinosa is traversed radially by numerous bundles of fine fibres passing from Lissauer's funiculus to the caput cornu dorsalis.

(4) **Clarke's cell-column.**—This is a very well marked group or column of large cells, which occupies in transverse section an area at the inner or mesial angle of the base of the dorsal horn (fig. 112, T6, T12), and appears cut off from the rest of the grey matter by a curved bundle of fibres derived from the dorsal column; it extends along the middle region of the cord from about the first lumbar below to the first thoracic nerve above (Bruce). The column in question was described by Lockhart Clarke[2] under the name of *posterior*

[1] Gierke, Arch. f. mikr. Anat. xxvi.

[2] Phil. Trans. 1851.

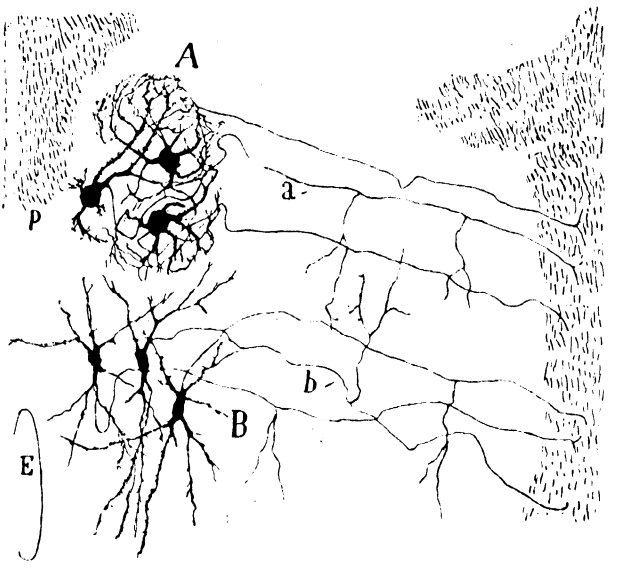


FIG. 115. — CELLS OF CLARKE'S COLUMN (A) AND OF THE MIDDLE OR INTERMEDIATE NUCLEUS (B) OF THE SPINAL CORD OF THE NEW-BORN MOUSE. Golgi method. (Cajal.)

E, central canal; *p*, dorsal column; *a*, axons of Clarke's cells passing to lateral column; *b*, axons of middle nucleus cells passing to lateral column. Both these sets of axons give collaterals to the grey matter, and bifurcate on reaching the white substance.

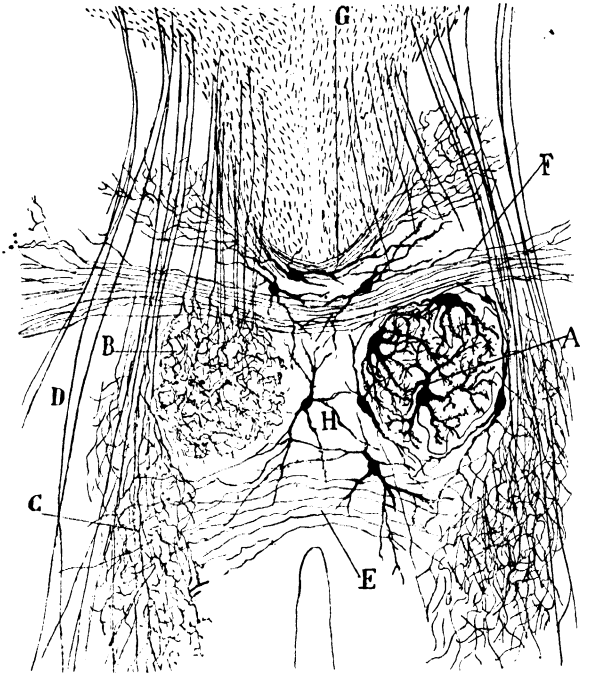


FIG. 116.—PART OF A SECTION ACROSS THE THORACIC CORD OF A NEW-BORN PUP. Golgi method. (Cajal.)

A, Clarke's column showing its cells; B, Clarke's column of the opposite side showing the collaterals from the mesio-dorsal column forming an arborisation within it; C, collaterals from the dorsal column arborising within the intermediate nucleus; D, longer collaterals passing to the ventral horn; E, anterior or ventral commissure; F, posterior or dorsal commissure; G, another part of the dorsal commissure close to dorsal median fissure; H, cells of the dorsal-commissure nucleus.

vesicular column, but it was first noticed by Stilling. It is best developed in the lower part of the thoracic region. From the fact that it is almost entirely confined to the thoracic region of the cord it was termed by Stilling the 'dorsal nucleus.' But, although ceasing above and below the points mentioned, it is not altogether unrepresented in other parts, for groups of cells are found in a similar situation opposite the origin of the second and third sacral nerves ('sacral nucleus' of Stilling) and opposite the origin of the third and fourth cervical nerves ('cervical nucleus'); and elsewhere there are scattered cells of the same character in the same part of the section of the cord. The cells of these 'cervical' and 'sacral' nuclei are, however, of a different type from those of Clarke's column, and their axons pass in various directions (dorsal and lateral columns, and ventral commissure). The cells of Clarke's column, like all the cells of the spinal cord, are multipolar. Their axis-cylinder processes tend towards the lateral column, where they are commonly stated to pass into the dorsal spino-cerebellar bundle of Flechsig. But there is reason to believe that in the first instance they take the direction of the part of the lateral column where Gowers' bundle is situated (see below). In their course through the grey matter they emit a few collaterals. The cells of Clarke's column are surrounded by a fine plexus of nerve-fibrils, derived from collaterals of the dorsal-column fibres, and the area also receives collaterals from the lateral pyramid-tract. The nucleus is marked off from the rest of the grey matter by encircling fibres, and the dendrons of the cells are confined within the area of the nucleus thus circumscribed (figs. 115, 116). They are furnished with spinous projections, and their ramifications form an intricate interlacement with the terminal ramifications of the collaterals which enter the nucleus from the dorsal column. The cells are mostly of large size, measuring, according to Mott, in their longest diameter, which is directed longitudinally, from 40 μ to 109 μ, the largest being found in the lowermost part of the column. In the fœtus, and even in the new-born child, the cells of Clarke's column are much smaller (25 μ to 30 μ), but by the second or third year after birth they have nearly attained the same size as in the adult. Besides the large cells, there are a certain number of somewhat smaller ones, lying at the periphery of the nucleus, against which they tend to be flattened (fig. 116). The dendrons of these smaller cells extend outside the nucleus into the neighbouring grey matter. Their axons pass partly towards the lateral column, partly towards the ventral commissure. They are termed by Cajal *limiting cells*, by Lenhossék *tangential cells*.[1]

After semi-section of the cord in the upper thoracic or in the cervical region, the large cells of Clarke's column undergo chromatolysis and eventually atrophy (Loewenthal); the same result follows section of the dorsal part of the lateral column alone, but in this case some of the large cells appear to remain unaffected. On this ground it has been conjectured that some of the fibres of Gowers' bundle may also come from the cells of Clarke's column.[2] Further, if a lesion be made (in the thoracic region) of the ventro-lateral column alone, degenerated fibres are at first seen (above the lesion) in the bundle of Gowers only; but in sections a few segments higher many are found in Flechsig's bundle as well, having evidently shifted posteriorly in ascending the cord.[3] In all probability, therefore, the fibres of both the spino-cerebellar tracts have a common origin—whether from Clarke's column or not is uncertain—and the separation of the tracts only takes place at the uppermost part of the cord.

In spite of the very marked and permanent atrophy of the cells of Clarke's column which follows section of the cervical region of the cord, there is no secondary degeneration of any long ascending fibres below the level of the section such as might perhaps be expected to occur as

[1] See, on Clarke's column, Mott, Journ. Anat. and Phys. 1888, and Brain, 1890; Lenhossék, Arch. f. mikr. Anat. xxxiii. 1889; Loewenthal, Recueil zool. Suisse, 1886; also the text-books of Kölliker, Van Gehuchten, and Cajal.

[2] Schäfer, Proc. Phys. Soc. Journ. Phys. xxiv. 1899.

[3] Schäfer and N. Bruce, Proc. Phys. Soc. Journ. Phys. xxxv. 1907. Barbacci (Riv. sper. d. fren. 1891, p. 34) describes a case in man of a lesion involving the lumbar enlargement, in which degenerated fibres were found in the situation of Gowers' bundle immediately above the lesion, and higher up passed into Flechsig's bundle.

the result of the atrophy of the cell-bodies. And a second semi-section in the thoracic region is followed by just as complete an ascending degeneration of the ascending tracts between the levels of the second and the first lesion as if no previous lesion had been established.[1] This observation tends to cast doubt upon the opinion that the origin of the cerebellar-tract fibres is from Clarke's column, which has usually been accepted as the nucleus of origin of at any rate the fibres of Flechsig's bundle.[2] Moreover, Loewenthal has shown that the atrophy of the cells of Clarke's column which results from injury to the lateral column of the cord is not proportionate to the injury of the dorsal spino-cerebellar tract.[3] (See also p. 97.)

The column of Clarke exhibits considerable variability in the number of its cells at adjacent levels, parts which are rich in cells alternating with other parts in which few or no cells may be present.

(5) **Cells of the reticular formation of the cord (interstitial nucleus** of Cajal).—These, best marked in the cervical region, are large and stellate, and their strong dendrons penetrate for some distance into the neighbouring white and grey matter. Their axons pass in various directions (ventral commissure, dorsal commissure, lateral column). These cells have been described as outlying or dislocated cells, since they are more or less enclosed, not by grey matter, but by the white columns. Such outlying cells may occasionally occur in other situations than in the reticular formation.[4]

(6) **Cells of the caput cornu.**—Near the apex of the dorsal horn, but ventral to the substance of Rolando, large stellate cells occur (fig. 113, A). Their long and spinous dendrons pass for the most part into the gelatinous substance of Rolando, but some extend towards the grey commissure and others into the ventral part of the dorsal horn. Their axons mostly tend in the direction of the lateral column, in which they join a bundle of fibres which lies close to the grey matter, between it and the pyramid-tract, and which is termed by Cajal the bundle of the dorsal horn (see p. 83). A certain number pass across to the other side in the ventral commissure. These cells of the apex of the dorsal horn lie in the path of the large collaterals which are passing from the dorsal column to the gelatinous substance.

(7) **Nucleus of the grey commissure.**—Certain cells which lie in this commissure (fig. 116, H), and which are of medium and small size, are described under this name. They are most numerous in the cervical and lumbar enlargements. Their axons are difficult to trace, but appear to tend towards the lateral columns.

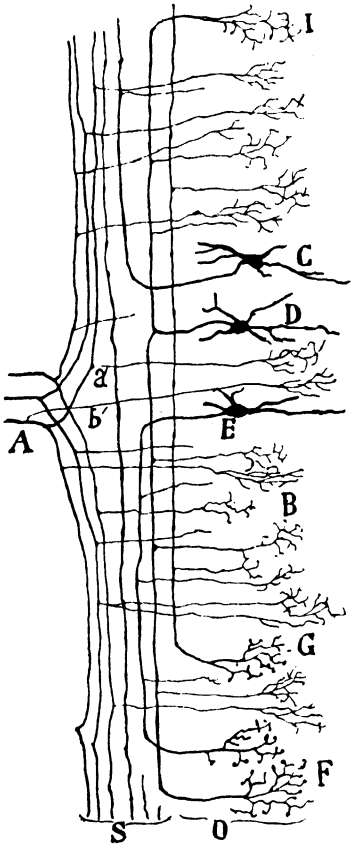


FIG. 117.—LONGITUDINAL SECTION OF THE SPINAL CORD OF CHICK-EMBRYO SHOWING THE BIFURCATION OF THE DORSAL ROOT-FIBRES AND THE PASSAGE OF THEIR COLLATERALS INTO THE GREY MATTER; AS WELL AS THREE CELLS OF THE DORSAL HORN SENDING THEIR AXONS INTO THE DORSAL COLUMN. Golgi method. (Cajal.)

A, entering root-fibres; S, dorsal column; O, grey matter; C, D, cells of dorsal horn; *a*, *b*, collaterals entering grey matter; B, G, F, I, arborisations of collaterals in dorsal horn.

It will be seen from the above account that of the cells in the grey matter of the spinal cord some are root-cells, giving origin to the efferent fibres of the ventral roots (and in the upper part of the cord to those of the spinal part of the eleventh cerebral nerve); others give rise to the fibres of long ascending tracts, such as the spino-cerebellar tracts; while a third class of cells

[1] Sherrington and Laslett, Journ. Phys. xxix. 1903. [2] Mott, *op. cit.*
[3] Int. Monthly Journ. of Anat. and Phys. x. 1893.
[4] Sherrington, Phil. Trans. vol. clxxxi. 1890. In birds and reptiles, as was first shown by Gaskell (Proc. Physiol. Soc. Journ. Physiol. 1885, and *ibid.* x. 1888), segmental groups of nerve-cells are seen at regular intervals along the cord close to or projecting from the surface in the ventro-lateral region. It is suggested by Kölliker (Zeitsch. f. wiss. Zool. lxxi. 1902) that these represent the intermedio-lateral cells of the mammalian cord, giving origin to the pre-ganglionic fibres of the sympathetic.

give origin to fibres which pass into one or other of the white columns—usually bifurcating as they leave the grey matter—and, running a short or long distance upwards or downwards, again enter the grey matter at a different level. These form what have been termed the cells of the white columns, or the propriospinal cells, since they give origin to intrinsic or propriospinal fibres. In addition to these three kinds, there are also in the dorsal horn a certain number of cells the axons of which do not leave the grey matter, but break up into a terminal arborisation at no great distance from the cell-body (cells of Golgi's type ii.). According to Cajal, these are by no means so abundant in the grey matter of the cord as has hitherto been supposed, nearly all the cells which are not radicular sending their axons into the white matter. Those fibres which only pass a short distance up or down before again ending in the grey matter run in a *limiting layer* or *boundary-zone* next to the grey crescent, while those which extend farther along the cord lie more peripherally, and the more so the longer the distance they travel. Most of the axons which pass to the white columns of the cord run upwards or downwards (or bifurcate, the branches running upwards and downwards) on the same side, but a certain number of cells send their axons across to the white columns of the opposite side. The cells which send their axons to the white columns of the same side are termed by Van Gehuchten 'tautomere cells'; those which send their axons to the opposite side 'heteromere cells'; while a certain number, the axons of which bifurcate near the cell-body and send branches one to the same side and one to the opposite side, are distinguished as 'hecateromere cells.'

Commissures.—The *ventral* or *anterior commissure of the cord* (fig. 118, B, *a.c.*) consists of medullated nerve-fibres which pass on each side, some into the ventral white column, others into the ventral horn of grey matter. Their course is not strictly transverse, many fibres which enter the ventral part of the commissure at one side leave it at the dorsal portion on the other side. There is thus an oblique decussation in the median plane (fig. 118). This decussation is most distinctly seen in the comparatively short and wide commissure of the lumbar region, and in the upper part of the cervical region. In the latter situation it appears as a continuation of the decussation of the pyramids of the medulla oblongata, to be afterwards described. In addition to the transverse fibres there are a few longitudinal bundles of fibres in the region of this commissure. Its fibres are often somewhat displaced by vessels which pass into the grey substance from the ventral fissure.

The *dorsal* or *posterior commissure of the cord* also contains medullated fibres running transversely or with a slight obliquity: they are collected mainly on the dorsal and ventral aspects of the substantia gelatinosa centralis. There are also nerve-cells in the commissure (see previous page), and amongst them some of the fibres appear to end, but most pass through. In this commissure is contained the central canal of the spinal cord surrounded by an area free from medullated nerve-fibres, and occupied by a substance which, like the superficial neuroglia and the substance of Rolando, has in the hardened condition a reticulated structure and in the fresh state a gelatinous aspect. This is the substantia gelatinosa centralis (p. 74). There is in most regions rather more of the commissure dorsal to the central canal than ventral. The fibres of the dorsal part curve backwards on reaching the crescents of grey matter and pass towards the bundles of the dorsal roots, whereas the rest diverge at various angles into the crescent.

The **central canal** is lined with a layer of ciliated epithelium (fig. 118, A, A'). Each cell is provided with a bunch of cilia on the side which is turned towards the lumen of the canal; the other end of the cell is prolonged into the reticular substance just mentioned, and there becomes lost to view.

In the adult human subject the lumen of the central canal is commonly obliterated, being filled with detached cells.[1]

Origin of the spinal nerves.—The roots of the spinal nerves are attached along the sides of the cord, opposite to the corresponding horns of the grey matter; the dorsal roots entering along a straight line at the dorso-lateral groove, and the ventral roots being scattered somewhat irregularly upon the surface (fig. 98, B). Ingbert[2] finds that about 653,000 dorsal root-fibres enter each side of the cord in man, and that rather more than 200,000 ventral root-fibres emerge. The numbers given by Stilling[3] are about 504,000 and 303,000 respectively. Both dorsal and ventral root-fibres increase in number with age in the rat.[4]

The **ventral** or **anterior roots** are seen in section to pass through the white substance, leaving the horn in several bundles which have a slight

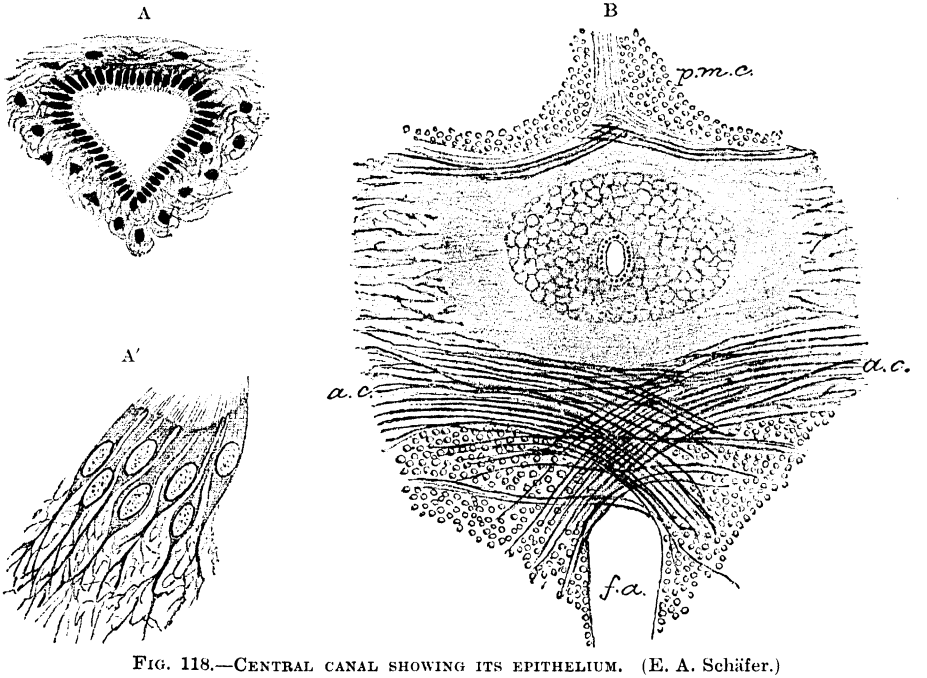


FIG. 118.—CENTRAL CANAL SHOWING ITS EPITHELIUM. (E. A. Schäfer.)

A, from a child of six. Magnified 150 diameters. A', some of the ciliated cells, highly magnified. B, section of the isthmus from the lumbar cord of an adult (æt. 33), showing the central canal in the middle surrounded by the substantia gelatinosa centralis. *f.a.*, anterior median fissure; *p.m.c.*, posterior white column; *a.c.*, anterior white commissure. Magnified 30 diameters.

inclination so as to be often cut obliquely if the section is exactly in a transverse plane. As the bundles leave the grey matter their fibres converge, some from the mesial, others from the lateral, and others from the dorsal part of the horn. Of those which pass from the mesial part, some are continued from the axis-cylinder processes of the mesial groups of cells of the ventral horn, and others from the other side of the cord through the ventral commissure, there perhaps being connected with corresponding cells. Those fibres of the root which take origin in the lateral part of the ventral horn are connected with the cells of its lateral groups, and with those of the intermediate cell-column.

[1] See on the central canal, Biach, Arb. a. d. neurol. Instit. Wien, 1907.
[2] Journ. Comp. Neurol. xiii. 1903 and 1904.
[3] *Loc. cit.* For the relative size of the nerve-fibres in different regions, see Gaskell, Journ. Physiol. vii. 1886, and Siemerling, Anat. Unters. ii. d. menschl. Rückenmarkswurzeln, 1887.
[4] Donaldson, Proc. Soc. of Neurol. of Chicago, 1901; Hatai, Journ. Comp. Neurol. 1903.

The middle fibres are connected with the more deeply lying cells of the ventral horn, but some can be traced from the dorsal horn, where they doubtless take origin from some of the cells there present.

In the cervical region of the cord, from the sixth nerve upwards, the root-fibres of the spinal part of the accessory nerve may also be seen passing from the ventral horn at first dorsally and then obliquely outwards through the lateral column. They arise from a group of somewhat large cells (fig. 112, *acc.*), which in the uppermost region lies in the lateral part of the horn, close to its ventral edge, but in the middle and lower cervical regions tends gradually to occupy a position nearer the base of the horn. This group of cells is the continuation downwards of the accessory nucleus which will be seen in the lower part of the medulla oblongata.

The fibres of the **dorsal** or **posterior roots** take origin in the cells of the spinal ganglia. These cells are not all of the same type, for, whereas some have large Nissl granules, others are almost free from chromatic substance, and yet others, chiefly of a small size, have an obscurely granular appearance. There is a marked difference in size in these cells, some, both clear and obscure, being comparatively small, others relatively large (see fig. 37, p. 30). Probably these differences are related to the distribution and functions of the fibres emanating from the cells; but what the correlation exactly may be is not known, although it may probably be assumed that the larger the cell the larger the diameter of the nerve-fibre arising from it. According to Warrington and Griffith [1] the largest cells occur in those spinal ganglia which supply sensory nerves to the limbs, and they suppose that the especially large cells there found give origin to the sensory fibres of the limb-muscles. Warrington states that cells under 26 μ in diameter are immature, and lack a fully developed axon. Dislocated cells are sometimes found in the dorsal roots at a distance from the ganglion.

According to the observations of Donaldson and Hatai upon the rat—which are confirmatory of previous observations on the frog and rabbit—the number of cells always exceeds that of the fibres in the corresponding posterior root.[2] This discrepancy is far greater in new-born animals, and tends gradually to diminish as age advances, but does not disappear. The number of cells remains about the same, but the number of fibres is more than doubled if an animal a few days old be compared with one at maturity. But although the actual number of cells in a ganglion remains the same during the period of growth, there is in the young animal a larger proportion of cells of the small type; as growth advances and more fibres become formed, this proportion is diminished. Doubtless, therefore, the new fibres are produced from the originally small cells, which increase in size with the growth from them of these fibres. As a matter of fact Donaldson and Hatai found the number of fibres in a cervical posterior root to be about equal to the number of *large* cells in the corresponding ganglion, but in the thoracic and lumbar region there were nearly twice as many large cells as fibres. And besides these there was in all the ganglia a considerable surplus of small cells.

The dorsal root-bundles are constricted at their entrance into the cord. They appear to separate into two sets. Of these, the lateral, which is small and contains mostly small fibres (?collaterals), enters opposite the tip of the horn. It is usually stated to join a bundle of fine longitudinal fibres which lies between the tip of the dorsal horn and the periphery of the cord. This bundle is known as the *marginal bundle* (Lissauer). Its fibres are evidently different from most of those which enter with the dorsal root; they acquire their medullary sheath considerably later (Bechterew), and according to Nageotti [3] they degenerate late in tabes. The supposition that they are radicular in origin may therefore be incorrect. But in position and appearance the bundle in question is very similar to the conspicuous bundle which is seen in the upper cervical cord and medulla oblongata lying lateral to the substantia gelatinosa of Rolando, and forming the descending root of the fifth cerebral nerve. The mesial set containing the larger

[1] Brain, 1904.

[2] Hatai, *loc. cit.*; Dunn, Journ. Comp. Neurol. 1900, and Hardesty, *ibid.* 1905 (frog); Lewin, Centr. f. Physiol. x. 1896 (rabbit).

[3] Nouv. Iconogr. d. l. Salpêtrière, xvii. 1904.

and some smaller fibres of the dorsal root passes into the latero-dorsal white column, with the longitudinal fibres of which its fibres become continuous; from this column many of them sweep with bold curves into the adjacent grey matter. At their attachment to the cord the direction of the dorsal roots, like that of the bundles of fibres of the ventral roots, is in most regions of the cord obliquely downwards towards the intervertebral foramina.

It was shown by Cajal that the fibres of the dorsal roots as they enter the cord join by a Y- or T-shaped junction with longitudinal fibres of the dorsal column; in other words, they bifurcate as they enter the cord into two principal branches which run upwards and downwards in the dorsal white column or in the adjacent part of the dorsal cornu (fig. 117). It has also been shown that both from the root-fibre before its bifurcation and from its ascending and descending stems there are

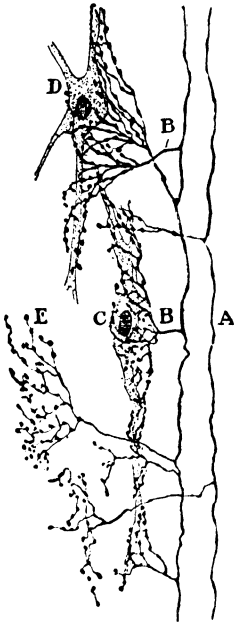


FIG. 119.—FIBRES OF DORSAL ROOTS PASSING UP DORSAL COLUMN (A) AND SENDING COLLATERALS (B) TO ARBORISE AROUND CELLS IN THE GREY MATTER OF THE CORD (C, D, E). (Cajal.)

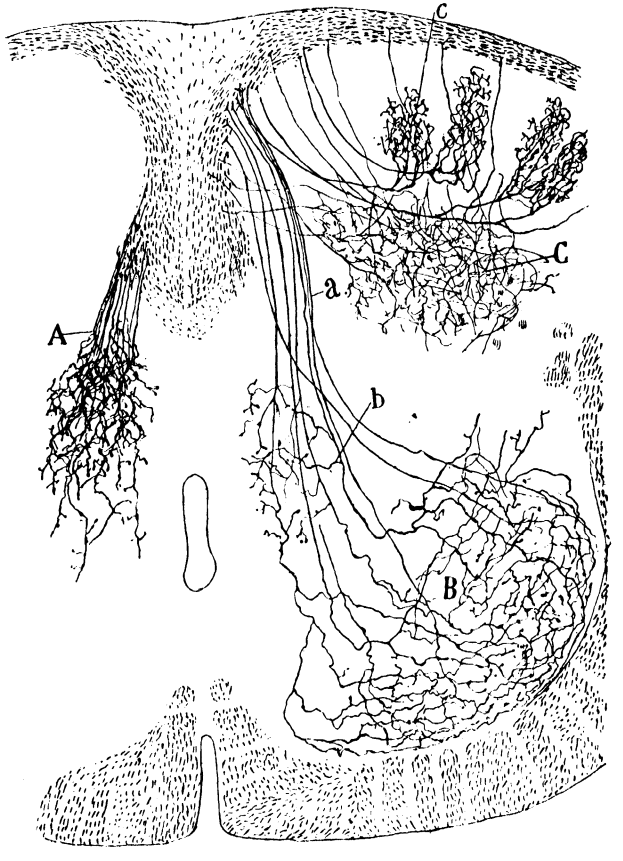


FIG. 120.—CHIEF COLLATERALS OF THE DORSAL-COLUMN FIBRES: NEW-BORN MOUSE. Golgi method. (Cajal.)

A, collaterals to the intermediate nucleus; B, to the ventral horn; *a*, main branches; *b*, side collaterals to the intermediate nucleus; C, to the apex of the dorsal horn; *c*, to the substance of Rolando.

given off at intervals, but most abundantly near the segment of entry, collaterals which are directed inwards towards the grey matter, into which they penetrate for a variable distance and within which they end by breaking up into a ramification of fibrils which may frequently be seen to have a close relationship to cells of the grey matter (fig. 119). In this way collaterals are

given off from the dorsal root-fibres and from their longitudinal extensions, some of which, the so-called 'reflex collaterals,' penetrate as far as the ventral horn of the same side (fig. 120, B); others pass through the dorsal commissure into the grey matter of the opposite side, others towards the lateral horn and intermediate cell-column, while others again pass into Clarke's column, into the intermediate nucleus, and into the substance of Rolando (fig. 120). Collateral fibres also enter the grey matter in large numbers from the dorsal columns, most of the fibres of which are prolongations of dorsal roots which have entered the cord lower down. But the collaterals are by no means confined to the fibres of the dorsal columns, for from all the longitudinal white columns of the cord the same convergence of fibres into the grey matter can be seen (see fig. 124).

Course of nerve-fibres within the spinal cord: conducting tracts. —It is impossible mechanically to unravel the tracts of nerve-fibres in their passage along the spinal cord, and it is difficult to trace the same fibre or fibres for any distance in microscopical sections of the normal adult organ. But the task of following out the course of certain sets of fibres has been much facilitated of late years by the application to the subject of two special methods. These methods have been already described (pp. 53, 54), in connexion with the more general question of nerve-structure, but their special applicability to the spinal cord may be here alluded to. Thus it is found that if the development of the spinal cord is carefully observed, the medullary substance of the nerve-fibres is formed later along some tracts of the white columns than in the rest of the white matter, appearing first in certain parts, and being longer delayed in others, so that in transverse sections of the cord these non-medullated tracts are easily distinguishable by their more transparent grey appearance and by their different behaviour with staining fluids (method of Flechsig).

The following statements regarding the time of myelination of the nerve-fibres and tracts of the cord are mainly founded on the observations of Flechsig[1] and of Trepinski[2]: (1) Ventral roots during fifth month; dorsal roots a little earlier, but finish considerably later. (2) Limiting layer (next to the grey matter in lateral column) during sixth month. (3) Dorsal columns, fifth to seventh month. (4) Ventro-lateral part of lateral column and adjacent part of ventral column, fifth to seventh month. (5) Dorsal spino-cerebellar tract, seventh month. (6) Ventral spino-cerebellar tract, seventh to eighth month. (7) Olivo-spinal tract, ninth month. (8) Pyramid tracts, at or soon after birth. The dorsal roots and dorsal columns (including Lissauer's bundle) myelinate at five different periods; this is doubtless an indication of differences of function.

The other method consists in tracing the course which the degeneration of the fibres pursues in consequence of a lesion either in the encephalon, or in the spinal cord itself, or even in the peripheral nerves; the lesions being produced by accidental injury, by pathological changes, or experimentally in animals. The changes which follow are either the result of the Wallerian law that separation of a nerve-fibre from the nerve-cell with which it is connected and from which it has grown out is followed by degeneration in the part of the fibre thus separated (*Wallerian degeneration*), or they may result from the prolonged disuse of a nervous tract, especially in young animals, as when a limb has been removed or from some other cause (*Gudden's atrophy*). The place of the degenerated nervous substance is ultimately taken by a non-nervous fibrillar tissue, which, by its difference of behaviour to staining fluids, can easily be distinguished from the surrounding undegenerated white substance (*sclerosed tract*). Further, after section of nerves or nerve-tracts

[1] Neurol. Centralbl. ix. 1890. [2] Arch. f. Psych. xxx. 1897.

groups of nerve-cells are affected by the degenerative processes (Nissl), and the cells may in new-born or young animals—or even in the adult—eventually disappear altogether.

Thus, in a rabbit in which immediately after birth the sciatic trunk is resected, when the animal is full-grown the corresponding ventral-horn cells are found to have become atrophied, and similar results are obtained with motor nerves generally, both spinal and cerebral (Gudden, Forel, Ganser, Mayser). Similarly, after section of the thoracic or cervical cord, the cells of Clarke's column undergo atrophy below the section; and after section of the pyramid tract, some of the giant-cells in the cerebral motor cortex become degenerated and disappear. As a result of the cell-atrophy the central part of the cut nerve-fibres sometimes undergoes secondary Wallerian degeneration (Van Gehuchten).

Tracts of the ventro-lateral column (see figs. 105, 121, 122).—Several tracts can be traced in the ventro-lateral column, not only along a great part of the spinal cord, but into or from certain parts of the encephalon. The long tracts in this column are (*a*) **descending,** the *direct* and *crossed pyramid* (or *pyramidal*) *tracts*, the *ponto-spinal* and *tecto-spinal*, the *rubro-spinal* or *prepyramidal*, and the *bulbo-spinal* or *triangular*; and (*b*) **ascending,** the *dorsal spino-cerebellar*, the *ventral spino-cerebellar*, the *spino-thalamic*, and the *spino-tectal* (the last three form collectively the *bundle of Gowers*).

Descending tracts in the ventro-lateral column.—The *pyramid tract* (*tract of the pyramid*) is directly traceable down from the opposite pyramid of the medulla oblongata, and ultimately from the cerebral cortex (precentral and paracentral gyri). The greater number of the fibres which compose the pyramid cross at the upper limit of the spinal cord, down which they pass in the dorsal part of the lateral column as a compact bundle of fibres occupying in transverse section a somewhat triangular area, which lies in the angle between the dorsal horn and the outer surface of the cord (fig. 105; fig. 122, 1), but is in most parts separated from both by fibres belonging to other systems. This *crossed lateral pyramid-tract* can be traced as far as the third sacral segment, becoming gradually smaller below and approaching the surface of the cord. A few fibres of this tract are found scattered in other parts of the lateral column.

Some of the fibres of the pyramids of the medulla oblongata do not cross over at the upper limit of the cord. Most of these pass down close to the anterior median fissure, forming the *uncrossed ventral* or *direct pyramid-tract* (fig. 122, 2) (*bundle of Türck*), which gradually diminishes as it is traced downwards, and usually ceases altogether at about the middle of the thoracic region of the cord, but descending fibres have been seen in this situation extending to as low as the fourth sacral nerve.[1] It is probable that the decussation of these ventral pyramid-tracts goes on along their whole course, their fibres passing through the ventral commissure and through the grey matter of the opposite side to reach the lateral pyramid-tract on the other side of the cord. Other non-crossed fibres pass to the lateral column of the same side, where they are mingled with the fibres which have crossed from the opposite pyramid of the medulla oblongata. They constitute the *uncrossed lateral pyramid-tract.* This tract, said to have been first noticed in man by Westphal,[2] and subsequently recognised in the dog and ape,[3] is of constant occurrence in the higher mammals

[1] Dejerine and Thomas, Comptes rendus de la soc. de biol. Feb. 8, 1896.
[2] Mentioned, but without reference, by A. W. Campbell, Brain, 1907.
[3] Pitres, Bull. Soc. de physiol. de Bordeaux, 1880 (dog), and Arch. de Physiol. 1884 (man); Schäfer, Journ. Physiol. iv. p. 324, 1883 (monkey).

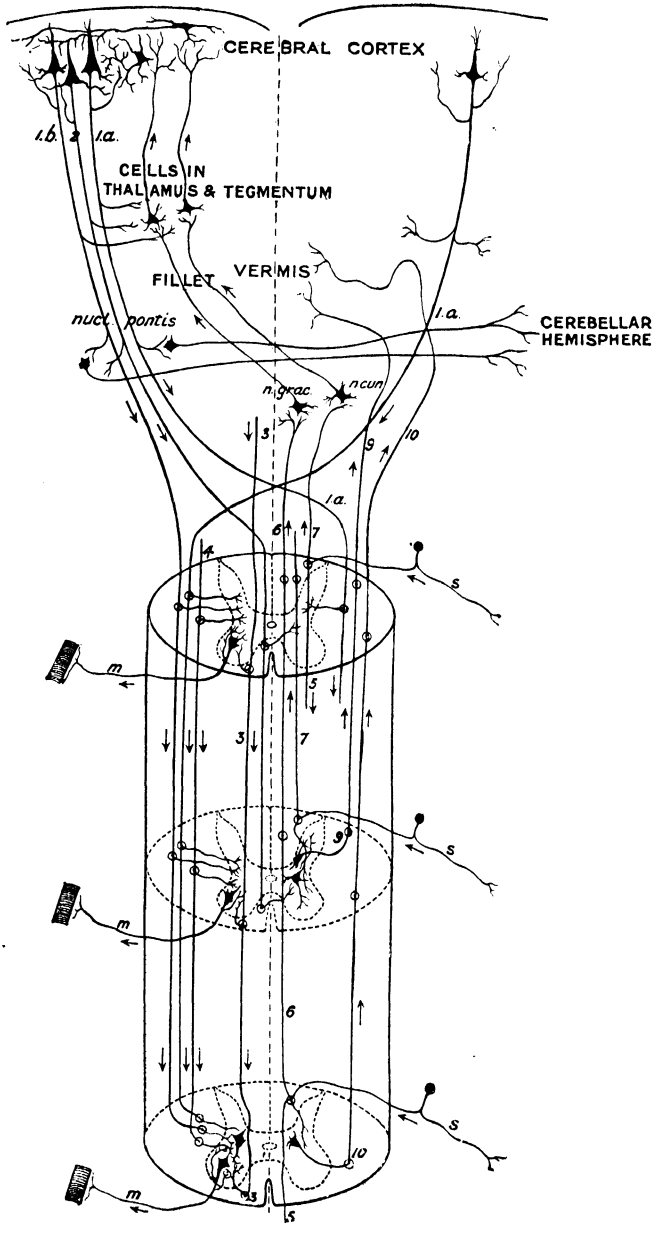


FIG. 121.—DIAGRAM SHOWING THE COURSE, ORIGIN, AND TERMINATION OF THE FIBRES OF THE PRINCIPAL TRACTS OF THE WHITE MATTER OF THE SPINAL CORD. (The numbers in this diagram refer to fibres of the tracts shown with corresponding numbers in fig. 122.)

Descending' tracts: 1*a*, a fibre of the crossed pyramid or cortico-spinal tract; 1*b*, an uncrossed fibre of the pyramid or cortico-spinal tract passing to the lateral column of the same side; 2, a fibre of the ventral pyramid or cortico-spinal tract; 3, a fibre of the ventro-lateral descending or ponto-spinal tract; 4, a fibre of the rubro-spinal tract; 5, a fibre of the comma tract. 'Ascending' tracts: 6, a fibre of the dorso-mesial spino-bulbar tract; 7, fibres of the dorso-lateral spino-bulbar tract; 9, one belonging to the dorsal spino-cerebellar; 10, a fibre of the ventral spino-cerebellar tract.

in which a lateral pyramid-tract exists.[1] Like the fibres of the crossed tract, it sends collaterals and terminals to the grey matter at the base of the posterior horn. It is well shown by the degeneration which follows all unilateral lesions of the motor area of the cerebral cortex.[2] The fibres in the pyramid-tracts do not appear to be grouped according to their destination, but those destined to different parts are intermingled.

There is much variation in the development of the ventral pyramid-tracts in different individuals. In some the tracts are so well marked as to form a visible prominence on the surface of the cord close to the ventral median fissure and separated from the rest of the anterior column by a groove, the *anterior intermediate sulcus* of Rauber. In others they are quite small, or may even fail altogether. In this case it may be assumed that the decussation of the pyramids, which is known to be subject to considerable variation, has been more complete than usual. In other instances, again, the ventral pyramid-tracts may be unsymmetrical, being more developed on one side than on the other, or the tract on one side may be wholly undeveloped. The direct tract is said to be wanting in 15 per cent. of cases in man. In different animals there is also much variation in the position and size of the pyramid-tracts.[3] A well-marked direct pyramid-tract appears to be absent in most animals, even in monkeys, although it is present in the anthropoid apes. In some (mouse, rat, guinea-pig, squirrel, sheep, kangaroo) the whole pyramid-tract runs in the posterior column, but in most animals (rabbit, cat, dog, monkey) it lies in the lateral column.

The fibres of the lateral pyramid-tract are connected with the grey matter by collateral fibres, which ramify in the formatio reticularis[4] and in the base of the posterior horn, some even penetrating to Clarke's column.[5] It is stated that there are about 160,000 fibres in the pyramid-tracts in the upper cervical region.

The pyramid-tracts are undoubtedly paths by which voluntary impulses, both motor and inhibitory, pass from the brain to the various spinal segments, although probably not the only paths for such impulses. All the fibres within the area embraced by the 'tract' do not, however, belong to the same system, although fibres of the one function predominate; and this is probably correct of all the so-called 'tracts' of conduction.

The other descending tracts in the ventro-lateral column are (1) the composite bundle of Loewenthal; (2) the rubro-spinal; and (3) the bulbo-spinal. The 'anterior marginal bundle' of Loewenthal[6] (fig. 122, 3) consists of fibres which undergo degeneration downwards and form an extensive circumferential tract in the ventral part of the ventro-lateral column. The tract involves (in the monkey and dog) a part of the ventral column which in man is occupied by the direct pyramid-tract, and also a part of the region of the bundle of Gowers, the fibres of these tracts being intermingled. Its nerve-fibres are continuous (1) with those of the *dorsal longitudinal bundle* (*vestibulo-spinal tract*) of the medulla oblongata. These are mainly derived from the nucleus of Deiters of both the same and the opposite side, but partly from scattered cells of the reticular formation of the medulla oblongata and pons, and perhaps also

[1] Langley and Sherrington, Journ. Physiol. v. 1884; Sherrington, Journ. Physiol. vi. 1885, and Brit. Med. Journ. 1890; Russell, Brain, 1895; Mellus, Proc. Roy. Soc. 1894 and 1895.

[2] Sutherland Simpson, Int. Monthly Journ. of Anat. and Phys. 1902; Sutherland Simpson and Jolly, Proc. Roy. Soc. Ed. 1907.

[3] For variations in the pyramid-tracts in man, see Obersteiner, Arb. a. d. neurol. Institut, Wien, 1902; Marie and Guillain, Semaine méd. 1902; Ugolotti, Rivista di patol. nerv. 1903; Matthew and Waterston, Rev. of Neurol. 1903; M. and Mme Dejerine, Rev. neurol. 1904; Hatschek, Arb. a. d. neurol. Institut, Wien, 1904.

[4] Monakow, Arch. f. Psych. xxvii. 1895.

[5] Schäfer, Proc. Phys. Soc. Journ. Physiol. 1899; confirmed for man by Collier and Buzzard, Brain, xxvi. 1903.

[6] Rev. méd. de la Suisse rom. 1885 and 1886; Int. Monthly Journ. Anat. and Phys. x. 1893.

of the tegmentum. (2) With the *ventral longitudinal bundle* (*tecto-spinal tract*) of the pons and medulla oblongata. All these fibres send numerous terminals and collaterals to end among the cells of the ventral horn..

The *rubro-spinal tract* (*bundle of Monakow*,[1] *prepyramidal tract*) (fig. 122, 4) runs down the lateral column ventro-lateral to the crossed pyramid-tract, with which in some animals its fibres become intermingled. It forms in section a triangular patch of scattered fibres, the origin of which is chiefly in the mid-brain (red nucleus of tegmentum of opposite side [2]). Some are said to originate in the red nucleus of the same side.[3] Mingled with these rubro-spinal fibres are a few derived from the reticular formation of the brain-stem and from the corpora quadrigemina of the opposite side (tegmento-spinal and tecto-spinal fibres).[4] The fibres and collaterals of the rubro-spinal tract enter the dorsal part of the ventral horn (Fraser).

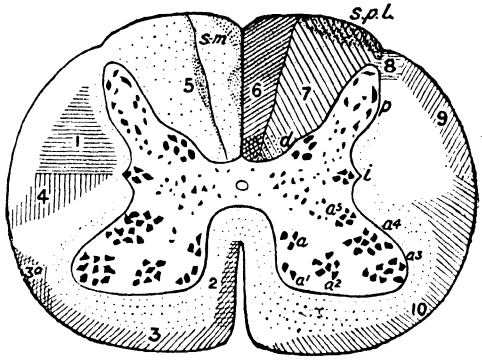


FIG. 122.—DIAGRAM SHOWING ON THE RIGHT SIDE THE 'ASCENDING' AND ON THE LEFT SIDE THE 'DESCENDING' TRACTS IN THE SPINAL CORD.

1, Crossed pyramidal; 2, direct pyramidal; 3, antero-lateral descending; 3*a*, bundle of Helweg; 4, pre-pyramidal; 5, comma; 6, postero-mesial; 7, postero-lateral; 8, marginal; 9, dorsal cerebellar; 10, antero-lateral ascending or ventral cerebellar; *s-m*, septo-marginal; *s.p.l.*, superficial postero-lateral fibres (dorsal root-zone of Flechsig); *a* to a^5, groups of cells in the anterior horn; *i*, intermedio-lateral group or cell-column in the lateral part of the grey matter; *p*, cells of posterior horn; *d*, dorsal nucleus or cell-column of Clarke. The dots represent 'endogenous' fibres (arising in grey matter of cord) having for the most part a short course.

Bulbo-spinal (*olivo-spinal*) *tract.*—Another descending tract of the antero-lateral column is the *bundle of Helweg* [5] (fig. 122, 3 *a*), the fibres of which form a small tract in the cervical region near the surface opposite the lateral angle of the anterior horn, and are traceable from the medulla oblongata dorsal to the olives. The situation of their cells of origin is uncertain, as is also their mode of termination in the cord.

Ascending tracts in the ventro-lateral column.—The *dorsal spino-cerebellar tract* (*direct cerebellar tract* of Flechsig) (fig. 122, 9) lies between the lateral pyramid-tract and the outer surface of the cord, occupying a somewhat narrow area of the transverse section, which in the upper regions of the cord reaches to the tip of the dorsal horn, but lower down becomes more limited, and is separated from the horn by the intervention of part of the adjoining pyramid-tract. It begins to appear at the lower thoracic region in man (between the second and third lumbar roots according to Bing), and is then seen in all sections of the cord and lower part of the bulb, passing eventually by the restiform body into the cerebellum (middle lobe, see fig. 123), some of the fibres decussating with fibres from the opposite side in the white substance of the vermis.

The axis-cylinder processes of the cells of Clarke's column are commonly stated to give origin to the fibres of the dorsal spino-cerebellar tract, but this is

[1] Arch. f. Psych. 1883 and 1890.

[2] Monakow, Monatschr. f. Psych. 1883 and 1891; Held, Neurol. Centralb. 1890; Thomas, Journ. de physiol. 1899; Probst, Zeitschr. f. Nervenheilk. 1899. Cf. also on this subject, Parhon, Névraxe, i. 1900; Pavlow, *ibid.* 1900; Rothmann, Neurol. Centralb. 1900, and Monatschr. f. Psych. 1901; Van Gehuchten, Névraxe, iii. 1901; E. H. Fraser, Journ. Phys. xxviii. 1902.

[3] Preisig. Journ. f. Psych. u. Neurol. 1904.

[4] Held, *loc. cit.* 1890; Boyce, Phil. Trans. 1894 and 1895; Lewandowsky, Unters. ü. d. Leitungsb. &c. 1904; Kohnstamm and Quensel, Neurol. Centr. 1908.

[5] Arch. f. Psychiatrie, xix. 1887; A. Bruce, Proc. Roy. Soc. Edin. xvii. See also Barker, Nervous System, 1899, pp. 954–958.

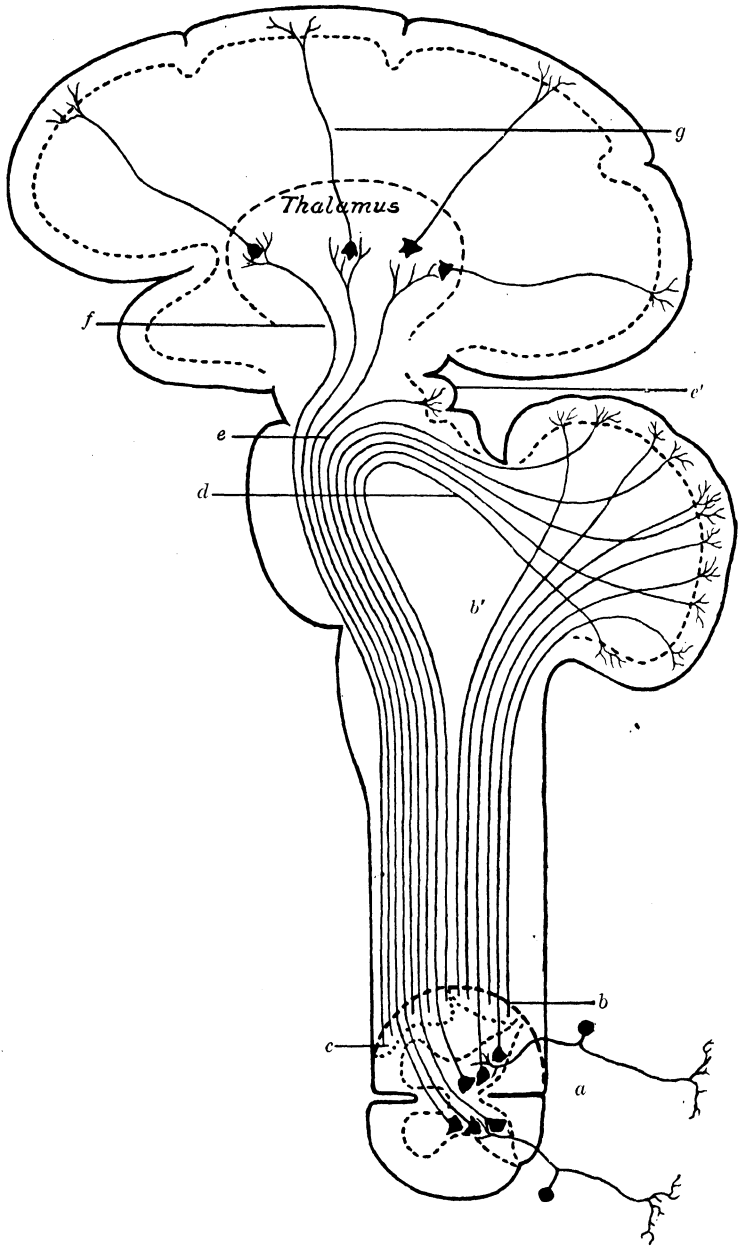


FIG. 123.—DIAGRAM SHOWING THE POSSIBLE COURSE OF THE ASCENDING FIBRES IN THE LATERAL COLUMNS OF THE SPINAL CORD AND THEIR CONTINUATIONS TO THE CEREBELLUM, CORPORA QUADRIGEMINA, THALAMUS, AND (BY OTHER NEURONES) TO THE CORTEX CEREBRI.[1] (E. A. Schäfer.)

a, dorsal root-fibres; *b*, bundle of Flechsig, passing at *b'* by the restiform body to the cerebellar vermis; *c*, bundle of Gowers; *d*, passage of most of its fibres along the superior peduncle to the cerebellum; *e*, fibres to the corpora quadrigemina, *e'*; *f*, others to the thalamus; *g*, fibres from thalamus to cerebral cortex.

[1] The origin of fibres of Gowers' bundle from cells of the opposite dorsal horn is not certain, but such crossing has been described (Grünbaum, Journ. Phys. xvi. 1894; Mott, Brain, xvii. 1895).

not certain (see p. 85). The fibres of this tract are of large size, and the tract is more compact and distinct than the ventral spino-cerebellar.

According to Sherrington and Laslett[1] the fibres of this tract which arise lower down in the cord lie nearer to the surface than those which have their cells of origin in the higher segments —an instance of a general principle which obtains—*for ascending tracts only*—viz. that the longer fibres run nearer the surface of the cord than the shorter ones. It would perhaps be more correct to state that there is a tendency for fibres of longer course belonging to the same system to be shifted dorsally.

The *ventral spino-cerebellar tract* (which is included in the *antero-lateral ascending bundle of Gowers*[2]) occupies a position in the sectional area of the lateral column which is anterior or ventral to the dorsal cerebellar tract, and it has in section an arched shape, curving from immediately in front of the crossed pyramid tract (where it is most strongly marked) round the superficial part of the lateral column in front of the dorsal cerebellar tract, and tailing off gradually between the issuing ventral roots to reach the ventral column. It begins to appear one or two segments lower than the bundle of Flechsig.[3] It can be traced upwards into the medulla oblongata and pons (fig. 123), and eventually enters the cerebellum by crossing over the superior peduncle and passing along this to the vermis.[4] A few of its fibres are said to pass by the middle peduncle of the cerebellum into the opposite hemisphere.[5] The dorsal and ventral spino-cerebellar tracts perhaps have a common origin, possibly from the cells of Clarke's column, but also from other cells in the grey matter of the same and perhaps of the opposite side (see p. 85). The fibres of this tract are intermingled with those of the ventro-lateral descending tract.

Spino-tectal and spino-thalamic fibres of Gowers' bundle.—The antero-lateral ascending tract of Gowers contains, intermingled with the spino-cerebellar fibres, a certain number of other fibres of smaller diameter which, in place of passing to the cerebellum, are continued up the pons and mid-brain, to end partly in the corpora quadrigemina and partly in the thalamus of the same side.[6]

Propriospinal or intrinsic fibres of the ventro-lateral column.—It has been shown that if a trans-section be made of the spinal cord (dog) and the animal be kept long enough for all trace of the resulting Wallerian degenerations to disappear, a subsequent section made below the level of the first section will be followed by descending degeneration of scattered fibres in this column. The fibres thus shown take origin in the cervical, thoracic, and upper lumbar regions, and are traceable down to the sacral region.[7]

Marie has described a tract of propriospinal fibres in man close to the anterior median fissure, scattered among the fibres of the direct pyramid tract. These fibres constitute the *ventral sulco-marginal tract* of Marie; but, according to Collier and Buzzard, they belong to the ventral longitudinal bundle.[8]

The remainder of the ventro-lateral column which is not comprised in specific tracts encircles the grey matter; it is termed the *ventro-lateral limiting layer*. It varies in sectional area with the size of the nerve-roots and of the grey matter, and many of its fibres not improbably are of a commissural nature,

[1] Journ. Phys. xxix. 1903.
[2] Neurol. Centralbl. 1886, and Lancet, 1886. Cf. Bastian, Med. Chir. Trans. 1867.
[3] Third lumbar, Risien Russell, Brain, 1898.
[4] Loewenthal, *op. cit.* 1885; Mott, Brain, 1892 and 1895; Tooth, *ibid.* 1892.
[5] Van Gehuchten, Système nerveux, 1906; Collier and Buzzard, Brain, xxvi. 1903. Cf. Tooth, Goulstonian Lectures, 1889, p. 58.
[6] According to R. Hunt (Cornell Univ. Med. Publ. i. 1904), the fibres of Gowers' bundle go in man wholly to the cerebellum. But this statement is not borne out by the observations of Horsley and Thiele (Brain, xxiv. 1901), nor of Collier and Buzzard, *op. cit.* Cf. Blumenau, Abstr. in Neurol. Centr. 1908, p. 264.
[7] Sherrington and Laslett, *op. cit.*
[8] Marie, Leçons s. l. maladies de la moelle, 1892; Collier and Buzzard, Brain, xxiv. 1901.

serving to connect the grey matter of successive segments of the cord. Certainly many axons of the nerve-cells of the neighbouring grey matter enter it, and there is a particularly well-marked bundle of such fibres close to the dorsal horn derived from the cells of that horn and especially of the substance of Rolando (bundle of dorsal horn, Cajal). The ventral column receives fibres from the grey matter of the other side through the ventral commissure (fig. 118, B, *a.c.*), and is in part composed of fibres of the ventral roots which course for a certain distance obliquely within it. Many intersegmental fibres also occur scattered among the fibres of the long tracts.[1]

At the dorsal part of the lateral column, close to the entering fibres of the dorsal roots and directly derived from them, is constantly to be seen the well-marked *marginal bundle* of fine nerve-fibres (p. 89), which was first described by Lissauer,[2] and since by Bechterew and others. It is not always confined to the lateral column, but may extend into the dorsal column. It is often not involved in degenerations affecting the ascending fibres of the posterior roots, as in tabes, and its fibres have therefore been regarded as endogenous.[3]

Tracts of the dorsal or posterior white column.—Ascending tracts.—This column is mainly composed of two long *ascending tracts*—viz. the *tract of Goll*, which above corresponds with the mesial dorsal column, and the *tract of Burdach*, which embraces the remainder of the dorsal column. In the lower part of the cord these two tracts are not marked off from one another in the adult, but from the middle of the thoracic region upwards the mesial dorsal column is separated from the lateral dorsal by a septum of pia mater.

Of the two parts of the dorsal column the *tract of Burdach* (*funiculus cuneatus*) is mainly composed of rather large fibres which are joined by—*i.e.* are continuous with—the large fibres of the entering dorsal roots. After a certain course, in which they give off collaterals to the grey matter, many of them enter the grey matter of the cord and come into intimate relationship, although not into actual continuity, with its cells. But other of the fibres of the lower roots, from the fifth thoracic downwards,[4] eventually pass into the tract of Goll and nucleus gracilis; while those from the upper thoracic and cervical roots pass into the nucleus cuneatus of the medulla oblongata and there terminate. As the posterior root enters the dorsal column it at first lies next to the posterior cornu. But as each successive root enters the cord those which have already entered become pushed by the newly entering fibres nearer to the dorsal median fissure.[5]

The fibres of the *tract of Goll* (*funiculus gracilis*) are for the most part of smaller diameter. They are derived from posterior root-fibres of the sacral, lumbar, and lower thoracic nerves, which, after having coursed a short distance in the tract of Burdach, instead of entering the grey matter of the cord, run up the mesial column into the medulla oblongata, where they terminate among the cells of the nucleus gracilis.

The fibres which ascend to and end in the nucleus of Goll and nucleus of Burdach give off most of their collaterals to the lumbar and cervical enlargements respectively.[6]

The column of Goll in the embryo shows a distinction into two parts—one mesial, close to the posterior median fissure, and one dorso-lateral, lying near the dorsal surface of the cord (Flechsig). The same author states that the column of Burdach is myelinated in three stages and shows a corresponding differentiation in the embryo into three parts—*ventral*, *middle*, and *dorsal root-zones*. The middle zone is said to be first attacked in tabes.[7]

[1] On the endogenous fibres of the human cord, see Bing, Arch. f. Psychiatrie, xxxix. 1904.
[2] Arch. f. Psychiatrie, 1886.
[3] Nageotti, Nouv. Icon. d. l. Salpêtrière, xvii. 1904. Orr and Rows, Brain, 1894, differ from this conclusion.
[4] Edinger, Bau d. nervösen Zentralorgane, 1904.
[5] Kahler, Berl. klin. Wochenschr. 1882.
[6] Sherrington, article 'Spinal Cord,' in Schäfer's Text-book of Physiology, vol. ii. p. 792.
[7] Nageotti, *op. cit.*

Descending fibres of the dorsal column.—In the middle of the sectional area of the lateral dorsal column a few fibres are constantly found, which undergo descending degeneration after lesions of the cord (p. 103). These are described as constituting a special tract ('comma' tract, Schultze),[1] but they are often a good deal intermingled with fibres of the adjacent ascending tracts. Whether they partly originate from cells higher up in the cord or are wholly derived from the descending branches of the dorsal root-fibres is uncertain. The latter, it may be remembered, extend a certain distance down the cord from the Y-shaped division of those fibres, giving off collaterals to the grey matter, and ultimately themselves turning into the grey matter. The extent to which these descending branches of the dorsal roots may pass down the cord has not as yet been fully determined.

Propriospinal or intrinsic fibres of the dorsal column.—These, which take origin in cells of the dorsal horn of grey matter, course both upwards and downwards in the posterior column (see fig. 117). The *ascending propriospinal fibres* lie for the most part in the ventral part of the column close to the median fissure and grey commissure; they are rendered evident by Stenson's experiment of temporary ligature (about an hour) of the abdominal aorta.[2]

In cases of degeneration of the dorsal roots, and hence of the dorsal columns, in man, the propriospinal fibres are found intact.[3]

Some of the ascending fibres can be traced as far as the nucleus gracilis of the medulla oblongata, but most of them have only a short course and soon pass again into the grey matter of the cord.

The *descending propriospinal fibres* of the dorsal columns are seen in total transverse lesions or in semi-sections of the cord to form two bundles—one lying close to the dorsal horn and commissure (*cornu-commissural bundle*), the other near the median fissure or septum, partly in the middle of the thickness of the column, partly close to the surface. The exact position of this tract varies in different parts of the cord; thus, in the sacral region it chiefly occupies a small triangle at the dorso-median angle of the column (*triangle* of Gombault and Philippe); in the lumbar region the corresponding fibres form a semi-oval patch close to the middle of the median fissure (*oval bundle* of Flechsig, *septo-marginal bundle* of Bruce and Muir) and a *superficial bundle* (Hoche); in the cervical and thoracic regions they tend to be less superficial and do not form definite bundles, but are scattered among the exogenous fibres which form the main substance of the column. Some authors consider that the comma tract (see above) is composed of endogenous fibres.[4] The cornu-commissural bundle occurs only in the lumbo-sacral region (Bruce), being most developed in the lower lumbar region. Its fibres are derived from cells in the dorsal horn.[5]

The collaterals of the white columns.—Dorsal column.—Besides the collaterals which pass into the grey matter of the dorsal horn from the

[1] Arch. f. Psych. u. Nervenh. 1883; but first observed by Bastian, Med. Chir. Trans. 1867. According to Collier and Buzzard, the comma tract is divided from the twelfth thoracic segment downwards into a dorsal and a ventral portion (Brain, xxvi. 1903). Kopezquski (Neurol. Centr. 1906) derives the comma tract wholly from the nerve-roots.

[2] Ehrlich and Brieger, Zeitschr. f. klin. Med. 1884, suppl.; Singer and Munzer, Abhandl. d. Wiener Akad. 1890; Sarbo, Neurol. Centralbl. 1895; Rothmann, Arch. f. Phys. 1899; Bochenek, Névraxe, 1901.

[3] Dejerine and Soltas, C. r. Soc. biol. 1896.

[4] H. H. Tooth, Goulstonian Lectures, 1889; Ziehen, *op. cit.* p. 328 *seq.*; Purves Stewart, Brain, xxiv. 1901.

[5] See on this subject Gombault and Philippe, Semaine méd. 1884; Flechsig, Neurol. Centralbl. 1890; Hoche, Neurol. Centralbl. 1896; Bruce and Muir, Brain, 1896; Bruce, Brain, 1897; Dejerine and Theobari, Journ. de Physiol. 1899; Goldstein, Monatschr. f. Psych. u. Neurol. xiv. 1903; Nageotti, Nouv. Iconogr. de la Salpêtrière, xvii. 1904; A. Gordon, Journ. Nerv. and Mental Diseases, xxxi. 1904, p. 533; Page May, Rev. of Neurol. 1905, where the literature of the subject will be found. Page May found in a monkey a small bundle of fibres in the mesio-dorsal column, close to the median fissure, degenerating downwards from a lesion of the mid-brain, and which he thinks may come from the thalamic region. It is, however, possible that they may have been aberrant fibres of the pyramid-tract, which are constantly present in many mammals, and are known sometimes to occur in man. Cf. Bumke, Neur. Centr. 1905, p. 938; D. Orr. Rev. of Neurol. 1903, p. 488 (also with a bibliography).

dorsal roots as they enter the cord and form synapses around the cells at the apex of the cornu, others pass in large number into the grey matter from the fibres of the dorsal columns, but fewer from the tract of Goll than from the tract of Burdach. Many of these end by ramifying in and near the apex of the cornu. Some traverse the whole thickness of the grey matter and, reaching the ventral horn, form a close interlacement around its cells (fig. 120). Others take the same direction dorso-ventrally through the grey matter, but break up into a terminal arborescence in the intermediate cell-column or nucleus. (This may also receive fine offsets from the collaterals to the ventral horn.) Others again sweep into the grey matter ventral to the substance of Rolando and, turning up into this, end in dense ramifications around its cells. And yet others from the same column skirt the lateral edge of the dorsal horn and pass with bold

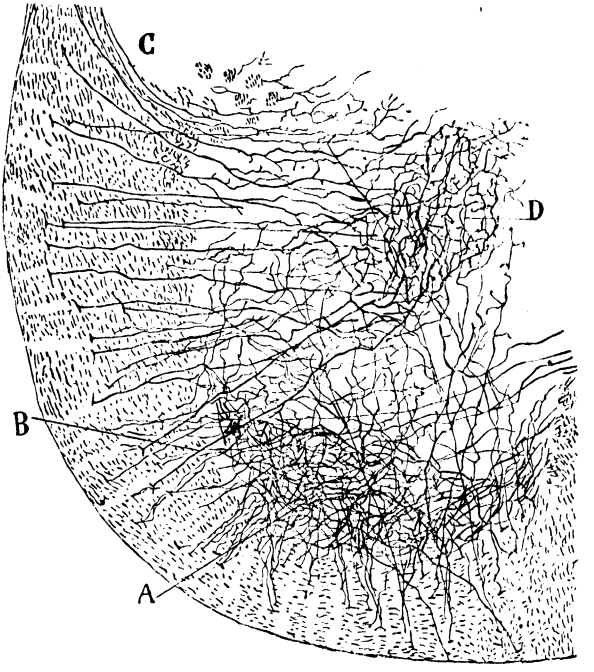


FIG. 124.—COLLATERALS OF THE VENTRO-LATERAL COLUMN PASSING INTO THE GREY MATTER: DORSAL CORD OF CAT-EMBRYO. (Cajal.)

A, close plexus around the cells of the ventral horn from fibres in the radicular zone of the ventral white column; B, long collaterals to the intermediate nucleus, D; C, dorsal horn of grey matter.

curves into Clarke's column, where they form a close interlacement of ramified fibrils among the cells, many becoming longitudinal. Besides these various collaterals, there are others which cross by way of the dorsal commissure to the dorsal horn of the opposite side.

Ventro-lateral column.—The collaterals from the fibres of this column are also both direct and crossed. The crossed collaterals pass both through the ventral commissure into the grey matter of the opposite side (where they are chiefly distributed around the ventral-horn cells, but partly pass more deeply into the grey crescent) and also through the dorsal commissure, mostly terminating in the dorsal horn. The direct collaterals pass from all parts of the ventro-lateral column vertically into the grey matter, into which they penetrate a variable distance (fig. 124) and in which they terminate in fine

arborisations. The collaterals from the crossed (lateral) pyramid-tract do not enter the ventral horn, but end in the grey matter of the formatio reticularis and in the base of the dorsal horn, some extending even into Clarke's column. The collaterals from the descending vestibulo-spinal, tecto-spinal, and rubro-spinal fibres in the ventral column end among the cells of the ventral horn.

Degenerations in the Spinal Cord as the Result of Lesions.

It necessarily results from the Wallerian law of degeneration of nerve-fibres (p. 53) that every lesion of the spinal cord in which fibres are cut or crushed must be followed by degeneration of nerve-fibres either above or below the lesion, according to the position of the cells from which the fibres have originally grown, and which serve throughout life to maintain the nutrition of the fibres with which they are connected. Any such degeneration which occurs above the lesion is, as already mentioned, termed 'ascending,' and below the lesion 'descending.'[1]

Similarly, if the nerve-cells from which the fibres are thus derived are removed or destroyed, the fibres, with any branches which they may give off, will degenerate along their whole course. Hence any tracts of fibres in the spinal cord which are derived from cells in parts of the brain degenerate on destruction of those parts. Further, those fibres which have grown into the spinal cord or brain from nerve-cells situated external to those organs (*e.g.* the fibres of dorsal roots of spinal nerves and corresponding fibres of cerebral nerves) will, if cut between the spinal cord or brain and the ganglion-cells from which they are derived, undergo degeneration from the point of section, not only as far as the surface of the central organ, but also along their whole course within that organ, and the degenerative process will include all their branches. Thus much having been said to explain the meaning of the results which are obtained by the study of cord-degenerations, we may proceed to consider the degenerations which follow (1) section of the dorsal roots of the nerves; (2) lesion or removal of parts of the brain; (3) section or other lesion of the spinal cord itself.

Degenerations in the spinal cord resulting from section of the dorsal roots.—These were originally investigated, among others, in the dog by Singer and Kahler, in the monkey by Mott and Tooth. It is convenient in describing the effect of section of the dorsal nerve-roots to consider them in the sacro-lumbar and in the cervico-thoracic regions respectively, although the course of the degenerative process is essentially similar in both.

(*a*) *Section of the dorsal roots of sacro-lumbar nerves.*—Section of these nerves —*e.g.* of the sixth lumbar to the second sacral—is followed by 'ascending' degeneration in the dorsal column of the same side along the whole length of the spinal cord and as far as the nucleus gracilis of the medulla oblongata. But the degeneration does not occupy the same position and extent in every part of the cord. At the lowest part it involves the whole of the dorsal column (fig. 125, *a*), but as soon as a point is reached at which uncut nerve-fibres enter the cord, these now occupy the part of the column nearest the horn of grey matter, while degenerated fibres are seen in that part only which is nearest the dorsal median fissure (*b*). In this situation they pass up the cord, diminishing in number, at first rapidly and afterwards more slowly, until at length a relatively small tract of degeneration is found, occupying the dorso-mesial part of Goll's tract, in which it runs to the nucleus gracilis (fig. 125, *c*).

(*b*) *Section of the dorsal roots of thoracic and cervical nerves.*—After section of one or more of these roots degeneration occurs immediately above the

[1] These terms must not be taken to imply either that the degeneration starts from the lesion and extends upwards or downwards along the fibres, or that the nervous impulses which the fibres conduct necessarily have an ascending or a descending direction. For it is known (1) that the degeneration in the peripheral part of a cut nerve-fibre occurs almost simultaneously along its whole course; (2) that a nerve-fibre may undergo 'descending' degeneration, although it normally conveys ascending impulses—*e.g.* the peripheral afferent nerves.

Since the terms 'ascending' and 'descending,' as applied to nerve-degeneration, lead to much confusion of ideas, it would be better, if possible, to discard them and to adopt words which merely imply that the degenerative process occurs above or below a lesion. But unfortunately those terms have taken such deep root in the literature of the subject that this course would be very difficult, and might lead to even worse confusion than their retention.

section in the part of the dorsal column which is next to the posterior horn (figs. 126, 127, *a*). Somewhat higher up this becomes separated from the horn by other uncut (and therefore undegenerated) nerve root-fibres, and approaches the mesial column. Still higher it is found to have reached that column, where it is represented by a smaller tract of degeneration, which in section lies obliquely across the column. With regard to this degeneration in the mesial column, it is to be noted that, while that which results from section of the lumbo-sacral roots occupies in the higher parts of the cord the dorso-mesial angle, as above described, the degeneration resulting from section of the thoracic roots from the fifth downwards lies next to this, passing up Goll's column in its lateral part next

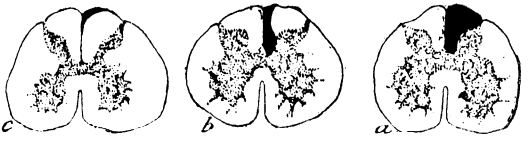


FIG. 125.—DIAGRAM SHOWING THE DEGENERATIONS IN THE POSTERIOR COLUMN WHICH RESULT FROM SECTION OF THE POSTERIOR ROOTS OF THE SECOND SACRAL TO THE SIXTH LUMBAR NERVES OF THE DOG. (Singer.)

a section at the level of the sixth lumbar ; *b*, at the fourth lumbar ; *c*, from the middle of the thoracic region.

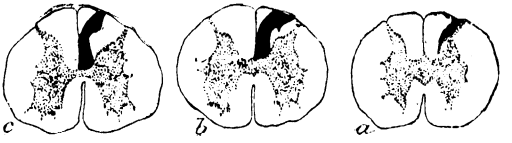


FIG. 126.—DIAGRAM OF DEGENERATIONS FOLLOWING SECTION OF THE ELEVENTH AND TWELFTH THORACIC POSTERIOR NERVE-ROOTS OF THE DOG. (Singer.)

a, section at the level of the twelfth thoracic ; *b*, at the third thoracic ; *c*, at the middle of the cervical region.

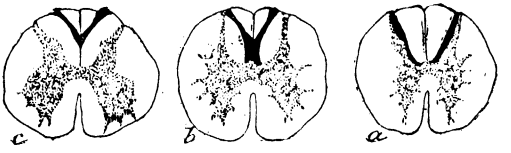


FIG. 127.—DIAGRAM OF THE DEGENERATIONS FOLLOWING BILATERAL SECTION OF THE SECOND THORACIC TO THE FIFTH CERVICAL POSTERIOR NERVE-ROOTS OF THE DOG. (Kahler.)

a, at the level of the first thoracic ; *b*, at the sixth cervical ; *c*, at the first cervical.

(Figs. 125, 126, and 127 are from Toldt's 'Gewebelehre.')

to the column of Burdach, and finally that resulting from section of upper thoracic and cervical roots is confined to Burdach's column, and ends in the nucleus cuneatus of the medulla oblongata. In other words, the lower the root the more mesial is the resulting long degeneration in the higher parts of the cord and in the medulla oblongata. The fibres, as they enter the cord with the dorsal nerve-roots, form in fact a succession of lamellar tracts, which lie in each case at first next to the dorsal horn, and become gradually shifted medianwards by those which enter the cord with the higher nerve-roots.[1]

It is further to be noted that in all cases the degeneration falls off markedly in amount as we trace it up the cord, and that what remains is eventually confined to a part of the dorsal column which contains normally fine or

[1] For a list of cases in the human subject of degeneration following lesions to one or two posterior roots, see Ziehen, *op. cit.* p. 288. To those given by Ziehen may be added a case of degeneration of the first cervical root alone described by Bumke, Neurol. Centr. xxiv. 1905. The fibres were traceable to the highest part of the nucleus cuneatus. For the course of the eighth cervical and first thoracic, see Van Gehuchten, Le Névraxe, ii. 1902.

medium-sized fibres only. From this it may be inferred that the larger fibres of the dorsal roots—which in fact form the bulk of those roots—have a relatively limited course after entering the cord. They probably end by their collateral branches, and ultimately by their main ascending branches, turning into the grey matter and breaking up into terminal ramifications in the fine interlacements of nerve-fibrils which occur in the neighbourhood of the nerve-cells and cell-groups. These terminal branches, and the nerve-fibrils which result from their ramifications, should also, of course, from the Wallerian law, degenerate after section of the roots, and there is no doubt that they actually do so, although from their scattered course in the grey matter it is difficult to prove the fact. It has, however, been shown by Mott that after section of the lower dorsal roots the fine nervous interlacement which surrounds the cells of Clarke's column disappears for some little distance above the entrance of the cut nerve-roots, and it may therefore be inferred that some of the fibres of the dorsal roots give origin directly and by collaterals to this interlacement; this can indeed be seen in Golgi preparations. Others, probably, are similarly related to other cells, both in the dorsal and ventral horns of the same side, and even on the other side of the cord, for it will be remembered that ramifying collaterals can be traced from the dorsal root-fibres to all these parts (see figs. 116 and 120). Thus all the larger and some of the smaller fibres of the dorsal roots gradually end as they are prolonged up the cord, until finally only those remain which pass up the mesio-dorsal column towards the medulla oblongata. Even these become gradually diminished in number, no doubt from the fact that some of them terminate in the grey matter as they proceed.

It will further be remembered that the fibres of the dorsal roots divide on their entrance into the cord into two main longitudinal branches, ascending and descending. Of these the ascending only has been traced by the above degenerations, but the descending branch must also undergo degeneration. It is, however, not easy to trace out its course. The only known 'descending' degenerations in the dorsal columns are (1) a degeneration along the narrow curved tract in the dorso-lateral column which is known as the 'comma' (Schultze), and (2) the degenerations in the septomarginal tract of Bruce and Muir, and in the triangular and oval and commissural areas (see p. 99), which are almost certainly endogenous. Mott and others have found that the comma degeneration results not only after section of the cord, but also after section of dorsal nerve-roots; although its extent is more limited than after transverse section of the cord (Dejerine). It is therefore not improbable that this degeneration in part represents the descending branches of the cut dorsal root-fibres (cf. p. 99, and fig. 128); but it is clear that their course is far more limited than that of the ascending branches. Moreover, the position and size of the comma tract vary in different regions of the cord, and the corresponding degeneration also varies in position and extent.

It will be convenient here to sum up what is known or may be inferred as to the course of the fibres of the dorsal roots within the cord as determined by anatomical, pathological, and experimental (degenerative) methods. Each fibre on entering the cord divides into an ascending and a descending branch, which form the longitudinal fibres of the dorsal column. Both from the root-fibre before division and, abundantly, from the branches collaterals come off, which lose themselves in ramifications enveloping nerve-cells in the grey matter. After a longer or shorter course, the main branches terminate by passing in like manner into the grey matter of the cord or of the medulla oblongata. Each root on entering the cord forms a large lamellar bundle of mixed large and small fibres, which run longitudinally in the latero-dorsal column close to the cornu of grey matter. From this lamellar bundle many fibres pass upward along the whole length of the cord, being gradually shifted inward towards the mesio-dorsal

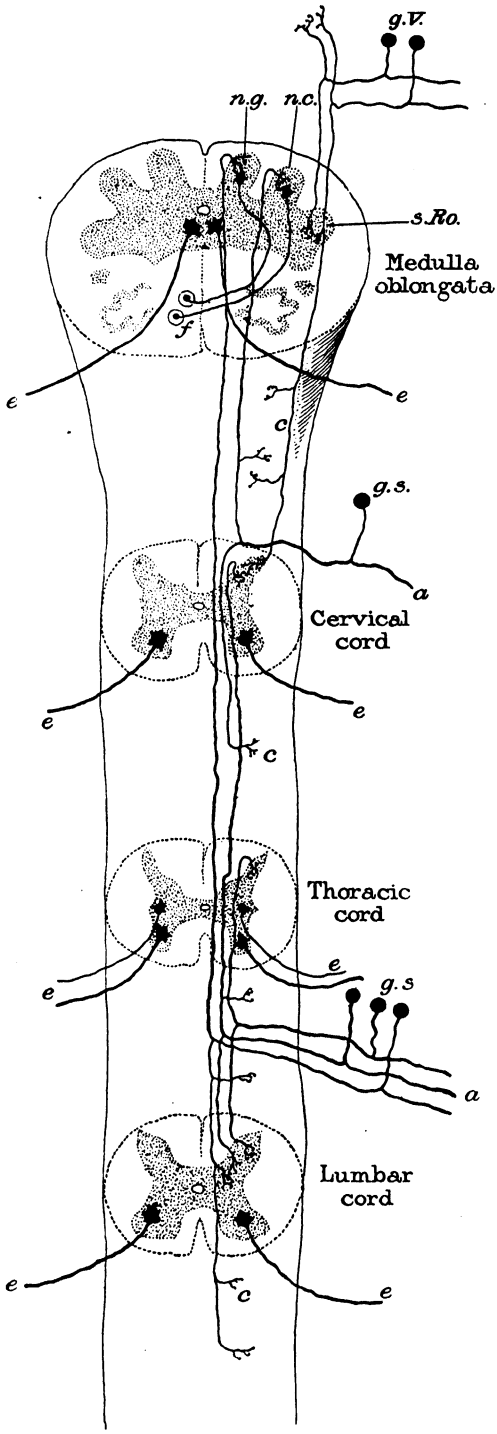


FIG. 128.—DIAGRAM, MODIFIED FROM CAJAL, TO SHOW THE COURSE OF THE FIBRES OF THE DORSAL ROOTS AFTER ENTERING THE CORD.

a, afferent fibres passing to ganglia; *e*, efferent fibres leaving cord, derived from motor cells; *g.s.*, spinal-ganglion cells; *g.*V., ganglion-cells of fifth nerve; *n.c.*, nucleus cuneatus; *n.g.*, nucleus gracilis; *f*, fibres of fillet; *c*, descending fibres giving off collaterals.

column, and forming as they reach this column the bundle of Goll or funiculus gracilis; these fibres eventually pass, some into the grey matter of the upper part of the spinal cord, others into grey matter in the nucleus gracilis of the bulb. On the other hand, the ascending fibres which are derived from the uppermost thoracic and the cervical roots do not form part of the bundle of Goll, but pass up to the bulb in the funiculus cuneatus and end in its nucleus. The remainder of the fibres which have entered by the dorsal roots have only a limited course up the latero-dorsal column, passing, as they ascend, into the grey matter, in which they and their collaterals form the fine nervous plexus around many of the nerve-cells which has been already mentioned. From some of the large fibres the plexuses around the cells of Clarke's column, and from others those around the cells of the substance of Rolando, are formed, whilst other collaterals furnish an enveloping plexus to the cells of the ventral horn and to those of other parts of the grey matter. The descending main branches of the dorsal root-fibres have, like many of the ascending branches, only a limited course, during which they give off collaterals, by means of which, and also ultimately by directly passing into the grey matter, they assist in forming the enveloping plexus around the nerve-cells of the segments of the cord immediately below that at which the parent root has entered (fig. 128).

Degenerations in the spinal cord resulting from lesions of parts of the brain.—*Lesions of the cerebral cortex.*—Removal of the cortex of the so-called 'motor' region of the cerebral hemisphere is followed by degeneration extending along the pyramid tract in the brain and cord. In the spinal cord this tract has for the most part crossed to the opposite side, but in man a portion runs as the direct tract along the ventral median fissure on the same side as the lesion (fig. 122). Although this direct pyramid tract is confined to the ventral column in man, it is found in the monkey as the result of lesions of the motor regions of the cortex that there are a very few scattered fibres in the circumferential part of the ventro-lateral column which undergo degeneration. The crossed tract lies in the dorsal part of the lateral column between the dorsal spino-cerebellar tract and the dorsal horn (fig. 129, I.), and in this situation the degeneration can be traced downwards, decreasing in amount, and, in the lower parts of the cord, with the disappearance of the dorsal spino-cerebellar tract, approaching the surface of the cord near the tip of the dorsal horn. In the cervical region the crossed pyramid degeneration may reach the surface of the cord in front of—*i.e.* ventral to—the dorsal cerebellar tract, which is partly enclosed by the degenerated fibres; this, at least, is the case in the monkey. After a unilateral lesion of the cortex there is also a certain amount of degeneration in the lateral tract of the cord on the same side as the lesion. This is especially the case when the lesion has involved the marginal convolution. This is due to fibres which pass from the pyramid of the medulla oblongata directly to the lateral column of the same side of the cord.

On the other hand, section of the pyramid-tract in the cord is followed by chromatolysis and eventual atrophy of the large cells in parts of the 'motor' area of the cortex.

Sherrington found, after removal of parts of the motor cortex, a few scattered degenerated fibres in the ventral and lateral cornua of the spinal cord. The same observer also noticed that, even when the cortical lesion was entirely confined to the so-called 'arm-area' of the cortex, a certain number of fibres were found to degenerate down the pyramid-tract of the opposite side, even as far as the lumbo-sacral region. This observation has been confirmed by Simpson and Jolly.[1]

Lesions of the cerebellum.—Marchi[2] described these as producing degenerations extending down the ventro-lateral column of the cord. But there seems no doubt that the degenerations which Marchi obtained were the result of the participation of the nucleus of Deiters in the experimental lesion, for, if care

[1] Proc. Roy. Soc. Edin. 1907.

[2] Arch. ital. d. biol. 1892.

be taken to avoid injury to this nucleus, no descending degeneration is observable in the cord even if the whole cerebellum be removed.[1]

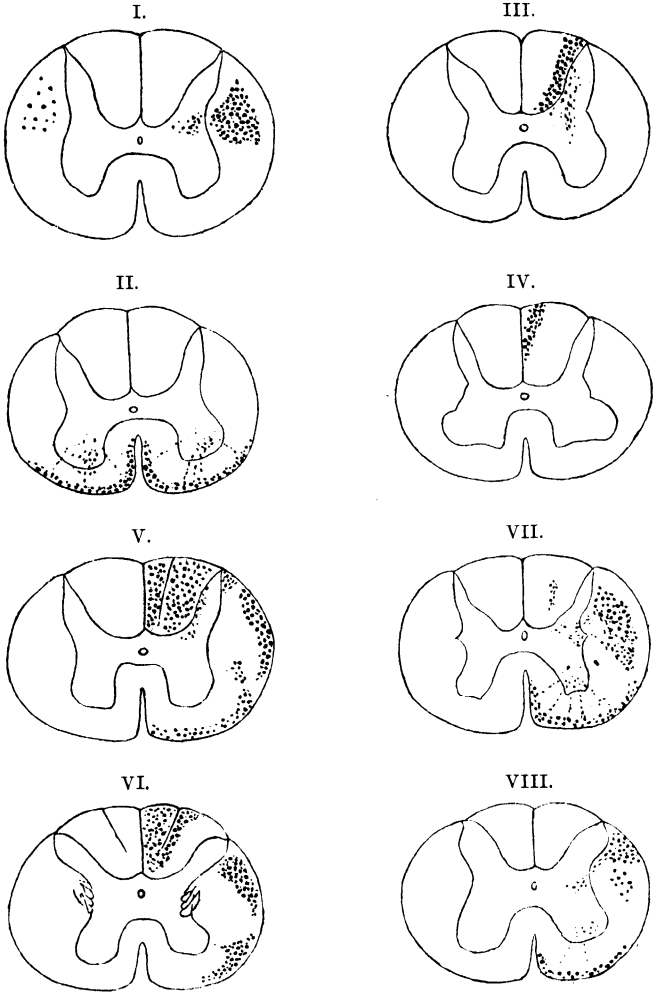


FIG. 129.—DIAGRAM OF SECTIONS OF THE SPINAL CORD OF THE MONKEY, SHOWING THE POSITION OF DEGENERATED TRACTS OF NERVE-FIBRES AFTER SPECIFIC LESIONS OF THE CORD ITSELF, OF THE AFFERENT NERVE-ROOTS, AND OF THE MOTOR REGION OF THE CEREBRAL CORTEX. The degenerations are shown by the method of Marchi. The left side of the cord is in all cases on the reader's left hand. (E. A. Schäfer.)

I. Degenerations resulting from extirpation of the motor area of the cortex of the left cerebral hemisphere.

II. Degenerations produced by section of the dorsal longitudinal bundles in the upper part of the medulla oblongata.

III. and IV. Result of section of dorsal roots of the first, second, and third lumbar nerves on the right side. III. is from the segment of cord between the last thoracic and first lumbar roots; IV. from the same cord in the cervical region.

V. to VIII. Degenerations resulting from (right) semi-section of the cord in the upper thoracic region. V. is taken a short distance above the level of section; VI. higher up the cord (cervical region); VII. a little below the level of section; VIII. lumbar region.

Lesions in the mid-brain.—Injury to the *red nucleus* of the tegmentum produces degeneration of fibres in the prepyramidal tract of the cord. Destruction

[1] Risien Russell, Phil. Trans. 1894; Ferrier and Turner, *ibid.*

of the *anterior corpora quadrigemina* is followed by degeneration of fibres (tecto-spinal) which in the spinal cord lie partly in the ventral, partly in the lateral column (Boyce). In these situations they are intermingled with the fibres of the vestibulo-(ponto)-spinal tract and with those of the rubro-spinal tract.

Lesions of the pons and medulla oblongata.—Any lesions of these parts which involve the descending tracts which are passing through them from the cortex cerebri or mid-brain necessarily produce degeneration of the fibres of such traversing tracts. Apart from this, there are certain portions of the grey matter the destruction of which is followed by degeneration of fibres down the ventral white column of the cord. This is especially true for the region containing the nucleus of Deiters; but it applies also to much of the reticular formation of the pons and bulb. The degenerated fibres end by terminals and collaterals arborising among the cells of the ventral horn (fig. 129, II.).

Degenerations resulting from lesions of the cord itself.—*Section of the spinal cord* in any part is followed by certain degenerations both above and below the section (fig. 129, V., VI., VII., and VIII.). These may be classed as (1) short degenerations, which extend only a limited distance above or below the plane of section; and (2) long degenerations, which extend an unlimited distance upwards or downwards in the cord. Of the short degenerations, the most marked are in the ventral column and the ventral part of the lateral column near the grey matter (ventro-lateral limiting layer), where there are seen numerous scattered degenerated fibres, both ascending and descending; they are due to the section of fibres which serve to connect cells of one segment of the cord to the grey matter of adjacent segments above or below. Of the long degenerations, the 'descending' ones are those of the pyramid-tracts, crossed and direct, the bulbo-spinal, ponto-spinal, tecto-spinal, and rubro-spinal, and, for a few segments, the small descending tract (comma) of the posterior column and the descending propriospinal fibres; the 'ascending' are in the posterior column, where they are the same as would have resulted from section of all the posterior roots below the point of section; in the lateral column in the situation of the dorsal spino-cerebellar tract and of the ventral spino-cerebellar tracts (including the spino-tectal and spino-thalamic fibres), and a certain number of proprio-spinal fibres, in the ventral and lateral columns.

Section of the ventral column alone is followed by both descending and ascending degeneration along the cord, and from the degenerated fibres numerous collaterals can be traced into the ventral horn. The whole column is not involved in these degenerations, but the fibres which degenerate below the lesion are for the most part situated near the surface of the cord and the ventral fissure, while those which degenerate above the lesion are scattered among the deeper fibres of the column.

Section of the dorsal column alone produces ascending degeneration, which is, for the first segment above the lesion, complete (except for a few descending fibres, mostly endogenous). But as the dorsal roots successively enter the cord above the lesion, they or the parts of them which are continued up the dorsal column occupy more and more of the lateral part of that column, and the degenerated fibres which have not passed into the grey matter are gradually shifted nearer to the dorsal fissure.

Section of the dorsal part of the lateral column in the mid-thoracic region produces descending degeneration of the lateral pyramid-tract and ascending degeneration of Flechsig's bundle.

Section of the ventral part of the lateral column in the mid-thoracic region produces ascending degeneration in Gowers' bundle. But a short distance above the lesion many of the degenerated fibres begin to shift backwards along

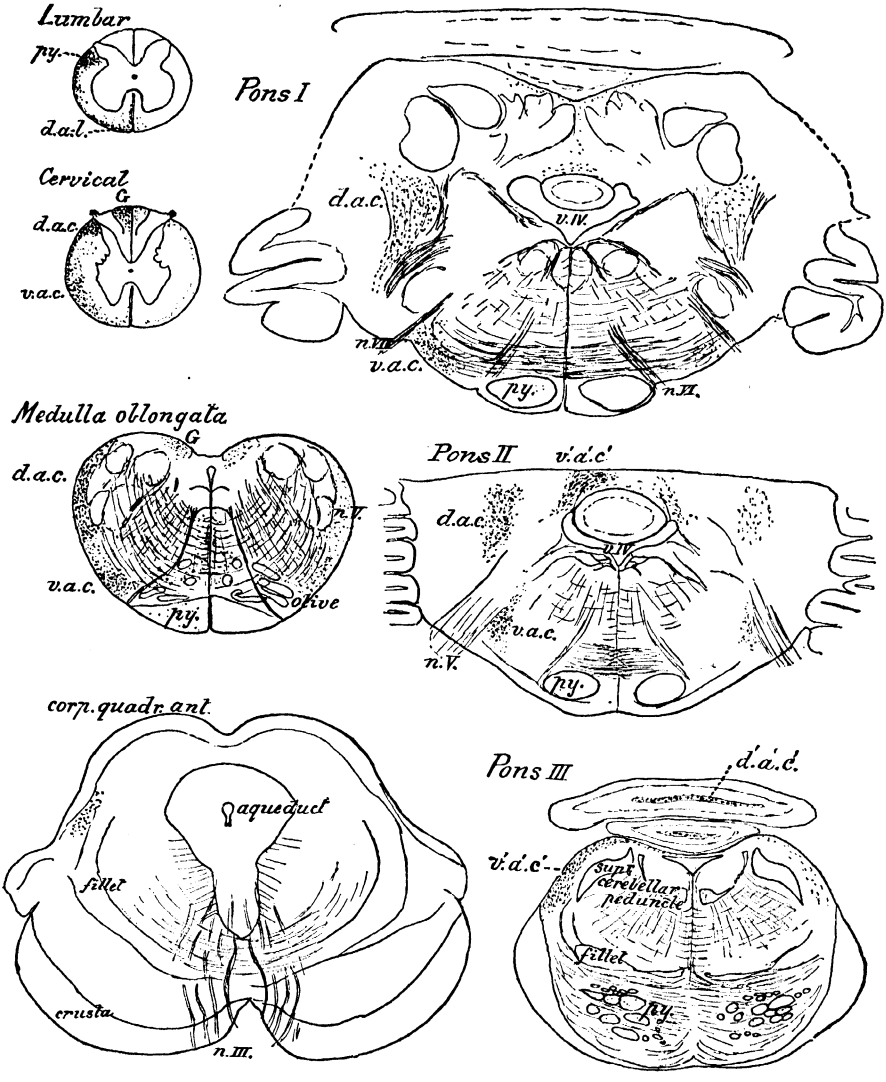


FIG. 180.—DEGENERATIONS IN THE SPINAL CORD, MEDULLA OBLONGATA, PONS, AND MESENCEPHALON OF A MONKEY, FOLLOWING HEMISECTION AT THE TWELFTH THORACIC NERVE. (E. A. Schäfer.)

The hemisection was on the left side of the cord, and complete. The section-outlines drawn to one scale with a camera lucida. The degenerated fibres shown by black dots. Those in the section of the lumbar cord descending, the rest ascending. *py.*, pyramid-tract; G, tract of Goll; *d.a.l.*, descending ventro-lateral fibres; *d.a.c.*, dorsal spino-cerebellar tract; *d'.a'.c'.* (in Pons III.), degeneration of this tract in the white matter of the cerebellar worm; *v.a.c.*, ventral spino-cerebellar tract (Gowers' bundle); *v'.a'.c'.* (in Pons II. and III.), degenerated fibres of this tract passing dorsally into the superior medullary velum (in Pons III.) and into the white matter of the vermis (in Pons II.); *n.III.*, *n.V.*, *n.VI.*, *n.VII.*, issuing fibres of the third, fifth, sixth, and seventh nerve-roots; *v.IV.*, fourth ventricle.

Nearly all the degeneration is on the same side as the lesion. A few fibres are degenerated on the opposite side (doubtless from a slight accidental injury of that side of the cord). Some degenerated fibres (spino-tectal and spino-thalamic) are seen in the region of the superior corpora quadrigemina.

the periphery of the cord, gradually passing into the bundle of Flechsig, so that in the higher regions of the cord both the dorsal and ventral cerebellar tracts show extensive degeneration (see p. 85). This passage of fibres from the one tract to the other continues up the medulla oblongata.

There is also descending degeneration in the prepyramidal (rubro-spinal) tract.

If the lesions of the cord are confined to one lateral half, the tracts of degeneration are limited to the side of the semisection; the few degenerated fibres sometimes seen in contra-lateral tracts are probably due to unavoidable injury to the other side of the cord in the performance of the operation.[1]

[1] For degenerations following total transverse lesions in the several regions of the cord, with list of literature, see Ziehen, *op. cit.* pp. 246 *seq.* A useful account of the tracts of the cord and degenerations in them is given by A. W. Campbell in Brain, 1897, with literature to that date. For later literature, as well as original observations, see Collier and Buzzard, Brain, 1901 and 1903. For a full account of clinical cases involving injury to individual segments of the cord, with notes of the symptoms observed, see K. Wichmann, Die Rückenmarknerven und ihre Segmentbezüge, Berlin, 1901. An abstract of this is given by Bechterew, Die Funktionen der Nervecentra, Jena, 1908.

THE PARTS OF THE BRAIN.

The brain or encephalon comprises the medulla oblongata and pons, the cerebellum, the mid-brain, and the cerebrum. The *medulla oblongata* or *spinal bulb* (fig. 131, D) is the part continuous with the spinal cord; it is the lowest part of the encephalon, and rests against the basilar process of the occipital bone. The *pons* (C) is a direct continuation upwards and forwards of the medulla oblongata, but the name includes the transversely coursing fibres of the middle cerebellar peduncle. The *cerebellum* (B) occupies the posterior fossa of the cranium. Its central part forms the dorsal boundary of a space which is bounded ventrally by the dorsal surface of the medulla oblongata and pons, and which is named the fourth ventricle of the brain. The cerebellum is connected by peduncles below with the medulla oblongata, above with the mid-brain, and in the middle with the pons. The *mid-brain* is continued from the pons and comprises the two peduncles of the cerebrum (*a*), upon the dorsal aspect of which are placed, in man and mammals, two pairs of tubercles named the *corpora quadrigemina* (*b*), but in oviparous vertebrates one pair only, then named the *corpora bigemina* or *optic lobes*. The *cerebrum* (A) includes all the remaining and by far the largest part of the encephalon. It is united with the parts below by the mid-brain, which forms a comparatively narrow portion (*isthmus* of older authors).[1] The cerebrum is mainly composed of the large convoluted *cerebral hemispheres*; within it are the third, and the two lateral ventricles. It occupies the vault of the cranium, the anterior and middle cranial fossæ, and the superior fossæ of the occipital bone. The cerebral hemispheres are united by a large commissure termed the *corpus callosum*, and by a small commissure (*anterior commissure of the brain*).

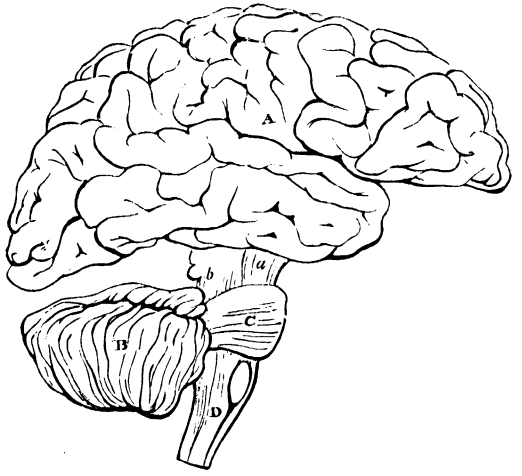


FIG. 131.—PLAN IN OUTLINE OF THE ENCEPHALON, AS SEEN FROM THE RIGHT SIDE. ½.

The parts are represented as separated from one another somewhat more than natural so as to show their connexions. A, cerebrum; B, cerebellum; C, pons; D, medulla oblongata; *a*, cerebral peduncle; *b*, corpora quadrigemina. *a* and *b* form the mid-brain.

The general relations and connexions of these various parts of the brain are shown in figs. 131 and 132. Of these figures, a median section is especially instructive as indicating the plan on which the brain is constructed. As explained in the part of this work dealing with the development of the nervous system, the neural tube above the level of the spinal cord acquires at an early period three dilatations termed the anterior, middle, and posterior primary cerebral vesicles, and from near the fore-part of the anterior vesicle two lateral processes are given off which undergo great expansion, so

[1] The term 'isthmus' is now more usually employed to indicate the region between the mid- and hind-brains, its situation being marked on the dorsal aspect by the decussation of the fourth nerves in the upper part of the superior medullary velum and on the ventral aspect by the upper border of the pons.

that ultimately these secondary offshoots form the main mass of the brain. In order to understand the general morphology of the adult brain, it is necessary to remember that the cavities of the various embryonic vesicles and their communications with one another persist, and that the brain acquires its fully developed form by certain flexures of the neural tube and by unequal growths of the different parts of the vesicle walls, so that, while some remain thin and even undergo atrophy, others acquire varying degrees of thickness.

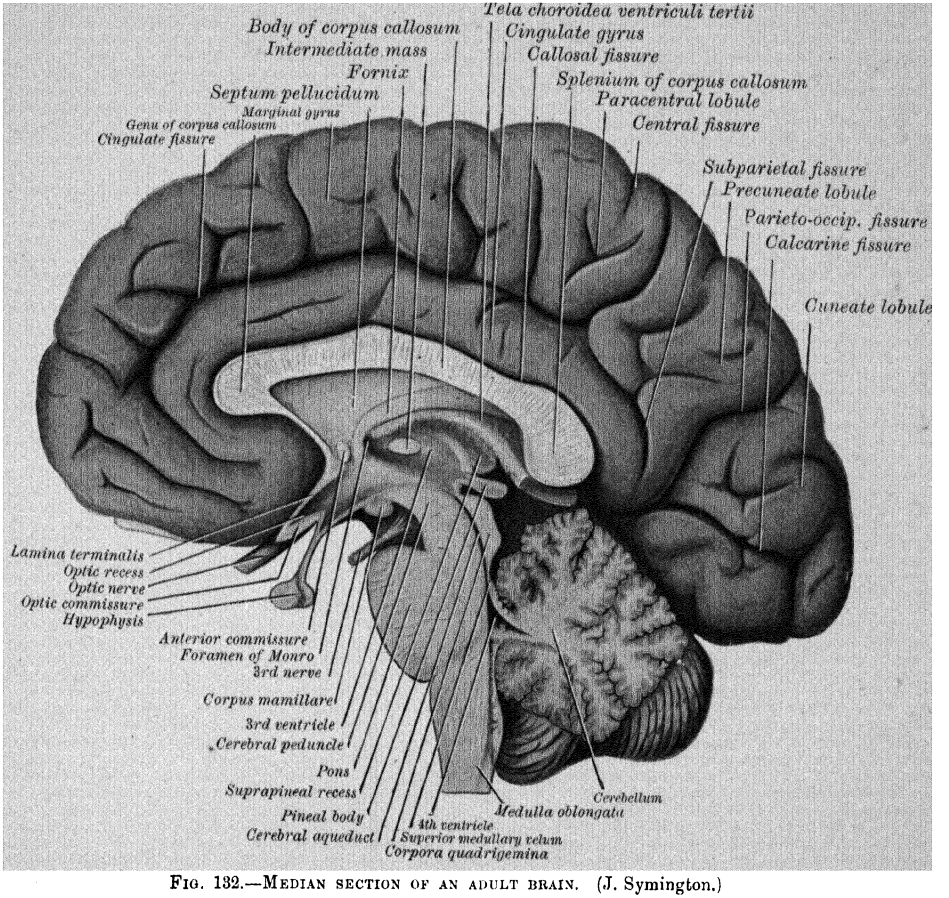


FIG. 132.—MEDIAN SECTION OF AN ADULT BRAIN. (J. Symington.)

The cavity of the posterior cerebral vesicle becomes the fourth ventricle, and its anterior or ventral wall thickens to form the medulla oblongata and pons. Its dorsal or posterior wall in its upper or cephalic part forms a thin median lamella, the superior medullary velum or valve of Vieussens, while laterally it becomes thickened and gives rise to the superior cerebellar peduncles. The inferior or caudal portion of this wall remains ependymal except in three places, one median and two lateral, where it and the adjacent covering of pia mater disappear, leaving apertures through which the cavity of the fourth ventricle communicates directly with the subarachnoid space on the external surface of the brain. The intermediate portion of the posterior wall undergoes very active growth to form the cerebellum, which extends not only backwards and to the

sides, but, as has already been explained, also upwards and downwards so as to conceal from the dorsal aspect all the other structures derived from the posterior cerebral vesicle. The cerebellum, from its size and from the fact that its cortical layer of grey matter possesses a distinctive structure and manner of folding, may be regarded as one of the main divisions of the brain.

The mid-brain, which is derived from the middle cerebral vesicle, is a very prominent structure during the earlier stages of development; but it grows afterwards very slowly, so that it constitutes only a comparatively small portion of the adult brain. Its cavity loses to a large extent the central dilatation and becomes a narrow canal, the aqueduct of Sylvius or aqueductus cerebri, which opens below into the fourth ventricle and above into the third. The ventro-lateral walls thicken and give rise to the pedunculi cerebri, and on the dorsal wall the corpora quadrigemina appear. These bodies, which at one period of embryonic life cause a marked prominence on the surface of the head, are now separated by a considerable interval from the cranial wall, and lie at the bottom of a deep cleft passing from behind forwards between the cerebellum below and the posterior part of the cerebrum above. This change in position is due to the more active growth and to the backward extension of the cerebellum and the cerebral hemispheres. The main axis of the parts of the neural tube derived from the posterior and middle cerebral vesicles is nearly vertical, but shows a tendency to bend forwards in the mid-brain, so that the upper end of the aqueduct of Sylvius inclines forwards (fig. 132).

Above the cerebral or Sylvian aqueduct the cavity of the neural tube is expanded in a sagittal plane to form the narrow median cleft known as the third ventricle. At the upper and anterior part of this cavity are the foramina of Monro, by which it communicates with the lateral ventricles. Nearly the whole of the third ventricle belongs to the inter-brain or diencephalon, but the part in front of a line uniting the posterior borders of the foramina of Monro with the optic commissure belongs to the end-brain or telencephalon. The lateral expansions of the dorsal part of this cavity into the cerebral hemispheres are the right and left lateral ventricles.

Some difference of opinion exists as to the direction and termination of the central axis of that part of the neural tube from which the inter- and end-brains are developed. According to Kupffer, this axis passes forwards from the opening of the Sylvian aqueduct to end in a small recess between the columns of the fornix and just above the anterior commissure. He considers this recess to correspond to the anterior neuropore and to the median olfactory lobe of Amphioxus. His, on the other hand, describes this axis as turning downwards anteriorly to end in the optic recess. The thin sheet of grey matter (end-plate, *lamina terminalis*) is therefore, according to Kupffer, ventral, and to His dorsal, to the main axis of the neural tube. In either case the brain-axis is bent so as to present a dorsal convexity. This bend appears at an early period of embryonic life, and is known as the primary cephalic flexure.

The lateral wall of the third ventricle is divided into an upper or dorsal, and a lower or ventral portion, by the sulcus of Monro. Above this sulcus the ventricle is bounded laterally by the thalamus, and below it by the hypothalamus. The ventral wall of the third ventricle is distinguished from that of the fourth ventricle and Sylvian aqueduct by its thinness, which is due to the divergence of the two cerebral peduncles as they pass towards the cerebral hemispheres. The term 'floor' is here more appropriate than when applied to the corresponding ventral boundaries of the hind- and mid-brain. The roof of the third ventricle remains ependymal, being represented by a layer of cells on the under-surface of the pia mater, which here forms a secondary roof, and is known as the tela choroidea. Two median diverticula are given off from this ventricle. One, the infundibulum, extends downwards from the floor to end in

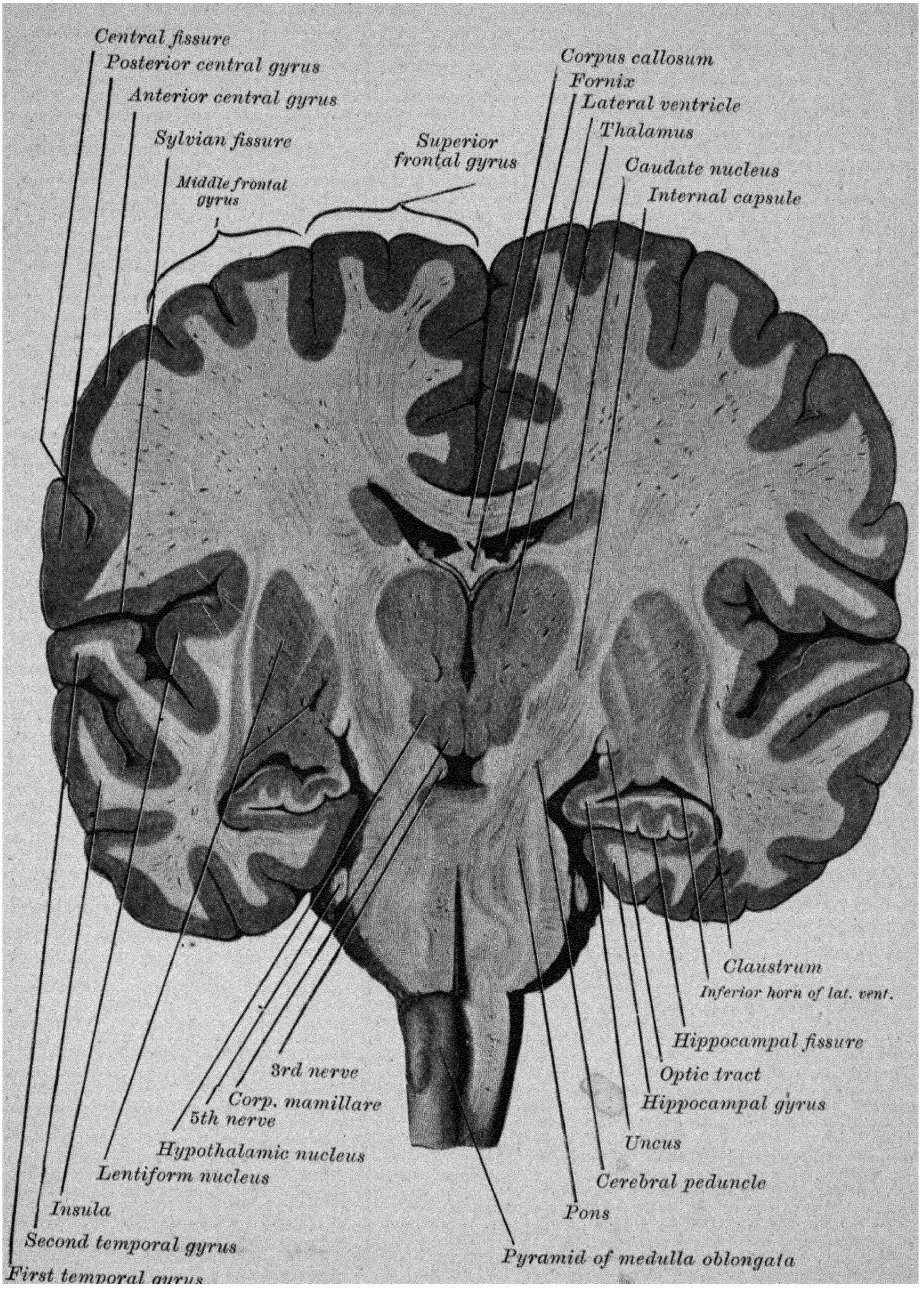


FIG. 133.—VIEW FROM THE FRONT OF A CORONAL SECTION OF AN ADULT BRAIN MADE THREE INCHES BEHIND THE FRONTAL POLE. The specimen was hardened and cut *in situ*. (J. Symington.)

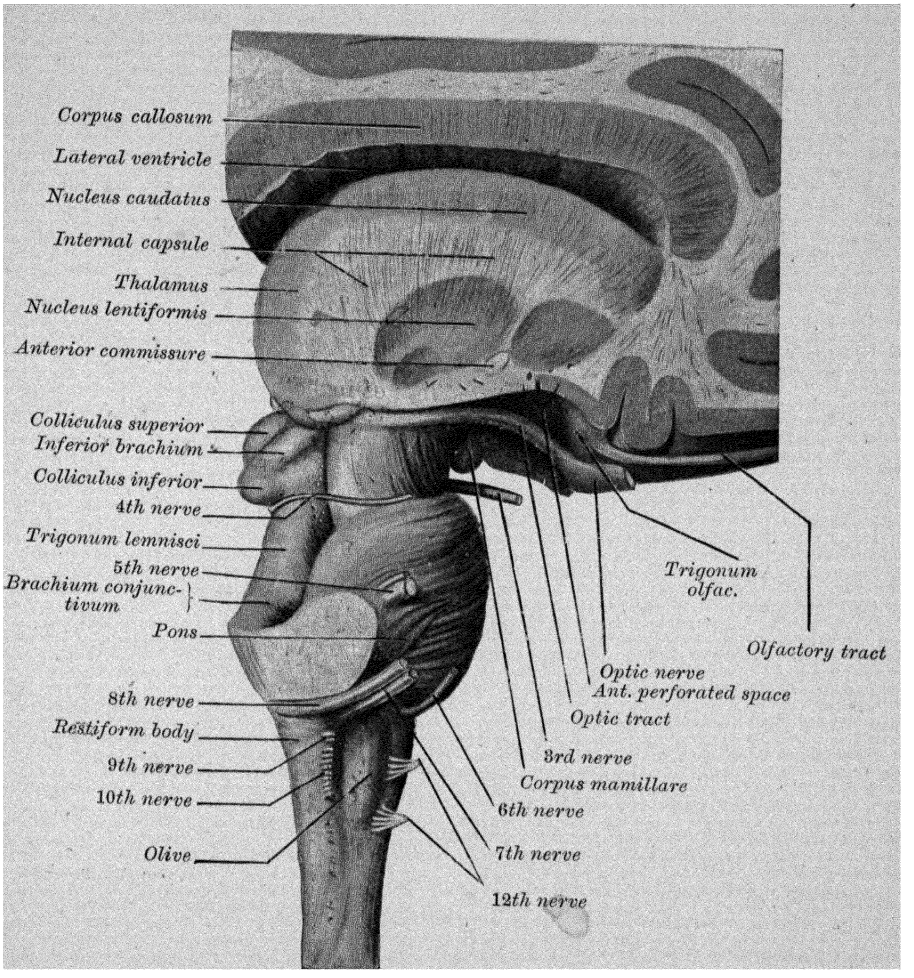
the posterior lobe of the pituitary body; the other extends backwards from the posterior part of the roof to enter the pineal body.

The two cerebral hemispheres conceal in a view from above all the other parts of the brain, and in a view from the lateral aspect all except the medulla oblongata and the lower parts of the pons and of the cerebellum. The surface of the hemispheres consists of a layer of grey matter, 2 to 3 mm. thick, forming the cortex; in nearly the whole of its extent this is thrown into numerous folds (convolutions or gyri), separated by fissures or sulci. Beneath the cortex is a large mass of white matter composed of nerve-fibres which connect the different parts of the brain with one another, or with the spinal cord. In addition to its cortical substance, the cerebrum contains various masses of grey matter situated more deeply and closely related to its peduncles, such as the corpora striata, thalami, &c. These are known collectively as the basal ganglia of the cerebrum. The great longitudinal fissure separates the two hemispheres in the major part of their extent, but is interrupted by certain commissures which cross the median plane and serve to unite the hemispheres.

The development of lateral outgrowths from the median part of the end-brain to form the cerebral hemispheres is associated with a median thickening of the wall of the neural tube just above the lamina terminalis and in front of the foramen of Monro. In this thickened area transverse commissural fibres appear. Those in the ventral part of the area become the small round anterior commissure, and those situated more dorsally form the corpus callosum or great transverse commissure, which grows forwards, upwards, and backwards, and constitutes the main connexion between the two hemispheres. As is evident from the examination of a median section of the brain (see fig. 132), the backward growth of the corpus callosum is so extensive that it overlaps not merely the third ventricle and the pineal body, but also the mid-brain and a considerable part of the cerebellum. Below the corpus callosum is the fornix. It is composed principally of two bundles of longitudinal fibres, which meet in the median plane in a part of their course. Posteriorly it is in close contact with the corpus callosum, but more anteriorly it is separated from it by a gradually widening interval as the longitudinal bundles of the fornix curve round to pass over the foramen of Monro and dip down into the hypothalamic region. Occupying this interval between the corpus callosum and the fornix is a narrow median cleft, triangular in shape, bounded laterally by two thin layers of nervous tissue known as the septum pellucidum. This cleft—the so-called fifth ventricle (cavum septi pellucidi)—differs from the other four (or true) ventricles in the fact that it is not formed from any part of the embryonic cerebral vesicles, nor is it lined, like the other ventricles, by ependymal epithelium. It is, moreover, completely closed, and does not communicate with the true ventricles. Further, in all the true ventricles some part of the nervous wall consists merely of a layer of ependyma-cells, and in these situations the blood-vessels of the pia mater are highly developed and form vascular tufts which project towards the cavity of the ventricle, pushing the ependyma-cells in front of them. In this way the choroid plexuses of the two lateral, the third, and the fourth ventricles are produced. No such vascular prominence is found in connexion with the fifth ventricle.

THE MEDULLA OBLONGATA AND PONS.

The medulla oblongata and pons are developed from the ventral portion of the posterior cerebral vesicle, and the upper or pontine part becomes differentiated from the lower portion or medulla oblongata, by a bulging (*tuber annulare*) of its



A SECTION OF PART OF THE CEREBRUM. Natural size. (J. Symington.)
The section of the cerebrum was inclined from below upwards and somewhat towards the middle line.

ventral wall. This prominence is due to the transversely coursing fibres of the middle peduncle of the cerebellum, many of which arch upwards so as to conceal from the ventral aspect the lower parts of the pedunculi cerebri.

The combined mass of the medulla oblongata and pons has an oblong or rhomboidal form, being expanded in the middle, where it is continuous with the cerebellar peduncles, and tapering towards the spinal cord below and the mid-brain above.

The **medulla oblongata** or **spinal bulb** is continuous below with the spinal cord, on a level with the lower margin of the foramen magnum. When the brain and spinal cord are removed together from their cavities it is not easy to define sharply the boundaries between the two. The hypoglossal nerves are attached to the medulla oblongata and the first pair of cervical nerves to the spinal cord, but occasionally some of the upper fibres of the first cervical spring from the medulla oblongata. The medulla oblongata is considered to extend to the lower end of the decussation of the pyramids, but the extent to which this decussation is visible on a surface view varies considerably in different cases.

The upper limit of the medulla oblongata is marked on the ventral and lateral aspects by the lower margin of the mass of transverse fibres which form the prominence of the pons, while its dorsal surface is directly continued into that of the pons without any visible line of demarcation between them. The ventral surface lies behind the basilar groove of the occipital bone, but separated from it by the vertebral arteries and some cerebrospinal fluid, and its dorsal or posterior surface occupies the fossa named the vallecula between the hemispheres of the cerebellum. From its front and sides the sixth to the twelfth cerebral nerves issue.

The length of the medulla oblongata from the lower part of the decussation of the pyramids to the pons is nearly an inch (20 to 24 mm.). At its lower end it is about half an inch in breadth (12 mm.); less in the dorso-ventral direction (9 mm.). From this level it enlarges in both these directions, at first slowly and then more rapidly, so that where it joins the pons it measures fully three-quarters of an inch (18 mm.); transversely rather less (15 mm.) from before backwards. Although in its general form it resembles the spinal cord, even the external markings of the medulla oblongata indicate important structural differences between the two.

The *ventral* and *dorsal median fissures* which partly divide the spinal cord are continued into similar fissures in the medulla oblongata. The ventral fissure terminates immediately below the pons in a recess, the *foramen cæcum* of Vicq d'Azyr; it is partly interrupted below by the decussating bundles of the pyramids; the dorsal fissure becomes gradually shallower as it is continued upwards to the lower end of the fourth ventricle, where it may be considered to terminate.

Certain of the cerebral nerve-roots issue from the lateral and ventro-lateral aspects of the bulb along imperfectly defined longitudinal sulci, which, as in the spinal cord, may be termed dorso-lateral and ventral respectively. Along the dorso-lateral sulcus issue from above downwards the *glosso-pharyngeal, vagus*, and *bulbar part of the accessory nerves*. This sulcus forms a shallow groove below, but above is so feebly marked that it can only be recognised by the line of exit of the nerves. This line passes near the dorsal margin of an oval prominence on the surface of the bulb termed the *olive*, but is separated from that prominence by a tract of longitudinal fibres. The larger part of the accessory nerve is attached to the spinal cord, its fibres joining the cord between the dorsal roots of the upper six cervical nerves and the ligamentum denticulatum. Not infrequently the accessory appears to arise along with the dorsal root of the first cervical nerve, more rarely also with the second cervical. At the junction of the pons with the medulla oblongata the seventh nerve is seen issuing from the brain just above the glosso-pharyngeal nerve, and still higher the roots of the fifth are given off from the lateral aspect of the pons nearly in the same line (see fig. 135). The dorso-lateral sulcus of the medulla oblongata is not precisely a continuation upwards of the groove on the spinal cord to which the dorsal roots are attached, but is situated rather farther forwards than the latter so that it appears on the lateral surface of the

medulla oblongata. In transverse sections of the lower part of the medulla oblongata it is seen that the bundles of fibres of these nerve-roots traverse the substance of the bulb to reach a group of nerve-cells in the grey matter near the central canal and thus mark off a somewhat oval area on each side at the posterior part of the section. This is the dorsal area of the medulla

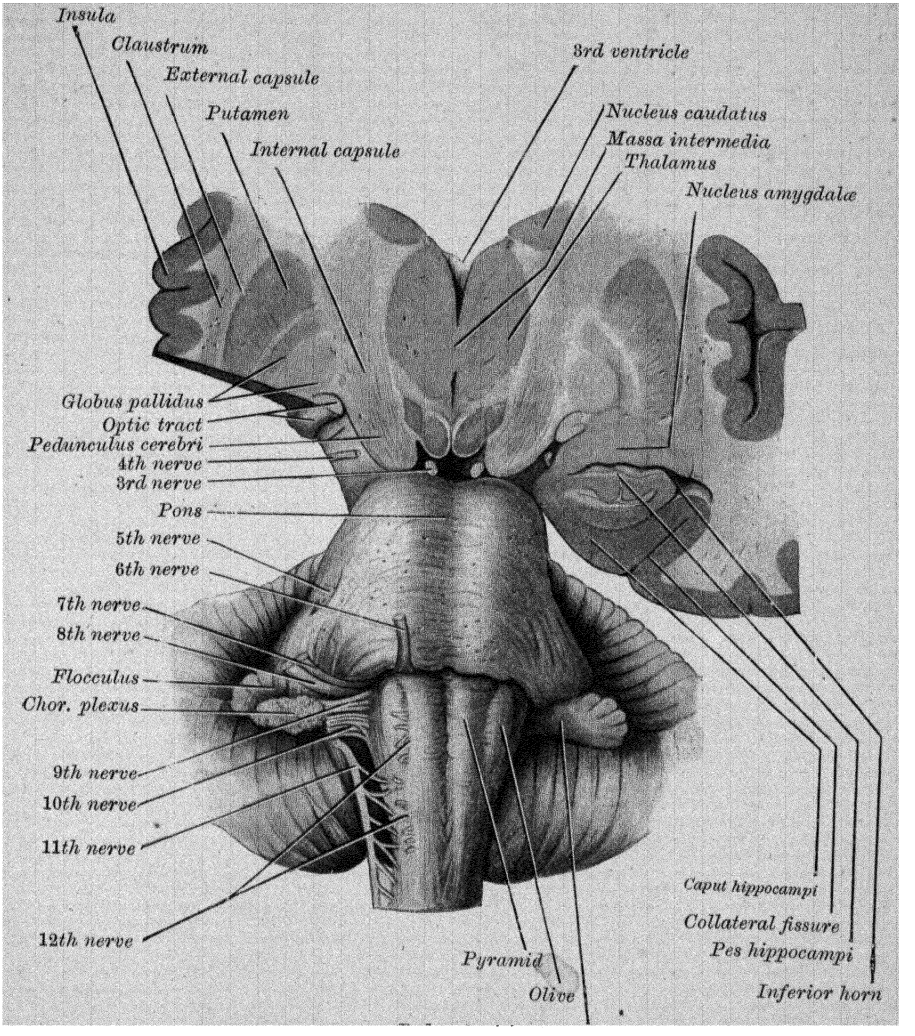


FIG. 135.—ANTERIOR OR VENTRAL ASPECT OF MEDULLA OBLONGATA AND PONS, AND A CORONAL SECTION OF PART OF THE CEREBRUM. Natural size. (J. Symington.)

On the right side the temporal lobe is removed to expose side of pedunculus cerebri, the optic tract, and the fourth nerve. The cerebral nerves attached to medulla oblongata and pons are shown on one side only.

oblongata, and the tracts of white fibres which can be traced upon the surface of this part are the dorsal columns.

The line of origin of the ventral roots of the spinal nerves, although not marked in the spinal cord by a distinct furrow like that at which the dorsal roots are attached, yet, when traced upwards into the bulb, deepens into a well-marked longitudinal groove which is continued almost vertically as far as the lower

border of the projecting mass of the pons. In its upper part this groove separates the olivary prominence from the prominence of the pyramid. Just below the olive it is often obliterated for a certain part of its course by a band of transverse fibres. The root-bundles of the *hypoglossal nerve* (fig. 135) pass out from this furrow, and those of the *sixth nerve* emerge in the same line with it, but at the lower border of the pons. In transverse sections of the medulla oblongata and pons these root-bundles may be traced back through the substance of the organ to a group or column of nerve-cells situated in a portion of grey matter close to the ventro-lateral side of the central canal in the lower closed part of the bulb, and close to the middle of the fourth ventricle in the upper opened-out parts. This portion of grey matter is continuous below with part of the ventral horn, and the roots of the hypoglossal and sixth nerve correspond generally with the ventral roots of the spinal nerves. In traversing the substance of the bulb they mark off a ventral area, wedge-shaped in transverse section, which is placed between them and the ventral median fissure. This area is on the surface marked by the prominence known as the *pyramid*, which corresponds in position (but only to a small extent in the fibres of which it is composed) with the ventral column of the spinal cord. The remainder of the transverse section of the bulb, after the dorsal and ventral areas are deducted, lies between the line of nerve root-bundles of the hypoglossus and sixth on the one side, and that of the successive bundles of the accessory, vagus, glosso-pharyngeal, and facial on the other. This is termed by Flechsig the lateral area, and on the surface it is marked by a continuation of part of the lateral column of the cord, and by the prominence of the olive already alluded to.

It will be remembered that in the upper region of the spinal cord a small portion of the dorsal column is marked off from the rest by a well-developed pia-matral septum, and is indicated on the surface by a distinct longitudinal prominence bounded laterally by a shallow groove. The portion thus marked off is the dorso-mesial column (tract of Goll), and the prominence, which is continued up into the medulla oblongata, becomes there still better marked, and is known as the *funiculus gracilis* (fig. 136). This, as it is traced upwards, especially as the fourth ventricle is approached, broadens out into an expansion termed the *clava*, and as the ventricle opens out the clavæ of opposite sides diverge and form the lateral boundaries to a triangular area of grey matter known as the *calamus scriptorius* of the fourth ventricle. Above, the clavæ are tapered off and soon become no longer traceable.[1]

Between the dorso-mesial column and the line of entrance of the dorsal roots of the cervical nerves there is found in the upper part of the cord a distinct column—viz. the dorso-lateral column (tract of Burdach). This is prolonged into the medulla oblongata as the *funiculus cuneatus*. Opposite the clava it shows a swelling called the *cuneate tubercle*, above which the fasciculus gradually disappears. Outside the funiculus cuneatus, and between it and the line of roots of the accessory nerve, another longitudinal prominence is caused by the fact that the substantia gelatinosa of Rolando begins near the lower end of the bulb to project towards the surface as a distinct prominence, narrow below but broadening as it is traced upwards, where it forms a considerable eminence known as the *tubercle of Rolando*. The longitudinal prominence is termed by Schwalbe the *funiculus of Rolando*. The clava and the cuneate and Rolandic tubercles are more distinct in the fœtus than in the adult.

In the upper part of the medulla oblongata the cuneate funiculus is covered by a set of fibres (*external arcuate fibres*) which issue from the ventral

[1] The funiculi graciles with their clavæ have been described as the *posterior pyramids*.

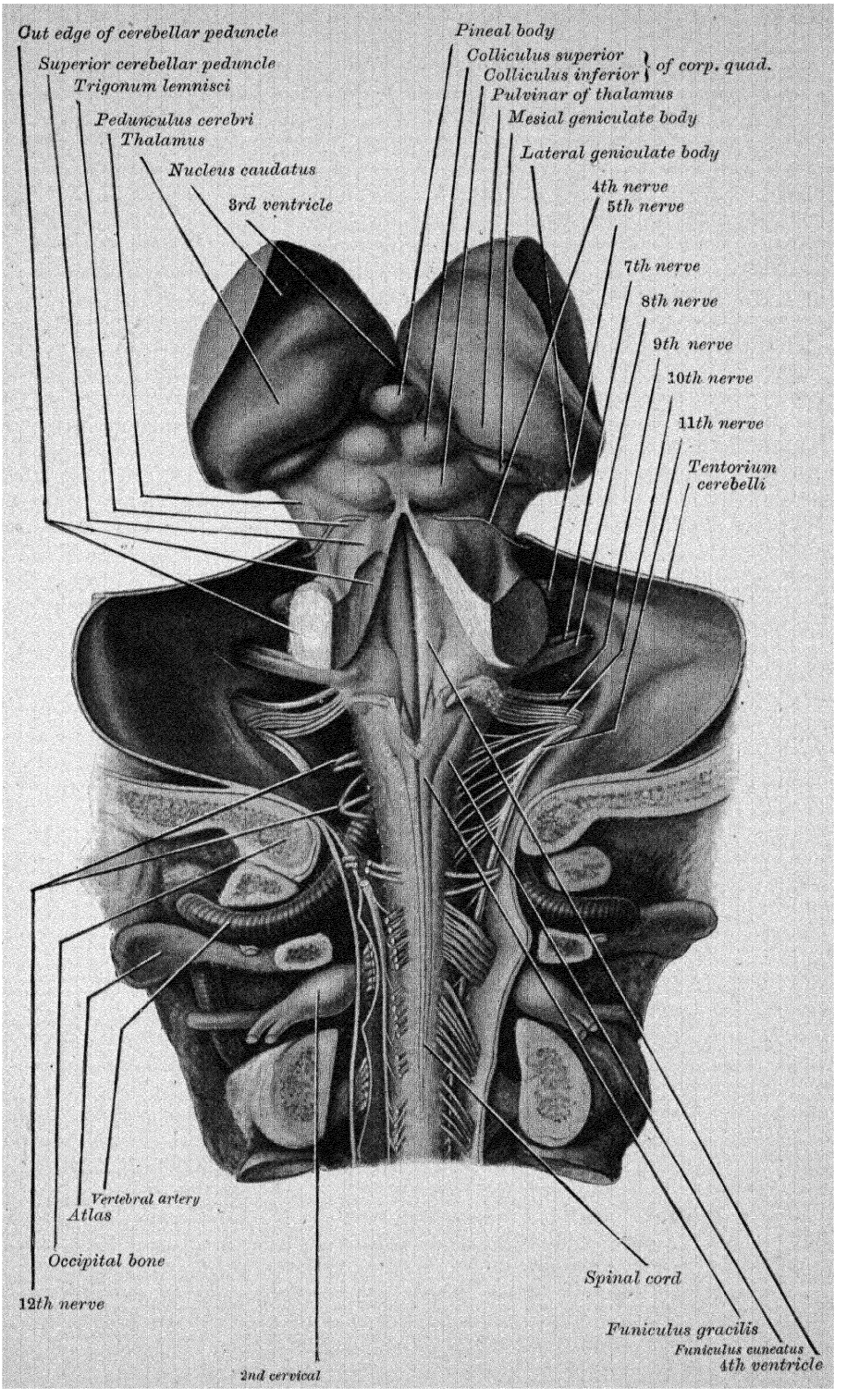


Fig. 136.—View from dorsal aspect of upper part of spinal cord, medulla oblongata, pons, fourth ventricle, mid-brain, thalamus, &c., dissected in situ. Natural size. (J. Symington.)

median fissure and, passing laterally over the surface of the pyramid and olive, turn obliquely upwards. There is also a narrow strand of fibres from the lateral column of the cord, marked by its white appearance, which joins this tract of oblique fibres just above the level of the tubercle of Rolando: this is the dorsal spino-cerebellar tract which has been already noticed in the description of the spinal cord. These two sets of fibres are reinforced by a large number of fibres coming from the opposite side of the bulb and passing from and through the olives. The whole mass of fibres thus produced forms a rounded, prominent cord, the *corpus restiforme*, or rope-like body (fig. 134), which passes directly into the corresponding hemisphere of the cerebellum, constituting its *inferior peduncle*.

The lateral column of the spinal cord appears, on the surface, to be directly continued upwards into the corresponding part of the medulla oblongata. In reality, however, a considerable tract of the white fibres—that which in the spinal cord we have noticed as the lateral pyramid-tract—is found, if we trace it upwards from the cord, to cross obliquely in stout bundles through the grey matter of the ventral horn, and across the ventral median fissure to the other side of the bulb, where it forms the mesial and larger part of the pyramid. The rest of the lateral column can be traced vertically upwards (with the exception of the dorsal spino-cerebellar tract, which, as just noticed, passes backwards into the restiform body) as far as the lower end of the olive, where its longitudinally coursing fibres become concealed by this prominence and by the arched fibres already noticed.

The *olive* or *lower olive* (figs. 134, 135) is, as its name implies, an olive-shaped prominence, which lies in the upper part of the bulb, immediately above the apparent termination of the lateral column, and extending nearly as far as the lower border of the pons, being only separated from this by a deep groove in which is sometimes a small band of arched fibres. The line of exit of the hypoglossal nerve-roots lies on its inner or mesial border, that of the accessory, vagus, and glosso-pharyngeal roots along its outer side; but the latter are separated from it by a groove in which longitudinal fibres prolonged from the ventro-lateral cerebellar tract can be seen. Sometimes there is a small longitudinal tract running along its inner border also, and in such case, with the arched fibres above and below, the olive appears to be entirely enclosed by a fibrous strand, which has sometimes been described as its capsule (*siliqua olivæ*). This name is, however, more applicable to a layer of fibres which immediately surrounds the dentate nucleus of the olive. The longitudinal tracts on either side of the olive are often concealed in great measure by the arched fibres, which may form a complete superficial layer over the olive, and indeed over the whole anterior and lateral surface of this upper part of the medulla oblongata.

The ventral columns of the cord, although on superficial inspection they appear to be prolonged into the pyramids of the bulb, are so only to a small extent. For the lateral pyramid-bundles, crossing the ventral median fissure from the lateral column, as above described, can be traced upwards close to that fissure, and, uniting with the comparatively small anterior pyramid-bundle, constitute the prominence known as the pyramid. The prolongation upwards of the rest of the ventral column of the cord lies deeply, being altogether concealed from view by the pyramids.

The *pyramids* (fig. 135) are more prominent above than below. They are bounded mesially by the ventral median fissure, and laterally by the olivary bodies, being separated from these by the groove from which the roots of the hypoglossal nerve issue. At their upper end they are constricted, and become more completely separated from the rest of the medulla oblongata.

They are here very frequently crossed by a band of arched fibres, the *ponticulus* of Arnold. Each pyramid then enters the substance of the pons in one large bundle, which soon breaks up into several bundles: these may be traced through the pons into continuity with fibres in the corresponding peduncle of the cerebrum.

The *decussation of the pyramids* is the name given to the obliquely crossing bundles of the pyramid-tract which are seen in the ventral median fissure at the lower part of the medulla oblongata. The extent to which the decussation is visible varies considerably in different individuals; for in some the bundles take a deeper, in others a more superficial course. Further, in some cases a larger share than usual of the longitudinal fibres of the pyramids passes down in the ventral pyramid-tract and a correspondingly smaller share in the lateral pyramid-tract. And since the ventral tract, which in the pyramid is external to the lateral tract, does not cross in the medulla oblongata, but merely passes obliquely at its lower end to attain the side of the ventral median fissure, the decussation in these cases is of less extent. On the other hand, in rare cases, the whole of the fibres of the pyramid may cross over at the lower part of the bulb and become lateral pyramid-tract, in which case the ventral or uncrossed tract is wanting in the cord, and the bulbar decussation is very well marked. All transitions are found between these two conditions (see p. 94).

The **pons** (pons Varolii) forms a prominence on the ventral aspect of the brain above the medulla oblongata, below the pedunculi cerebri, and between the lateral hemispheres of the cerebellum (fig. 135). It is marked by transverse fibres which on each side are gathered together into a compact mass, passing into the cerebellum, and named the *middle peduncle of the cerebellum*. The *fifth nerve* is attached to the side of the pons near its upper border and close to where it becomes continuous with the middle peduncle of the cerebellum. The ventral surface of the pons is convex from above, downwards, and from side to side, but has a shallow median groove along which the basilar artery runs, and it is perforated by small branches of the artery. The groove is in some measure due to the circumstance that the pyramids of the medulla oblongata are continued up through the pons with a slightly divergent course, and thus produce a prominence on either side of the middle line, covered, however, by the superficial transverse fibres. The lower border of the pons is transverse, while the upper one external to its median depression inclines obliquely outwards and downwards.

The dorsal part of the pons is free over a triangular area, which forms the upper part of the anterior (ventral) wall of the fourth ventricle; external to this it is continuous with the superior cerebellar peduncles.

The pons is about an inch (25 mm.) long, rather more broad, and somewhat less from before backwards.

In a series of horizontal sections, the pons is seen to consist of a ventral or basal portion (*pars basilaris pontis*) and a dorsal or tegmental part (*pars dorsalis pontis*). The ventral portion consists of transverse cerebellar fibres, which in fresh specimens have a white appearance; between these the longitudinal bundles of pyramid-fibres, which are mixed with a considerable quantity of grey matter (*nuclei pontis*), are readily distinguished. Sections across the upper half of the pons show it to be bounded on each side by a free convex border, which reaches as far inwards on the dorsal aspect as a longitudinal groove between the pons and the superior cerebellar peduncle; but in sections lower down, the pons passes on either side without any distinct line of demarcation into the middle peduncle of the cerebellum. The *pyramid-fibres* near the lower end of the pons form two compact masses, situated one on each side

of the median plane, but as they are traced upwards through the pons they are seen to spread outwards and become divided into bundles flattened ventro-dorsally. These fibres are most numerous in the upper part of the pons. The dorsal or tegmental part of the pons has to the naked eye a fairly uniform grey colour, which appears to be due to the fact that its fibres, most of which run in a longitudinal direction, are mixed with a large amount of grey matter. The tegmental part diminishes in size from below upwards, so that while near the lower end of the pons it measures about 15 mm. from side to side and 10 mm. from before backwards, towards the upper end the corresponding measurements are about 10 mm. by 6 mm. This part forms the floor of the upper division of the fourth ventricle, but it also reaches outwards on each side beyond the lateral borders of the ventricle where it comes into relation with the fibres of the middle and superior cerebellar peduncles. As the ventricle narrows, the pigmented mass of nerve-cells forming the *locus cæruleus* is seen on each side in the lateral part of its floor. The other nuclei and the various tracts of nerve-fibres cannot be satisfactorily distinguished by the naked eye in unstained specimens.

The fourth ventricle.—The external characters of the medulla oblongata and pons may be completed by a description of those parts of these structures which enter into the boundaries of the fourth ventricle.

This ventricle lies behind the upper half of the medulla oblongata and behind the whole length of the pons, so that the anterior (ventral) wall or so-called floor of the ventricle is made up of a lower or medullary, and an upper or pontine portion. Each of these is triangular and their bases are in contact; consequently the floor is lozenge- or diamond-shaped, and is sometimes named the *fossa rhomboidalis*. The pointed lower end of the ventricle has the shape of a writing-pen, and is termed the *calamus scriptorius* (fig. 136). At its widest part the fourth ventricle is continued outwards on either side, round the upper end of the medulla oblongata, nearly to the outer border of the olivary body in the form of the pointed *lateral recess*. From this point its upper part again narrows, converging gradually above to be continued into the comparatively narrow Sylvian aqueduct.

The *lateral boundaries of the ventricle* are, in its lower or medullary part, the clavæ of the funiculi graciles, the funiculi cuneati, and the restiform bodies; in its upper half the *superior peduncles of the cerebellum* (fig. 136). These pass gradually to the roof of the ventricle as they extend upwards. They are at first separated from one another by a tolerably wide interval, which, however, gradually narrows near the end of the ventricle, the two peduncles of opposite sides there approaching one another, and their margins coming in contact.

The *floor or ventral boundary of the fourth ventricle* is generally marked at its widest part—*i.e.* at the level of the lateral recesses—by some transverse white lines, which cross the grey matter of the floor, and are known as the *striæ medullares seu acusticæ* (fig. 137, *str.*). These striæ vary greatly in number, breadth, direction, and degree of distinctness, while occasionally they are absent. It is mainly owing to these variations that the floor of the fourth ventricle presents such a variety of appearances. The striæ are caused by bundles of white fibres which are connected laterally with the cochlear division of the auditory nerve, and mesially pass to the median groove and raphe, where they disappear in a ventral direction.

One bundle of these striæ is sometimes seen, usually on one side only, taking a course obliquely upwards and outwards, passing at the lateral boundary of the ventricle into the middle cerebellar peduncle (*aberrant bundle of striæ medullares, Klangstab* of Bergmann).

The floor of the ventricle is bisected by a slight median groove. A little on either side of this groove, and immediately below the striæ medullares, is a small triangular depression (*inferior fovea*, fig. 137, *i.f.*), the apex of which extends only as far as the striæ, while the base is prolonged into two grooves extending one from each angle. The inner of the two grooves passes with a slightly curved course towards the point of the calamus scriptorius, and thus cuts off a pointed triangular area, which is bounded mesially by the median sulcus, and the base of which is turned towards the striæ acusticæ. This area (*trigonum hypoglossi*) is slightly prominent, and constitutes the lower end of the fasciculus teres; in it is the prolongation of the tract of nerve-cells from which the roots of the hypoglossal nerve take origin. The outer of the two grooves passes downwards with a slight outward obliquity nearly to the lateral boundary of the ventricle, and marks off externally another triangular area (*trigonum acustici*, *t.a.*), the base of which is also directed upwards, where it can be traced into a prominence (best marked in children) over which the striæ acusticæ course. To this prominence the name *tuberculum laterale seu acusticum* has been applied, since the cochlear part of the acoustic nerve comes into connexion with its grey matter and with that of the trigonum acustici.

Included between the two grooves is a third triangular area (*trigonum vagi*), the apex of which is at the inferior fovea, while its base looks downwards and outwards. This area has a distinctly darker colour than the rest of the floor of the ventricle, and especially than the trigonum hypoglossi on the inner side, which has a whitish-grey appearance, and it has accordingly been named the *ala cinerea* (*a.c.*). Towards the apex it is somewhat depressed, but below it is elevated into a distinct prominence (*eminentia cinerea*). It corresponds with the dorsal nucleus of the vagus, and superiorly, near the inferior fovea, of the glosso-pharyngeal nerve.

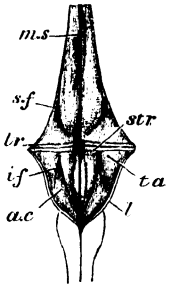


FIG. 137. — ANTERIOR BOUNDARY (FLOOR) OF THE FOURTH VENTRICLE. Natural size. (E. A. Schäfer.)

m.s, median sulcus; *str*, striæ acusticæ, marking the limit between the pontine part of the ventricle and the medullary part or calamus scriptorius; *lr*, lateral recess; *if*, inferior (posterior) fovea; *a.c*, ala cinerea; *ta*, trigonum acustici; *s.f*, superior (anterior) fovea, close to the lateral margin of the superior part of the ventricle.

Below (postero-lateral to) this area is an uneven elongated brownish eminence (*area postrema* of Retzius) directed downwards and inwards along the lateral border of the calamus scriptorius to the opening of the central canal. It is usually separated from the area cinerea by a white ridge termed the *funiculus separans*.

The central canal as it approaches the fourth ventricle expands in a dorsal direction to form an elongated median cleft (fig. 144, p. 130). This cleft has on each side two grooves dividing the lateral wall into three longitudinal zones—dorsal, intermediate, and ventral. The dorsal zone, corresponding to the alar lamina of His, turns outwards on the floor of the fourth ventricle to form the area postremæ, the ventral zone or basal lamina becomes the trigonum hypoglossi, and the intermediate zone passes into the ala cinerea. The obex (see next page) is formed from the thickened free edge of the roof-plate.[1]

Above the striæ acusticæ the floor of the fourth ventricle is marked in the middle of each lateral half by a distinct somewhat angular depression in a line with the inferior fovea, from which it is separated by the eminence over which the striæ acusticæ pass. This depression is termed the *superior fovea* (*s.f.*). Between it and the median sulcus is the prolongation of the

[1] J. T. Wilson, Jour. Anat. and Phys. vol. xl.

funiculus teres, which is prominent (*eminentia teres*) opposite the fovea, but becomes gradually less so above and below. Extending from the superior fovea to the upper end of the ventricle, where this narrows to the Sylvian aqueduct, is a shallow depression (*locus cæruleus*) distinguished in the adult by its dark-grey or slaty tint, which is due to a subjacent tract of pigmented nerve-cells (*substantia ferruginea*).

Dorsal (posterior) wall, or roof of the fourth ventricle (figs. 132, 183).—While the floor is a nearly flat lozenge-shaped area, the roof, which is covered by the cerebellum, is tent-like, presenting a deep transverse sulcus (*fastigial* or *posterior recess*) above its middle, above and below which it slopes towards the floor. The roof may therefore be divided into two parts, upper and lower. The upper part is formed by the *superior (anterior) medullary velum*, and the *superior (anterior) cerebellar peduncles*; these are separated from one another by longitudinal grooves. The lower part is more irregular in form and more complicated in structure. Mesially the *nodule* of the inferior vermiform process of the cerebellum projects prominently towards the ventricle, and on either side of this the *inferior (posterior) medullary velum* is prolonged outwards to the lateral recess. From the nodule and the free edge of the inferior medullary velum the pia mater, covered on its ventricular surface by a layer of ependyma-cells, is prolonged downwards on to the back of the medulla oblongata, to which it is attached along the lateral aspects of the calamus scriptorius. In the lower part of this fold of pia mater is a median aperture termed the *foramen of Magendie (apertura medialis ventriculi quarti)*. Opposite each lateral recess the pia mater extends outwards to form its posterior wall, and at its extremity is an aperture known as the *foramen of Luschka (apertura lateralis ventriculi quarti)*. This opening is placed behind the glosso-pharyngeal and vagi nerves, and in front of the inner part of the flocculus.

Both the median and lateral openings, although varying considerably in size and form, are fairly constant. Thus Retzius found the foramen of Magendie present in 98 out of 100 brains, and the foramina of Luschka in 195 out of 200.

The epithelium covering the ventricular surface of the pia mater is continuous with the epithelium on the floor of the ventricle, but it is somewhat thickened by the addition of white nervous matter before reaching the lateral boundary of the floor. This thickening is left as a slightly prominent and often ragged membrane when the epithelium of the roof of the ventricle is torn off with the pia mater. It commences internal to the clava, and accompanies the lateral boundary for about a quarter of an inch (6 mm.); it then turns outwards over the posterior surface of the restiform body and terminates close to the place where the roots of the vagus and glosso-pharyngeal issue. It is termed the *tænia* or *ligula* (fig. 144), and its upper transverse portion forms the lower boundary of the lateral recess of the ventricle. Another thickening of the roof is sometimes seen at the apex of the ventricle covering the point of the calamus scriptorius; this is named the *obex* (seen in fig. 136).

Two longitudinal vascular inflexions of the pia mater, known as the *choroid plexuses of the fourth ventricle*, project from the lower half of the posterior wall into the cavity, one on either side of the middle line, covered everywhere by the epithelium of the roof. Offsets from these pass also into the lateral recesses, from the apices of which they emerge and appear below the flocculus and behind the ninth and tenth nerves (see fig. 135). These vascular tufts were termed by Bochdalek the *cornucopiæ*. The epithelial layer of the roof of the ventricle follows all the convolutions of the choroid plexuses, but is nowhere pierced by them; it is generally described as the epithelium of the plexuses.

The dorsal outgrowth from the posterior cerebral vesicle from which the cerebellum is formed only involves the intermediate part of that vesicle. The cerebellar thickening extends from this part in a cephalic and caudal as well as in a dorsal direction so as to overlap and conceal from the dorsal aspect the other parts derived from this vesicle, which separate the cerebellum from the fourth ventricle. This is well seen in a median section (fig. 132), from which it may also be observed that the cephalic and caudal borders (represented by the lingula and nodule) remain near one another. These are covered on their ventricular surfaces by the superior and inferior medullary vela, so that it is only at the posterior recess where these join the cerebellum that the latter really forms part of the posterior wall of the fourth ventricle, although at first sight it appears to constitute the dorsal boundary of that space.

INTERNAL STRUCTURE OF THE MEDULLA OBLONGATA.

The internal structure of the medulla oblongata, like the external form, will be best understood by tracing its several parts upwards from the spinal cord;

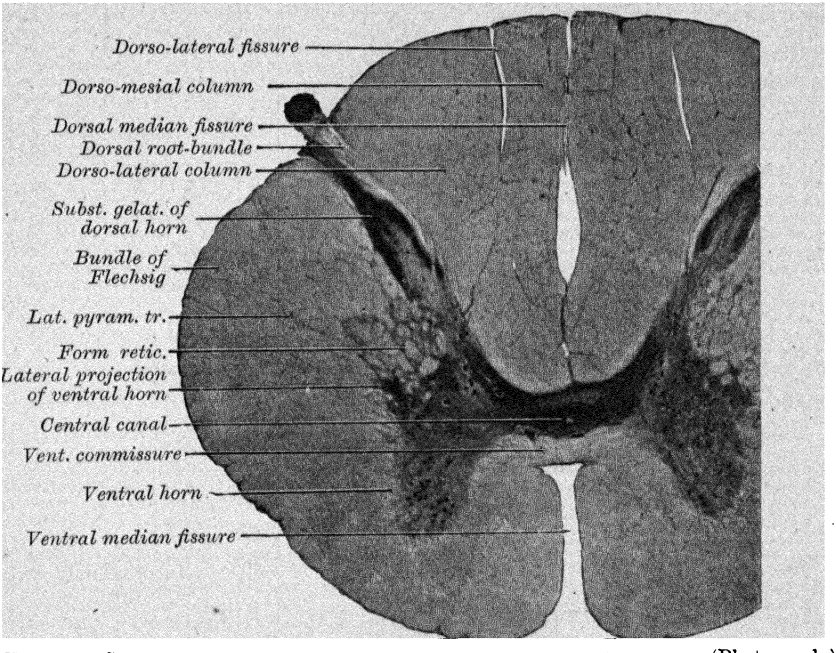


FIG. 138.—SECTION OF HUMAN SPINAL CORD FROM UPPER CERVICAL REGION. (Photograph.) Magnified about 8 diameters. (E. A. Schäfer.)

and this can be most readily done by a comparison of the appearances of successive transverse sections.

The first changes are produced, in its internal structure as in its external form, by the passage of the fibre-bundles of the crossed pyramid-tract from the lateral column of the cord (fig. 138) obliquely through the base of the ventral horn, and across the ventral fissure (figs. 139 to 142), to form, along with the ventral pyramid-tract (which now becomes separated from the fissure by the fibres of the lateral tract) and the uncrossed lateral pyramid-tract of the cord, the *pyramid* of the medulla oblongata. By this abrupt passage of a large number of white fibres through it, the ventral horn is broken up, and one part, the caput cornu, is entirely separated from the rest; while the base of the horn remains as a small portion of grey matter close to the ventro-lateral aspect of the central canal. Within this *central grey matter* two groups or columns of large nerve-cells make their

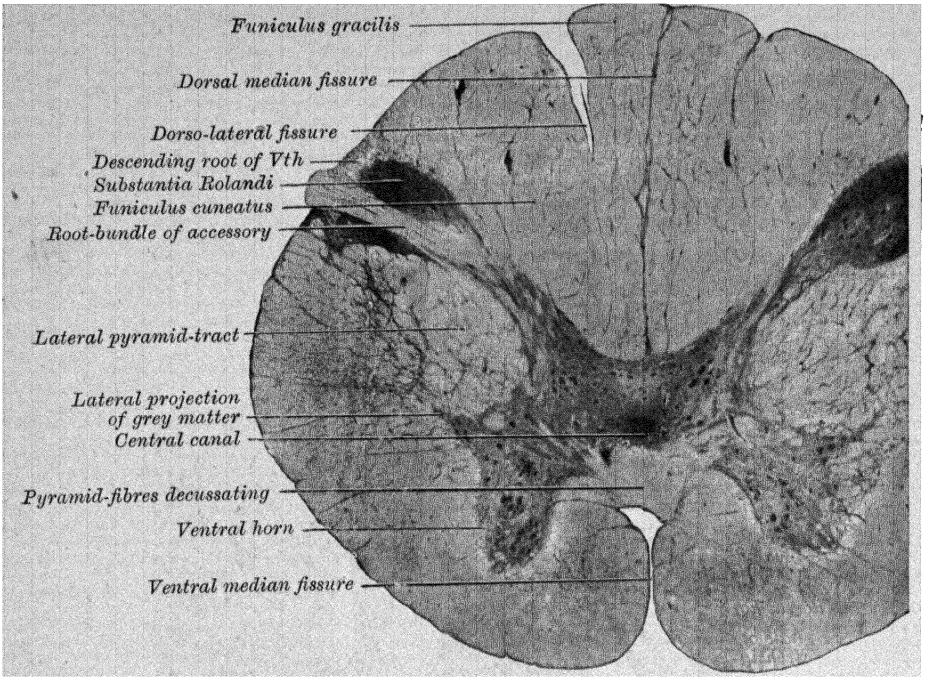


FIG. 139.—SECTION ACROSS THE LOWERMOST PART OF THE MEDULLA OBLONGATA AT ITS JUNCTION WITH THE MEDULLA SPINALIS. Magnified 6 diameters. (E. A. Schäfer.)

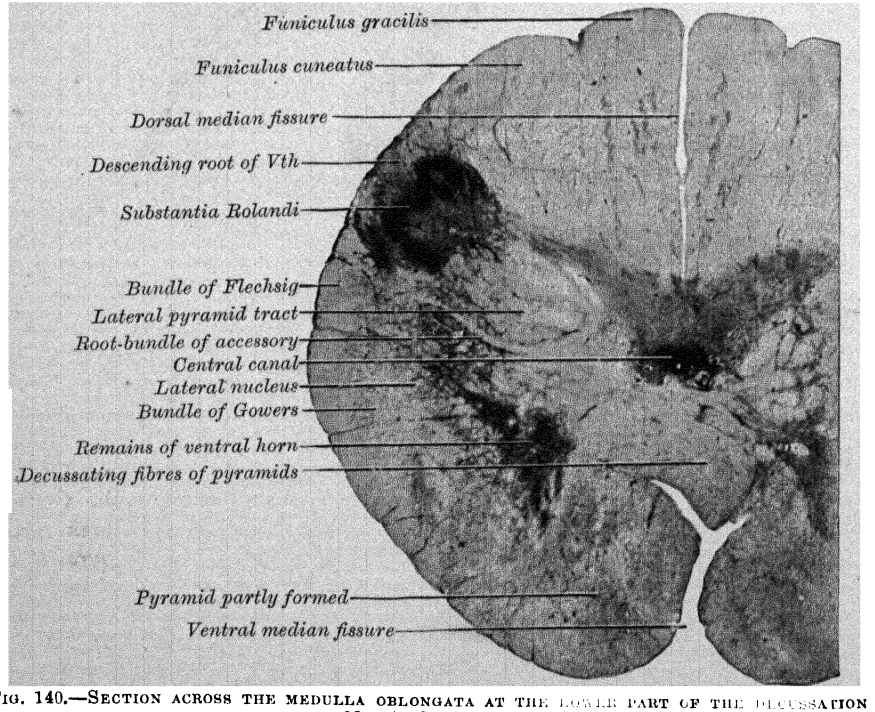


FIG. 140.—SECTION ACROSS THE MEDULLA OBLONGATA AT THE LOWER PART OF THE DECUSSATION OF THE PYRAMIDS. Magnified 6 diameters. (E. A. Schäfer.)

appearance. One of these lies ventro-lateral to the canal (fig. 143, *N. XII.*) and is traceable upwards in the same situation until the central canal opens out into the fourth ventricle (figs. 144 to 148). This is the *hypoglossal nucleus*; its cells are similar in character to those of the ventral-horn cells of the spinal cord — that is to say, they are large and multipolar with well-marked Nissl granules. Their dendrons extend a considerable distance from the cell-body: some pass across the middle line into the nucleus of the opposite side. The nucleus is very richly supplied with arborising collaterals derived from the secondary sensory paths (of the fifth, tenth, and eleventh cerebral nerves) adjacent to it: some of these collaterals come from the opposite side. No collaterals enter the nucleus from the pyramid-tract. At its ventral part there is a space nearly free from cells, and below this is a compact nucleus —the *nucleus of Roller* (fig. 148, D)—which, however, does not give off fibres to the twelfth nerve, but sends its axons into the adjacent white columns of the formatio reticularis, in which they bifurcate, one branch ascending and the other descending. It is probably a sensory nucleus of the second order (Cajal). The other group of cells lies dorso-lateral to the canal (fig. 143, *N. XI.*) and is a continuation of the *accessory nucleus* in the dorso-lateral group of the ventral horn of the cervical region of the cord. This nucleus is traceable upwards to the ventricular part of the medulla oblongata, where it passes into continuity with the dorsal nucleus of the vagus (see p. 134). It receives many collaterals —a large number from the dorsal columns, but also others from other sensory tracts. Some of the cell-dendrons cross the middle line to reach the nucleus of the opposite side.

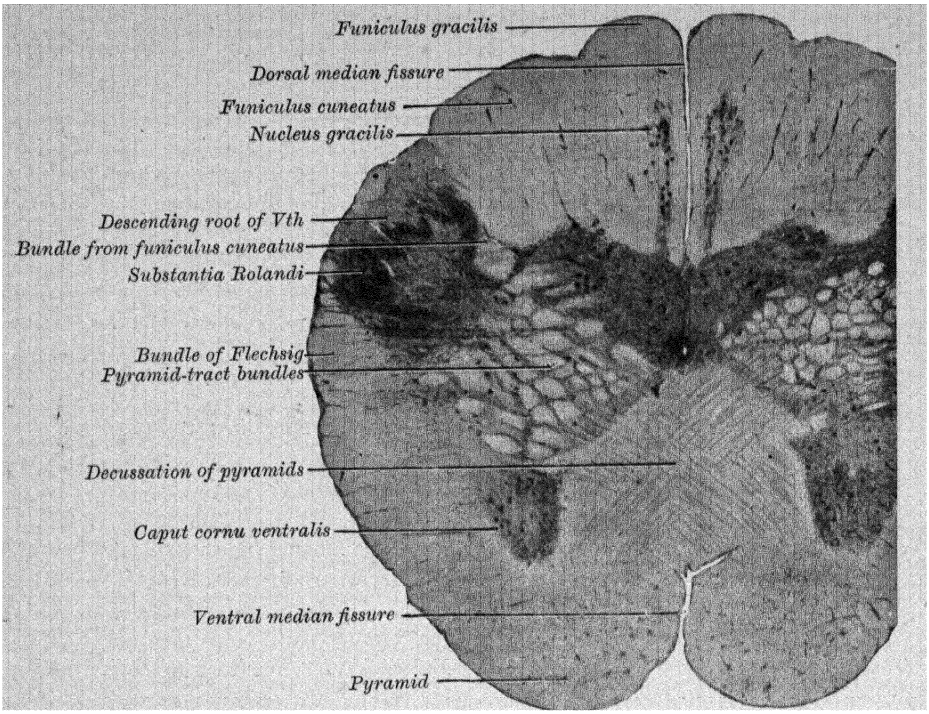
The separated portion of the ventral horn becomes pushed over to the side by the development of the pyramid and the interpolation, somewhat higher up, of the olivary body between them, so that it comes to lie close to the separated caput cornu dorsalis (see below). The greater part of the grey substance is broken up into a *formatio reticularis—i.e.* a comparatively coarse network of grey matter containing nerve-cells, intersected by bundles of white fibres; but a small part containing numerous nerve-cells remains for a time in the lateral column, and is known as the *nucleus lateralis* (fig. 140).

This nucleus, which is also known as the *nucleus of the lateral column*, lies dorso-lateral to the olive, when this has made its appearance, between it and the descending root of the fifth nerve. In the rabbit Cajal distinguishes three parts—one mesial, large-celled; one lateral, small-celled; and one linear in form and partly detached. In man this distinction into three parts is not apparent, but the nucleus tends to bifurcate (at the lower end of the calamus scriptorius) into two parts, a mesial and a lateral, which are separated by the nucleus ambiguus. The axons of the cells are said by Cajal to enter the neighbouring lateral column and to divide there into ascending and descending branches; but according to Yagita [1] the main connexion of the cells of this nucleus is with the cerebellum, for if the restiform body (of one side) be severed the cells of the lateral nucleus of the same side show chromatolysis.

The two halves of the medulla oblongata are united by a septum of grey matter with dorso-laterally disposed cells and fibres which is termed the *raphe*. Emerging from this at the anterior (ventral) median sulcus fibres are seen which form a thin superficial layer covering the pyramids and sweep round laterally over the olives to join the restiform body.

The **formatio reticularis** occupies the whole of the ventral and lateral areas of the bulb, dorsal to the pyramids and olives respectively. It is thus named on account of the appearance which it presents in a transverse section viewed under a moderate magnifying power. This reticular appearance is caused by the intersection of bundles of fibres belonging to two

[1] Sonderabdr. a. d. Okayama-Igakkwai-Zasshi, 1906.



DECUSSATION OF THE PYRAMIDS. Magnified about 6 diameters. (E. A. Schäfer.)

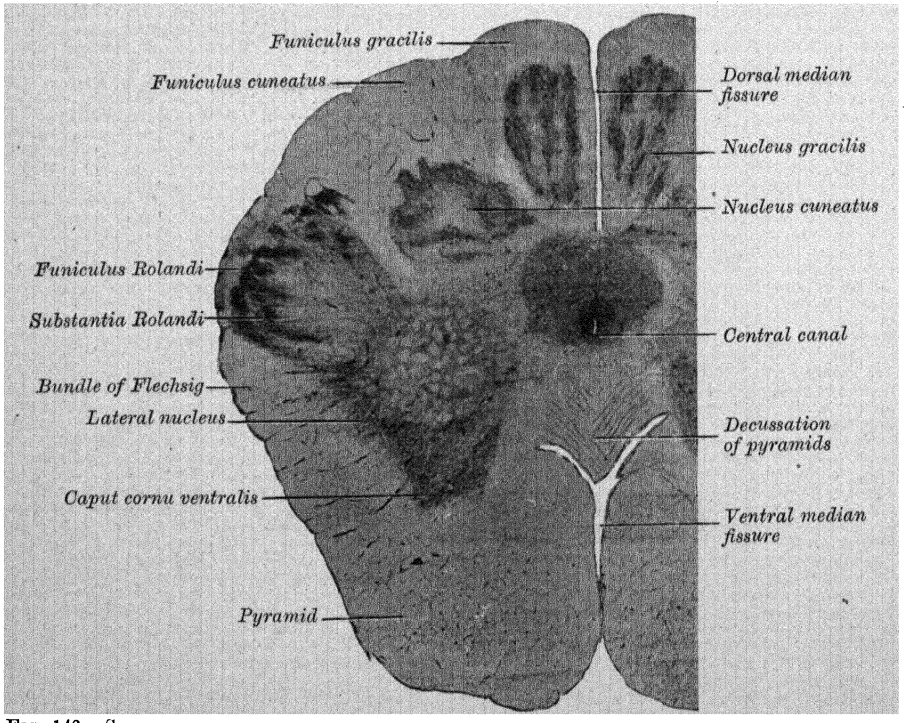


FIG. 142.—SECTION ACROSS THE MEDULLA OBLONGATA AT THE LEVEL OF THE UPPERMOST PART OF THE DECUSSATION OF THE PYRAMIDS.

sets which run at right-angles to one another. Those of the one set are longitudinal, and these are intersected by transverse arched fibres, passing obliquely to the raphe with a curved course from the nuclei of the funiculus gracilis and funiculus cuneatus, and from the olivary nucleus; in the upper part of the medulla oblongata those from the olivary nucleus converge towards the restiform body after crossing the raphe, whereas those from the dorsal nuclei become longitudinal fibres in both lower and upper portions of the bulb, and run upwards in the inter-olivary region as the commencement of the *fillet*.

In some parts grey matter with nerve-cells enters largely into the constitution of the formatio reticularis. The cells are especially large and numerous in the reticular formation of the lateral area near the ventral area, where in the lower part of the medulla oblongata is situated a remnant of the ventral horn; and its grey matter is presumably derived in great measure from the latter. In the ventral or mesial area of the bulb nerve-cells are less abundant in the formatio reticularis, and this is therefore sometimes distinguished as the *formatio reticularis alba*, from the other or *formatio reticularis grisea*. The cells of the formatio reticularis vary much in size, some being small, but many very large and containing large Nissl granules. They appear to lie without any definite arrangement. Their axons join the adjacent longitudinal white bundles, bifurcating for the most part as they enter the bundles. The *raphe* should probably be looked upon as part of the reticular formation; its cells have a general resemblance to those of the adjoining formatio reticularis, but they are chiefly disposed dorso-ventrally. The reticular formation receives numerous collaterals from the pyramid-fibres—at least in some animals (Cajal).

The longitudinal fibres of the reticular formation of the ventral area belong to at least three tracts—viz. (1) those which occupy the part nearest to the pyramids and form the tract of the fillet (fig. 147); (2) and (3) those which are prolonged into the anterior column of the spinal cord. The former (2) lie most dorsal and next to the central grey matter: these become in the upper regions of the medulla oblongata very distinct, and are collected into a compact bundle known as the *dorsal* or *posterior longitudinal bundle*, which is still better marked in the pons or mid-brain. Between these fibres of the posterior longitudinal bundle and those of the fillet is (3) an ill-defined tract which is largely formed of fibres passing downwards from the corpora quadrigemina of the opposite side into the ventral column of the cord: these fibres constitute the *ventral longitudinal bundle*. It is, however, nowhere so distinctly marked off from the rest of the reticular formation as is the adjacent posterior or dorsal bundle.

At the side of the bulb two tracts which are prolonged upwards from the cord are visible in all transverse sections of this part. These are the *bundles of Flechsig and of Gowers*. The latter lies dorso-lateral to the olivary nucleus in the medulla oblongata, but in the pons it passes deeply towards the dorsal surface. The former is in the lower part of the bulb, as in the cord, in close contact with the bundle of Gowers, but as the restiform body develops Flechsig's bundle gradually passes into it and is conducted to the cerebellar worm.

Arched fibres.—The *arched* or *arcuate fibres* of the medulla oblongata are the curved fibres which are seen in transverse sections coursing in the plane of the section. From their position they are distinguished into external and internal, or superficial and deep.

The *outer* or *superficial arched fibres* emerge for the most part from the raphe at the ventral median fissure, and, passing over the pyramids and olives, go to the restiform body. They are added to by deep fibres which come to

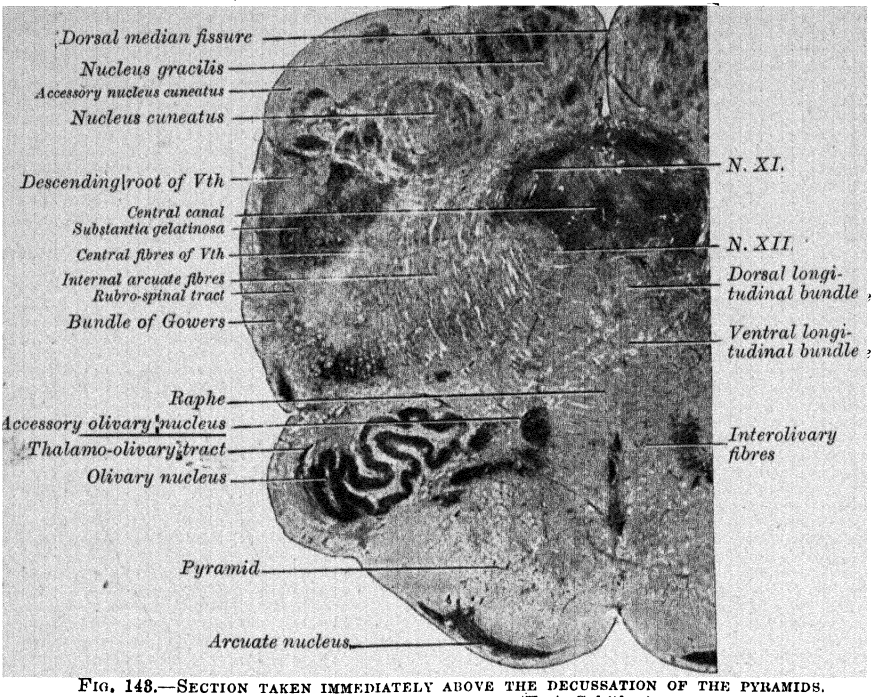


FIG. 148.—SECTION TAKEN IMMEDIATELY ABOVE THE DECUSSATION OF THE PYRAMIDS. Magnified about 6 diameters. (E. A. Schäfer.)

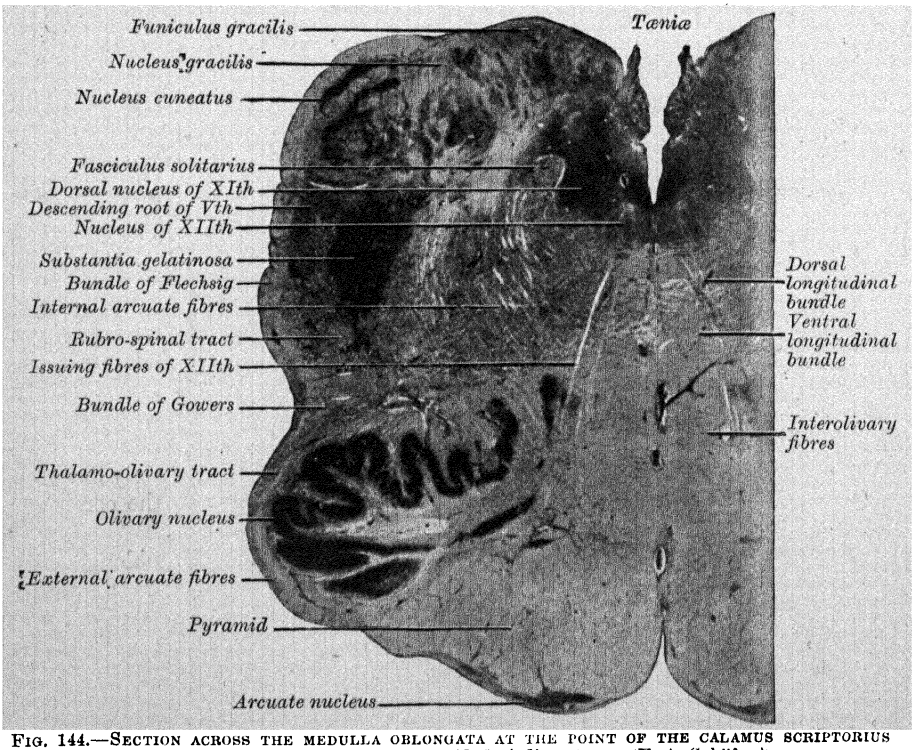


FIG. 144.—SECTION ACROSS THE MEDULLA OBLONGATA AT THE POINT OF THE CALAMUS SCRIPTORIUS OF THE FOURTH VENTRICLE. Magnified 6½ diameters. (E. A. Schäfer.)

the surface partly in the groove between the pyramids and olives, partly after passing through the olives, as before mentioned. In the raphe they may be seen to come from the opposite side; their origin is not certainly known, but is perhaps the olivary nucleus. Connected with them, and lying between them and the ventro-lateral part of the pyramid, is a collection of grey matter, known as the *nucleus of the arched fibres*. The axons of its cells mingle with the superficial arcuate fibres and probably pass to the cerebellum. Accessory arcuate nuclei of a similar character are here and there met with in the course of these fibres. The arcuate nuclei become very largely developed at the junction of the medulla oblongata with the pons. They are probably a continuation of the nuclei pontis (see p. 147).[1]

The *inner* or *deep arched fibres* originate: some in the nucleus gracilis and nucleus cuneatus and sensory nuclei of cerebral nerves, some in the opposite olive and some from cells of the reticular formation. Those from the dorsal and other sensory nuclei traverse the formatio reticularis and enter the raphe, in which they cross to the opposite side. Emerging from the raphe, they become longitudinal, and pass upwards in the tract of the fillet, and in the central tract of the cerebral nerves. Those from the olivary nucleus also cross in the raphe, pass through or around the other olivary nucleus, and enter the cerebellum through the restiform body. Those from the cells of the reticular formation bifurcate and become longitudinal near the raphe, one branch passing downwards and one upwards. Many of these pass into the dorsal longitudinal bundle of the same and of the opposite side.

Raphe.—The *raphe* or *seam* contains fibres which run in part dorso-ventrally (fibræ rectæ), in part longitudinally, and in part across more or less obliquely. Intermixed with the nerve-fibres are the nerve-cells already noticed. The fibræ rectæ are continuous ventrally with the superficial arched fibres which emerge at the anterior median fissure; dorsally in the upper part of the bulb others enter the raphe from the medullary striæ (p. 122). The longitudinal are chiefly fibres which have passed into the raphe as fibræ rectæ or as superficial or deep arched fibres, and in it have altered their direction and become longitudinal. The obliquely crossing fibres are the deep arched fibres which enter or emerge from the raphe.

Descending root of the fifth nerve.—As we trace the sections upwards from the cord the dorsal horns become gradually shifted laterally, simultaneously with an increase in size of the posterior columns, so that in place of forming an acute angle with the dorsal median fissure they come to lie almost at right-angles to it (figs. 138 to 141). Moreover, the apex of the cornu enlarges and comes close to the surface, where it presently forms a distinct projection, the funiculus of Rolando, which, a little higher up, swells into the tubercle of Rolando. At the same time the cervix cornu diminishes in size and like the ventral horn is eventually broken up, by the passage of transverse and longitudinal bundles of white fibres through it, into a reticular formation, which then separates the caput cornu from the rest of the grey matter. In the tubercle of Rolando the caput cornu is near the surface, but above the tubercle it lies deeper; it is covered by a well-marked bundle of white fibres, the *descending root of the fifth nerve*, and by fibres which are passing over it to form the restiform body.

The fibres of the descending trigeminal root were at one time supposed to take origin from the cells of the tubercle of Rolando, but this is not the case, for firstly they do not grow from these cells, but from the cells of the Gasserian (semilunar) ganglion (His), and secondly, if

[1] Jelgersma, Centr. f. Nervenh. 1889; Zingito Neurol. Centr. 1908.

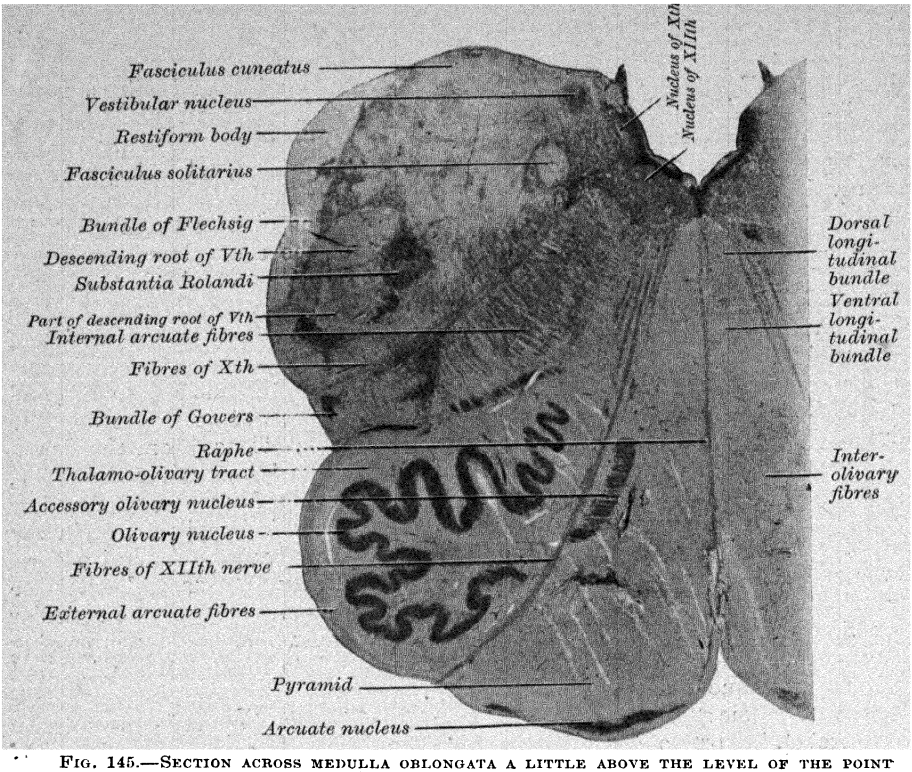


FIG. 145.—SECTION ACROSS MEDULLA OBLONGATA A LITTLE ABOVE THE LEVEL OF THE POINT OF THE CALAMUS SCRIPTORIUS. Magnified about 6 diameters. (E. A. Schäfer.)

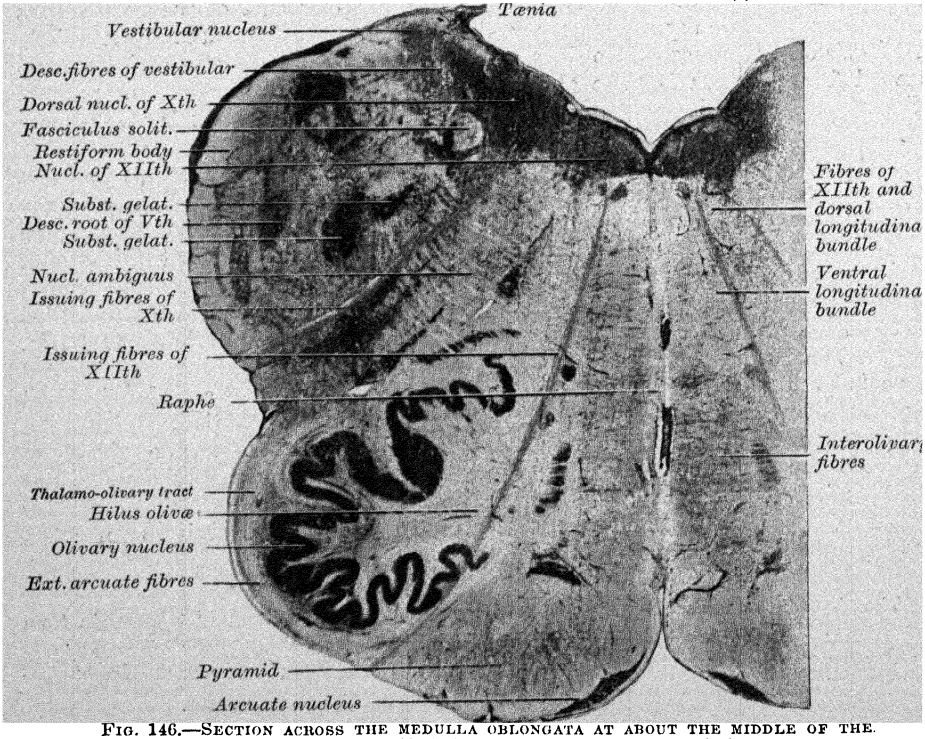


FIG. 146.—SECTION ACROSS THE MEDULLA OBLONGATA AT ABOUT THE MIDDLE OF THE OLIVARY BODY. Magnified about 6 diameters. (E. A. Schäfer.)

the sensory root of the fifth is cut at its exit from the pons, the fibres of this root degenerate, but the cells of the adjacent gelatinous substance remain unaffected (Bechterew). There is, however, a physiological connexion established with these cells by means of collateral fibres, as in the case of the fibres of the dorsal columns of the cord and the substance of Rolando of the dorsal horn.

Nuclei of dorsal columns.—The grey matter of the base of the dorsal horn undergoes a considerable increase as we trace it upwards in sections.

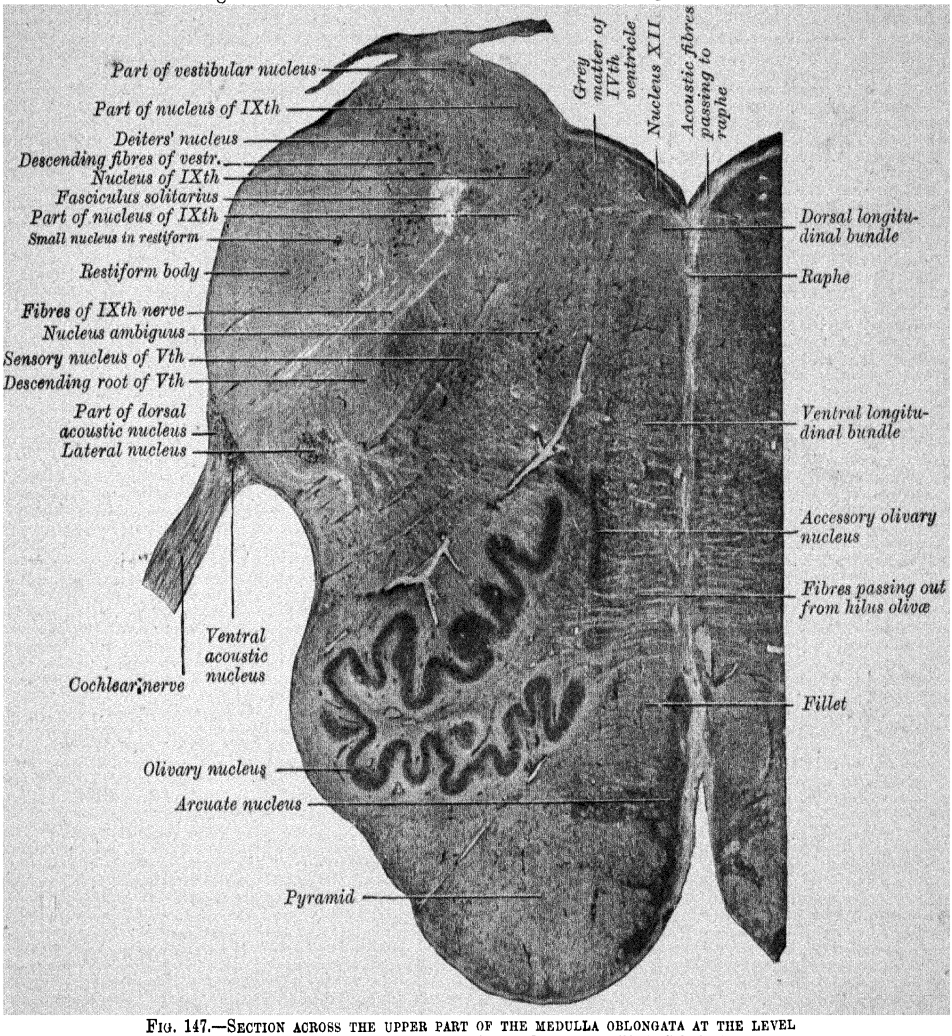


FIG. 147.—SECTION ACROSS THE UPPER PART OF THE MEDULLA OBLONGATA AT THE LEVEL OF THE EIGHTH NERVE. Magnified about 6 diameters. (E. A. Schäfer.)

Portions of grey matter are soon found extending into the funiculi graciles and cuneati, forming the nuclei of those columns (*nuclei of Burdach and of Goll*). The appearance of grey matter is seen in the column of Goll lower down than in the column of Burdach (fig. 141). These nuclei are at first narrow in transverse section, but as the central canal approaches the dorsal surface of the medulla oblongata they appear as comparatively thick masses, which produce externally the eminences of the clava and the cuneate

tubercle (figs. 143, 144). Outside the nucleus of the funiculus cuneatus an *accessory* or *external nucleus* is seen at one part in sections of the medulla oblongata (fig. 143). This is considered by Cajal to represent a separated portion of the substance of Rolando. In the grey matter of the nucleus gracilis and principal nucleus cuneatus the ascending fibres of the dorsal columns of the cord become lost.

The *nucleus of Burdach* (*nucleus cuneatus*) has cells of two kinds. Some are small and arranged in groups or islets, their dendrons ramifying densely near the cell-body. Other cells of the nucleus have widely spreading dendrons: these cells are both small and large in size.

The *nucleus of Goll* (*nucleus gracilis*) also shows two kinds of cells—one with closely ramifying dendrons which are beset with spines, and the other with open widely spreading dendrons.

The axons from these nuclei emerge from their ventral border and sweep forwards and inwards in a curved manner as *internal arched fibres* towards the raphe or seam which unites the two halves of the medulla oblongata. Having here intercrossed with those from the opposite side in a decussation (*decussation of the fillet*) which lies above that formed by the fibres of the pyramids, they form a considerable bundle of longitudinally coursing fibres which lies just dorsal to the pyramid and is known as the *main fillet* (*lemniscus*).[1] Its fibres receive their myelin much earlier than those of the pyramid. The fillet-fibres from the nucleus of Goll begin to make their appearance at a lower level than those of the nucleus of Burdach; and in the fillet-tract itself they occupy a more ventral position.[2]

Nuclei of central grey matter and motor nuclei.—When the slit-like upper end of the central canal opens out into the fourth ventricle, the small remaining portion of the base of the ventral horn, which in the closed part was ventro-lateral to the central canal, comes to the surface at the floor of the ventricle, and as the sections are traced upward increases gradually in size, producing the prominence of the funiculus teres. In it, as in the lower part of the bulb where the canal is still closed, a group of large nerve-cells (*nucleus of hypoglossal*) is seen in all transverse sections. From this group (column) of cells the successive bundles of the roots of the hypoglossal or twelfth cerebral nerve arise and pass obliquely through the substance of the bulb to leave it on its anterior aspect.

At the fourth ventricle the hypoglossal nucleus lies a short distance from the surface covered by a flattened bundle of longitudinally running white fibres, which gives this mesial triangle of the calamus scriptorius (trigonum hypoglossi) a white appearance. Nearer to the surface of the floor and nearer also to the median groove is a small group of cells, known as the *nucleus of the funiculus teres* (fig. 148, I; fig. 151, *n.f.t.*). The cells are small, and have been said to give origin to fibres which belong to the vago-glosso-pharyngeal roots, but this is now regarded as incorrect.

The nucleus of the accessory nerve, which is seen at the dorso-lateral aspect of the central canal in the lower part of the bulb (fig. 143), is found to be pushed to the side as the central canal opens out into the fourth ventricle, so that in the floor of the ventricle it lies lateral or dorso-lateral to the hypoglossal nucleus. These cells form the upper part of the *nucleus of the accessory*, or *dorsal vago-accessory nucleus* (see figs. 144 to 146; fig. 148, E). They give origin to the bulbar part of the accessory and to some of the efferent fibres of the vagus; the spinal part of the accessory takes origin in a dorso-lateral group of cells

[1] Injury to the cuneate and gracile nuclei produces ascending degeneration in the tract of the fillet (Mott).

[2] Van Gehuchten, Le Névraxe, iv. 1902.

of the ventral horn of the spinal cord (extending from the level of the olive as low down as the fifth cervical nerve) (see p. 80).

The dorsal vago-accessory nucleus where it appears in the floor of the fourth ventricle is separated from the nucleus of the hypoglossal by the *intercalary nucleus* of Standerini (fig. 148, F), the connexions of which are unknown.

Lying in the reticular formation and ventral to the principal mass of grey matter which here occupies the floor of the fourth ventricle, is a small detached pear-shaped mass of grey matter containing nerve-cells which is connected by a kind of stalk with the rest of the grey matter. This nucleus, the *nucleus ambiguus*, gives origin to fibres which pass along the stalk obliquely towards the floor of the fourth ventricle and then turn outwards and forwards to issue

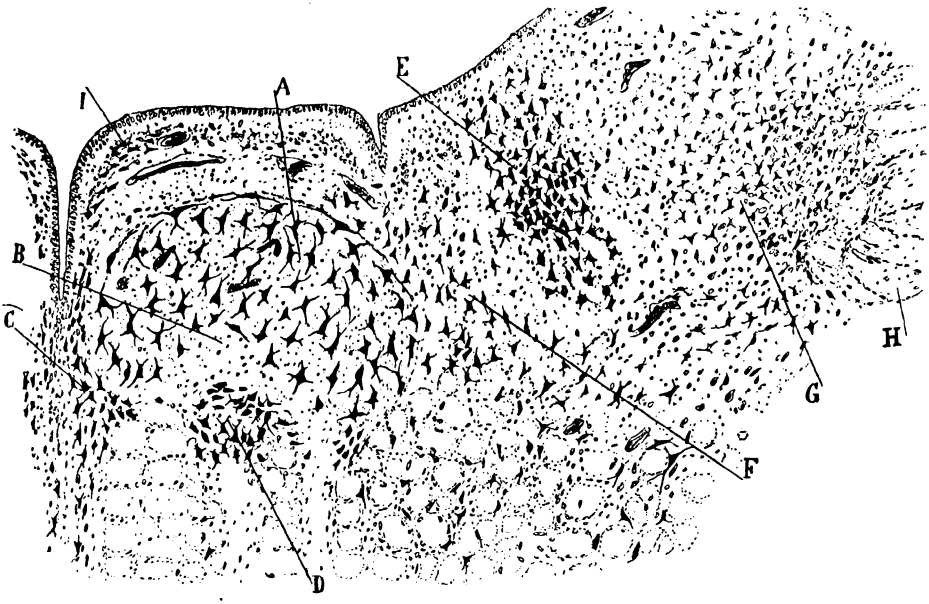


FIG. 148.—SECTION OF MEDULLA OBLONGATA THROUGH THE FLOOR OF THE FOURTH VENTRICLE, SHOWING THE MOTOR NUCLEI OF THE TENTH AND TWELFTH NERVES. Nissl method. (Cajal.)

A, nucleus of twelfth with large cells; B, part of nucleus containing only small cells; C, nucleus of raphe; D, nucleus of moderate-sized cells described by Roller; E, dorsal motor nucleus of tenth nerve; F, intercalated nucleus of Standerini; G, sensory nucleus of ninth and tenth nerves; H, fasciculus solitarius; I, cells in grey matter of floor of ventricle.

with the root-bundles of the tenth nerve and higher up with those of the ninth nerve from the side of the bulb (fig. 146). It is the *ventral motor nucleus* of these nerves, and in its relation to the grey matter and in the size and character of its cells it is a counterpart of the nucleus of the seventh nerve, which appears in sections somewhat higher up (in the pons) in a similar situation.

The nucleus ambiguus and the nucleus of the facial represent a continuation into the medulla oblongata of the motor cell-column of the ventral horn of the cord. Some of the cells send their axons across the raphe to the opposite side (Cajal). The nucleus receives collaterals from fibres arising in the sensory nucleus of the fifth (substance of Rolando) and from ascending fibres derived from other sensory nuclei.[1]

[1] On the nuclei of origin of the eleventh, tenth, and ninth nerves, see Van Gehuchten, Journ. de Neurol. 1898 and 1899, and Système nerveux, 1906.

Sensory nuclei of the seventh, ninth, and tenth cerebral nerves.—Above the level where the roots of the accessory nerve cease to come off, a mass of grey matter with numerous cells is seen lying lateral to the hypoglossal nucleus in a situation near the floor of the ventricle corresponding to the prominence of the ala cinerea (trigonum vagi) which appears on the surface, and it extends upwards as far as the fovea inferior. In connexion with it there are successively seen bundles of fibres of the roots of the vagus and glosso-pharyngeal nerves (tenth and ninth cerebral nerves): those of the vagus beginning at the commencement of the ventricle and continuing along the length of the ala cinerea, and those of the glosso-pharyngeal connected with the upper part of the ala cinerea and with the part beneath the inferior

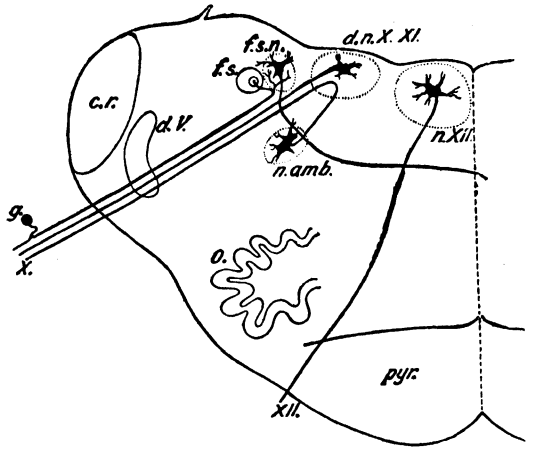


FIG. 149.—PLAN OF THE ORIGIN OF THE TWELFTH AND TENTH NERVES. (E. A. Schäfer.)

pyr., pyramid; *n.XII.*, nucleus of hypoglossal; *XII.*, hypoglossal nerve; *d.n.X.XI.*, dorsal nucleus of vagus and accessory; *n.amb.*, nucleus ambiguus; *f.s.*, fasciculus solitarius (descending root of vagus and glosso-pharyngeal; *f.s.n.*, its nucleus; *X.*, issuing fibres of vagus; *g*, ganglion-cell in vagus giving origin to a sensory fibre; *d.V.*, descending root of fifth; *c.r.*, corpus restiforme.

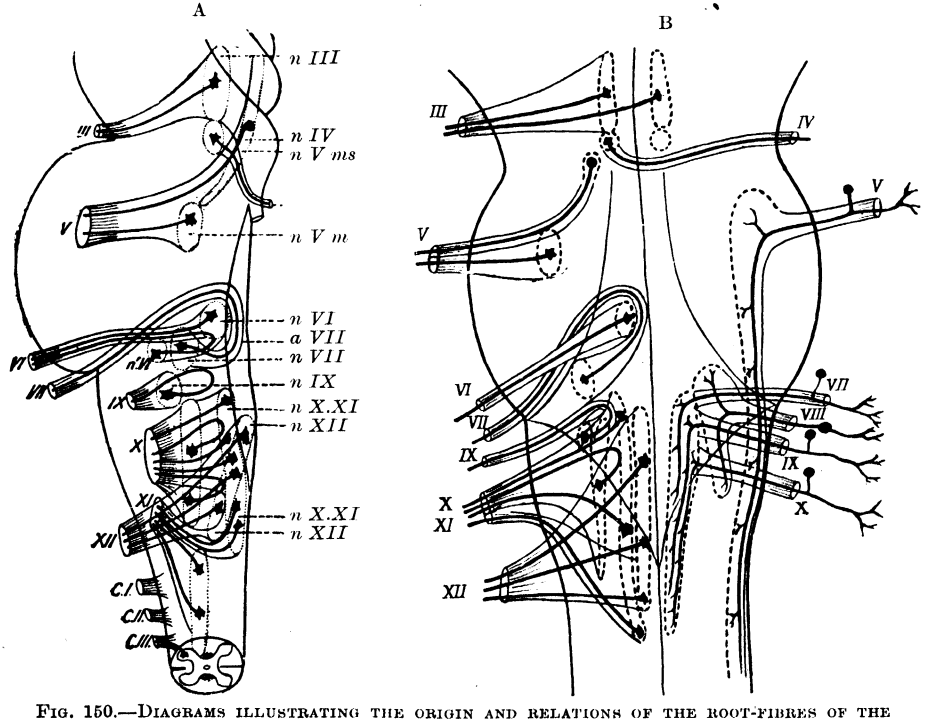


FIG. 150.—DIAGRAMS ILLUSTRATING THE ORIGIN AND RELATIONS OF THE ROOT-FIBRES OF THE CEREBRAL NERVES. (E. A. Schäfer.)

A, efferent fibres only: profile view. B shows on the left the motor nuclei and efferent fibres, except those of the fourth nerve, and on the right side the afferent fibres: surface view.

fovea. The grey matter in question is connected with the entering sensory root-fibres of the vagus and glosso-pharyngeal (*principal sensory nucleus* of these nerves).

Close to this nucleus, but placed somewhat more deeply in the grey matter, is a round longitudinal bundle of white fibres termed the *fasciculus solitarius* (figs. 144, 145, 146, 147). This bundle, which is accompanied by gelatinous grey matter with many small nerve-cells (*nucleus of fasciculus solitarius, descending sensory nucleus of facial, glosso-pharyngeal, and vagus*), occupies the same relation to the seventh, ninth, and tenth nerves that the descending root of the fifth occupies to that nerve. Its fibres lose themselves among the cells of the enclosing grey matter, and this and the bundle are traceable downwards into the uppermost part of the cervical region of the spinal cord, where they blend with those of the opposite side: traced upwards they are seen to enter the bulb with the bundles of nerve-roots which form the vagus, glosso-

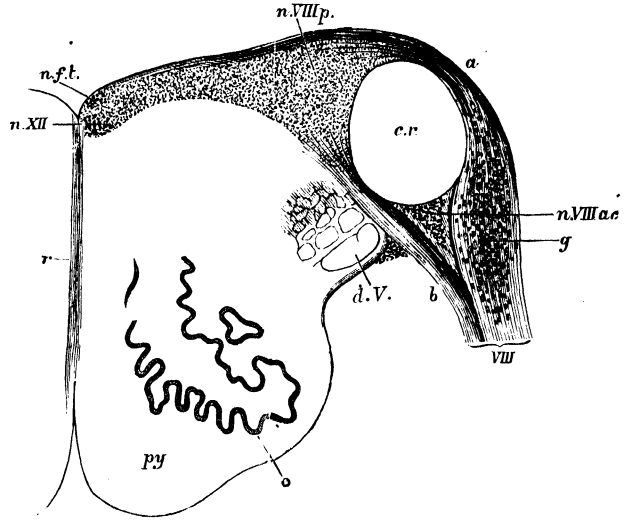


FIG. 151.—TRANSVERSE SECTION AT THE UPPER PART OF THE MEDULLA OBLONGATA. (Schwalbe.)

py, pyramid; *o*, olivary nucleus; *d.V.*, descending root of the fifth nerve; *VIII*, root of the acoustic nerve, formed of two parts, *a* (cochlear) and *b* (vestibular), which enclose the restiform body, *c.r.*; *n.VIIIp*, dorsal nucleus of the vestibular nerve; *n.VIIIac*, ventral acoustic nucleus; *g*, ganglion-cells of the acoustic tubercle (lateral acoustic nucleus); *n.f.t.*, nucleus of the funiculus teres; *n.XII*, nucleus of the hypoglossal; *r*, raphe.

pharyngeal, and pars intermedia of the facial. Both this bundle and the descending root of the fifth have their myelin sheath developed at an early period. They grow into the bulb from the ganglia of the fifth, seventh, ninth, and tenth nerves in the same way that the dorsal roots grow into the medulla spinalis from the spinal ganglia.

In some animals the nuclei of the solitary bundles of opposite sides blend below dorsal to the central canal to form the *commissural nucleus* of Cajal.

The nucleus of the solitary bundle lies mainly on the inner side of the bundle, but in part intercalated among its external fascicles. The cells of the nucleus resemble those of the substantia gelatinosa of Rolando. Their axons pass into the adjacent white columns and form the secondary ascending or sensory tract

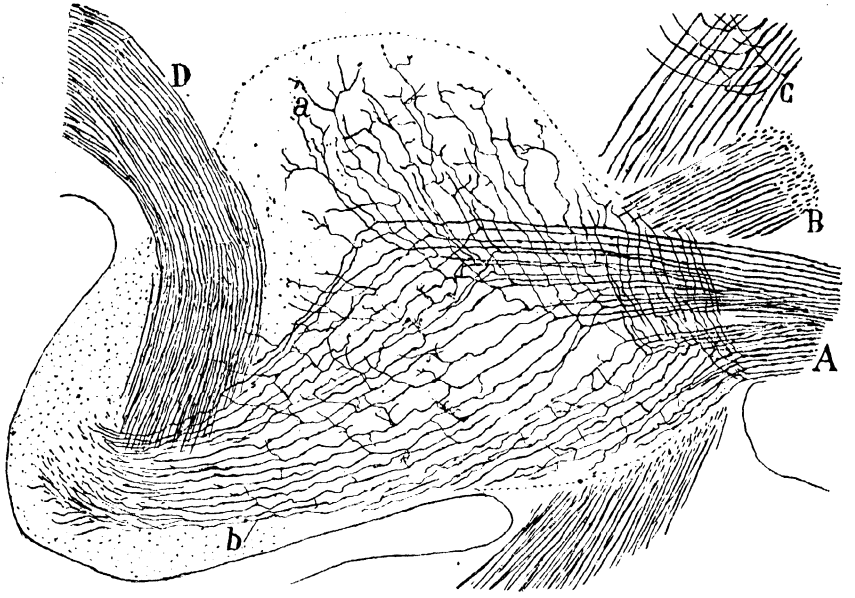


FIG. 152.—LATERAL SAGITTAL SECTION OF BULB OF MOUSE-FŒTUS, SHOWING ENTERING FIBRES OF COCHLEAR NERVE. (Cajal.)

A, fibres of cochlear nerve passing in and bifurcating into *a* ascending, and *b* descending branches B, vestibular nerve; C, descending root of fifth; D, restiform body.

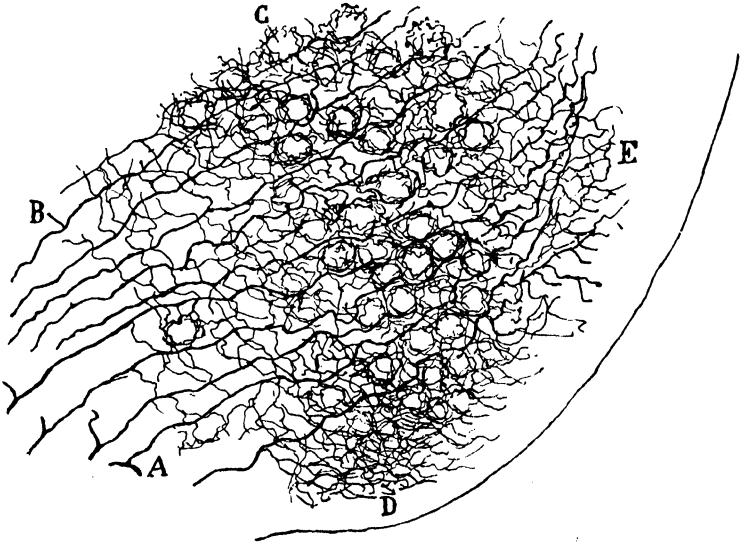


FIG. 153.—DESCENDING BRANCHES OF COCHLEAR NERVE ENDING IN THE ACOUSTIC TUBERCLE. (Cajal.)

A, entering fibres; B, a descending branch; C, a pericellular nest; D, E, plexus of collaterals in the granule-zone.

of the cerebral nerves, which eventually passes along with the fibres of the main fillet and the ascending tract of the fifth to the thalamus.

Nuclei of the cochlear and vestibular divisions of the eighth nerve.—The bundles of the acoustic nerve pass partly dorsal and partly ventral to the restiform body. The *dorsal* or *cochlear division* is connected with two nuclei, one termed the *dorsal* or *lateral cochlear nucleus*; the other being known as the *ventral* or *accessory nucleus*. The fibres of the **cochlear division**, which originate in the cells of the spiral ganglion of the cochlea, like all other sensory fibres bifurcate as they enter the cerebro-spinal centre. One of the branches—the shorter or ascending—enters the ventral nucleus; the other—the larger or descending—passes into the dorsal nucleus, in each case ending in pericellular arborisations of a peculiarly close character.

Of the two nuclei the dorsal is the larger and more prominent, occupying a rounded projection on the lateral and dorsal aspects of the restiform body (acoustic tubercle). The grey matter of the dorsal nucleus or acoustic tubercle is described by Cajal as composed of four zones—viz. (1) ependymal epithelium of the lateral recess of the fourth ventricle; (2) plexiform zone, containing small nerve-cells; (3) a zone of granules; (4) a zone of large fusiform cells, some of which send their axons into the trapezium; the rest pass dorsally and form the striæ acusticæ in the floor of the fourth ventricle. These dip in at the raphe and eventually mingle with the fibres of the trapezium of the opposite side (fig. 157).[1]

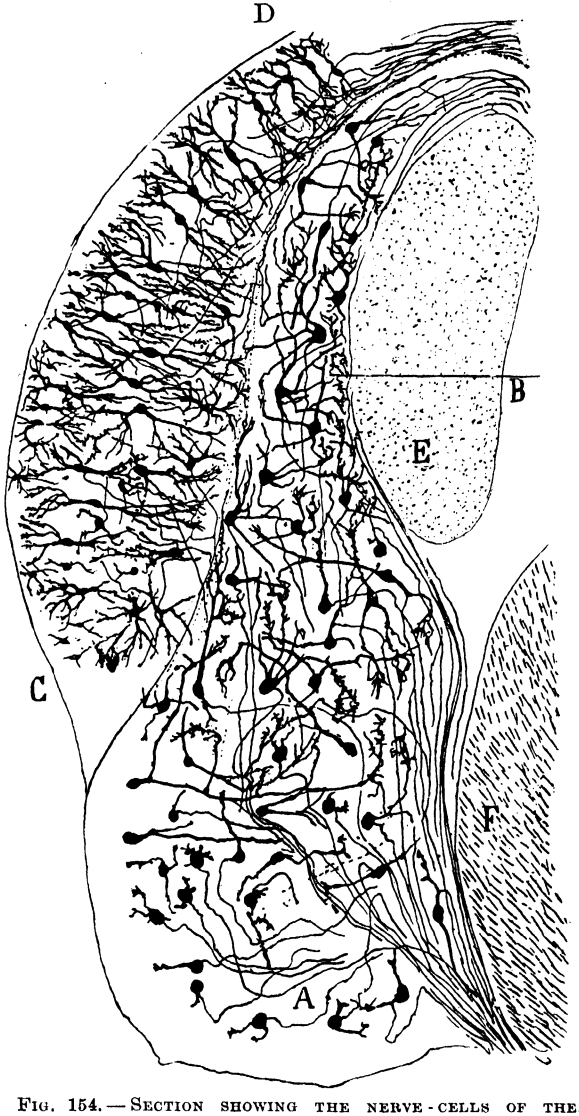


FIG. 154.—SECTION SHOWING THE NERVE-CELLS OF THE VENTRAL AND LATERAL GANGLIA OF THE COCHLEAR NERVE, FROM AN EIGHT-DAY RABBIT. (Cajal.)

A, B, ventral (accessory) ganglion; C, D, lateral ganglion (acoustic tubercle); E, restiform body; F, descending root of fifth.

Ventral to the restiform body and between the two roots of the eighth nerve is another mass of ganglion-cells, the *ventral* or *accessory cochlear nucleus*

[1] The further course of these auditory fibres will be noticed with the pons.

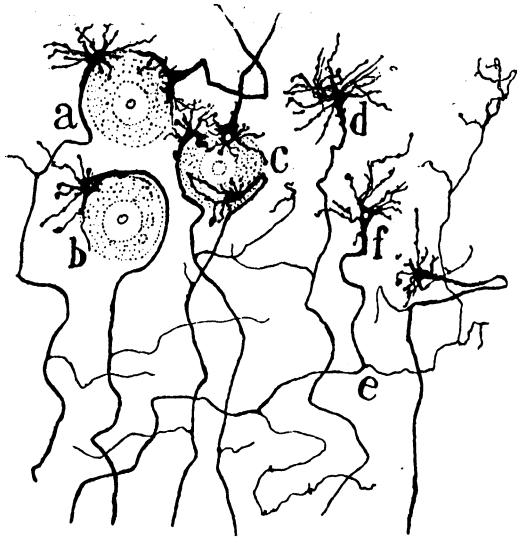


FIG. 155.—ASCENDING BRANCHES FROM BIFURCATIONS OF COCHLEAR NERVE-FIBRES ENDING IN THE VENTRAL OR ACCESSORY GANGLION IN EXPANSIONS OF HELD.

a to *f*, various kinds of terminals and collaterals.

(fig. 151, *n.VIIIac*), which receives the endings of the ascending branches of the cochlear fibres (fig. 155). From its cells fibres are seen passing transversely towards the opposite side (fig. 156); they belong to the system of the *trapezium* (p. 149). Some do not pass directly into the trapezium, but first pass dorsalwards around the restiform body. The ventral ganglion has many small nerve-cells (granules) which lie near the periphery, and a deep layer of large cells from which the trapezium fibres originate.

Towards the upper part of the bulb an extensive tract of grey matter containing small nerve-cells becomes developed outside the vago-glossopharyngeal nucleus. This tract corresponds to the lateral triangular area (*trigonum acustici*) which is seen on the surface outside the ala cinerea. Into it pass most of the fibres of the **vestibular division** of the eighth nerve, which originate in the bipolar cells of the vestibular ganglion; it is termed the *dorsal vestibular nucleus* or *principal nucleus of the vestibular division* (fig. 151, *n.VIIIp.*). Continuous below with it is a column of grey matter (*descending vestibular nucleus*) which is associated with longitudinal bundles of nerve-fibres termed by Roller the 'ascending root of the acoustic nerve' (fig. 163, *R.*), but which is really formed of the *descending branches of the vestibular division* (fig. 158, *d*), which, like all afferent nerve-fibres, bifurcate on entering the nerve-centre (figs. 159, 160), one branch passing upwards and the other

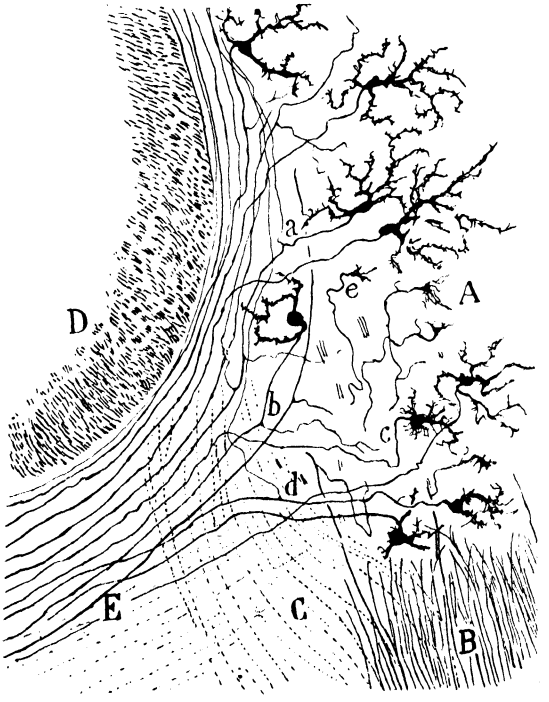


FIG. 156.—VENTRAL COCHLEAR GANGLION OF CAT A FEW DAYS OLD. (Cajal.)

A, ventral ganglion with multipolar cells; B, cochlear fibres; C, vestibular fibres; D, descending root of fifth; E, fibres from cells (*c*) of ventral ganglion passing to trapezium; *a*, *d*, dorsally directed collaterals; *b*, ventrally directed collaterals; *e*, pericellular expansions of Held.

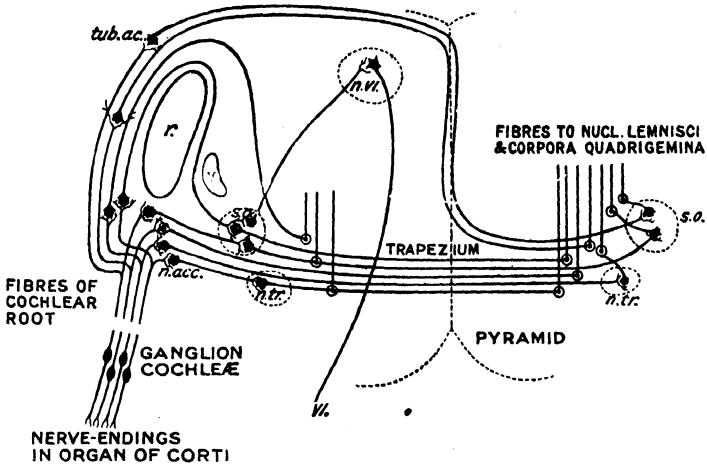


FIG. 157.—PLAN OF THE COURSE AND CONNEXIONS OF THE FIBRES FORMING THE COCHLEAR ROOT OF THE AUDITORY NERVE. (E. A. Schäfer.)

r., restiform body; *V*, descending root of the fifth nerve; *tub.ac.*, tuberculum acusticum; *n.acc.*, accessory nucleus; *s.o.*, superior olive; *n.tr.*, nucleus of trapezium; *n.VI.*, nucleus of sixth nerve; *VI.*, issuing root-fibre of sixth nerve.

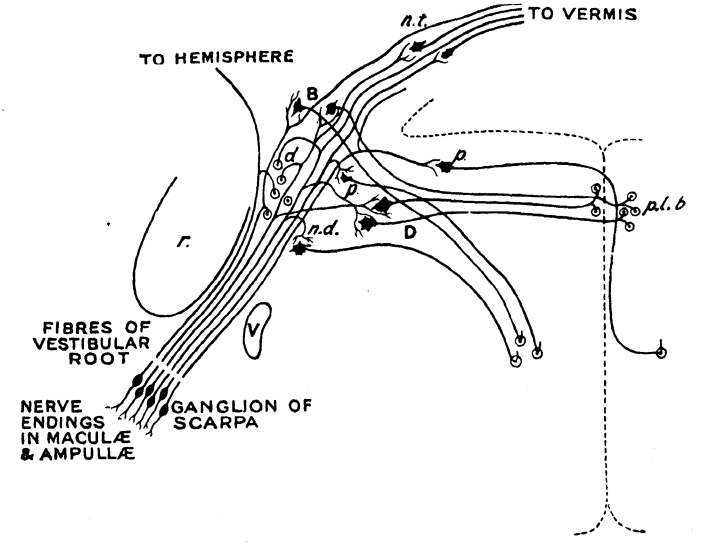


FIG. 158.—PLAN OF THE COURSE AND CONNEXIONS OF THE FIBRES FORMING THE VESTIBULAR ROOT OF THE AUDITORY NERVE. (E. A. Schäfer.)

r., restiform body; *V*, descending root of fifth nerve; *p.*, principal nucleus of vestibular root; *d*, fibres of descending vestibular root; *n.d.*, a cell of the descending vestibular nucleus; *D*, nucleus of Deiters; *B*, nucleus of Bechterew; *n.t.*, nucleus tecti (fastigii) of the cerebellum; *p.l.b.*, posterior (dorsal) longitudinal bundle.

downwards. Ventral to the vestibular nucleus is a collection of grey matter with very large nerve-cells, the *nucleus of Deiters* (figs. 147, 158, 169). Its cells send their axons into the posterior longitudinal bundles of both sides, where they bifurcate, one branch passing upwards towards the mid-brain and another downwards towards the cord. The nucleus of Deiters was formerly regarded as giving

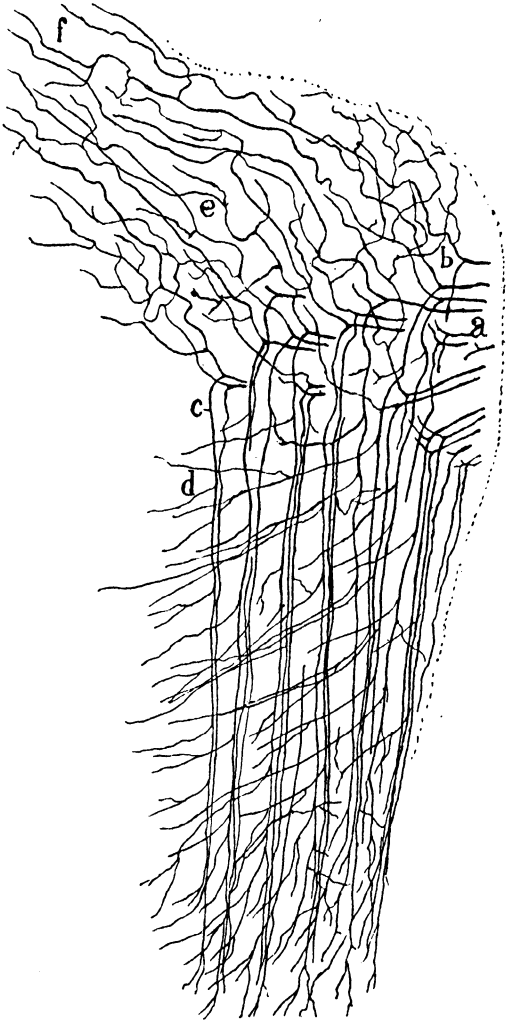


FIG. 159.—FROM A LONGITUDINAL LATERAL SECTION OF BULB OF MOUSE-FŒTUS, SHOWING THE ENTERING FIBRES OF THE VESTIBULAR NERVE. (Cajal.)

a, entering fibres; *b*, a bifurcation; *c*, *d*, descending branches with collaterals *e*, *f*, ascending branches.

origin to part of the auditory nerve, and was known as the outer or superior acoustic nucleus. Many collaterals proceed to it from the entering fibres of the vestibular division, while others can be traced to another group of cells dorso-lateral to the nucleus of Deiters and known as the *nucleus of Bechterew* (figs. 158, 160). The axis-cylinder processes of some of the cells of the last-named

nucleus pass to the reticular formation, and there become longitudinal fibres, but others pass along with the fibres from Deiters' nucleus to the dorsal longitudinal bundle (fig. 158). Most of these collections of cells will be again noticed in dealing with the structure of the pons. The remaining ascending branches of the vestibular nerve pass beyond the nuclei of Deiters and Bechterew into the cerebellum, entering especially the nucleus tecti (fig. 160). Some small groups of nerve-cells

FIG. 160.—TRANSVERSE SECTION OF THE LATERAL PART OF THE BULB OF A RECENTLY BORN MOUSE, CLOSE TO THE CEREBELLUM. (Cajal.)

A, restiform body; B, entering fibres of vestibular nerve; C, descending root of fifth; D, nucleus tecti in cerebellar worm; E, nucleus of Bechterew; F, branches of vestibular ramifying in nucleus of Deiters; G, dentate nucleus of cerebellum; *a*, bifurcation of vestibular fibres; *b*, ascending branches and collaterals; *e*, descending branches; *c*, collaterals from restiform body to nuclei of Bechterew and Deiters; *d*, axons of cells of nucleus of Bechterew; *f*, *g*, collaterals from restiform to cerebellar hemisphere; *i*, a cell of Bechterew's nucleus.

occur among the entering bundles of the vestibular nerve (*interstitial nucleus* of Cajal).

The axons from the nuclei of Deiters and Bechterew form a secondary vestibular tract which connects those nuclei through the dorsal longitudinal bundles and other longitudinal white fibres of the reticular formation with the motor nuclei of the oculo-motor and other cerebral nerves, and with the anterior horns of the spinal cord, and which doubtless subserves vestibular reflexes.

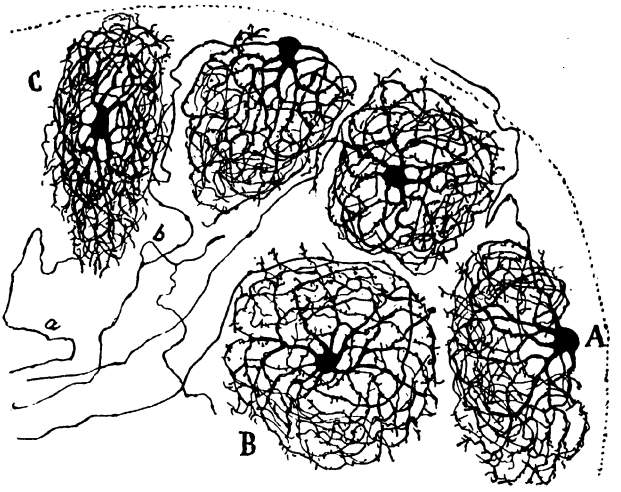


FIG. 161.—CELLS OF OLIVARY NUCLEUS OF NEW-BORN CHILD. (Cajal.)
A, C, superficial cells; B, deep cell; *a*, axons passing towards hilus; *b*, a collateral.

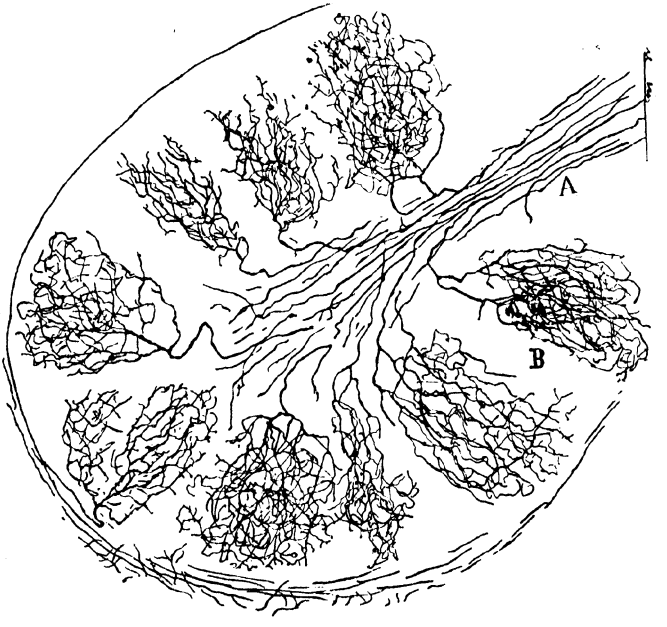


FIG. 162.—FIBRES ENTERING THE OLIVARY NUCLEUS AND ARBORISING AMONG ITS CELLS: NEW-BORN CHILD. (Cajal.)
A, fibres entering hilus; B, bunches of terminal ramifications among the cell-groups. The cells themselves are not stained.

Nucleus of the olivary body.—The *nucleus of the olivary body*, or *inferior olivary nucleus*, which has been termed, from its appearance in section, the *corpus dentatum of the olive* (figs. 143 to 147), is enclosed in the olivary prominence, but the grey matter is not visible from the surface, being covered by both longitudinal and transverse white fibres. It takes the form of a thin wavy lamina, which is curved round at its edge so as to form an ovoid scalloped capsule. The open part or hilus of this looks towards the middle line. A considerable tract of white fibres passes into and out of the hilus along its whole extent, forming the so-called *olivary peduncle* (*p.o.*).[1]

The cells of the olivary nucleus are peculiar (fig. 161). They are small with many closely bunched dendrons, and each cell is more or less isolated from the rest by the white bundles which traverse the nucleus. Their axons pass out of the hilus in the direction of the raphe and are mingled with those which come from the opposite olive. After crossing in the raphe they pass round and through the opposite olivary nucleus and stream towards the restiform body (as internal arched fibres), in which they pass into the cerebellar hemisphere of the opposite side. Very numerous collaterals ramify around the cells of the olivary nucleus; the majority of these come from the anterior column behind the pyramids, but they are also added to by collaterals from the lateral column and from the pyramids (Cajal). The internal arched fibres which are derived from the olivary nucleus are distinguishable by their smaller diameter from the larger internal arched fibres which belong to the tract of the fillet; moreover, they develop their myelin-sheath later. Others of the olivary fibres, after coursing through the grey lamina, reach the surface, where they are continued as external arched fibres into the restiform body. The cerebellar hemisphere of one side is connected in this way with the olivary nucleus of the opposite side (*olivo-cerebellar tract*). In cases of atrophy or of removal in the new-born animal of the cerebellar hemisphere of one side, the olive of the opposite side is atrophied, while that of the same side is intact. There appears also to be a direct relationship between each olive and the cerebral hemisphere of the same side, for cases have been recorded in which one cerebral hemisphere, the homo-lateral olive, and the hetero-lateral cerebellar hemisphere, all show signs of atrophy. But the anatomical path by which the connexion between cerebral hemisphere and olive is brought about is not known. The olives are, perhaps, to be looked upon as intermediary stations between the cerebrum and cerebellum: they have no direct connexion with the cord (Flechsig), unless the olivo-spinal tract of Helweg may be looked upon as a uniting tract.

Besides the main olivary nucleus, two smaller isolated bands are generally seen (figs. 145, 146), looking like separated portions of the chief nucleus. They are situated one on the dorsal and the other on the mesial aspect of the chief nucleus, and are known as the outer and inner *accessory olivary nuclei*. They are traversed like the main nucleus by bundles of internal arched fibres going to the restiform body, and are not infrequently connected at one or two places with the main nucleus.

INTERNAL STRUCTURE OF THE PONS.[2]

Sections of the pons, as compared with the medulla oblongata, are greatly modified by the appearance of the transversely coursing fibres passing to the

[1] Some fibres emerge from the hilus and turn sharply round the ventral and lateral borders of the dentate nucleus, to which they form a kind of capsule.

[2] See on the general structure and on the nerve-tracts, A. Bruce, Illustrations of the Nerve-tracts in the Mid- and Hind-brain, 1892; and Florence B. Sabin, Model of medulla oblongata, pons, and mid-brain of a new-born child, Johns Hopkins Hosp. Rep. ix.

hemispheres of the cerebellum. These occupy the whole of the ventral portion and enclose and conceal from view the bundles of the pyramids, which can be traced upwards into and through the pons from the medulla oblongata.

Between the bundles of fibres of this ventral portion of the pons a large amount of grey matter with multipolar nerve-cells is everywhere found (*nuclei pontis*: fig. 163, *n.p.*). The transverse fibres originate in this grey matter, which, on the other hand, receives innumerable collaterals from the fibres of the pyramidal bundles. These bundles are concealed ventrally by the transverse fibres of the middle peduncle, which lie over and partly between them. Behind them is another system of transverse fibres termed the *trapezium* (from its aspect

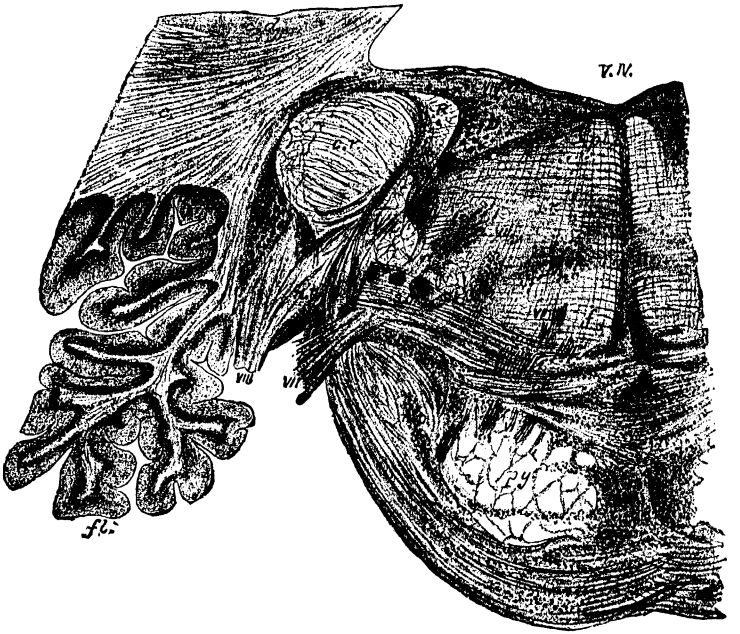


FIG. 163.—TRANSVERSE SECTION OF PONS THROUGH THE ORIGIN OF THE AUDITORY NERVE. From a photograph. Magnified about 4 diameters. (E. A. Schäfer.)

v.IV., fourth ventricle; *c.*, white matter of cerebellar hemisphere; *c.d.*, corpus dentatum cerebelli; *fl.*, flocculus; *c.r.*, corpus restiforme; *R*, Roller's 'ascending' auditory bundle (really formed of descending fibres of vestibular nerve); *D*, Deiters' nucleus; *VIII*, root of auditory nerve; *VIII.d.*, principal nucleus of vestibular division; *VIII.v.*, ventral nucleus of cochlear nerve; *n.tr.*, small-celled nucleus traversed by fibres of the trapezium; *tr.*, trapezium; *f.*, main fillet; *p.l.b.*, posterior or dorsal longitudinal bundle; *f.r.*, formatio reticularis; *n*, *n'*, *n''*, nuclei in formatio reticularis; *V.a.*, so-called ascending root of fifth (really descending); *s.g.*, substantia gelatinosa; *s.o.*, upper olivary nucleus; *VII*, issuing root of facial; *n.VII.*, nucleus of facial; *VI*, root-bundles of abducens; *py.*, pyramid-bundles; *n.p.*, nuclei pontis.

in the lower animals where it appears between the diverging pyramid-bundles). This system forms an important part of the central acoustic tract.

The posterior or dorsal portion of the pons is constituted by a continuation upwards of the reticular formation and of the central grey matter of the medulla oblongata. As in the bulb, there exists here also a median seam or raphe, which is similar in structure to that of the medulla oblongata. In the ventral part of the pons it is almost obliterated by the great development of the obliquely and transversely passing fibres, except near the upper and lower borders, where the superficial transverse fibres of the pons turn in at the middle line; especially at the upper border, where bundles of the same fibres encircle the peduncles of the cerebrum as they emerge from the pons.

In the reticular formation, in addition to the scattered and reticularly arranged grey matter with nerve-cells everywhere met with, there are one or two more condensed collections of cells which lie imbedded in this formation and from which nerve-fibres arise; and as in the reticular formation of the medulla oblongata we find longitudinal and transverse white bundles intersecting one another, the transverse fibres corresponding with the internal arcuate fibres of the medulla oblongata.

The **nuclei pontis** contain stellate nerve-cells, which vary much in size. Some are large and possess thick axons which tend towards the middle line, which they cross, decussating with those of the opposite side, and passing into the opposite cerebellar hemisphere as the fibres of its middle peduncle. Other cells are smaller, with finer axons, which take, however, the same course as those just noticed. But there are, in addition, a number of small nerve-cells belonging to Golgi's type ii., the axons of which have only a short course, and end by ramifications in the adjacent grey matter. The fibres which go to form the middle cerebellar peduncle appear to be devoid of collaterals.

As has already been mentioned, the nuclei pontis receive many collaterals from the pyramid-fibres, and apparently some of the latter send end-arborisations into this grey matter.

A part of the grey matter of the pons, which is indistinguishable in its general appearance from the rest of the nuclei pontis, lies dorsally near the raphe, and just ventral to the tract of the fillet. This part receives collaterals not from the pyramid-fibres, but from the fibres of the fillet, and therefore must be considered to form a separate nucleus of grey matter, since it is connected with afferent fibres, not with efferent fibres like the nuclei pontis generally. It is distinguished by Cajal under the name of *dorsal nucleus of the raphe*, but might be better termed *nucleus pontis dorsalis*.

Central grey matter.—The rest of the grey matter of the pons lies near the dorsal surface and appears in the floor of the upper part of the fourth ventricle. Besides scattered nerve-cells, others are collected within it into definite groups or nuclei. One of these nuclei, in the lower part of the pons, is the continuation of the vestibular nucleus already seen in the upper part of the medulla oblongata; another is the continuation of the acoustic tubercle; another, near the lower extremity of the pons, is the nucleus of the sixth nerve; whilst in the uppermost part of the pons another group of motor cells forms the lower end of the nucleus of the fourth nerve. This will be noticed more particularly in the description of the mid-brain.

Vestibular nuclei and secondary vestibular path.—The *chief nucleus of the vestibular nerve* is composed of two parts, continuous with one another—a *dorsal part* (fig. 151, *n.VIIIp.*) which appears in the grey matter at the side of the fourth ventricle; and a *descending part* which accompanies the descending root of the nerve. The nucleus is prolonged upwards underneath the striæ acusticæ into the pons (fig. 163, *VIII.d.*). It is widest at about the junction of the medulla oblongata and pons, where it extends almost to the middle line; farther up it rapidly narrows and becomes shifted towards the lateral boundary of the ventricle as the nucleus of the sixth nerve makes its appearance between it and the median sulcus. The entering fibres of the vestibular division of the eighth nerve bifurcate (figs. 158, 159). The ascending branches go to the nucleus of Deiters, the nucleus of Bechterew, and the nucleus tecti of the cerebellum (fig. 160). The descending branches send off numerous collaterals into the dorsal nucleus, and they then pass down in the latero-dorsal part of the medulla oblongata in close relation to the descending nucleus, and end in it by terminals and collaterals. In both the dorsal and descending nuclei the cells

are for the most part small; their axons pass into the reticular formation and become longitudinal, but their exact destination has not been ascertained.

The *nucleus of Deiters* (fig. 158, *D*; fig. 163, *D*), also continued up from the medulla oblongata, lies immediately ventro-lateral to the nucleus which has just been described, and is characterised by the large size of its cells. It does not begin to be visible so far down as the main vestibular nucleus, but is continued as far upwards, rather increasing in size superiorly, whereas the main vestibular nucleus diminishes.

The cells of Deiters' nucleus are very large, and are very closely invested by the terminal arborisations of the ascending branches of the vestibular nerve. The axons have numerous collaterals, some of which are distributed to the dorsal part

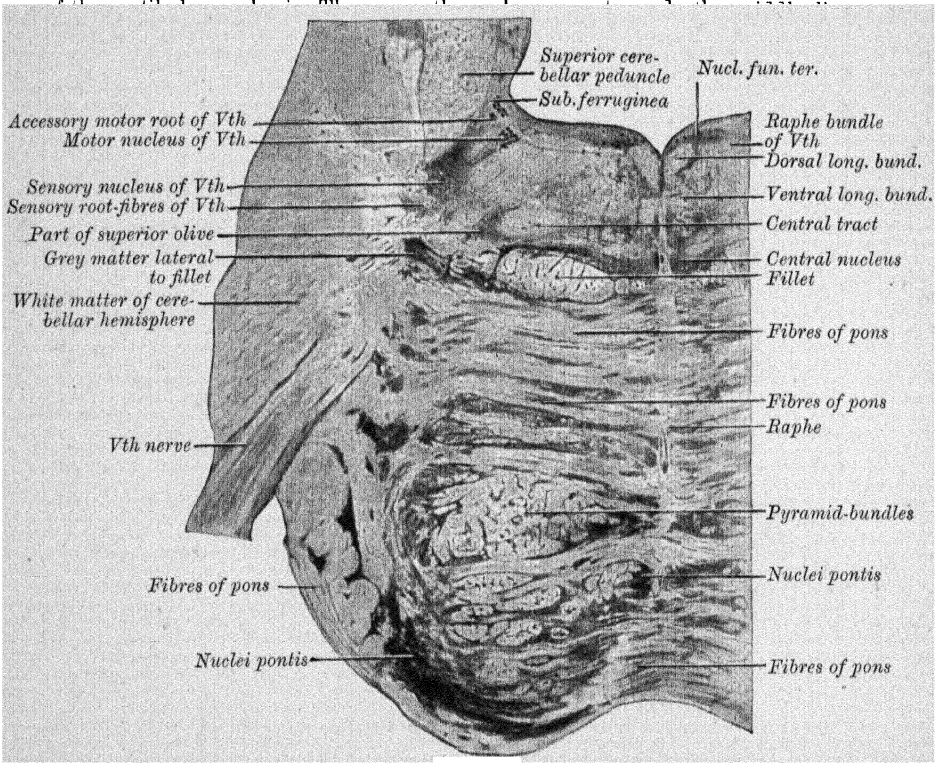


FIG. 164.—SECTION ACROSS THE MIDDLE OF THE PONS. Magnified about 4 diameters.

and enter the dorsal longitudinal bundles of both sides, bifurcating as they enter them, and the resulting fibres pass upwards and downwards (Cajal). Hence, if Deiters' nucleus be destroyed on one side, there is Wallerian degeneration in the dorsal longitudinal bundles of both sides (Fraser); above the level of the lesion, at least as far as the oculo-motor nucleus, and below the lesion even to the lower end of the spinal cord (ventral column).

The *nucleus of Bechterew* lies lateral to Deiters' nucleus, of which it is regarded by Kölliker as an appendage. Its cells are smaller than those of Deiters' nucleus, but, like those, they are invested, although less closely, with arborisations of the ascending branches of the vestibular nerve. Their axons pass through Deiters' nucleus, and, mingling with the axons of its cells, also pass towards the middle line and join the posterior longitudinal bundles of both sides.

Some, however, become longitudinal fibres of the formatio reticularis of the same side, especially just mesial to the seventh nucleus. The nerve-fibres which are derived from these two nuclei and from the cells of the dorsal and descending nuclei—which, as we have seen, form the posterior longitudinal bundles and other longitudinal bundles in the reticular formation—compose the *secondary vestibular paths*. Of these the dorsal longitudinal bundle-fibres must be looked upon as constituting an important factor in the reflex path between the vestibular nerve and the chief motor nuclei, both cerebral and spinal. The fibres in the reticular formation, on the other hand, may carry impressions towards the thalamus and cerebrum, but the exact path of these is not known.

Acoustic nuclei and central acoustic path.[1]—The *ventral nucleus of the cochlear nerve*, which, as we have seen, is represented in the upper part of the medulla oblongata by a collection of nerve-cells lying in the angle between

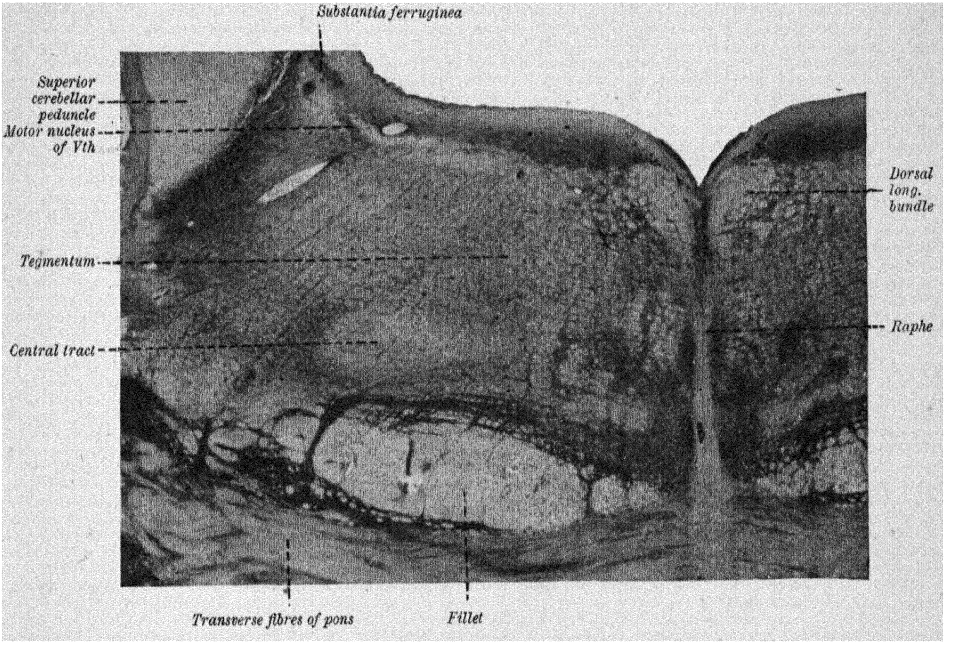


FIG. 165.—DORSAL PART OF PONS FROM SAME SECTION AS SHOWN IN FIG. 164, BUT MORE MAGNIFIED. Photograph. (E. A. Schäfer.)

the restiform body and the two divisions of the root of the acoustic (fig. 151, *n.VIIIac.*), is continued in the region of the pons by a collection of cells lying between the restiform body and the flocculus; the short ascending branches of the fibres of the cochlear root pass directly into it (figs. 154, 155). On the other hand, the descending branches of the bifurcated fibres turn downwards and enter the tuberculum acusticum.

The *trapezium*, which is constituted by a large number of horizontally disposed fibres running behind the pyramid-bundles, is derived from the

[1] The chief recent work on the central acoustic path and its nuclei is contained in the following: v. Monakow, Arch. f. Psych. 1890; Held, Arch. für Anat. 1891, 1892, and 1893; Van Gehuchten, Le Névraxe, iv. 1902, and Système nerveux, 1907; Cajal, Sistema nervioso, &c., Madrid, 1904; F. Hofmann, Arb. a. d. Wiener neur. Institut, xiv. 1907. An excellent account will be found in L. F. Barker, The Nervous System, 1899, with full literature to that date. For a good diagram of the path, see Allen Starr, Journ. Nerv. and Mental Dis. xxix. 1902. On the trapezium nucleus, Nils and Björk, Anat. Anz. xxix. p. 273, 1906.

secondary acoustic nuclei (dorsal and ventral nuclei of the cochlear nerve, p. 139), which, on the other hand, receive, as we have already seen, the terminations of the entering branches of the cochlear division of the eighth nerve. The fibres which enter the trapezium are conducted in it towards the raphe (fig. 157), where they decussate with those of the opposite side. After crossing the raphe they become longitudinal, and passing somewhat more dorsally they become accumulated to form a well-marked tract which in sections of the pons lies in the ventral or ventro-lateral part of the reticular formation lateral to the main tract of the fillet (which latter is nearer the middle line and is continued up from the inter-olivary tract in the medulla oblongata). The superadded tract forms the *lateral fillet*, and above the pons it comes to the surface at the side of the tegmentum (trigonum lemnisci), where it is seen as the *fillet of Reil* passing towards the posterior corpora quadrigemina. The lateral fillet thus represents the continuation of the central acoustic path.

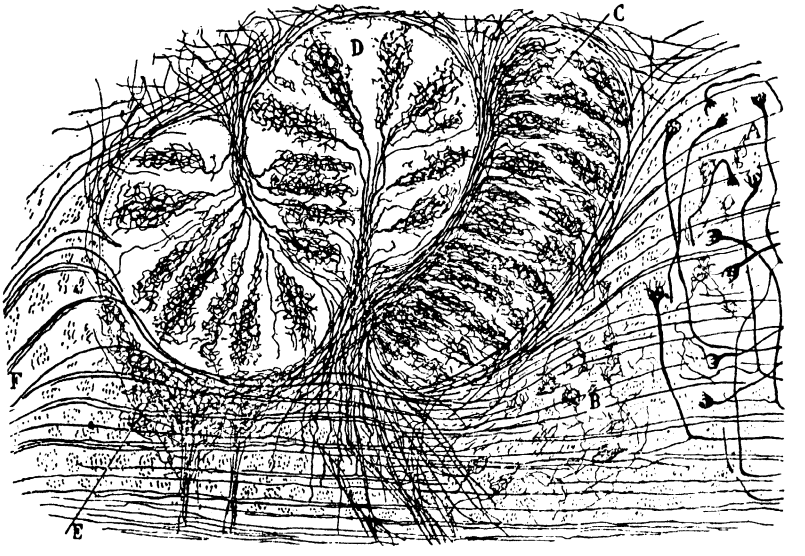


FIG. 166.—LEFT SUPERIOR OLIVARY, ACCESSORY OLIVARY, AND TRAPEZIUM NUCLEI OF KITTEN A FEW DAYS OLD. (Cajal.)

A nucleus of trapezium, showing calices of Held; B, mesial pre-olivary nucleus; C, accessory olivary nucleus; D, superior olivary nucleus; E, lateral pre-olivary or semilunar nucleus; F, fibres of trapezium.

In their course through the trapezium and lateral fillet, the fibres of the central acoustic path give off collaterals to, and receive additions from, a series of nuclei which are intercalated in this path and which are known as the *superior olivary nucleus*, the *accessory nucleus*, the *mesial pre-olivary nucleus*, the *lateral pre-olivary* or *semilunar nucleus*, the *nucleus of the trapezium*, and the *nucleus of the lateral fillet*.

The *superior olivary nucleus* (figs. 166, 167) is an **S**-shaped mass of grey matter, which lies just above the lateral part of the trapezium. In general appearance it resembles the substantia Rolandi, and like that has fusiform cells with many close dendrons disposed vertically to the surface. It receives a large number of collaterals from the trapezium, which enter mainly at the folds of the **S**, and some from the axons of its own cells. These axons pass partly

into the neighbouring formatio reticularis, in which they are continued upwards as a homolateral prolongation of the acoustic path, partly into the trapezium, by which they are conveyed to the opposite side of the pons, there to turn upwards. The cells and their axons thus form acoustic neurones of the third order (the first and second being respectively those belonging to the spiral ganglion of the cochlea and to the dorsal and ventral acoustic nuclei), and the fibres derived from them eventually join the lateral fillet and end in the

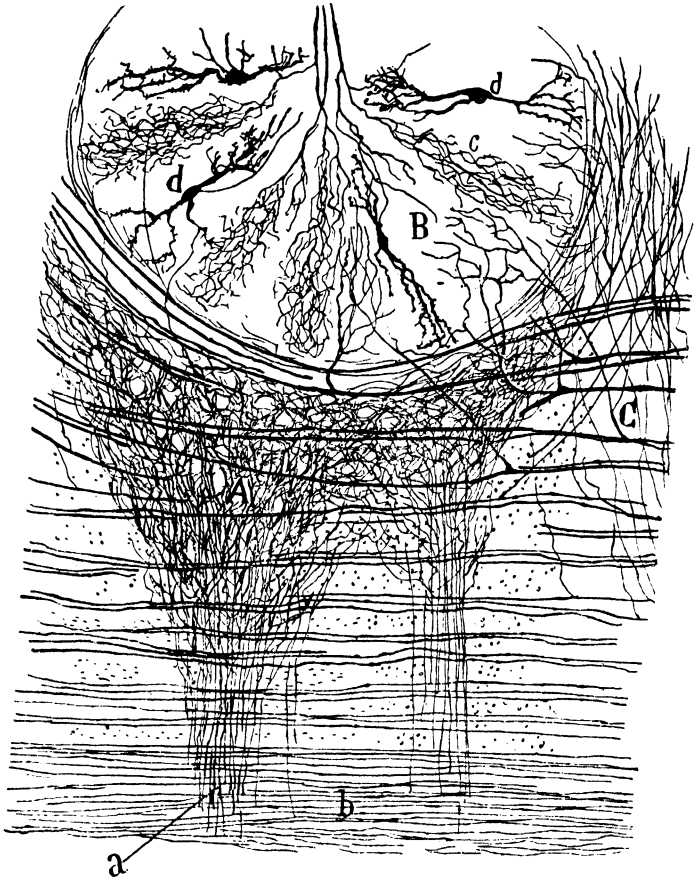


FIG. 167.—PART OF SUPERIOR OLIVARY NUCLEUS AND SEMILUNAR NUCLEUS OF KITTEN A FEW DAYS OLD. More magnified. (Cajal.)

A, lateral pre-olivary or semilunar nucleus; B, superior olivary nucleus; C, coarse collaterals passing into it; *a*, fine collaterals entering semilunar nucleus; *b*, fine superficial trapezium-fibres; *d*, *d*, cells of superior olivary nucleus.

posterior corpora quadrigemina and mesial geniculate body. The superior olive is larger and better-developed in many animals than in man.

An *accessory superior olivary nucleus* lies against the mesial side of the main nucleus, which it resembles in general structure. The axons of its cells, which are somewhat larger and provided with fewer dendrons than those of the main nucleus, leave the nucleus on its dorsal aspect and join fibres of the lateral fillet by a Y-shaped junction. It receives both terminal fibres and collaterals

from the trapezium, which arborise closely around the cells, forming pericellular nests of fine fibrils.

The *nucleus of the trapezium* is closely connected with the accessory superior olive, and with the mesial pre-olivary nucleus. Its cells are rounded in shape and of medium size; their axons pass into the trapezium, and within this are conducted across the middle line to the opposite side; they probably there join the fibres of the lateral fillet. The trapezium nucleus receives a large number of afferent fibres and collaterals from the fibres of the trapezium, which have mainly originated in the ventral cochlear nucleus of the opposite side, but perhaps partly from that of the same side: some, also, may be derived from the opposite trapezium nucleus. These afferent fibres end in two ways—viz.

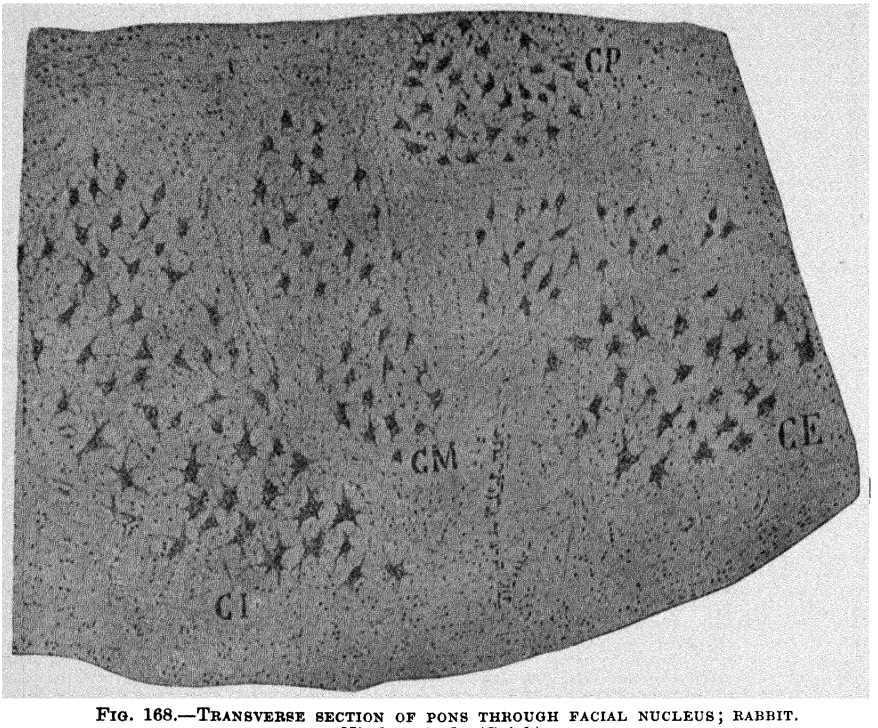


FIG. 168.—TRANSVERSE SECTION OF PONS THROUGH FACIAL NUCLEUS; RABBIT. Nissl method. (Cajal.)

CI, mesial cell-group; CE, lateral cell-group; CM, middle cell-group; CP, dorsal or posterior cell-group.

(*a*) in fine and somewhat diffuse arborisations; (*b*) in the calices of Held. The latter are cup-like expansions of the axis-cylinder, which closely embraces the body of the cell around which it terminates; the edge of the cup is jagged, and sometimes one or more of the points are prolonged to an adjacent cell (as in fig. 155). According to some authorities, the fibres which end in the calices of Held are direct continuations from the cochlear root of the opposite side; others look upon them as derived from the cells of the trapezium nucleus of the opposite side.

The *nucleus semilunaris* or *lateral pre-olivary nucleus* lies immediately ventral to the superior olive. Its cells are collected into groups, and are imbedded in a very close plexus of afferent fibrils derived from fibres in the trapezium, and doubtless from the cochlear nuclei of the opposite side. The

axons of the cells mingle with the adjacent fibres of the trapezium, and join the central acoustic path.

The *mesial pre-olivary nucleus* lies ventral to and in continuity with the trapezium nucleus. It receives many collaterals from the trapezium which form close pericellular arborisations, but not calices of Held. The cells are smaller and less globular than those of the trapezium nucleus; their axons join the central acoustic path.

Nuclei of seventh (facial). — The *motor nucleus of the facial nerve* (fig. 163, *n.VII.*) lies in the reticular formation just dorsal to the superior olivary nucleus, and at some depth therefore below the floor of the fourth ventricle. It begins to be visible in sections immediately above the medulla oblongata, in the form of groups of nerve-cells, from which separate bundles of fibres proceed, and extends three or four millimetres upwards. Its cells are of medium size, and their axis-cylinder processes are directed inwards and backwards towards the grey matter of the floor of the ventricle, where they collect to form a longitudinal bundle, oval in section, which runs for a short distance upwards in the grey matter and then turns sharply in a ventro-lateral direction, traversing the thickness of the pons to emerge on its lateral aspect (fig. 169). The groups of cells within the facial nucleus are related to the supply of motor fibres to the different sets of muscles innervated by this nerve-trunk. Three of these groups lie ventrally and one dorsally (fig. 168). From the mesially situated ventral group the muscles of the tympanum receive their fibres; next to this is a cell-group supplying fibres to the muscles of the pinna; next, and placed still more laterally, a cell-group supplying the muscles of the mouth and face; whilst the fourth group, which lies dorsal to the rest, gives off the fibres which pass into the superior branch and supply the frontalis, corrugator supercilii, and orbicularis palpebrarum.[1] A few fibres have been described as coming from the nucleus of the opposite side, but this is denied by Van Gehuchten. The facial nucleus receives many collaterals from the adjacent fibres of the lateral columns, from the fibres of the fillet and of the secondary acoustic path, and from the secondary trigeminal path.

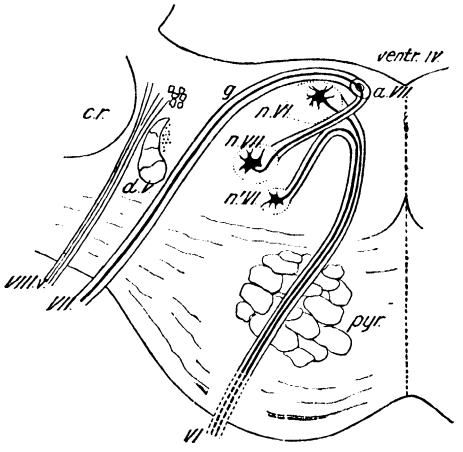


FIG. 169.—PLAN (TRANSVERSE) OF THE ORIGIN OF THE SIXTH AND OF THE MOTOR PART OF THE SEVENTH NERVE. (E. A. Schäfer.)

VI., sixth nerve; *VII.*, seventh nerve; *a.VII.*, ascending part of root of seventh shown cut across near the floor of the fourth ventricle; *g*, genu of seventh nerve-root; *n.VI.*, chief nucleus of the sixth nerve; *n'.VI.*, accessory nucleus of sixth; *n.VII.*, nucleus of seventh; *d.V.*, descending root of fifth; *pyr.*, pyramid-bundles; *VIII.v.*, vestibular root of eighth nerve.

The *sensory portion of the facial* (*nerve of Wrisberg, pars intermedia*) takes origin from the unipolar cells of the geniculate ganglion of the facial in exactly the same way as the posterior roots of the spinal nerves from the cells of the spinal ganglia. The peripherally directed branches pass into the chorda tympani and supply the anterior part and side of the tongue with taste-fibres. The centrally directed branches enter the side of the pons in company with the rest of the nerve and curve round in the reticular formation to join the upper

[1] Van Gehuchten, Journ. de Neurol. 1898, and Système nerveux, 1906. See also Parhon and Minea, Presse méd., 1907.

end of the solitary bundle, down which they pass for a certain distance, giving collaterals and terminals to the grey matter at the side of the bundle forming its nucleus, as in the analogous case of the glosso-pharyngeal and vagus, but confined to the upper part of the nucleus. This part of the nucleus of the solitary bundle also receives fibres from the glosso-pharyngeal and from the descending root of the trigeminal, and in all probability represents a bulbo-pontine gustatory centre.[1]

Nucleus of sixth (abducens).—The *nucleus of the sixth nerve* consists of a group or short column of large multipolar cells lying on each side of the median sulcus (fig. 169, *n.VI.*). It corresponds to the part of the fasciculus teres which lies immediately above the medullary striæ on the floor of the fourth ventricle. The fibres of the nerve run in bundles obliquely ventralwards and downwards (caudalwards) to emerge at the lower border of the pons. Between this nucleus and the median groove, along the middle of the fourth ventricle, is an oval bundle of nerve-fibres, which runs longitudinally upwards for about 5 mm., and occupies nearly the same position with regard to the nucleus of the sixth nerve that the longitudinal fibres which cover the hypoglossal nucleus occupy with regard to the origin of the twelfth. The bundle in question is the ascending part of the root of the seventh nerve (p. 153), and when followed upwards in sections its fibres are seen to turn sharply outwards and ventralwards, and to become the issuing root of the facial. Into the nucleus of the abducens, collaterals pass from the posterior longitudinal bundle and from the adjacent reticular formation. Some of the fibres of the sixth nerve are said by Van Gehuchten to arise from a small *ventral nucleus* close to the facial nucleus, and, like that nucleus, sending fibres obliquely backwards towards the fourth ventricle, which, near the principal nucleus, turn ventralwards to join the issuing fibres of the nerve (fig. 169).

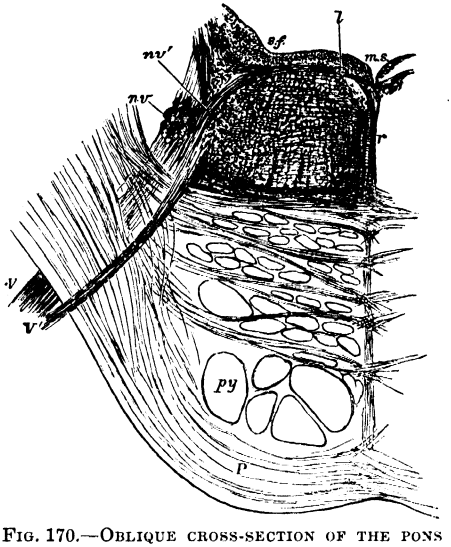


FIG. 170.—OBLIQUE CROSS-SECTION OF THE PONS ALONG THE LINE OF EXIT TRAVERSED BY THE FIFTH NERVE. Magnified 3 diameters. (E. A. Schäfer.)

The section passes through the lower part of the motor nucleus (*nv'*), from which a bundle of fibres of the motor root, *V'*, is seen passing; a part of the upper sensory nucleus (*nv*) is also shown in the section in the form of a number of small isolated portions of grey matter. Among these are a few bundles of the descending root cut across, but most of these have already become diverted outwards to join and assist in forming the issuing part of the main or sensory root, *V*; near the fourth ventricle are seen some transverse fibres which come partly from the raphe, partly from a small longitudinal bundle of fibres (*l*) near the median sulcus (*m.s.*), and pass outwards to join the root of the fifth nerve; *f.r.*, formatio reticularis; *r.*, raphe; *s.f.*, substantia ferruginea; *p*, fibres of pons passing to cerebellum.

Nuclei of fifth (trigeminal).—The *motor nucleus of the fifth nerve* (fig. 164 and fig. 170, *nv'*) comes to view in sections through the higher part of the pons, situated a little below the surface close to the lateral margin of the fourth ventricle. It contains large pigmented multipolar nerve-cells, the axis-cylinders of which pass out into the motor root of the trigeminal. It receives numerous collaterals, some of which are sensory and derived from the central

[1] Cf. Nageotti, Review of Neurology, iv. 1906; also Cajal, Testura d. sistema nervioso, t. ii. p. 180; and Van Gehuchten, Système nerveux, 1906, p. 601.

tract of the fifth, and some motor derived from the axons of the accessory motor nucleus.

The *upper sensory nucleus of the fifth nerve* (fig. 164 and fig. 170, *nv*) lies on the outer side of the motor root. The cells are of large and medium size and

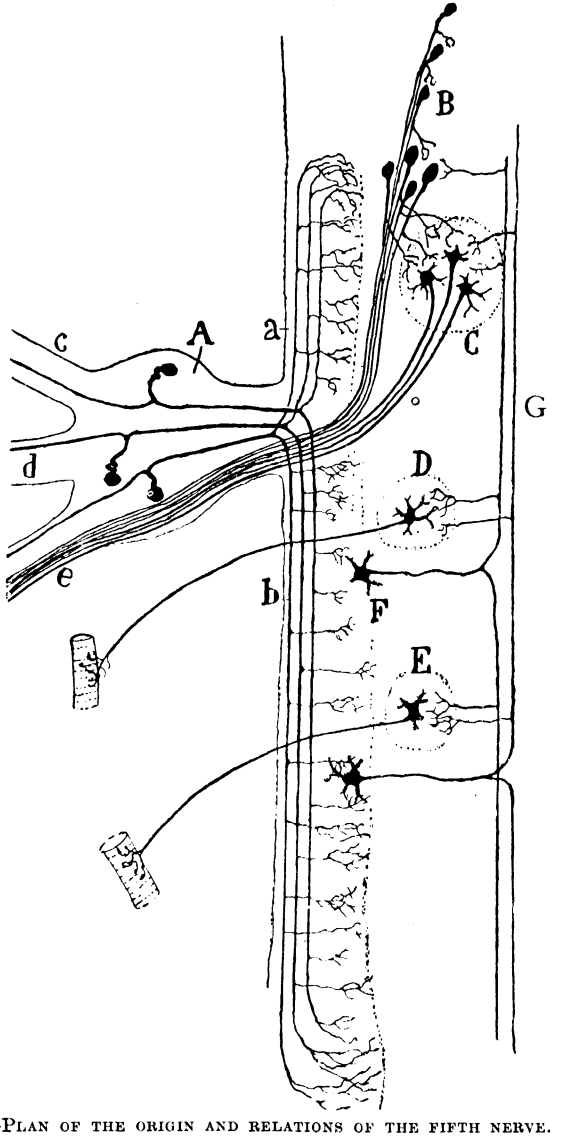


FIG. 171.—PLAN OF THE ORIGIN AND RELATIONS OF THE FIFTH NERVE. (Cajal.)

A, Gasserian ganglion; B, accessory motor nucleus; C, main motor nucleus; D, facial nucleus; E, nucleus of hypoglossal; F, sensory nucleus of trigeminal; G, cerebral tract of trigeminal; *a*, ascending branches; *b*, descending branches of sensory root-fibres; *c*, *d*, *e*, ophthalmic, maxillary, and mandibular branches of trigeminal trunk.

arranged in clusters, separated by the fasciculi of the sensory nerve-root. This collection of cells is much more extensive than the motor nucleus, being seen in sections higher up the pons, and passing below into the *lower sensory nucleus*,

which is a continuation of the grey matter of the tubercle of Rolando. Passing towards the middle line in all sections through the middle part of the pons is a well-marked tract of fine fibres which are traceable over the dorsal longitudinal bundle to the raphe, in which they become lost. This tract is the *raphe-bundle* of the trigeminal. Its fibres pass by and may in part be continuous with a small oval bundle of longitudinal fibres (fig. 170, *l*), which lies in the grey matter not far from the median sulcus, and which resembles in appearance the ascending part of the facial root.

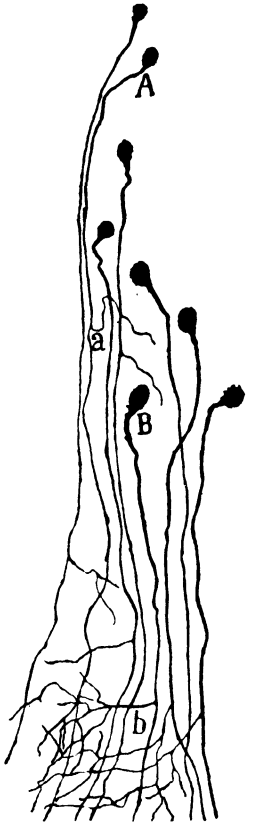


FIG. 172.—CELLS OF THE ACCESSORY MOTOR NUCLEUS OF THE FIFTH NERVE. (Cajal.)

A, an upper cell with smooth cell-body; B, lowermost cells with small projections on cell-body; *a*, collaterals within the accessory nucleus; *b*, collaterals passing into the principal motor nucleus.

The fibres of the sensory root (which are derived from the centrally directed branches of the axons of the Gasserian ganglion-cells) bifurcate as they enter the pons into ascending and descending branches (fig. 171). The ascending branches are short and arborise in the upper sensory nucleus. The descending branches are collected into one or more bundles which extend down in the lateral part of the reticular formation, accompanied by the downward extension of the sensory nucleus known as the substantia gelatinosa. This *descending trigeminal root* is traceable down into the upper cervical cord, and its nucleus here comes into close contiguity with the gelatinous substance of the apex of the posterior horn. The fibres of the descending root give off many collaterals as well as terminals to the accompanying substantia gelatinosa.

The cells of the sensory nucleus of the trigeminal are either large or of medium size. Their axons pass towards the raphe, and either on the same or more frequently on the opposite side of this they become longitudinal (or join longitudinally running fibres by a T-shaped junction), and take part in the formation of the great sensory tract which passes to the thalamus (fillet-system). The bundles into which they are collected retain, however, their individuality, and can be traced up through the reticular formation and tegmentum into a part of the thalamus distinct from that reached by the remainder of the fillet-system (*trigemino-thalamic tract*).

In their course through the reticular formation these axons give off many collaterals to the motor nuclei of the medulla oblongata and pons, especially to the nucleus ambiguus, the facial nucleus, and the principal motor nucleus of the fifth. In addition to these cells, which give origin to the fibres of the secondary or central path of the fifth, the sensory nucleus includes a number of small cells of Golgi's second type, with closely massed dendrons, and axons extending only a short distance from the cell-body and ramifying in the grey matter of the nucleus itself.

The *accessory motor nucleus of the fifth nerve* is composed of large globular unipolar cells (fig. 172) arranged (in groups or intermittently) in a somewhat linear fashion in the central grey matter along the lateral aspect of the anterior

end of the fourth ventricle, and traceable up as far as the region of the inferior corpora quadrigemina. Below, as it approaches the principal motor nucleus, the accessory nucleus expands into a triangular mass (fig. 164) of similar cells, except that the cell-bodies are rather less smooth and may show fine spines like commencing dendrons. Occasionally one or more multipolar cells are seen amongst them, but these may belong to the neighbouring substantia ferruginea. Each cell of this nucleus sends a single large axon down to join the motor root of the fifth.[1] As these fibres pass the principal motor nucleus they give off to it many collaterals; others are distributed around the cells of the lower part of the accessory nucleus itself, and this also has many collaterals derived from the axons of the sensory nucleus, and others from the nucleus of Bechterew (Cajal).

The substantia ferruginea, which has sometimes been regarded as belonging to the motor system of the fifth, is, according to Cajal, a sensory nucleus of the third order, and sends its axons to the central grey matter.

Transition from the pons to the mid-brain.—In sections through the upper part of the pons the fourth ventricle, which here becomes rapidly narrowed, is at first roofed over dorsally by the two superior peduncles of the cerebellum which are passing to the mesencephalon, and by the superior medullary velum and lingula, which lie between them. The grey matter of the floor of the ventricle (central grey matter) shows on each side near the median groove a group of nerve-cells continuous below with the nucleus of the funiculus teres, and above with the nucleus of the aqueduct. More to the side is the mass of pigmented nerve-cells known as the *substantia ferruginea* (figs. 164, 165, 170, *s.f.*), and still more laterally, at the angle which the roof makes with the floor, the accessory motor nucleus of the fifth, along the outer border of which a well-marked white bundle—the accessory (descending) motor root of the fifth nerve—runs downwards towards the middle of the pons, where it issues with the motor root. The cells of the accessory nucleus and the fibres of the accessory root can be traced from the region of the superior corpora quadrigemina. Between the central grey matter and the reticular formation on each side of the raphe is the now sharply defined dorsal longitudinal bundle (fig. 165). The fillet is also now distinct from the neighbouring longitudinal bundles of the reticular formation, and a considerable part of it, the lateral fillet, is seen to be passing to the side of the pons, and, higher up, its fibres, as they cross obliquely towards the corpora quadrigemina, overlap the superior cerebellar peduncle of the same side (fig. 173). As the lateral fillet thus passes gradually to the side it gives place mesially to a bundle of longitudinal fibres, which begins to be distinct in this region, and which is traceable upwards into the *mesial bundle of the crusta*; a part of this enters the tegmentum and is seen as far as the base of the thalamus (the so-called 'mesial fillet'). The superior cerebellar peduncle as the sections are traced upwards is seen gradually to shift ventral- and mesial-wards, until in sections through the uppermost part of the pons it reaches the raphe, and begins to decussate with its fellow of the opposite side (fig. 173).

In sections through the uppermost part of the pons (fig. 173) the fibres of the middle peduncles, which arch upwards as before mentioned, are cut obliquely, and their entrance into the cerebellar hemisphere is no longer seen. The fillet is passing to the side and the superior cerebellar peduncles are approaching the middle line and beginning to cross. Bundles belonging to

[1] According to Terterjanz, these fibres go to the tensor palati muscle (Arch. f. mikr. Anat. liii. 1899).

the fourth nerve are seen passing in the grey matter at the side of the ventricle to intercross in its roof with those of the opposite side.

Tænia pontis (fig. 174).—One or more small bundles of fibres are frequently seen—usually on one side only—emerging from the middle line on the ventral aspect and turning round the cerebral peduncle parallel with the uppermost pontine fibres to pass with these into the hemisphere of the cerebellum. According to Horsley,[1] the bundle or bundles in question are ponto-cerebellar, arising in the nuclei pontis and ending in the nucleus dentatus cerebelli.

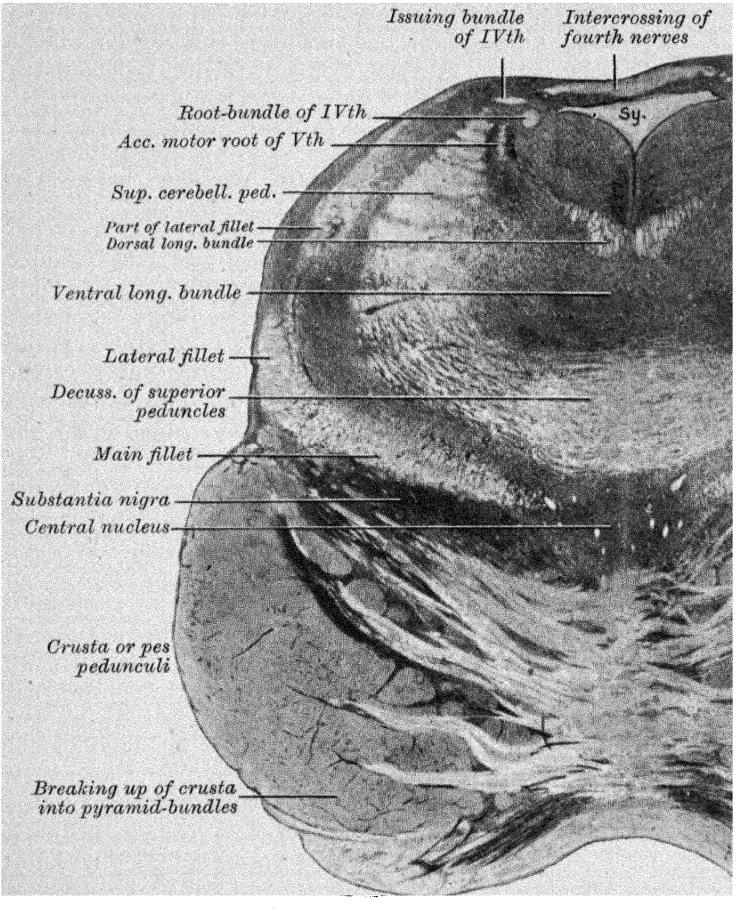


FIG 173.—TRANSVERSE SECTION THROUGH THE UPPERMOST PART OF THE PONS.

The pyramid-bundles are more scattered and also more numerous in the upper than in the lower part of the pons, and the grey matter between them is increased in amount. In the highest sections (fig. 175) this grey matter is beginning to accumulate ventral to the fillet and reticular formation, and to contain a considerable amount of pigment in its cells (commencement of *substantia nigra* of mesencephalon). The pyramid-fibres now again collect into a compact bundle, which tends to be flattened dorso-ventrally. In fact, but for the obliquely cut fibres of the middle peduncles of the cerebellum, a section through this part of the pons exhibits all the characters of sections through the lowest part of the mid-brain.

[1] Brain, 1906.

Course of nerve-tracts through the medulla oblongata and pons.[1]—**Ascending tracts.**—The tracts of the *dorsal column* of the cord are continued in the medulla oblongata as the white substance of the funiculus gracilis and funiculus cuneatus. The fibres end by arborisations in the grey matter which forms the corresponding nuclei (fig. 128, p. 104); and numerous deep arched fibres emerge from the same collections of grey matter, and pass through the raphe to the other side of the medulla oblongata, where they are continued into the longitudinal fibres dorsal to the pyramids and form the *main tract of the fillet* (Edinger) (inter-olivary layer of Flechsig).

The fillet is not well marked off from the adjacent tracts of longitudinal fibres in the medulla oblongata, but in the pons it is very apparent as a distinct flattened mass of white matter, composed of a number of bundles lying in the ventral part of the formatio reticularis (fig. 165), and in this form it is continued up into the mid-brain. At the upper part of the pons it tends towards the lateral aspect and begins to appear on the exterior, just above the fibres of the middle peduncle.

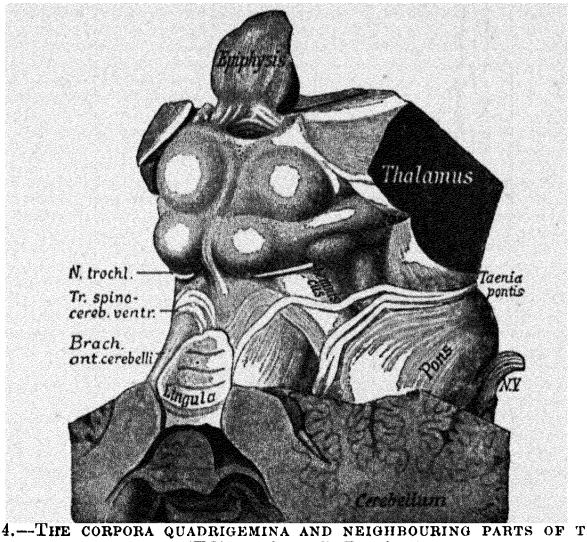


FIG. 174.—THE CORPORA QUADRIGEMINA AND NEIGHBOURING PARTS OF THE BRAIN. (Edinger from G. Retzius.)

Brach. ant. cerebelli, the superior cerebellar peduncles, between them the anterior medullary velum partly covered by the lingula; *Tr. spino-cereb. ventr.*, ventral spino-cerebellar tract curving round the peduncle; *Lemniscus*, the lateral fillet; *N. trochl.*, fourth nerve; *N.V.*, fifth nerve. The pineal body (epiphysis) is turned upwards to show the posterior commissure.

Here, as the *lower* or *lateral fillet*, a part of it forms a prominent superficial band (*fillet of Reil*), which passes obliquely at the side of the mid-brain to enter the corpora quadrigemina (fig. 174, lemniscus). This lateral fillet is formed mainly, if not entirely, of fibres of the central acoustic path (p. 149). This path is traceable from the accessory and lateral nuclei of the cochlear division, the cells of which send their axons mainly by way of the trapezium to the superior olivary and other nuclei (pre-olivary, semilunar, and trapezoid) of the opposite side. In these nuclei the fibres in question for the most part terminate, and the path is continued by other neurones, the cell-bodies of which lie in those nuclei, while the axons pass into the lateral part of the fillet and are continued up, as we have seen, towards the corpora quadrigemina.

[1] The literature of these tracts is much the same as for the tracts between the mid-brain and spinal cord. See especially the description given by Collier and Buzzard in Brain, xxiv. 1901. A bibliography of the spino-cerebellar tracts will be found in Bing, Die Bedeutung d. spino-cerebellaren Systeme, 1907. See also L. F. Barker, Nervous System, 1899, and Ziehen, *op. cit.*

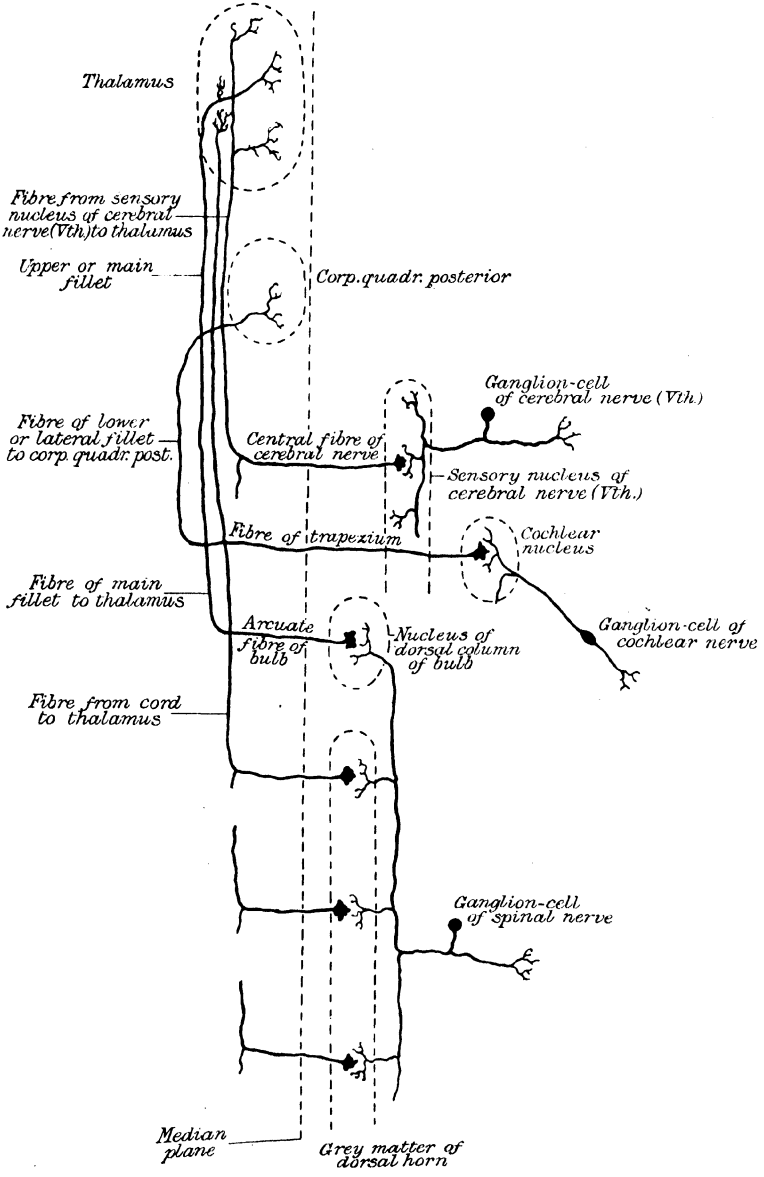


FIG. 175.—DIAGRAM OF SENSORY PATH FROM PERIPHERAL NERVE TO CORPORA QUADRIGEMINA AND THALAMUS. (E. A. Schäfer.)

The wavy bundles of fibres which constitute the lateral fillet are separated by islets of cells which are accumulated at two places into larger masses termed the *nucleus of the lateral fillet* and the *superior nucleus of the lateral fillet*. In some animals these are more or less united, and lie lateral to the tract of the fillet, appearing like a prolongation of the superior olivary nucleus.

The *nucleus of the lateral fillet* is formed of large stellate cells with few and long dendrons; the axon is directed towards the raphe. The *superior nucleus* is formed of fusiform cells with transversely extended dendrons, the axon passing towards the middle line and taking part in a ventral decussation.

The lateral fillet contains some *descending* fibres which are probably passing from the nuclei which are connected with it downwards towards the motor nuclei in the medulla oblongata and spinal cord.

The remainder of the tract of the fillet (*upper* or *main fillet*) is formed by a continuation upwards of the interolivary tract of the medulla oblongata. Its fibres are chiefly derived from the gracile and cuneate nuclei of the opposite side; besides which, fibres belonging to the same system pass up from the lateral column of the cord (*spino-thalamic fibres*). The fillet is reinforced throughout the whole extent of the medulla oblongata and pons by other fibres which emanate from the masses of grey matter in which the sensory roots of the cerebral nerves have their terminal arborisations.[1] But many of the fibres which continue the sensory path of the cerebral nerves upwards run in the formatio reticularis apart from the bundles which constitute the fillet, forming a similar but less defined tract, which is known as the *central* or *thalamic tract of the cerebral nerves*, and passes to the thalamus.

Homologous fibres belonging to the central path of the fifth nerve are conducted upwards towards the thalamus by a separate tract in the formatio reticularis and tegmentum: this is known as the *trigemino-thalamic tract* (p. 156). In all cases the central paths pass upwards mainly on the opposite side of the brain-stem, but a certain number of fibres are continued upwards on the same side.

Collaterals pass off from all the longitudinal tracts of the posterior and lateral regions of the medulla oblongata and pons to end by terminal ramifications in the adjacent nuclei (Kölliker).

The part of the lateral column of the cord which forms the *dorsal spino-cerebellar tract* (see fig. 123 and fig. 130, *d.a.c.*) passes at about the middle of the medulla oblongata obliquely backwards in the restiform body to the cerebellum, in which it terminates for the most part in the upper part of the worm, both on the same and on the opposite side. In its passage up the medulla oblongata this tract gives off two sets of collaterals, one (ventral) passing to a small special nucleus, and the other (more dorsal) to the grey matter of the solitary bundle.[2]

The *ventral spino-cerebellar tract* (fig. 123; fig. 130, *v.a.c.*) passes into the upper part of the pons, and turning dorsally at about the level of the exit of the fifth nerve curves backwards and enters the cerebellum over the superior peduncle and in the superior medullary velum. Its fibres end mainly in the lower part of the worm, many crossing the middle line. As it passes up the medulla oblongata some of its fibres join those of the dorsal spino-cerebellar system and enter the restiform body. But a part of the bundle of Gowers is continued up through the reticular formation of the pons and mid-brain towards the region of the superior corpora quadrigemina and thalamus.[3]

Descending tracts.—The *lateral pyramid-tract* seen in the cord is traceable from the opposite pyramid of the bulb, and through this and the ventral part of the pons from the crusta of the mid-brain. Together with the small part

[1] Gee and Tooth, Brain, xxi. 1898; Van Gehuchten, Le Névraxe, 1902.
[2] Horsley and Thiele, Brain, xxiv. 1901.
[3] Schäfer, Quain's Anatomy, 10th ed.; Mott, Phil. Trans. 1891; Brain, 1892 and 1895.

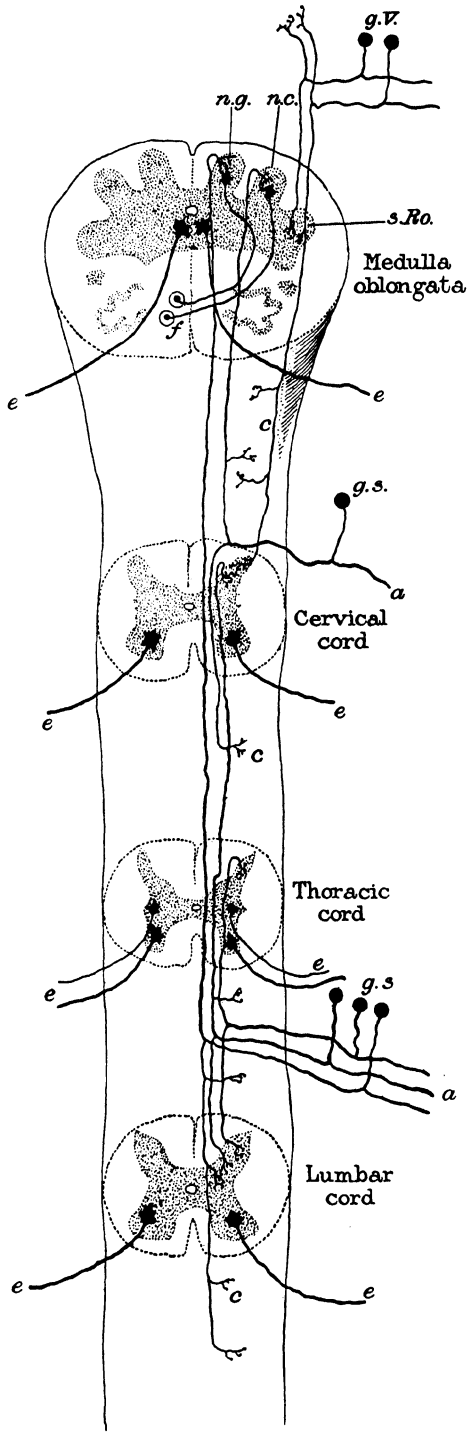


FIG. 176.—DIAGRAM, MODIFIED FROM CAJAL, TO SHOW THE COURSE OF THE FIBRES OF THE DORSAL ROOTS AFTER ENTERING THE CORD.

a, afferent fibres passing to ganglia; *e*, efferent fibres leaving cord, derived from motor cells; *g.s.*, spinal-ganglion cells; *g.V.*, ganglion-cells of fifth nerve; *n.c.*, nucleus cuneatus; *n.g.*, nucleus gracilis; *f*, fibres of fillet; *c*, collaterals.

of the ventral column of the cord which also enters into the constitution of the pyramid-system, it there forms the *pyramid-tract of the crusta* (*peduncular tract*, Meynert). The pyramid-tract is hardly larger in the medulla oblongata than in the upper cervical region of the spinal cord, but is much larger in the pons than in the medulla oblongata, many of its fibres ending in the pons. Those which are continued down into the pyramids of the medulla oblongata run

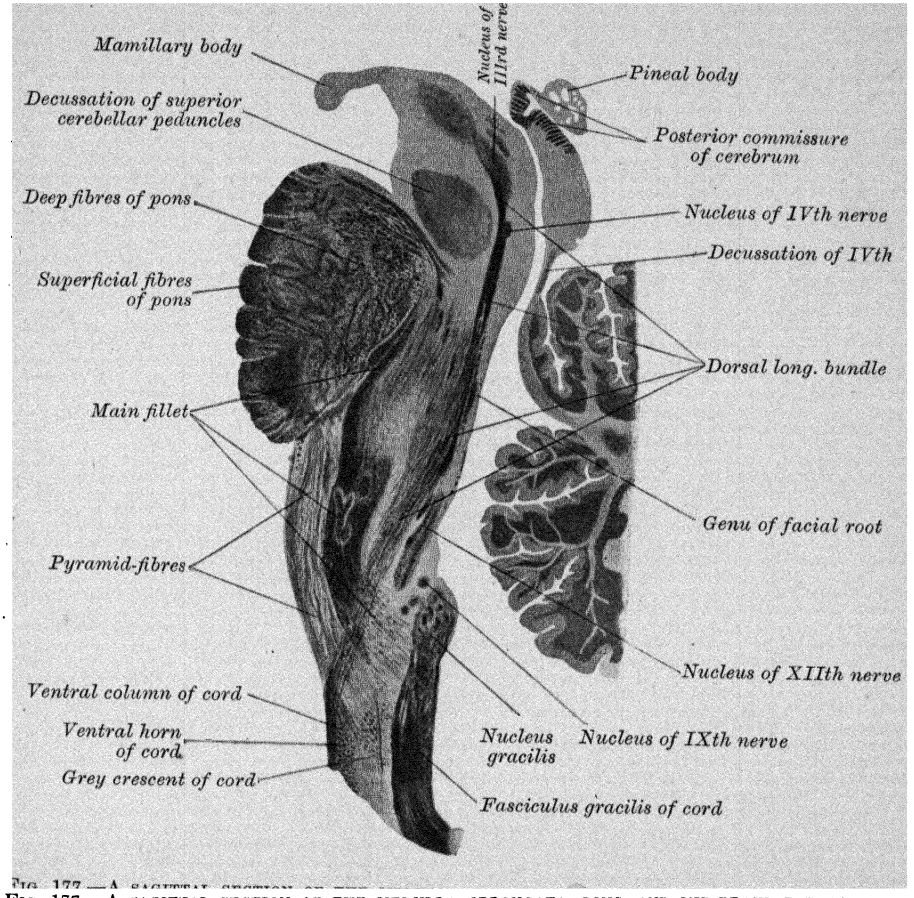


FIG. 177.—A SAGITTAL SECTION OF THE MEDULLA OBLONGATA, PONS, AND MID-BRAIN, PARALLEL AND CLOSE TO THE MESIAL PLANE, FROM A THREE MONTHS' CHILD. Weigert method. (From A. Bruce, 'Nerve-tracts in the Mid- and Hind-brain,' 1892.)

The manner in which the dorsal longitudinal bundle follows the shifting of the position of the motor nuclei from the dorsal part of the pons and medulla oblongata to the ventral part of the medulla spinalis is well seen both in this and in the next figure.

down the pons they give off numerous collaterals to the nuclei pontis and some to the tegmentum. Those fibres which terminate in the pons itself probably chiefly end in the grey matter of the nuclei pontis. In the medulla oblongata hardly any fibres, terminal or collateral, can be seen to leave the pyramids. They have been described by many authors as ending in the nerve-nuclei of the efferent cerebral nerves which arise here and in the medulla oblongata, but this does not appear to be founded on actual observation, and, as a matter of fact,

none can be seen to enter those nuclei.[1] From the cells of the nuclei pontis nerve-fibres pass across the raphe to form the opposite middle peduncle of the cerebellum. These fibres reach the cortex of the opposite cerebellar hemisphere, and thus constitute part of a *cerebro-ponto-cerebellar path.* On the other

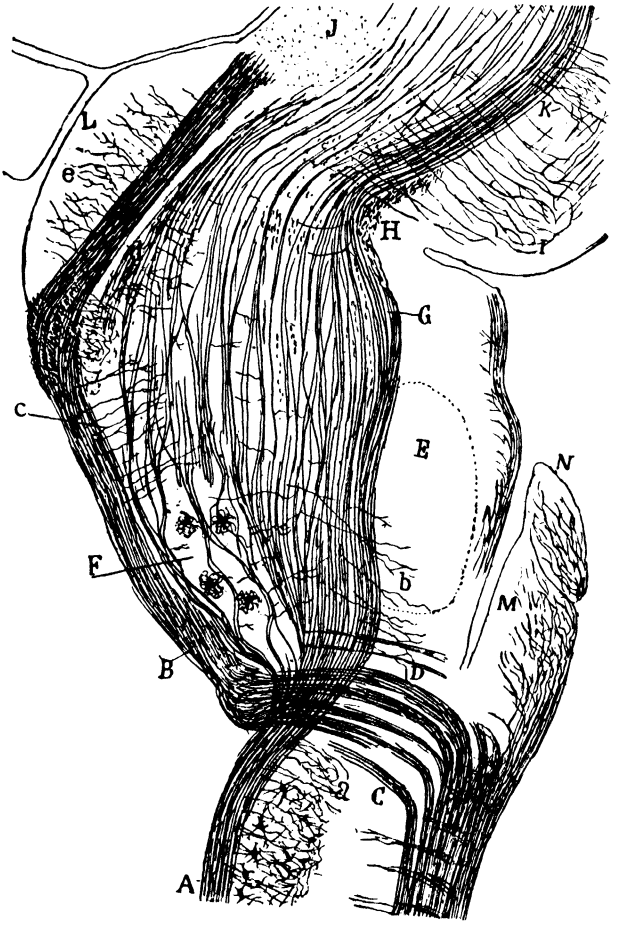


FIG. 178.—SAGITTAL SECTION OF PONS AND MEDULLA OBLONGATA OF MOUSE A FEW DAYS OLD. (Cajal.)

A, ventral column of cord; B, pyramid of medulla oblongata; C to D, decussation of pyramids; D, fibres of sensory decussation; E, situation of nucleus of twelfth nerve; F, cells of olivary nucleus; G, dorsal longitudinal bundle; H, fibres of seventh nerve near floor of fourth ventricle; I, central grey matter; J, situation of interpeduncular ganglion; K, collaterals passing from dorsal longitudinal bundle into oculo-motor nucleus; L, pons; M, central canal opening into fourth ventricle at N; *a*, collaterals from ventral-column fibres into ventral horn of cord; *b*, collaterals into nucleus of twelfth; *c*, *d*, *e*, collaterals of pyramid-fibres.

hand, the nuclei pontis receive many collaterals and terminals from the traversing fibres of the pyramid-tract (figs. 178, 179, 180).

In its passage through the cerebral peduncle, pons, or medulla oblongata the pyramid-tract often gives off aberrant bundles, which may leave the main tract in or above the pons and rejoin it lower down (Pick), or may pass away from it altogether and end in the grey matter of the nuclei pontis. One such aberrant bundle is not uncommonly found in the

[1] Sutherland Simpson, Int. Monthly Jour. Anat. and Physiol. 1902; Cajal, Textura &c. 1904.

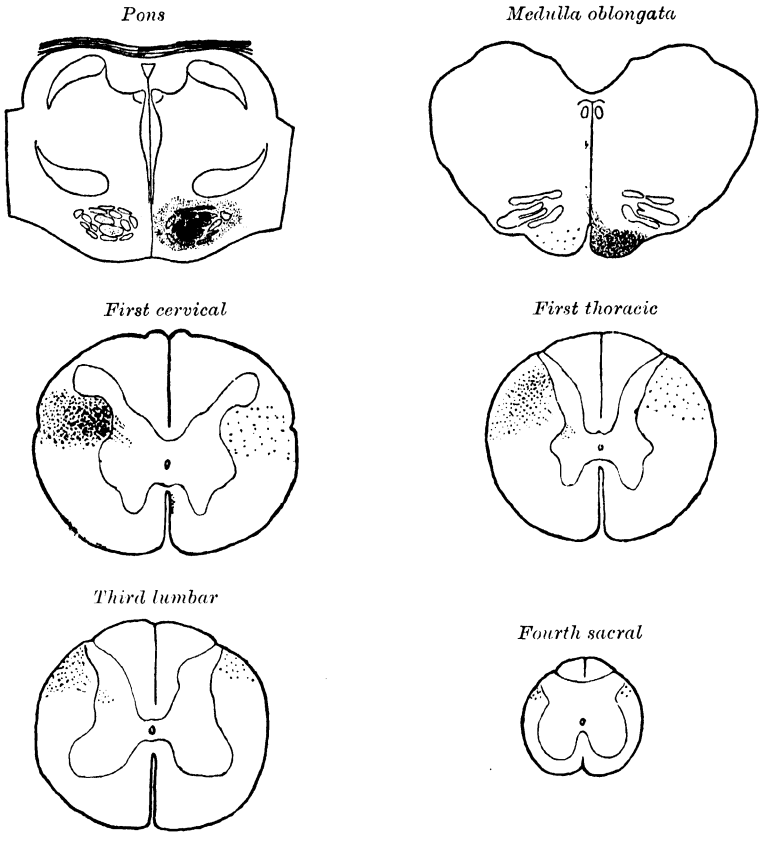


FIG. 179.—SECTIONS ACROSS THE PONS, MEDULLA OBLONGATA, AND SPINAL CORD OF A MONKEY IN WHICH THE MOTOR CORTEX OF THE RIGHT HEMISPHERE HAD BEEN REMOVED SOME WEEKS PREVIOUSLY. (Sutherland Simpson and Jolly.)

Notice a few fibres degenerated in the pyramid-bundles of the left side, *above the decussation*; these must have crossed in the corpus callosum. Also some degeneration in the homolateral pyramid-tract in the cord and the passage of fine fibres into the base of the dorsal horn from the main pyramid-tract degeneration.

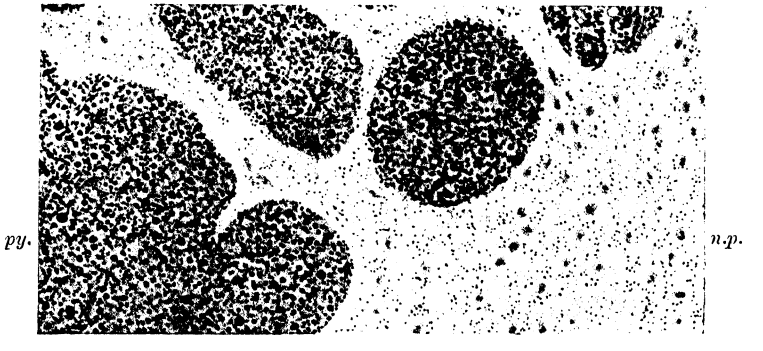


FIG. 180.—PYRAMID-BUNDLES OF THE PONS AFTER AN EXTENSIVE LESION IN THE MOTOR CORTICAL REGION OF THE SAME SIDE: MONKEY. (Sutherland Simpson.)

The degenerated fibres are shown by the Marchi method. Notice the extensive fine degeneration of the collaterals of the pyramid-fibres (*py.*) in the nuclei pontis (*n.p.*).

medulla oblongata, leaving the pyramid—usually the *left* pyramid—and passing round below the olivary body to become lost in the lateral column.[1]

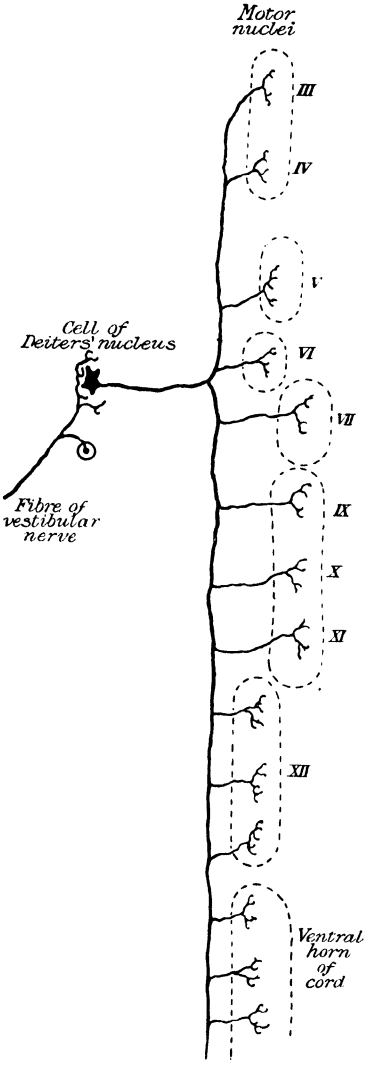


FIG. 181. — DIAGRAM OF A FIBRE OF THE DORSAL LONGITUDINAL BUNDLE ARISING FROM A CELL OF DEITERS' NUCLEUS. (E. A. Schäfer.)

The *rubro-spinal tract* is traceable down from the tegmentum of the mid-brain, where it takes origin in the cells of the red nucleus, mainly of the opposite side. It is at first mesial to the fillet, but lower down passes to the side of the reticular formation (figs. 143, 144).

Another tract in the lateral part of the reticular formation is the *ponto-spinal* (Bechterew), which is formed of fibres derived from cells of the reticular formation, and running downwards into the ventral column of the cord along with those of the ventral longitudinal bundle. But some cross the raphe and pass into the opposite lateral column. Associated with this tract are *vestibulo-spinal fibres* derived from the cells of the nucleus of Deiters and the nucleus of Bechterew. These are similar both in origin and ultimate destination to the fibres of the dorsal longitudinal bundle (see below).

The *thalamo-olivary tract* or *central tract of the tegmentum* (Bechterew) is another tract of descending fibres which, in the mid-brain and pons, runs in the middle of the tegmentum, but in the medulla oblongata comes to lie somewhat more ventrally and approaches the olivary nucleus, which is believed to be its destination. The origin of its fibres is said to be the thalamus. It myelinates later than most of the other tracts.

The *ventral column* of the cord is found when traced upwards to be (in man) in part continuous with the pyramid of the same side. The rest (the whole in animals) dips under the pyramid and forms the longitudinal fibres of the white reticular formation in the dorsal part (fig. 178). These are traceable upwards to the tegmentum. In the pons one tract of them becomes collected into the well-marked fasciculus termed the *posterior* or *dorsal longitudinal bundle* (figs. 164, 165; fig. 178, G), and others form the less-marked *anterior* or *ventral longitudinal bundle* (fig. 164 and fig. 178, ventral to the last). In the region of the medulla oblongata, as in the cord, these two tracts are indistinguishable from one another in the adult, but in the fœtus they are found to myelinate at different periods, and are then readily differentiated. Both give off numerous collaterals to the motor nuclei which they pass (fig. 178, *a*, *b*, I, K).

[1] Elliot Smith, Rev. of Neurol. ii. 1904; *ibid.* 1907. See also Karplus and Spitzer, Arb. a. d. neurol. Instit. Wien, 1904.

THE CEREBELLUM.

The **cerebellum** (figs. 182, 183, and 184) consists of two lateral lobes or *hemispheres* joined together by a median lobe called, from the peculiar appearance caused by the transverse furrows or ridges upon it, the *worm* (*vermis*) or *vermiform process*. This is seen on the under-surface in the fossa between the hemispheres as a well-marked projection named the *inferior vermis*, but above it forms an elevation (the *superior vermis*) which passes into the lateral lobes without any distinct line of demarcation. In most mammals, as in man, the lateral lobes are much better developed than the median lobe, whereas in birds and reptiles the reverse is the case. In amphibia and fishes the cerebellum is quite rudimentary.

The cerebellum occupies most of that part of the cranial cavity which lies below the level of the tentorium cerebelli. Its upper or dorsal surface is in contact with the tentorium, which separates it from the cerebral hemispheres. The outer part of its ventral aspect comes into relation with the petrous portion of the temporal bone external to the internal auditory meatus. Its highest portion projects slightly into the opening in front of the tentorium and, below, it often sinks into the foramen magnum. The transverse sinus, commencing behind at the torcular Herophili, passes round its outer and anterior aspects to reach the jugular foramen. The medulla oblongata, pons, and lower part of the mid-brain lie in a hollow, concave from side to side, on its anterior (ventral) aspect, called the *anterior cerebellar notch*, and the cerebellum is connected with each of these parts by a pair of peduncles (see fig. 190). On the inferior surface each hemisphere is convex both from before backwards and from side to side, and lies in a cerebellar fossa of the occipital bone. The hemispheres are separated by a deep median fossa, named the *vallecula*, in which the inferior vermiform process (figs. 183, 184) lies partially concealed. On a surface view the vallecula is lozenge-shaped, being narrow in front and behind, but expanded in the middle where the pyramidal lobule of the inferior worm is seen (see fig. 184). The deeper part of the vallecula is divided into two lateral parts by the vermis, and the deep antero-posterior grooves thus formed which mark off the lower worm from the hemispheres may be termed *sulci vallecul*æ (*dexter et sinister*). The vallecula is continuous behind with a deep but narrow notch (*posterior cerebellar notch*) which separates the projecting posterior margins of the hemispheres, and into which the falx cerebelli dips. The upper vermiform process, as already mentioned, is not sharply marked off from the dorsal surface of the hemispheres, so that the upper surface of the organ, which is ridged in the middle (*culmen monticuli*), slopes downwards uninterruptedly on each side and behind (*clivus monticuli*).

The greatest diameter of the organ is transverse, and extends to about 4 inches (10 cm.); its greatest vertical diameter is about 2 inches (5 cm.); and its greatest dorso-ventral measurement about 2 inches; it thins out towards the lateral border. It weighs about 5 oz. (142 grammes).

The cerebellum is characterised by its laminated or foliated appearance, its surface being everywhere marked by deep, closely set, transverse and somewhat curved, fissures, which extend a considerable depth into its substance, but do not all entirely encircle the organ, for many of them coalesce with one another, and some of the smaller furrows have even an oblique course between the others. Moreover, on opening the larger fissures, other folia are seen to lie concealed within them, not reaching the surface of the cerebellum.

The depth of the fissures can best be estimated in sections through the organ taken across the laminæ: in such sections each lamina is seen to

have a white centre and a grey cortex, and the white centres of the laminæ appear in the form of processes ramifying from a larger white centre near the middle and anterior part of the organ: to the arborescent appearance thus obtained in section the name *arbor vitæ cerebelli* has been applied (fig. 185).

Externally the most conspicuous fissure is the *great horizontal fissure* (figs. 183, 184), which beginning in front at the middle peduncle of either side extends round the peripheral part of each hemisphere, dipping down into the posterior notch. This fissure pursues a somewhat wavy course and, except near the middle line behind, lies distinctly below the border which separates the tentorial from the cranial surface, so that in the greater part of its extent it is visible on looking at the cerebellum from below (see fig. 184). It may, however, be conveniently regarded as dividing the cerebellum into an upper and lower portion, in each of which several lobes, separated by fissures for the most part deeper than the rest, are described. We may first consider the parts which are present upon the upper part and which compose the upper half of the organ in both the worm and the hemispheres.

Upper surface (fig. 182).—The greater part of this surface is visible from above and lies against the tentorium, but it also extends downwards in front into the anterior cerebellar notch, and at the sides reaches round the outer margin on to the inferior aspect.

The upper worm begins at the superior medullary velum between the two superior peduncles and ends at the bottom of the posterior notch in a short, concealed transverse lamina, termed the *folium cacuminis*. It is usually described as being formed of five successive parts or lobules, which are termed from before back (1) the *lingula*, (2) the *central lobule*, (3) the *culmen* (*culmen monticuli*), (4) the *clivus* (*clivus monticuli*), and (5) the *folium cacuminis*. Corresponding with these in each hemisphere are (1) a small lateral extension of the lingula, (2) the *ala lobuli centralis* continued laterally from the central lobule, (3) the *anterior lunate lobule* continued from the culmen, (4) the *posterior lunate* continued from the clivus, and (5) most posteriorly the large *postero-superior lobule* continued from the small folium cacuminis.

Of the **fissures** or **sulci** which separate these lobules of the upper surface from one another, four in number, the first, or most anterior, which may be termed the *precentral sulcus*, lies in front of the central lobule, and separates it from the lingula. The next, or *postcentral sulcus*, divides the central lobule and its alæ from the culmen and anterior lunate lobules. The third, or *preclival fissure*, separates the culmen and anterior lunate from the clivus and posterior lunate lobules. This fissure is of considerable morphological importance on account of its early development and the regularity with which it appears in nearly all mammals. Lastly, the fourth, or *postclival fissure*, lies immediately above the folium cacuminis, and after extending outwards in each lateral lobe for about an inch turns almost directly forwards. It separates the folium cacuminis and the postero-superior lobules from the clivus and posterior lunate. Below the folium cacuminis and the postero-superior lobules comes the great horizontal fissure which has already been described.

Besides these interlobular fissures, all of which extend deeply down towards the central white substance, there are certain other sulci which on the upper surface of the hemispheres are almost or quite as well marked as those, but which are less deep or are not seen on the upper worm. They are best made out in sagittal sections of the hemisphere (see fig. 185, A to E). Thus between the postcentral and preclival sulci there is a fissure dividing the culmen and anterior lunate lobules into anterior and posterior portions. According to

Bradley,[1] this fissure ought to be regarded as one of the primary or lobar fissures. The laminæ and fissures of the upper surface all have a sub-parallel arched direction, curving forwards as they traverse the hemispheres to end above the middle cerebellar peduncles and the anterior part of the great horizontal fissure.

We may now describe in detail the subdivisions of the upper surface, taking (since they are directly continuous with one another) those of the worm and hemispheres together.

The lingula.—This is usually confined to the worm, and from the surface it is entirely concealed by the next lobe; it is best seen in a median section of the organ (figs. 185, A and B). It consists of a small tongue-shaped group of four or five transverse laminæ, which may be said to lie upon the middle of the

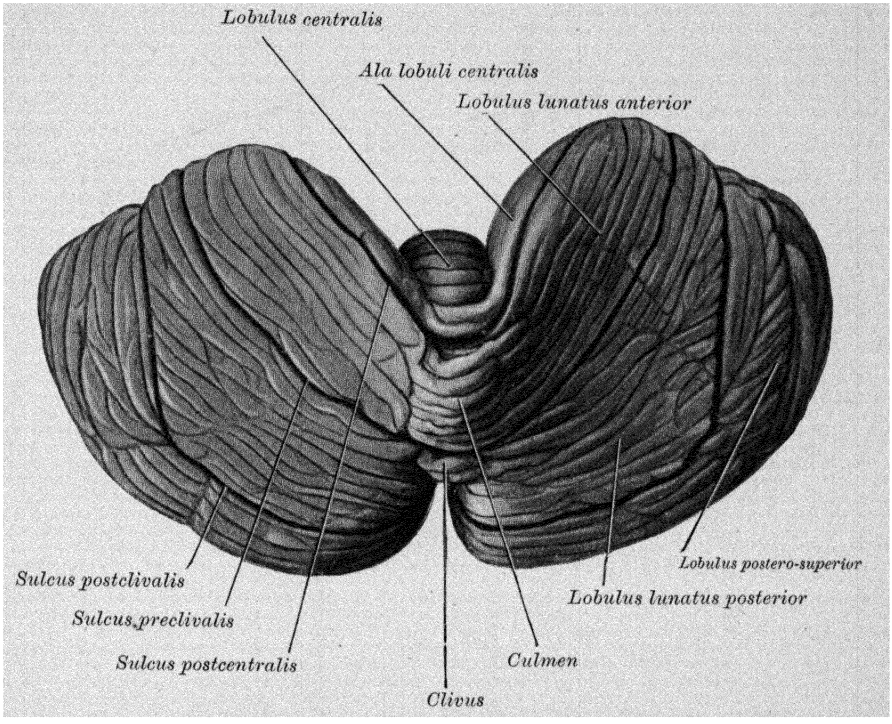


FIG. 182.—VIEW OF THE CEREBELLUM FROM ABOVE. Natural size. (J. Symington.)

superior medullary velum. Its medullary centre is in continuity with the velum, and forms part of the dorsal boundary of the fourth ventricle, which here has a tent-shaped projection into the middle of the cerebellum (fig. 185, A).

The lingula gradually shades off at the sides and is usually unrepresented in the hemispheres, but its laminæ are sometimes prolonged laterally for a little distance over the lower part of the superior cerebellar peduncle (*frænulum lingulæ*, fig. 185, C).

The central lobe and its alæ.—When the cerebellum is cut away from the adjacent structures this lobe is seen in the anterior notch (figs. 182, 183), where it forms a convex prominence. Its laminæ are prolonged beyond the limit of the

[1] Jour. Anat. and Physiol. xxxvii.

worm for some distance along the anterior aspect of the hemispheres, where they form wing-like continuations of the central lobe which are known as the *alæ lobuli centralis*. The central lobe receives a primary branch of the arbor vitæ which passes upwards and forwards into it from the enlargement of the white centre which is known as the trapezoidal body, but the fissures (*precentral* and *postcentral*) which separate it from the lingula and culminate lobe respectively are not better marked at the surface than those which intervene between the laminæ of the culminate lobe, and, as a glance at the sections (fig. 185) shows, its laminæ all belong to the same (ascending) group of folia as those which constitute the culminate lobe.

The culmen and anterior lunate lobules : lobus culminis.—The culmen occupies rather more than half of the upper surface of the worm, and, as its name implies, constitutes the most prominent part of the upper worm. Its surface shows three or four well-marked laminæ, beset by a number of secondary and tertiary folia. It is separated from the next part of the worm by a deep groove which descends to the middle of the organ ; this sulcus is prolonged, as we have already seen, on to either hemisphere, and passes in a curved manner parallel with the general disposition of the laminæ on this surface to the antero-lateral margin, where it runs into the anterior part of the great horizontal fissure. The subdivision of the hemisphere which is cut off between this preclival fissure behind and the postcentral sulcus in front has been known as the *anterior lunate lobule*. The two anterior lunate lobules, together with the culmen with which they are in complete lateral continuity, form a main subdivision of the upper surface of the cerebellum, which may appropriately be termed the *lobe of the culmen*. The lateral parts of the lobe each receive three well-marked branches of the medullary centre of the hemispheres ; in the central part they come off by a common stem from the corpus trapezoides of the worm (fig. 185, A).

The clivus and posterior lunate lobules : lobus clivi.—Behind the preclival fissure, and extending as far as the folium cacuminis (from which it is separated by the *postclival fissure*), is another considerable group of laminæ which receive their branches from the upper aspect of the horizontal stem of the arbor vitæ. In a median section of the worm these laminæ, owing to the great depth of the preclival and postpyramidal sulci, appear to form one group with the folium cacuminis and the laminæ of the tuber valvulæ (fig. 185, A), and this group has been described as constituting a posterior lobe. In fact, however, the great horizontal fissure below the folium cacuminis and the postclival fissure above this folium separate the group into three well-marked divisions ; of very unequal size it is true in the worm, owing to the rudimentary character of the central or cacuminate division, but far more distinct and equal in the hemispheres ; they may therefore be conveniently thus subdivided in the worm also, and of them, two (the clivus and folium cacuminis) belong to the upper worm, the third, tuber valvulæ, to the lower.

Two or three secondary laminæ of the clivus reach the surface of the worm, but they are beset with many tertiary folia, and other important folia belonging to the same group lie concealed in the preclival fissure.

The lateral extension of the clivus on to each hemisphere is known as the *posterior lunate lobule*, and the two posterior lunate lobules with the clivus between them, bounded in front by the preclival, behind by the postclival fissure, may collectively be termed the *lobe of the clivus*. The lateral parts of this lobe each receive two or three primary branches of the medullary centre of the hemisphere (fig. 185, D, E).

The combined anterior and posterior lunate lobules of each hemisphere are sometimes termed the *pars anterior* and *pars posterior* of the *lobulus quadrangularis*.

The folium cacuminis and postero-superior lobules : lobus cacuminis.—The folium cacuminis is formed by the extremity or apex of the main horizontal stem of the arbor vitæ vermis (fig. 185, A). As the median section shows, it is composed of but a single primary folium, which may be either plain or beset with rudimentary folia. But at the side of the worm it rapidly expands, with divergence of its bounding fissures and a great increase of size of its main branch of the arbor vitæ and the formation of numerous secondary and tertiary folia, a large lobule being thereby produced at the posterior and upper part of each hemisphere which has been termed the *postero-superior lobule* (figs. 182, 183;

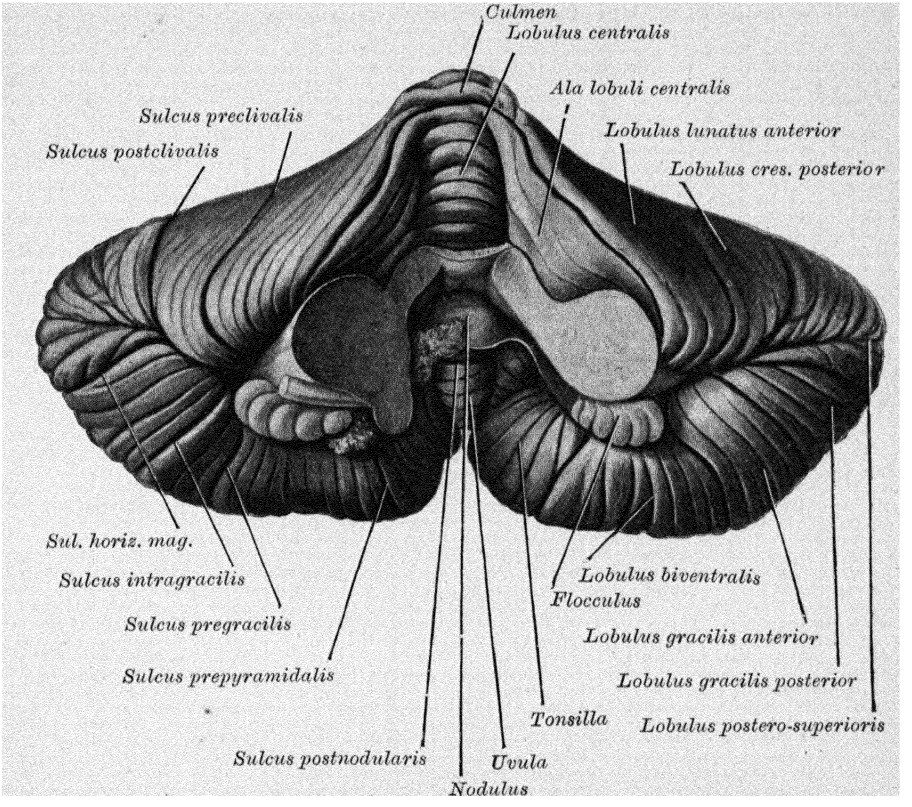


FIG. 183.—VIEW OF THE CEREBELLUM FROM THE FRONT. Natural size. (J. Symington.)

The medulla oblongata, pons, and mid-brain were removed after division of the cerebellar peduncles and superior medullary velum. On the left side of the cerebellum the inferior cerebellar peduncle and choroid plexus were removed to expose the inferior medullary velum and the peduncle of the flocculus.

fig. 185, B). The expansion occurs mostly above the horizontal plane, and its branch of the arbor vitæ has a direction no longer directly backwards, but rather upwards and backwards; this upward shifting appears to be due to the great development of the lobules of the lower surface of the hemisphere. The postero-superior lobules are bounded, like the folium cacuminis itself, in front and above by the postclival fissure, below by the great horizontal fissure; joined as they are in the middle line by the folium cacuminis, they form a great winged mass which occupies the posterior and lateral part of the upper surface of the cerebellar hemispheres, and forms the rounded postero-lateral border; to this conjoined mass the term *lobus cacuminis* may be applied.

Under surface (fig. 184).—Turning now our attention to the under surface of the organ, we here meet with considerably greater complexity, and the correspondence between the parts of the worm and those of the hemisphere is less clearly apparent. The lower worm extends from the inferior medullary velum to the folium cacuminis (great horizontal fissure), and the parts or lobules which are enumerated in it are four in number—viz. from before back (1) the *nodule*, (2) the *uvula*, (3) the *pyramid*, and (4) the *tuber valvulæ*. On the hemisphere a greater number of lobules is distinguished—viz. (1) the *flocculus*, corresponding with the nodule; (2) the *tonsil*, corresponding with the uvula; (3) the *biventral lobule*, corresponding with the pyramid; (4) the *slender lobule*, formed of an anterior and a posterior part well marked off from one another; and (5) the *inferior semilunar lobule*, which also shows a tendency to subdivision. This last lobule corresponds with and is directly in lateral continuity with the tuber valvulæ of the worm. The slender lobules are interpolated in the hemisphere, and have not any obvious prominence of the worm corresponding with them, but they appear to represent a development of certain rudimentary folia which are seen in sagittal sections of the worm on the lower part of the stalk of the tuber valvulæ, entirely concealed by the pyramid (see fig. 185, B). If this is the case, then the combined slender and inferior semilunar lobules may be reckoned as collectively forming a primary subdivision of the hemisphere, corresponding with the tuber valvulæ of the worm and to which the term postero-inferior may be applied, and the two postero-inferior lobules, together with the tuber valvulæ which unites them in the middle line, may collectively be spoken of as the *lobus tuberis*. This large lobe occupies at least two-thirds of the inferior surface of the cerebellum; of the remaining third more than one-half is occupied by the combined pyramid and biventral lobes, about one-third by the uvula and tonsils, and the small remaining portion by the nodule and flocculus.

The lobules of the under surface of the organ are separated from one another by fissures extending deeply into both the worm and hemispheres. In the worm there are three such interlobular depressions—viz. one between the nodule and the uvula (*postnodular*), one between the uvula and pyramid (*prepyramidal*), one between the pyramid and tuber valvulæ (*postpyramidal*), besides the middle of the great horizontal fissure separating the tuber valvulæ from the folium cacuminis. In the hemispheres a larger number is apparent. The *postnodular sulcus* passes laterally into a groove curved with its convexity forwards which first limits the tonsil in front and then passes between the flocculus and biventral lobule to join the anterior end of the great horizontal fissure. The *prepyramidal sulcus* curves laterally round the outer side of the tonsil, separating it from the biventral lobule: it joins the postnodular external to the tonsil. From the sides of the *postpyramidal sulcus* three deep fissures, concentric with one another, curve outwards and forwards over the under surface of the hemisphere. The most anterior of these, and also the shortest, passes at first behind the tonsil before curving across the hemisphere. It lies between the biventral and slender lobes, and may be termed the *pregracile sulcus*. The second of the three concentric fissures subdivides the slender lobule into two nearly equal parts (lobulus gracilis anterior and lobulus gracilis posterior); we may distinguish it as the *intragracile*. The third, which is the longest, separates the slender lobule from the inferior semilunar lobule; like the other two, it arises at the mesial edge of the hemisphere opposite the depression (postpyramidal sulcus) between the pyramid and the tuber valvulæ, and arches round on the lower surface of the hemisphere with its concavity forward to fall into the great horizontal

fissure at the antero-lateral margin. This fissure may be termed the *post-gracile.*

The lobes of the under surface of the organ as already enumerated may be now more particularly described in order from before back.

The nodule, inferior medullary velum, and flocculus: lobus noduli.—The nodule occupies much the same position relatively to the inferior medullary velum and tent of the fourth ventricle that the lingula occupies with regard to the superior medullary velum, but it is better developed than the lingula. Although sometimes merely composed of a few transverse laminæ set upon the median part of the inferior medullary velum, it more often appears as a distinct prominence having a separate branch of the arbor vitæ (fig. 185, A). It

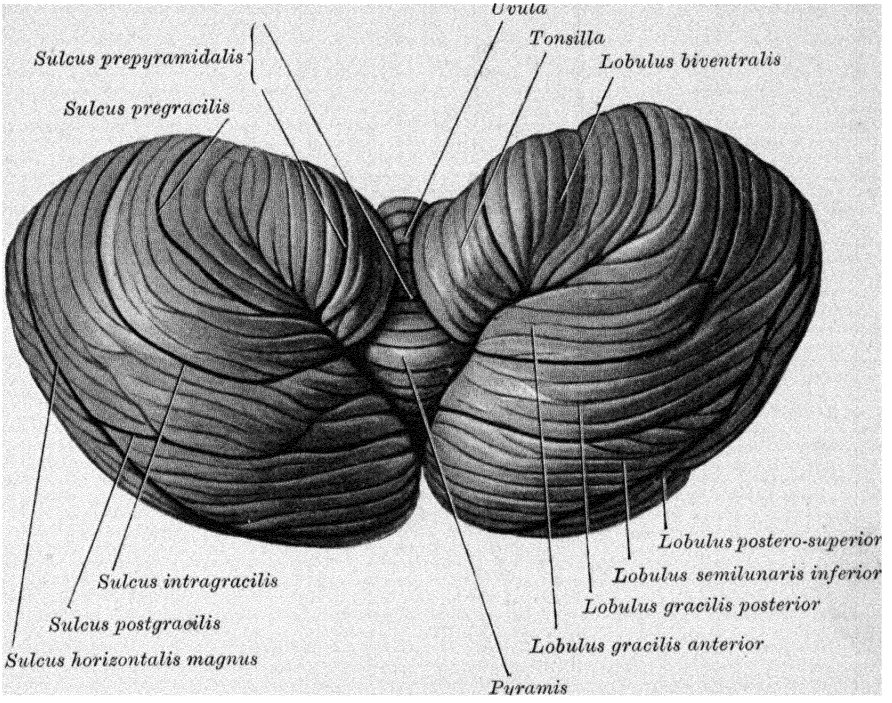


FIG. 184.—VIEW OF CEREBELLUM FROM BELOW. Natural size. (J. Symington.)

can only be seen after the cerebellum is separated from the medulla oblongata and pons, or in a median section, being almost entirely concealed by the uvula when the organ is viewed from below. The median part of the inferior medullary velum is adherent to the nodule and forms the lower boundary of the posterior tent-like recess of the fourth ventricle, and at the apex of this recess it becomes continuous with the superior medullary velum and the white core of the cerebellum. It is covered in front and below by the folia of the nodule. The lateral part of the inferior medullary velum is continued on either side of the nodule as a thin white semilunar lamina with a thickened concave free border (fig. 185, B, C, D). Each lamina possesses an antero-superior surface which looks towards the fourth ventricle, and a postero-inferior one which is covered by pia mater and rests upon the tonsil. The attached border is

continuous with the white matter of the cerebellum, and from its free border the pia mater, covered with ependyma-cells, is prolonged downwards to the back of the medulla oblongata. Traced laterally, the inferior medullary velum becomes thickened and covered with grey matter, forming the peduncle of the flocculus, which curves outwards and forwards behind and external to the lateral recess of the fourth ventricle and expands into a small irregular lobule (*flocculus*) lying between the biventral lobule and the middle peduncle of the cerebellum, and composed of a few short irregular laminæ, which tend to diverge from the attachment of the stalk (fig. 185, E). The nodule, with the inferior medullary velum, the stalk of the flocculus, and the flocculus itself, constitute collectively a small but distinct subdivision of the cerebellum (*lobus noduli*).

Other small portions of laminated grey matter sometimes appear just behind the stalk of the flocculus. They represent the *paraflocculus*, which, although very rudimentary in man, in many mammals is much larger than the flocculus and projects into a well-marked fossa on the petrous part of the temporal bone.

The uvula and tonsils: lobus uvulæ.—The uvula forms a considerable portion of the lower worm, for, although narrow at its upper attached end, it becomes elongated from before backwards towards its lower border. It is least prominent close to the nodule, and from this part it enlarges rapidly downwards and backwards to attain its greatest prominence next to the pyramid. Like the nodule and the pyramid, it is purely a median prominence, being separated from the tonsils by the sulcus valleculæ. At the bottom of this groove on each side of the uvula is a low corrugated greyish ridge which connects the narrow stalk of the uvula with the stalk of the tonsil; this concealed connecting ridge is known as the *furrowed band.*

The tonsil is of an irregular ovoid form compressed from within outwards and separated by deep fissures from the other lobules of the cerebellum. It measures about $1\frac{1}{4}$ inch (nearly 32 mm.) in a vertical direction, $\frac{3}{4}$ inch (19 mm.) from before backwards, and rather less than $\frac{1}{2}$ inch (12·5 mm.) from side to side, and lies in a depression called the *nidus avis.* Its inner surface above is related to the outer surface of the nodule and uvula, and below is separated by a narrow cleft from the opposite tonsil. Between its outer surface and the biventer lobe is a deep fissure (prepyramidal), above which the tonsil is attached to the main mass of the hemisphere. The upper border reaches the inferior medullary velum and the anterior lies behind the medulla oblongata. The lower border forms with the adjacent part of the biventer lobule a prominence which may project into the foramen magnum, and the posterior border conceals the narrow fold uniting the pyramid and the biventer lobule. The uvula, furrowed band, and tonsils constitute collectively another distinct subdivision of the cerebellum (*lobus uvulæ*). The tonsil consists of about ten or twelve folia, which run nearly in a sagittal direction, so that in a sagittal section of the cerebellum passing through the tonsil its branch of the arbor vitæ appears expanded and not obviously dendritic (fig. 185, C).

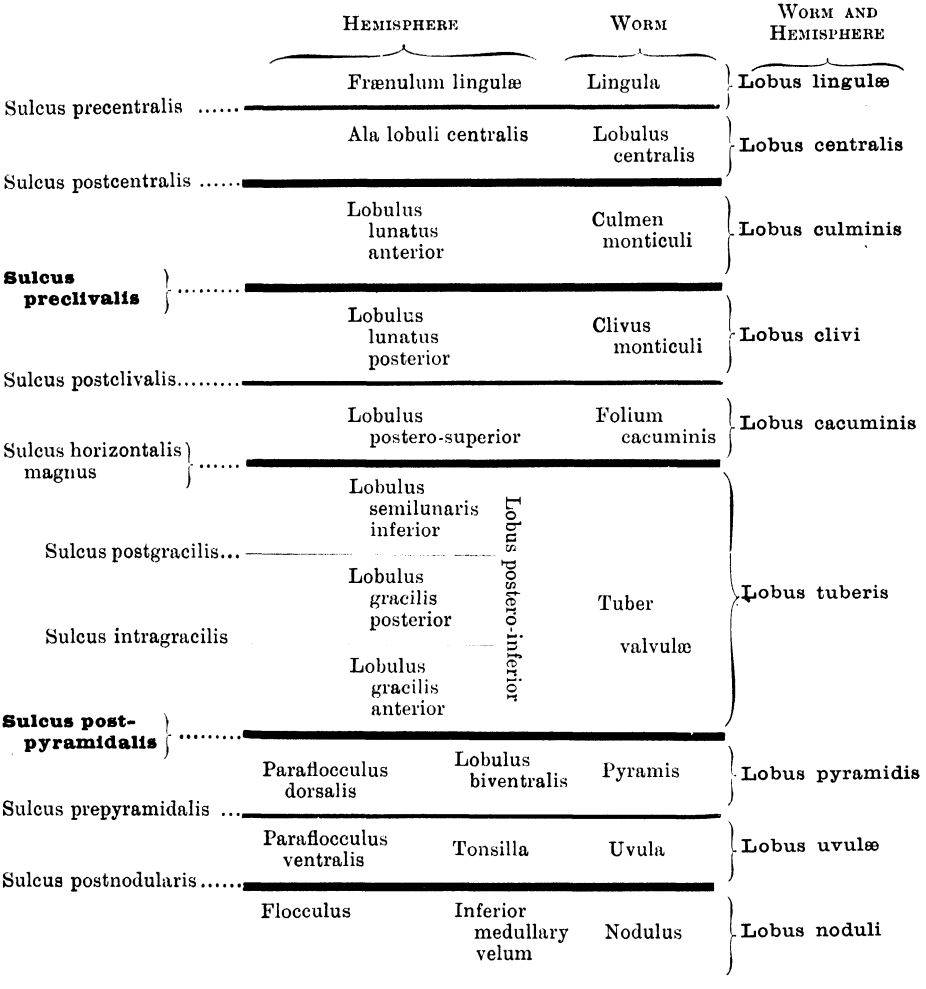
The pyramid and biventral lobules: lobus pyramidis.—The pyramid forms the most marked prominence of the lower worm, but as seen from the surface it shows only three or four transverse laminæ. It is in reality a long clavate projection attached to the stem of the arbor vitæ by a narrow stalk, and it is not only separated from the uvula and tuber valvulæ by deep fissures, but also from the hemispheres by the sulcus valleculæ on each side of it. Its connection with the biventral lobule of the hemisphere is here maintained by a narrow S-curved ridge, which joins the stalk of the pyramid with the mesial pointed

extremity of the biventral lobe. This *connecting ridge* is evidently analogous with the furrowed band of the preceding lobe. To see it the tonsil must be removed or a vertical section made through the organ, passing just to the outer side of the pyramid. The exposed surface of the biventral lobule is roughly triangular, and is bounded internally by the deep antero-posterior fissure separating it from the tonsil and externally by the outwardly curved lateral portion of the postpyramidal fissure, while in front the base of the lobule extends on to the anterior aspect as far as the flocculus. The apex of the lobule is directed backwards and inwards towards the pyramid, and its laminæ have a curved direction radiating from the apex towards the base of the triangle. The lobule is partly bisected by a fissure (midventral) deeper than the rest, and becoming better marked towards the base. This fissure divides the lobule into an inner and an outer portion; from this subdivision its name has been derived. The inner part forms with the tonsil a rounded prominence, while the outer is grooved by the ridge of bone separating the cerebellar fossa from the foramen magnum. Collectively, the pyramid, the connecting ridges, and the biventral lobules constitute a distinct division of the cerebellum, to which the name *lobe of the pyramid* may be applied.

The tuber valvulæ and postero-inferior lobules: lobus tuberis.—The tuber valvulæ, which constitutes the hindmost division of the inferior worm, exposes about five or six tertiary folia (laminæ transversales inferiores) at the surface, between those of the pyramid and the folium cacuminis. It differs from the other constituents of the inferior worm, and resembles those of the superior worm in being obviously prolonged laterally into and gradually enlarging to form the corresponding hemisphere lobules. These conjoined postero-inferior lobules of the hemispheres with the tuber valvulæ of the worm collectively form a large alate mass (*lobus tuberis*), bounded in front by the anterior arcuate or pregracile fissure, which separates it from the pyramidal (biventral) lobe; behind by the great horizontal fissure, which also limits it antero-laterally. Its laminæ run in a curved manner, concentrically with these fissures, and it is separated into four crescentic parts by three concentric fissures—two deep and complete, the intragracile and the posterior gracile, and a third only slightly less deep, the lesser horizontal fissure. Of these four parts the two anterior, about equal in size, form what has been termed the slender lobule (lobulus gracilis); the two posterior, of which the hinder one is the larger, together form what has been termed the inferior semilunar lobule.

The whole cerebellar worm may thus be regarded as subdivided by deep sulci into nine parts or lobules, each of which has the corresponding lobule of the hemispheres continuous with it. This continuity is obvious upon the upper and posterior aspects of the organ, but on the inferior aspect it tends to be rudimentary, and is moreover concealed within the sulci valleculæ. The combined lobes which are thus formed by the union of the lobules of the worm with those of the hemispheres are as follows: (1) lobus lingulæ, (2) lobus centralis, (3) lobus culminis, (4) lobus clivi, (5) lobus cacuminis, (6) lobus tuberis, (7) lobus pyramidis, (8) lobus uvulæ, and (9) lobus noduli. The hemisphere-parts of the lobus lingulæ and of the lobus centralis are rudimentary, but otherwise the hemisphere-parts of the lobes are considerably larger than those of the worm, in some cases, as in that of the lobus cacuminis and the lobus tuberis, the difference of size being very great. The former (lobus cacuminis) is, in fact, represented in the worm by a single concealed folium only, while a large portion of the lobus tuberis—viz. the lobus gracilis—can hardly be said to be represented in the worm. These nine lobes are separated from one another by interlobar fissures, which are all nearly equally well marked in the hemispheres, whilst in the worm some are less developed, particularly those above and below the folium cacuminis. This median part of the lobus cacuminis is therefore imperfectly marked off from the clivus above and the tuber valvulæ below, the three together forming a very distinct posterior subdivision of the worm.

The relations between the parts of the worm and those of the hemispheres, and the fissures which separate the several lobes from one another, as well as those which serve to subdivide the lobus tuberis, are indicated in the accompanying diagrammatic table, in which are shown the corresponding parts of the worm and hemispheres and the fissures which separate them into lobes. The positions of the principal intralobar fissures of the hemisphere are marked by thick lines.



The above table represents, with some modifications, the usual plan of subdividing the adult human cerebellum. It has, however, been shown by the researches of Stroud,[1] Knithan,[2] Elliot Smith,[3] Bradley,[4] Ziehen,[5] and Bolk,[6] that these subdivisions are based mainly upon a study of the cerebellum in the adult human subject, and ignore to a large extent the

[1] 'The Mammalian Cerebellum,' Journ. of Comparative Neurology, v. 1895.
[2] Die Entwickelung des Kleinhirns bei Säugethieren, Münchener medicinische Abhand. vii. Reihe 6 Heft, 1895.
[3] 'The Brain of the Edentates,' Trans. Linn. Soc. London, Zoology, 1899 ; and various papers in Journ. of Anatomy and Physiology, xxxvi. and xxxvii.
[4] 'On the Development and Homology of the Mammalian Cerebellar Fissures,' Journ. of Anatomy and Physiology, xxxvii.; and 'The Mammalian Cerebellum: its Lobes and Fissures,' *ibid.* xxxviii.
[5] 'Makroscopische und mikroscopische Anatomie des Gehirns,' Bardeleben's Handbuch der Anatomie des Menschen, 10 Lief. 1903.
[6] 'Beiträge zur Affen-anatomie,' Morph. Jahrbuch, xxxi. 1902 ; and 'Hauptzüge der vergleichenden Anatomie des Cerebellum der Säugethiere mit besonderer Berücksichtigung des menschlichen Kleinhirns,' Monatsch. f. Psych. u. Neurologie, xii 1902.

development and comparative anatomy of the organ; and various attempts have been made to devise a more scientific mode of subdivision and to distinguish between primary or *interlobar*, and secondary or *interlobular*, fissures. It is generally admitted that the preclival is one of the first cerebellar fissures to be developed and the most constant throughout the mammalian series. Stroud termed it the *fissura prima* and described it as dividing the cerebellum into two main lobes, anterior and posterior. Of these the anterior is so much the smaller that this division is not of much use for topographical purposes. Elliot Smith described, in addition to the fissura prima of Stroud, a *fissura secunda* represented by the prepyramidal sulcus of man. These two fissures separate three primary lobes called *anterior*, *central*, and *posterior*; a large part of the human cerebellum belongs to the central lobe. According to Bradley, the typical mammalian cerebellum is divided by four primary fissures into five lobes. The most anterior of these fissures is not recognised in the current descriptions of the human brain, but it appears to be represented by a sulcus subdividing the lobus culminis; the second fissure is the preclival, the third the postpyramidal, and the fourth the postnodular. Bradley maintains that the *fissura secunda* of Elliot Smith is only an interlobular fissure, while the postnodular, on account of its early appearance, ought to be considered a primary fissure, and the nodule a lobe, since it is not only bounded by a well-defined fissure, but is the only part of the vermis which is connected with the flocculus.

The great horizontal fissure is usually considered the main fissure of the cerebellum, but when its development is taken into consideration it is hardly entitled to that position. Thus it is later in its appearance than the preclival and postpyramidal, and is at first limited to the lateral lobes. Although it afterwards crosses the median plane it remains rather shallow in the vermis; indeed, according to Ziehen, its two lateral portions occasionally fail to join one another.

The significance of the division of the cerebellum into a median and two lateral lobes has been exaggerated, for it is of a secondary character. The cerebellum is developed from two lateral plates which meet in the median plane, and the subsequent division into three parts is due to the more rapid growth of the lateral portions as compared with the median. Further, a paramesial fissure separating the median from the lateral lobes does not appear to be formed in any mammal on the anterior (superior) part of the cerebellum.

It has been proposed (Elliot Smith) to divide the cerebellum into two floccular lobes and an interfloccular mass. The flocculus, however, consists of at least two lobules on each side, the flocculus proper and the paraflocculus. Each of these lobules is connected with a different part of the vermis and they vary greatly in their relative development in different mammals, so that it does not appear advisable to group them together as forming one of the main divisions of the cerebellum. The paraflocculus is very rudimentary in man, and its peduncle cannot be traced to the vermis. It is probably separated from the uvula and pyramid by the tonsil and biventer lobules.

Arbor vitæ cerebelli.—When a section is made through the worm or through either hemisphere across the direction of the folia, the organ is seen, as already mentioned, to be composed of a white or medullary centre and of a uniform cortex of grey matter, and the section presents a dendritic appearance (arbor vitæ cerebelli) in consequence of the fact that the larger laminæ are themselves formed of secondary, and these again are beset with tertiary folia. It is only in such sections that the relative depth and importance of the fissures can be estimated, and a description of the sections is therefore fully as important as that of the surface-markings, and is in fact necessary for the elucidation of the latter.

The mode of transition of the parts of the worm into those of the hemispheres can also best be made out by the inspection of successive sagittal sections; beginning with a median section through the worm, and passing gradually to the side, the successive sections being made in planes parallel with the median plane, or only so far inclined to it, and to one another, as to cut the majority of the lamellæ at right-angles.

1. *Section of the cerebellum in the median plane of the worm* (fig. 185, A). In front we notice the tent of the fourth ventricle projecting with a sharp angle (dorsal recess of fourth ventricle) into the enlargement of the white substance known as the *corpus trapezoides*. The apex of the angle is

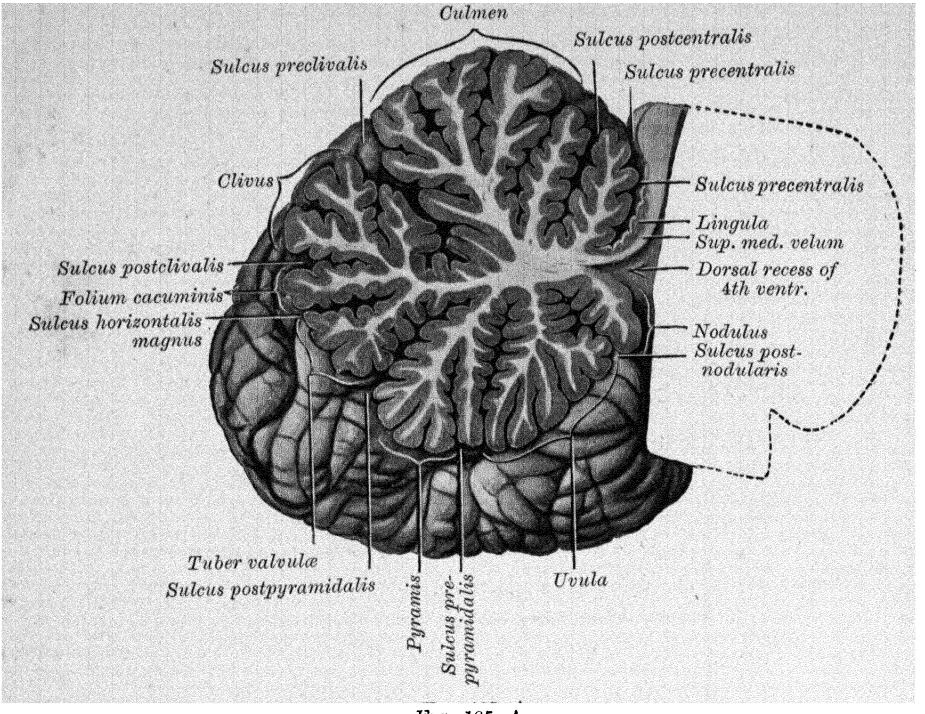


FIG. 185, A

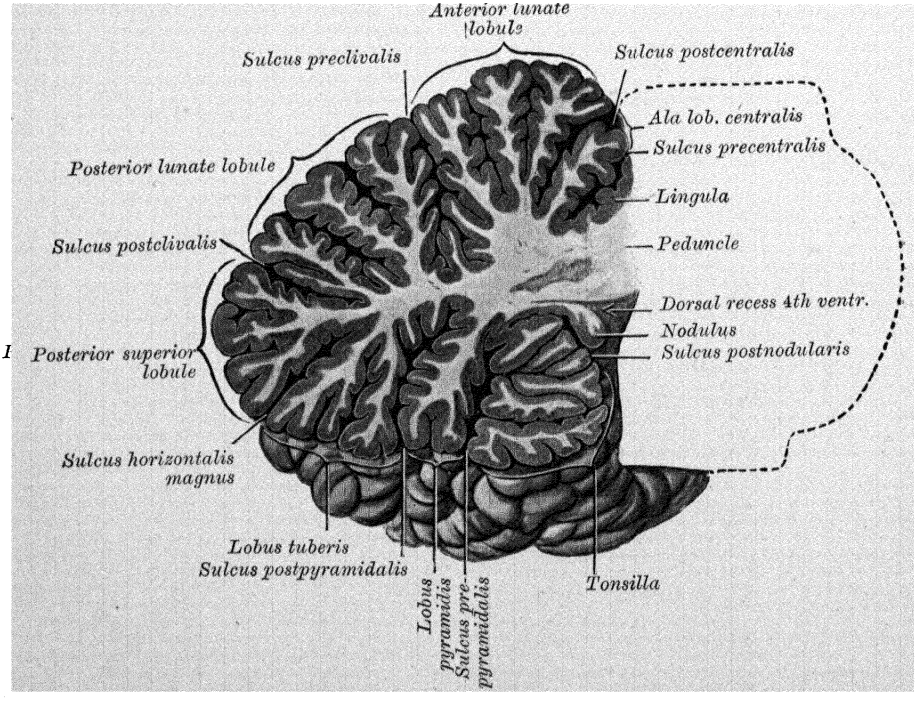


FIG. 185, B.

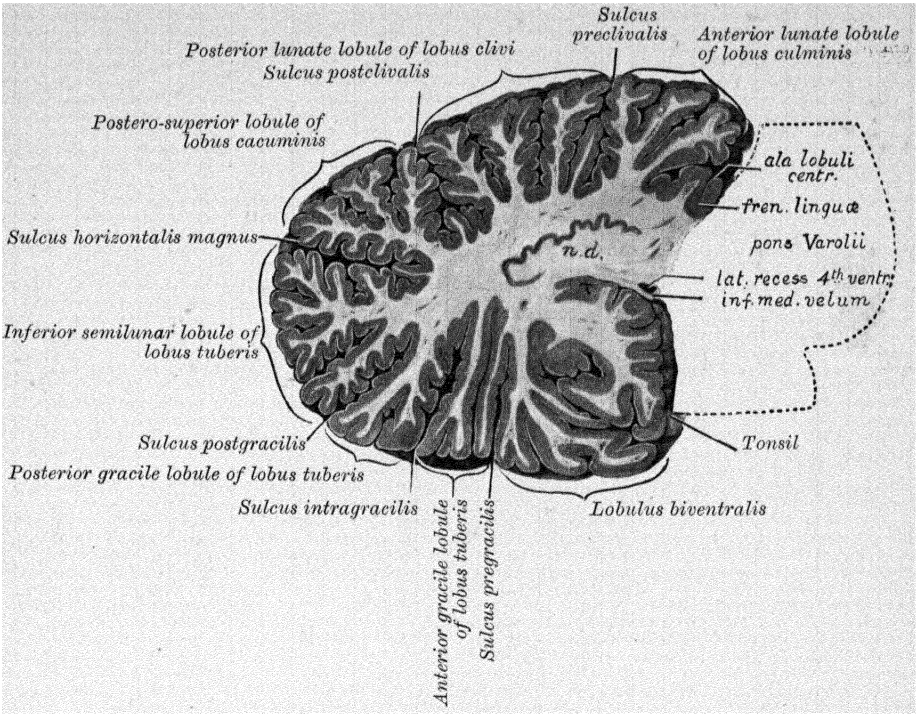


Fig. 185, C.

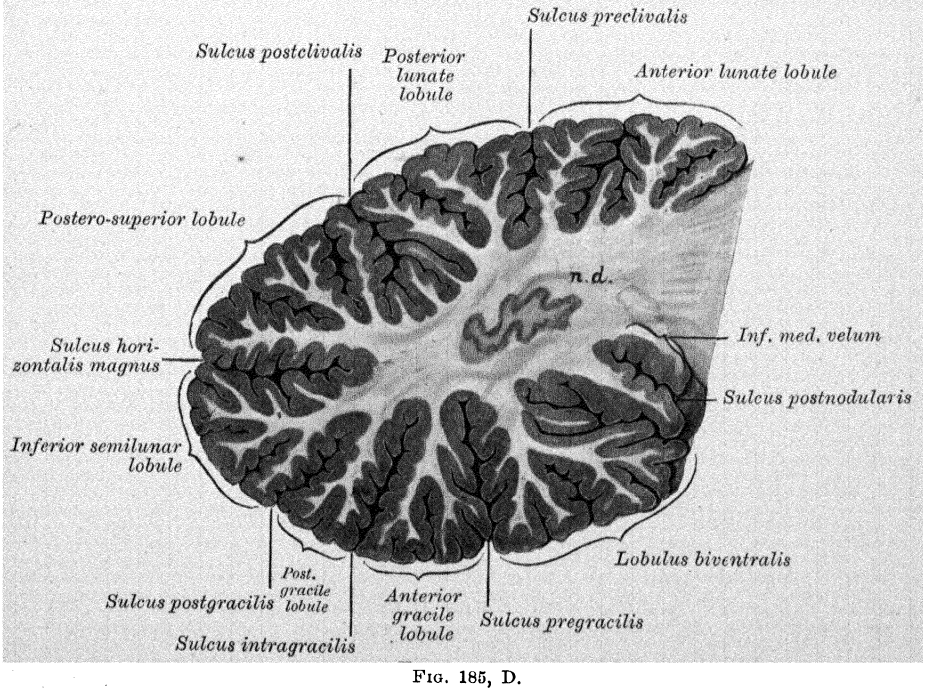


Fig. 185, D.

directed backwards with a slight downward tilt, so as to leave only a thin layer of white matter—the middle part of the inferior medullary velum—between it and the nodule. The corresponding layer of white matter between the cavity of the fourth ventricle and the lingula is the middle part of the superior medullary velum. The two vela are prolonged forwards from the anterior or ventral side of the corpus trapezoides, and diverging from one another bound the dorsal or fastigial recess of the fourth ventricle above and below. From the upper part of the corpus trapezoides two branches of the white centre diverge, one upwards with a slight inclination forwards—this is the branch to the central lobe; the other, the thickest and strongest of all the branches of the arbor vitæ of the worm, upwards and backwards into the culmen. This stem of the culmen gives off secondary branches. Of those

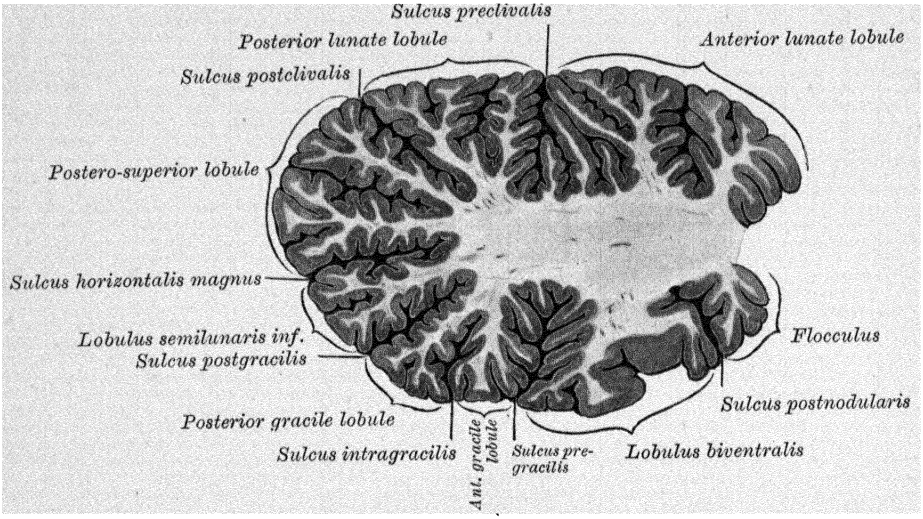


FIG. 185, E.

FIG. 185, A TO E.—FIVE SUCCESSIVE SAGITTAL SECTIONS OF THE CEREBELLUM TO SHOW ITS INTERNAL STRUCTURE, THE RELATIVE DEPTH OF THE FISSURES, AND THE GROUPING OF THE LAMINÆ. From photographs. (E. A. Schäfer.)

A, median section of the worm.
B, section near the edge of the worm at the transition into the hemisphere.
C, at the mesial edge of the hemisphere.
D, nearer the middle of the hemisphere.
E, through the middle of the hemisphere.

which are directed upwards and forwards, the one nearest the base is rudimentary, and enters a small lamina concealed at the bottom of the postcentral fissure; the next two are large, and enter laminæ which reach the surface, but before attaining it they may themselves fork. The prolongation of the stem also reaches the surface, being first bifurcated, but the branches from the dorsal or posterior side of the stem of the culmen, two, three, or more in number, pass into short laminæ which mostly lie concealed within the preclival fissure.

Prolonged backwards from the postero-inferior angle of the corpus trapezoides is a narrow horizontal stem, which after a course of about 2 cm. ends directly in the medullary centre of the folium cacuminis, often passing round a slight curve just before reaching this. From the upper side of this horizontal stem about five branches pass upwards and backwards, and from the lower side about as many pass downwards and backwards, but all are not of equal import-

ance, for some merely enter rudimentary lamellæ which are concealed at the bottom of the interlobar fissures, and only a few enter lamellæ which reach the surface.

Of those which pass from the upper side of the horizontal stem all may be considered to belong to the clivus. Of the more anterior of these some are rudimentary, one or two less so, but all enter lamellæ which are completely concealed in the preclival fissure. The hindmost is larger and longer and reaches the surface; it gives off a vertical branch which passes into the upper part of the lobule nearest the culmen, bifurcating near the surface, and is then continued on in a nearly horizontal direction parallel to and overlying the folium cacuminis.

Of the branches from the lower side of the white centre and its horizontal prolongation three are of great importance. The foremost one passes from the corpus trapezoides almost vertically downwards for about 6 or 8 mm. into the uvula, giving off only small lateral branches; it then gives off successively two or three branches which course downwards and forwards, usually bifurcating before reaching the surface. Only short branches are given off backwards from the main part of the uvula stem.

About 2 or 3 mm. behind the branch to the uvula, that to the pyramid passes off. This has a general direction downwards and backwards; it gives off lateral branches as it proceeds, most of which are small, but one or two longer branches come off on its anterior aspect and pass to the surface nearly vertically downwards.

Following the horizontal stem back, two or three rudimentary offshoots are seen entering small lamellæ which are concealed within the postpyramidal fissure, until finally, about 15 mm. from the corpus trapezoides and 5 mm. from the base of the folium cacuminis, another considerable branch passes off at an acute angle, with a curve forwards and downwards into the tuber valvulæ. Its lateral offshoots, which are at first short, become gradually longer, corresponding with the expanding form of this lobe of the worm.

The deepest fissures of the median section are the precentral, the postcentral, the preclival, the postpyramidal, the prepyramidal, and the postnodular (see fig. 185, A). The postclival fissure is here quite shallow, the great horizontal only slightly deeper. The general grouping of the branches of the arbor vitæ is into five divisions (irrespective of the white matter of the lingula and nodule)—viz. two ascending (central lobe and culmen), a posterior group (clivus, folium cacuminis, and tuber valvulæ), and two descending (pyramid and uvula).

2. *Arbor vitæ at transition of worm into hemisphere* (fig. 185, B). With the general enlargement of the organ as the worm passes into the hemisphere the white centre becomes greatly increased in amount. This affects all parts of it, but first and most markedly the corpus trapezoides and the root of the branch into the anterior lunate lobule, which is here a large square mass of white matter from which three distinct branches pass towards the upper surface of the culmen, which is subdivided by two deep fissures into as many parts. A short branch also passes forwards from the corpus trapezoides into the ala lobuli centralis. The lingula is still seen in this section, and the superior medullary velum is becoming thickened by the fibres of the superior cerebellar peduncle. The horizontal stem of the arbor vitæ is also much thicker, and from it the branches of the posterior lunate lobule pass upwards as two main stems, which go towards the surface, bifurcating as they approach it; there are concealed folia in the pre- and post-clival fissures. The postclival fissure is now deep, as is also the great horizontal, and between the two a lobule, fan-shaped in section (the postero-superior), is now visible, having a distinct large bifid branch of the arbor vitæ

directed upwards and backwards into it, each ramus dividing more than once before reaching the surface. Between the great horizontal and the postpyramidal fissure a large branch passes downwards and backwards, and gives off several well-marked rami from its lower border, three or more reaching the surface. The branch into the pyramid is broader at its root; in fig. 185, B, the section passes outside the uvula, and has taken a slice off the tonsil.

3. *In a sagittal section altogether beyond the vermis and just within the limit of the hemisphere* (fig. 185, C), what in the worm constitutes the horizontal stem

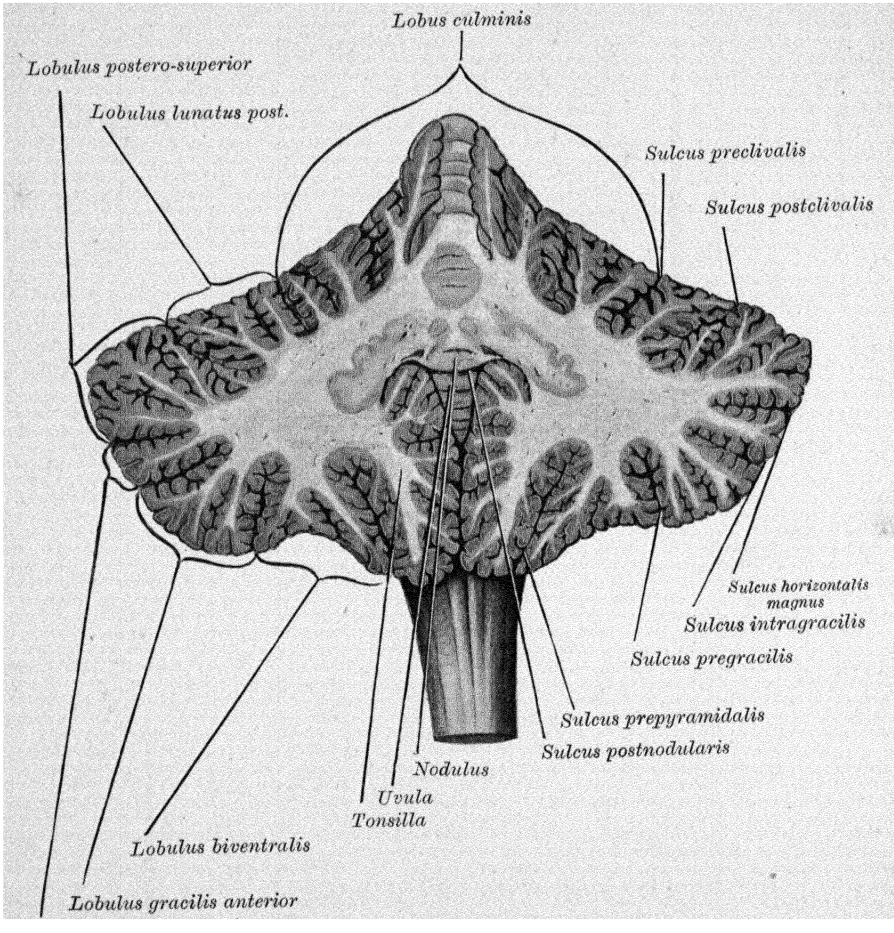


FIG. 186.—CORONAL SECTION OF CEREBELLUM ABOUT 1 CM. BEHIND VENTRAL WALL (FLOOR) OF FOURTH VENTRICLE, VIEWED FROM BEHIND. Natural size. (J. Symington.)

The lobus culminis is formed by a median elevation (culmen) and two lateral portions (anterior lunate lobules).

of the arbor vitæ has become greatly enlarged, and has now blended with the enlarged corpus trapezoides to form the large central white mass of the hemisphere. In this the nucleus dentatus (*n.d.*) is now seen, and appears as a thin irregularly triangular wavy band of grey matter, with the blunt apex of the triangle directed posteriorly towards the horizontal fissure and the open base looking forwards and giving off the great mass of fibres of the superior cerebellar peduncle which now replaces the superior medullary velum. Above the level of

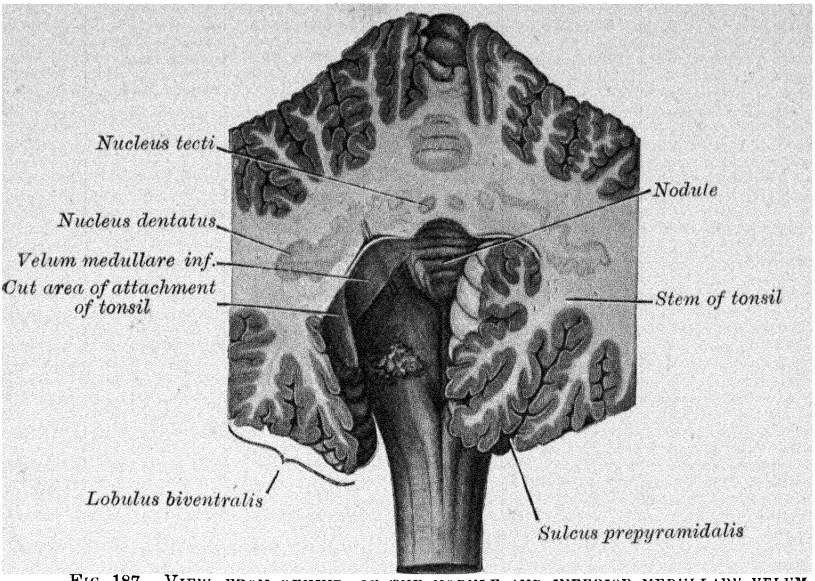


FIG. 187.—VIEW, FROM BEHIND, OF THE NODULE AND INFERIOR MEDULLARY VELUM. Natural size. (J. Symington.)

A sagittal section was made through the cerebellum about 1 cm. behind the ventral wall of the fourth ventricle and on the left side the tonsil was removed after the division of its stem. Some folia belonging to the uvula were removed to see the nodule, and the pia mater with its epithelial lining extending downwards from the nodule and inferior medullary velum to the back of the medulla oblongata were also taken away and the cavity of the fourth ventricle exposed. A bristle was passed under the left lateral part of the inferior medullary velum.

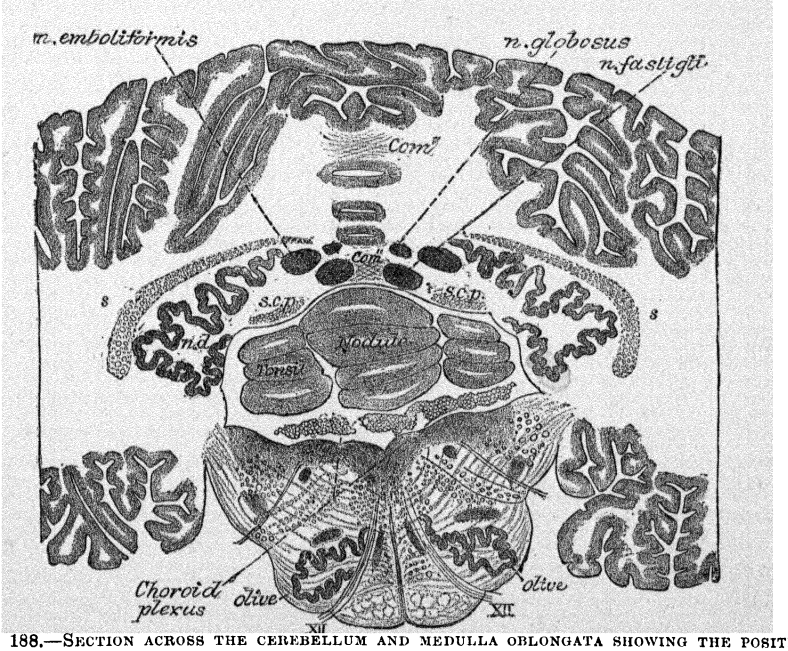


FIG. 188.—SECTION ACROSS THE CEREBELLUM AND MEDULLA OBLONGATA SHOWING THE POSITION OF THE NUCLEI IN THE MEDULLARY CENTRE OF THE CEREBELLUM. (Stilling.)

n.d., nucleus dentatus cerebelli; *s*, band of fibres derived from restiform body, partly covering the dentate nucleus; *s.c.p.*, commencement of superior cerebellar peduncle; *com'*, *com''*, commissural fibres crossing in the median white matter.

the horizontal fissure seven or eight principal processes of the white centre extend into the lobes of the upper surface : the most anterior is small, and passes forwards into the diminishing ala lobuli centralis ; three enter the anterior lunate lobule (in the section here figured they still appear to come off from a common stalk) ; two or three, the posterior lunate ; and a large branch directed obliquely upwards and backwards passes into the postero-superior lobule ; between these principal branches are a few rudimentary ones passing into concealed laminæ, of which there are groups at the bottom of the pre- and post-clival fissures. Besides the postcentral and the pre- and post-clival fissures, two other fissures divide the anterior crescentic lobe into three parts, and other fissures divide the posterior lunate. The postero-superior lobule is not thus subdivided by complete fissures.

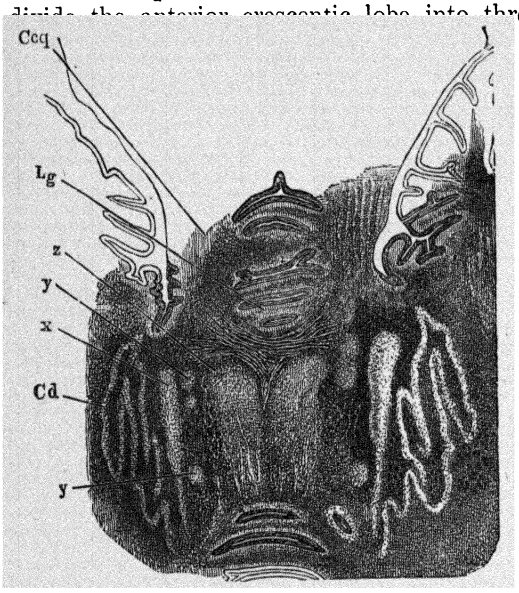


FIG. 189.—HORIZONTAL SECTION THROUGH THE WHITE CENTRE OF THE CEREBELLUM SHOWING THE NUCLEI OF GREY MATTER. $\frac{3}{4}$. (From Henle, after Stilling.)

The section is taken just over the roof of the fourth ventricle. The nuclei are represented lighter than the white matter in which they are imbedded.

Cd, corpus dentatum; *x*, nucleus emboliformis; *y*, *y*, nucleus globosus; *z*, nucleus tecti. Above the two coalesced roof-nuclei are seen some of the fibres of the superior (anterior) decussation, and above these again the laminæ and furrows of the lingula (*Lg*); whilst below the roof-nuclei one or two laminæ and furrows of the inferior vermiform process are included in the section. *Ccq*, superior cerebellar peduncle.

Below the level of the great horizontal fissure six or seven main branches come off from the white centre. Two of these pass into the inferior semilunar lobule, one, the posterior, being very large and bifid or trifid ; one passes into each division of the lobulus gracilis, one into the biventral lobule, and a broad anteriorly directed branch into the tonsil. A seventh small offshoot, directed almost due forward, belongs to the stalk of the flocculus.

4. *Sagittal sections through the hemispheres* (fig. 185, D, E). In sections still farther outwards the conditions are much the same as just described, except that the ala lobuli centralis and the tonsillar branch are no longer seen, and the branch into the biventral has become distinctly bifid. The nucleus dentatus does not extend far into the lateral part of the hemisphere, and the superior cerebellar peduncle is no longer cut ; but fibres are seen streaming from the white centre of the hemisphere into the middle and inferior peduncles. The general conformation of the section is somewhat altered, but the number and relations of the subdivisions of the hemisphere are not materially different, and the several branches of the arbor vitæ and the more important fissures are readily recognisable.

Nuclei in the white matter of the cerebellum.—The *dentate nucleus* (corpus ciliare, corpus dentatum) of the cerebellum (figs. 185 to 188) has in section the appearance of a wavy line of compact yellowish-brown substance, containing white matter within. The wavy character is more apparent in horizontal than in vertical sections through the hemisphere. The line is interrupted at its anterior and mesial part (*hilus*), where the superior cerebellar peduncle emerges from it. The dentate nucleus may be described as

consisting of a plicated pouch or capsule of grey substance open at one part and enclosing white matter in its interior, like the dentate nucleus of the lower olivary body.

In addition to the corpus dentatum certain other portions of grey matter, which have been more recently recognised, are found in the white centre of the cerebellum (Stilling). They are three in number on each side and are termed respectively the nucleus emboliformis, nucleus globosus, and nucleus tecti (figs. 186 to 189). The *nucleus emboliformis* is a small clavate mass of grey substance lying mesially to and partly covering the hilus of the dentate nucleus. On the inner side of the nucleus emboliformis, between it and the middle line, is a streak of grey matter passing antero-posteriorly and ending behind in an enlarged extremity. This has been named the *nucleus globosus*. Finally, close to the middle line, where it is only separated from its fellow by a narrow septum of white matter, is a rather larger portion of grey substance, which lies in the anterior part of the white centre of the worm, and close to the upper wall of the tent-like projection in the roof of the fourth ventricle. It is termed the *nucleus of the roof* (*nucleus tecti; nucleus fastigii*). These several portions of grey matter are not entirely isolated, but are connected here and there both with one another and with the dentate nucleus.

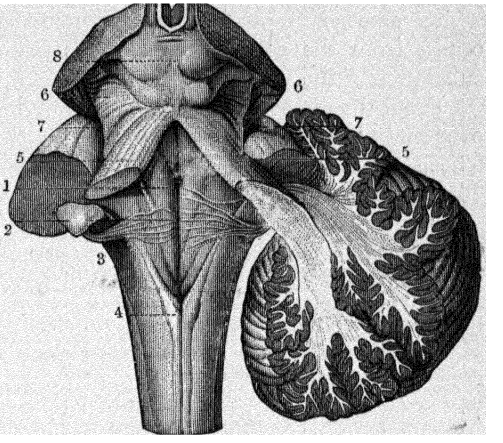


FIG. 190.—FIGURE SHOWING THE THREE PAIRS OF CEREBELLAR PEDUNCLES. (From Sappey after Hirschfeld and Leveillé.)

On the left side the three cerebellar peduncles have been cut short; on the right side the hemisphere has been cut obliquely to show its connection with the superior and inferior peduncles. The cut ends of the cerebellar peduncles have been artificially separated from one another and are displayed diagrammatically.

1, median groove of the fourth ventricle; 2, the same groove at the place where the auditory striæ emerge from it to cross the floor of the ventricle; 3, inferior peduncle or restiform body; 4, funiculus gracilis; 5, superior peduncle: on the right side the dissection shows the superior and inferior peduncles crossing each other as they pass into the white centre of the cerebellum; 6, lateral fillet at the side of the pedunculi cerebri; 7, lateral grooves of the pedunculi cerebri; 8, corpora quadrigemina.

Commissural and association fibres in the white matter of the cerebellum.—Two chief sets of *decussating commissural fibres* were described by Stilling in the middle line of the cerebellum: one at the superior part of the worm at the base of the central lobule—*the superior commissure* (fig. 188, *com'*); the other at the inferior part (*inferior commissure* (*com''*)). Commissural fibres also pierce the nuclei of the roof. In addition to these crossing fibres, *association fibres* are said to connect one lamina with another, passing in the white substance of the laminæ across their general direction, and arching round the fissures between the laminæ.

Peduncles of the cerebellum.—The cerebellar peduncles are constituted by white fibres which pass out from or into the white medullary substance of the hemispheres.

The *superior peduncles* (*crura ad cerebrum, brachia conjunctiva*) emerge from the upper and mesial part of the medullary substance of the hemispheres, and run upwards and forwards towards the tegmentum. They are situated at first at the side, but subsequently in the roof, of the upper part of the

fourth ventricle. These peduncles are concealed by the upper part of the cerebellum, so that to see them properly this must be divided in the middle line and turned aside. When this is done, the superior peduncles, with the superior medullary velum stretched out between them, are brought into view. They have already been noticed in sections across the upper part of the pons, and are found for the most part to pass into the red nucleus of the tegmentum. Their further course will be subsequently traced.

The fibres of the superior peduncle pass almost entirely out of the hilus of the dentate nucleus, but some fibres appear to curve round the outer side of this, and some of the mesial fibres are traceable directly from the white substance of the worm. Probably most of the fibres of these peduncles which emerge from the dentate nucleus are derived from its cells, and the others from the cells of the nucleus fastigii and adjacent nuclei of the white substance of the worm.

From the superior medullary velum longitudinal fibres can be seen passing over and along with the superior peduncle into the white centre of the worm. These are fibres belonging to the ventral spino-cerebellar tract (see pp. 97 and 161, and fig. 174).

Although the fibres of the superior peduncle originate in cells within the nucleus dentatus, and undergo degeneration as the result of lesions of the hemisphere, in a case, reported by Mendel,[1] of lesion of the left thalamus, a well-marked bundle of degenerated fibres was traced through the tegmentum of the left side mesial to the nucleus tegmenti, across to the right side at the decussation of the superior peduncles, and along the outer side of the right superior peduncle to the right hemisphere.

The *inferior peduncles* (*crura ad medullam*) are connected with the white matter of the lateral hemispheres, between the other two, and are traceable forwards immediately outside the superior peduncles to the lateral wall of the fourth ventricle. Here they turn sharply downwards, at a right-angle, and become continuous with the restiform bodies of the medulla oblongata.

The *middle peduncles* (*crura ad pontem*) are distinguished by the small size of their fibres. These come from the nuclei pontis and enter the lateral part of the white matter in two main bundles. One of these bundles, composed of the superior transverse fibres of the pons which pass obliquely downwards over the others, radiates into the lateral and lower parts of the medullary centre of the hemispheres. The other bundle, which is formed of the lower transverse fibres of the pons, is joined at its passage into the white centre by the restiform body or inferior peduncle, and the fibres of both turn upwards. Those from the pons radiate into the upper parts of the medullary centre of the hemisphere; those from the restiform body into the upper part of the worm.

The fibres of the middle peduncles originate in the cells of the nuclei pontis, reach the middle line, and there undergo decussation. After this intercrossing the fibres pass into the hemisphere and are traceable to the cortex.

[1] Neurol. Centr. 1882.

MICROSCOPIC STRUCTURE OF THE CEREBELLUM.

Each lamina of the cerebellum has a central part of white substance, which is an offshoot from the white centre, and a cortex of grey matter consisting of two layers, an inner and outer, the outer being covered superficially by pia mater. Between the inner and outer layers of grey matter is an incomplete stratum of large nerve-cells, the *corpuscles of Purkinje*. The fibres of the white matter are disposed in bundles which have a parallel course as they pass from the principal offshoots of the white centre of the organ into the secondary laminæ. This parallelism is maintained in their passage through the centre of the laminæ, but the fibres gradually turn off obliquely into the grey matter, so that the white core gradually thins off towards the extremities of the laminæ. Owing to the turning outwards and passage into the grey matter of these bundles of white fibres, the white core is not sharply marked off under the microscope from the grey cortex; but the limits are more distinctly marked at the bottom of the fissures which separate the laminæ than in the laminæ themselves. As the fibres pass radially into the grey matter they lose their parallel arrangement, and tend to branch among the small nerve-cells of the adjacent inner or granule layer of the grey matter; many pass through this layer, and some are traceable to the cells of Purkinje, from which they actually take origin, while others can be followed beyond these cells into the outer or molecular layer of the grey matter.

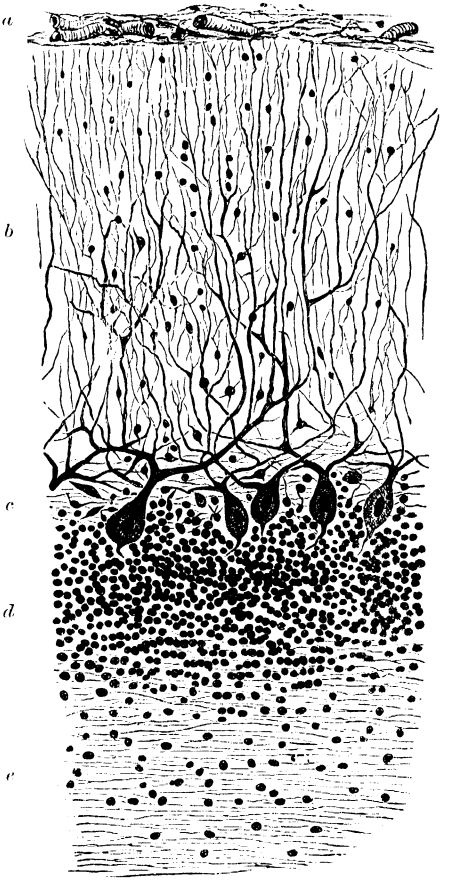


FIG. 191.—SECTION OF CORTEX OF CEREBELLUM. (Sankey.)

a, pia mater; *b*, external layer; *c*, layer of corpuscles of Purkinje; *d*, inner or granule layer; *e*, medullary centre.

The grey matter of the cerebellar cortex is disposed, as already intimated, in two distinct layers. The *inner layer* or *layer of granules* is so called because it contains numerous small nerve-cells known as 'granules': this layer has a reddish or yellowish-brown colour in the fresh condition, hence it has been termed the 'rust-coloured' layer. The granules are more closely packed in the outer part of the layer; near the medullary centre of the lamina they are separated by the radiating bundles of white fibres, between which they may penetrate for some distance within the white centre. Besides small nerve-cells, the granule-layer includes a few large nerve-cells and also neuroglia-cells. The *outer, molecular,* or *plexiform layer* has, under the microscope, in sections taken across the laminæ, a finely punctated appearance. It is of fairly uniform thickness, whereas the granule-layer is thicker near the extremities of the laminæ than

in the furrows. It contains scattered nerve-cells, but they are neither so numerous nor so small as the 'granules' of the inner layer. It also has many nerve-fibres, mostly running parallel to the surface, and also a number of elongated cells which run vertically to the surface (*Bergmann's fibres*) and end below the pia mater. Their cell-bodies are situated in the granule-layer, and they are regarded as neuroglia-cells (see p. 195).

The molecular layer is further in large part occupied by the dendritic processes of the large nerve-cells which lie at the junction of the granule and medullary layers, already mentioned as the *cells* or *corpuscles of Purkinje*. These have conspicuous flask-shaped cell-bodies from 35 μ to 65 μ in diameter, each

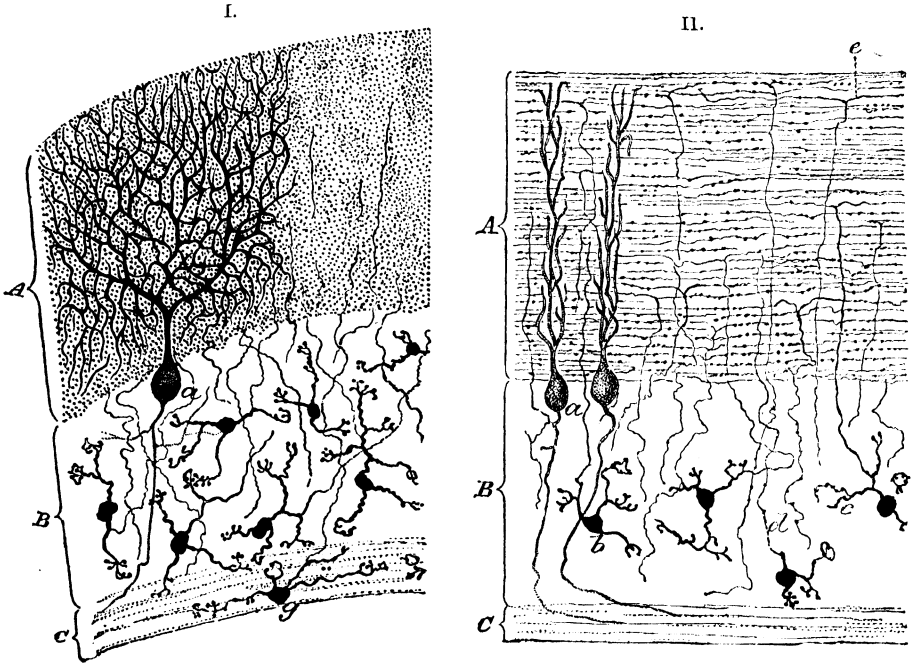


FIG. 192.—SECTIONS OF CORTEX CEREBELLI STAINED BY GOLGI'S METHOD. (Cajal.)
I. Section taken across the lamina. II. Section made in the direction of the lamina.
A, outer or molecular layer; B, inner or granule layer; C, medullary centre.
a, corpuscle of Purkinje; *b*, small granules of inner layer; *c*, dendritic process of a granule; *d*, nerve-fibre process of a granule passing into the molecular layer, where it bifurcates and becomes a longitudinal fibre (in I. these longitudinal fibres are cut across and appear as dots); *e*, bifurcation of another fibre; *g*, a granule lying in the white centre.

with a greatly ramified dendritic process directed peripherally, and an axis-cylinder or nerve process which passes centrally into the granule-layer, where it becomes medullated, and passes directly into a nerve-fibre of the medullary centre. As with the axis-cylinder processes of the cells of the cerebral cortex, and, according to Golgi, with those of the ventral-horn cells of the spinal cord, these axis-cylinder processes of Purkinje's cells also give off lateral ramuscles (collaterals) which lose themselves among the granules, some turning backwards to enter the molecular layer (fig. 193). The dendritic processes of the cells of Purkinje are spread out in planes which run transversely to the laminæ (Stilling), so that they are seen in their full extent only in sections cut vertically to the surface but across the laminæ (fig. 192, I.); whereas in

vertical sections taken parallel to the laminæ, the ramifications appear limited to a comparatively narrowed tract (fig. 192, II.). The dendrons may arise by a single root or by two roots; in either case there is a frequent dichotomous division, with slight enlargements at the points of division, and also the giving off laterally of numerous ramuscles which take a horizontal or curved course in the molecular layer. The branches do not anastomose nor join with those of other cells, but have free terminations, often curling back for a short distance before ultimately ending (fig. 193).

The dendrons of the Purkinje cells exhibit a very close fibrillation throughout their whole extent (fig. 194). Near the place where they come off from the body of the cell they are beset with small button- or disc-like endings of nerve-fibres, which, according to Cajal and Illera,[1] are probably derived from the recurrent collaterals of the axons of the Purkinje cells.

Besides these dendritic processes of Purkinje's cells, the molecular layer contains great numbers of very fine horizontal fibres, running longitudinally as regards the laminæ. These pass into the molecular layer from the small cells of the granule-layer. The axis-cylinder processes of the small 'granules' in fact pass vertically between the corpuscles of Purkinje and enter the molecular layer, where they join, by a T- or Y-shaped junction, with one of the horizontal fibres just mentioned (fig. 192, II.); these fibres may therefore be regarded as the branches of the axis-cylinder processes of the granule-cells. They appear to end after a short course either simply or by slightly ramifying.

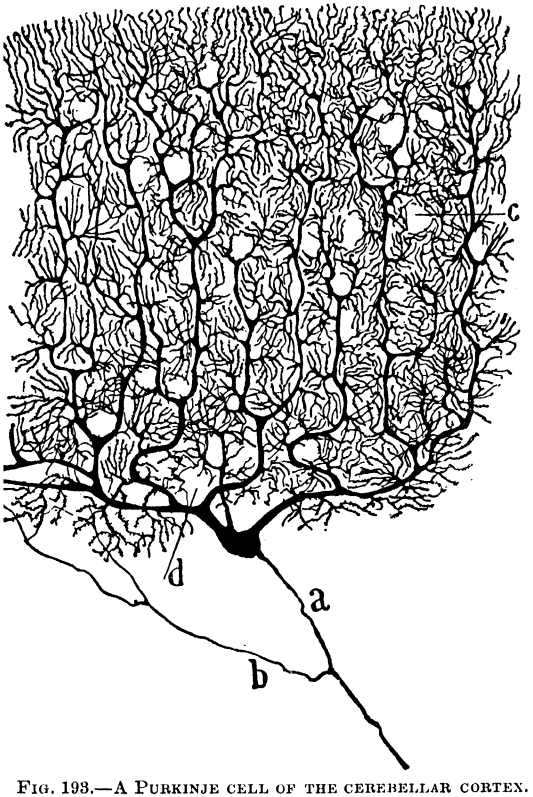


FIG. 193.—A PURKINJE CELL OF THE CEREBELLAR CORTEX. Golgi method. (Cajal.)

a, axon; *b*, collateral; *c*, *d*, ramifications of dendrons.

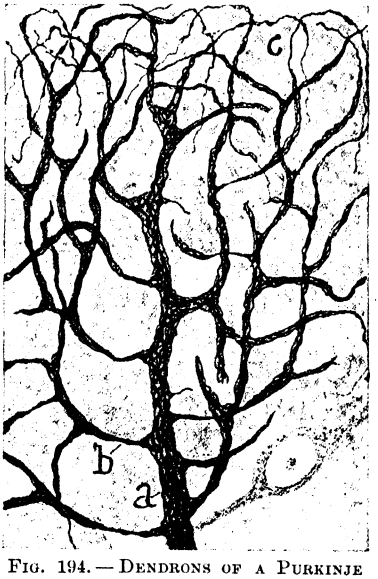


FIG. 194. — DENDRONS OF A PURKINJE CELL SHOWING THE NEURO-FIBRILS. (Cajal.)

a, a large branch; *b*, a secondary branch; *c*, endings of the ramifications.

[1] Travaux du Laboratoire d'Histologie, v. 1907, Madrid.

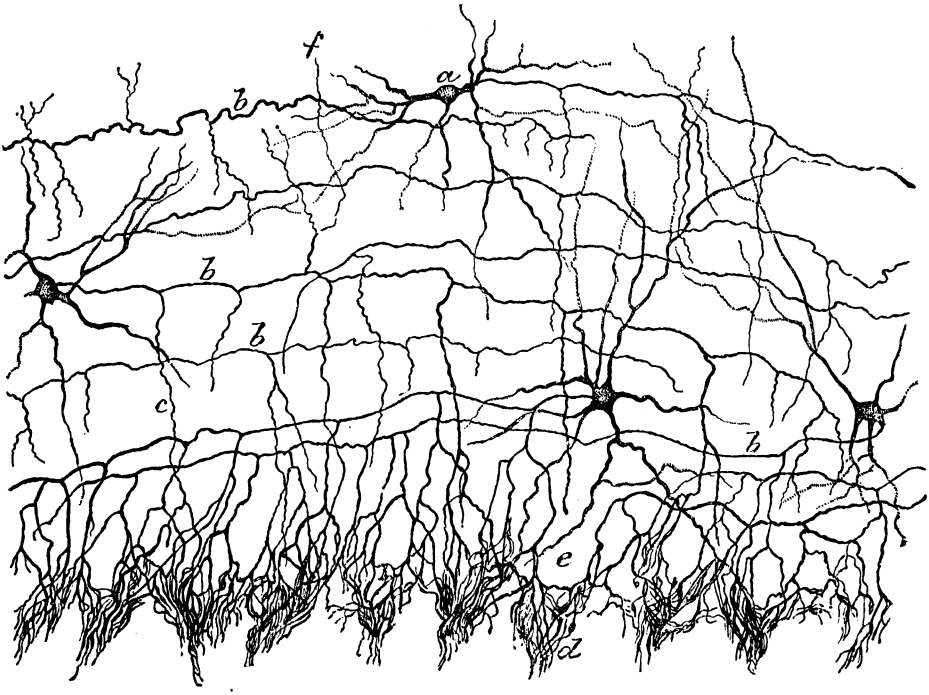


FIG. 195.—CELLS OF THE MOLECULAR LAYER OF THE CEREBELLUM. (Cajal.)

a, a cell from the outer part of the layer with a horizontally directed branched axis-cylinder process; *b*, nerve-fibre processes of cells which send processes *c* to aid in forming the basket-work *d e* around the cells of Purkinje; *f*, a process directed towards the surface of the lamina.

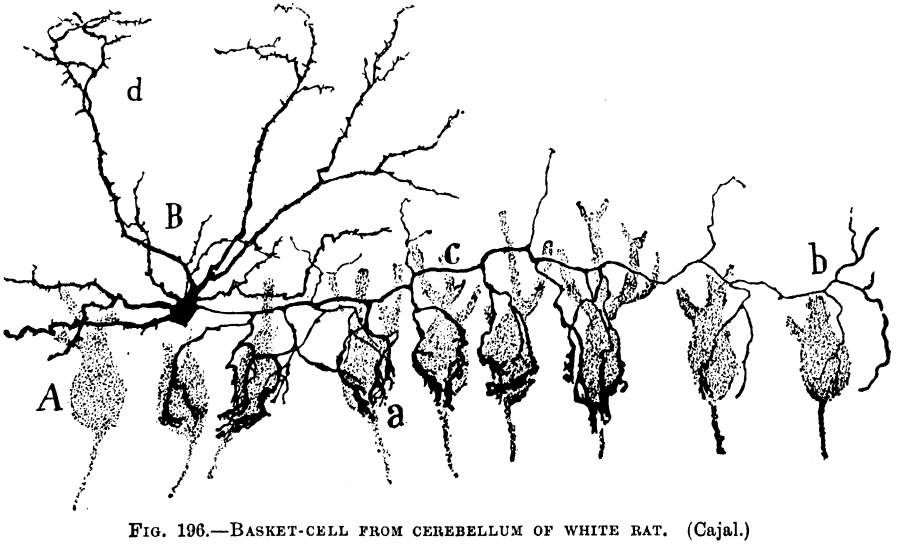


FIG. 196.—BASKET-CELL FROM CEREBELLUM OF WHITE RAT. (Cajal.)

A, row of Purkinje cells; B, basket-cell; *c*, *b*, its axon *a*, its pericellular ramifications.

The nerve-cells of the molecular or plexiform layer are divisible, according to their relative position in the layer, into two kinds, outer and inner. The outer cells—*i.e.* those in the outer half or so of the layer—somewhat smaller than the inner, have extensive dendritic processes and an axis-cylinder process which extends for some distance horizontally or obliquely in the layer, ramifying freely (fig. 195, *a*). The inner cells, called also 'basket'-cells, usually lie near the cells of Purkinje, but they may be placed some little distance within the molecular layer. Their dendrons pass in all directions, some of them even reaching the surface of the organ; the axon, which seems not to be provided with a medullary sheath, usually emerges from the side of the cell and extends laterally for some distance, giving off at intervals, as it passes along, a number of branches which pass inwards towards the cell-bodies of Purkinje's corpuscles, near which they become considerably enlarged (fig. 195, *b*, *c*): they are especially

FIG. 197.—BASKET-WORK OF FIBRES AROUND TWO CELLS OF PURKINJE. (Cajal.)

a, axis-cylinder or nerve-fibre process of one of the corpuscles of Purkinje; *b*, fibres prolonged over the beginning of the axis-cylinder process; *c*, branches of the nerve-fibre processes of cells of the molecular layer, felted together around the bodies of the corpuscles of Purkinje.

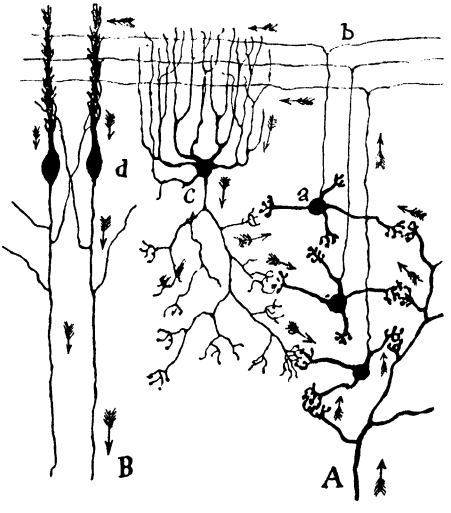


FIG. 198.—CELLS OF THE CEREBELLAR CORTEX, SHOWING THE PROBABLE PATH OF NERVE-IMPULSES. (Cajal.)

A, a moss-fibre (afferent); B, an axon of a Purkinje cell (efferent); *a*, granules; *b*, their axons; *c*, a Golgi cell; *d*, two Purkinje cells.

thick in birds. Having reached these, they break up into a close felt-work of filaments (terminal ramification) which surrounds the corpuscles of Purkinje, and with similar ramifications from other cells envelops the corpuscle in a sort of basket-work of nerve-filaments. This basket-work extends even for a short distance along the axis-cylinder process of the corpuscle (figs. 196, 197, 199).

The 'granules' of the inner, or rust-coloured, layer of the grey matter are small nerve-cells, nearly spherical, and provided with several small protoplasmic processes, which soon end in close bunch-like terminal ramifications within the layer (fig. 192, B). These form synapses with the branches of the moss-fibres immediately to be described (fig. 198). But the axis-cylinder process of is far greater extent, and, taking a peripheral course, passes vertically beyond the corpuscles of Purkinje for a variable distance into the molecular layer, where it becomes connected with the horizontal fibres of that layer in the manner before described.

A few cells in the granule-layer are larger; their cell-bodies lie chiefly in the outer part of the granule-layer, near the cells of Purkinje. They are stellate, and have long dendritic processes: these may penetrate both into the white centre of the lamina and into the molecular layer. Their axis-cylinder processes are singularly branched, losing themselves in a ramification which may extend throughout the whole thickness of the granule-layer; it is not certainly known if they are medullated, nor if they are connected with fibres of the white centre. The corpuscles in question are known as the *cells of Golgi* (fig. 198, *c*). In addition to these short-axoned cells, there is yet another kind of large cell (*solitary cells*) occurring in the granule-layer or in the neighbouring part of the white substance. These are fusiform and placed for the most part parallel to the surface: they have a long axon, the destination of which has not been determined, and long branching dendrons. These cells are surrounded closely by

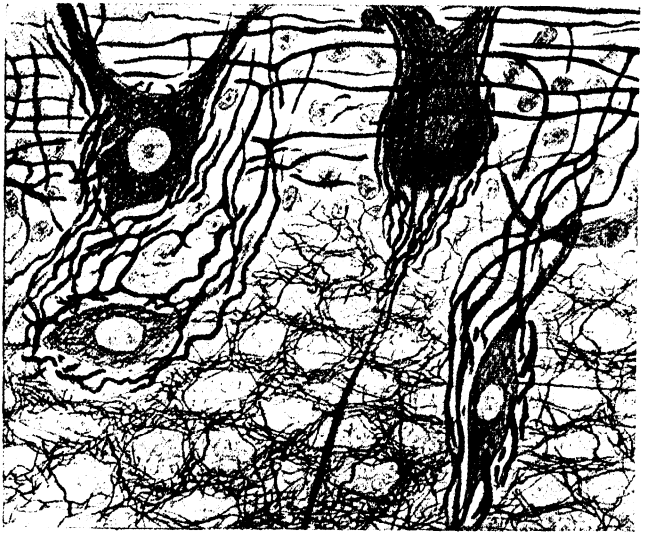


FIG. 199.—CELLS OF PURKINJE AND THE ADJACENT PART OF THE GRANULE-LAYER OF THE CEREBELLUM. (Cajal.)

Two large cell-bodies of Purkinje's cells and two more deeply situated fusiform cells are shown. These are all surrounded by a feltwork of fibres derived from the basket-cells. From one of the large cells of Purkinje the axon is seen passing obliquely through the granule-layer. The granules are not stained, but a fine feltwork of nerve-fibrils is visible in their interstices.

nests or baskets derived from collaterals of the tangential fibres in the deeper part of the molecular layer, which fibres are themselves derived from the ordinary granules.

Of the fibres which connect the white centre with the grey matter of the laminæ, some, which have already been described, are the nerve-processes of the cells of Purkinje. These pass to the nucleus dentatus of each hemisphere or to the grey matter in the white substance of the vermis. But others pass to the grey cortex from the fibres of the white centre. These have two modes of termination in the grey matter. (1) Some of these fibres (*moss-fibres* of Cajal) traverse the granule-layer, and, branching within that stratum, exhibit peculiar moss-like appendages, both on their ramuscles and at the places whence these come off (fig. 201). The moss-like tufts form synapses with the dendrons of the granules as the moss-fibres pass through the granule-layer (fig. 198);

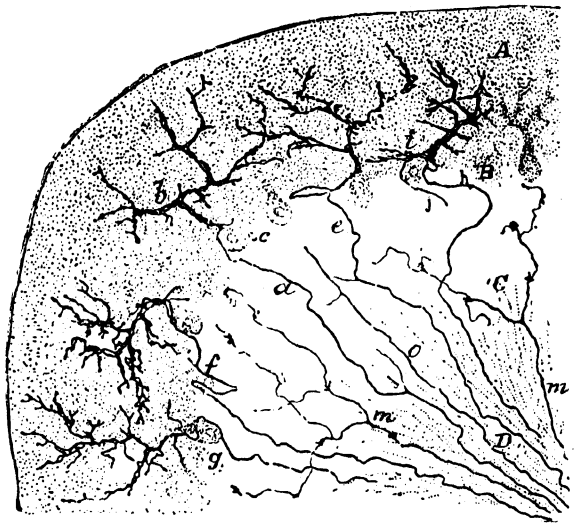


FIG. 200.—TRANSVERSE SECTION OF A CEREBELLAR LAMELLA OF THE ADULT BAT SHOWING THE FIBRES WHICH PASS FROM THE WHITE CENTRE TO THE GREY MATTER. (Cajal.)

A, molecular layer; B, cells of Purkinje; C, granule-layer; D, white substance; *a*, *e*, *f*, *g*, fibres which end in 'tendrils' enveloping the protoplasmic processes of the cells of Purkinje; *b*, an enveloping plexus; *c*, body of cell of Purkinje; *m*, 'moss'-fibres.

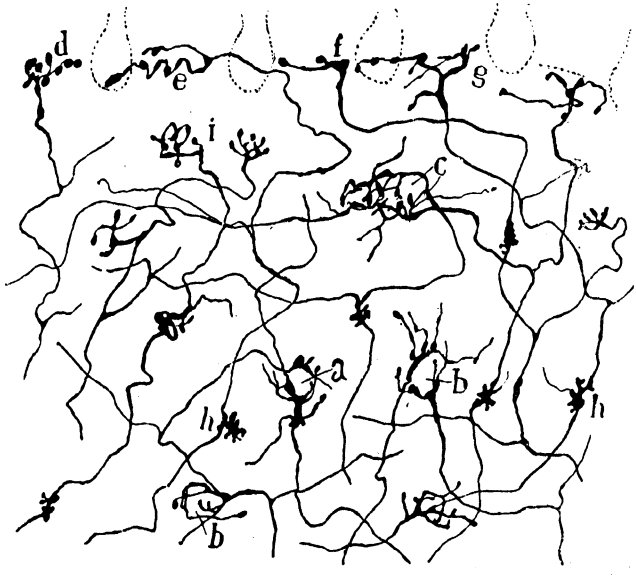


FIG. 201.—MOSS-FIBRES FROM CEREBELLUM OF YOUNG PIGEON. Golgi method. (Cajal.)

a, *b*, *c*, ramified tufts of moss-fibres enveloping 'granules' (the latter are not represented); *d*, *e*, *f*, *g*, terminal tufts near bodies of Purkinje cells; *h*, *h*, lateral tufts on moss-fibres; *i*, terminal tufts below level of Purkinje cells.

the ramifications of the two are not in close contact, but seem to be separated by a small amount of protoplasmic material. These synaptic interlacements are termed by Cajal and Illera 'glomeruli,' and they describe the axons of the cells of Golgi as contributing ramuscles to the same structures. Each moss-fibre, with its ramifications, extends over a considerable area of the granule-layer, but the branching and moss-like efflorescences are especially well marked near the level of the cells of Purkinje, beyond which the fibres pass into the molecular layer, where they appear to become longitudinal and horizontal, while breaking up yet again into fresh branches. (2) The fibres of the second kind (*tendril or climbing fibres*) from the medullary centre (fig. 200, *a*, *e*, *f*, *g*; fig. 202) pass towards the cells of Purkinje, and envelop their principal

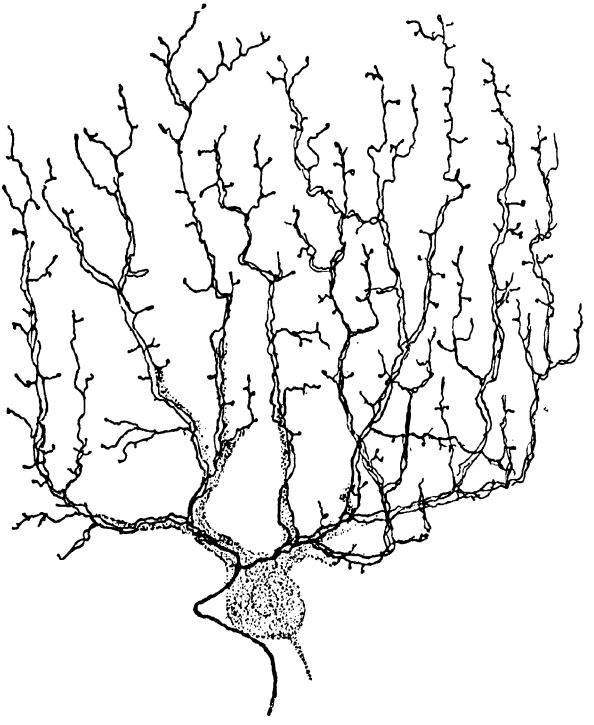


FIG. 202.—ENDING OF A TENDRIL FIBRE ON A PURKINJE CELL, SHOWING THE MANNER IN WHICH ITS BRANCHES TWINE ROUND THE BRANCHES OF THE DENDRONS. From the human cerebellum. (Cajal.)

dendrons in a terminal ramification, or plexus, in the same manner that the bodies or bases of the cells and the commencement of their axis-cylinder processes are enveloped in 'basket-work' formed by the vertical branches of the nerve-processes of the inner cells of the molecular layer. The cell-origin of the fibres which pass from the white centre into the grey cortex is not known, but fibres pass to the cortex cerebelli both from the nuclei pontis by the middle peduncle, from the spinal cord by the inferior peduncle and along the superior peduncle, and also from the opposite olivary nucleus of the medulla oblongata by the inferior peduncle. The opinion is expressed by Cajal that the tendril-fibres are derived from the cells of the nuclei pontis and the moss-fibres from fibres entering the cerebellum by the inferior peduncle. Cajal and Illera were unable to distinguish neuro-fibrils in the tendril-fibres.

Neuroglia-cells.—Lying among the nerve-cells of the granule-layer which are nearest the cells of Purkinje are a number of relatively large cells (fig. 204) giving off dendritic processes which are directed towards the periphery, and which course through the molecular layer as the fibres of Bergmann before mentioned. From the opposite side of these cells other processes pass off and become lost, partly among the granules, partly among the fibres of the white centre. These centrally directed fibres somewhat resemble commencing axis-cylinder processes of nerve-cells, but the cells in question are neuroglia-cells, belonging therefore to the supporting tissue of the nerve-centre. The peripherally directed fibres expand at the surface of the organ immediately underneath the pia mater into small conical enlargements, with their bases directed superficially: here they form a sort of limiting membrane similar to the internal

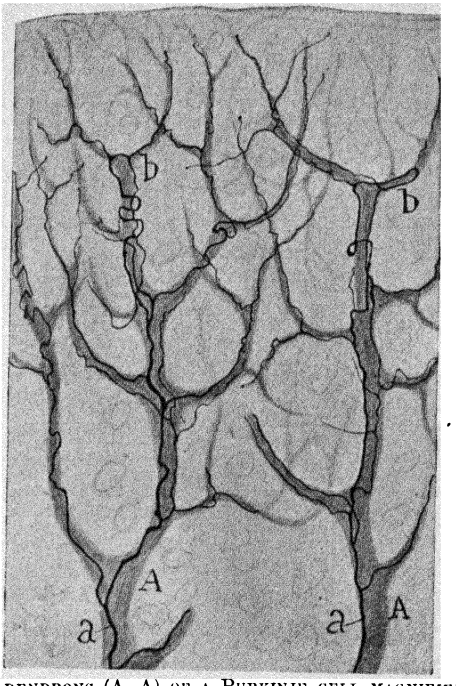


FIG. 203.—PARTS OF DENDRONS (A, A) OF A PURKINJE CELL MAGNIFIED TO SHOW THE ENDINGS OF THE TENDRIL FIBRES (*a*, *b*). (Cajal.)

limiting membrane of the retina, which is formed by the fibres of Müller. Although many of the neuroglia-cells have this arrangement, others, which are stellate or arborescent, lie more deeply among the granules, or among the nerve-fibres of the medullary centre.

Nuclei of the white centre of the cerebellum.—The grey matter of the *nucleus dentatus cerebelli* somewhat resembles both macroscopically and microscopically that which constitutes the inferior olivary nucleus. Its cells are of medium size and possess many short and rapidly ramifying dendrons and an axon which is directed towards the hilus and enters the superior cerebellar peduncle. Nerve-fibres which are derived from the cells of Purkinje of the cortex of the hemisphere arborise in the grey matter among its cells. It also receives collaterals from some of the fibres of the restiform body. This nucleus is a station between cerebellar cortex and red nucleus of tegmentum.

The *embolus* and *nucleus globosus* are similar in general structure to the nucleus dentatus, and like that receive nerve-fibres from the cells of Purkinje; probably chiefly, if not entirely, from those of the cortex of the middle lobe. In like manner the cell-axons are directed towards the superior cerebellar peduncles in which they become intermingled with those from the nucleus dentatus. But in the decussation they tend rather more dorsally, and pass to the large-celled part of the red nucleus (Preisig).

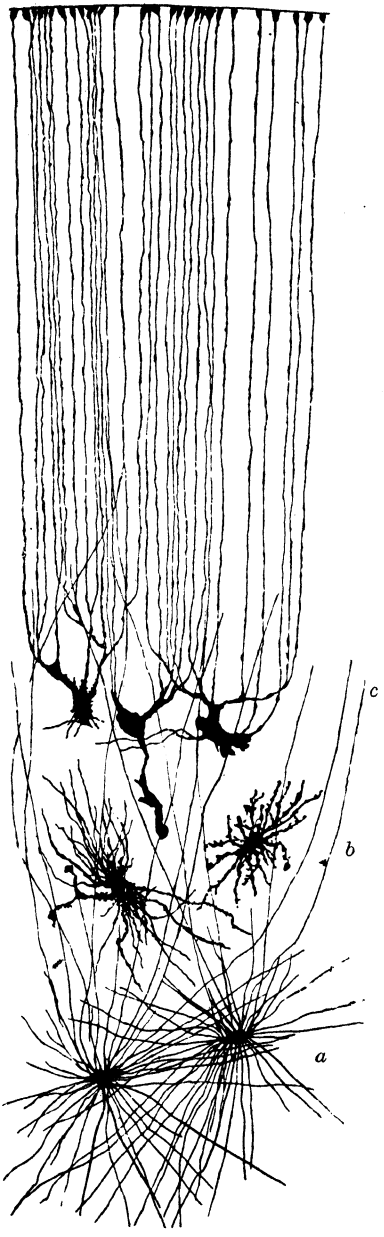


FIG. 204. — NEUROGLIA-CELLS OF THE CEREBELLUM. Golgi method. (G. Retzius.)

a, cells with long parallel processes extending to surface; *b*, arborescent cells; *c*, 'spider'-cells.

In the *nucleus tecti* the cells are smaller than in the nuclei just described and have long divergent dendrons. They are collected into groups which are separated from one another by bundles of fibres derived from the secondary vestibular nuclei of the medulla oblongata (vestibulo-cerebellar path). Whether this nucleus also receives fibres from the cells of Purkinje is uncertain. The cell-axons enter the adjacent white matter and may pass to the superior peduncle of the opposite side, decussating over the roof of the fourth ventricle; but their actual course has not hitherto been successfully followed out.

Degenerations following cerebellar lesions.—After removal of one-half of the organ extensive degeneration is seen in the superior peduncles of the same side. The degenerated fibres pass mainly to the tegmental (red) nucleus of the opposite side, partly to that of the same side; in other words, the decussation of these peduncles in the region of the inferior corpora quadrigemina is not complete. Some can be traced as far as the thalamus. These fibres of the superior peduncle take origin in the cells of the nucleus dentatus, and the adjacent nuclei in the white centre.

After extirpation of the middle lobe only of the cerebellum the degeneration in the superior peduncles is comparatively slight.

The middle peduncle, after removal of the corresponding half of the cerebellum, shows no degeneration unless sufficient time be allowed to elapse for secondary degeneration to intervene.[1] This may then ultimately occur as the

[1] Van Gehuchten, Système nerveux.

result of atrophy of the cells of the nuclei pontis from which the fibres of the middle peduncle arise.

The restiform body shows no descending degeneration. Some authors (Marchi, Biedl) have described descending degeneration in it as the result of section or of cerebellar lesions, but if the cerebellar cortex alone be injured no such degeneration is visible, and the positive effects recorded were therefore in all probability due to accidental injury of the medulla oblongata.[1] But Risien Russell found that when the middle lobe is involved in the lesion some degenerated fibres are seen hooking round the superior peduncle alongside those of Gowers' bundle; then passing round its external aspect and finally along the internal part of the restiform body towards the olivary nucleus.[2] According to Van Gehuchten, this bundle of Russell comes from the nucleus tecti and passes to Deiters' nucleus and to various parts of the formatio reticularis of the opposite side of the medulla oblongata.[3]

It follows therefore that only the superior peduncles contain efferent fibres, and these end for the most part in the opposite tegmentum (red nucleus) and in both thalami: the middle and inferior peduncles contain only afferent or cerebellopetal fibres (see p. 194).

Composition of the cerebellar peduncles.—The *inferior peduncle* was described by Stilling as composed of two parts, an external part—the restiform body—and an internal segment. Frequently, however, the term 'restiform body' is employed as the equivalent of inferior peduncle. The peduncle is almost wholly formed of afferent fibres. These are derived from several sources:

1. The *bundle of Flechsig*, the fibres of which are believed to take origin in the cells of Clarke's column of the spinal cord, and which, after passing up the cord and lower part of the medulla oblongata, enter the restiform body, where they run chiefly in the lateral and superior part. From the restiform body they are distributed mainly to the grey matter of the cephalic half of the vermis, a few of the fibres crossing the middle line. This bundle is composed of relatively large fibres.

2. The *olivary fibres*, which are derived from the cells of the opposite olivary nucleus, and are of relatively small diameter. They cross the raphe, traverse the other olivary nucleus, to which they give off many collaterals, and sweep round dorsally to enter the restiform body, of which they occupy the mesial and ventral part. They are distributed to all parts of the cerebellar cortex.

3. According to Edinger, some of the *internal arcuate fibres* which are derived from the cells of the nucleus cuneatus and nucleus gracilis pass to the restiform body both on the opposite and on the same side of the medulla oblongata. Edinger's view is founded mainly upon the study of the comparative anatomy of those parts in the lower vertebrates. Experiments on mammals have for the most part not borne out this view; destruction or injury of the nucleus gracilis and nucleus cuneatus is not followed by Wallerian degeneration in the restiform body.[4]

4. *Reticulo-cerebellar fibres*, coming from cells of the reticular formation of the same or of the opposite side and passing as arcuate fibres into the mesial and ventral part of the restiform body. Some of the fibres of this system come from the lateral nucleus of the medulla oblongata (Van Gehuchten).

[1] Ferrier and Turner, Phil. Trans. clxxxv. 1894; Van Gehuchten, Système nerveux. Horsley and Clarke (Brain, 1905) state also that no fibres can be seen degenerated in any of the peduncles as the result of lesion of cerebellar cortex, the axons of the cortical cells going exclusively to the nucleus dentatus, n. tecti, n. globosus, and n. emboliformis.

[2] Phil. Trans. clxxxvi. 1895.

[3] Système nerveux, pp. 645, 646.

[4] Van Gehuchten, Système nerveux, p. 654. But some authors describe results confirmatory of Edinger's view (Ferrier and Turner, Tschermak, Collier and Buzzard).

5. *Fibres derived from the vestibular nerve* and from the nuclei in which it terminates. These pass upwards in the internal segment of the inferior peduncle into the nucleus tecti. Many of the *descending branches* of the same nerve pass

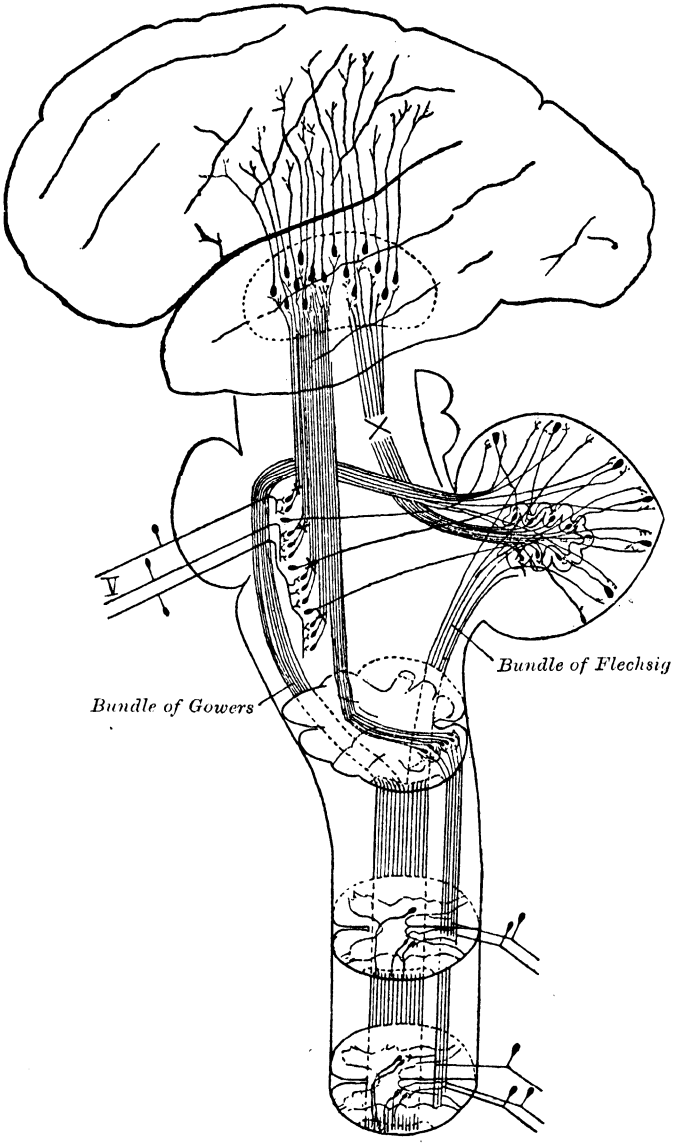


FIG. 205.—DIAGRAM OF THE SPINO-CEREBELLAR, BULBO-TEGMENTAL, CEREBELLO-TEGMENTAL, PONTO-TEGMENTAL, AND PONTO-CEREBELLAR TRACTS. (Van Gehuchten.)

downwards in the internal segment, which also contains the descending cerebello-bulbar fibres of Russell's bundle which have just been described.

The inferior peduncle is an important path of connexion between the cerebellar hemisphere on the one hand and the opposite olivary nucleus and

reticular formation, and through these possibly with the opposite side of the cord. It also serves by the bundle of Flechsig to unite the same side of the cord with the vermis; it is therefore mainly a spino-cerebellar path.

The inferior peduncle in man contains a very small nucleus of grey matter (Dejerine) (see fig. 147).

The *middle peduncle* is wholly formed of fibres derived from the cells of the nuclei pontis, passing from one side of the pons to the contra-lateral hemisphere; the opinion at one time held that its fibres are derived from the cerebellar hemisphere having been founded upon the result of secondary Wallerian degeneration (see p. 196). It is said to contain a few fibres derived from Gowers' tract; but these, if present, are probably aberrant, and it is certain that in the main this peduncle is to be regarded as forming the last stage of the cerebro-cerebellar path.

The *superior peduncle* is composed of cerebellofugal fibres which are passing from the nucleus dentatus and the nuclei globosus and emboliformis to the red nucleus of the opposite side (see p. 196), to which and to the oculomotor nucleus they give off numerous collaterals. Many then pass on towards the thalamus, and bifurcate. One of the branches goes to the internal medullary lamina of the thalamus of that side; the other crosses the middle line beneath the third ventricle and enters the thalamus of the other side.[1] The fibres of the superior peduncle, after crossing, give off descending branches which run in the formatio reticularis towards the medulla oblongata and cord. The passage down to the cord is, however, denied by Van Gehuchten, who states that they do not descend beyond the lower border of the pons. Some fibres are said to pass to the red nucleus of the same side; these also were found in the rabbit by Van Gehuchten. From the larger cells of the red nucleus the bundle of Monakow (rubro-spinal tract) originates, and crossing the middle line runs down the lateral column of the medulla oblongata and cord: this path therefore exhibits a double crossing. Thus there is an indirect connexion established between the cerebellar hemisphere and the same side of the cord. In their passage downwards the fibres of the rubro-spinal tract communicate with the various motor nuclei. There are also connexions between the red nucleus (its small-celled part) and the thalamus, and through this with the cortex cerebri; and some fibres of the superior peduncle go past the red nucleus and enter the thalamus. These represent a cerebello-cerebral path.

Besides the true peduncular fibres of the superior peduncle, it must be remembered that the greater part of Gowers' bundle enters the cerebellar worm by turning round and coursing backwards along the peduncle. This portion of the peduncle, therefore, represents a spino-cerebellar connexion of a direct character, comparable to that which is formed by the bundle of Flechsig through the inferior peduncle. The fibres from Gowers' bundle are distributed mainly to the caudal half of the vermis, on both sides.

Histogenesis of the cerebellar cortex. — In the embryonic cerebellum, and in most animals for a few days after birth, there is a cap-like layer of granule-like cells, several deep, superficial to the molecular layer (Obersteiner). This has been termed by Cajal the *zone of superficial granules*, and he has shown that it is formed at a certain stage of development of two distinct strata, one the more superficial, composed of epithelium-like elements (indifferent cells, neuroblasts) set perpendicularly to the surface, and the other next to the molecular layer composed of bipolar cells placed parallel to the surface and to the direction of the cerebellar lamellæ (fig. 208, A, B; fig. 209). The further development of the superficial cells has not been fully ascertained, and it can only be conjectured that they become gradually transformed into cells of the molecular layer, for no such superficial zone is

[1] Van Gehuchten, Névraxe, vii. 1905 (rabbit).

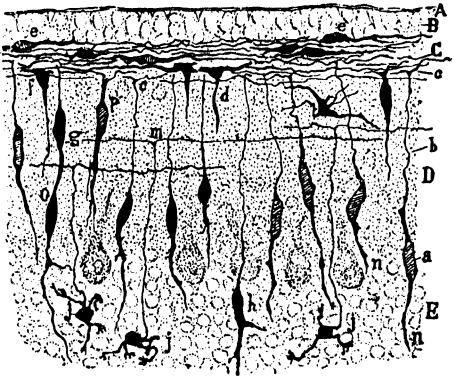


FIG. 206.—SECTION OF CEREBELLUM OF RAT A FEW DAYS AFTER BIRTH. (Cajal.)

A, basement-membrane; B, undifferentiated neuroblasts; C, horizontally disposed bipolars; D, vertically disposed bipolars in molecular layer; E, granule-layer. The small letters for the most part indicate cells in various stages of transition between the horizontally disposed cells and the cells of the molecular and granule layers. The Purkinje cells are already formed, but are not stained in the section.

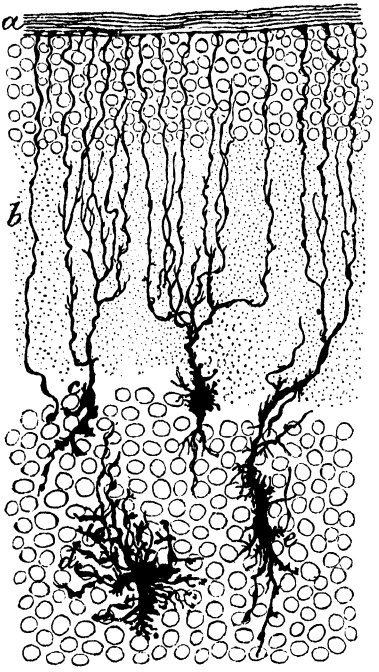


FIG. 207.—SECTION OF CEREBELLAR LAMINA OF A FIFTEEN-DAY KITTEN, SHOWING SOME OF THE NEUROGLIA-ELEMENTS. Golgi method. (Cajal.)

a, pia mater; *b*, processes of the neuroglia-cells passing towards the surface, where they end in conical enlargements; *c*, *e*, elongated neuroglia-cells; *d*, stellate neuroglia-cell.

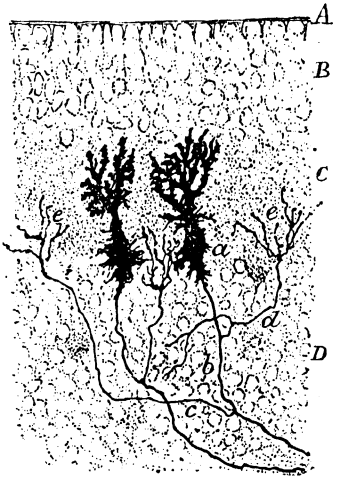


FIG. 208.—TWO CELLS OF PURKINJE FROM THE CEREBELLUM OF A NEW-BORN PUPPY. Golgi method. (Cajal.)

A, cuticular layer of cerebellum with insertion of radial fibres; B, layer of superficial granules; C, molecular layer showing the longitudinal fibres derived from the granules of the next layer, D, cut across and appearing as points; D, granule-layer; *a*, bodies of Purkinje's cells, the protoplasmic processes of which are still short and very irregular; *b*, nerve-fibre process of one of the cells; *c*, *d*, two collaterals from the same fibre; *e*, *e*, their terminal arborisations in the molecular layer.

seen in the adult cerebellum. At a certain stage of development there are also to be seen deeper in the molecular layer bipolar cells placed vertically, and having protoplasmic processes extending down towards or into the granule-layer, and axis-cylinder processes extending towards the surface: these become continued by T-shaped junctions into fibres running parallel with the processes of the horizontal bipolar cells which have just been described. The vertical bipolar cells appear to be derived from the horizontal ones, and represent a stage in the formation of the granules of the granule-layer. The basket-cells are formed from others of the superficial cells which become horizontally bipolar and remain more or less so, but soon send their axons down to the cells of Purkinje. The neuroglia-cells are early differentiated (fig. 207). The cells of Purkinje in the cerebellum of embryonic and very young animals are

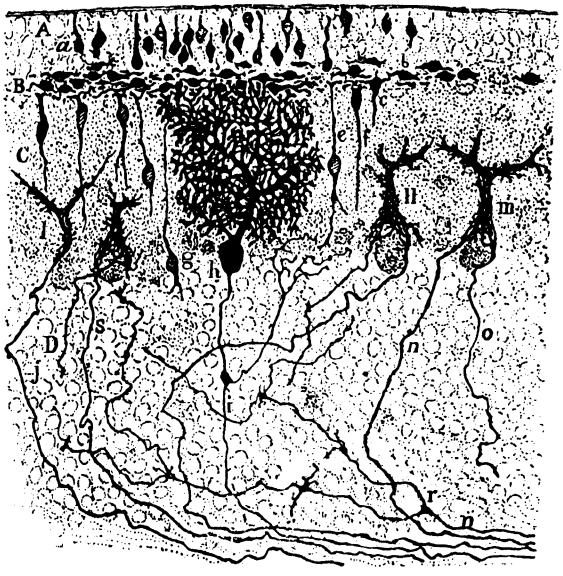


FIG. 209.—TRANSVERSE SECTION OF THE CEREBELLUM OF A SIXTEEN-DAY-OLD PUPPY. Golgi method. (Cajal.)

A, epithelium-like layer of superficial zone; B, layer of horizontal bipolar cells; C, molecular layer; D, granule-layer; *a*, epithelium-like cell; *b*, bipolar horizontal cell; *c*, cell sending a process downwards into the molecular layer; *e*, *f*, *g*, bipolar vertical cells; *h*, cell of Purkinje; *i*, its nerve-fibre process giving off a collateral towards the molecular layer; *j*, *n*, *o*, *s*, fibres from the white substance passing to form plexuses (*l*, *m*) which envelop the upper part of the bodies and the proximal part of the dendrites of cells of Purkinje; *r*, 'moss'-fibre.

very irregular multipolar cells (fig. 208), with relatively short protoplasmic processes, but a well-developed axis-cylinder process, which already has two or three collateral fibres extending towards and ramifying in the deeper part of the molecular layer (fig. 209). It is not until two or three weeks after birth (in the dog) that the dendrons begin to assume their characteristic form and arrangement. The arborescence which in the adult cerebellum envelops the principal dendrons of the cells of Purkinje (see p. 194 and fig. 200) is at this early stage chiefly confined to the upper part of the body of the cell (fig. 209). It is uncertain whether the cells of Purkinje and the cells of Golgi develop from neuroblasts *in situ* or whether they migrate downwards from the cells of Obersteiner's layer.[1]

[1] On the histogenesis of the cerebellum, see Cajal, *op. cit.* Also Berliner Arch. f. mikr. anat. lxvi. 1905.

MID-BRAIN, OR MESENCEPHALON.

This is a short and constricted part of the brain uniting the pons and cerebellum below with the cerebrum above. It passes through about the centre of an opening in the dura mater, bounded behind and at the sides by the free edge of the tentorium, and in front by the dura mater covering the back of the dorsum sellæ. Owing to the small size of this division of the brain as compared with the cerebral hemispheres above, and the pons and cerebellum below, it is sometimes called the *isthmus encephali* (see p. 110). The main axis is directed upwards and somewhat forwards, and measures about half an inch, but the length of the posterior surface is a little more and the anterior rather less than half an inch. Below it measures an inch or so from side to side and from before backwards, but owing to the lateral divergence of the two pedunculi cerebri, as they ascend, the transverse diameter is increased to one and a-half inches at its upper end.

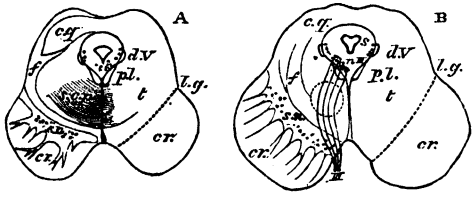


FIG. 210.—OUTLINE OF TWO SECTIONS ACROSS THE MESENCEPHALON. Natural size. (E. A. Schäfer.)

A, through the inferior pair of the corpora quadrigemina; B, through the superior pair.

cr., crusta; *s.n.*, substantia nigra; *t*, tegmentum; *s*, Sylvian aqueduct with the central grey matter; *c.q.*, grey matter of quadrigeminal bodies; *l.g.*, lateral groove; *p.l.*, posterior longitudinal bundle; *d.V*, descending motor root of fifth nerve; *s.c.p.*, superior cerebellar peduncle; *f*, fillet. The dotted circle in B indicates the red nucleus.

The mid-brain consists of a large ventral portion composed of the two pedunculi cerebri and a smaller dorsal part formed by the corpora quadrigemina (fig. 210). It is traversed by a canal called the cerebral or Sylvian aqueduct.

The **aqueductus cerebri** (*aqueduct of Sylvius, iter a tertio ad quartum ventriculum*) is a passage into which the upper end of the fourth ventricle gradually narrows, and which above turns forwards and expands abruptly into the third ventricle. It is rather more than half an inch long. In shape it varies in different parts, being **T**-shaped in section below (near the fourth ventricle), triangular above (near the third), and in the intermediate part of an elongated oval form, and larger than at its extremities. This dilatation of the aqueduct is the remains of a relatively more marked expansion found in the fœtus, and might, as Retzius suggests, be termed the ventricle of the mid-brain. It is lined by an ependyma with ciliated columnar epithelium, outside which is a thick layer of grey matter, the *central grey matter of the aqueduct*, continuous with that of the fourth ventricle.

The **pedunculi** or **crura cerebri** (fig. 133) emerge from the upper border of the pons and diverge from one another, leaving between them the posterior perforated space and the corpora mamillaria, and disappearing in the cerebral hemispheres, where they are crossed by the optic tracts. The triangular interval seen at the base of the brain to be enclosed between the diverging peduncles has been termed *trigonum interpedunculare* by Schwalbe. Near the point of the angle of divergence the roots of the third nerve issue in several bundles from a groove along their inner side (fig. 210, B, *III.*); and this groove serves to indicate the separation between the more prominent ventral part of the peduncle (*basis*

s. crusta pedunculi, fig. 210, *cr.*) and the dorsal and larger part (*tegmentum*, *t.*) which is in great measure concealed from view by the crusta when viewed from below and in front, since it only comes to the surface on the ventral aspect at the trigonum interpedunculare, or posterior perforated spot. A section across the pedunculus cerebri shows the two parts of which it is composed to be separated from one another by a tract of dark-coloured grey substance known as the *substantia nigra* (fig. 212, *sn*), which comes to the surface on the inner side at the groove above mentioned from which the third nerve issues (*sulcus oculomotorii*), and on the outer side also along a grooved line—the *sulcus lateralis* (fig. 210, *l.g.*).

Of the two main parts of each peduncle the *crusta* is formed almost entirely of lamellated bundles of longitudinal fibres, some of which are continuous with the pyramid-fibres of the medulla oblongata and pons, while others are superadded; and the *tegmentum* is a continuation of the formatio reticularis of those parts, with the addition of much grey matter and white fibres, among

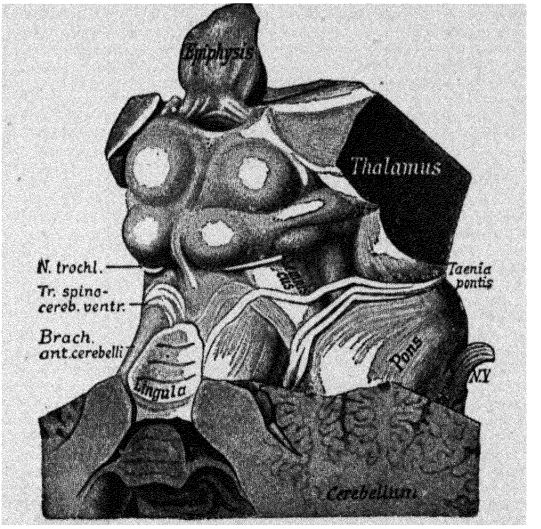


FIG. 211.—VIEW OF THE MID-BRAIN AND ADJOINING PARTS: LATERO-DORSAL ASPECT. (Edinger, from G. Retzius.)

The epiphysis has been turned forwards to display the posterior commissure.

the latter being those of the superior peduncle of the cerebellum. The two crustæ, semilunar on transverse section, are entirely distinct from one another (see fig. 210), and each is marked off from the tegmentum of the same side by the superficial sulci just mentioned; but the two tegmenta are united in the median plane by a raphe, and extend dorsally at the sides of the aqueduct to become continuous with the bases of the corpora quadrigemina. Transverse sections through the lower part of the mid-brain show that the tegmentum contains a large mass of decussating fibres (fig. 212, *s.c.p.*), while a similar section higher up discloses two rounded reddish masses, the red nuclei of the tegmentum (fig. 213, *r.n.*).

The Sylvian aqueduct is covered on its dorsal aspect by the *lamina quadrigemina*, bearing the eminences termed superior and inferior (anterior and posterior) quadrigeminal bodies or the superior and inferior colliculi (fig. 211). The median part of the lamina is marked by a comparatively wide groove (*sulcus longitudinalis s. sagittalis*), shallower inferiorly, which serves to separate the corpora

quadrigemina of opposite sides. This grooved surface, which is raised above the level of the upper medullary velum, is connected with the velum by a small median strand of longitudinal fibres termed the *frænulum veli*. In front of the upper (anterior) pair of corpora quadrigemina the groove is interrupted by a transverse white prominence—the *posterior commissure*; but both this and the upper end of the median groove are in the natural condition concealed by the *pineal body* or *epiphysis*, which projects backwards and downwards from the posterior wall of the third ventricle above and between the upper pair of quadrigeminal bodies. On raising the pineal body, the

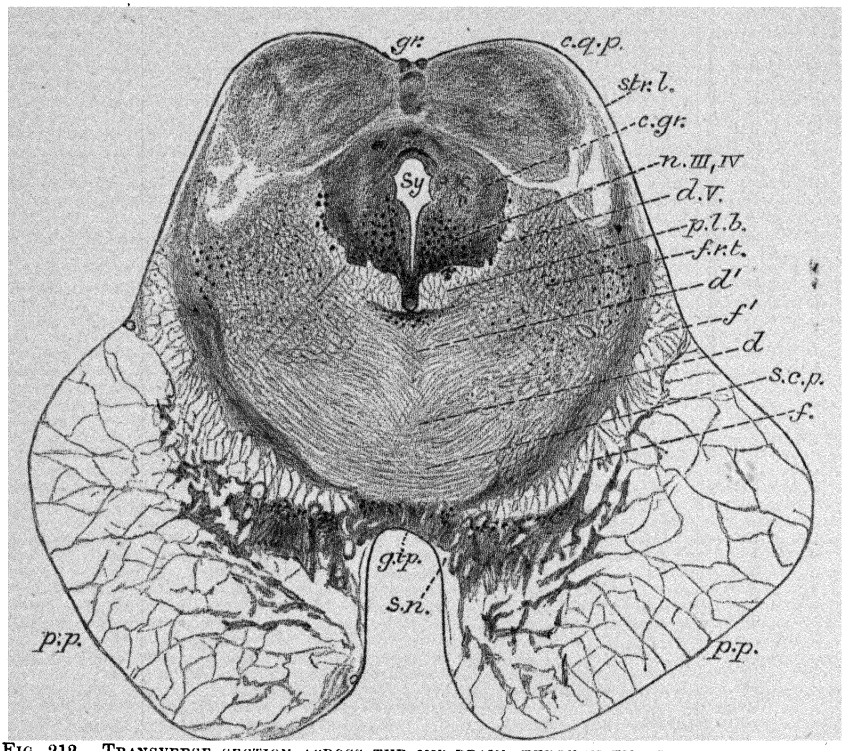


FIG. 212.—TRANSVERSE SECTION ACROSS THE MID-BRAIN, THROUGH THE POSTERIOR CORPORA QUADRIGEMINA. Magnified about 3½ diameters. (E. A. Schäfer.) From a photograph.

gr., dorsal quadrigeminal groove (sulcus longitudinalis); *c.q.p.*, corpus quadrigeminum posterius; *str.l.*, stratum lemnisci; *c.gr.*, central grey matter; *n.III, IV*, oculomotor nucleus; *d.V.*, descending motor root of fifth nerve; *p.l.b.*, posterior longitudinal bundle; *f.r.t.*, formatio reticularis tegmenti; *d*, *d'*, decussating fibres of tegmentum (fountain-like decussations of Forel and Meynert); *s.c.p.*, decussating fibres of superior cerebellar peduncles; *f*, main fillet; *f'*, lateral fillet; *p.p.*, crusta pedunculi; *s.n.*, substantia nigra; *g.i.p.*, interpeduncular ganglion; *Sy*, Sylvian aqueduct.

triangular area beneath it (*trigonum subpinealis*) is found to be separated from the posterior commissure by a deep transverse groove (fig. 211). A well-marked narrow transverse groove (*sulcus transversus*), which commences a short distance from the middle line and is curved round the lower border of the upper tubercle, separates this from the lower tubercle of the same side.

The **corpora quadrigemina** are two pairs of rounded eminences which are mainly composed of grey matter, although covered externally by and containing in their interior many white fibres. The upper or anterior tubercles (*colliculi superiores*) are broader and longer and also darker in colour, but slightly less prominent than the lower or posterior (*colliculi inferiores*). Laterally the corpora

quadrigemina are not bounded by a distinct groove, but each appears to be prolonged obliquely upwards and forwards into a white tract known as the *brachium* of the corresponding tubercle.

The lower (posterior) brachium (fig. 211) extends outwards and upwards towards the mesial geniculate body, from which it is separated by a well-defined sulcus. It is about a third of an inch in length, and the groove which forms its upper boundary marks it off from the superior quadrigeminal body. The upper (anterior) brachium is narrower, longer, and not so well defined. It passes outwards towards the lateral geniculate body, opposite the inner end

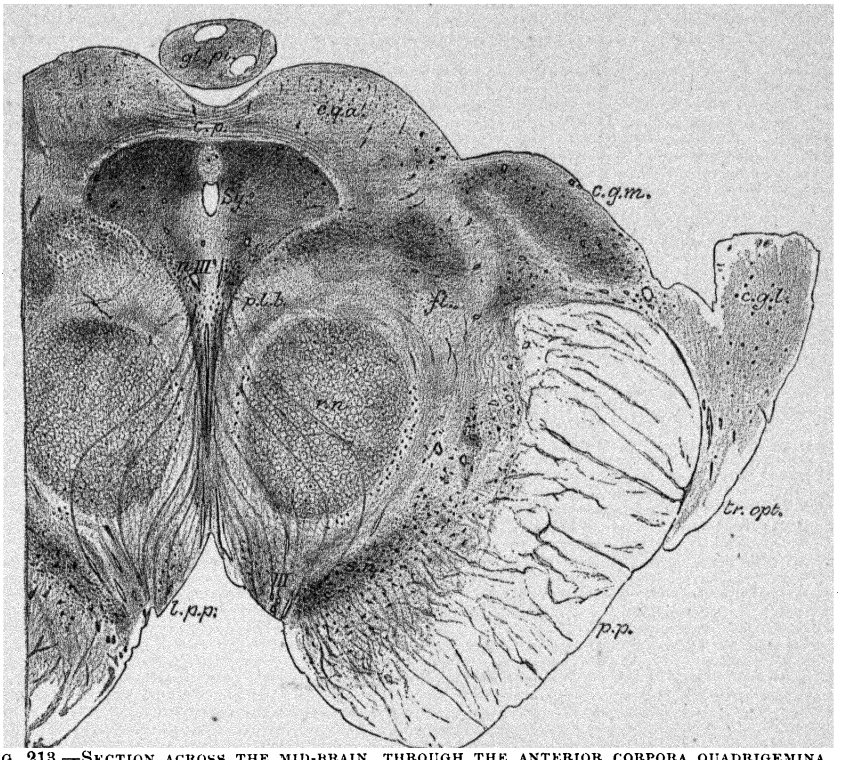


FIG. 213.—SECTION ACROSS THE MID-BRAIN, THROUGH THE ANTERIOR CORPORA QUADRIGEMINA. Magnified about 3½ diameters. (E. A. Schäfer.) From a photograph.

Sy., aqueductus Sylvii; *c.p.*, commissura posterior; *gl.pi.*, corpus pinealis; *c.q.a.*, grey matter of one of the anterior corpora quadrigemina; *c.g.m.*, corpus geniculatum mesiale; *c.g.l.*, corpus geniculatum laterale; *tr.opt.*, tractus opticus; *p.p.*, pes pedunculi; *p.l.b.*, posterior longitudinal bundle; *fi.*, upper fillet; *r.n.*, red nucleus; *n.III*, nucleus of third nerve; *III*, issuing fibres of third nerve; *l.p.p.*, locus perforatus posticus.

of which it often appears to divide into two bundles, which embrace this prominence and are then continued into the optic tract. The anterior of these bundles runs outwards in the narrow groove between the mesial geniculate body and the under surface of the pulvinar of the thalamus, while the posterior (*fasciculus peduncularis transversus* of Gudden) crosses the outer end of the inferior brachium. The two divisions of the upper brachium and their continuity with the optic tract vary considerably in their degree of prominence. These bundles are better marked in some animals than in man.[1]

[1] See G. Retzius, 'Zur Kenntniss der lateralen Fläche des Mesencephalons und ihrer Umgebung,' Biologischen Untersuch. viii. 1898.

MICROSCOPIC STRUCTURE OF THE MID-BRAIN.

Cerebral aqueduct or aqueduct of Sylvius.—The epithelium which lines the Sylvian aqueduct is ciliated (as elsewhere in the ventricles of the brain), and the attached ends of the cells extend as radiating ependymal fibres through the thickness of the mid-brain to reach the surface—at least, this can be seen to be so in the embryo and in small vertebrates, and is perhaps true for all. But some of the radiating fibres which are seen belong to neuroglia-cells at various levels in the course of the fibres; these are probably detached epithelium-cells. The fibres which extend from them often branch dichotomously, besides possessing many small lateral offsets.

The **central grey matter of the aqueduct** (fig. 212, *c. gr.*) is a layer 2 to 3 mm. thick, which surrounds the aqueduct and is prolonged from the grey matter of the fourth ventricle. It contains, scattered through its substance, nerve-cells of varying size, the largest being prolonged upwards from the locus cœruleus of the fourth ventricle; the cells are very numerous and small at the dorsal side of the aqueduct. In addition to these scattered cells, the grey matter of the aqueduct contains certain more defined groups or columns of cells which are connected with the roots of the third and fourth and of the fifth cerebral nerves. Among the cells there is a network of fine medullated nerve-fibres, while near the aqueduct and immediately under the ependymal layer many fine longitudinal fibres are seen.

The **nuclei of the third and fourth nerves** (figs. 212, 213, *n.III, IV*) extend on either side along almost the whole length of the ventral part of the aqueduct, close to the middle line, the nuclei of the two sides being only separated from one another by the raphe; at one part they even meet across this (fig. 213, *n.III*). The cells of these nuclei are large and irregular in shape, and of a yellowish colour. The nucleus from which the root-bundles of the fourth nerve spring does not begin to show itself until the level of the upper part of the inferior corpora quadrigemina; it lies just below and rather to the side of that from which the bundles of the third originate. From its nucleus the bundles of the fourth pass obliquely downwards towards the pons, and just before reaching this the nerve turns sharply dorsalwards, and passes into the superior medullary velum, in which it crosses horizontally, decussating with the nerve of the opposite side (fig. 173).

According to Van Gehuchten a few fibres of the fourth nerve pass out on the same side, but this is somewhat doubtful. On the other hand, with a few exceptions, the fibres of the third nerve pass out on the same side as the cells from which they originate. The dendrons of the cells of these nuclei extend across the middle line into the contralateral nuclei. The nuclei also receive many collaterals and terminals, especially from the dorsal longitudinal bundle, but also from other sources, which form a close interlacement among the cells. The pyramid-tract fibres send no branches to the oculomotor nuclei: the connexion therefore of these nuclei with the volitional path must be indirect. In this respect they agree with other motor nuclei.

The nucleus from which the third nerve takes origin extends upwards underneath the superior corpora quadrigemina, ventral to the Sylvian aqueduct, and even into a corresponding situation in the posterior part of the third ventricle. The anterior part is composed of smaller cells than the rest: it extends forwards into the wall of the third ventricle, and appears to be subdivided into two portions, of which that which is mesial, and which lies just above the corpora mamillaria, is said to be connected with the fibres of the third nerve to the ciliary muscle; while that which is lateral is believed to be connected with the fibres to the sphincter pupillæ. The main part of the oculomotor nucleus is formed by large cells, which tend to be

grouped (see diagram, fig. 214). Thus, there are two distinct groups on each side which are dorso-lateral (*anterior* and *posterior dorsal nuclei*), and two which are ventro-mesial (*anterior* and *posterior ventral nuclei*). These four nuclei are grouped round a *central nucleus*[1] which lies in the middle line. Besides these, there is an elongated nucleus of small cells which posteriorly (caudalwards) lies in close contact with the central nucleus, but anteriorly curves outwards, and another small-celled nucleus in front on either side just below the posterior commissure. The former is known as the *nucleus of Edinger and Westphal*, but it is uncertain whether it gives origin to any fibres of the third nerve. The latter is termed the *nucleus of Darkschewitsch*. It receives fibres from the dorsal longitudinal bundle, and according to some authors also gives off fibres to that bundle, but it is now not believed to give origin to oculomotor fibres. According to Kölliker, its fibres pass to the posterior commissure; but other authorities, on the other hand, state that it receives fibres from the superior

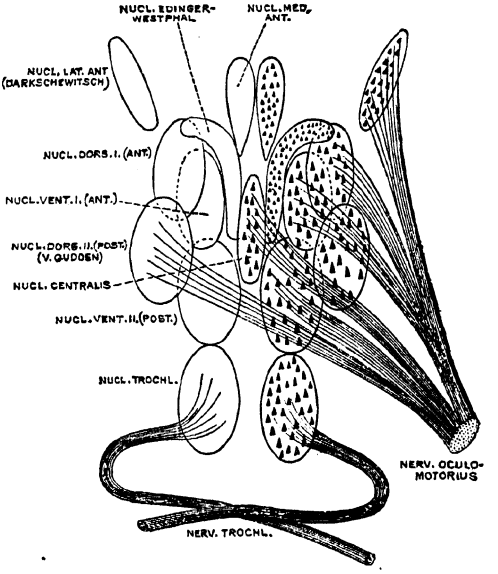


FIG. 214.—DIAGRAM OF THE GROUPS OF CELLS FORMING THE NUCLEI OF THE THIRD AND FOURTH NERVES. (Perlia.)

The fibres from the nucleus of Darkschewitsch to the oculo-motor nerve are doubtful.

corpora quadrigemina through that commissure. From the groups of cells which constitute the oculomotor nucleus proper the fibres of the third nerve pass with a curved course through the tegmentum, to emerge at the inner margin of the crusta of the same side; but the fibres from the posterior of the dorsal groups undergo decussation.

These last-mentioned fibres were believed to pass to the internal rectus of the opposite side, but according to Schwalbe they go to the opposite superior rectus, and the corresponding fibres of the ventral groups go to the inferior oblique of the same side. On the other hand, Bernheimer states that the mesial groups of cells supply the nerves of the external rectus of the globe, and the lateral groups those to the ciliary muscle and sphincter pupillæ.

In a case recorded by Kahler and Pick, in which there was paralysis of the levator palpebræ, the rectus superior, and the obliquus inferior, a lesion was found involving the dorso-lateral bundle of the nerve-roots. The observations of Starr point to these three muscles being

[1] Perlia, Arch. f. Ophthal. 1887.

innervated from the dorsal (dorso-lateral) groups, and the rectus internus and rectus inferior from the ventral (ventro-mesial) groups, in the order here given (from above down).

Leube has also described a case of hæmorrhage into the dorso-lateral part of the nucleus, which was accompanied by ptosis and dilatation of the pupil of the same side.

Hensen and Voelckers endeavoured to arrive at the localisation within the nucleus by studying the effects of faradic excitation in the living animal of the issuing bundles of the root of the third nerve. They found the order of movement from before back (above down in man) to be ciliary muscle, sphincter iridis, internal rectus, superior rectus, levator palpebræ superioris, inferior rectus, inferior oblique.

According to Cajal (anatomical evidence), the order from before back is rectus superior, obliquus superior, smooth muscles, rectus inferior, rectus internus. It is clear therefore that there is great uncertainty as to the topographical relations of these nuclei to the ocular muscles.

Duval and Laborde were of opinion that the third nerve receives fibres from the mesial part of the dorsal longitudinal bundle of the opposite side and perhaps some fibres from the dorsal longitudinal bundle of the same side. These fibres they supposed to be derived mainly from the nucleus of the sixth nerve, and to pass out along with the fibres of the third nerve to the internal rectus, so that the nucleus of the sixth would supply both the external rectus of the same side entirely, and the internal rectus of the opposite side partially (fibres derived from the nucleus of the third also going to the internal rectus). These are the muscles which are brought together into action in conjugate deviation of the eyes to either side; and the cases which are sometimes met with of conjugate paralysis involving the internal rectus of one side and the external rectus of the other side, which are accompanied by atrophy of the nucleus of the sixth, might thus be accounted for. But, although no doubt the dorsal longitudinal bundle contains fibres which bring the ocular muscles into correlation (for its fibres give off collaterals to all the oculomotor nuclei), it has not been proved that any of these fibres pass out with the nerve-roots. As a matter of fact, the fibres of the posterior longitudinal bundle are derived mainly from the cells of Deiters' nucleus in the pons and medulla oblongata and from other cells of the reticular formation of those parts; and these fibres divide on reaching the bundle, one branch passing upwards past the nucleus of the sixth nerve, to which it gives collaterals, to end by both collaterals and terminal branches in the combined nucleus for the fourth and third nerves; while the other branch runs down into the ventral column of the cord, and forms similar connexions with the motor nuclei of the ventral horn. No fibres from the sixth nucleus pass into the bundle, and the conjugation of movements of the eyes cannot therefore be brought about in the manner suggested by Duval and Laborde.

The prolongation of the **upper nucleus of the fifth nerve** consists of a small number of large globose cells (figs. 172, 173, 212) which lie at the extreme lateral margin of the grey matter of the aqueduct close to the bundles of the descending root of the fifth nerve, towards which their axis-cylinder processes are directed. This nucleus and root gradually become smaller, and disappear before the superior end of the mesencephalon is reached.

Crusta, or basis.—The crusta is semilunar in section, the substantia nigra projecting into it with an irregular convex border. It is made up of longitudinal white fibres which become arranged in the higher parts of the mid-brain into flattened bundles, with their edges dorsal and ventral, separated from one another by processes of pia mater. The crusta is directly prolonged into the longitudinal bundles of the ventral part of the pons and is continuous superiorly with the internal capsule of the cerebral hemisphere.

Close to the substantia nigra, the bundles of white fibres are smaller and somewhat separated by projections of the grey matter extending between them. The layer they form has received the name of *stratum intermedium*. They are usually stated to have a different origin and destination from the other fibres of the crusta, passing, according to Meynert, between the lenticular nucleus of the corpus striatum, and the substantia nigra and reticular formation of the bulb and pons. It is doubtful, however, if this is true for any of these fibres, and is certainly not the case with the majority, for (in monkeys) after a lesion of the Rolandic region, most if not all the fibres of the stratum intermedium undergo degeneration along with the fibres of the pyramid-tract, to which therefore

they must be regarded as belonging. They may perhaps be branches or collaterals of pyramid-tract fibres on the way to terminate in the substantia nigra.[1] In the cat a certain number of fibres from the cortical tract of the crusta leave this and pass round the side of the mid-brain to enter the anterior corpora quadrigemina (R. Boyce, S. Simpson).

The continuation of the pyramid-bundles of the pons occupies about the middle three-fifths of the crusta, but the area occupied shades off on both sides and some fibres are found close to the mesial border; the extreme lateral part is, however, free from them (fig. 197). Superiorly its fibres come through the middle part of the internal capsule from the Rolandic region of the frontal lobe. By far the majority arise from the cortical cells in that part and degenerate after lesions in it, but a few have their cell-origin elsewhere. From such degenerations it is evident that the fibres from the various areas (leg, arm, face) become largely intermingled in the internal capsule, and still more so in the crusta, although the facial fibres are more numerous in the mesial part, the arm fibres in the centre, and the leg fibres towards the lateral part of the crusta (fig. 215).[2]

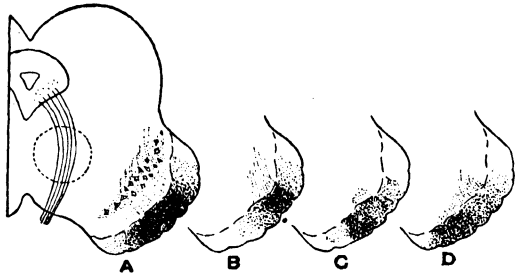


FIG. 215.—SECTIONS OF THE MID-BRAIN OF THE MONKEY, AFTER LESIONS OF THE MOTOR AREA OF THE CEREBRAL CORTEX. THE DARK POINTS REPRESENT DEGENERATED NERVE-FIBRES. Marchi method. (Sutherland Simpson and Jolly.)

A, after destruction of the whole motor cortex; B, of the leg area; C, of the arm area; D, of the face area (the arm area having been also somewhat involved).

It is remarkable that, whereas in the lower part of its course (spinal cord and bulb) the fibres of the cortical tract acquire a medullary sheath later than do the other fibres of the white columns, in the upper part (pedunculi cerebri and cerebrum) it is acquired earlier.

The fibres of the outer or lateral part of the crusta are traceable downwards to the lateral longitudinal bundles of the pons, and upwards to the posterior part of the internal capsule, but their origin and destination have not yet been satisfactorily made out. They are probably connected superiorly with the occipito-temporal regions of the cerebral cortex, and end below among the cells of the nuclei pontis.

Some of the mesially situated bundles of the crusta (about one-fifth of the whole) are also distinct from the cortical tract proper (Flechsig), being developed at a later period. They are connected through the anterior part of the internal capsule with the lower frontal region of the hemisphere, and possibly bring this into relation with the nuclei of the facial and hypoglossal. Finally, one well-marked bundle in the crusta is connected with the fillet (*mesial fillet*, pp. 157 and 215). This bundle is at the lateral border of the cortical tract in the

[1] S. Simpson, Internat. Monatschr. f. Anat. u. Physiol. xix. 1902; Simpson and Jolly, Proc. Roy. Soc. Edin. xxvii. 1907.

[2] Mellus, Proc. Roy. Soc. lv. 1894, and lvii. 1895; Simpson and Jolly, *op. cit.* Stanley Barnes (in man), Brain, xxiv. 1901.

upper part of the crusta, but lower down crosses obliquely over or between the fibres of that tract to attain the mesial border of the crusta, whence it is traceable to the fillet. Spitzka states that it contains the afferent cerebral tracts of the cerebral nerves, but it is probably a descending tract, taking origin in the thalamus and extending down to the medulla oblongata (*thalamo-bulbar tract*; see p. 215).

Interpeduncular ganglion (fig. 212, *g.i.p.*).—This is a median collection of nerve-cells, mostly large; the more superficial ones arranged tangentially and the deeper ones vertically to the surface. It receives from each side the fibres of the fasciculus retroflexus of Meynert (fig. 216), which passes obliquely downwards from the ganglion of the habenula, and it gives off a bundle which passes parallel with the plane of the raphe to enter the dorsal tegmental nucleus (see next page). The fibres of this bundle are fine and come from the

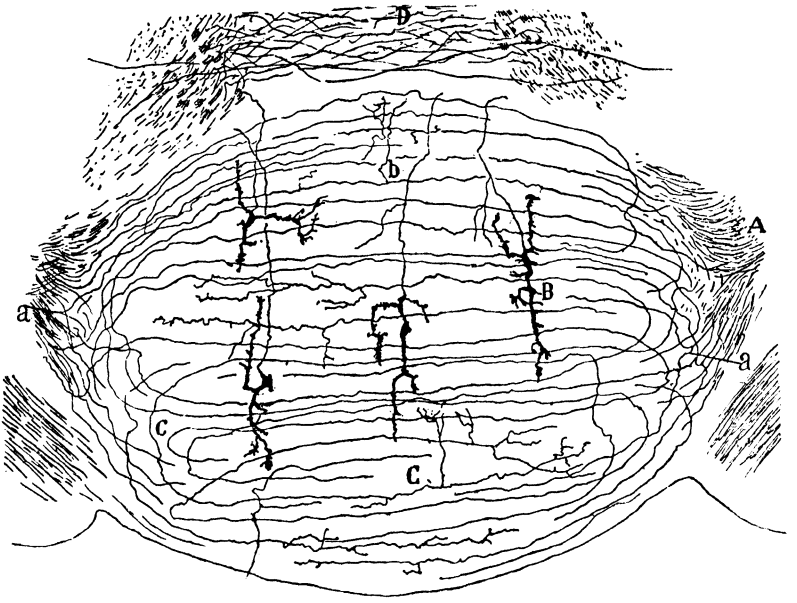


FIG. 216.—CORONAL SECTION, SOMEWHAT OBLIQUELY FROM BEFORE BACKWARDS, OF THE REGION OF THE INTERPEDUNCULAR GANGLION FROM A FOUR-DAY OLD MOUSE. Golgi method. (Cajal.)

A, fasciculus retroflexus of Meynert; *a*, *a*, bifurcations of its fibres; *b*, collaterals within the ganglion; *c*, some of the fibres turning round after crossing to the opposite side of the ganglion; C, terminal arborisation of such a fibre; B, cells of the ganglion seen in profile, sending their axons towards the tegmentum; D, ventral tegmental decussation.

more central part of the ganglion. The axons from the lateral parts are thicker: their destination has not hitherto been traced.

The **substantia nigra** is a mass of grey matter which is characterised by the presence of a number of very darkly pigmented irregular nerve-cells, which give the substance in which they are scattered the appearance from which it derives its name. It forms a layer which separates the crusta from the tegmentum. It is thicker near the mesial border of the peduncle than laterally, where the tract of the fillet may be but incompletely separated by it from the longitudinal bundles of the crusta. It commences at the upper part of the pons, and can be traced as far forwards as the posterior border of the corpora mamillaria. At the origin of the third nerve it is traversed in its mesial part by some of the issuing fibres of the nerve-root. The cells of the substantia nigra are large in the dorsal part and smaller in the ventral part of the mass. Their axons pass

into the tegmentum, but it is not known how and where they terminate. There are also a certain number of short-axoned cells with their axons terminating in the substantia nigra itself. The grey matter of the substantia nigra projects here and there between the adjacent bundles of the crusta: one considerable projection in particular in the lower part of the mesencephalon serving to mark off the mesial portion of the crusta from the rest. The cells in this projection are much smaller and relatively more numerous than in the rest of the substantia nigra.

The substantia nigra receives many branches (collaterals) from the pyramidal bundles of the crusta, and it is stated to undergo atrophy as a result of lesions of the motor cortex cerebri.

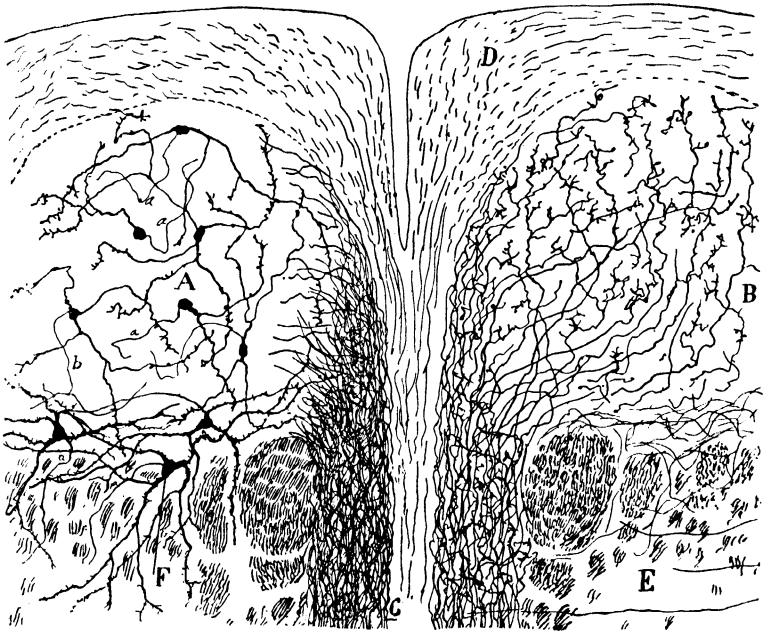


FIG. 217.—CORONAL SECTION OF TEGMENTUM OF YOUNG KITTEN, SHOWING THE DORSAL TEGMENTAL NUCLEI OF GUDDEN.

A, cells of nucleus, for the most part small, but with larger cells in the ventral part, F, of the nucleus; B, terminal arborisations of the tegmental bundle, C, the fibres of which take origin in the interpeduncular ganglion (see previous figure); D, central grey matter of aqueduct; E, situation of ventral tegmental nucleus.

Tegmentum.—The tegmentum, like the formatio reticularis of the pons, of which it is the prolongation upwards, is composed of small longitudinal bundles of white fibres, separated by transversely coursing or arched fibres, together with a considerable amount of reticularly disposed grey matter containing scattered nerve-cells.

Nuclei of the tegmentum and raphe.—The *dorsal tegmental nucleus* (fig. 217) is a collection of small cells in the central grey substance in the lower part of the mid-brain and upper part of the pons. This nucleus receives the termination of *Gudden's tegmental bundle*, which arises in the interpeduncular ganglion and passes on either side of the raphe to its destination. The axons of the cells of the nucleus in question have not been definitely traced; according to Kölliker, they pass dorsally and join the longitudinal fibres which surround the aqueduct.

The *ventral tegmental nucleus* lies in the same region as the last described, but ventral to the dorsal longitudinal bundle in the formatio reticularis alba, close to the raphe. Its cells are larger than those of the dorsal nucleus, and send their axons into the adjoining bundles of the white reticular formation, from which also the nucleus receives many collaterals.

Another nucleus in this region is the *central large-celled nucleus of the raphe*, which lies in the middle line in the region of the fourth nucleus and sends its fibres towards the dorsal longitudinal bundle. In the raphe of the pons there is a similar nucleus of considerable dorso-ventral extent, composed of cells of medium size sending their axons into the adjacent longitudinal bundles; this is the *superior central nucleus* of Bechterew.

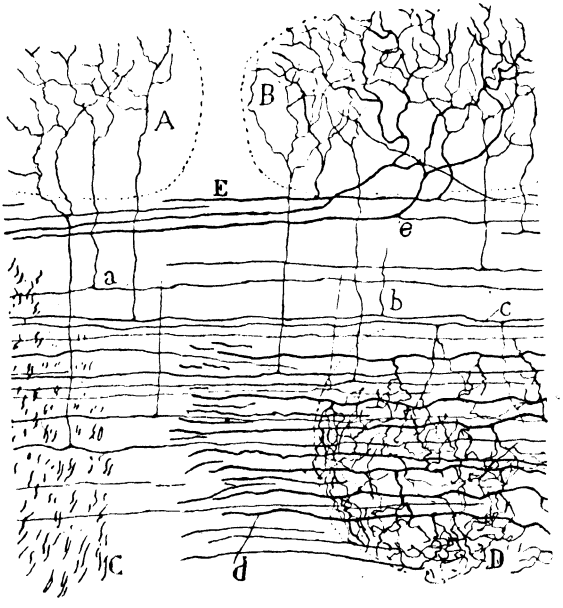


FIG. 218.—PART OF SAGITTAL SECTION OF THE MID-BRAIN OF A NEWLY BORN MOUSE. Golgi method. (Cajal.)

A, nucleus of fourth nerve; B, nucleus of third nerve; C, decussation of superior cerebellar peduncle; D, red nucleus; E, fibres of dorsal longitudinal bundle passing oculomotor nuclei; *a*, *b*, *c*, longitudinal fibres of formatio reticularis sending collaterals to nuclei of fourth and third nerves and to red nucleus; *d*, fibres of superior cerebellar peduncle passing to red nucleus; *e*, bifurcation of a fibre of the dorsal longitudinal bundle.

The *red nucleus* appears in sections of the region of the superior corpora quadrigemina as a nearly circular mass of grey matter with many longitudinal white fibres occupying the middle of the tegmentum on either side of the raphe (fig. 213). It is surrounded by a kind of capsule of white matter, and the fibres of the superior cerebellar peduncle of the opposite side are directly continued into it and partly end by forming arborisations and nests among its cells. It also receives collaterals from the ventral longitudinal bundle, from Gudden's bundle, and from the fillet. Some of its cells are large, have large Nissl granules, and give off many dendrons (see fig. 219, on right-hand side of cut). The axons pass across the raphe in the decussation of Forel and form the bundle of Monakow, which is traceable downwards into the spinal cord (prepyramidal tract). There are also other and smaller cells, some with short axons ending in the nucleus itself, and yet others sending their axons into the adjacent white matter of the tegmentum, in which they are conducted to the thalamus. Some

of the fibres of the superior cerebellar peduncle go direct to the thalamus, without being interrupted in the red nucleus.

Tracts of tegmentum.—In addition to more diffuse longitudinal fibres there are others which are collected into defined tracts. One such tract (*vestibulo-motor*) is the *dorsal* or *posterior longitudinal bundle*, which is seen in all sections of this part of the brain as a pyriform area of transversely cut fibres which lies on each side of the middle line between the grey matter underlying the aqueduct and the formatio reticularis (figs. 212, 213, *p.l.b.*). The fibres which constitute this bundle below have already been noticed (see p. 166 and fig. 181); traced upwards its fibres become related to the nuclei of the third and fourth nerves, to which it furnishes numerous collaterals and terminal ramifications (fig. 218, E), which form synapses with the cells of those nuclei. Below it forms similar connexions with the abducens nucleus and with the motor nuclei of the spinal cord; in the anterior column of the cord its fibres are intermingled with those of other tracts. The fibres take origin in the cells of Deiters' nucleus and of the reticular formation of the pons, medulla oblongata (see p. 142), and mid-brain (fig. 219, *e*), and also from certain large cells in the sensory nucleus of the fifth nerve. The dorsal longitudinal bundle is composed exclusively of large nerve-fibres, which acquire their myelin at an early stage—in fact, as soon as the roots of the nerves themselves. It appears to be developed in nearly all vertebrates, and in some is better marked than in mammals; in the lizard it can be traced as a separate bundle right down the cord, dorsal to the ventral commissure. After giving off fibres to the nucleus of the third nerve the bundle appears to be continued up as far as the posterior commissure. This continuation cerebralwards is, however, constituted differently from the bundle proper, for it consists of much finer fibres, which have a descending direction and which originate in a small nucleus—the so-called *nucleus of the dorsal longitudinal bundle*—which is found in the grey matter at the side of the posterior part of the third ventricle, a little in front of the termination of the aqueduct. Some of the fibres of the dorsal longitudinal bundle are said to be continued into the hypothalamus.

The dorsal longitudinal bundles come close together at the raphe, and fibres pass from one to the other. These have been supposed to be connecting fibres between the motor nuclei of opposite sides, which the bundles pass and supply with collaterals and terminals, but evidence for such direct connexion is wanting. The dorsal longitudinal bundle is very small in the mole (Forel), large in reptiles and amphibia (Spitzka).

Brachium conjunctivum or superior cerebellar peduncle.—Another tract of longitudinal and decussating fibres is derived from the superior peduncle of the cerebellum, which we have already traced as it passes forwards over the superior end of the fourth ventricle. Reaching the sides of the aqueduct as a well-marked bundle of semilunar shape in section (fig. 173), it gradually takes a more ventral position as it is traced upwards in the mesencephalon, and its fibres soon begin to pass across the raphe, decussating with those of the other side (fig. 210, A, and fig. 212, *s.c.p.*), the decussation extending as far upwards as the superior pair of corpora quadrigemina. Having crossed to the opposite side, the tract in question pursues its course longitudinally upwards, appearing at first as a round white bundle, but higher up losing itself in a circular tract of grey matter with numerous large pigmented cells, known as the *nucleus of the tegmentum* or *red nucleus* (fig. 210, B, and fig. 213, *r.n.*). Some fibres do not cross, but enter the red nucleus of the same side. Many of the fibres only give collaterals to the red nucleus, and are then continued to the thalamus. Before crossing, each fibre sends off a descending branch, which, according to

Cajal, passes downwards in the pons and medulla oblongata on the mesial side of the descending root of the fifth, giving off collaterals to the motor nuclei of the fifth, seventh, ninth, and tenth nerves and perhaps to the ventral horn of the cord. These fibres form Cajal's *descending cerebellar bundle* of the brachium conjunctivum, but the extent to which the branches pass downwards is doubtful. According to Van Gehuchten, the bifurcation of the fibres does not occur until the opposite side is reached.

A small bundle of fibres in the brachium conjunctivum has been described as taking origin in the thalamus and passing to the cerebellar hemisphere.

Ventral longitudinal bundle: tecto-spinal tract.—From each superior colliculus of the corpora quadrigemina a bundle of fibres passes on each side,

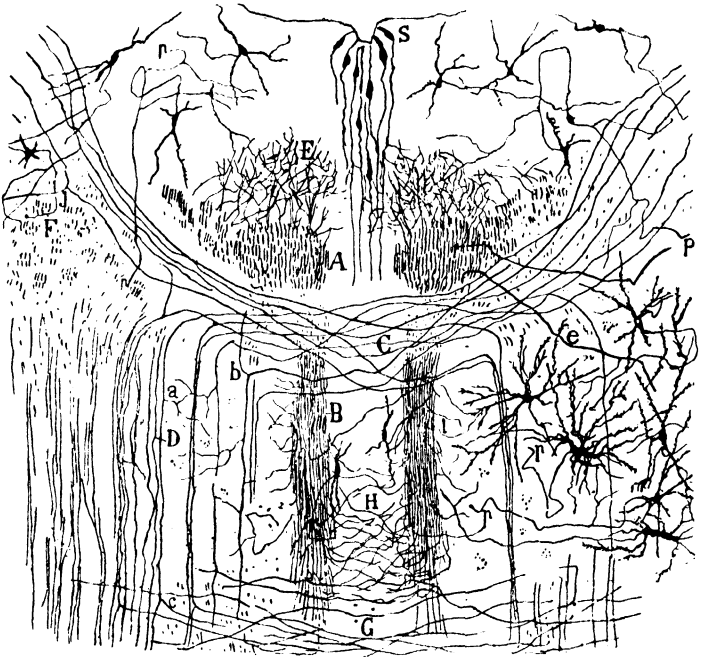


FIG. 219.—CORONAL SECTION, SOMEWHAT OBLIQUE, OF THE TEGMENTUM OF A NEWLY BORN MOUSE. Golgi method. (Cajal.)

A, dorsal longitudinal bundle; B, tegmental bundle of Gudden; C, Meynert's fountain-decussation, composed of fibres arising in the anterior corpora quadrigemina and passing into the ventral longitudinal bundle, D; *a*, collaterals of these fibres; *b*, a bifurcation; E, collaterals of the fibres of the dorsal longitudinal bundle in the oculomotor nucleus; F, longitudinal fibres of the tegmentum probably belonging to the main tract of the fillet; G, decussation of collaterals from the ventral longitudinal bundles; H, decussation of Forel, formed by the axons of cells of the red nucleus (some of its cells are seen on the right of the figure); *p*, axons of cells in the red nucleus and central grey matter; *e*, fibre passing from the tegmentum into the dorsal longitudinal bundle; S, ependyma-cells of the aqueduct.

sweeping round the central grey matter of the aqueduct close to the ventral part of the dorsal longitudinal bundle, and decussates with its fellow in the raphe, where the two bundles form the *fountain-decussation of Meynert* (fig. 219, C), to become longitudinal in the part of the tegmentum ventral to the dorsal longitudinal bundle. The fibres of this tecto-spinal tract pass partly through the red nucleus, giving off to it many collaterals, and then run downwards in the formatio reticularis of the mid-brain, pons, and medulla oblongata to reach the ventral column of the spinal cord, where its fibres are distributed to the ventral cornu. They are intermingled in the cord with those

of the dorsal longitudinal bundle, but some are said to pass down the lateral column (Boyce) along with those of the rubro-spinal tract.

Monakow's bundle: rubro-spinal tract.—This is formed of fibres derived from the cells of the red nucleus, which decussate in the raphe somewhat lower down than do those of the tecto-spinal tract, forming the *fountain-decussation of Forel* (fig. 219, H).[1] As they descend in the pons and medulla oblongata the bundles of Monakow tend to occupy a more lateral position, and in the cord they are seen in the lateral column as the *prepyramidal tract.*

The *central tract of the tegmentum* (Flechsig; Bechterew) is a collection of fibres which is said to take origin either in the thalamus or in the nucleus lenticularis, and which passes down almost in the centre of the tegmentum towards the pons and medulla oblongata. In the last-named it trends laterally, and is traceable to the neighbourhood of the olivary nucleus, in which its fibres are supposed to end.

Other descending tracts are the *bundle of Münzer*, the fibres of which take origin in cells of the inferior colliculi, and pass downwards in the tegmentum to reach the reticular formation of the pons near its lateral border; and the *fasciculus retroflexus* (Meynert) passing, mesially to the red nucleus, to end in the interpeduncular ganglion (fig. 216).

Tract of the fillet.—The fillet, which, in sections across the upper part of the pons, forms a considerable flattened bundle of longitudinal fibres at the ventral border of the formatio reticularis, is traceable upwards into the ventral part of the tegmentum of the mid-brain. Soon, however, the laterally situated part of this tract is seen to pass obliquely outwards and emerge at the side of the pedunculi cerebri, curving obliquely over the outer side of the prolongation of the cerebellar peduncle (fig. 210, A, *f*), and tending towards the inferior corpora quadrigemina. It is seen on the surface as a band of obliquely curved fibres, occupying a triangular area at the side of the tegmentum (fig. 212, *str.l.*), and it was to this band that the name of fillet (lemniscus) was originally applied by Reil. It is known as the *lower* or *lateral fillet* (see p. 159). It is covered externally by a thin layer of grey matter containing nerve-cells (*nucleus of the lateral fillet*).

The remaining fibres of the tract of the fillet take a different course, being continued upwards, at first in the ventral part, but subsequently in the dorso-lateral part of the tegmentum as the *upper* or *main fillet*; some of the fibres become lost in the tegmentum, and the rest are not traceable farther as a distinct bundle. But many fibres of this portion pass to the superior corpora quadrigemina, and others extend beyond the quadrigeminal region to the thalamic region (Flechsig). The lateral fillet is the continuation upwards of the central auditory path, mainly from the opposite cochlear nuclei, through the trapezium; the upper fillet is derived chiefly from the interolivary tract of the medulla oblongata—*i.e.* from the nucleus gracilis and nucleus cuneatus of the opposite side, reinforced by fibres from various sources (see p. 161 and fig. 175), and is the continuation of the sensory path of the posterior columns of the cord.

Lying on the mesial side of the upper fillet, and apparently forming a portion of the same tract, is a bundle of fibres which differ from those of the true fillet in having a descending course. They originate in cells of the thalamus, enter the crusta at its mesial part, leave this to join the fillet, and run down as far as the formatio reticularis of the medulla oblongata. They form a *thalamo-bulbar tract*, and were formerly known as the mesial fillet, a term which has also sometimes been applied to the main or upper fillet. More or less intermingled

[1] This is partly formed, however, by collaterals of Gudden's bundle (see p. 211).

with them are some fibres which are said to originate in the cortex cerebri and to leave the other fibres of the pyramid-tract in the crusta in order to enter this mesial part of the fillet and eventually to end in the formatio reticularis of the pons and medulla oblongata (*cortico-bulbar tract*).

The *central tract of the cerebral sensory nerves* and the *central tract of the sensory division of the fifth nerve* pass upwards in the tegmentum distinct from the bundles of the fillet proper, although these tracts are homologous with the tract of the fillet, and, like the upper fillet, have their endings in the thalamus.

The *ventro-lateral ascending bundle of Gowers* sends a number of its fibres upwards beyond the pons into the dorso-lateral part of the tegmentum. These are traceable as far as the superior corpora quadrigemina; a few pass to the hypothalamus: they probably form a part of the sensory or higher reflex path.

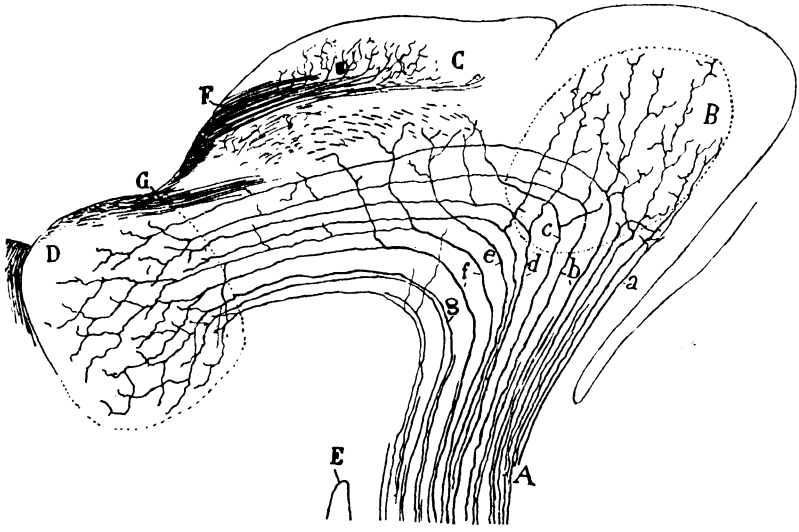


FIG. 220.—SAGITTAL SECTION, SEMI-DIAGRAMMATIC, OF THE LATERAL FILLET AND ITS UPPER TERMINATIONS IN THE MOUSE. Golgi method. (Cajal.)

A, lateral fillet; B, posterior colliculus; C, anterior colliculus; D, mesial geniculate body; E, bend above pons; F, optic fibres; *a*, fibres of lateral fillet passing to posterior colliculus; *b*, *c*, *d*, fibres giving collaterals to posterior colliculus and passing on to geniculate body; *e*, *f*, *g*, fibres giving off collaterals to anterior colliculus and passing on to geniculate body.

Transverse peduncular bundle.—This is a compact bundle of fibres, occurring only occasionally in man but fairly constant in most animals, which is seen emerging at the side of the mid-brain just anterior to the anterior colliculus and passing round the cerebral peduncle across the direction of its fibres, to reach the mesial border between the issuing fibres of the third nerve and the corpus mamillare. Here it takes a sagittal direction for a short distance and then dips into the interior, passing between the substantia nigra and the formatio reticularis of the tegmentum.

The bundle in question was first noticed by Gall and Spurzheim,[1] but more particularly described by Gudden,[2] who gave it the name of *tractus peduncularis transversus*, and found that it undergoes atrophy after enucleation of the eyes in the new-born rabbit and is absent in the mole. This fact, as well as the observation of Monakow that the tract in question also atrophies after removal of the cortical visual area, leads to the supposition that it is related to the secondary visual path. Nevertheless the origin and ending of its fibres are still obscure. According to Marburg,[3] it is to be regarded as an aberrant part of the optic tract, and its fibres take origin in the retina and are connected with a nucleus lateral to the corpus mamillare.

[1] Atlas du Système nerveux, 1810.
[2] Arch. f. Psychiatrie, ii. 1870. See also Kölliker, Gewebelehre, ii. 1896.
[3] Quoted by Edinger, Nervöse Zentral-organe, 1904.

According to Cajal,[1] the fibres of the tract, after dipping into the tegmentum, have numerous small nerve-cells interspersed among them. They cross the bundles of the upper or main fillet in the interior of the tegmentum and end in free arborisation in a nucleus outside and dorsal to the red nucleus.

The **inferior** or **posterior colliculi**[2] (*lower* or *posterior quadrigeminal bodies*) are composed almost entirely of grey substance, the so-called *nucleus* of these bodies (fig. 212, *c.q.p.*), which is covered by a *superficial white layer* and is separated by a thin layer of white matter from the central grey matter of the aqueduct (*deep white layer*). It contains numerous small and some larger nerve-cells. The superficial white layer is derived partly from the brachium, partly from fibres originating in the nucleus. The deep white layer is also derived

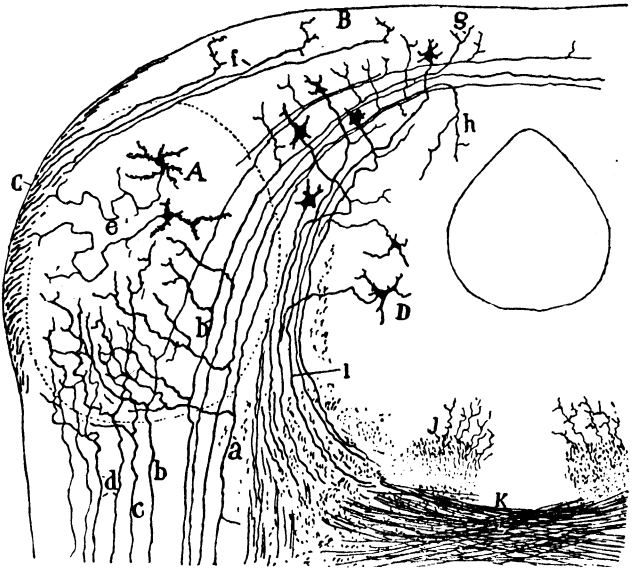


FIG. 221.—DIAGRAM SHOWING THE GENERAL STRUCTURE OF THE POSTERIOR CORPORA QUADRIGEMINA. (Cajal.

A, principal mass of grey matter; B, C, cortical layer; D, grey matter around Sylvian aqueduct; K, decussation of superior peduncles of cerebellum; *a*, *b*, *c*, *d*, fibres of central acoustic path from lateral fillet; *e*, axons from cells of principal nucleus passing towards brachium; *f*, fibres from brachium passing into superficial layer; *g*, fibres from fillet passing into superficial layer; *h*, a fibre of fillet passing to central grey matter of aqueduct; *j*, collaterals from dorsal longitudinal bundle passing to oculomotor nucleus; *l*, axons of cells in dorso-mesial part of colliculus curving round grey matter of aqueduct and forming the deep white layer.

in part from fibres originating in cells of the nucleus and in part from the fillet. Many of the fibres of the lateral fillet pass directly into the nucleus, where they end in terminal arborisations (fig. 221). Before entering they send off a branch to the mesial geniculate body. The destination of the axons of the cells of the grey nucleus is twofold. Some pass into the superficial white layer and appear to go towards the mesial geniculate body in the lower brachium; these lie for the most part in the lateral part of the nucleus. Others, mainly from large cells in the dorso-mesial part of the nucleus, pass into the deep white layer, and partly pass downwards in the tegmentum of the

[1] Sistema nervioso, ii. 1904.

[2] The term *nates* is often applied to the superior or anterior corpora quadrigemina, and *testes* to the inferior or posterior. These names were used by Vesalius, but are somewhat misleading, and have fallen into disuse.

same side, partly cross to the opposite side, and then take a descending direction. A few fibres of the deeper white layer pass over the roof of the aqueduct to attain the opposite side. The connexions of these have not yet been satisfactorily worked out, but they are believed to be closely related to the termination of the fibres of the lower fillet. The nuclei are united across the middle line by a commissural portion of grey matter which is bounded superficially and deeply by transverse white fibres derived from the fillet.

The connexion of the inferior colliculi with the lower or lateral fillet would appear to indicate a close connexion between these posterior or inferior quadrigeminal bodies and the auditory sense; and in conformity with this it is noticeable that it is only those animals (mammals) which have a well-developed spirally wound cochlea that show the inferior corpora quadrigemina as distinct prominences. In nearly all vertebrates below mammals there are merely corpora

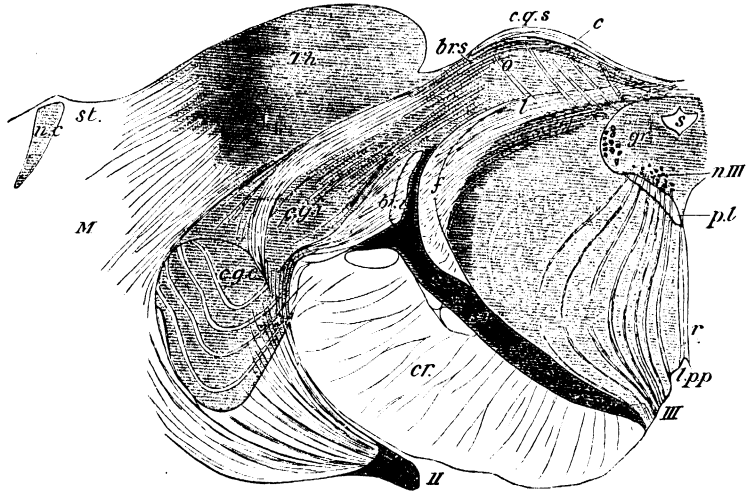


FIG. 222.—SECTION THROUGH THE UPPER PART OF ONE OF THE ANTERIOR CORPORA QUADRIGEMINA AND THE ADJACENT PART OF THE THALAMUS. (After Meynert.)

s, aqueduct; *gr*, grey matter of the aqueduct; *c.q.s*, quadrigeminal eminence, consisting of: *l*, stratum lemnisci; *o*, stratum opticum; and *c*, stratum cinereum; *Th*, thalamus (pulvinar); *c.g.i*, *c.g.e*, internal and external (mesial and lateral) geniculate bodies; *br.s*, *br.i*, superior and inferior brachia; *f*, fillet; *p.l*, posterior (dorsal) longitudinal bundle; *r*, raphe; *III*, third nerve; *nIII*, its nucleus; *l.p.p*, posterior perforated space; *s.n*, substantia nigra; above this is the tegmentum with its nucleus, the latter being indicated by the circular area; *cr*, crusta; *II*, optic tract; *M*, medullary centre of the hemisphere; *n.c*, nucleus caudatus; *st*, stria terminalis.

bigemina, and these seem mainly to represent the anterior pair of the quadrigemina of mammals. This anterior pair is chiefly connected with the optic nerves and therefore with the visual sense. It is atrophied in the mole, in which animal the posterior pair is well developed. And if one eye be removed in a new-born animal, the opposite superior colliculus and its brachium undergo arrest of development, whereas the inferior colliculi develop normally (Gudden).

The **superior** or **anterior colliculi** (*upper* or *anterior quadrigeminal bodies*) show externally and uppermost a thin layer of neuroglia, fine stellate glia-cells, and the ends of glia-fibres, which radiate from the central canal (aqueduct) towards the periphery. Excluding this neuroglia-layer, and also the central grey matter around the Sylvian aqueduct, four strata are distinguished in vertical sections (Tartuferi):

1. *Stratum zonale: superficial white layer.*—This is a relatively thin stratum of transversely coursing fine nerve-fibres, which are derived from the superior brachium (perhaps from the optic tract) and some, in the cat, from the cerebral cortex, through the pyramid-tract (see p. 209). Many of them dip down and lose themselves in the next layer, but some appear to be continued towards the middle line and to decussate with others over the central grey matter from the same stratum of the opposite side. Among the fibres of this layer are a few medium-sized and small cells, of fusiform or angular shape, disposed tangentially in the layer.

2. *Stratum cinereum: grey cap.*—A layer of grey matter, crescentic in section, of considerable thickness opposite the most prominent part of the tubercle, but thinning off at its margins. Its nerve-cells are numerous but vary in size, the smaller ones being near the stratum zonale, the larger in the deeper part of the layer. They are for the most part placed vertically, and send their

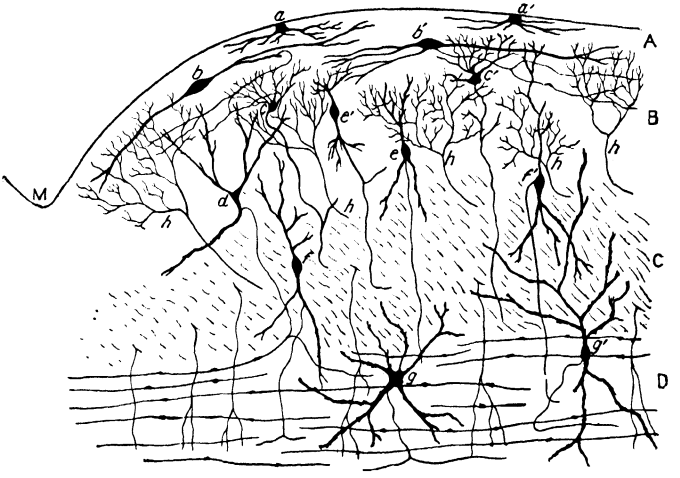


FIG. 223.—DIAGRAM SHOWING THE CHARACTERS OF THE CELLS IN THE GREY MATTER OF THE ANTERIOR CORPORA QUADRIGEMINA. (After Cajal.)

M, portion of dorsal median groove; *A*, superficial white layer; *B*, grey cap; *C*, optic-fibre layer (upper grey-white layer); *D*, layer of the fillet (lower grey-white layer).

a, *a'*, marginal nerve-cells: their axons are not represented; *b*, *b'*, horizontal spindle-shaped cells of Golgi's type ii.; *d*, small cells with much branched dendrons and an axon extending to the optic-fibre layer; *e*, *e'*, spindle and stellate cells of the grey cap; *f*, *f'*, cells of the stratum opticum, sending their axons into the stratum lemnisci; *g*, *g'*, cells of the stratum lemnisci; *h*, *h*, fibres of the optic-nerve layer ending in the grey and superficial white layers.

dendrons outwards—*i.e.* towards the stratum zonale—while their axons are directed inwards towards the deeper layers. The optic nerve-fibres from the next layer end among its cells (fig. 224).

3. *Stratum opticum: upper grey-white layer.*—The grey matter of this layer is largely interrupted by nerve-fibres from the optic tract, which enter by the superior brachium at the antero-lateral aspect and run obliquely upwards and forwards. The layer may be subdivided into (α) a dorsal zone of coarse fibres, (β) an intermediate zone of fine fibres, and (γ) a central zone containing much grey matter interspersed with bundles of white fibres.

These are described by Ganser as three distinct layers, and termed the third or superficial medullated layer, the fourth or middle medullated, and the fifth or middle grey layer; whil the fourth layer of Tartuferi, immediately to be mentioned, becomes the sixth and seventh of Ganser.

The optic fibres turn up dorsally into the grey cap and there end in terminal arborisations. The whole stratum is richly beset with large nerve-cells, which send their axis-cylinder processes mostly into the next or fourth stratum, and from this the fibres sweep round the ventral aspect of the central grey matter (fountain-decussation of Meynert) to form the opposite ventral longitudinal bundles. Of the nerve-fibres, those of the intermediate zone (β) are, according to Tartuferi, retinal fibres; those of the central zone (γ) are probably derived from the corona radiata of the occipital region of the brain; while the coarse fibres of the dorsal zone (α) are perhaps derived from the opposite side.

4. *Stratum lemnisci: deep grey-white layer.*—This, although composed of grey matter, is also occupied by many transversely coursing nerve-fibres which are derived from the upper fillet, and probably end in the layer. Some of the fibres, however, are, as just stated, derived from the large cells of the fourth layer, and others from the nerve-cells of the stratum itself, which contains many cells of large size, the axons of which pass for the most part

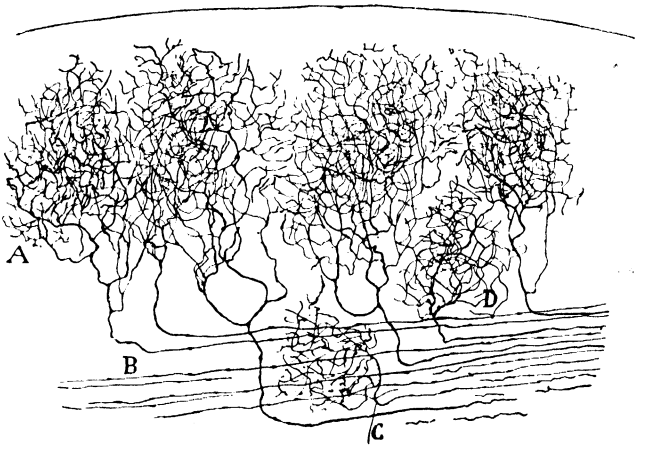


FIG. 224.—TERMINAL ARBORISATIONS OF OPTIC FIBRES IN THE ANTERIOR COLLICULUS OF A TWENTY-DAY-OLD MOUSE: SAGITTAL SECTION. Golgi method. (Cajal.)
A, more superficial arborisations of optic fibres, B; C, D, deeper arborisations.

across the middle line, decussating with those of the opposite side as arcuate fibres in the raphe and forming the fountain-decussation of Meynert (fig. 219). Some may pass downwards in the tegmentum of the same side. As was shown by Redlich and Probst, they are continued down in the *ventral longitudinal bundle* into the medulla oblongata and ventral column of the spinal cord. It is possible that some of the fibres are derived (over the aqueduct) from the opposite side. Part of the ventro-lateral ascending bundle of the spinal cord passes into this layer. Ganser subdivides the layer into two, which he terms respectively the deep white (sixth) and the deep grey (seventh) layers.

No fibres pass to the cerebral cortex from the colliculi.

Structure of the optic lobes of birds.—All who have specially worked at this subject distinguish more strata in the optic lobes of birds than in the corresponding bodies of mammals. Thus Bellonci makes the number of layers (exclusive of the central grey matter of the aqueduct) nine, Stieda twelve, whilst Cajal distinguishes as many as fourteen strata (fig. 225). Of these the most superficial (fig. 226) is a layer of thick medullated fibres coming directly through the optic tract and chiasma from the retina of the opposite side. (In birds all the optic nerve-fibres cross

at the chiasma.) They pass in from the side (so that they are cut across in a sagittal section, fig. 225), and after a variable course turn downwards into the deeper layers, where they end at four different levels (as far as the seventh layer) in terminal arborisations. Of these terminal ramifications, that in the seventh layer is flattened horizontally, the others are more extended vertically

FIG. 225.—SAGITTAL SECTION OF OPTIC LOBE OF BIRD. Golgi method. (Cajal.)

a, optic fibres cut across; *b*, stellate cell of second layer; *c*, fusiform horizontal cell of third layer; *d*, vertical cell of third layer with axon passing into eighth layer; *e*, large horizontal cell of fourth layer; *f*, *g*, *h*, cells of fourth layer with axons ramifying in the eighth and ninth layers; *i*, cell of fourth layer with axon passing to deep nerve-fibre layer; *j*, vertical cells with long ascending dendron giving off an axon at *z* which passes to optic layer and sends collaterals at *k* into seventh layer; *m*, similar cells, but with recurrent axons passing to deep nerve-fibre layer; *n*, a pyramidal projection-cell; *o*, *p*, *q*, *r*, cells of the deeper layers with axons passing into deep nerve-fibre layer, *s*.

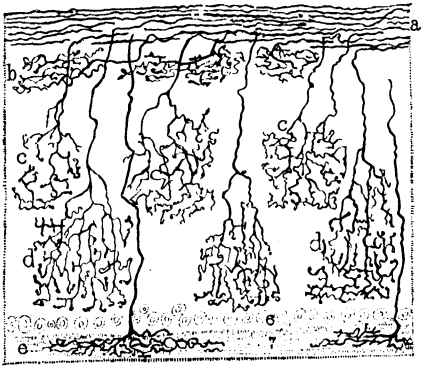


FIG. 226.—TRANSVERSE SECTION OF OPTIC LOBE OF BIRD. Golgi method. (Cajal.)

The superficial part only is represented, as far as the seventh layer.

a, optic fibres; *b*, their arborisation in the second layer; *c*, that in the fourth layer; *d*, that in the fifth layer; *e*, that in the seventh layer.

(fig. 226). Some of these terminal arborisations end in a special circumscribed part of the lobe, which is known as the *ganglion of the roof*. This contains a large number of nerve-cells, the dendrons of which interlace with the optic arborisations, while their nerve-fibre processes are directed towards the deeper layers of the lobe. All the layers below the first contain nerve-cells, as well as nerve-fibres, but the seventh is mainly composed of the expanded ramifications of the optic fibres just mentioned, and of similar expansions of the superficially directed nerve-fibre processes of cells from the tenth layer (fig. 225, *j*, *j*). The cells vary in size and shape in the different layers, but on the whole they are smallest nearer the surface and largest in the deeper layers (tenth to thirteenth). With the exception of the cells of the tenth layer just mentioned, the cells send their axis-cylinder processes downwards to pass away as nerve-fibres of the fourteenth layer, which is chiefly formed of large medullated nerve-fibres, although some nerve-cells are even here interspersed. But some of the smaller cells of the more superficial layers (fig. 225, *d*) belong to Golgi's second type of nerve-cell—*i.e.* their axis-cylinder processes do not pass into nerve-fibres, but break up into a terminal arborisation a short distance from the cell, and interlace among the cells of some of the other layers. The third, fifth, seventh, and ninth layers all have relatively few cells and a molecular aspect, due apparently to the fine arborisations of the nerve-fibre or axis-cylinder processes which they contain. The protoplasmic processes of the cells are, some of them, very long, and when coursing vertically often extend as far as the layer of optic

fibres on the one hand, and the deep medullary layer on the other. The axis-cylinder processes sometimes come off from the dendrons, sometimes from the body of the cell. Of the fibres which form the deepest layer, although many, as just stated, are derived from the cells of the optic lobe, and are therefore passing away by that layer, some have a contrary direction and are passing *into* the grey matter, where they end in extensive ramifications extending as far towards the surface as the sixth layer.

The fibres of the deep medulla, on leaving the optic lobe, partly encircle, partly traverse, four groups of nerve-cells, which are known as the *optic ganglia*. It is possible that these in part represent the external or lateral geniculate body of mammals. The fibres give off collaterals, which end in ramifications among the cells of these ganglia; some of the fibres appear altogether to terminate in this way.

DIENCEPHALON, THALAMENCEPHALON, OR INTER-BRAIN.

Under this head are included the cavity of the third ventricle and the structures forming its walls. Although a small part of the third ventricle in front and certain structures bounding it in this situation ought, strictly speaking, to be regarded as belonging to the telencephalon, they will be more conveniently considered here.

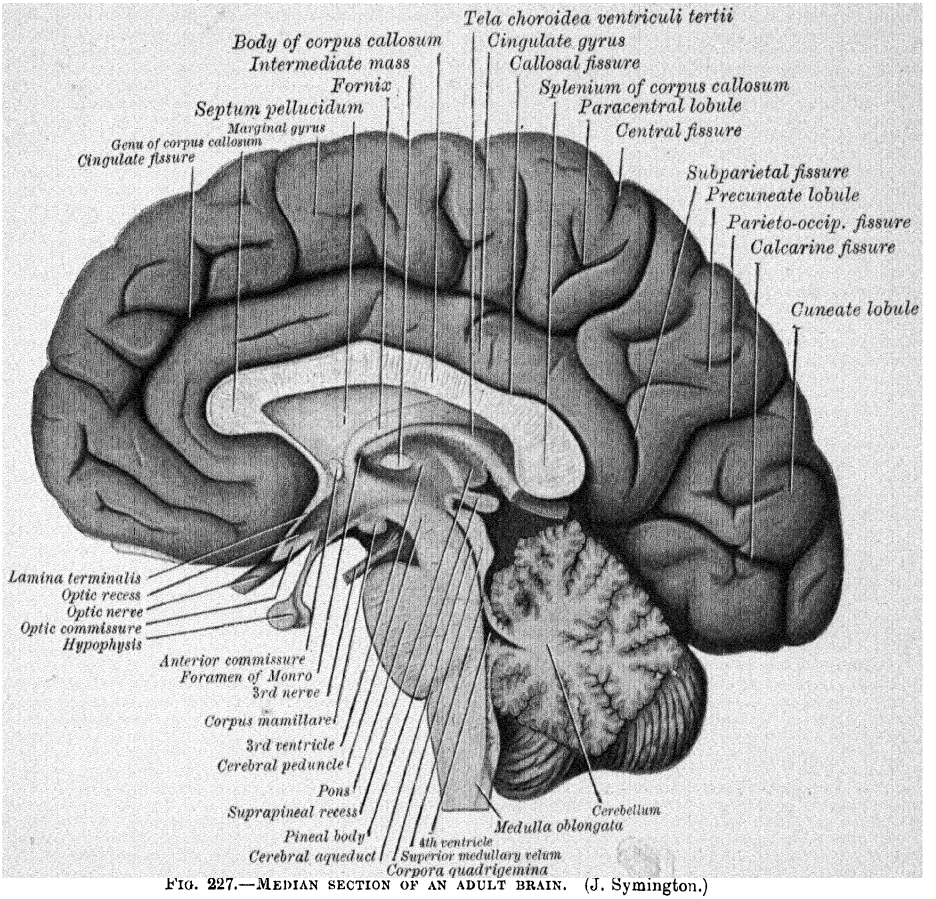


FIG. 227.—MEDIAN SECTION OF AN ADULT BRAIN. (J. Symington.)

The **third ventricle** is a narrow median cleft which communicates posteriorly with the cerebral or Sylvian aqueduct, and at its anterior and upper part with the lateral ventricles by the interventricular foramina (*foramina of Monro*). It is prolonged downwards and forwards into a gradually narrowing recess, which becomes divided below into two by the projection towards the cavity of the optic commissure. Each lateral wall is marked by a shallow groove (*sulcus of Monro*, *sulcus limitans* of His) extending from the Sylvian aqueduct to the foramen of Monro, and indicating the direction of the main axis of this part of the neural tube.

According to Kupffer, this axis is prolonged forwards into a small recess, between the columns of the fornix and immediately above the anterior commissure, which represents the anterior pole of the neural axis. His, on the other hand, considers that the axis turns downwards and forwards to end in the optic recess, while others maintain that the cephalic end of the neural tube is at the infundibulum.

Along the upper curved margin of the lateral wall, from the column of the fornix to the pineal body, runs a white stria, known as the *stria medullaris* or *stria pinealis*. A little above the *sulcus of Monro* the lateral walls of the ventricle are united by a connecting band of grey matter of variable extent, termed the *intermediate mass* (middle commissure) (fig. 228; fig. 229, *m.c.*). This

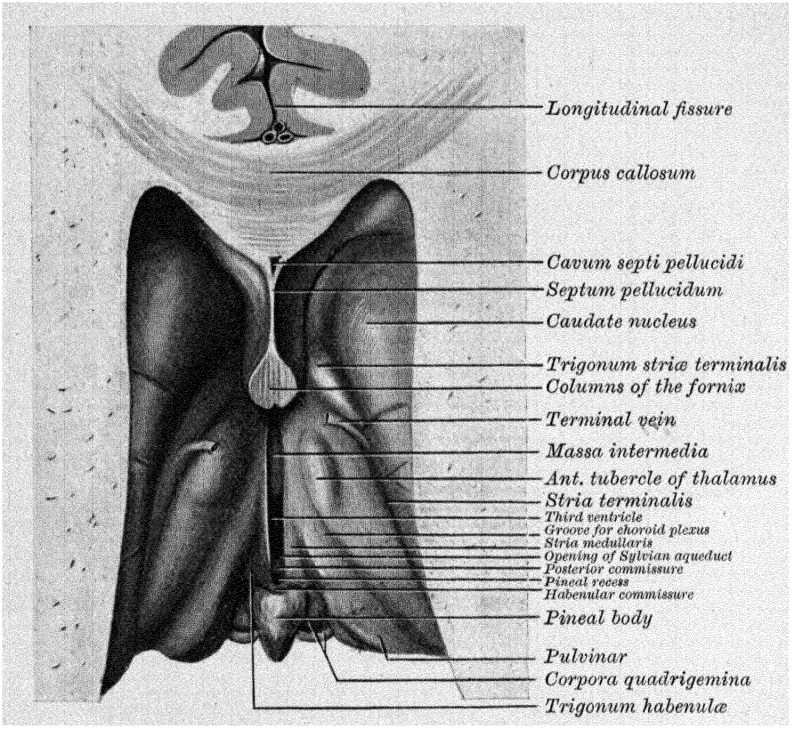


FIG. 228.—VIEW OF THE CAUDATE NUCLEI, THALAMI, THIRD VENTRICLE, ETC., FROM ABOVE. Natural size. (J. Symington.)

is sometimes double and occasionally wanting: it is liable to be torn across in removing the brain.

Each lateral wall is formed above the sulcus of Monro by the corresponding *thalamus* and below the sulcus by the *hypothalamus*. The *floor* of the third ventricle is very narrow, being represented by a groove which is the morphological equivalent of the median sulcus on the anterior wall of the fourth ventricle. Traced from behind forwards, this groove will be found to lie between the diverging cerebral peduncles, and then on the thin lamina uniting the *corpora mamillaria*; beyond this it sinks into the *recess of the infundibulum* and, passing forwards over the eminence caused by the *optic commissure*, it ends in the *optic recess*. This recess is expanded transversely for about 2 mm. on each side of the median plane and is the widest part of the floor. The *roof* is also narrow and

consists of a layer of ependyma lined by ciliated cells which extend from one *stria medullaris* to the other on the under surface of the median portion of the *tela choroidea*. At the striæ medullares the cells become continuous with those lining the lateral walls of the ventricle. The vessels of the *tela choroidea*, which project downwards into the third ventricle and form its choroid plexuses, are likewise covered by these cells, which also line a recess projecting backwards above the pineal body, and hence termed the *suprapineal recess*. Between this recess and the opening of the Sylvian aqueduct are the *habenular commissure*, the *pineal recess*, and the *posterior commissure*. The *anterior wall* contains the *columns of the fornix*, the *anterior commissure*, and the *lamina terminalis*, all of which are derived from the telencephalon.

The **thalami** (figs. 228 to 230) are two large masses of grey matter situated in the dorsal portion of the lateral walls of the third ventricle, or ventricle of the diencephalon: hence this division of the brain is also termed the thalamencephalon. Each thalamus is of an irregular oval form with the smaller end

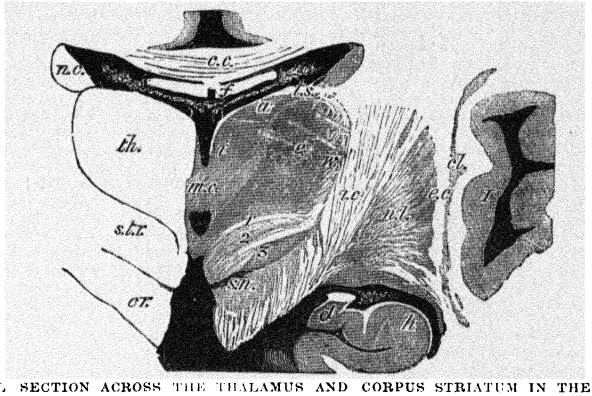


FIG. 229.—CORONAL SECTION ACROSS THE THALAMUS AND CORPUS STRIATUM IN THE REGION OF THE MASSA INTERMEDIA. Natural size. (From a preparation by S. G. Shattock.)

th, thalamus; *a*, *e*, *i*, its anterior, external, and internal nuclei respectively; *w*, its latticed layer; *m.c.*, massa intermedia; above and below it is the cavity of the third ventricle; *c.c.*, corpus callosum; *f*, fornix, separated from the third ventricle and thalamus by the tela choroidea. In the middle of this are the two veins of Galen and the choroid plexuses of the third ventricle; and at its edges the choroid plexuses of the lateral ventricles; *t.s.*, stria terminalis; *cr.*, forward prolongation of the crusta passing laterally into the internal capsule, *i.c.*; *s.t.r.*, subthalamic prolongation of the tegmentum, consisting of (1) the dorsal layer, (2) the zona incerta, and (3) the nucleus of Luys; *s.n.*, substantia nigra; *n.c.*, nucleus caudatus of the corpus striatum; *n.l.*, nucleus lenticularis; *e.c.*, external capsule; *cl.*, claustrum; *I*, insula.

directed forwards and inwards. Its length, measured from before backwards and outwards, is nearly 1½ inch (35 mm.), its greatest transverse diameter is about ¾ inch (18 mm.), and its vertical extent a trifle more than its transverse. It has four surfaces—superior, inferior, external, and internal; and two extremities, of which the anterior is narrow and the posterior broad and prominent. The *upper* or *dorsal surface*, as seen after the removal of the corpus callosum, fornix, and tela choroidea with its choroid plexus, is a large oval-shaped mass of grey substance covered by a thin stratum of white fibres. It is marked by a shallow longitudinal groove (see fig. 228), which inclines inwards as it passes forwards and terminates a short distance behind and internal to the anterior extremity of the surface. This extremity is raised into a prominence termed the *anterior tubercle* (fig. 228), and, together with the part of the upper surface which is placed outside the groove just described, appears in the floor of the ventricle of the corresponding hemisphere, and is covered by the lining epithelium of that cavity

(*lamina affixa* of the fornix; Hochstetter). This part of the upper surface is limited externally by a white band, the *stria terminalis*, which separates it from the *nucleus caudatus*. The longitudinal groove above mentioned corresponds with the margin of the fornix and is covered by the *choroid plexus*. The part of the upper surface internal to and behind the groove does not appear in either the third or the lateral ventricle, and is therefore not covered with epithelium. It is limited internally in about the anterior half of its extent by a sharp edge which separates it from the mesial surface, and which is marked by the white stria before noticed (*stria medullaris*, fig. 228), connected behind with the *pineal body*. It is along this stria, which is surmounted by a ridge-like extension of ependymal tissue, that the thin epithelium roofing the third ventricle is attached laterally; this epithelium always comes away when the *tela choroidea* is removed. Behind this the inner border is free and rounded, and inclines backwards and outwards to join the posterior projecting extremity of the thalamus (*posterior tubercle* or *pulvinar*). Just external to the posterior part of the stria medullaris is a small triangular area separated posteriorly from the mesencephalon by a transverse groove and bounded externally by the *sulcus habenulæ*. This triangular area is termed the *trigonum habenulæ* and contains a small collection of nerve-cells (*ganglion habenulæ*). The upper surface of the thalamus is convex, and towards its inner and posterior borders slopes distinctly downwards. The mesial surface of the thalamus is situated at the side of the third ventricle; it is covered with epithelium and is joined with the opposite thalamus by the massa intermedia. The posterior rounded surface is occupied almost entirely by the pulvinar. Below and external to this is the external geniculate body, and a little farther inwards the internal geniculate body, which is overlapped by the pulvinar. The *lateral and ventral surfaces* of the thalamus are continuous with other parts of the brain. The ventral surface is united with a prolongation of the tegmental part of the pedunculi cerebri (*hypothalamus*); and more anteriorly the corpus mamillare and the side of the tuber cinereum lie below it. The lateral surface is in contact with and is bounded by the cerebral peduncle, which is passing out of the white centre of the hemisphere between the thalamus and the lenticular nucleus as a thick band of fibres known as the *internal capsule*.

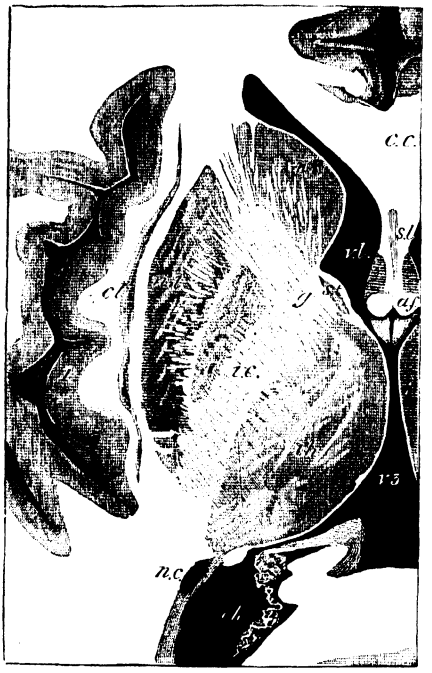


FIG. 230.—HORIZONTAL SECTION THROUGH PART OF THE CEREBRAL HEMISPHERE. Natural size. (From a preparation by S. G. Shattock.)

The section is viewed from below. *v.l.*, lateral ventricle, anterior cornu; *c.c.*, corpus callosum; *s.l.*, septum pellucidum; *a.f.*, columns of the fornix; *v3*, third ventricle; *th*, thalamus; *s.t*, stria terminalis; *n.c.*, nucleus caudatus, and *n.l*, nucleus lenticularis of the corpus striatum; *i.c.*, internal capsule; *g*, its angle or genu; *n.c.*, tail of the nucleus caudatus appearing in the inferior cornu of the lateral ventricle; *cl*, claustrum; *I*, insula.

The **posterior commissure** is composed of fibres which cross the posterior wall of the third ventricle immediately above the upper opening of the Sylvian

aqueduct and below the recess of the pineal body. In a sagittal section this commissure has the form of a folded lamina (fig. 177, p. 163). According to Cajal its fibres are derived from cells in the anterior corpora quadrigemina, many of them being branches of bifurcated axons; the one branch passing across in the commissure, the other passing downwards outside the central grey matter past the nucleus of Darkschewitsch, sending collaterals to the grey matter of the anterior colliculus (fig. 231). Edinger, on the other hand, states that the fibres arise partly in a nucleus in the caudal part of the thalamus, but chiefly from a nucleus common to the posterior commissure and the dorsal longitudinal bundle, and that after crossing in the commissure the fibres dip

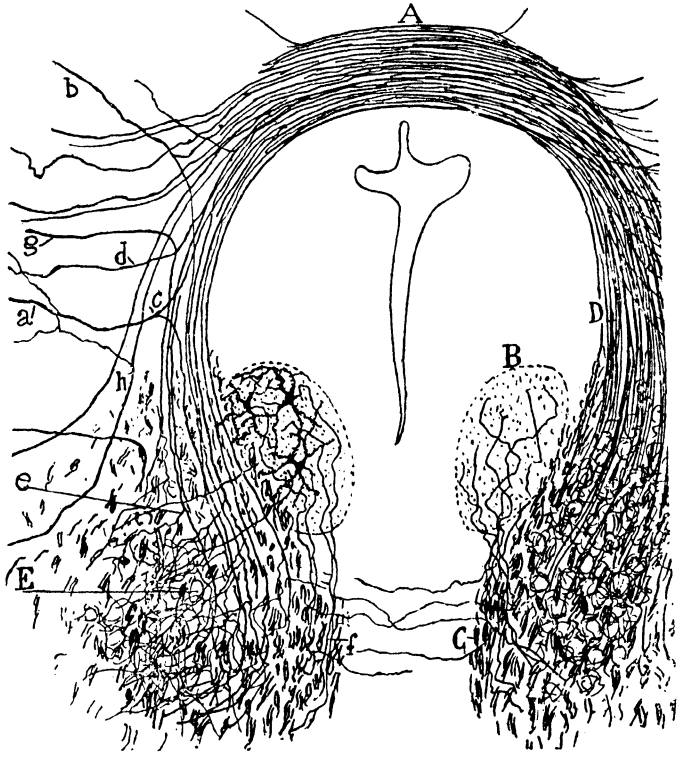


FIG. 231.—CORONAL SECTION OF POSTERIOR COMMISSURE OF EIGHT-DAY KITTEN. (Cajal.)

A, posterior commissure; B, nucleus of Darkschewitsch; C, remainder of dorsal longitudinal bundle; D, fibres of commissure curving round central grey matter; E, interstitial nucleus; *a*, *b*, *c*, *d*, fibres passing into the commissure; *e*, collaterals passing to interstitial nucleus; *f*, axons of cells of nucleus of Darkschewitsch; *g*, a fibre passing down to interstitial nucleus; *h*, a collateral to the anterior colliculus.

down into the tegmentum, in which they are continued to the medulla oblongata. In all vertebrates the fibres of the posterior commissure are among the first to be medullated.

Commissure of the habenula.—This, although frequently regarded as a part of the posterior commissure, is an independent and very constant band of commissural fibres, found throughout the vertebrate series, and generally known in comparative anatomy as the *superior commissure*. It is smaller than the posterior commissure, and consists mainly of fibres connecting the two ganglia

habenulæ, but some after decussating in the median plane turn backwards into the pineal body.[1]

Other commissural fibres of the thalamic region are the *posterior thalamic decussation* behind the mamillary bodies, which, according to Dejerine, is probably connected with the corpora Luysii; and the *commissure of Meynert*, which lies just over the chiasma and may perhaps unite the two sides of the supra-optic nucleus.

The **pineal body** (*epiphysis cerebri*, *conarium*) (figs. 132, 136, 232) is a small reddish body of a flattened oval form, with the smaller end directed downwards and backwards. In its long diameter it measures 7 mm. to 10 mm., and in its transverse 5 mm. to 7 mm. It is attached at its base to the posterior and habenular commissures. Its superior surface is closely attached to the pia mater, where this membrane passes forwards below the splenium of the corpus callosum to form the *tela choroidea* of the third ventricle. Its inferior surface

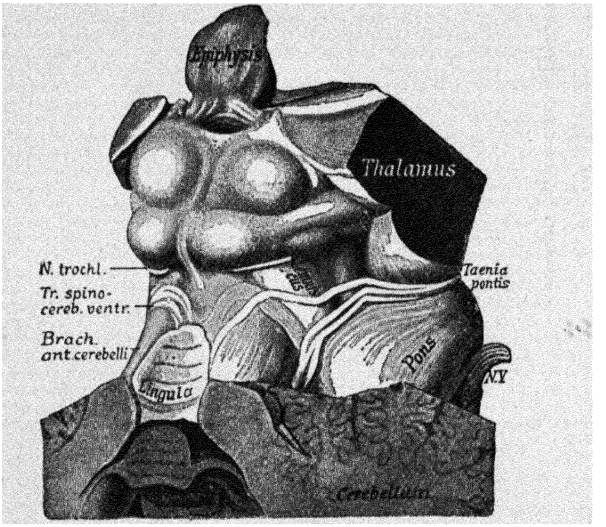


FIG. 232.—THE CORPORA QUADRIGEMINA AND NEIGHBOURING PARTS OF THE BRAIN. (Edinger from G. Retzius.)

Brach. ant. cerebelli, the superior cerebellar peduncles, between them the superior medullary velum partly covered by the lingula; *Tr. spino-cereb. ventr.*, ventral spino-cerebellar tract curving round the peduncle; *Lemniscus*, the lateral fillet; *N. trochl.*, fourth nerve; *N.V.*, fifth nerve.

rests in the hollow between the superior colliculi of the corpora quadrigemina. Owing to its slender connexion with the brain, it is very liable to be torn away in removing the pia mater. The base of the pineal body has a small depression, continuous in front with the cavity of the third ventricle, and leading backwards a short distance into the substance of the pineal body. This *pineal recess* is separated below from the upper opening of the Sylvian aqueduct by the posterior commissure, and is bounded above by the commissure of the habenula. Above the latter commissure is another recess of the ventricle (*suprapineal recess*). The stalk of white fibres on either side of the pineal recess is termed *pedunculus conarii*; it broadens out in front into the trigonum habenulæ.

The pineal body is composed of a number of hollow follicles, spherical or tubular, lined and almost filled with epithelium, and separated by vascular connective tissue. It receives sympathetic nerve-fibres, which are probably destined

[1] Cameron, 'On the Presence and Significance of the Superior Commissure throughout the Vertebrata,' Journ. Anat. and Phys. xxxviii. April 1904.

for the blood-vessels. There are no recognisable nerve-cells or neuroglia-cells. The pineal body contains calcareous matter (*brain-sand*) composed of microscopic particles aggregated into masses, and formed of earthy salts (phosphate and carbonate of lime, with a little phosphate of magnesia and ammonia) combined with animal matter.

The same calcareous matter is frequently found on the outside of the pineal body, or deposited upon its peduncles. It is found also in the choroid plexuses,

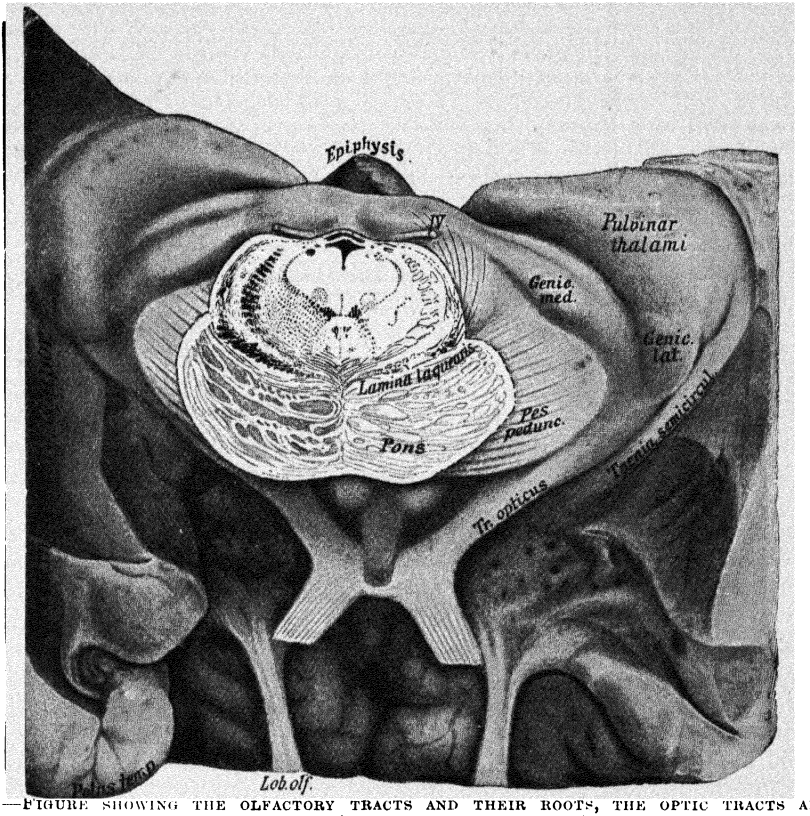


FIG. 233.—FIGURE SHOWING THE OLFACTORY TRACTS AND THEIR ROOTS, THE OPTIC TRACTS AND CHIASMA, AND PARTS OF THE THALAMUS (GENICULATE BODIES, ETC.) FROM THE VENTRAL AND POSTERIOR ASPECT. (Edinger.)

The pons is cut across at its upper part. Its section shows the aqueduct, the fillet (lamina laquearis), superior cerebellar peduncles, fourth nerve, etc. The corpora mamillaria are partly concealed by the pons; between these and the chiasma is seen the tuber cinereum with the infundibulum.

and in a scattered form in other parts of the membranes of the brain. It occurs at all ages, frequently in young children and sometimes even in the fœtus. It cannot therefore be regarded as the product of disease. The pineal body is larger in the child and the female than in the adult male (Huschke). In the brains of other mammals it is proportionately larger than in the human subject, and less loaded with brain-sand.

The pineal body is developed originally as a hollow outgrowth from that part of the embryonic brain which afterwards forms the third ventricle; the diverticulum becomes subsequently cut off from the ventricle, and undergoes ramification to form tubes which are afterwards separated for the most part into isolated vesicles.

The pineal body is present in all vertebrates, Amphioxus only excepted. In elasmobranch fishes and in most reptiles, as the researches of de Graaf, Baldwin Spencer, and others have shown, it is continued into a long tubular prolongation from the third ventricle, which passes through an aperture in the skull (parietal foramen) and ends under the skin in a small vesicle lined with ciliated epithelium. In some reptiles (*e.g.* Hatteria, blind-worm, lizard) this vesicle becomes developed into a structure which bears a close resemblance to an invertebrate eye (*pineal eye*), the part nearest the surface being thickened to form a kind of lens, and the part connected with the stalk being pigmented and stratified like a retina, while the stalk itself becomes solid and has nerve-fibres developed in it. It is doubtful how far this structure serves as an eye in any living reptile, but in certain extinct forms it was probably more completely developed. In birds and mammals the pineal eye is not developed, but the organ is similar in structure to that of man. In lower vertebrates the pineal body arises in the form of two lateral recesses, and, according to Dendy,[1] 'the ancestors of vertebrates must have possessed a pair of parietal eyes which may have been serially homologous with the ordinary vertebrate eyes.'

Paraphysis.—C. S. Minot[2] distinguishes six structures in the roof of the diencephalon—viz. from before backwards, paraphysal arch, velum transversum, postvelar arch, superior commissure, epiphysis, and posterior commissure. The velum transversum forms the tela choroidea of the third ventricle, and in front of the velum a glandular organ—the paraphysis—is developed. It is present in most vertebrates, but it has not yet been demonstrated in placental mammals.

Interpeduncular or optico-peduncular space.—This is a lozenge-shaped area at the base of the brain bounded behind by the median part of the upper border of the pons and the diverging cerebral peduncles, and in front by the optic commissure and by the optic tracts, as these pass outwards and backwards to reach the cerebral peduncles (fig. 233). Within this area are situated the *fossa interpeduncularis*, the *corpora mamillaria*, and the *tuber cinereum* with its prolongation—the *infundibulum*—to the posterior lobe of the *hypophysis*. The median portion of this space corresponds to the floor of the third ventricle.

The fossa interpeduncularis (locus perforatus posticus) lies in a deep fossa (*fossa Tarini*, His) at the base of the brain, at the bottom of which is greyish matter, connecting the diverging peduncles. It is perforated by numerous small openings for the passage of blood-vessels; and some horizontal white striæ usually pass out of the grey matter and turn round the peduncles close to the upper border of the pons, into which they enter, passing eventually into the cerebellar hemisphere (*tænia pontis*) (p. 158). The fossa corresponds posteriorly, as far as a line joining the anterior borders of the third nerves, to the floor of the aqueduct of Sylvius, but in front of those nerves to the posterior part of the floor of the third ventricle. In the grey matter is the collection of cells known as the interpeduncular ganglion (p. 210).

The **corpora mamillaria** (fig. 233; they are shown in section in fig. 135) are two round white eminences in front of this fossa, each about the size of a small pea, connected together across the middle line. They lie close together, and the limits of each are well defined except on the outer side where the eminence is prolonged outwards into a more or less distinct *brachium corporis mamillaris* (Retzius). Sometimes the brachium is replaced by a small elevation like a diminutive corpus mamillare.

Each corpus mamillare contains grey matter concealed within its superficial white fibres, the nerve-cells being arranged in two groups, the *lateral* and *mesial nuclei*; of these the lateral contains larger nerve-cells than the mesial. The white matter of the corpora mamillaria is formed by the columns of the fornix (hence the corpora mamillaria have also been named *bulbs of the fornix*), and by the bundle of Vicq d'Azyr, which leaves the anterior part of each tubercle at the dorso-mesial aspect (fig. 234). Posteriorly each corpus mamillare gives off a bundle of nerve-fibres which is termed its *peduncle*. This,

[1] Quar. Journ. Mic. Science, 1899, p. 111.
[2] 'On the Morphology of the Pineal Region,' Amer. Journ. Anat. vol. i. No 1.

which in man is concealed within the grey matter of the floor of the third ventricle, but which is seen at the base of the brain in many animals, and is connected with the lateral nucleus of the mamillary body, is traceable to the tegmentum (Gudden). The fibres which pass to the corpus mamillare through the columns of the fornix arise from cells of the hippocampus. Some of them, according to Edinger, are derived directly from the olfactory tract. The cells of the mamillary body give off axons which bifurcate within the grey matter (fig. 234, A). One branch, the coarser (*f*), turns dorsalwards and becomes one of the fibres of the bundle of Vicq d'Azyr, which enters the dorsal part of the thalamus; the other and finer branch (*g*) turns caudalwards

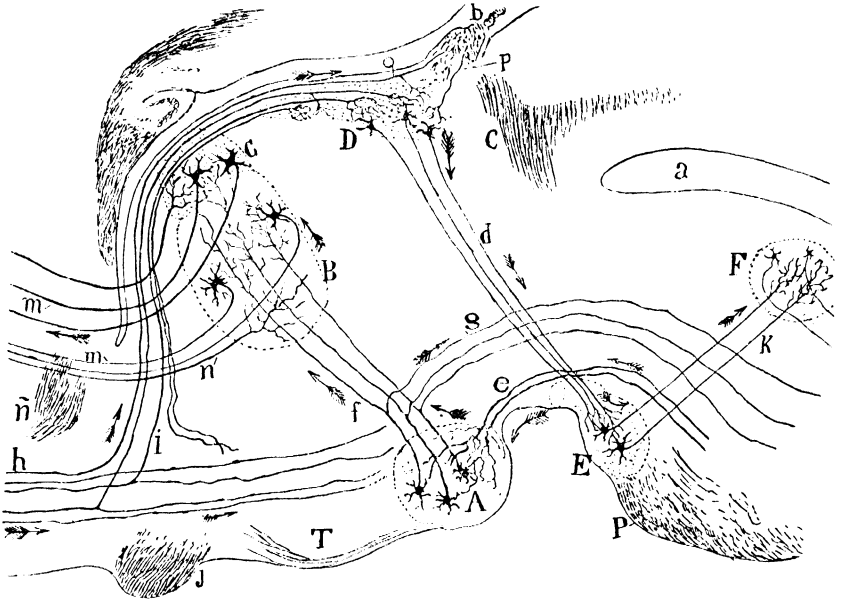


FIG. 234.—DIAGRAM SHOWING THE RELATIONS OF THE MAMILLARY APPARATUS, THE GANGLION OF THE HABENULA, AND THE DORSAL THALAMIC NUCLEUS. (Cajal.)

A, mesial mamillary nucleus; B, dorsal nucleus of thalamus; G, its upper segment; D, ganglion of habenula; E, interpeduncular ganglion; F, dorsal tegmental nucleus; K, fibres of Gudden's ventro-dorsal tegmental bundle (p. 211) passing from interpeduncular ganglion to dorsal nucleus; J, chiasma; P, pons; C, posterior commissure; T, tuber cinereum; *a*, aqueduct; *b*, interhabenular commissure; *d*, fasciculus retroflexus of Meynert (p. 210); *e*, fibres of mamillary peduncle; *f*, bundle of Vicq d'Azyr; *g*, bundle from mamillary body to tegmentum (Gudden); *h*, olfactory projection-fibres; *i*, branches passing to stria medullaris; *m*, thalamo-cortical fibres; *n*, cortico-thalamic fibres; *ñ*, anterior commissure; *o*, fibre of stria medullaris passing to habenular commissure; *p*, fibre from opposite stria medullaris ramifying in habenular ganglion.

and becomes a fibre of the mamillo-tegmental bundle of Gudden. In most vertebrates there is one (median) corpus mamillare in place of the two of mammals.

Nuclei of the mamillary body.—Two nuclei are recognisable in the interior—one the *mesial*, the larger, and the other the *lateral*, crescentic in shape, closely applied to it, and much smaller. Above and in front of the mesial nucleus is a thin layer of grey matter which is termed by Cajal the *limiting nucleus*.

The cells of the *mesial nucleus* are small and without Nissl granules; those of the lateral nucleus are larger and rich in chromatin-granules. The axons from both nuclei pass as just described into the bundles of Vicq d'Azyr and

Gudden. The former end in the dorsal nucleus of the thalamus, the latter in the red nucleus and adjacent grey matter of the tegmentum. Neither of these bundles crosses the middle line. Afferent fibres pass to the corpus mamillare partly through its peduncle (brachium), and partly by way of the columns of the fornix. The former originate (*a*) in the tegmentum from arcuate fibres, which course below the superior cerebellar peduncles; (*b*) from the main fillet. The fibres which enter the corpus mamillare by its peduncle bifurcate, one branch passing to the mesial, one to the lateral nucleus; some cross the middle line and enter the opposite mamillary body. They arborise among the cells,

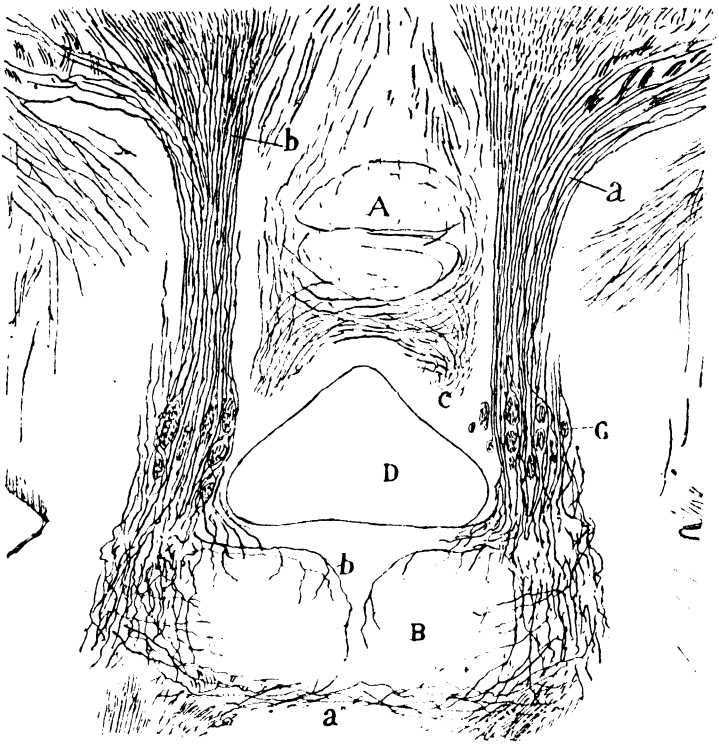


FIG. 235.—HORIZONTAL SECTION THROUGH CEREBRAL PEDUNCLE AT LEVEL OF MAMILLARY BODIES: YOUNG KITTEN. (Cajal.)

A, interpeduncular ganglion; B, mesial nucleus of mamillary body; D, depression between pons and mamillary bodies; G, root-bundles of third nerve cut across; *a*, lateral, and *b*, mesial fibres of mamillary peduncles: the same letters repeated in the lower part of the figure indicate ramifications of their fibres within the mesial nucleus.

forming a dense interlacement (fig. 235). A few pass beyond the corpus mamillare and reach the tuber cinereum.[1]

The fibres which reach the corpora mamillaria by way of the columns of the fornix are chiefly collaterals which are given off from these columns as they pass through the bodies, although some terminate within them. By far the larger number of the fibres of the columns of the fornix pass beyond the corpora mamillaria, crossing the middle line and turning downwards in the reticular formation, in which they are said to be traceable as far as the pons, and possibly farther.

[1] The account given by Cajal has here been followed. Most authorities have looked upon the peduncle as containing purely efferent fibres passing to the tegmentum. Cf. Hatschek, Arb. a. d. neurol. Instit. Wien, x. 1903.

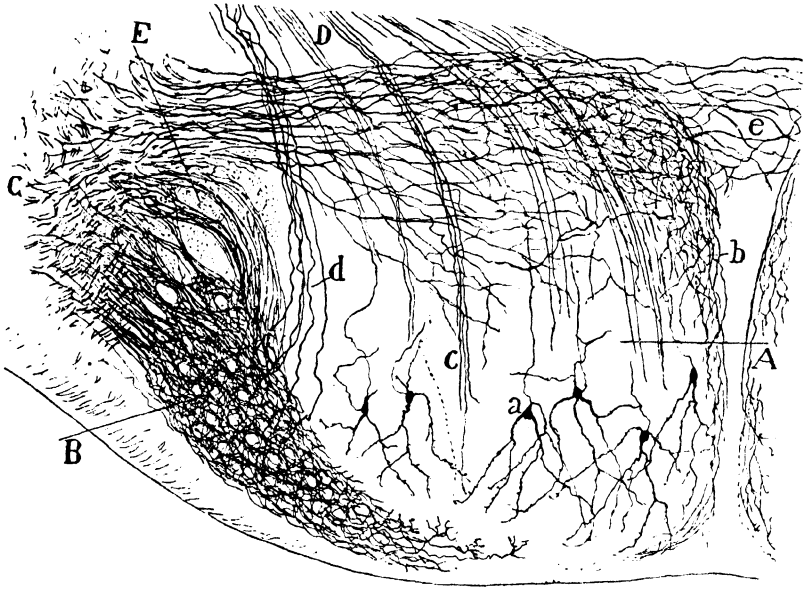


FIG. 236.—CORONAL SECTION THROUGH THE MAMILLARY BODY OF A YOUNG KITTEN. (Cajal.)

A, mesial nucleus; B, lateral nucleus with close nerve-plexus formed by the fibres of the mamillary peduncle; C, bundles of this peduncle cut obliquely; D, bundles of efferent fibres from the mamillary body; E, section of bundles of column of fornix; *a*, cells of mesial nucleus; *b*, terminal ramifications of mesial branches of mamillary peduncle; *c*, axons from mesial nucleus; *d*, axons from lateral nucleus; *c*, commissure formed by intercrossing of mesial fibres of mamillary peduncles.

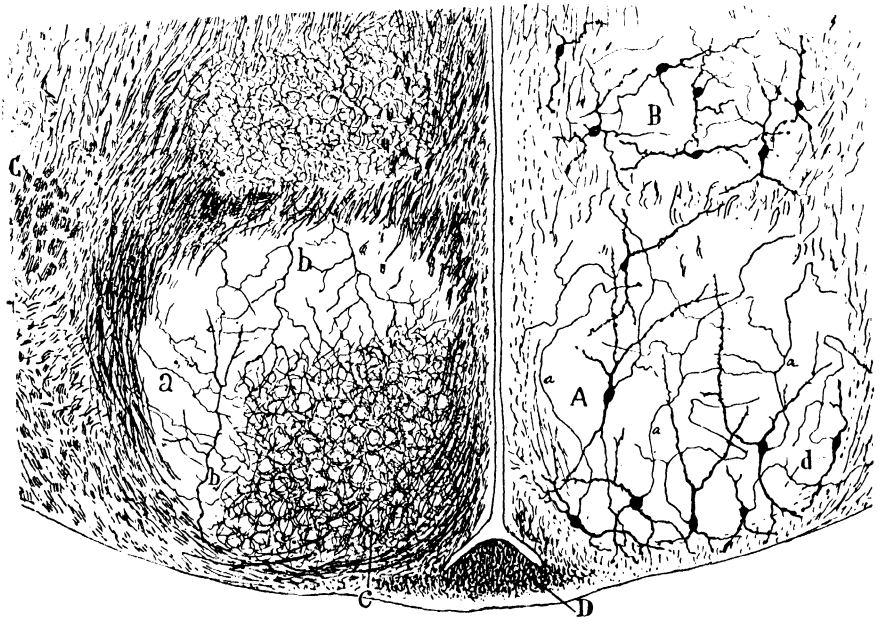


FIG. 237.—CORONAL SECTION OF TUBER CINEREUM OF MOUSE A FEW DAYS OLD. (Cajal.)

A, anterior nucleus; B, dorsal nucleus; C, column of fornix; D, bundle of tuber cinereum; *a*, collaterals from fibres of the capsule; *b*, terminals of capsule-fibres; *c*, closely interwoven plexus within the main nucleus.

An isolated bundle of one of the columns of the fornix is sometimes visible at the base of the brain passing to the corpus mamillare (*stria alba tuberis*, Lenhossék).

The **tuber cinereum** (fig. 233; fig. 234, T) is a lamina of grey matter extending forwards from the corpora mamillaria to the optic commissure, to which it is attached. It forms part of the floor of the third ventricle. In the middle it is prolonged downwards into a hollow conical process, the *infundibulum* (figs. 227, 238), to the extremity of which is fixed the pituitary body. On

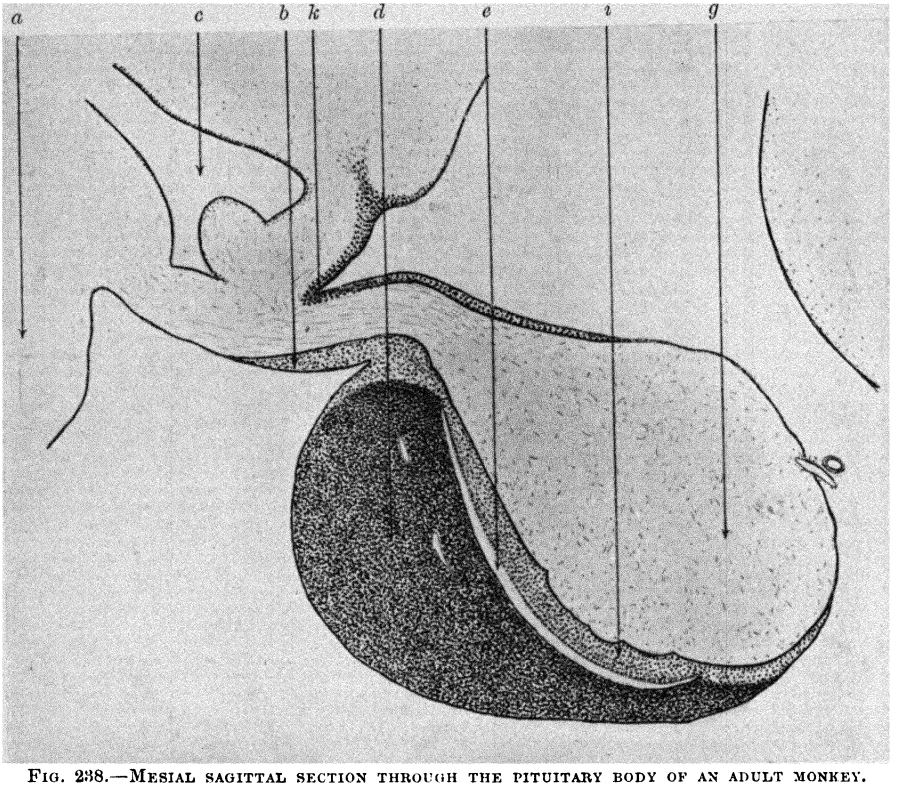


FIG. 238.—MESIAL SAGITTAL SECTION THROUGH THE PITUITARY BODY OF AN ADULT MONKEY. Semi-diagrammatic. (P. T. Herring.)

a, optic chiasma; *b*, tongue-like process of pars intermedia; *c*, third ventricle; *d*, anterior lobe proper; *e*, epithelial cleft; *g*, nervous substance of posterior lobe; *i*, epithelial investment of posterior lobe (pars intermedia); *k*, pars intermedia extending over and into adjacent brain-substance. The dark shading indicates the anterior lobe proper; the lighter shading shows the position of the epithelium of the pars intermedia. The arrangement is similar to that found in man, but the posterior lobe is relatively rather larger in the monkey. It must, however, be remembered that the anterior lobe and pars intermedia almost surround the posterior lobe, and do not merely lie ventral to it as they appear in a median section. In the cat and many other animals the infundibular recess is prolonged right into the posterior lobe.

its outer side, close to the optic tract, is a tract of grey matter with nerve-cells, termed by Meynert the *basal optic ganglion* (*supra-optic nucleus* of Cajal) (see p. 240). According to Lenhossék, this is subdivided into three successive groups of nerve-cells, the most anterior being just above the chiasma, the most posterior near the corpus mamillare.

Nuclei of the tuber cinereum.—Three collections of nerve-cells are described within the tuber cinereum, and are termed respectively the *anterior* or *principal*, the *posterior* or *accessory* and the *superior* or *dorsal nuclei*. The anterior nucleus (fig. 237) has medium-sized cells, the

axons of which pass from before backwards. It is enveloped by a capsule of white fibres, most of which are derived from nuclei in front of the tuber cinereum and are passing backwards partly to end in the nucleus, partly behind it. The posterior nucleus receives many of these.

The basal optic ganglion perhaps gives origin to the fibres of Gudden's commissure, which accompanies the optic tract.

Retzius[1] describes another median prominence which is situated behind the tuber cinereum. He terms this the eminentia saccularis, as he considers that it represents the saccus vasculosus found in this situation in fishes and some other lower vertebrates.

The **pituitary body** or *hypophysis cerebri* (figs. 227, 238, and 241) (called pituitary gland, from its having been erroneously supposed to discharge *pituita* into the nostrils) is a small reddish-grey mass, of a somewhat flattened

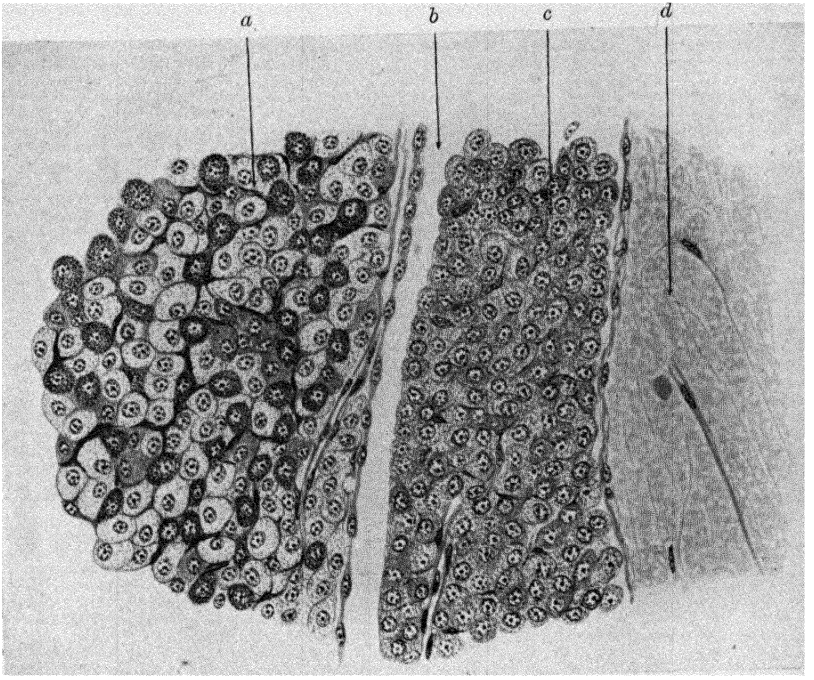


FIG. 239.—MESIAL SAGITTAL SECTION THROUGH PART OF THE PITUITARY BODY OF AN ADULT CAT. (P. T. Herring.)

a, anterior lobe showing different forms of epithelial cells: the blood-channels are collapsed and their position indicated only by endothelial cells; *b*, epithelial cleft separating anterior from posterior lobe; *c*, epithelial investment of posterior lobe ('Epithelsaum' of Lothringer); *d*, nervous substance of posterior lobe.

oval shape, widest in the transverse direction, and occupying the sella turcica of the sphenoid bone. The pituitary body has a special prolongation of the dura mater completely enclosing it, except above, where there is a small aperture for its connexion with the infundibulum. The body consists of two lobes, of which the anterior is the larger; it is concave behind, where it embraces the smaller posterior lobe. The two lobes differ both in their structure and development.

The *posterior lobe* is developed as a hollow downgrowth of the part of the embryonic brain which afterwards becomes the third ventricle. The extension of the cavity into the lobe becomes obliterated in man. But in some animals

[1] Biol. Untersuch. vii. 1895.

(*e.g.* cat) not only does the infundibulum extend into the posterior lobe, but may even, in rare instances, connect up with a cleft-like cavity which lies between the lobes. The part of the posterior lobe which is adjacent to this cavity becomes invaded by the epithelium of the invagination which has formed the anterior lobe and acquires distinctive characters. It is termed the *pars intermedia*. The cleft which separates the lobes contains a yellowish fluid, which is probably secreted by the cells bounding the cleft.

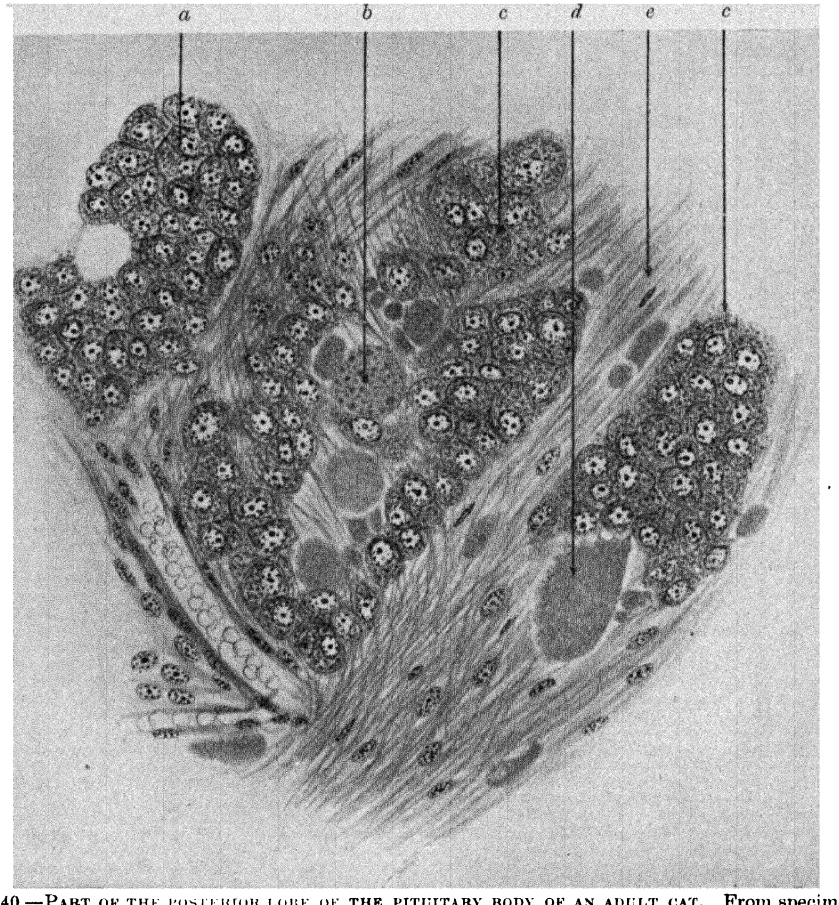


FIG. 240.—PART OF THE POSTERIOR LOBE OF THE PITUITARY BODY OF AN ADULT CAT. From specimen fixed in Flemming's solution and stained with eosin and methylene blue. (P. T. Herring.)

a, cells of epithelial investment (pars intermedia); *b*, cells containing globules of colloid; *c*, *c*, islets of epithelial cells similar in character to those of the epithelial investment; *d*, colloid or hyaline body in posterior lobe; *e*, ependyma and neuroglia fibres. The drawing is from part of the section in the neighbourhood of the neck of the posterior lobe. Globular colloid bodies occur in close proximity to the epithelial cell islets.

Although the posterior lobe receives a few fibres which pass into it from the adjacent basal portion of the brain, the pars nervosa contains no cells which can be identified as nerve-cells, but many which have the appearance of neuroglia-cells.[1] The pars intermedia is formed by an epithelial stratum a few cells deep which bounds the intraglandular cleft posteriorly (fig. 239). The layer of

[1] Berkley, Retzius, and others have described cells with axon-processes, but others who have made a careful study of the hypophysis by the Golgi method have failed to confirm this.

epithelium next to the cleft has the appearance of ependymal epithelium. Within interstitial spaces of this lobe Herring has noticed in sections of the gland a material staining like colloid, in the form of globular masses extending from the pars intermedia to the prolongation of the third ventricle. This probably represents the secretion of the lobe. It appears to be greatly increased in amount after thyroidectomy (fig. 242). It is stated by several authorities that the anterior lobe also becomes hypertrophied in cases of thyroid deprivation.

The *anterior lobe* is developed as a prolongation (*Rathke's pouch*) from the ectoderm of the buccal cavity, with which it is therefore originally in connexion.

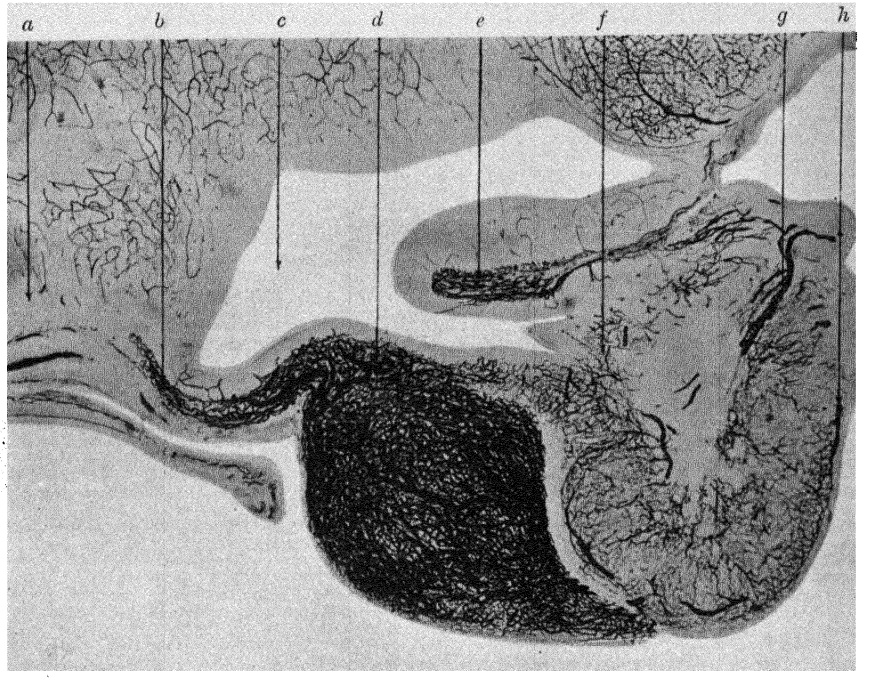


FIG. 241.—MESIAL SAGITTAL SECTION OF PITUITARY BODY OF ADULT CAT; BLOOD-VESSELS INJECTED WITH CARMINE GELATINE. Photograph. (P. T. Herring.)

a, optic chiasma; *b*, tongue-like process of pars intermedia; *c*, third ventricle; *d*, anterior lobe; *e*, pars intermedia lying above neck of posterior lobe; *f*, posterior lobe; *g*, central artery entering posterior lobe at its postero-superior angle; *h*, large vein lying between nervous substance and epithelial investment of posterior lobe.

It is formed entirely of epithelium arranged in trabeculæ. The blood-vessels are very numerous (fig. 241) and large, and the sinus-like capillaries form a close network around the trabeculæ. The lymphatics originate in cleft-like spaces between the tubules, and pass to a network in the capsule. The epithelium contains two kinds of cells— one kind containing granules (chromophil-granules) staining darkly with eosin, the others remaining colourless (fig. 239, *a*). But it may be that these represent two different physiological conditions of the same cell, since cells of intermediate character are also described.[1] The chromophil-cells are usually found to be increased in number and the anterior lobe enlarged in the disease known as acromegaly. The secretion of the anterior

[1] The above account of the structure of the pituitary body is based on the description given by Herring (Quart. Journ. Exp. Physiol. i. 1908), where the literature of the subject will also be found.

lobe probably enters the blood-vessels, whereas that of the pars intermedia passes into the third ventricle.

Lamina terminalis.—In the middle line of the base of the brain, in front of the optic commissure, is the anterior portion of the great longitudinal fissure, which separates the two hemispheres. At a short distance in front of the chiasma this fissure is crossed transversely by the anterior recurved extremity of the corpus callosum. On gently turning back the optic commissure, the thin connecting layer of grey substance known as the *lamina terminalis* is seen occupying the space between the corpus callosum and the chiasma, and continuous above the chiasma with the tuber cinereum. It is connected at the

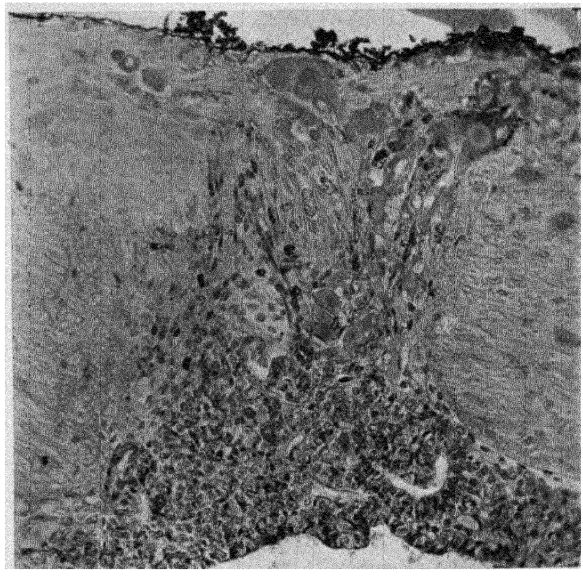


FIG. 242.—SECTION OF PART OF THE POSTERIOR LOBE OF THE PITUITARY OF A DOG, SHOWING MASSES OF COLLOID MATTER PASSING TOWARDS AND INTO THE CAVITY OF THE INFUNDIBULUM. Photographed from a preparation by P. T. Herring. Magnified 160 diameters.

The animal had undergone thyroidectomy nineteen days before being killed for examination of the pituitary, and the colloid secretion is present in unusual amount. Some of the colloid appears to be present in nucleated cells, but for the most part it forms irregular clumps which appear to be streaming from the pars intermedia (below) to the cavity of the infundibulum (above).

sides with the grey substance of the anterior perforated space, and forms part of the anterior boundary of the third ventricle (fig. 227). It is somewhat liable to be torn in removing the brain from the skull; and in that case an aperture is made into the fore-part of the third ventricle.

The optic tracts and optic commissure or chiasma.—The optic tracts curve round the crusta on each side to unite with one another immediately in front of the tuber cinereum, where they form the X-shaped commissure which is known as the chiasma. The optic tracts form the posterior limbs of the X; the optic nerves, passing through the optic foramina, the anterior limbs (fig. 242).

Each tract is described as arising posteriorly[1] by a broad root, which is divided by a longitudinal groove into two parts, a lateral and a mesial. The

[1] The optic fibres actually take origin *anteriorly* in the nerve-cells of the retina.

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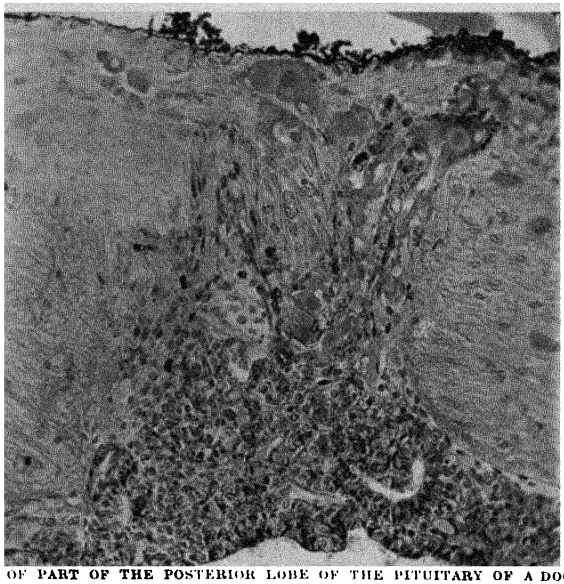

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Each tract is described as arising posteriorly[1] by a broad root, which is divided by a longitudinal groove into two parts, a lateral and a mesial. The

[1] The optic fibres actually take origin *anteriorly* in the nerve-cells of the retina.

lateral root is the larger. It is connected with the posterior and ventral part of the thalamus (lateral geniculate body and pulvinar), and is partly continuous with the brachium of the superior colliculus of the quadrigeminal bodies. The mesial root, when traced backwards, is seen to curve round the crusta and then to lose itself beneath the mesial geniculate body, in which it appears to merge. Although this root thus appears connected with the internal geniculate body, it is doubtful if there is any functional connexion between the latter and the optic nerve-fibres, the part of the tract which enters the mesial geniculate body being Gudden's commissure, which joins the mesial geniculate bodies of the two sides (see next page). Before reaching the chiasma the optic tract lies postero-mesially to the anterior perforated space.

In some animals there is a small nucleus between the optic tract and the crusta, receiving collaterals from the optic fibres. It is termed by Cajal the *nucleus of the optic tract.*

Darkschewitsch described the passage of some of the fibres of the optic tract to the ganglion habenulæ and pineal peduncle, and ultimately by the posterior commissure to the oculomotor nucleus. He regarded these as fibres subserving the reflex changes of the pupil.

As for the course of the optic fibres in the tract and chiasma, it may be stated that, although in many mammals (mouse, guinea-pig), and in all vertebrates below mammals, the decussation is complete, so that all the fibres pass from one tract into the opposite optic nerve, in other mammals (rabbit, dog, cat, monkey) and in man it is incomplete, so that some of the fibres from the left optic nerve pass into the left tract and others into the right tract, and the same, *mutatis mutandis*, for those of the right nerve. This fact has been conclusively proved both by experiment and clinical observation. At the same time it must be stated that cases have occasionally been recorded which, if correct, may be explained on the supposition that the crossing is complete: in these we might suppose that there has been a reversion to the lower and more primitive type of chiasma.

The two sets of nerve-fibres are usually spoken of as the crossed and uncrossed bundles, although they are not to be regarded as formed into entirely separate funiculi, nor are their limits sharply defined either in the nerve, chiasma, or tract. The uncrossed bundle is distributed exactly to the lateral half of the retina, the crossed bundle to the mesial half; and on the whole the fibres of the uncrossed bundle keep to the lateral side of the optic nerve, whilst the crossed bundle is on the mesial side of the nerve. In the chiasma and tract they are usually more commingled, and their relative position is very variously given. In a case of atrophy of one nerve which has been clearly described by Williamson, the uncrossed fibres chiefly occupied the middle of the tract, the crossed being chiefly at the periphery and lower part. Similar results were obtained by Henschen.

According to Salzer's enumeration, there are nearly half a million fibres in each optic nerve.[1] The fibres vary in size. According to Gudden they are divisible, according to their calibre, into two classes, finer and coarser. The former of these he regarded as being concerned in the production, as afferent fibres, of the pupil-reflexes, the latter as conveying visual impressions. The finer fibres undergo atrophy after destruction of the superior corpora quadrigemina in young animals (cat and rabbit).

[1] Boughton (Journ. Comp. Neurology, xvi. 1906) found the fibres of the optic nerve to increase in number in growing animals as age advances (rat, cat).

It must be remembered that not only centripetal, but also some centrifugal impressions are carried by the optic tracts; governing the chemical changes which occur in the retina, and also the movements of some of its elements (pigment-cells, cones).

Besides the optic nerve-fibres, there is a bundle at the posterior part of the chiasma, running along the mesial side of the optic tracts to join the internal geniculate bodies of the two sides. This is known as the *inferior commissure* or *commissure of Gudden*. It appears to have no relation to the visual function, for it undergoes no change when the rest of the optic tracts atrophy after extirpation of both eyes in young animals. Its fibres are of extremely small diameter.

In structure the optic tract resembles an extension of the white matter of the brain, being very soft and not divided up into bundles by connective tissue, nor are its fibres provided with membranous sheaths. These structures are found, however, in the chiasma, and in the optic nerve, both of which are firm and tough, and invested with sheaths continuous with the pia mater and arachnoid. At its entrance into the orbit the optic nerve receives a strong investment from the dura mater, which is continued around it into the sclerotic coat of the eye. The nerve is subdivided by intercommunicating connective-tissue septa into a large number of compartments, which contain the nerve-fibres, but the latter are not gathered up into round funiculi invested by perineurium, as in the case of the ordinary peripheral nerves.

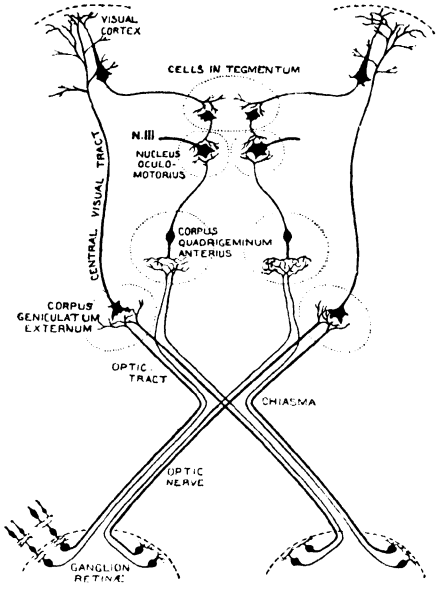


FIG. 243.—DIAGRAM TO SHOW THE PROBABLE COURSE AND RELATIONS OF THE OPTIC FIBRES.

To simplify the diagram, only single neurones are represented as continuing the two neurones from the retinæ in the geniculate and quadrigeminal bodies of each side with the visual cortex. This must not be taken to imply that the retinal impressions from the two retinæ are fused in these intermediate nuclei.

As regards the course of the optic fibres, the results of experiment show that whilst most have their cell-origin in the periphery—presumably in the nerve-cells of the retina—some take origin in nerve-cells of parts of the brain (superior corpora quadrigemina, external geniculate body, and pulvinar). Of those nerve-fibres which have their cell-origin in the retina, and which therefore undergo degeneration backwards after section of the optic nerve or tract, some end by arborisations between the nerve-cells of the external geniculate body and pulvinar (figs. 243, 244), others by arborisations in the more superficial layers of the superior corpora quadrigemina (see figs. 223, 224). It has been found that after enucleation of the eye the grey matter between the cells in these several parts undergoes atrophy. Those fibres which have their cell-origin in the nerve-centres end by terminal arborisations within the retina. Their course will there be followed in the part of this work which deals with the structure of the eye.

In the grey matter which lies between the third ventricle and the optic chiasma, a small collection of nerve-cells (*basal optic ganglion*) is seen on each side, as already noticed (p. 234). These ganglia do not appear to have any direct connexion with the optic nerve, as was supposed by Meynert to be the case, but from each a tract issues, which, after decussating with that of the

opposite side (*Meynert's commissure*), applies itself to the mesial side of the optic tract, close to Gudden's commissure, and passes backwards to the subthalamic region to enter the nucleus of Luys (Dejerine). Antero-laterally this tract may be connected, beyond the basal optic ganglion, with the lenticular nucleus.

The **geniculate bodies** are intimately related to the corpora quadrigemina, but are also continuous with the posterior part of the thalamus. The lateral geniculate body receives many of the fibres of the optic tract, and undergoes partial atrophy if the opposite eye be extirpated in the new-born animal. It is darker in colour than the adjacent part of the thalamus, with which it is closely connected, and it is formed of several curved layers of grey matter, with white lamellæ of optic-nerve fibres separating them (fig. 222, *c.g.e.*)

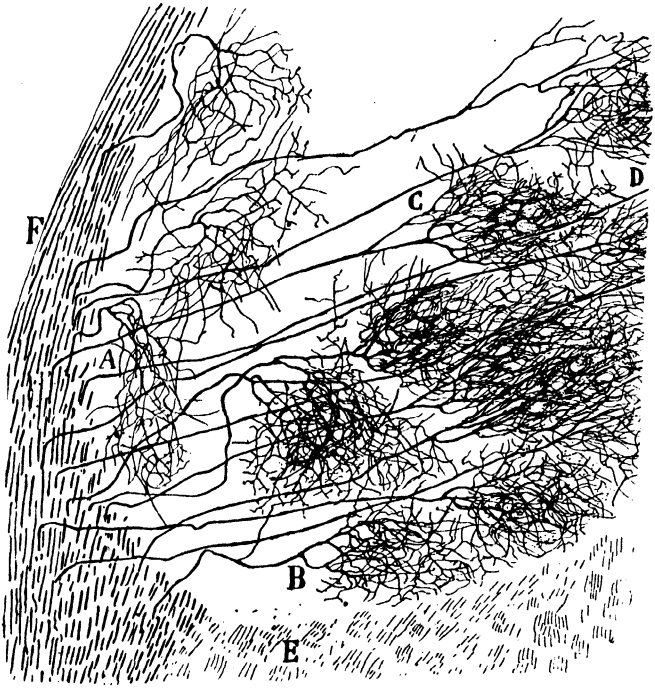


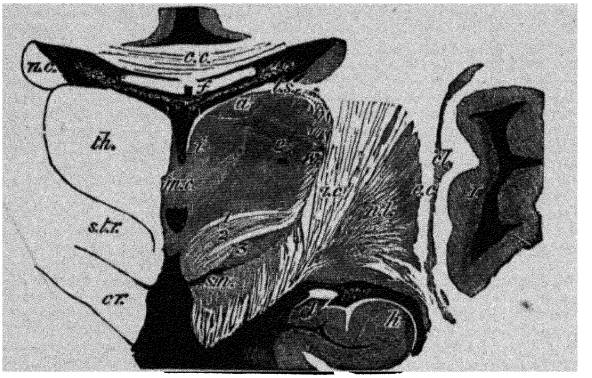
FIG. 244.—PART OF THE VENTRAL NUCLEUS OF THE LATERAL GENICULATE BODY OF THE CAT. (Cajal.)

A, superficial optic arborisations; B, C, D, deep optic arborisations; E, F, optic fibres.

Most of the cells (with the exception of a few belonging to type ii. of Golgi) are medium-sized and pigmented, and send their nerve-fibre processes to the cortex of the occipital region by the optic radiations; they are in man joined by a large number of arcuate fibres which arise in the pulvinar thalami. They pass horizontally backwards across the retro-lenticular part of the internal capsule to the cortex bounding the calcarine fissure. If the visual region of the occipital cortex is removed on one side in young animals, the cells of the lateral geniculate body of the same side undergo atrophy (Monakow). On the other hand, if the eyes are extirpated, the atrophy which extends along the optic tracts involves the grey matter between the cells, but not the cells themselves. Lesions of the retina cause Wallerian degeneration in the lateral geniculate body (and in

the anterior quadrigeminal body) of the same or of the opposite side, according to the part which is injured.[1] The intercellular grey matter of these bodies is mainly composed of ramifications of the retinal fibres. The same statement applies to the adjacent part of the thalamus (pulvinar), which is intimately associated both in structure and function with the lateral geniculate bodies.

The mesial geniculate body, which is connected with the inferior colliculus by the inferior brachium, appears on a superficial view to receive a part of the optic tract, but the connexion is only apparent, for the fibres of the tract sweep round and under it to pass to the superior colliculus. This mesial geniculate body receives (through its brachium) many of the fibres of the secondary acoustic path from the lateral fillet: these fibres end in the ventral nucleus in fine arborisations. It is much better developed in animals with an acute sense of hearing, such as the bat, than in man. It is also said to receive fibres from the cerebral cortex (temporal region), but probably more fibres pass from the body in question to the cortex.



IG. 245.—CORONAL SECTION ACROSS THE THALAMUS AND CORPUS STRIATUM IN THE REGION OF THE MASSA INTERMEDIA. Natural size. (From a preparation by S. G. Shattock.)

th, thalamus; *a*, *e*, *i*, its anterior, lateral, and mesial parts respectively; *w*, its latticed layer; *n.c.*, massa intermedia; above and below it is the cavity of the third ventricle; *c.c.*, corpus callosum; , fornix, separated from the third ventricle and thalamus by the tela choroidea. In the middle of this re the two veins of Galen and the choroid plexuses of the third ventricle; and at its edges the horoid plexuses of the lateral ventricles; *t.s.*, stria terminalis; *cr.*, forward prolongation of the crusta assing laterally into the internal capsule, *i.c.*; *s.t.r.*, subthalamic prolongation of the tegmentum, onsisting of (1) the dorsal layer, (2) the zona incerta, and (3) the nucleus of Luys; *s.n.*, substantia igra; *n.c.*, nucleus caudatus of the corpus striatum; *n.l.*, nucleus lenticularis; *e.c.*, external capsule; *l.*, claustrum; *I*, insula.

The cells of the mesial geniculate body are collected into two chief groups or uclei, *dorsal* and *ventral*. The dorsal is poor in cells, but has a close network of ell-dendrons, and is traversed by bundles of arcuate fibres. The ventral is rich in ells, which are for the most part small, but in the deepest part is a group of large ells. The cell-axons pass into the brachium and probably to the cerebral cortex.

The **thalami** are covered on their free surfaces (mesial and dorsal) (figs. 245, 46) by a layer of white fibres, most marked upon the dorsal surface (*stratum onale*), and mainly running antero-posteriorly. On their outer surface is the hite matter of the inner capsule (*i.c.*) formed by fibres converging towards the rusta from the hemispheres. Next to the thalamus on this side is a denser ayer of white fibres, termed the *outer medullary lamina*. All along this surface adiating fibres pass out of the thalamus to mingle with the fibres of the internal

[1] For the literature of this subject, see Parsons, Brain, xxv. 1902; also Dean and Usher, *ibid.* xvi. 1903. In both these papers the results of experiments upon the monkey are given, and the legenerations resulting from unilateral retinal lesions are described.

capsule, to pass to the surface of the cerebral hemispheres. Those in front pass to the frontal lobe of the hemisphere; those in the middle region to the posterior part of the frontal and to the parietal lobe, besides some to the temporal lobe; those behind partly to the temporal lobe, but chiefly to the occipital lobe. The fibres to the occipital lobe pass out from the lateral margin of the pulvinar, and have at first a curved course round the posterior horn of the lateral ventricle, afterwards radiating, with a generally sagittal direction, towards the cortex of the occipital lobe. They are often spoken of as the *optic radiations*. These radiating fibres are apparently continuous with others passing from the optic tract to the pulvinar, but there is a cell-station for them in the latter. The lower surface of the thalamus is continuous posteriorly with the prolongation of the tegmentum (*subthalamic tegmental region*), but in front this prolongation inclines outwards and merges into a layer of grey matter which is continuous internally with the grey matter of the floor of the ventricle, and is seen at the base of the brain as the anterior perforated lamina. At the anterior end of the thalamus is a tract of fibres which stream from it through the internal capsule into the frontal lobe of the hemisphere (*anterior stalk of thalamus*). Other fibres curve downwards and outwards towards the white substance of the hemisphere, forming the so-called *lower stalk of the thalamus* (*ansa peduncularis*).[1] Above this is another tract (*ansa lenticularis*, p. 250) sweeping from under the thalamus round the mesial part of the crusta in the direction of the lenticular nucleus of the corpus striatum (fig. 252). The layer of grey substance which is interpolated between the two tracts is the *substantia interansalis*; including the two ansæ, it has been designated *substantia innominata*.

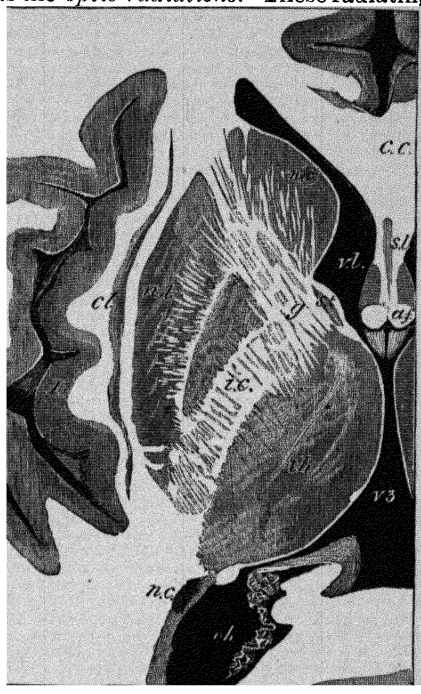


FIG. 246.—HORIZONTAL SECTION THROUGH PART OF THE CEREBRAL HEMISPHERE. Natural size. (From a preparation by S. G. Shattock.)

The section is viewed from below; *v.l.*, lateral ventricle, anterior cornu; *c.c.*, corpus callosum; *s.l.*, septum lucidum; *a.f.*, columns of the fornix; *v3*, third ventricle; *th*, thalamus; *st*, stria terminalis; *n.c.*, nucleus caudatus, and *n.l*, nucleus lenticularis of the corpus striatum; *i.c.*, internal capsule; *g*, its angle or genu; *n.c*, tail of the nucleus caudatus appearing in the inferior cornu of the lateral ventricle; *cl*, claustrum; *I*, insula.

The body of the thalamus is chiefly formed of grey matter with large and small nerve-cells scattered in it, but their arrangement and connexions with nerve-tracts have not been fully ascertained. Its grey matter is partially subdivided into two parts, inner and outer (mesial and lateral), by a vertical white lamina, S-shaped in section (*internal medullary lamina*). The *lateral* part (fig. 245, *e*) is the larger, and extends into the pulvinar; it is marked externally by the radiating white lines before mentioned as passing from the thalamus into the inner capsule, and these confer upon its external layer somewhat of a reticulated aspect (*latticed layer*, *w*). The *mesial* part (*i*) does not extend into the anterior tubercle,

[1] The term 'anse pédonculaire' was originally used (by Gratiolet) to include the whole substantia innominata.

but this part of the grey substance of the thalamus is cut off from it by another septum of white matter. The anterior separated part contains comparatively large nerve-cells. The thalamus receives below a well-marked bundle (*bundle of Vicq d'Azyr*), which emerges from the corpus mamillare, and passes obliquely upwards to diverge into the anterior part of the thalamus (fig. 234). The intermediate grey mass or middle commissure unites the mesial nuclei across

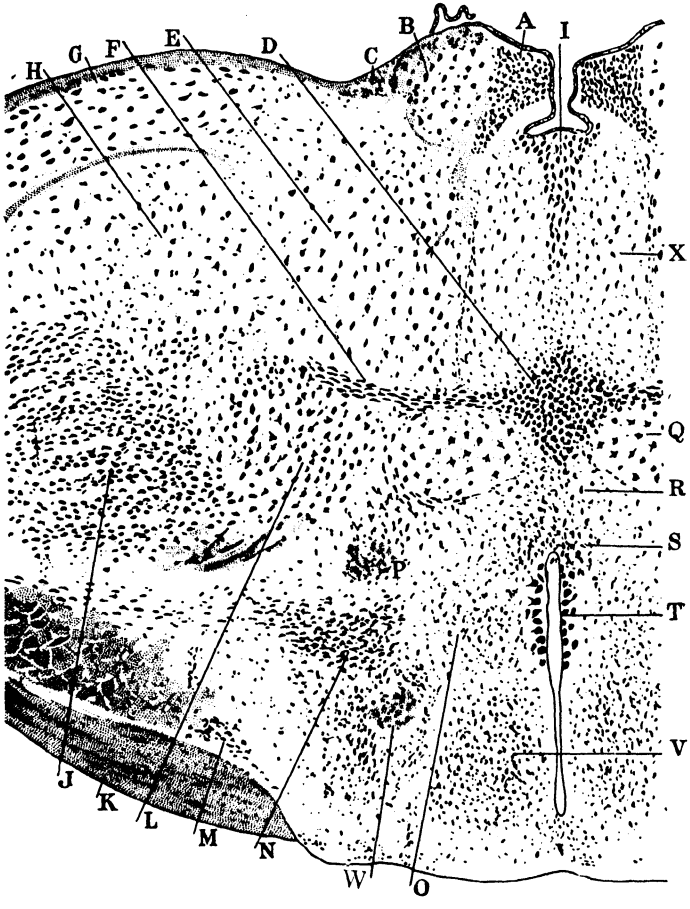


FIG. 247.—SOME OF THE NUCLEI OF THE THALAMUS AS SHOWN IN CROSS-SECTION OF POSTERIOR PART OF THALAMUS OF GUINEA-PIG. Prepared by Nissl's method. (Cajal.)

A and B, nuclei of habenula; C, stria medullaris; D, median rhomboid nucleus; E, intermediate dorsal nucleus; F, falciform nucleus; G, nucleus of lateral geniculate body; H, lateral dorsal nucleus; I, median dorsal nucleus; J, ventro-lateral or main sensory nucleus; K, optic tract; L, intermediate ventral nucleus; M, supra-optic nucleus; N, postero-mesial part of nucleus of internal capsule; O and V, nuclei of tuber cinereum; P, bundle of Vicq d'Azyr; Q, ovoid mesial nucleus; R, S, median ventral nuclei; T, third ventricle; W, column of fornix; X, dorsal nucleus of raphe.

the third ventricle, and is also continuous below on each side with the grey matter of the cavity. It contains nerve-cells and transversely coursing fibres, but many of the fibres are said to loop backwards near the median plane in place of passing across to the opposite side.

Structure and connexions of the thalamic nuclei.—The nuclei of the thalamus are numerous. In the ensuing account the description given

by Cajal is followed. He describes three series of thalamic nuclei lying in planes which may be roughly described as lateral, intermediate, and mesial. The lateral series comprises (1) the geniculate bodies and the pulvinar, and (2) the radiate nucleus (lattice-nucleus of Nissl). The intermediate series consists from before back of (1) the angular; (2) the dorsal; (3) the main sensory nucleus of Cajal (ventro-lateral, Nissl, Kölliker), with its accessory or semilunar nuclei; and (4) the posterior nucleus. The mesial series comprises, from before back, (1) the median nucleus of Kölliker; (2) the commissural nuclei; (3) the middle nucleus; (4) the internal nucleus; and

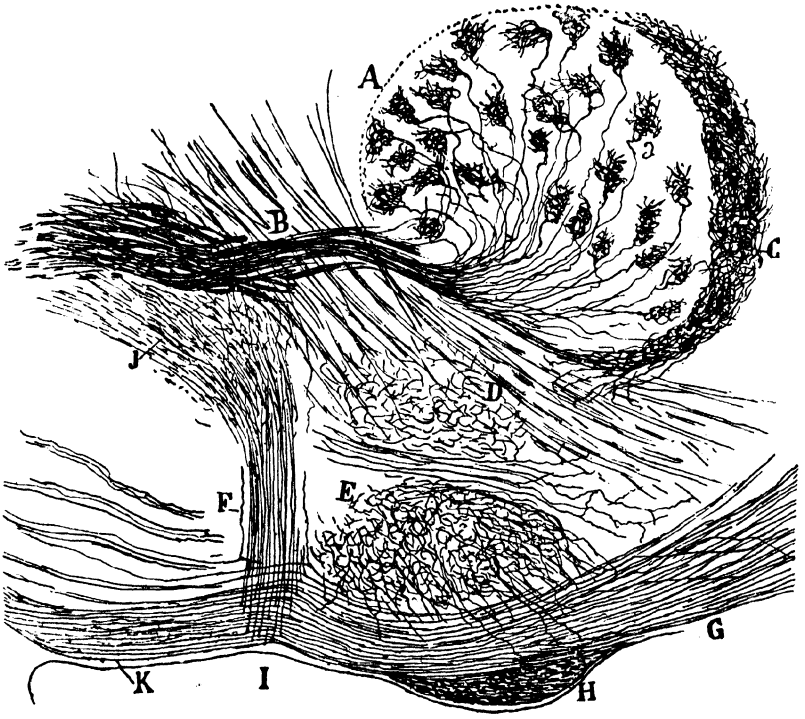


FIG. 248.—SAGITTAL SECTION OF INFERIOR THALAMIC AND PEDUNCULAR REGION OF YOUNG MOUSE. THE SECTION IS SOMEWHAT LATERAL AND PASSES ALONG THE CEREBRAL PEDUNCLE. (Cajal.)

A, main sensory nucleus of thalamus; B, sensory bundle (fillet); C, anterior semilunar nucleus; D, radiate nucleus, or lattice nucleus of Nissl; E, nucleus of Luys; F, bundle of collaterals from peduncular fibres, K, G, passing off at I and entering the area of Forel, J; H, optic tract.

(5) the ganglion of the habenula. Some of those enumerated have already been described.

Of the **lateral series**, the *geniculate bodies* and the *pulvinar* have been noticed. The *radiate nucleus* (lattice-nucleus of Nissl) lies among the fibres which radiate between the thalamus and cortex cerebri, separating the thalamus from the corpus striatum and internal capsule. Its cells are large; their axons pass downwards, but their destination is not known. It receives many collaterals from the thalamo-cortical fibres among which it lies.

Of the **intermediate** or **central series** of thalamic nuclei the most important appears to be the *ventro-lateral nucleus* (main sensory nucleus of Cajal) (fig. 247, J; fig. 250, B; figs. 248, 254, A). This receives all the fibres of the main fillet which have penetrated as far as the thalamus, and also fibres from the cortex cerebri,

to which it also gives off many fibres which pass from its cells into the corona radiata. The cells of this nucleus are of medium size and possess many dendrons, but there are, in addition, short-axoned cells of Golgi's type ii.

Lying in contact with the anterior surface of the ventro-lateral nucleus is the *anterior semilunar nucleus* (fig. 248, C; fig. 250, D; fig. 254, C). This also receives afferent fibres from various sources—through the central white lamina of the thalamus—viz. from the central tract of the fifth, from the reticular formation of the pons and mid-brain, from the superior cerebellar peduncle, and from the anterior end of the dorsal longitudinal bundle. The nucleus also receives large 'centrifugal' fibres from the cortex cerebri. The axons of its cells enter the corona radiata to pass to the cortex cerebri.

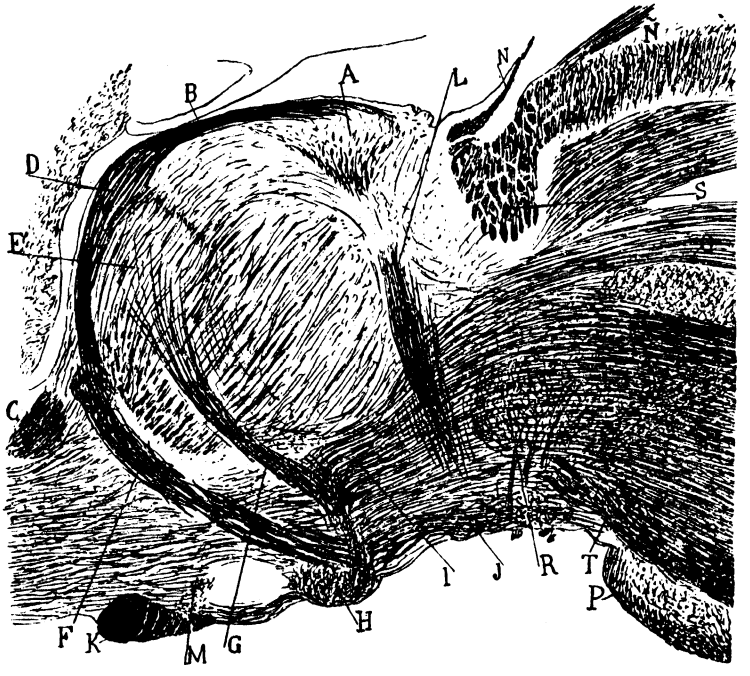


FIG. 249.—SAGITTAL SECTION OF THALAMUS OF GUINEA-PIG. Weigert-Pal method. (Cajal.)

A, ganglion of habenula; B, medullary stria; C, anterior commissure; D, angular nucleus; E, dorsal nucleus; F, column of fornix; G, bundle of Vicq d'Azyr; H, mamillary body; I, mamillo-tegmental bundle of Gudden; J, mamillary peduncle; K, chiasma; L, fasciculus retroflexus of Meynert; M, supra-optic nucleus; N, interhabenular commissure; N, anterior colliculus; O, grey matter of tegmentum; P, pons; R, red nucleus; S, posterior commissure; T, sensory tract (fillet).

The *posterior semilunar nucleus* (fig. 250, E; fig. 254, B) lies between the ventro-lateral and the posterior nucleus. It also receives many collaterals from the central white lamina and large and numerous fibres from the cortex cerebri. It contains cells similar to those of the anterior semilunar nucleus; their axons pass to the corona radiata.

The *posterior nucleus* (fig. 250, C; fig. 254, D) is a group of medium-sized cells, the destination of the axons of which is undetermined. It is traversed by optic fibres and by fibres derived from the central path of the fifth, and receives numerous collaterals from the fillet and a few large fibres from the cortex.

The *angular nucleus* of Cajal (*antero-lateral* of Nissl) (fig. 249, D) lies in the anterior and upper part of the thalamus, where it is bounded by

the stria medullaris. It is composed of large cells with conspicuous Nissl granules and with a close intercellular nerve-plexus which is supplied partly from the bundle of Vicq d'Azyr (this passes first through the dorsal nucleus) and partly by fibres from the cortex which enter it through the radiate nucleus. The axons of its cells appear to pass to the corona radiata.

The *dorsal nucleus* of Cajal (fig. 249, E) occupies the antero-internal part of the thalamus. It receives fibres and collaterals from the bundle of Vicq d'Azyr.

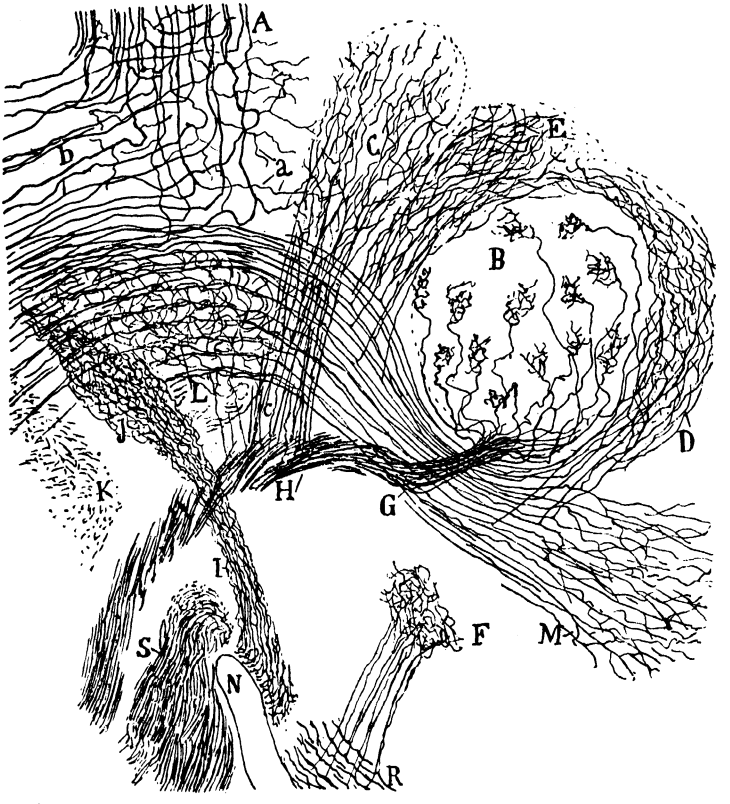


FIG. 250.—SAGITTAL AND SOMEWHAT LATERAL SECTION OF THALAMUS AND PART OF MID-BRAIN OF AN EIGHT-DAY-OLD MOUSE. Golgi method. (Cajal.)

A, posterior commissure; *b*, its fibres passing backwards and sending collaterals, *a*, forwards to thalamus; B, main sensory nucleus of thalamus; C, its posterior nucleus; D, E, accessory (semilunar) nuclei; F, a sub-thalamic nucleus, receiving collaterals from the mamillary peduncle, R; G, main fillet; H, collaterals passing from fillet-fibres to posterior thalamic nucleus; I, transverse peduncular tract; J, its nucleus of termination; L, red nucleus with fibres of superior cerebellar peduncle passing through it, and with the fibres of the central tract of the trigeminal and cerebral nerves passing by it to the thalamus and below this to the zona incerta, M; N, fold at upper part of pons; S, pyramid-tract.

Its cells are smaller than those of the angular nucleus. Their axons pass into the radiating bundles which penetrate the corpus striatum and form part of the thalamo-cortical system of fibres.

The *intermediate ventral nucleus* (fig. 247, L) lies mesial to the main sensory nucleus (J), of which it appears a prolongation. It has large cells with long axons, passing to the corona radiata, and small short-axoned cells. It receives numerous fibres from the cerebral cortex, but it is uncertain whether fibres of the ascending sensory tracts end in it.

Above the central nucleus, between it and the ganglion of the habenula, is the *intermediate dorsal nucleus* (fig. 247, E) (supero-internal of Cajal, postero-internal of Nissl), containing medium-sized cells sending their axons to the cortex cerebri.

Of the **mesial series of nuclei** of the thalamus, some lie just outside the median plane, others in the commissural grey matter (massa intermedia).

The *ganglion of the habenula* lies in the thalamus just in front of the pineal body and below the stria medullaris. It is better developed in the lower mammals than in Primates, and belongs to the olfactory apparatus (Edinger). Two cell-groups or nuclei can be made out in it, *mesial* and *lateral*—the former composed of very small cells with numerous dendrons, the latter of larger cells with

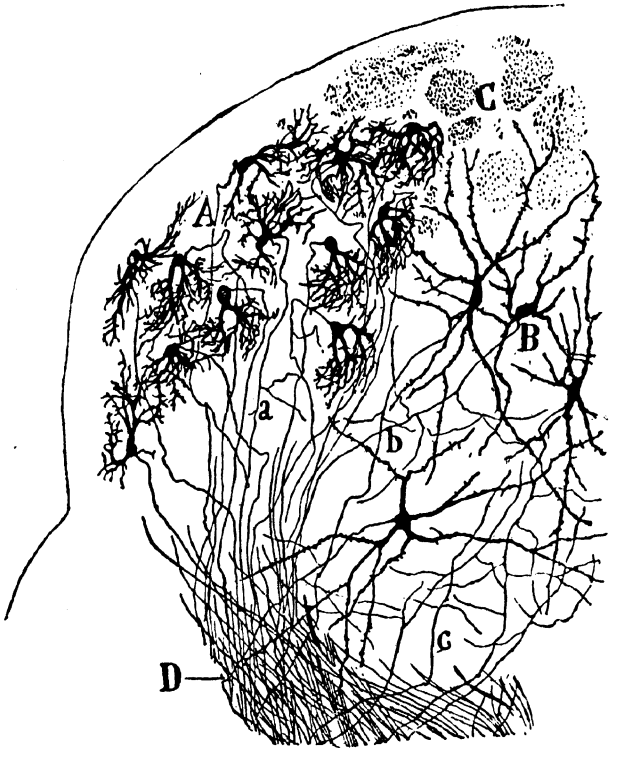


FIG. 251.—CORONAL SECTION OF THE HABENULAR NUCLEI OF DOG. Golgi method. (Cajal.)
A, mesial, B, lateral nucleus; C, stria medullaris; D, fasciculus of Meynert; *a*, axons from cells of mesial nucleus; *b*, *c*, axons from cells of lateral nucleus.

fewer and longer dendrons (fig. 251). The efferent fibres from the cells (fig. 249, L; fig. 251, D) pass away from the ganglion in the fasciculus retroflexus of Meynert (Gehuchten), which itself goes to the interpeduncular ganglion. Afferent fibres reach it from the stria medullaris: they come, for the most part, from the olfactory tubercle and olfactory bulb (deep olfactory radiation of Dejerine). It is also said to receive fibres from the column of the fornix, septum pellucidum, and stria terminalis; but according to Cajal these sources are doubtful. The afferent fibres form in the internal nucleus a close interlacement; in the external, a more open arborisation, each spreading over a large part of the nucleus.

The so-called commissure of the habenulæ is really a decussation of fibres of the stria medullaris, not of fibres derived from the habenulæ.

The *nucleus of the stria medullaris* lies at the extremity of that stria after it has passed the ganglion of the habenula. It receives collaterals from the stria and from the columns of the fornix. The *middle nucleus* lies ventral to it.

The nuclei in the **commissural part** of the thalamus are numerous. The following are enumerated by Cajal in the rabbit—viz. the *supero-internal*, the *superior*, *middle*, and *inferior commissural*, the *interdorsal commissural*, and the *oval*, *triangular*, and *falciform nuclei* (some of these are shown in fig. 247).

The *middle commissural nucleus*, of rhomboidal shape, lies in the middle of the massa intermedia. Its cells are of moderately large size, and the nuclei falciformes lie on either side of it, forming its wings. Somewhat lower down on each side is the *oval nucleus*, and outside this,

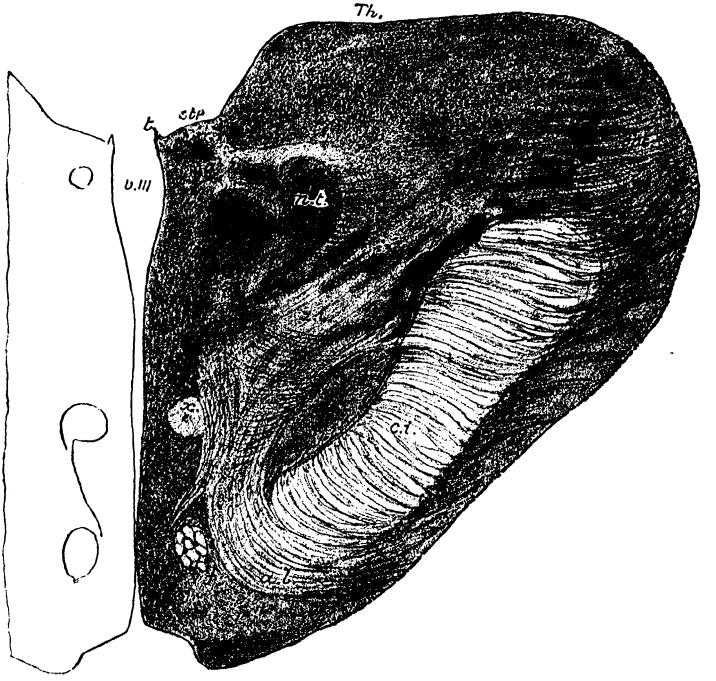


FIG. 252. — SECTION OF THE INTER-BRAIN NEAR THE JUNCTION WITH THE MID-BRAIN, SHOWING THE SUB-THALAMIC TEGMENTAL REGION. Magnified about 2½ diameters. From a photograph. (E. A. Schäfer.)

The section passes nearly horizontally, so as to cut the fibres of the internal capsule across transversely. It is just above the corpora mamillaria.

t., tænia (attachment of epithelial roof of ventricle); *v.III*, ventriculus tertius; *str*, stria medullaris; *Th.*, thalamus; *n.t.*, part of mesial nucleus of thalamus; *opt.*, optic fibres passing into pulvinar; *z.i.*, zona incerta; *c.s.*, corpus subthalamicum of Luys; *c.i.*, capsula interna; *a.l.*, ansa lenticularis; *f*, pillar of fornix passing backwards towards corpus mamillare; *V.A.*, bundle of Vicq d'Azyr, passing upwards and forwards from corpus mamillare into thalamus; *x.*, white bundle containing a central nucleus of grey matter (fasciculus retroflexus of Meynert); *g*, *g'*, groups of nerve-cells, of which *g* is part of the nucleus of the tuber cinereum, and *g'* is the hinder end of the ganglion habenulæ.

and between it and the lateral nucleus of the thalamus, is the *triangular nucleus*. The cells of the last-named are not unlike those of the lateral nucleus, and their axons pass downwards to join with those from the lateral nucleus and enter the thalamo-cortical path. The nucleus receives fibres from the internal capsule (cortico-thalamic), which bifurcate, one branch entering the nucleus on the same side, the other passing across the middle line.

In the front part of the thalamus, lying in the median plane between the two dorsal nuclei, is the *median dorsal commissural nucleus* composed of small cells with descending axons joining the thalamo-cortical path. This nucleus has many commissural fibres traversing it.

The *subventricular nucleus* forms a group of large cells lying close to the epithelium of the cavity of the third ventricle.

In man, as compared with the rabbit and lower mammals generally, the lateral geniculate body is very large and shows a series of grey and white zones; the pulvinar is also large; but this is especially the case with the lateral nucleus, which is much extended from before back. On the other hand, the dorsal nucleus is relatively small.

The angular nucleus appears to be represented in man by the so-called *centre of Luys*, which is a spheroidal group of nerve-cells lying between the pulvinar, the lateral nucleus, and the internal nucleus of Burdach. Its cells are surrounded by a close plexus of medullated fibres. According to Dejerine it receives fibres from the central sensory tract and from the superior cerebellar peduncle.

The *internal nucleus* of Burdach lies in the anterior part of the thalamus mesial to the internal medullary lamina and partly in front of the centre of Luys, and contains many small cells and few medullated fibres.

Hypothalamus.—The prolongation of the tegmentum under the posterior part of the thalamus was divided by Forel into three layers, which are named respectively, from above down, the *stratum dorsale*, the *zona incerta*, and the *corpus subthalamicum* or *nucleus of Luys* (fig. 245, 1, 2, 3; fig. 252, *c.s.*). The latter has here taken the place of the substantia nigra, lying next to the prolongation of the crusta, the fibres of which are seen at the side of the subthalamic region forming the internal capsule. The *stratum dorsale* consists chiefly of fine longitudinal fibres—continued into the dorsal longitudinal bundle according to Meynert, into the fibres enclosing the red nucleus according to Forel. The red nucleus of the tegmentum is prolonged into its posterior part, and from this a considerable number of fibres stream into the internal medullary lamina of the thalamus, and a well-marked bundle passes across the internal capsule to the lenticular nucleus. Some fibres of this layer, which are traceable from the upper fillet (Wernicke), turn into the external medullary lamina of the thalamus, which lies along the mesial side of the internal capsule. Finally another bundle of fibres is said to be traceable from the mesial part of the thalamus backwards through the subthalamic region into the dorsal part of the posterior commissure, and over the Sylvian aqueduct into the tegmentum of the opposite side.

The *ansa lenticularis* (Forel) is composed of a bundle of collaterals from the motor fibres in the peduncle which originate behind the nucleus of Luys between this and the substantia nigra and sweep backwards into the tegmentum, where they become disseminated in a grey area near the raphe, termed the *area of Forel* or *interstitial nucleus* (fig. 248, J). Its fibres, as they spread out, partly envelop the red nucleus—some appear to enter it. Forel thought that these fibres came from the lenticular nucleus; hence the name of ansa lenticularis applied to the bundle.

The *zona incerta* is a reticular formation prolonged from that of the tegmentum; it passes anteriorly into the substantia interansalis. It contains moderate-sized cells disposed horizontally: the destination of their axons has not been traced. It receives afferent fibres from the sensory path of the fifth and from the superior cerebellar peduncle. In front of the nucleus of Luys is a continuation of the zona incerta which is known as the *nucleus of the internal capsule* (fig. 247, N); this also receives collaterals and terminals from the peduncular fibres. The cells are small.

The *corpus subthalamicum*, or *nucleus of Luys* (fig. 252, *c.s.*), is a well-marked brown stratum in the grey matter, containing numerous moderately large

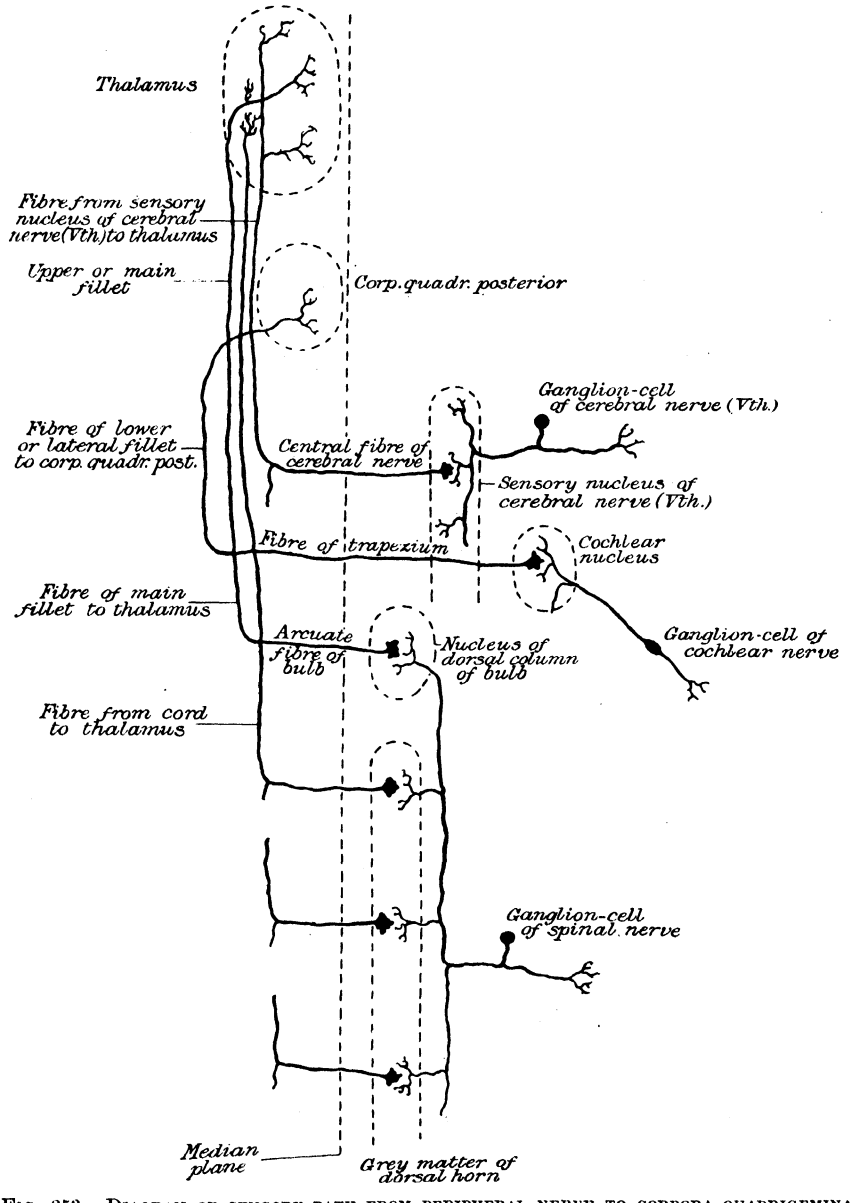


FIG. 253.—DIAGRAM OF SENSORY PATH FROM PERIPHERAL NERVE TO CORPORA QUADRIGEMINA AND THALAMUS. (E. A. Schäfer.)

nerve-cells, with extended dendrons, and a close plexus of very fine medullated fibres. The cell-axons tend in a mesial direction and enter the mesial third of the crusta, from which the nucleus receives also numerous collaterals. The body is lens-shaped in section, and has an enclosing envelope of white substance, through which strands of fine fibres pass from the interior mesially towards the zona incerta, and outwards and downwards through the internal capsule. This stratum is distinct only in the Primates.

Ending of sensory tracts in thalamus: termination of fillet.—The sensory fibres which are traceable to the thalamus from the spinal cord, medulla oblongata, pons, and mid-brain pass for the most part into the lateral nuclei.

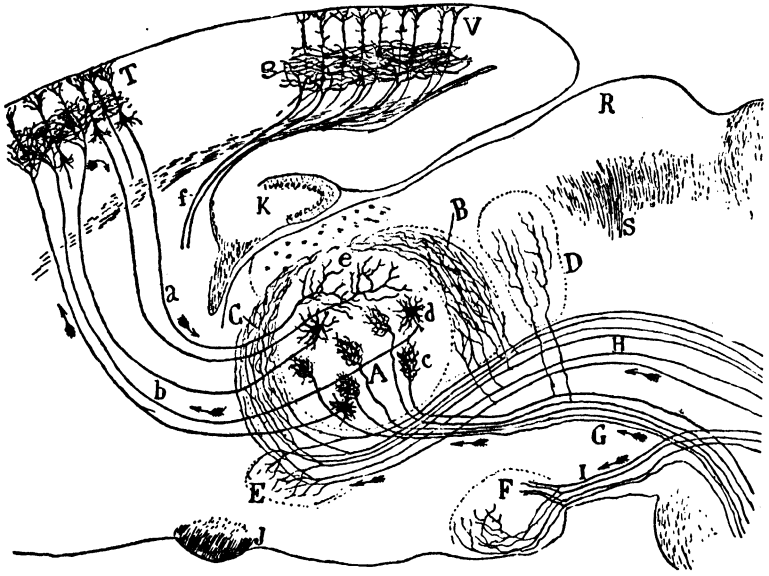


FIG. 254.—DIAGRAM OF THE CONNEXIONS OF THE THALAMUS WITH THE ASCENDING FIBRES OF THE FIFTH NERVE, AND OF THE UPPER FILLET ON THE ONE HAND, AND WITH THE CORTEX CEREBRI ON THE OTHER. (Cajal.)

A, principal sensory nucleus of thalamus; B, C, accessory (semilunar) nuclei; D, posterior nucleus; E, nucleus of zona incerta in hypothalamus; F, lateral nucleus of mamillary body; G, fibres of fillet passing into principal nucleus and ending in arborisations, *c*: on their way they give off collaterals to the posterior nucleus; H, central tract of trigeminal passing to the posterior and anterior accessory nuclei and to the zona incerta; I, peduncle of mamillary body; J, chiasma; K, hippocampus; R, anterior colliculus; S, optic fibres; T, cells in motor cortex cerebri sending axons, *a*, to end in sensory nucleus of thalamus, *e*; *b*, axons of thalamus-cells passing to grey matter of motor cortex; V, visual cortex receiving fibres, *f*, from lateral geniculate body and thalamus: these fibres are seen ending in the stria of Gennari, *g*. The arrows indicate the course of nerve-impulses.

Most of these fibres arise in the dorsal nuclei of the medulla oblongata of the opposite side, and, crossing the raphe as internal arcuate fibres, turn upwards and form the *main or upper fillet*. This is reinforced by fibres derived from the cells of the sensory nuclei of the afferent cerebral nerves, but many of these fibres occupy a separate tract which adjoins that of the fillet and is known as the *central tract of the cerebral nerves*. In addition to these two tracts, a third is formed of ascending fibres derived from the cells in the sensory nucleus of the fifth (*central tract of the trigeminal*). Besides the fibres of these three tracts, a certain number of the fibres of Gowers' bundle of the ventro-lateral column of the spinal cord do not pass into the cerebellum along its superior peduncle with the rest of the bundle, but are continued upwards in

the lateral part of the tegmentum, and some are traceable into the lateral part of the thalamus, where they break up into a fine arborisation (monkey). Another set of afferent fibres is derived from the continuation of the fibres of the superior cerebellar peduncle, some of which, after giving off collaterals to the red nucleus, are prolonged up into the thalamus. The main fillet fibres enter the lower part of the principal sensory nucleus (figs. 248, 250, 254), but before doing so they give off numerous collaterals to the posterior semilunar nucleus (fig. 250, C; fig. 254, D). The corresponding fibres of the central tract of the cerebral nerves and of the trigeminal, which run in the tegmentum dorsal to the main fillet, give off collaterals to the posterior semilunar nucleus (fig. 250, E; fig. 254, B), and then pass on below the main sensory nucleus, and crossing the course of the tract of the upper fillet end in the anterior semilunar nucleus (fig. 250, D; fig. 254, C), sending collaterals into the zona incerta (fig. 250, M; fig. 254, E).

From the thalamic nuclei the afferent or sensory path is continued to most parts of the cerebral cortex by fibres which arise as axons of the thalamic cells. On the other hand, the thalamus receives fibres from cells of most parts of the cortex. How the nervous impulses which descend along these fibres are continued to the lower centres is not certainly known, but fibres are observable passing from the cells of the thalamus to the corpus striatum, and others become lost in the internal capsule.

A certain number of authorities (*e.g.* Flechsig, Hösel, Tschermak) are of opinion that some of the afferent fibres—or branches of them—pass further and directly enter the cerebral cortex by the corona radiata. In following up fibres which have undergone Wallerian degeneration as a result of experimental lesions in animals, I have never seen such degeneration proceed beyond the thalamus; this conforms with the statements of most others who have investigated the question by this method (Ferrier and Turner, Probst, Van Gehuchten).

THE CEREBRAL HEMISPHERES.

EXTERNAL CONFORMATION.[1]

The **cerebral hemispheres** together form an ovoid mass, irregularly flattened on its under side, and placed in the cranium with its smaller end forwards, its greatest width being opposite to the parietal eminences. The hemispheres are separated in a large part of their extent by a deep fissure, the *great longitudinal fissure*. On opening this fissure by drawing asunder the two hemispheres, it is seen, both before and behind, to pass quite through to the base of the cerebrum; but for 10 cm. in the middle it is interrupted, at a depth of about 35 mm. at the front to 50 mm. at the back, by a large transverse mass of white substance, named the *corpus callosum*, which connects the two hemispheres together. While the brain is within the skull, the greater part of the longitudinal fissure is occupied by a vertical process of the dura mater—the falx cerebri—which dips down between the two hemispheres, not quite reaching to the corpus callosum in front, but touching it behind. Where the fissure is unoccupied by the falx, the inner surfaces of the two hemispheres lie in close contact with one another.

Each cerebral hemisphere has an outer, convex surface, in contact with the vault of the cranium; an inner or mesial, flat surface, which forms one side of the longitudinal fissure; and an irregular under surface, in which is a deep cleft, the *vallecula Sylvii*. In front of this cleft the under surface (orbital division), which looks somewhat outwards as well as downwards, and is slightly concave, rests in the anterior fossa of the base of the skull. Behind the cleft the under surface lies in the middle fossa, and, farther back still, on the tentorium cerebelli. These two parts of the under surface are concave from before backwards, and look inwards and downwards. The three surfaces of the hemisphere pass into one another at the borders, which are also three in number—viz. two mesial (superior and inferior) and one lateral. The superior mesial border is the most distinct of the three. It separates the mesial and external surfaces, and lies at the side of the superior sagittal sinus. The inferior mesial border is well marked in its anterior third, where it separates the orbital part of the under surface from the mesial surface; in the middle it is interrupted by the various structures uniting the two hemispheres; posteriorly it inclines obliquely backwards and downwards from the splenium to the posterior extremity of the hemisphere, and occupies the angle at the attachment of the falx cerebri to the tentorium cerebelli. The lateral border anteriorly separates the orbital and external surfaces of the frontal lobe, and this part is sometimes termed the superciliary border. Behind the stem of the Sylvian fissure it forms the lower edge of the temporal and occipital lobes. The anterior extremity of each hemisphere is known as the *frontal pole*, the posterior as the *occipital pole*, while the free rounded anterior extremity of the temporal lobe is sometimes termed the *temporal pole*.

The surface of the hemispheres is composed of grey matter, and is moulded into numerous smooth and tortuous eminences, named *convolutions* or *gyri*, which are marked off from each other by *fissures* or *sulci* of varying depth.

The convolutions are covered closely throughout by the vascular investing membrane, the pia mater, which sends processes down to the bottom of the sulci, while the arachnoid membrane passes from one convolution to another, without dipping between them. In general, the breadth of a convolution is some-

[1] The most important work on the naked-eye anatomy of the human cerebral convolutions that has appeared since the last edition of this text-book is Retzius's Das Menschenhirn, 1896, which has been freely consulted in the preparation of this edition.

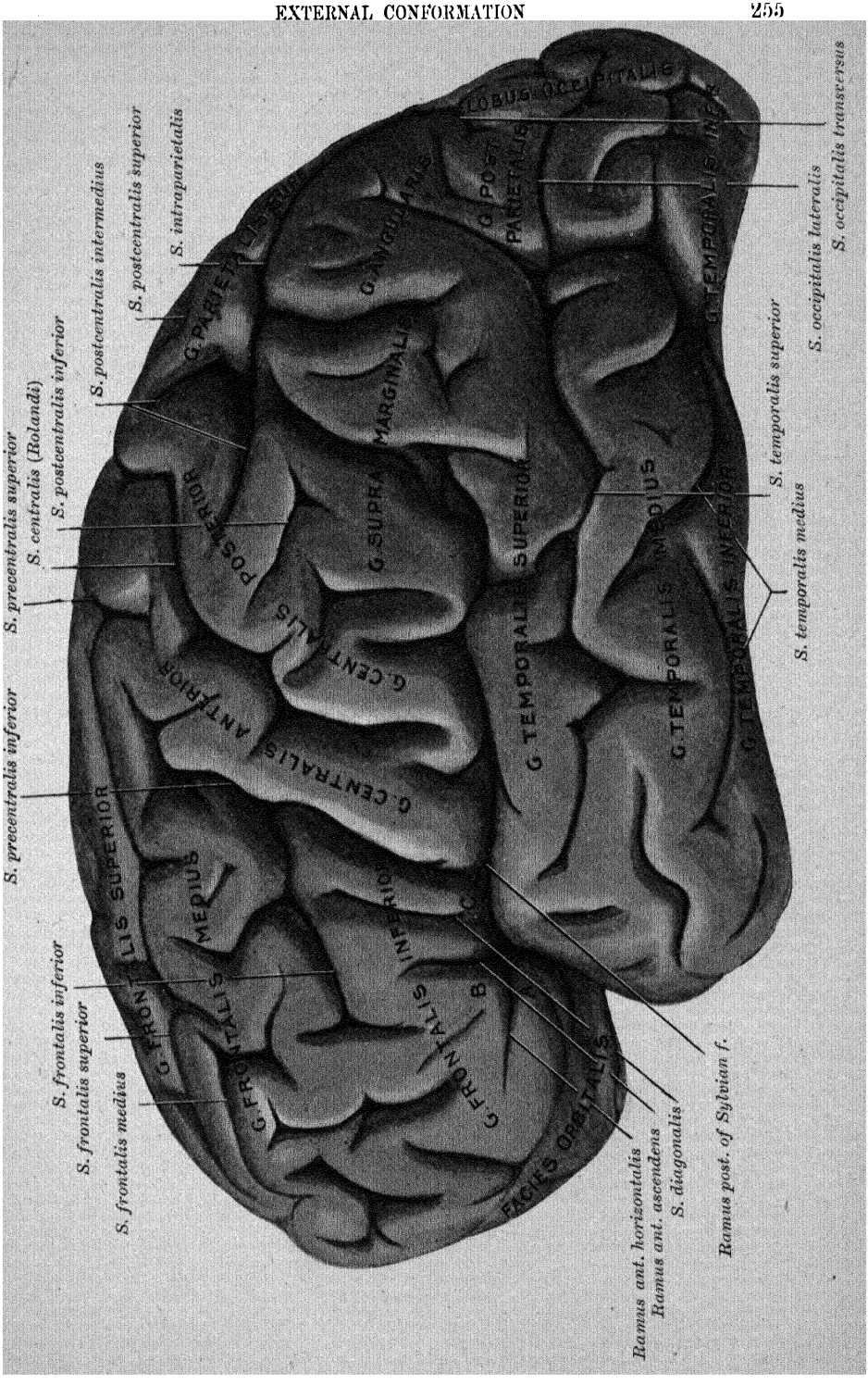


FIG. 255.—LEFT CEREBRAL HEMISPHERE FROM THE LATERAL ASPECT. Natural size. (J. Symington.)
This and the next three figures are from the same cerebral hemisphere.

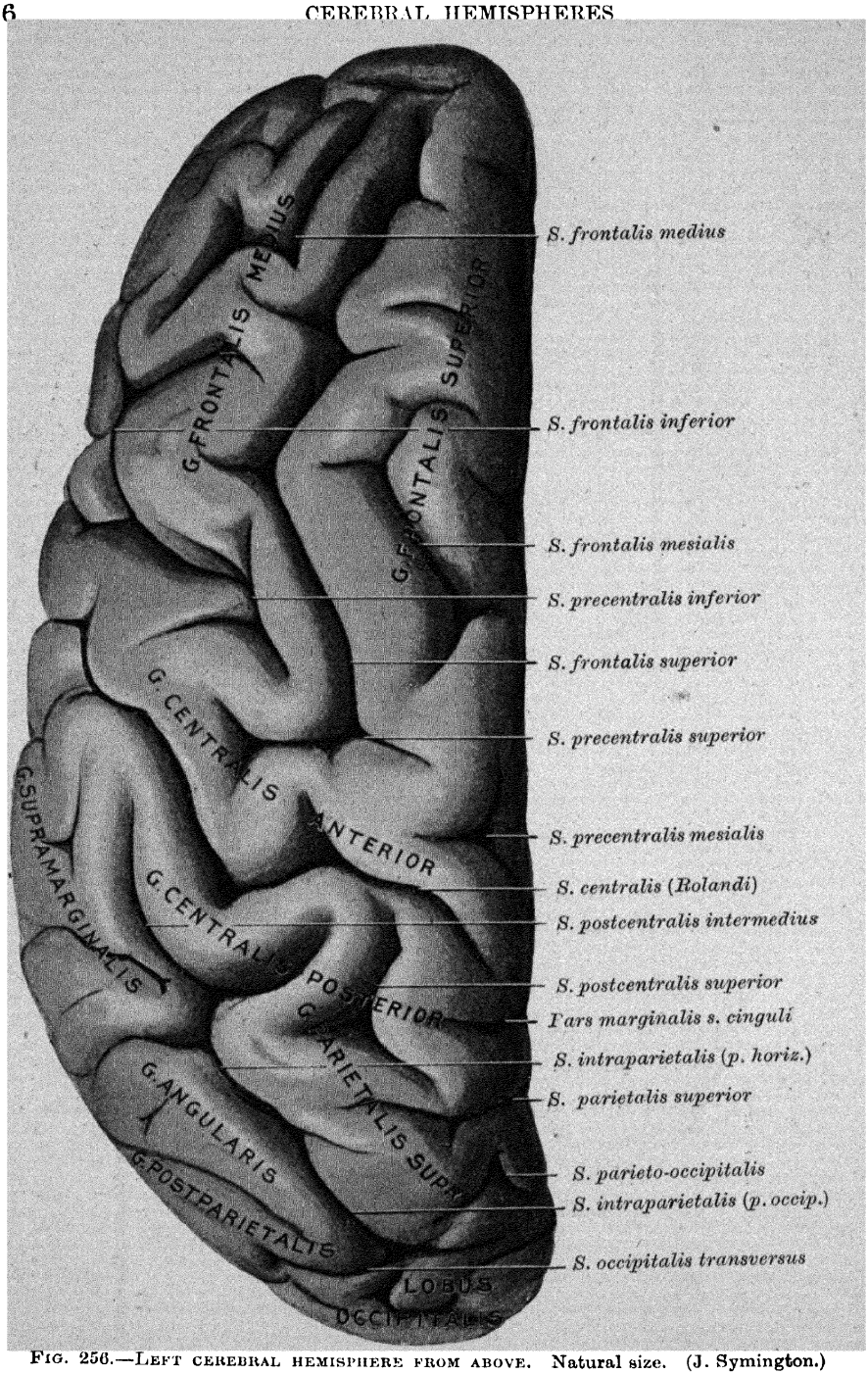


FIG. 256.—LEFT CEREBRAL HEMISPHERE FROM ABOVE. Natural size. (J. Symington.)

what greater at the surface than at the base. The convolutions present considerable variations of position, direction, and complexity in the brains of different individuals, and even in the two sides of the same brain, but they are usually recognisable without much difficulty. It is far easier, however, to trace the more important fissures and convolutions on the brain of a monkey, where they are much less obscured by tortuosities and secondary sulci.

Since the external grey or cortical substance is continuous over the whole surface of the cerebral hemispheres, being found alike within the sulci and upon the gyri, it is obvious that a far greater extent of grey matter is thus provided for with a given size of the brain than could have been the case had the hemispheres been plain and destitute of convolutions; indeed, it is

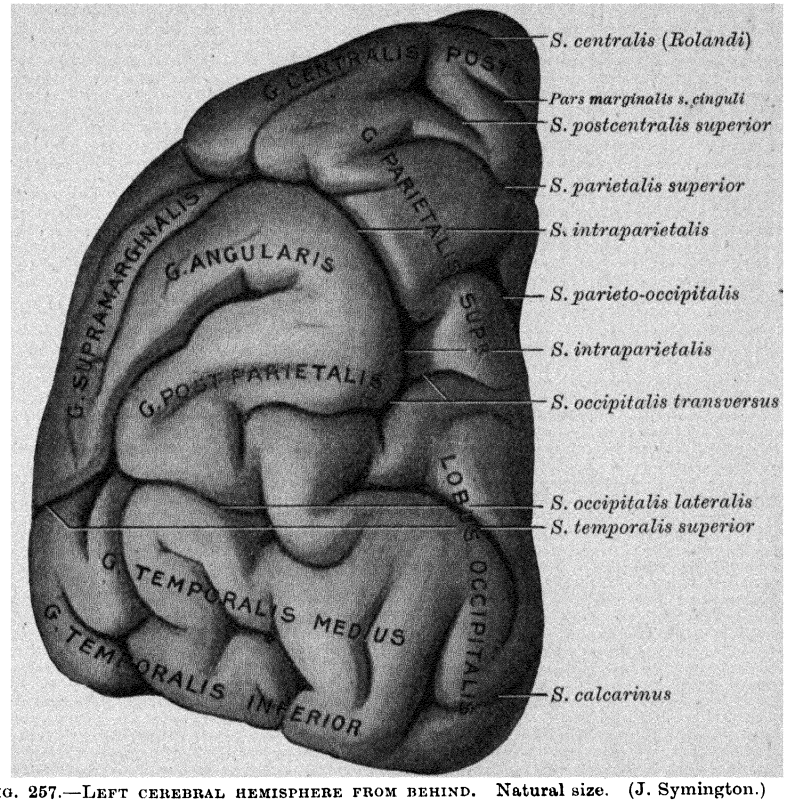


FIG. 257.—LEFT CEREBRAL HEMISPHERE FROM BEHIND. Natural size. (J. Symington.)

calculated that the extent of 'sunken' or 'concealed' surface is twice that of 'exposed' surface.

The sulci between the convolutions vary greatly in depth, being in some parts quite shallow, in others as much as 25 mm. (1 inch) or more deep. The average depth is about 10 mm. or 12 mm.

In the examination of the surface of the hemispheres the student should first ascertain the position of those fissures which by their depth, length, or regularity are most easily recognised, since these will serve as landmarks to assist in the determination of the smaller and less regular ones. The relations of many of the fissures cannot be completely studied without opening them up, as sulci which on a surface view are continuous will often be found to be separated by well-marked deep, or concealed, annectent gyri.

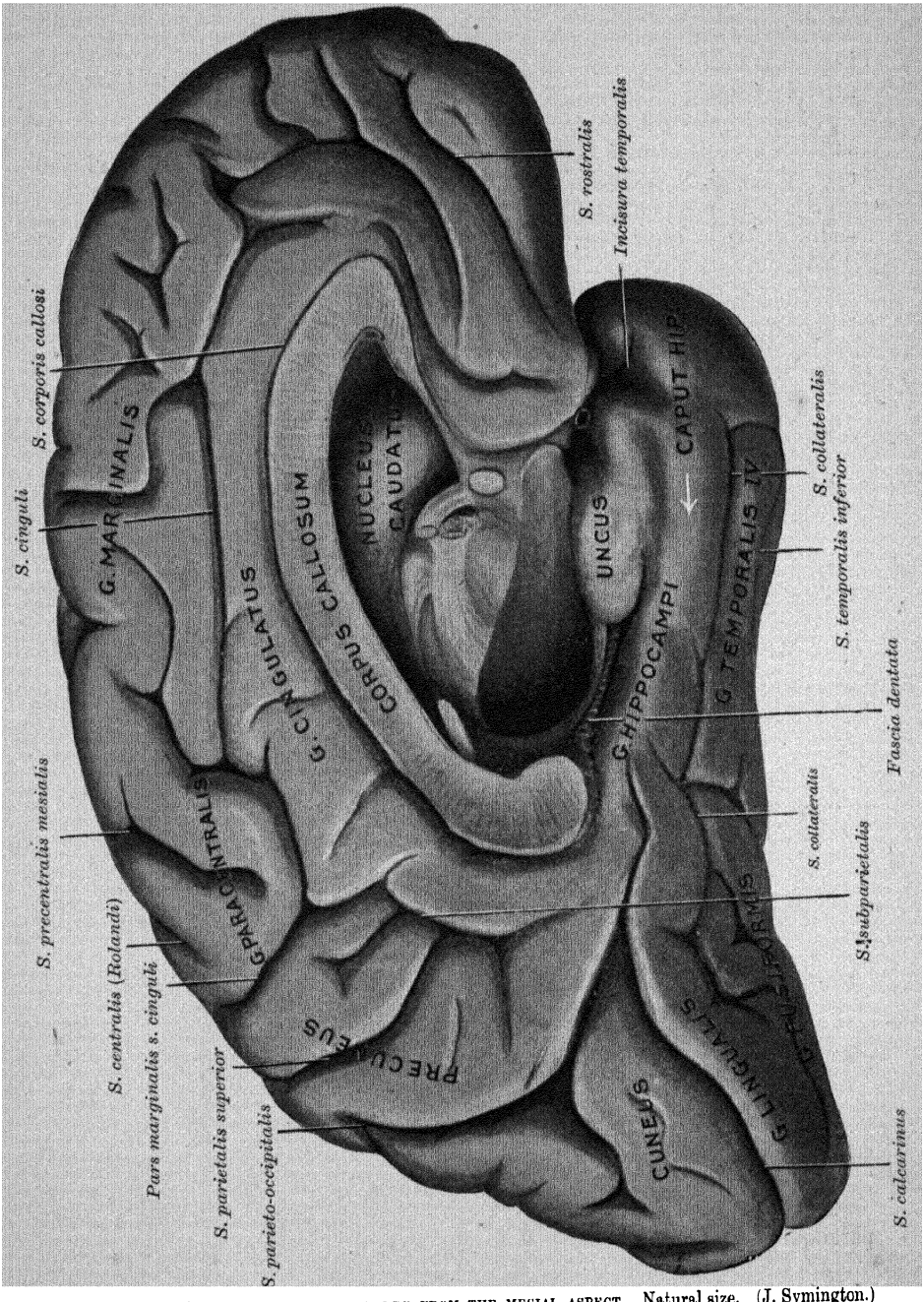


FIG. 258.—LEFT CEREBRAL HEMISPHERE FROM THE MESIAL ASPECT. Natural size. (J. Symington.)
The label 'caput hippocampi' has been placed too far forwards. The caput hippocampi does not extend in front of the incisura temporalis

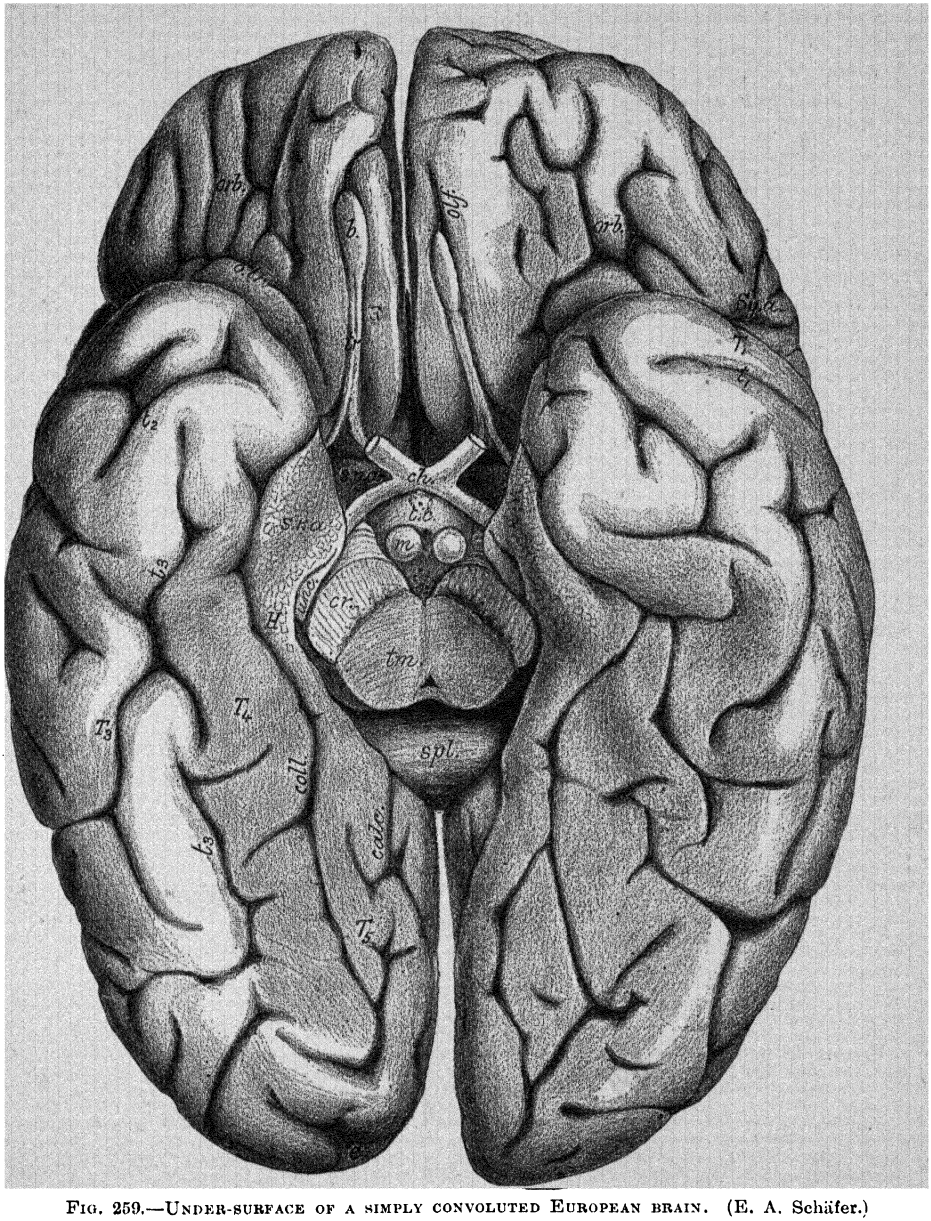


FIG. 259.—UNDER-SURFACE OF A SIMPLY CONVOLUTED EUROPEAN BRAIN. (E. A. Schäfer.)

Sulci—*orb.*, orbital (sagittal rami); *o.tr.*, transverse orbital; *olf.*, olfactory; t_1, t_2, t_3, first, second, and third temporal; *coll.*, collateral (fourth temporal); *calc.*, calcarine.

Gyri—*R*, gyrus rectus; T_1, T_2, T_4, T_5, first, third, fourth, and fifth temporal; *H*, hippocampal; *s.r.a.*, caput gyri hippocampi; *unc.*, uncus.

ch., chiasma; *s.p.a.*, substantia perforata antica; *t.c.*, tuber cinereum; *m*, corpora mamillaria, accidentally separated from one another in the preparation; *cr*, crusta; *tm*, tegmentum; *spl.*, splenium of callosum.

INTERLOBAR FISSURES.

It may be well in the first instance to describe the six chief or 'interlobar' fissures, so called because they are used to mark the hemisphere off into lobes; the lobes themselves, with the convolutions and fissures which are included within them, can then conveniently be taken in order.

Lateral cerebral or **Sylvian fissure** (see figs. 255, 260).—The most distinct fissure in the adult brain, and also one of the first to make its appearance in the development of the embryo, is the *fissure of Sylvius*. This deep and

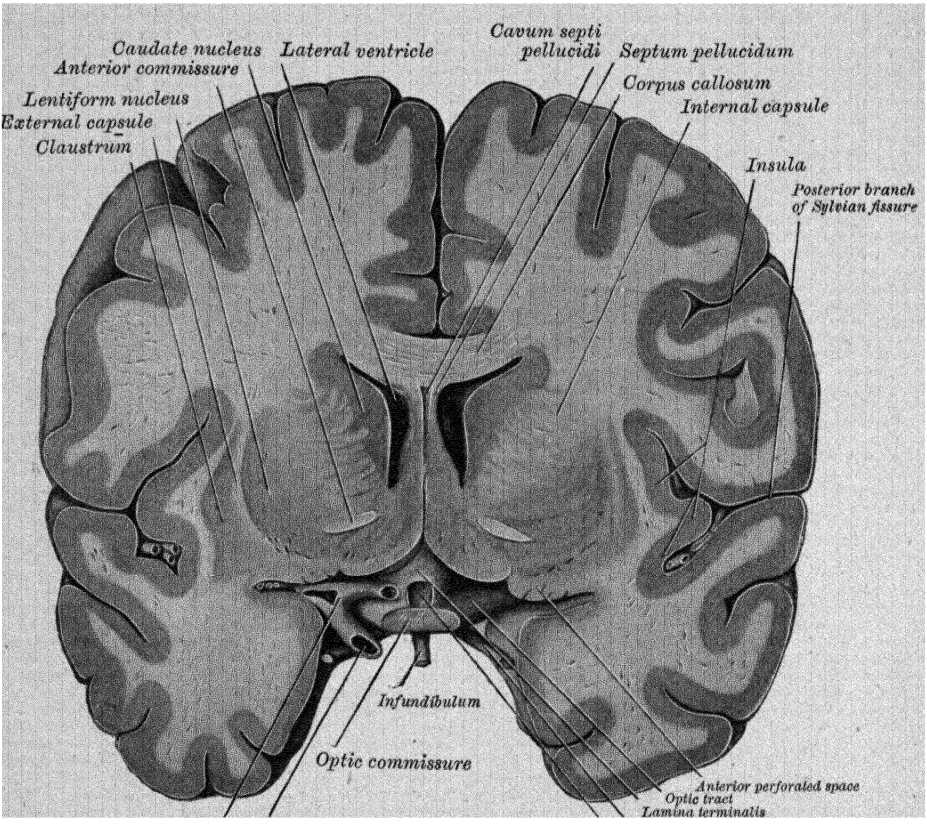


FIG. 260.—VIEW FROM THE FRONT OF A CORONAL SECTION OF AN ADULT BRAIN MADE TWO AND A-HALF INCHES BEHIND THE FRONTAL POLE AND NEARLY ONE INCH BEHIND THE TEMPORAL POLE AND ABOUT HALF AN INCH POSTERIOR TO THE ANTERIOR END OF THE LATERAL VENTRICLES. $\frac{5}{6}$. (J. Symington.)

This and figs. 261 and 262 were made from a brain hardened and cut *in situ* (see fig. 263).

The vallecula Sylvii is seen on each side external to the optic commissure; on the right side of the brain the internal carotid artery is shown dividing in this space into the anterior and middle cerebral arteries.

conspicuous fissure is seen at the base of the brain, opening out as the *vallecula Sylvii* (Broca) below the anterior perforated space. From this origin the fissure passes outwards between the frontal and temporal lobes to the lateral surface of the hemisphere, where it divides into a short anterior and a much longer posterior branch. The anterior branch, after a short course upwards and forwards, usually ends by dividing into an *anterior horizontal* and an *anterior ascending* branch. The posterior branch is continued nearly horizontally as a deep fissure for a considerable distance (8 or 9 cm.) obliquely backwards and upwards in the direction

of the parieto-occipital fissure, having a slightly curved course. It ends at about the junction of the middle and posterior thirds of the lateral surface (midway

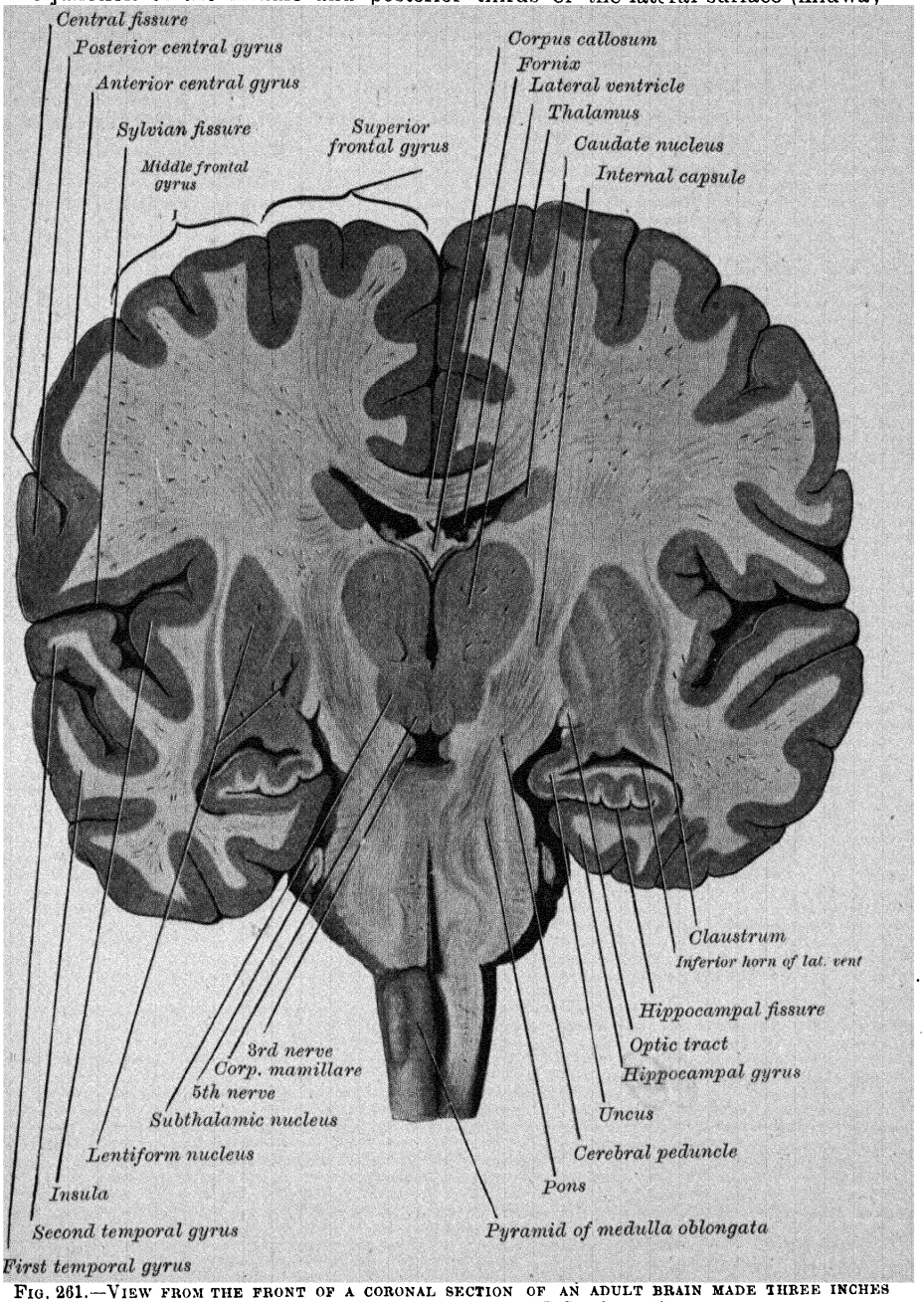


FIG. 261.—VIEW FROM THE FRONT OF A CORONAL SECTION OF AN ADULT BRAIN MADE THREE INCHES BEHIND THE FRONTAL POLE. ⅔. (J. Symington.)

from superior-mesial to lateral border), usually by bifurcating, one branch passing obliquely upwards, the other backwards and somewhat downwards. If the lips of the Sylvian fissure are separated the insula is exposed and the various

branches of the fissure will be found to extend into the sulcus surrounding the insula. The posterior branch, however, extends backwards beyond the insula for a distance of 2 cm. to 3 cm., and this post-insular part passes inwards to within about 1 cm. of the cavity of the descending part of the body of the lateral ventricle. The convolutions which bound the various branches of the Sylvian fissure are folded over the insula so as to conceal it from view (see figs. 260, 261). They form the insular opercula, and belong to the frontal, parietal, and temporal lobes of the brain.

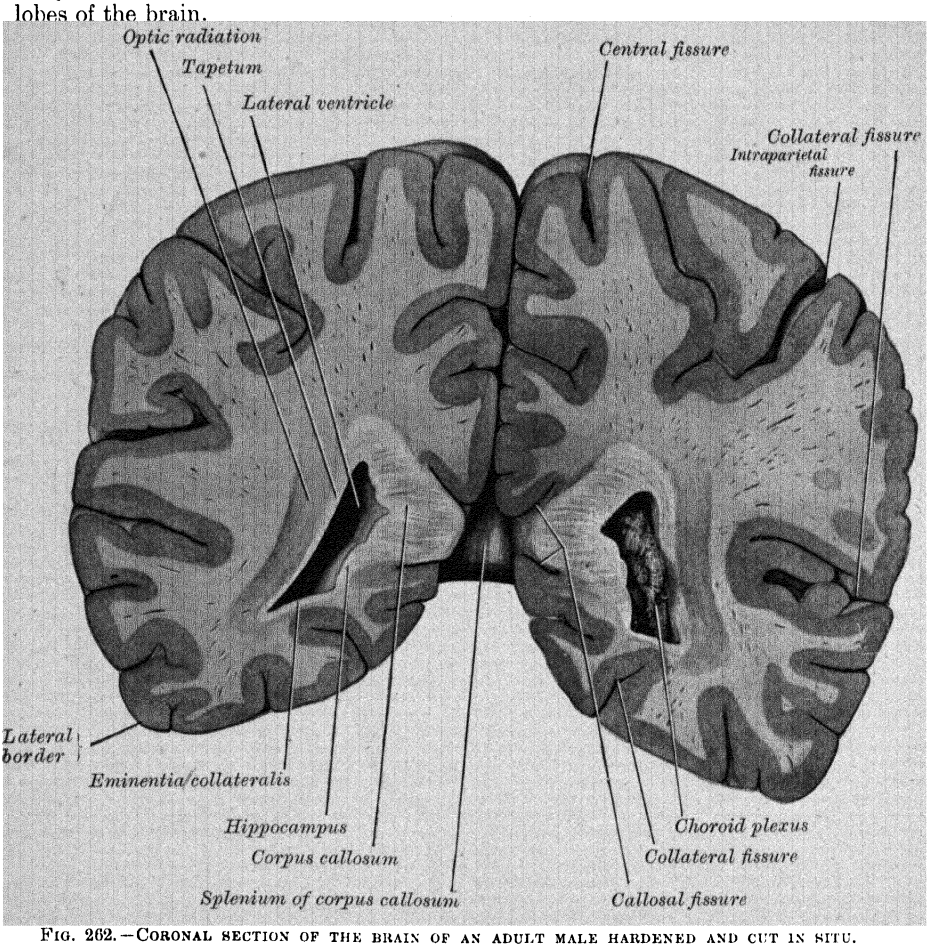


FIG. 262.—CORONAL SECTION OF THE BRAIN OF AN ADULT MALE HARDENED AND CUT IN SITU.

The section was 2¼ inches in front of the occipital pole and just posterior to the splenium of the corpus callosum. On the left side the choroid plexus of the lateral ventricle has been removed. ⅔. (J. Symington.)

The frontal operculum is subdivided by the anterior horizontal and anterior ascending branches of the Sylvian fissure into three parts—an *anterior*, an *intermediate*, and a *superior* (Retzius). The *anterior frontal* portion lies internal to the anterior horizontal branch and is formed by the posterior part of the orbital surface of the frontal lobe; hence it is often termed the *orbital operculum*. The *intermediate frontal operculum* is the smallest and the most irregular owing to the variations in the two anterior branches of the Sylvian fissure between which it is placed. These branches may arise independently from the main fissure (**U** form), from a common stem (**Y** form), or as a single limb (**I** form), in which

case this operculum is absent. The intermediate is often known as the *pars triangularis, cap of Broca,* or *frontal operculum.* Retzius objects to this last name as being misleading, and has suggested the term here adopted (operculum frontale intermedium). The *superior frontal operculum* lies behind the anterior ascending branch of the Sylvian fissure. Its anterior portion belongs to the inferior frontal convolution, and its posterior to the lower end of the anterior central. The *parietal operculum* bounds the posterior horizontal branch of the Sylvian fissure behind the level of the lower end of the central fissure. It is described by Cunningham [1] with the superior part of the frontal operculum as the *fronto-parietal operculum.* The convolution bounding the fissure of Sylvius below is described as the *temporal operculum.*

The relations of the opercula to the branches of the Sylvian fissure and to the insula are best understood by a study of the development of these parts of the brain. In a five months fœtus

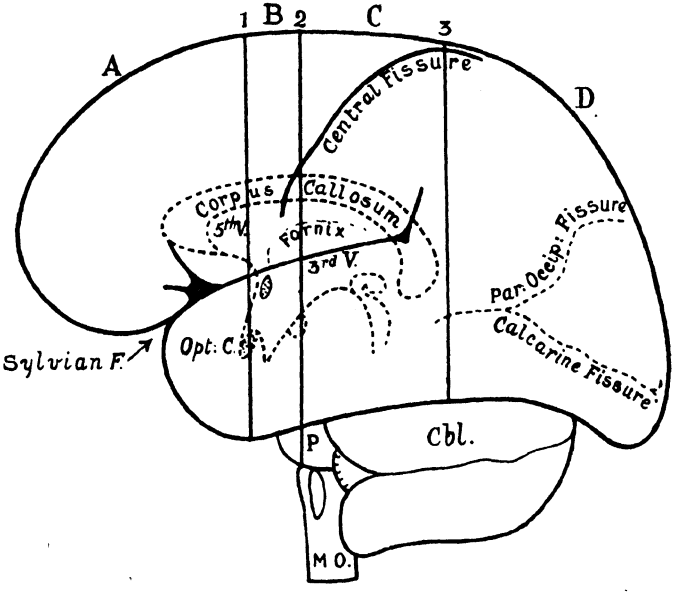


FIG. 263.—THE LATERAL ASPECT OF THE LEFT SIDE OF THE BRAIN, WITH THE POSITION OF CERTAIN STRUCTURES ON THE MESIAL ASPECT INDICATED BY DOTTED LINES.

The three vertical lines 1, 2, and 3 show the position of the three coronal sections represented in figs. 260, 261, and 262. A, B, C, D are the four pieces into which the cerebrum was divided. (J. Symington.)

(see fig. 264) the insula is uncovered, occupies a somewhat depressed triangular area on the lateral aspect of the cerebral hemispheres, and is separated by a limiting sulcus from the adjacent cortex, which is more prominent and represents the developing opercula. In a seven months fœtus (see fig. 265) the growth of the opercula is more advanced, but a considerable part of the insula is still visible, as the superior frontal and the temporal opercula have not yet met the inferior frontal operculum. At full time a small area of the insula remains uncovered, but in the adult the whole lobe is generally concealed (see fig. 255).

The horizontal and ascending branches arose by a common stem from the main fissure (Y form) in 32 per cent. of the hemispheres examined by Cunningham; independently (V and U form) in 37·5 per cent.; and as a single limb (I form) in 30 per cent. Eberstaller [2] found a single branch in 24 per cent. of his cases, but it only occurred fourteen times in 100 hemispheres examined by Retzius.[3] The posterior branch of the Sylvian fissure is both absolutely (Eberstaller)

[1] Contribution to the Surface Anatomy of the Cerebral Hemispheres, 1892.
[2] Das Stirnhirn, 1890. [3] Das Menschenhirn, 1896.

and relatively to the length of the hemisphere (Cunningham) longer on the left than on the right side. There are sometimes two secondary extensions of the Sylvian fissure on to the orbital lobe (orbital limbs), but these are less deep and have not the same morphological importance as the others.

Central fissure.—The *central sulcus*, or *fissure of Rolando*[1] (fig. 255 and fig. 256), extends across the lateral convex surface of the hemisphere inter-

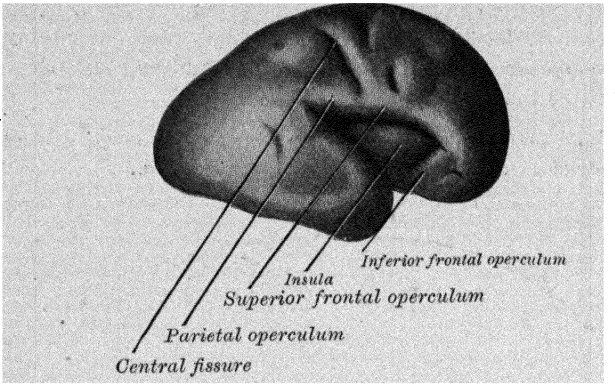


FIG. 264.—RIGHT CEREBRAL HEMISPHERE OF FIFTH MONTH FŒTUS, VIEWED FROM THE LATERAL ASPECT. Natural size. (J. Symington.)

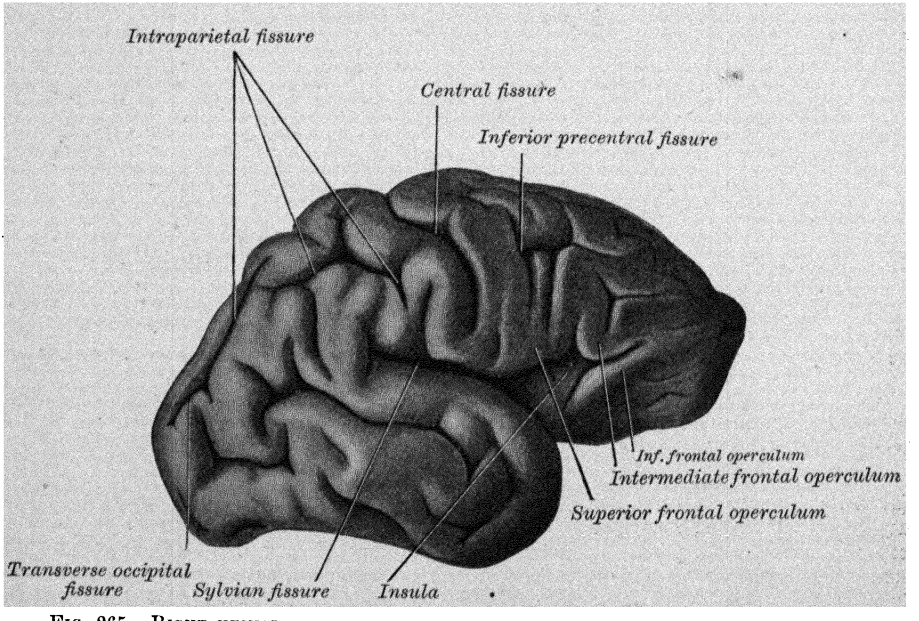


FIG. 265.—RIGHT HEMISPHERE OF BRAIN OF SEVEN MONTHS FŒTUS, VIEWED FROM THE LATERAL ASPECT. Natural size. (J. Symington.)

rupting the general longitudinal course of the gyri and sulci. The parallel convolutions which bound it are named the *anterior* and *posterior central* gyri.

[1] Although thus named by Leuret (Anatomie comparée du système nerveux, 1839), from attention having been directed to it by Rolando a few years previously, this fissure was noticed and figured by Vicq d'Azyr (Traité d'Anatomie et de Physiologie, 1796).

It begins above, near the vertex or highest point of the hemisphere, somewhat behind the middle of the great longitudinal fissure, and passes outwards, downwards, and forwards to end near the middle of the fissure of Sylvius, the posterior limb of which it sometimes (but rarely) joins. The junction when present is effected by the medium of a small sulcus, *anterior subcentral sulcus* (*inferior transverse sulcus* of Eberstaller), which is usually separated from the lower end of the central fissure by an annectent gyrus joining the two central convolutions. The central fissure usually reaches the superior mesial border of the hemisphere, but sometimes stops short of that line; it generally exhibits a hook-like backward inclination at this extremity. The anterior and posterior walls have several buttresses which fit into corresponding recesses on the opposite wall, but as a rule these buttresses do not cross the floor, so that the fissure is of fairly uniform depth (2 cm.), except near its two extremities, where it rapidly becomes shallower. One of the largest and the most constant buttress is found on the anterior wall about an inch to an inch and a half from the middle line (fig. 256). It produces a curve on the central fissure with its concavity forwards, known as the *superior genu*. Below this the fissure forms another curve (inferior genu) with its convexity forwards. The lowest part of the fissure is nearly vertical and is often slightly bent. This fissure is very rarely interrupted in its course, although on separating its lips it may sometimes be seen that there is a slight tendency to the appearance of an annectent gyrus about the level of the superior genu, and it is here that the interruption is liable to occur. The central fissure appears early (end of fifth month), being laid down in two parts—an upper shorter, and a lower longer portion (Cunningham). In this double mode of origin it resembles the precentral and postcentral sulci.

R. Wagner found the fissure interrupted in the brain of Professor Fuchs. Eberstaller met with this anomaly twice in 200 brains, and in both cases it was unilateral. It did not occur at all in 100 hemispheres examined by Retzius. A. W. Campbell[1] observed the interruption 13 times in 1,400 brains, and he believes it to be produced by an excessive development of a precentral buttress which is constantly present just above the superior genu.

The acute angle which the slope of the fissure of Rolando (central fissure) forms with the superior border of the hemisphere is known as the Rolandic angle. According to Cunningham it averages 71·7°. The two Rolandic fissures form therefore, when looked at from above, a wide **V**, open forwards and forming an angle of 143°. The length of the fissure is about $3\frac{3}{4}$ inches (8 cm.) when the measurement is made along a straight line on the surface of the brain between its two extremities. It is relatively longer and more curved in the anthropoid apes than in man.

This fissure has once been found duplicated, the two fissures replacing it being separated by a gyrus (g. Rolandicus) along their whole length (Giacomini). The condition was present in both hemispheres of the same brain.

Parieto-occipital fissure.—The *parieto-occipital fissure* is best marked on the mesial surface of the hemisphere, where it appears as a deep cleft (fig. 258)—*internal part of the parieto-occipital fissure*—extending downwards and a little forwards from the superior margin of this surface to near the posterior extremity of the corpus callosum, where it usually joins the calcarine fissure, the two together forming a **Y** which encloses a wedge-shaped portion of the occipital lobe (*cuneus*). On the convex surface the fissure is continued transversely outwards for a variable distance, generally about half an inch (12 mm.), forming the *external part of the parieto-occipital fissure* (fig. 256). This fissure is here taken as the division between the parietal and occipital lobes.

If the parieto-occipital fissure be opened up it will be seen that it does not really join the calcarine, being separated from it in the depth of the fissure by a cuneo-limbic annectent gyrus (gyrus cunei of Ecker). This gyrus is better developed in the anthropoid apes, where it usually

[1] Histological Studies on the Localisation of Cerebral Function, 1905.

appears on the surface and completely separates the parieto-occipital and calcarine fissures, whereas in man this only occurs as an occasional variation (3·9 per cent. of cases, Cunningham).

The parieto-occipital fissure is seldom a simple fissure of uniform depth. Cunningham [1] described a deep annectent convolution crossing the internal part of the parieto-occipital fissure at about the junction of its upper and middle thirds. Retzius [2] has shown that there may be several such deep cuneo-precuneate convolutions; while in other cases the fissure divides above into two branches separated by a superficial *parieto-occipital lobule*.[3] Elliot Smith [4] has described a *fossa occipito-parietalis* in the depths of which are found a large convolution, *arcus intercuneatus*, with three fissures, a sulcus limitans præcunei, an incisura parieto-occipitalis, and a sulcus paracalcarinus. All of these may appear on the surface, in which case there is no parieto-occipital fissure in the usual meaning of this term. The size of its external portion depends (inversely) on the size of the annectent gyrus which curves round its outer extremity and connects the parietal with the occipital lobe. In Primates the external portion of this fissure is concealed within a deep transverse cleft (*Affenspalte*, figs. 278 to 291) which intervenes between the parietal and occipital lobes, the cleft tending obliquely backwards, so that the occipital edge somewhat overlaps the parietal (*occipital operculum*).

The question as to whether or not the 'Affenspalte' is represented in the human brain, and if so by what fissure, is still disputed. Bischoff [5] considered it was represented by a temporary fissure (external perpendicular) which appears during the fifth and sixth months of fœtal life. Cunningham [6] supported this view and believed that the fissure, at least in the great majority of cases, gradually disappears, so that an 'Affenspalte' is not usually present in the adult. Hochstetter [7] has brought forward important evidence to show that the so-called temporary fissures are due to post-mortem changes, so that the existence under normal conditions of Bischoff's external perpendicular fissure is doubtful. Ecker [8] held that the 'Affenspalte' of the apes was homologous with a fissure which he terms *sulcus occipitalis transversus*, and Eberstaller [9] supported this view. Cunningham considered that this fissure belongs to the intra-parietal system of fissures, being the bifid extremity of its occipital portion and not the representative of the 'Affenspalte.' Elliot Smith [10] maintains that the 'Affenspalte' is present in the great majority if not in all human brains as a curved sulcus (*sulcus occipitalis lunatus*) situated on the lateral aspect of the occipital lobe. The principal reason which Elliot Smith advances in support of his view is that the stria of Gennari extends into the caudal lip of the 'Affenspalte' in apes and of the sulcus occipitalis in man.

The calcarine fissure (Huxley).—This is seen on the mesial surface of the hemisphere (fig. 258). It is a deep fissure, extending from near the posterior extremity of the brain, where it usually begins in a T-shaped fork, in a course curved at first upwards and then downwards, and ending below the splenium of the corpus callosum. The forked posterior extremity near the occipital lobe is sometimes cut off from the rest of the fissure, and appears as an independent sulcus (*sulcus extremus* of Schwalbe; *fissura extrema* of Seitz). In many Primates the anterior extremity appears to be continued into the hippocampal fissure, but this is usually superficial only, and occurs but rarely in the human brain.

J. S. Bolton [11] found the calcarine fissure bifurcated at its posterior extremity in 35 out of 40 hemispheres; the average lengths of the upper and lower limbs were $\frac{5}{8}$ inch and $\frac{3}{4}$ inch respectively. Not infrequently one or both of these limbs extend on to the outer surface of the hemisphere.

D. J. Cunningham [6] showed that the calcarine fissure is divisible developmentally into an anterior and a posterior portion. The former appears early as a simple total fissure; the latter is developed later as two shallow depressions which subsequently join one another and the

[1] Contribution to the Surface Anatomy of the Cerebral Hemispheres, 1892.
[2] Menschenhirn, 1896.
[3] He found the lobule in 22 out of 100 hemispheres.
[4] Studies in the Morphology of the Human Brain. Cairo, 1904.
[5] Die Grosshirnwindungen des Menschen. München, 1868.
[6] Contribution to the Surface Anatomy of the Cerebral Hemispheres, 1892.
[7] Beiträge zur Entwickelungsgeschichte des Gehirns, 1898.
[8] Zur Entwickelungsgeschichte der Furchen und Windungen der Grosshirnhemisphären im Foetus des Menschen, 1869.
[9] 'Zur Oberflächen-Anatomie der Grosshirnhemisphären,' Wiener Med. Blätter. 1884.
[10] 'The so-called "Affenspalte" in the Human (Egyptian) Brain,' Anat. Anzeiger, Oct. 1903.
[11] 'The Exact Histological Localisation of the Visual Area of the Human Cerebral Cortex,' Phil. Trans. 1900.

anterior fissure. He holds that the anterior fissure is morphologically much the more important, since it is deeper and more constant; and it is this part which indents the posterior horn of the lateral ventricle and forms the calcar. The anterior calcarine fissure cuts into the hippocampal gyrus in front, and behind extends between two deep annectent gyri, cuneo-limbic and anterior cuneo-lingual. The greater part of the calcarine fissure lies within an area where the cortex is distinguished by having a white line, visible to the naked eye, in the grey matter, termed the line of Gennari. This area is the chief end-station of the optic radiations and is termed the visuo-sensory area. Its limits were mapped out by J. S. Bolton,[1] and subsequently by A. W. Campbell and Elliot Smith. It occupies the bottom and sides of the posterior calcarine fissure and extends on to the adjacent superficial cortex, but it does not reach quite to the anterior end of the anterior calcarine fissure, and where present is confined to the lower wall of the fissure and a narrow strip of superficial cortex below it. Elliot Smith considers that the calcarine fissure ought to be described as consisting of a prestriate and an intrastriate portion (see p. 372).

Two annectent gyri (*anterior* and *posterior cuneo-lingual*) are often found in the calcarine fissure, one between the anterior and posterior parts of the fissure, the other crossing the posterior part.

The collateral fissure (Huxley).—This is seen on the inferior surface, where it lies below and parallel to the anterior part of the calcarine (figs. 258, 259, *coll.*). It extends forwards towards the tip of the temporal lobe, but does not reach the extremity of the lobe. The middle part of this fissure, which mainly causes the projection of the collateral eminence in the lateral ventricle, is formed independently of the two extremities. The anterior portion often remains distinct from the middle part and with the incisura temporalis partly separates the enlarged anterior extremity of the hippocampal gyrus (pyriform lobe) from the temporal lobe, and occasionally these two fissures are continuous with one another, forming as in apes a distinct *rhinal fissure*.[2]

The **sulcus cinguli** or **calloso-marginal fissure** (Huxley) is an extensive fissure of the mesial surface, which begins below the rostrum of the corpus callosum close to the anterior perforated space, and sweeping round the genu of the callosum runs parallel to that body, separated from it by the gyrus cinguli, and from the upper margin of the hemisphere by the marginal gyrus, as far as a little behind the middle of the hemisphere, where it turns obliquely upwards, and ends a short distance behind the commencement of the central fissure (fig. 258). Both the anterior and the posterior parts of this fissure are developed independently of and are often permanently distinct from the middle part. The anterior part or *prelimbic fissure* sweeps round the genu of the corpus callosum, and when distinct from the middle part passes obliquely upwards towards the upper margin of the hemisphere. In any case it usually sends a well-marked ascending branch towards the margin. The posterior part of the cingulate (*pars marginalis*, fig. 258) hooks round the inflected end of the central fissure, and is curved round the paracentral lobule, which it bounds below and behind.

The six fissures which have been described are used by anatomists to map out the surface of the brain into regions to which the name of 'lobes' has, not very appropriately, been applied. In all, seven lobes are enumerated—viz. the *frontal*, *parietal*, *occipital*, *temporal*, *insular*, *limbic*, and *olfactory*. It must, however, be understood that these so-called lobes have by no means an equal morphological value, nor do they correspond precisely with the functional differentiations of the hemisphere which can be made out as the result of experiments on animals, and clinical and pathological observations in man. The distinction is further artificial because the so-called lobes are in many places not marked off from one another otherwise than by imaginary lines. Nevertheless it is found convenient for purposes of anatomical description to consider the surface of the brain as thus constituted, and the lobes will accordingly be here described in the order in which they have been above enumerated.

[1] Phil. Trans. 1900.

[2] See Retzius, Das Menschenhirn, Tafel lx.

FRONTAL LOBE.

The central fissure, passing obliquely downwards from the superior mesial border of the hemisphere towards the Sylvian fissure, marks off the anterior part of the hemisphere—constituting in man nearly one-third of the whole—as the *frontal lobe*. This term, however, includes not only the part of the external surface which is thus marked off, but the corresponding adjacent part (marginal convolution) of the mesial surface, as far as the cingulate fissure, and also the under or orbital surface situated in front of the stem of the Sylvian fissure. In the description of the fissures and convolutions within the lobe these three surfaces will be separately considered.

EXTERNAL SURFACE OF THE FRONTAL LOBE.

The **precentral sulcus** (*pre-Rolandic sulcus* of Broca) (fig. 255) has a direction parallel with that of the central fissure, from which it is separated by the anterior central gyrus. It is sometimes complete, but more usually is subdivided into two or three separate portions by annectent gyri, which connect the anterior central with the superior and middle frontal respectively; a third annectent gyrus passes below the lower end of the fissure, and unites the anterior central with the inferior frontal. The uppermost portion (*sulcus precentralis mesialis*, fig. 256) cuts the upper border of the hemisphere, and appears on the mesial surface (fig. 258), often as a well-marked vertical fissure, which occasionally runs into the cingulate, to which it has sometimes been regarded as belonging.[1] The next portion (*sulcus precentralis superior*) is very often continued forwards into the first frontal sulcus (fig. 256). Its middle part is opposite the upper genu of the central fissure. The inferior portion (*sulcus precentralis inferior*) is by far the best marked. It separates the anterior central from the inferior and part of the middle frontal gyri, and usually gives off a well-marked branch anteriorly into the middle frontal gyrus. The inferior precentral sulcus is often joined to the Sylvian fissure, either directly or through the intermediation of the sulcus subcentralis anterior or of the sulcus diagonalis, but there is usually, perhaps invariably, an annectent gyrus concealed in the depth of the fissure even in these cases. The inferior frontal sulcus sometimes appears to spring from the inferior precentral, near its middle, but the two are probably more frequently separated by an annectent gyrus which here joins the middle and inferior frontal gyri.

Two well-marked sagittal sulci (*superior* and *inferior frontal*) course over the external surface of the frontal lobe in front of the precentral fissure; they subdivide this part of the lobe into three sagittal gyri—*superior*, *middle*, and *inferior*. Besides these constant sulci, there are certain others which are less constant in their occurrence and in the extent to which they are developed as connected fissures—viz. one running along the middle of the superior frontal gyrus, which we will term, from its position near the upper border, the *sulcus mesialis* (Cunningham) (fig. 256), and one running along the centre of the middle frontal gyrus (*sulcus frontalis medius* of Eberstaller) (fig. 256). Both of these are not only inconstant in their occurrence, but when present are frequently interrupted, and then appear to consist of a series of separate parts, which are often united here and there with the other frontal sulci.

The mid-frontal sulcus (*s. frontalis medius*) usually bifurcates in front, and becomes transverse (*s. transversus anterior*, *fronto-marginal sulcus* of Wernicke).

The **superior frontal sulcus** is developed after the inferior, and along with the superior precentral, with which it is usually in direct continuity. This

[1] Schwalbe, Lehrbuch der Neurologie, 1881.

sulcus is often interrupted by superficial annectent gyri passing obliquely from before backwards from the superior to the middle frontal convolution. Anteriorly, the superior frontal often passes into the mid-frontal sulcus (Cunningham). Posteriorly, its line may be continued by a branch from the superior precentral sulcus into the anterior central gyrus.

The **inferior frontal sulcus** usually curves forwards from the middle of the inferior precentral sulcus towards the frontal pole of the hemisphere. Several small secondary furrows pass from it above and below, and it is sometimes subdivided by superficial annectent gyri into three portions. Anteriorly it bifurcates, forming a transverse piece, which may develop separately. At the apex of the lobe, in front of and sometimes forming part of this fissure, are one or two transverse sulci forming the *sulcus radiatus* and *lateral fronto-marginal sulcus* of Eberstaller.

Gyri.—Four convolutions are described upon this surface, three of which run antero-posteriorly, while the fourth takes a direction obliquely across the brain, and parallel with the central fissure. The three antero-posterior convolutions are termed respectively the *superior*, *middle*, and *inferior*, or *first*, *second*, and *third frontal gyri*. They are separated from one another by the upper and lower longitudinal frontal sulci, and from the fourth or anterior central gyrus by the precentral sulci, which run parallel to the central fissure.

The **superior frontal gyrus**, which is much the longest, runs parallel with the upper margin of the hemisphere, over which it is continuous with the marginal convolution of the mesial surface, the two in fact really forming a single convolution to which the name first frontal is frequently applied. This convolution reaches the frontal pole of the hemisphere in front; behind it is partly continued into the upper end of the anterior central gyrus, partly separated from that gyrus by the upper end of the precentral sulcus; below it is marked off from the middle frontal by the irregular and somewhat interrupted superior frontal sulcus. It is sometimes subdivided by a longitudinally coursing sulcus mesialis (see fig. 256) into two parts, but less often than the middle gyrus. This subdivision is rarely found in the brain of the negro.

The **middle frontal gyrus** runs below and parallel to the first. It is separated from the anterior central by the superior and inferior precentral sulci, between which there is usually a well-marked annectent gyrus. The inferior frontal sulcus separates it from the third gyrus. It is also often partially subdivided by a longitudinally coursing sulcus frontalis medius (see fig. 256) into two parts, an upper and a lower, which are sometimes described as distinct convolutions.

The **inferior frontal gyrus**, the smallest of the three, is curved around both the horizontal and ascending branches of the anterior limb of the Sylvian fissure, which deeply indent the gyrus and subdivide it into three parts—*anterior* (pars orbitalis), *intermediate* (pars triangularis), and *superior*, or posterior (pars basilaris) (see fig. 266, A, B, C). The left gyrus is often called Broca's convolution, and is more developed than the right one, perhaps corresponding with the localisation of the speech centre on the left side. This increased development chiefly affects the triangular or intermediate part. When well developed the triangular part entirely separates the horizontal and ascending fissures; when less marked they are confluent below; if the triangular part is absent they are entirely confluent. This inferior frontal gyrus is connected at its lower and posterior end by an annectent gyrus with the lower end of the anterior central gyrus, while at its anterior end it passes round to the orbital surface of the lobe. This gyrus is bounded posteriorly by the inferior precentral, and sometimes also by the anterior subcentral sulcus.

It is occasionally subdivided into two by a longitudinal sulcus concentric with the inferior frontal (Giacomini).

The posterior portion of the gyrus (pars basilaris) is subdivided into an anterior and a posterior portion by the sulcus diagonalis of Eberstaller (see fig. 255). This is usually distinct, and lies in front of the lower end of the inferior precentral sulcus, but sometimes joins this sulcus, the inferior frontal, or even the Sylvian. The pars triangularis is also often scored by secondary sulci.

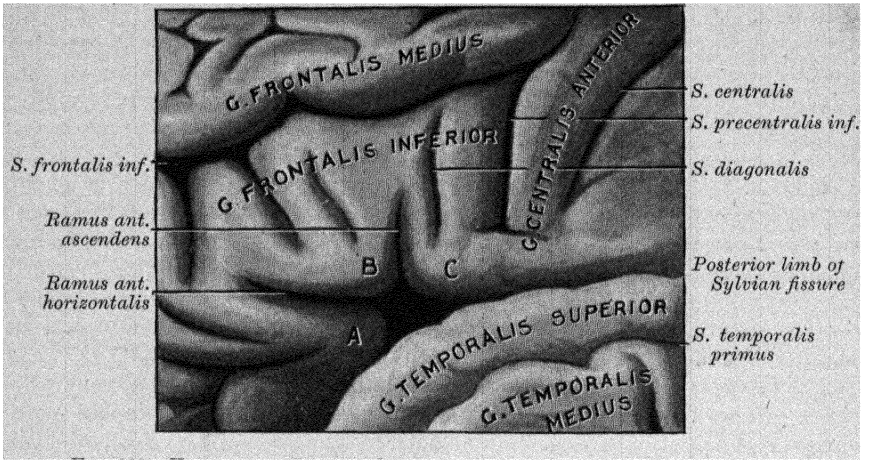


FIG. 266.—VIEW OF THE INFERIOR FRONTAL GYRUS OF THE LEFT HEMISPHERE, FROM THE SAME BRAIN AS FIG. 267. (E. A. Schäfer.)

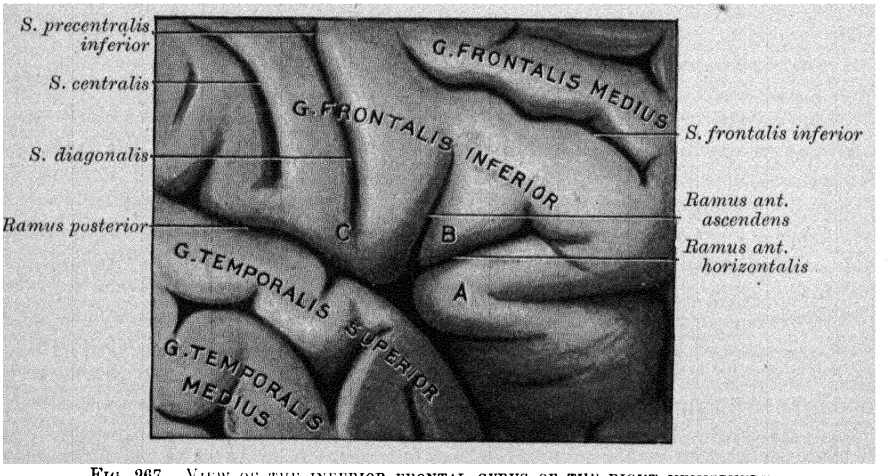


FIG. 267.—VIEW OF THE INFERIOR FRONTAL GYRUS OF THE RIGHT HEMISPHERE, FROM THE SAME BRAIN AS FIG. 266. (E. A. Schäfer.)

The **anterior central, precentral,** or **ascending frontal gyrus** (figs. 255 and 256) lies between the central and the precentral sulci, and extends from the superior margin of the hemisphere (where it is continuous with the posterior part of the marginal gyrus on the mesial surface) to the Sylvian fissure. It is narrowest in the middle, enlarging somewhat above and below. It is usually connected, as just mentioned, with each of the three longitudinal frontal convolutions by an annectent gyrus, the precentral sulcus

being thereby considerably interrupted. There is a similar connexion by a curved annectent gyrus below the central fissure with the posterior central convolution.

MESIAL SURFACE OF THE FRONTAL LOBE.

On the mesial surface of the hemisphere there is only one convolution which is considered to belong to the frontal lobe—viz. the **marginal gyrus** (fig. 258). This, as above explained, is continuous over the upper border with the superior frontal gyrus on the external surface. It is separated from the cingulate gyrus of the limbic lobe by the sulcus cinguli, and is partially interrupted by the ascending branches of that fissure. Besides these, there is often, but not constantly, a sagittal fissure running along the middle of the convolution. This fissure (*sulcus marginalis*) subdivides the middle of the gyrus into superior and inferior parts. The antero-inferior part of the marginal gyrus is marked by two or three sulci which are curved concentrically with the prelimbic part of the cingulate sulcus. These have been termed by Eberstaller the *rostral sulci*. Below the genu of the callosum the marginal gyrus is continuous with the limbic lobe by one or more broad *fronto-limbic annectent gyri*. Other annectents are found between the several parts of the cingulate sulcus, when this is subdivided; when it is not subdivided they are concealed in its depth. At its posterior end the marginal gyrus becomes continuous with the two central gyri on either side of the upper extremity of the central fissure. But this posterior part of the marginal gyrus is sometimes nearly cut off from the rest of the gyrus by the sulcus precentralis mesialis, and is distinguished as the **paracentral lobule** (fig. 258).

ORBITAL SURFACE OF THE FRONTAL LOBE.

The **orbital sulcus** (H-shaped sulcus, triradiate sulcus) is a complex of sulci, which extends over the greater part of the concave orbital surface of the frontal lobe. It consists of a posterior part (*sulcus orbitalis transversus* of Weisbach, fig. 259), which curves inwards from near the anterior branch of the Sylvian fissure in an arch convex forwards, to end mesially near the lateral root of the olfactory tract; and of three or four sulci having a general sagittal direction (*sulci orbitales sagittales*), and usually communicating posteriorly with the transverse orbital. These sagittal sulci vary greatly in their number and extent, and in the number and direction of the secondary and tertiary sulci, which come off from them, and they frequently produce, with the transverse sulcus, the figure of an H, K, or X. Weisbach has endeavoured to connect these variations with racial and sexual differences, but there does not seem to be any foundation for such connexion, and in fact (as is well shown in fig. 259) two entirely different types may be found on opposite hemispheres of the same brain.

Three convolutions are described as lying in front of the transverse orbital sulcus, named, according to their position, the **inner, middle,** and **outer orbital gyri**. The last of these is continuous at the side with the inferior frontal, the first and second are the continuations of the superior and middle frontal convolutions.

On the inner gyrus is seen the **olfactory sulcus** (*olf.*) in which the olfactory tract and bulb lie. It has a straight course nearly parallel with the great longitudinal fissure, somewhat inclining towards it. The part of the inner gyrus between the olfactory sulcus and the mesial border is sometimes known as the *gyrus rectus* (*R*). Behind the transverse orbital sulcus, between it and the anterior limiting sulcus of the insula, is a fourth gyrus, the **posterior**

orbital, which is continuous externally with the inferior frontal and is often grooved by the posterior border of the lesser wing of the sphenoid bone.

The continuity of the convolutions of the external with those of the orbital surface is often interrupted by a sulcus which crosses their direction, extending across the front of the lobe from the anterior end of the Sylvian fissure (*sulcus fronto-orbitalis*, Giacomini; *fronto-marginalis lateralis*, Eberstaller).

CONCEALED AREA OF THE FRONTAL LOBE.

In addition to that part of the frontal operculum which is exposed on the external surface of the hemisphere there is an area of cortex belonging to this operculum which is fully as extensive as the exposed area, although it has been almost entirely ignored by anatomists except Rüdinger [1] and Retzius.[2] This area may be termed the deep or concealed part of the inferior frontal gyrus, and all the three opercula into which this gyrus is usually divided take part in its formation. It may be seen by widely separating the lips of the various branches of the Sylvian fissure, or by removing the temporal lobe and the insula, as shown in fig. 268.

The deep surface of the anterior or orbital operculum is of a triangular form, looks mainly backwards towards the anterior aspect of the insula, and consists of three or four convolutions. In fig. 272 this surface is divided close to its inner border, which is fully an inch long and is separated from the insula by the anterior limiting sulcus.

The deep surface of the intermediate operculum (pars triangularis), like the exposed surface, is very variable in its extent, but it usually forms a single nearly straight convolution about an inch long running inwards to the anterior end of the superior limiting sulcus of the insula (see fig. 268).

The deep surface of the superior part of the frontal operculum is divisible into two parts—an inferior looking downwards towards the temporal lobe, and an internal which lies against the insula. The *inferior* portion is irregularly rectangular in form, measuring from within outwards and from before backwards about an inch. It is separated by a sharp ridge from the inner portion, but joins the outer surface of the operculum by a more rounded border. Its anterior boundary is formed by the ascending branch of the Sylvian fissure, and behind it joins the concealed surface of the parietal operculum. It does not usually present any independent and well-defined fissures, but the diagonal sulcus and the anterior subcentral sulcus often cross its outer border and extend inwards on to this aspect, and sulci on the inner surface of the frontal operculum may pass outwards on to it.

The *inner* or insular surface is also somewhat quadrangular, and has its long axis in the sagittal direction. It is bounded in front by the ascending branch of the Sylvian fissure, above by the superior limiting sulcus, and below by the prominent ridge between it and the inferior surface of the operculum. A well-defined posterior boundary separating it from the parietal operculum is not so readily determined. Opposite the central fissure this aspect is marked by a convolution which Retzius terms the *gyrus anticentralis*. He regards this convolution as belonging to the frontal operculum, and describes a fissure immediately behind it (*sulcus transversus primus*) as forming the posterior boundary of this part of the frontal operculum. In front of the gyrus anticentralis there are usually three convolutions on the inner aspect of the superior frontal operculum, which Retzius terms from behind forwards the *gyrus antiprecentralis*, *gyrus antidiagonalis*, and *gyrus posterior rami anterioris ascendentis*.

PARIETAL LOBE.

This lobe lies behind the frontal, in front of the occipital, and above the temporal. It is bounded in front by the central fissure, behind by the parieto-occipital and transverse occipital fissures (fig. 257), laterally and below by the posterior branch of the fissure of Sylvius as far as this preserves its horizontal direction, and then by a line connecting this with the anterior end of the lateral occipital. Above and mesially it extends within the great longitudinal fissure and appears on the mesial side of the hemisphere as the precuneate or quadrate lobule.

[1] Ein Beitrag zur Anatomie des Sprachcentrums, 1882.
[2] Das Menschenhirn, 1896.

EXTERNAL SURFACE OF THE PARIETAL LOBE.

The **intraparietal sulcus** (Turner) (fig. 255) arches through the parietal lobe, commencing near its anterior inferior angle, where it is sometimes, though rarely, continued into the fissure of Sylvius. It ascends at first parallel to the central fissure (*s. postcentralis inferior* or *pars ascendens inferior*), and then turns backwards horizontally to the back of the lobe (*pars horizontalis s. posterior*), extending nearly to the termination of the parieto-occipital fissure, past which it is continued (*pars occipitalis, paroccipital* of Wilder) to join the transverse occipital. Its horizontal portion divides the parietal lobe into two parts, the superior and inferior parietal lobules, and it is frequently bridged across by annectent convolutions connecting those lobules. One or two well-marked rami pass into the superior parietal lobule from the upper side of the pars horizontalis, and as many shallow sulci extend from its lower concave side into the inferior parietal lobule.

Above the sulcus postcentralis inferior, and often separated from it by an annectent gyrus connecting the superior parietal lobule with the posterior central gyrus, is a short vertical fissure (*s. postcentralis superior*), which is termed by Cunningham the *pars ascendens superior*, since in a large number of instances it is directly continuous with the pars ascendens inferior (the bridging gyrus being then absent), and the two conjoined parts then constitute a sulcus which runs parallel to the central fissure, and is termed the *postcentral sulcus* (Ecker). In the hemisphere shown in figs. 255, 256, the sulcus postcentralis consisted of four elements; the two lower represent the inferior, the next the intermediate, and the highest the superior postcentral.

Although the condition with a detached superior postcentral is to be regarded as typical of this sulcus as shown both by its occurrence in most of the Primates and the course of its development in the human embryo, it is by no means the most common in the adult human brain, the usual condition being that in which there is a complete postcentral sulcus from which the horizontal arm passes off backwards at an oblique angle towards the occipital lobe, although generally interrupted near the anterior limit of that lobe by an annectent gyrus. An arrangement of this character was met with by Cunningham in 56 per cent. of his cases. In 16 per cent. a more or less complete postcentral sulcus was present, and was cut off from the horizontal part of the fissure by an annectent gyrus. Occasionally the postcentral sulcus communicates above, and sometimes also below, with the central fissure. Three deep annectent gyri partially interrupt the horizontal part of this fissure and join the superior and inferior parietal lobules (Eberstaller); these have been supposed to be a human characteristic, but they occur in the chimpanzee and occasionally in the baboon (Cunningham).

In rare cases the pars ascendens inferior of this fissure is cut off from the pars horizontalis, and the latter is continuous with the pars ascendens superior alone. In other and also rare instances all the parts of the fissure are separated from one another by bridging convolutions, so that the fissure appears as four distinct parts—viz. the two portions of the postcentral sulcus (lower and upper), the pars horizontalis, and the pars occipitalis (Cunningham).

The occipital continuation of the intraparietal fissure is sometimes separated from the rest of the fissure (*paroccipital fissure* of Wilder). It usually terminates posteriorly by joining a sulcus which is nearly transverse to its direction, the sulcus occipitalis transversus (see figs. 256, 257). This will be further noticed in connexion with the occipital lobe. In the monkey's brain the occipital termination is concealed within the deep cleft ('Affenspalte') formed by the occipital operculum.

Below the inferior postcentral sulcus, and cutting into the margin of the fronto-parietal operculum, is a small oblique sulcus (*s. retrocentralis transversus* of Eberstaller). This sometimes serves to prolong the intraparietal fissure into the fissure of Sylvius.

The intraparietal fissure is usually developed in the fœtus in four segments (Cunningham), which appear in the following order—viz. inferior postcentral, horizontal, occipital, and superior postcentral. It is better developed—*i.e.* more continuous and deeper—in apes than in man; but the superior postcentral part is either not developed or is rudimentary in them. The so-called

horizontal part is not truly horizontal, but has an upward inclination which is more marked in the male human brain than in the female.

The **posterior central** or **ascending parietal convolution** (fig. 255) lies behind the central fissure, between this and the postcentral sulcus, and parallel to the anterior central convolution, with which it is usually continuous below the central fissure. Above, it is connected by a broad annectent gyrus with the superior parietal convolution, and is continued on to the mesial surface by a narrow annectent which unites it with the posterior part of the marginal gyrus (paracentral lobule).

The **superior parietal convolution** or **superior parietal lobule** (fig. 256) is that part of the parietal lobe which lies above the pars horizontalis of the intraparietal sulcus, and behind the upper part of the last described convolution, from which it is imperfectly separated by the upper part of the postcentral sulcus. Its posterior limit is the boundary of the parietal lobe—viz. the parieto-occipital fissure, round the extremity of which an annectent convolution connects this lobule with the occipital lobe (*upper parieto-occipital annectent gyrus*). The superior parietal is continuous on the mesial surface of the hemisphere with the precuneus. Retzius describes a constant fissure (*sulcus parietalis superior*) (fig. 256) in this lobule, which appears in the seventh or eighth month of fœtal life. It passes from the precuneus across the superior border of the hemisphere on to the superior parietal convolution, and in the course of its development may join the horizontal part of the intraparietal sulcus, and, less frequently, the precuneate sulcus.

The **precuneus** or **quadrate lobule** (fig. 258) is the part of the parietal lobe which is seen on the mesial surface of the hemisphere. It is bounded in front by the marginal portion of the cingulate fissure, and behind by the parieto-occipital fissure, and is incompletely separated from the gyrus cinguli by the subparietal fissure. Its surface is indented by one or two furrows which cut the margin of the hemisphere and extend downwards a variable distance over the surface of the lobule (*precuneate sulci*).

The **inferior parietal lobule** is embraced within the curve of the intraparietal sulcus. It is bounded behind by the lower limb of the transverse occipital fissure. It is divided into three gyri—viz. the supramarginal, the angular, and the postparietal (fig. 255). The **supramarginal convolution** lies behind and below the anterior part of the intraparietal sulcus, beneath the lower end of which it is continuous with the posterior central convolution. It arches round the upturned extremity of the fissure of Sylvius, to become continuous with the superior temporal convolution below, and with the angular behind. The **angular gyrus**, connected in front with the supramarginal, bends over the end of the superior temporal (parallel) sulcus, and is continued below into the first and second temporal gyri. Behind, it is separated from the postparietal gyrus by a shallow vertical sulcus, which may be absent. The **postparietal gyrus** lies above the lateral occipital sulcus.

CONCEALED AREA OF THE PARIETAL LOBE (see fig. 268).—The parietal lobe possesses a considerable area of cortex concealed within the Sylvian fissure. The concealed or opercular surface may be divided into an anterior and a posterior part, the anterior being opposite the posterior part of the insula and the posterior corresponding to the post-insular region of the Sylvian fissure. The anterior consists of an inferior surface lying against the temporal lobe and a much smaller internal surface in contact with the insula. The ridge between these two surfaces is well defined in front, but gradually fades away behind. The inferior surface consists of two and sometimes three well-developed convolutions running nearly transversely outwards. The posterior part of the parietal operculum, very variable in extent, consists of two or three small convolutions forming the anterior wall of the terminal ascending branch of the posterior limb of the Sylvian fissure.

OCCIPITAL LOBE.

The occipital end of each hemisphere is of a pyramidal shape, and is usually described as possessing three surfaces—mesial, external, and inferior. Of these the mesial is the only one that is separated by well-defined fissures from the adjacent parietal and temporal lobes. In the apes the external surface is limited anteriorly by a deep cleft ('Affenspalte'), but in man this is either absent, or represented by a smaller fissure (the sulcus lunatus) (see fig. 269). On the inferior

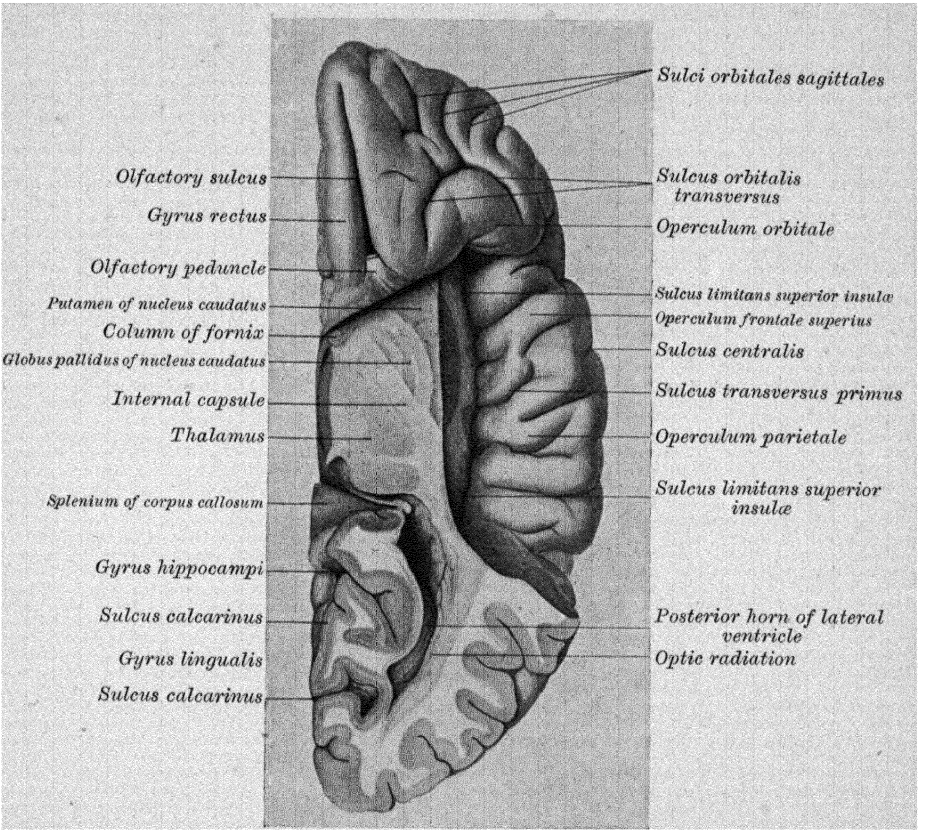


FIG. 268.—VIEW, FROM BELOW, OF THE OPERCULO-INSULAR SURFACES OF THE FRONTAL AND PARIETAL LOBES OF A LEFT CEREBRAL HEMISPHERE. (J. Symington.)

The hemisphere was divided horizontally just below the anterior perforated spot and the splenium of the corpus callosum, and the upper piece was placed with its under-surface upwards. The insula and the temporal lobe were then removed in order to expose the concealed opercular surfaces of the superior frontal and the parietal opercula.

or tentorial surface there is no sulcus separating the temporal and occipital lobes. Under these circumstances considerable difficulty has been experienced in mapping out the boundaries of the occipital lobe. Some anatomists assign to this lobe all the hemisphere situated behind the plane of the parieto-occipital fissure and include in it the posterior parts of the parietal and temporal lobes (as here described). In this work Eberstaller's plan has been followed. He describes the whole of the inferior surface as belonging to the temporal lobe, so that the occipital lobe is regarded as having only two surfaces—a mesial and an external.

On the mesial surface of the hemisphere the lobe is marked off by the parieto-occipital fissure from the precuneus, and by the posterior calcarine from the lingual gyrus of the temporal lobe (fig. 258).

On the external surface it is bounded in front by the external parieto-occipital fissure and by the transverse occipital sulcus, and lower down it is continuous externally with the middle and inferior temporal convolutions.

MESIAL SURFACE OF THE OCCIPITAL LOBE.

The mesial surface of the occipital lobe is occupied by a well-marked gyrus termed the cuneus (**cuneate lobule,** fig. 258). This is of a triangular shape, and is bounded in front by the parieto-occipital fissure and below by the calcarine, while above and behind it reaches the margin of the hemisphere and is continuous with the external surface. It is indented by two or three shallow vertical sulci.

The parieto-occipital and calcarine fissures which bound the mesial surface have already been described, as well as the deep annectent gyri which pass across them and connect the cuneus with the adjacent lobes (see p. 266). Owing to variations in these fissures and annectent gyri the cuneus varies considerably in size and form. Thus when the internal parieto-occipital fissure divides above into two branches which bound a well-marked parieto-occipital lobule (Retzius) the cuneus is reduced in size and becomes less distinctly triangular.

The superior sagittal (longitudinal) venous sinus in passing downwards causes an impression on the inner side of the occipital pole of the hemisphere (Bastian). This impression is generally found on the right side, but sometimes on the left.

EXTERNAL SURFACE OF THE OCCIPITAL LOBE.

The anterior bounding sulci of the external surface of the occipital lobe are, as we have seen, the external part of the parieto-occipital and the transverse occipital, while the lateral occipital runs into it. The parieto-occipital has already been described (p. 264). The **transverse occipital sulcus** (Ecker) is a transverse furrow, which is laid down as a distinct sulcus in the fœtus, but is later almost invariably joined by the horizontal part of the intraparietal, of which it then appears to be the bifurcated posterior end (p. 257). In Primates it is usually concealed by the occipital operculum, but on drawing this aside it may still be seen on the anterior wall of the 'Affenspalte.' Its inner end approaches the mesial border of the hemisphere, behind the parieto-occipital fissure, from which it is separated by an annectent gyrus which joins the occipital lobe with the superior parietal lobule. Its outer end, which is often curved forwards, is usually separated from the lateral occipital by the *inferior parieto-occipital annectent gyrus* uniting the occipital lobe with the post-parietal gyrus (see fig. 257).

The **lateral occipital sulcus** runs somewhat obliquely backwards a short distance below the outer end of the transverse occipital towards the occipital pole of the hemisphere. It is separated from the lateral border of the hemisphere by the second and third temporal gyri which are passing to the occipital pole. This fissure may join the superior temporal, or transverse occipital, or be broken up into two or three pieces.

Not unfrequently the calcarine fissure extends backwards from the inner aspect of the hemisphere on to the external surface of the occipital lobe so that its bifid extremity (fissura extrema of Seitz) is visible when the hemisphere is viewed from behind (see fig. 269). Bolton [1] describes two small occipital polar sulci situated a short distance from the extremity of the

[1] 'The Exact Histological Localisation of the Visual Area of the Human Cerebral Cortex,' Phil. Trans. 1900.

calcarine fissure and usually distinct from both the transverse and lateral occipital sulci. These polar sulci are shown though not labelled in fig. 257. They define, according to Bolton, the external limits of the visuo-sensory area as determined by the presence of the line of Gennari in the cortex. As has already been mentioned, Elliot Smith [1] holds that there is usually a fissure on the external surface of the occipital lobe, which is the homologue of the Primate 'Affenspalte.' This fissure (*sulcus lunatus*) is curved, has its convexity directed upwards and outwards, and is bounded below and behind by an occipital operculum (see fig. 269).

TEMPORAL LOBE.

The temporal lobe is somewhat pyramidal in shape, having three surfaces—viz. a lateral, an inferior, and a superior concealed within the fissure of Sylvius.

The rounded apex of the pyramid is free, is directed forwards, and lies underneath the orbital surface of the frontal lobe, from which it is separated by the broad commencement of the Sylvian fissure.

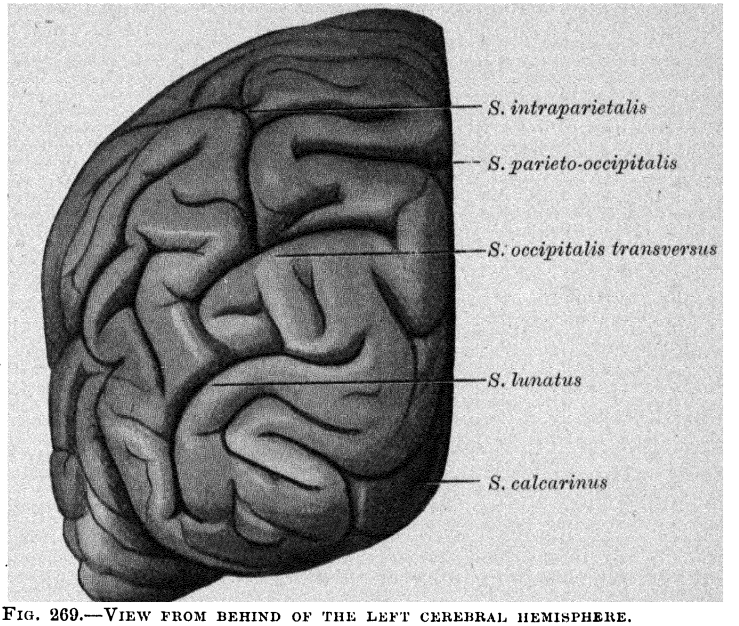


FIG. 269.—VIEW FROM BEHIND OF THE LEFT CEREBRAL HEMISPHERE.
From the brain of an Egyptian Fellah, presented to the Anatomical Museum, Queen's College, Belfast, by Professor Elliot Smith of Cairo.

The external or lateral surface of this lobe is bounded above for two-thirds of its length, at first by the stem and afterwards by the posterior branch of the fissure of Sylvius, which separates it from the frontal and parietal. At the posterior end of this fissure it is continuous above with the postero-lateral part of the parietal lobe, and behind with the occipital lobe. On its inferior surface the temporal lobe extends backwards to the occipital pole and it is bounded internally by the calcarine, the anterior part of the collateral, and incisura temporalis, which separate it from the occipital and limbic lobes.

LATERAL AND INFERIOR SURFACES OF THE TEMPORAL LOBE.

On these surfaces there are four sulci with an antero-posterior direction. The **first** or **superior temporal sulcus,** also termed from its relation to the

[1] 'The so-called Affenspalte in the Human (Egyptian) Brain,' Anat. Anzeiger. Oct. 1903.

Sylvian fissure the *parallel fissure* (fig. 255), is an important furrow, appearing in the sixth month, and being constant in the Primates. In many monkeys it is more extensive than in man, nearly reaching the parieto-occipital fissure at the margin of the hemisphere. The angular gyrus curves round its posterior extremity. Both this and the second temporal turn upwards as they pass back. The fissure is sometimes interrupted by a small gyrus connecting the convolutions above and below it. The **second temporal sulcus** runs parallel to and below the last, but is less constant in extent and direction. It is often interrupted by one or more vertical connecting gyri. The **third temporal sulcus** (t_3) is seen on the under surface of the lobe, extending behind nearly to the occipital pole. It is often interrupted near its anterior and posterior ends, and sometimes also about the middle, by annectent gyri. In front it generally fails to reach the extremity of the lobe, which forms a smooth 'pole' from which most of the sulci diverge. A **fourth temporal sulcus** (t_4) is formed by the collateral fissure, which has already been noticed (p. 267) (figs. 258, 259).

On the lateral surface of the lobe three convolutions can usually be distinguished. The **first** or **superior temporal gyrus** (fig. 255) bounds the posterior branch of the Sylvian fissure below, and is continuous behind with the supramarginal and to a less extent with the angular convolution of the parietal lobe. The **second temporal gyrus** is separated from the postparietal gyrus by the lateral occipital sulcus and ends behind in the occipital lobe. The **third temporal gyrus** is also continuous with the occipital lobe. On the under surface of the lobe is the **fourth temporal gyrus,** lying between the third temporal sulcus and the collateral fissure. The second and third gyri are convolutions of some thickness, and are a good deal interrupted by transverse and oblique secondary sulci. The fourth, which was formerly known as the first occipito-temporal, is narrower, and more sharply marked off by its bounding sulci. Its posterior part, which has been termed the *fusiform lobule*, is sometimes described as belonging to the occipital lobe. Lastly, between the posterior part of the collateral and the calcarine fissure is the **fifth temporal gyrus** or **lingula.** This is continuous in front with the hippocampal gyrus of the limbic lobe. It is joined by two deep annectent gyri, which pass across the posterior calcarine fissure, connecting this gyrus with the cuneus.

SUPERIOR, CONCEALED, OR OPERCULO-INSULAR SURFACE OF THE TEMPORAL LOBE (see fig. 270).—This surface is of considerable extent, measuring 9 cm. or 10 cm. from before backwards. Near its posterior end its transverse diameter is between 3 cm. and 4 cm.; from this it narrows as it passes forwards until it reaches the level of the anterior end of the insula, where it expands in an anterior and an internal direction, reaching about 3 cm. in front of the insula and turning inwards to become continuous with the upper surface of the hippocampal convolution. It is divided into two portions, an opercular and an insular. The *opercular* portion is opposite the parietal and frontal opercula. The area lying below the parietal operculum consists of two or three gyri which have a direction mainly in the transverse direction—*transverse temporal gyri* (Heschl). The most anterior of these is the largest, and is directed obliquely outwards and forwards. In front of this gyrus the opercular surface lies against the superior, intermediate (if well developed), and orbital portions of the frontal operculum, and is marked by a number of short, shallow, and irregular sulci, dividing it into a series of anterior transverse temporal gyri. The *insular* surface, looking inwards and upwards towards the postero-inferior surface of the insula, is often separated by a well-marked border from the opercular surface.

THE INSULA OR ISLAND OF REIL.

This lobe is entirely concealed in the adult human brain within the fissure of Sylvius, the margins of which form opercula (see p. 262) which overlap the lobe. The insula corresponds with the lentiform nucleus in the interior of the hemi-

sphere (fig. 260), and probably in consequence of its close connexion with this mass of grey matter, which appears early as a thickening of the lateral wall of the vesicle of the cerebral hemisphere, the insula does not keep pace with the general expansion which the hemisphere-vesicles undergo, and hence in consequence of that expansion it becomes overlapped and concealed by the rest of the hemisphere. On account of this early fixation and the close topographical relation between it and the largest of the basal ganglia, the insula (along with the basal ganglia and the continuation of the peduncles between them) is frequently spoken of as the *stem* (Germ. *Stammtheil*) of the hemisphere, the remainder of the cerebrum, which covers it in, being termed by some authorities

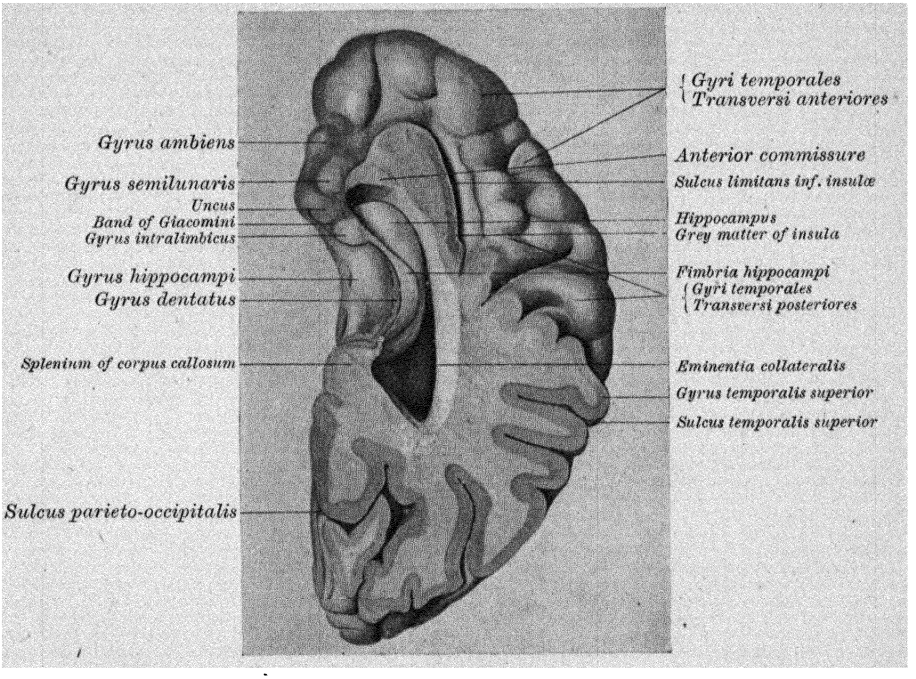


FIG. 270.—VIEW, FROM ABOVE, OF THE OPERCULO-INSULAR SURFACE OF THE TEMPORAL LOBE OF THE RIGHT CEREBRAL HEMISPHERE. (J. Symington.)

The Sylvian fissure was opened and a knife was inserted into it and then carried nearly horizontally backwards through the insula and the posterior part of the hemisphere. The inferior horn of the lateral ventricle was subsequently opened up, and the lower part of the insula removed to expose the insular surface of the temporal lobe.

the mantle or pallium. To obtain a general view of the island it is necessary to cut away its opercula (fig. 271), but some of its relations are best seen in sagittal (fig. 272), coronal (figs. 260, 261), and horizontal (fig. 246) sections through the hemispheres.

As Marchand[1] has shown, the insula appears in a hardened brain as an irregular three-sided pyramid with the apex or pole directed outwards and forwards. It is separated from the adjacent convolutions by a triangular sulcus (*sulcus limitans insulæ*) which almost entirely surrounds it, and which is itself formed by an anterior, a superior, and an inferior part. The anterior and inferior limiting sulci do not, however, quite meet, and the space between them is known as the *limen insulæ*. At this point, which is opposite the outer part of the

[1] Die Morphologie des Stirnlappens und der Insel der Anthropomorphen, 1898.

anterior perforated spot, the insula becomes continuous with the orbital part of the third frontal convolution, and the upper surface of the caput of the hippocampal convolution.

SURFACES AND SULCI OF THE INSULA.

The three surfaces of the insula are termed anterior, superior, and postero-inferior. They are moulded against the insular portions of the various opercula. The *anterior surface* lies in contact with the orbital and the intermediate opercula of the frontal lobe; the *superior*, which is the largest, opposite the superior frontal and the parietal opercula; and the *postero-inferior* against the temporal operculum.

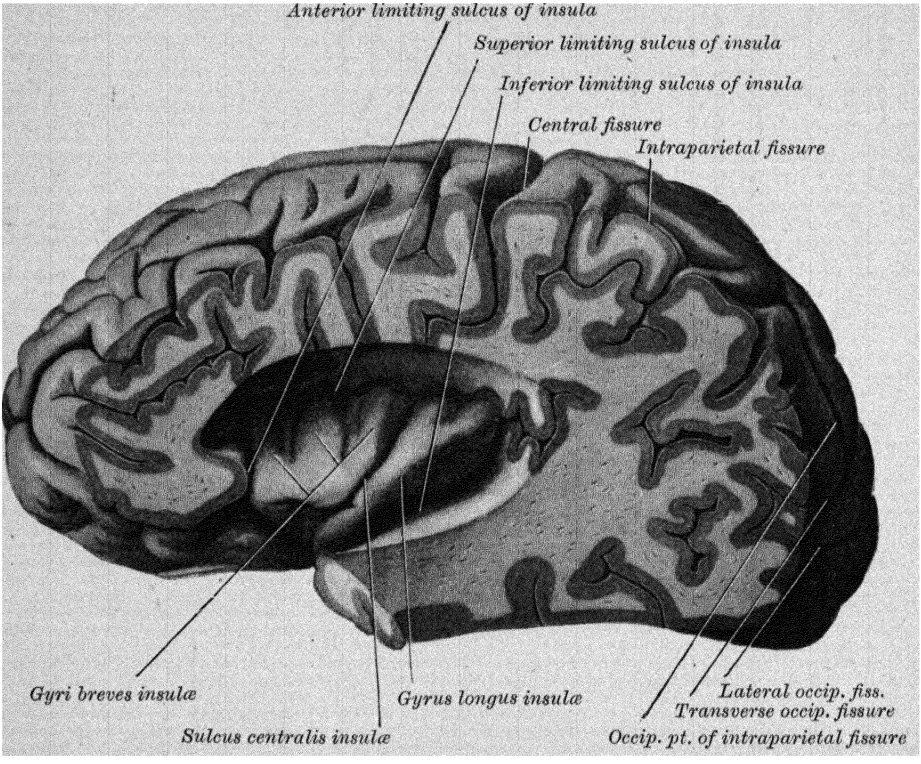


FIG. 271.—DISSECTION TO EXPOSE THE LEFT INSULA FROM THE LATERAL ASPECT. (J. Symington.)

The insula is marked out by shallow sulci, which diverge from its pole, into several straight gyri having a similar divergent course. One of these sulci, which is deeper and appears earlier than the rest, and is also more constant in lower Primates, has been termed the **sulcus centralis insulæ** (Guldberg), since the line of direction of this sulcus nearly corresponds with that of the central fissure in the mantle. This serves to subdivide the lobe into two parts, a *precentral* and *postcentral lobule.*

The **precentral lobule** of the insula is formed of a few short convolutions (*gyri breves*, fig. 271) converging from the superior limiting sulcus but falling short of the apex of the lobule, which is smooth and forms a slight prominence. These convergent gyri are usually three in number (anterior, middle, and

posterior), being subdivided in this manner by secondary and somewhat shallow sulci, having the same direction. The most marked of these sulci lies between the middle and posterior gyri breves, and has been named *sulcus precentralis insulæ*. A fourth small gyrus is described by Eberstaller as lying deeply underneath the orbital operculum. This he has termed the *gyrus brevis accessorius*. This accessory gyrus, and usually also the anterior of the three gyri breves, look forwards, lying upon the *anterior surface* of the insula, which is sometimes nearly at a right-angle with the superior surface.

The **postcentral lobule** (*gyrus longus insulæ* of Giacomini) (fig. 271) is also often subdivided at its upper end by a longitudinal furrow (*sulcus postcentralis insulæ*) into two parts, anterior and posterior. Its grey matter is continuous below with the tip of the hippocampal gyrus, laterally with that of the first temporal gyrus, above and posteriorly over the limiting sulci with the grey matter of the parietal and temporal opercula.

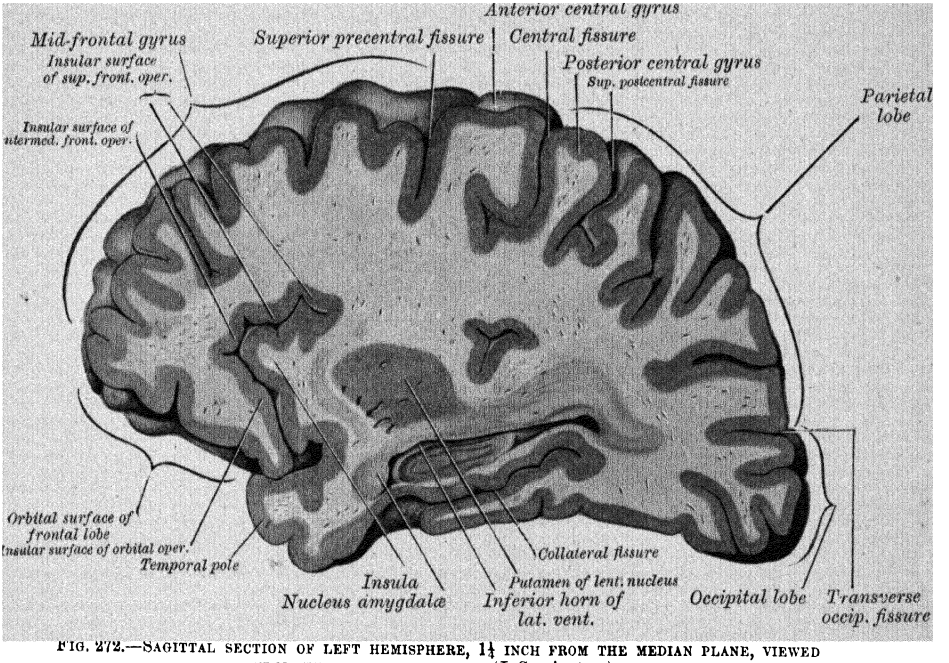


FIG. 272.—SAGITTAL SECTION OF LEFT HEMISPHERE, 1¼ INCH FROM THE MEDIAN PLANE, VIEWED FROM THE LATERAL ASPECT. (J. Symington.)

The three principal furrows of the insula (sulcus centralis, s. precentralis, and s. postcentralis insulæ), which radiate from the vallecula Sylvii, have been compared with the three similarly radiating fissures of the mantle—viz. the central fissure, the precentral fissure, and the intraparietal fissure. They are not, however, directly continuous with those, being arrested at the superior sulcus limitans insulæ. Sometimes the central fissure is continued by a small sulcus (anterior subcentral) almost into the sulcus centralis insulæ.

Marchand [1] and more recently Holl [2] take a different view from that adopted here regarding the primary subdivision of the insula. They consider that its main fissure is not the sulcus centralis but the sulcus postcentralis (sulcus longitudinalis of Marchand), and according to Holl

[1] 'Die Morphologie des Stirnlappens und der Insel der Anthropomorphen,' Arbeiten aus dem pathologischen Institute zu Marburg, 1893.

[2] 'Über die Insel des Menschen und Anthropoidengehirnes,' Archiv für Anatomie, 1902.

the human insula is a submerged arcuate gyrus folded round the sulcus longitudinalis, and consisting of a narrow, nearly simple and straight posterior limb, and a large convoluted anterior limb. Retzius,[1] in view of certain statements by Holl regarding the relative development of the central and postcentral fissure, examined 100 insulæ of children and adults from brains hardened in formol. In 94 he found the sulcus centralis single and well developed, while the sulcus postcentralis presented a similar condition in only 17 out of the 100 specimens, and in 67 it was broken up into two or three portions.

LIMBIC LOBE.

The *cingulate gyrus*, with its continuation the *hippocampal gyrus*, forming together the *gyrus fornicatus*, were separated by Broca, on morphological grounds, from the other parts of the hemisphere, as a distinct lobe, intimately united in front and below with the olfactory lobe; and the name of *grande lobe limbique* was given by him to these combined gyri, because it formed the *limbe* or edge of the hilus on the inner aspect of the hemisphere through which various structures pass to unite the hemisphere with its fellow of the opposite side, or with lower parts of the brain. This lobe has been compared in shape to a tennis-racket, the olfactory bulb and its peduncle forming the handle of the racket, while the cingulate and hippocampal gyri, united anteriorly with the inner and outer roots of the olfactory peduncle, constituted the ring-like edge of the body of the racket. Broca regarded this limbic lobe as olfactory in function.

To this lobe of Broca, Schwalbe added the other central parts of the mesial wall of the hemisphere—viz. the *lamina septi pellucidi* and the *dentate convolution*, as well as the *fornix*—looking upon these as representing an inner encircling convolution concentric with the gyrus cinguli and gyrus hippocampus. Schwalbe named the whole lobe, thus reconstituted, the 'falciform lobe,' the olfactory tract and bulb being, however, excluded from it.

To the parts included by Schwalbe within Broca's limbic lobe, certain other structures, which, although in a rudimentary condition in man, are well developed in certain mammals, have since been added by Giacomini, Zuckerkandl, and Retzius. One of these occurs in the human brain as a thin layer of grey matter on the upper surface of the corpus callosum; this is termed (by Zuckerkandl) the *gyrus supracallosus*. This gyrus is continuous round the splenium of the corpus callosum with the dentate gyrus, and is described as ending anteriorly in the rudimentary *gyrus geniculi*. It represents a part of the hippocampal formation, which has become opened out and thinned by the rapid growth of the corpus callosum, and has also shared in the atrophy of this formation in man as well as other microsmatic mammals. Retzius has directed special attention to a narrow ridge of grey matter which appears between the fimbria hippocampi and the posterior part of the gyrus dentatus, and extends backwards on to the under surface of the splenium of the corpus callosum internal to the dentate gyrus. This *gyrus fasciolaris* ends anteriorly in a pointed process, in front of which the gyrus dentatus and fimbria are separated by a narrow sulcus. If this sulcus be traced forwards it will be found to broaden out again, and the grey matter in its floor to become continuous with the tip of the uncus. The part of the uncus behind the place where it is crossed by the band of Giacomini is called by Retzius the *gyrus intralimbicus*. Occasionally in the fœtus the gyrus fasciolaris and the gyrus intralimbicus are continuous with one another, and both must be regarded as belonging to the inner part of the limbic lobe. Elliot Smith describes them as consisting of 'inverted hippocampus.'

[1] 'Zur Morphologie der Insula Reili,' Biologische Untersuchungen, x. 1902.

Hidden beneath the posterior part of the gyrus cinguli, and lying external to the subsplenial part of the gyrus dentatus, a small projection of the cortex is usually to be found, about 1 cm. long and 2 mm. to 4 mm. broad, marked by one to seven semicircular eminences. This has been described (by A. Retzius originally, and more recently and fully by Zuckerkandl and G. Retzius) under the somewhat misleading name of *callosal gyrus* (Balkenwindung), but is not to be confounded with the gyrus cinguli which has often been so denominated. It is best developed in osmatic mammals. The so-called peduncles of the corpus callosum (*gyri subcallosi* of Zuckerkandl) also belong to the inner part of the limbic lobe.

Zuckerkandl divides the limbic lobe into three concentric portions—an outer, the great limbic lobe of Broca formed by the cingulate and hippocampal gyri; an intermediate or outer marginal by the dentate, supracallosal and geniculate gyri; and an inner marginal by the fornix, lamina septi pellucidi, and gyrus subcallosus. The two marginal gyri have become separated from one another by the development of the corpus callosum.

As thus constituted, the limbic lobe is bounded circumferentially mainly by two important fissures, the cingulate above and the anterior part of the collateral and the rhinal fissures below, while the less constant subparietal or postlimbic sulcus separates it behind from the parietal lobule, and the anterior end of the calcarine cuts into it just below the splenium. The inner limit of the lobe is formed by the fissura choroidea (Schwalbe), through which the choroid plexus is invaginated into the lateral ventricle. The outer limbic gyrus is bounded internally by the callosal and hippocampal fissures, and the intermediate and inner limbic gyri are separated from one another in the temporal lobe by the fimbrio-dentate fissure; but on the under aspect of the splenium the fimbria and gyrus dentatus become widely separated, the gyrus dentatus being prolonged round the splenium on to the dorsal surface of the corpus callosum, as the gyrus supracallosus and the fimbria turning forwards on its ventral surface to become continuous with the crus of the fornix.

As already stated (see p. 267), the division of the cerebral hemispheres into lobes is not based upon any clearly defined morphological or physiological principle, but is largely artificial and has been adopted to facilitate the description of the cerebral surface. The limbic lobe, although associated by Broca with the centre for smell, is no exception to this rule, as only a comparatively small part of his limbic lobe appears to be specially olfactory in function.

CONVOLUTIONS AND FISSURES IN THE LIMBIC LOBE (fig. 258).

Gyrus cinguli or **callosal gyrus.**—This is an extensive convolution which lies between the marginal gyrus of the frontal lobe and the quadrate lobule of the parietal lobe above and the corpus callosum below. The convolution sweeps round the corpus callosum, beginning below its rostrum, where it abuts on the subcallosal gyrus, and ending a little below the level of the splenium by becoming continuous with the posterior end of the hippocampal gyrus. Where it passes into that gyrus it is much narrowed (isthmus gyri fornicati). It is separated from the corpus callosum by a fissure which is termed the *callosal sulcus*.

The **hippocampal gyrus** is continuous posteriorly, at the anterior end of the calcarine fissure, with the cingulate gyrus above and the lingual gyrus below. As it passes forwards it first lies between the hippocampal and anterior part of the collateral fissures and then expands to form the *caput gyri hippocampi*, which sends a hook-like process (*uncus*) backwards and outwards on the upper aspect

of the anterior end of the hippocampal fissure. The caput gyri hippocampi does not reach the apex of the temporal lobe, being partly separated from it by the incisura temporalis above and the anterior part of the collateral fissure below. As a rule these two fissures do not meet, and the caput gyri hippocampi is joined to the temporal pole by a bridging convolution (*gyrus rhinencephalo-temporalis anterior*) of very variable breadth. Occasionally the anterior part of the collateral fissure is separated from the posterior part and joins the incisura temporalis to form the rhinal fissure which is very distinct in many apes. The surface of the caput is marked by a small depression to which Retzius has applied the term sulcus rhinencephali inferior. In addition to the inferior aspect of the caput gyri hippocampi, just described, there is an upper surface which is overlapped by the optic tract, anterior perforated spot, and frontal lobe. Upon this upper concealed surface Retzius has described two constant elevations—a median (*gyrus semilunaris*) and a lateral (*gyrus ambiens*), separated by the *sulcus semiannularis*. The caput gyri hippocampi is the cortical centre for smell and corresponds to the *lobus pyriformis* of osmatic mammals. The hippocampal gyrus is covered superficially by a well-marked reticular layer of white fibres (*substantia reticularis alba*, Arnold, fig. 259, *s.r.a.*). The part of the hippocampal gyrus which is adjacent to the gyrus dentatus and forms the lower lip of the hippocampal sulcus is termed the subiculum.

Uncus.—This small process is crossed about its middle by a continuation of the gyrus dentatus, generally known as the band of Giacomini. The portion of the uncus behind this band forms the *gyrus intralimbicus* of Retzius; that in front is similar in structure to the caput gyri hippocampi (fig. 270).

The **dentate gyrus** (*fascia dentata Tarini*, figs. 258, 270) lies above the hippocampal gyrus, from which it is separated by the *hippocampal* or *dentate fissure*. It is a narrow convolution having a toothed or notched appearance at its free border: hence the name. Above and overlapping it is the *fimbria*, from which it is separated superficially by a shallow sulcus (*fimbrio-dentate*), narrow in front but broadening out behind, where it forms a triangular depression below the splenium of the callosum. The gyrus dentatus begins posteriorly just behind and above the splenium by a fine curved lamina (fasciola cinerea), which is continuous with the longitudinal striæ (both lateral and mesial) of the corpus callosum. From this point it bends downwards, lying along the isthmus of the gyrus fornicatus and then along the upper border of the hippocampal gyrus; here the crus of the fornix passes to its upper border in continuity with the fimbria (see p. 314). Anteriorly it is continued into the cleft between the hippocampal gyrus and its uncus, where it becomes lost to view. But if this cleft be opened out the dentate gyrus is seen to exhibit a sharp curve within it, and in continuity with the curved end a greyish band emerges from the cleft and passes transversely over the uncus to disappear on the ventricular surface of that gyrus (Luschka, Giacomini).

The part of the gyrus dentatus which lies below the splenium is sometimes much more developed than usual, and shows strongly marked folds or dentations which recall the broad and secondarily convoluted gyrus dentatus which covers the under surface of the splenium in some mammals (G. Retzius).

The **fimbria hippocampi** (fig. 270) represents the white matter of the hemisphere, which here comes to the surface along the side of the dentate gyrus. It is continuous with the alveus which covers the hippocampus within the lateral ventricle, and this is continuous with and forms part of the central white matter. The fimbria itself, however, appears to be actually formed of fibres which are

prolonged into it posteriorly from the crus of the fornix; anteriorly it is continued into the white matter of the uncus. In section the fimbria appears as a somewhat club-shaped expansion of the alveus, exhibiting a hook-like lateral prolongation. This is the section of a thin lamina (*tænia fimbriæ*) continuous with the epithelium covering the choroid plexuses which here invaginate the ventricular epithelium.

The only sulcus within the limbic lobe which remains to be described (the *callosal sulcus* and the *fimbrio-dentate sulcus* having been already noticed) is the **hippocampal** or **dentate fissure**. This begins as a shallow furrow just below the posterior end of the splenium corporis callosi, between the fasciola cinerea and the end of the gyrus cinguli; it then lies between the remainder of the dentate gyrus above and the isthmus gyri fornicati and hippocampal gyrus below, and becoming deeper as it passes forwards ends in the bend between the hippocampal gyrus and its uncus. This fissure causes the elevation of the hippocampus or cornu Ammonis in the inferior horn of the lateral ventricle (fig. 261).

The **fornix** (see p. 313) also belongs to the limbic lobe as above defined. It contains a bundle uniting the hippocampus with the olfactory lobe. This bundle, the *olfactory bundle of the cornu Ammonis* (Zuckerkandl), best developed in osmatic mammals, is contained within the body of the fornix. Traced forwards, it is found to leave the column to pass in front of the anterior commissure, and then to run in the subcallosal gyrus to the vallecula Sylvii. Here it divides into two parts, one (pars olfactoria) passing by the anterior circumference of the lamina perforata anterior to the inner root of the olfactory tract, and the other (pars temporalis) at the hinder border of the anterior perforated lamina to the point of the hippocampal gyrus. This is the band which has been described (by F. Arnold and Broca) as continuing the peduncle of the corpus callosum with the hippocampal gyrus.

In some mammals (*e.g.* monkeys) there is a band of grey matter running along the upper surface of the fornix, on each side near the middle line, wedged in between it and the corpus callosum. This closely resembles the supra-callosal gyrus above the callosum (see below), and appears to be part of another rudimentary gyrus which may be termed *gyrus infracallosus*, or, including certain patches of grey matter which occur here and there in the substance of the fornix, *gyrus fornicis*.

The **cingulum**, which also belongs to the limbic lobe, is a tract of fibres running in the gyrus hippocampi and gyrus cinguli. The bundle has for the most part a longitudinal course within the white matter of these gyri. Beevor thought that its fibres connect the hippocampal and cingulate gyri with the cortex of the outer surface of the hemisphere. According to Flechsig and Cajal, however, the cingulum consists of projection fibres, and is not to be regarded as an association bundle. A bundle of fibres having a somewhat similar course in the anterior descending part of the gyrus fornicatus is usually described as part of this tract; but according to Beevor it is doubtful if these fibres can be considered to belong to the cingulum; at all events, their continuity with the remainder of that tract could not be traced. A fuller description of the origin and course of the fibres of the cingulum, based upon Cajal's observations, will be given subsequently (see p. 400).

Gyrus limbicus.—The longitudinal striæ of the corpus callosum (p. 310) belong to a thin lamina of grey matter which extends over the surface of the corpus callosum from the lower edge of the gyrus fornicatus, and is much better developed in osmatic mammals than in Primates (Valentin, Jastrowitz). The striæ, together with this grey matter, represent a degenerated convolution

(*supracallosal gyrus*, Zuckerkandl), which is continuous posteriorly with the fasciola cinerea—*i.e.* with the dentate gyrus. Together with another degenerated gyrus in front, which is represented only by the prolongation of the stria medialis (*gyrus geniculi* of Zuckerkandl), these form a rudimentary gyrus (*bordering gyrus*, *gyrus marginalis*, Germ. *Randwindung*), which is curved around the brain-stem and the central parts of the hemisphere, lying within and concentric with the larger and well-developed gyrus formed by the cingulate and hippocampal gyri. The lamina of the septum pellucidum, and the so-called peduncle of the corpus callosum (gyrus subcallosus of Zuckerkandl) also belong to this bordering gyrus, but have become separated from the supracallosal part by the development of the corpus callosum; and the gyrus infracallosus (where this exists) and the fornix and fimbria may also be considered to form part of it.

OLFACTORY LOBE.

Under this head are included the *olfactory bulb*, its *peduncle* (olfactory tract), the *trigonum olfactorium*, and the *anterior perforated space*. The other portions of the brain connected with the olfactory apparatus have already been described in connexion with the limbic lobe.

The **olfactory bulb** lies on the under surface of the frontal lobe, its anterior extremity being about 1 cm. behind the level of the frontal pole in man, although in many mammals the bulb extends forwards considerably in front of the other parts of the hemisphere. It (fig. 259) is oval in shape and of a reddish-grey colour when viewed from the ventral aspect. It is nearly a centimetre long and about a third of this in width; from its posterior extremity the olfactory tract emerges. Its dorsal surface, which is in contact with the frontal lobe, is white and is directly prolonged into the tract. This surface is marked by a longitudinal ridge which fits into the anterior end of the sulcus olfactorius of the frontal lobe.

The bulb is rudimentary in man and other Primates, and in the seals, and is lacking in Cetacea, but in macrosmatic mammals (Turner), and in vertebrates generally, it is well developed and forms a distinct portion of the cerebral hemisphere, enclosing an extension of the ventricular cavity. In some mammals (*e.g.* horse) this extension remains throughout life in free communication with the anterior horn of the lateral ventricle; in others (*e.g.* dog) the communication is lost. In the human fœtus of from two to four months it appears as a hollow projection of the fore-brain; but as the walls of this projection thicken by the development of nervous tissue within them, the cavity becomes gradually obliterated, and is ultimately entirely occupied by neuroglia (central neuroglia of the olfactory tract and bulb).

The **olfactory tract (peduncle)**, sometimes erroneously spoken of as the olfactory nerve, is a band of white matter, flattened on the ventral aspect but ridged along the dorsal aspect (where it fits into the olfactory sulcus), and therefore triangular in section. It measures about 2 cm. in length and 2½ mm. in breadth, being broadest anteriorly where it passes out of the bulb, and narrowing posteriorly, owing to lateral compression, until just before its termination, where it broadens to form the roots.

Trigonum olfactorium (fig. 299).—The olfactory peduncle joins the convoluted grey matter of the frontal lobe situated just in front of the anterior perforated spot. If the olfactory tract be thrown backwards it will be seen to pass into a small triangular area bounded at the sides by the bifurcated

end of the sulcus olfactorius, and having its base directed towards the anterior perforated spot. This is termed the *trigonum olfactorium* or *gyrus tuberis olfactorii* (Retzius). The two roots of the peduncle curve inwards and outwards respectively into the grey matter which is directly continuous with the sides of the gyrus tuberis olfactorii. The *inner root* (*gyrus olfactorius medialis*) is situated behind the gyrus rectus, and is sometimes separated from it by a shallow fissure. This grey matter is often termed the *area of Broca*. The fibres of this root curve sharply round the posterior limit of Broca's area, and its fibres pass partly into this, partly into the callosal gyrus. The *outer* and larger *root* (*gyrus olfactorius lateralis*) is directed outwards towards the limen of the insula, and often appears as though it passed on to the island. In reality, however, as is best shown in the fœtus, it turns sharply inwards and backwards towards the gyrus semilunaris and gyrus ambiens of the caput gyri hippocampi (Retzius). The

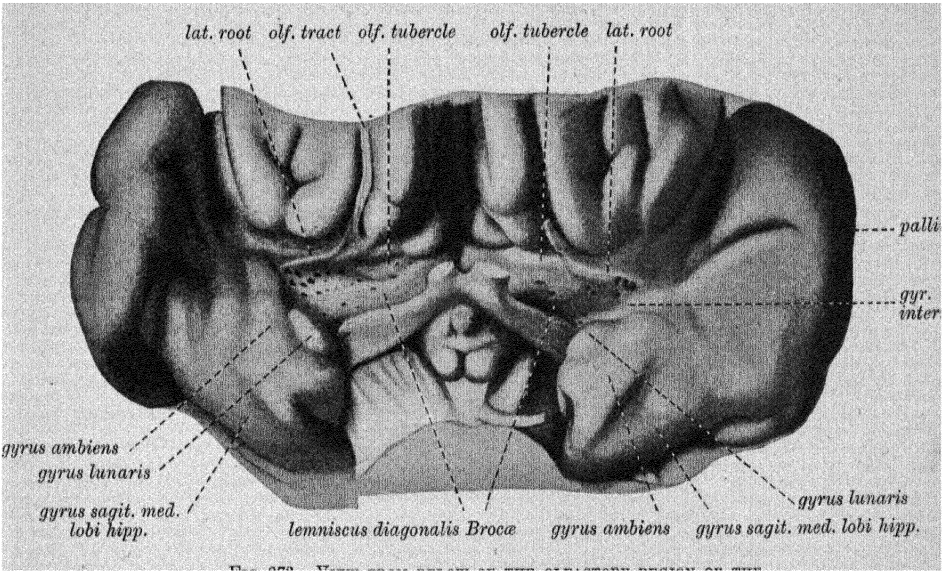


FIG. 273.—VIEW FROM BELOW OF THE OLFACTORY REGION OF THE HUMAN BRAIN. (G. Retzius.)

roots of the olfactory peduncle are largely composed of grey matter, and hence they are termed by Retzius *gyri*; the grey matter is traversed by the white fibres of the olfactory peduncle, which are more or less distinctly visible according to their distance from the surface.

The **anterior perforated space** is a nearly smooth depressed area of grey matter which owes its name to the fact that it is perforated by numerous small branches from the commencement of the anterior and middle cerebral arteries. It is somewhat triangular in shape, and is bounded in front by the *fissura prima* (His), which separates it from the trigonum olfactorium and the mesial and lateral roots of the olfactory peduncle. Behind it is limited internally by the anterior part of the optic tract and externally by the sulcus between it and the projecting temporal lobe. On the outer side it is separated from the insula by the external root of the olfactory nerve, and is concealed by the temporal lobe which overlaps it.

If the optic commissure be turned inwards and backwards, a smooth whitish band will be seen to pass across the space immediately external to the optic commissure. This, which is known as the *diagonal band of Broca*, is continuous in front with the gyrus subcallosus, and behind joins the temporal lobe. In macrosmatic mammals there is a considerable swelling of the grey matter at the anterior perforated space, called the *tuberculum olfactorium*. According to Retzius, there is frequently to be seen in man an oval elevation on the anterior perforated space, which represents this tubercle. The grey matter forming the floor of the space is continuous above with the corpus striatum.

Rhinencephalon and pallium.—Phylogenetically the olfactory is the first of the nerves of special sense to acquire a cortical centre, and this lies on the basal aspect of the hemisphere. With the gradual evolution of other cortical centres, the surface of the hemisphere becomes divisible into two main portions—a ventral, the *rhinencephalon*, and a dorsal, the *pallium*—separated by a longitudinal cleft, the *rhinal fissure*. Turner describes the rhinencephalon as consisting of an olfactory bulb, a crus, and a lobus hippocampi (natiform protuberance or pyriform lobe). As there are other parts of the hemisphere which belong to the olfactory apparatus, the rhinencephalon may be regarded as formed by the olfactory bulb and its peduncle, the trigonum olfactorium with the mesial and lateral olfactory roots or gyri, the anterior perforated spot and tuber olfactorium, the caput gyri hippocampi, the hippocampus (cornu Ammonis), gyrus dentatus and supracallosal gyrus, the fornix, and the septum pellucidum. The term 'pallium' includes all the cortex of the hemisphere which does not belong to the rhinencephalon. It is distinguished from the latter by its progressive development in the vertebrates and its tendency to become convoluted in the higher mammalia until in the Primates it attains a remarkable degree of complexity, in striking contrast to the rudimentary convolutions of the rhinencephalon. Elliot Smith [1] suggests that, as part of the rhinencephalon is pallial, all those portions of the cortex which do not belong to the rhinencephalon should be termed the neopallium. T. H. Bryce divides the pallium into the rhinopallium and the neopallium.

DEVELOPMENT OF THE CEREBRAL FISSURES AND CONVOLUTIONS.

Soon after their formation from the anterior cerebral vesicle, as described in the volume on 'Embryology,' the cerebral hemispheres present the same general outline as in the adult, the ventral portions having already grown downwards and forwards, giving rise to the temporal lobes and the stems of the Sylvian fissures. The backward extension of the hemispheres by which the occipital lobes are formed is, however, at first faintly marked. At this stage each hemisphere, except at its base, is very thin, and a relatively highly developed choroid plexus protrudes into its cavity and is covered by ependymal cells continuous at the choroidal fissure with the wall of the hemisphere. Until the fourth month the hemisphere-walls remain thin and the ventricles are relatively large, a condition obviously favourable to the formation of folds of the entire thickness of the wall, so that fissures appear on its outer aspect, with corresponding projections towards the ventricular cavity. Such fissures have been described as of normal occurrence by numerous anatomists, and termed *transitory* or *temporary*, since they apparently disappeared as the cerebral wall thickened. As already stated, Hochstetter [2] has shown that these so-called temporary fissures are the result of *post-mortem* changes, or imperfect methods of preservation, and this view has been confirmed by Retzius [3] and Mall.[4]

[1] 'Notes on the Natural Subdivisions of the Cerebral Hemispheres,' Journ. Anat. and Phys. July 1901.
[2] Bibliotheca Medica, Abtheilung A. Anatomie, Heft 2, 1898.
[3] Biol. Untersuch, Bd. x. 1902. [4] American Journal of Anatomy, vol. ii. 1903.

Until the fifth or sixth month of fœtal life the external surface of the cerebral hemispheres remains smooth and devoid of fissures with the exception of the Sylvian. The peculiar manner in which this fissure is formed has already been described (see p. 262). On the median aspect there are several fissures—viz. the hippocampal, calcarine, and collateral—which are termed 'complete' since they involve the whole thickness of the wall. Of these the hippocampal is probably the first to appear, but Hochstetter found, in a series of sections of a human fœtus

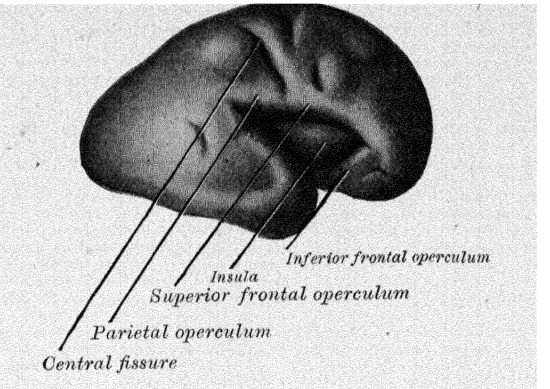


FIG. 274.—RIGHT CEREBRAL HEMISPHERE OF FIVE MONTHS' FŒTUS, VIEWED FROM THE LATERAL ASPECT. Natural size. (J. Symington.)

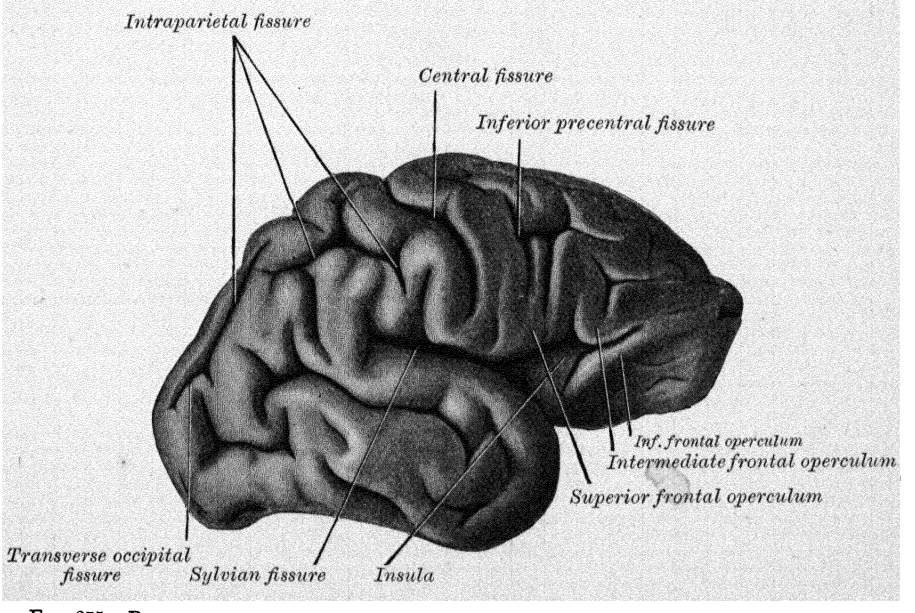


FIG. 275.—RIGHT HEMISPHERE OF BRAIN OF SEVEN MONTHS' FŒTUS VIEWED FROM THE LATERAL ASPECT. Natural size. (J. Symington.)

with a vertex-perineal length of 49 mm., that the projection of the hippocampus into the ventricle was almost entirely due to a thickening of the cerebral wall in this region, the hippocampal fissure itself being very faintly indicated. The hippocampal fissure was formerly regarded as due to the persistence of the posterior part of the arcuate fissure, which was described as pursuing an arched course, from near the foramen of Monro towards the temporal pole, parallel with the choroidal fissure. The arcuate, like the other transitory fissures, is, however, an artefact.

The calcarine is often found well marked when the outer surface of the hemisphere is smooth. It is usually joined by a complete parieto-occipital fissure, but while the calcarine gives rise to a permanent prominence (calcar) in the ventricle, the parieto-occipital eminence gradually disappears.

Until about the beginning of the sixth month of fœtal life the only fissures usually present are the Sylvian and the complete fissures on the median aspect, but sometimes the central fissure appears in the fifth month (fig. 274). During the last three months of fœtal life the development of the convolutions is rapid (fig. 275), so that at birth they are nearly as complicated as in the adult. There is considerable variation as to the time and mode of appearance of the fissures. As a rule the central, the precentral, the first and second frontal, the intraparietal, the collateral, the first temporal, and the cingulate fissures are present at the seventh month, in addition to those already described. In the eighth month these fissures tend to become more tortuous, and various tertiary fissures are formed. This increase in complexity is still more marked during the last month of fœtal life, so that practically all the fissures are present at full time.

Nearly all the principal fissures have been shown to commence as two or more shallow pits, which gradually increase in length and depth and then join one another. Thus the central is usually formed by two such depressions, the cingulate by three, and the intraparietal by four. On the other hand, fissures normally arising from several elements may be produced by extension from a single depression. A large number of the variations in the arrangement of the fissural pattern are due to non-union of one or more of the elements of the complex fissures.

ON THE VARIATIONS WHICH OCCUR IN THE DISPOSITION OF THE FISSURES AND CONVOLUTIONS IN INDIVIDUALS OF DIFFERENT AGE, SEX, INTELLECTUAL DEVELOPMENT, AND RACE.

Very considerable variations are found in the course and relative development of the fissures and convolutions, and this not only in different individuals, but also on opposite sides of the same brain. Even the principal fissures, under which term may be included both those which occur as complete folds of the hemisphere-wall (Sylvian, hippocampal, calcarine, parieto-occipital, and collateral), and those which are the first to make their appearance (about the sixth month of fœtal life) as indentations of the smooth surface of the mantle (precentral, central, intraparietal, parallel, olfactory, cingulate), are very subject to modification, as may partially be inferred from the detailed accounts which have already been given. Although a considerable amount of attention has been paid by several observers to these variations, and of late years especially by Spitzka, Giacomini, Eberstaller, Cunningham, G. Retzius, Elliot Smith, and Duckworth, it cannot be considered as proved that there is any constant relationship between any of the variations which are found to occur and either the age, sex, occupation, or even the race of the individual. Various attempts have from time to time been made to determine in particular a sexual distinction, but it has invariably appeared that the inferences which had been drawn from an insufficient number of observations are not borne out by a more extended series. It is more probable that certain racial differences may ultimately be established when a sufficient number of brains belonging to individuals of other than European races shall have been carefully examined, but up to the present the materials for such comparison have not been abundant enough. In brains of individuals belonging to lower races which have been described (Bushmen, Fuegians, Lapps, and others) it has not appeared that there is any distinct lack of complexity in the convolutions as compared with ordinary European brains; but it is probable that if a large number were to be examined the average complexity in such races would be below that of the average European brain. This is in fact stated by Parker to be the case for the brain of the negro, but the number examined was not sufficient for the statement to be considered conclusive. There is apparently, however, some evidence to show that complexity of convolution, especially in certain regions, generally goes hand in hand with intellectual development of the individual; for in many cases[1] in which the brains of men of known intellectual capacity have been examined, the complexity, due partly to the greater development of secondary and tertiary sulci, partly to the more curved course taken by the principal sulci, has been decidedly, in some instances extraordinarily, marked, more particularly in the frontal and parietal regions. Indeed,

[1] See especially the following by G. Retzius which have appeared in his Biologische Untersuchungen: (*a*) 'Das Gehirn des Astronomen, Hugo Gyldén,' viii. 1898; (*b*) 'Das Gehirn des Mathematikers, Sonja Kovalevski,' ix. 1900; (*c*) 'Das Gehirn des Physikers und Pädogogen, Adam Siljeström,' x. 1902; (*d*) 'Das Gehirn eines Staatsmannes,' xi. 1904. Also E. A. Spitzka, 'A Study on the Brain of the late Major J. W. Powell,' American Anthropologist, v. 1903 (in which will be found an excellent summary of the literature of this subject), and 'A Study of the Brains of six Eminent Scientists and Scholars,' Trans. Amer. Phil. Soc. xxi. 1907.

in some cases a relationship seems to have been apparent between a particular type of mental development and a special part of the brain. Thus it was found that the brain of the great French orator, Gambetta, showed an especial degree of complexity of the third left frontal convolution; and in some eminent mathematicians the region of the supramarginal convolution has been found particularly well developed. In skilled artisans it might be expected that the part of the brain which is connected with the voluntary movements of the hands and fingers would be found more developed than the rest, and in one or two individual cases this has been noticed; but the material for a general statement regarding such relationship is insufficient. Benedikt, from the examination of the brains of a large number of individuals belonging to the criminal class, was of opinion that there exists among these an undue tendency to the formation of four antero-posterior convolutions in the frontal lobe, or, in other words, an undue tendency to the appearance of the paramesial and middle frontal sulci. Although apparently supported by a few observations by other anatomists, this supposition has not borne the test of more extended observation; and, indeed, this so-called 'criminal' type was actually less frequent in the brains of convicts examined by Giacomini than in those of ordinary persons.

ON THE CAUSATION OF THE GYRI AND SULCI OF THE BRAIN.

Various explanations have been offered to account for the convoluted form of the cortex. These are based partly on mechanical considerations—*e.g.* the resistance offered by the larger blood-vessels and undue growth of the brain as compared with that of its enclosing skull-capsule; partly on physiological or physiologico-mechanical considerations, which suppose that there is a relative increase of functional activity of certain parts as compared with others, resulting in an increased growth of those parts, and hence their projection in the form of gyri. These theories, however, are quite insufficient to account for the convoluted formation, since it can be shown (1) that the blood-vessels for the most part do not correspond with the fissures, nor do they lie in the depth of the fissures, when they happen to coincide with them; (2) that the brain does not fill the skull at the time the permanent fissures make their appearance; (3) that in the animal series there is no direct relationship between intellectual development and cerebral convolution. Further, it may be stated that no theory which will not also account for the fissures and laminæ of the cerebellum as well as the convolutions of the cerebrum can be regarded as satisfactory.

It has been pointed out by Jelgersma that a simple mathematical explanation exists for the presence of a convoluted surface. The one feature which mammals with smooth brains have in common is smallness of body; whereas those mammals which possess convoluted brains are invariably found to be of relatively large size (Dareste). In other words, small mammals have smooth brains, however high they may be on the animal ladder, and in spite of their possessing a high degree of intelligence (*e.g.* certain monkeys); while large mammals have convoluted brains, although their intellectual development may be relatively low (*e.g.* cetaceans). 'The grey cortex of the brain, which in members of the same species maintains a tolerably constant thickness, increases by surface extension. Further, with every advance in the growth of the grey matter there must be a proportionate increase of the subjacent white matter. The geometrical law involved is simply this—that in the growth of a body the surface increases with the second, but the interior with the third power of the radius. From this it is evident, seeing that the proportion of internal white matter and external grey matter is in all cases a uniform one, that in the evolution of a large animal out of a small animal a disproportion between the grey capsule and the white core of the cerebrum must result. This is compensated for by the extended cortex placing itself in folds or puckers. Jelgersma further points out that the extent of the cerebral surface depends upon two factors—namely, (1) the absolute quantity of the grey matter, and (2) the thickness with which this is spread over the surface. The absolute quantity of grey matter present is determined by the bulk, or by the psychical endowments of the animal, or by both of these factors together. On the other hand, although the thickness of the grey cortex is very much the same in the same species, it differs considerably in different animal groups; and it follows from the theory which he has advanced that the more sparsely the grey substance is spread over the surface of the white matter, the richer will be the convolution type. In the cetacean cerebrum the grey cortex is exceedingly thin, and it is due to this that the surface shows such an extreme condition of complexity.'[1]

Cases in which there is a congenital absence of the corpus callosum are characterised by a peculiar type of convoluted surface, the fissures and convolutions showing a strong tendency

[1] D. J. Cunningham, Address delivered at the opening of the section of Anatomy and Physiology at the annual meeting of the British Medical Association, 1890.

to radiate from the Sylvian fossa. There is often in these cases an intricacy of pattern displayed which is comparable to that of the cetacean hemisphere, and may be very possibly produced in a similar manner.

The same law by which the formation of the cerebral convolutions is accounted for likewise explains the development of the cerebellar folia, and of the wavy outline of the corpora dentata of the cerebellum and olives.

Jelgersma's theory is not complete in so far that it does not explain why the convolutions should tend to assume certain patterns in certain groups. It is not improbable that these differences may be determined by variations in the relative functional importance of different parts, producing a corresponding variation in the extent of grey matter which has to be provided for; and relative increase of this can only be obtained by local puckering (Cunningham). There is no doubt, however, that the formation of the various cerebral patterns, fairly constant for the same species, is scarcely susceptible of any very simple explanation, and that for the present we must rest satisfied with the statement of the fact.

THE CEREBRAL HEMISPHERES IN THE PRIMATES.[1]

Our knowledge of the morphological significance of the various fissures and convolutions of the adult human brain has been largely due to the study of the evolution of the Primate brain, and this department of comparative anatomy has acquired special importance owing to the numerous experimental observations that have been made to ascertain the functions of the different parts of the cerebral cortex in various apes.

In all the Primates the cerebral hemispheres present the same general form. The portion devoted to the sense of smell (rhinencephalon) is relatively small as compared with many of the lower mammals; and the hemispheres extend in a caudal direction so as to overlap to a greater or less extent the dorsal surface of the cerebellum. The cerebral fissures and the associated convolutionary pattern differ, however, very widely in their degree of complexity. In the common marmoset—a small platyrrhine monkey—the surface of the hemisphere is nearly smooth. Between this brain and that of man a series of Primate brains can be found exhibiting a fairly gradual increase in the number and complexity of the cerebral sulci and gyri, but all belonging to the same general type.

In the **marmoset** (Hapale jacchus) (figs. 276, 277) the hemispheres are small and very simple, the only distinct fissure on the outer aspect being the

FIG. 276. — OUTER ASPECT OF THE LEFT HEMISPHERE OF A MARMOSET, Hapale jacchus. Natural size. (J. Symington.)

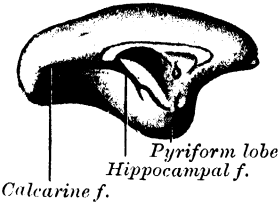


FIG. 277. — INNER ASPECT OF THE LEFT HEMISPHERE OF A MARMOSET, Hapale jacchus. Natural size. (J. Symington.)

Sylvian, while on the inner side there is merely a *hippocampal* fissure, and a *calcarine* which does not branch posteriorly. This fissure produces a very distinct *calcar* in the posterior horn of the lateral ventricle. The *rhinal* fissure, which separates the pyriform from the temporal lobe, is visible from the front, but not from either the inner or outer aspect. This fact is of interest, since in macrosmatic mammals it appears on the outer aspect, while in the Primates generally, with the great development of the pallium and the diminution in the size of the rhinencephalon, the rhinal fissure becomes shifted over to the inner aspect.

The brain of the **capuchin monkey** (Cebus capucinus) shows a marked advance both in size and in cerebral foldings on that of the marmoset, but various members of the family Cebidæ, such as Callithrix and Chrysothrix, present intermediate characters. On the outer aspect (fig. 278) of the capuchin brain the *Sylvian* fissure joins superficially the well developed *parallel* fissure; beyond this union the parallel fissure is continued upwards and backwards into the concavity of the *intraparietal* fissure. The *central* fissure is straight and

[1] I am indebted to the Council of the Royal College of Surgeons of England for permission to draw the brain of a gorilla in the Hunterian Museum. Prof. D. J. Cunningham kindly placed at my disposal the brains of the gibbon and orang. The other figures of Primate brains are from specimens in the Anatomical Department, Queen's College, Belfast.—J. S.

shallower than the intraparietal. On the outer surface of the frontal lobe the *inferior precentral* (sulcus arcuatus) and the *inferior frontal* (sulcus rectus) are well formed, but the *superior precentral* is only indicated by a small shallow depression. The intraparietal fissure is curved round the upper end of the parallel fissure, and is joined on its convex border by the *parieto-occipital* fissure. The 'Affenspalte' (simian sulcus) is seen on the surface of the brain, behind the

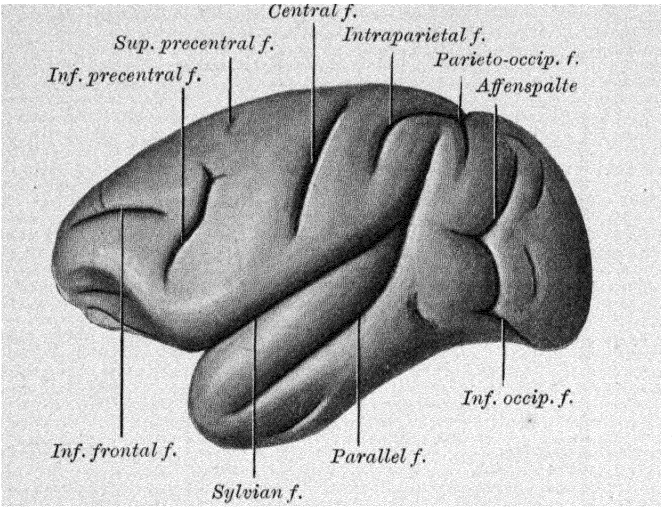


FIG. 278.— OUTER SURFACE OF THE LEFT HEMISPHERE OF A CAPUCHIN MONKEY, Cebus capucinus. Natural size. (J. Symington.)

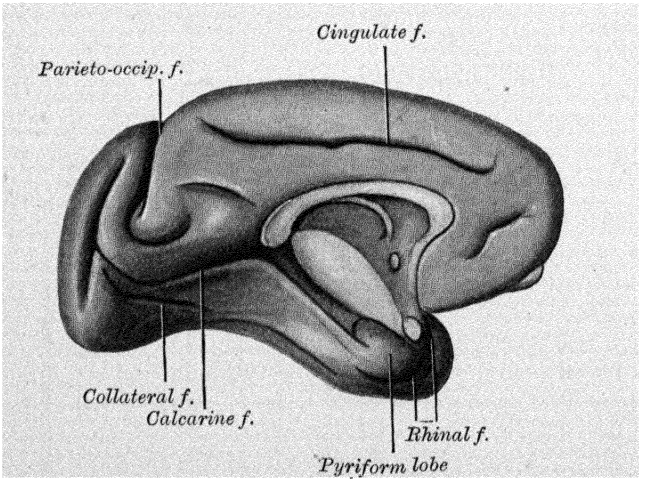


FIG. 279.—INNER SURFACE OF THE LEFT CEREBRAL HEMISPHERE OF A CAPUCHIN MONKEY, Cebus capucinus. Natural size. (J. Symington.)

parieto-occipital and intraparietal fissures. In some of the Cebidæ the 'Affenspalte' approaches much more closely these fissures. On the inner aspect (fig. 279) the *cingulate*, *parieto-occipital*, *calcarine*, *hippocampal*, and *collateral* fissures are all present. A deep fissure curves round the lower end of the parieto-occipital, and becomes lost on its posterior wall. The calcarine terminates posteriorly in an ascending and a descending vertical branch. The *rhinal* fissure, divided into

two portions, is now visible on the inner aspect. It separates the pyriform lobe in front and below from the temporal lobe.

Bonnet monkey (Macacus sinicus).—The brain of this old-world monkey has frequently been the subject of experiment, and on that account is of special interest. It presents a considerable resemblance to the brains of the larger Cebidæ, but there are certain points of difference. The 'Affenspalte' (fig. 280) is now a deep transverse sulcus bounded posteriorly by a well-developed occipital

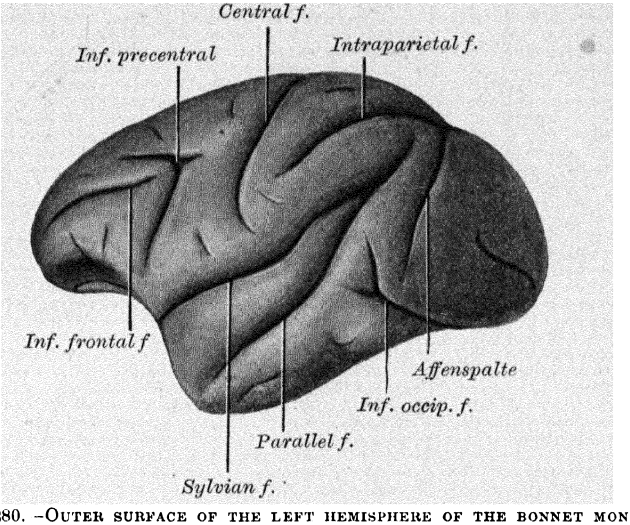


FIG. 280. –OUTER SURFACE OF THE LEFT HEMISPHERE OF THE BONNET MONKEY, Macacus sinicus. Natural size. (J. Symington.)

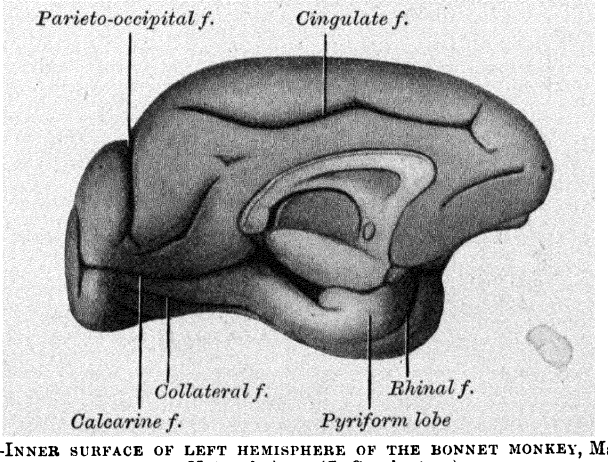


FIG. 281.—INNER SURFACE OF LEFT HEMISPHERE OF THE BONNET MONKEY, Macacus sinicus. Natural size. (J. Symington.)

operculum, and within this sulcus are concealed the posterior bifid end of the intraparietal and the parieto-occipital fissures. In the frontal lobe there is a distinct anterior branch at the upper end of the inferior precentral fissure, and several pits represent the superior frontal fissure, and another the superior precentral. The orbital surface is marked by a triradiate sulcus and also a small orbito-frontal. In the parietal lobe the superior postcentral sulcus is represented by a small pit, and there is another but shallower depression below

the anterior end of the intraparietal fissure. The inner aspect of the hemisphere (fig. 281) closely resembles that of Cebus.

Baboon.—The brain of the yellow baboon (Papio babouin) is larger and more richly convoluted than that of Macacus, but the general pattern is very similar. On the outer aspect (fig. 282) the *Sylvian* fissure has several small

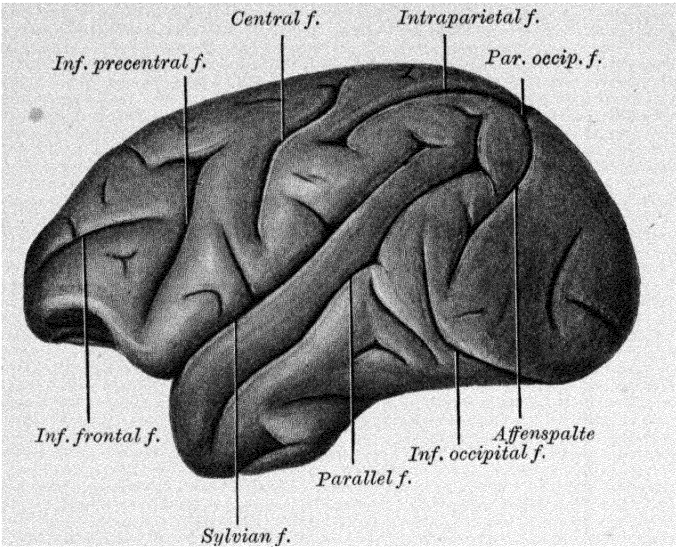


FIG. 282.—OUTER ASPECT OF THE LEFT HEMISPHERE OF A YELLOW BABOON, Papio babuin. Natural size. (J. Symington.)

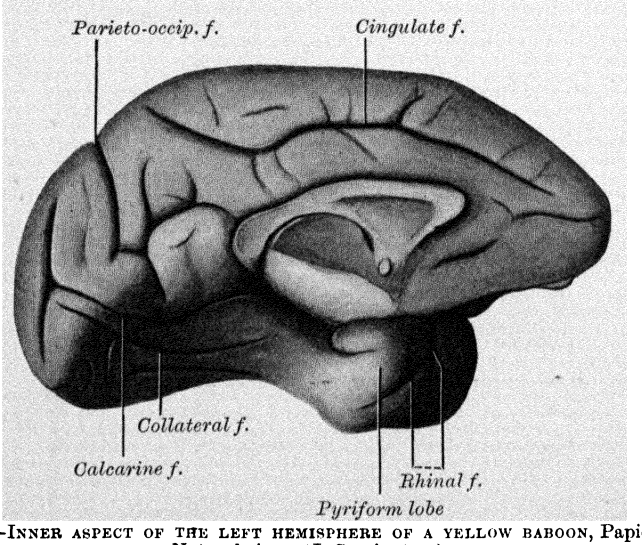


FIG. 283.—INNER ASPECT OF THE LEFT HEMISPHERE OF A YELLOW BABOON, Papio babuin. Natural size. (J. Symington.)

fissures cutting into its upper edge; its extremity is bifid, and it does not join the parallel as it appears to do in both Cebus and Macacus.

The *central* fissure is not so straight as in Cebus or Macacus, and external to the superior precentral impression presents a distinct curve, with the concavity forwards—the so-called *superior genu*. Below this there is a curve,

with its convexity forwards, which is in front of the anterior end of the intraparietal fissure and represents the inferior genu of higher apes. The fissure does not reach the superior mesial border of the hemisphere, and its lower end is separated by a broad annectent gyrus from the Sylvian fissure. On the frontal lobe the *superior precentral* depression is much better marked than in Macacus, while below the central fissure two fissures are seen in an area where only one is developed in Macacus. These fissures are the *transverse precentral*, and farther forwards the *diagonal*. The *intraparietal* begins in a small transverse branch, but its general course is the same as in Macacus. The *superior postcentral* depression is rather more distinct than in Macacus. The 'Affenspalte' runs a considerable distance outwards, and is bounded behind by a distinct occipital operculum. On the inner aspect (fig. 283) the *rhinal* fissure, as in Cebus, is divisible into two parts. The *calcarine* fissure resembles the corresponding fissure in both Cebus and Macacus in dividing posteriorly into an upper and a lower branch.

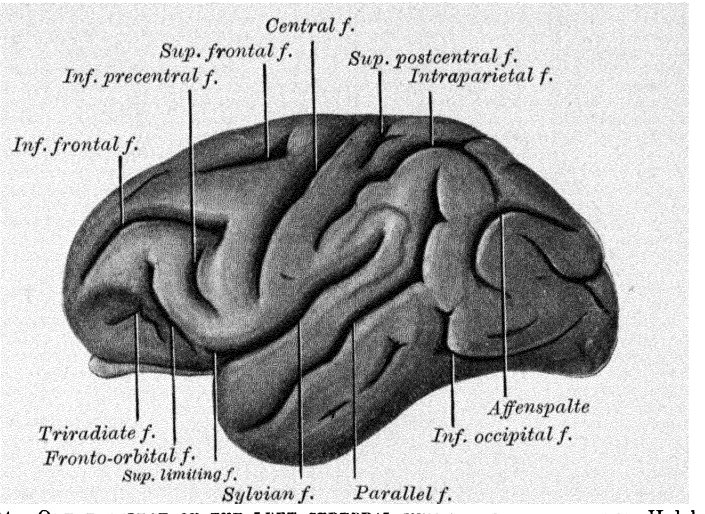


FIG. 284.—OUTER ASPECT OF THE LEFT CEREBRAL HEMISPHERE OF A GIBBON, Hylobates lar. Natural size. (J. Symington.)

Gibbon (Hylobates lar).—The brain of the gibbon is much smaller and simpler than any of the other anthropoid apes, but it possesses certain features which readily distinguish it from that of the lower Quadrumana and associate it with the brain of the higher apes. It therefore forms an interesting link between the two groups.

In the Sylvian region there is a well-developed *fronto-orbital* sulcus, and the *superior limiting* sulcus of the insula extends forwards so as to be visible in front of the Sylvian fissure. In neither the macaque nor the baboon is the superior limiting sulcus visible without opening up the Sylvian fissure, but in all the anthropoid apes it is continued forwards so as to appear in front of the Sylvian fissure. The *fronto-orbital* sulcus is generally admitted to represent the anterior limiting sulcus of the insula in man, but in the anthropoids the inferior and intermediate frontal opercula are not developed; consequently the anterior part of the insula is exposed, and there is no anterior branch to the Sylvian fissure.

The *superior frontal* sulcus is represented by two distinct longitudinal depressions, and the *inferior frontal* is well defined, but the *precentral* fissures

are feebly developed. The *superior precentral* may exist as the slightly bifid posterior end of the superior frontal sulcus; the *inferior precentral* is situated entirely below the posterior end of the inferior frontal, from which it is separated by a narrow annectent gyrus. In the parietal lobe the *intraparietal* fissure forms, as in many of the lower apes, a curved sulcus, beginning behind the central fissure and terminating in the 'Affenspalte.' Some little distance before its termination it gives off a branch which runs inwards towards the superior mesial border of the hemisphere. In addition to the main intraparietal fissure, two other fissural elements belonging to this system are present—viz. a well-formed *superior postcentral* and a *transverse occipital*. The latter is concealed by the occipital operculum, but is not continuous with the posterior end of the main portion of the intraparietal fissure, which only slightly notches the anterior wall of the 'Affenspalte.' The *parallel* fissure is decidedly longer than the Sylvian, extending from near the temporal pole upwards and backwards almost to the horizontal portion of the intraparietal fissure.

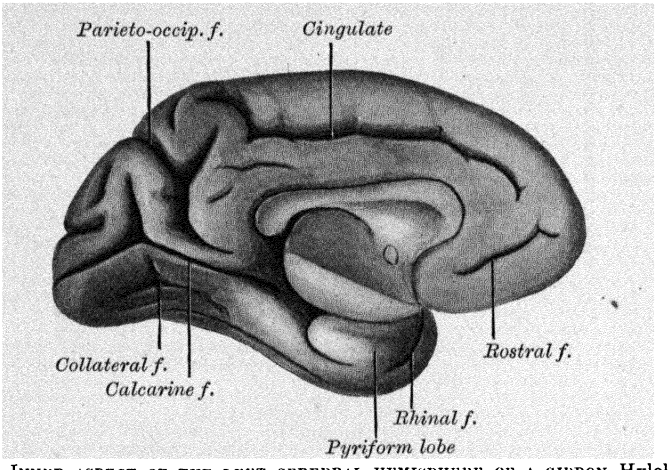


FIG. 285.—INNER ASPECT OF THE LEFT CEREBRAL HEMISPHERE OF A GIBBON, Hylobates lar. Natural size. (J. Symington.)

The mesial aspect of this brain (see fig. 285) does not call for any extended notice. As is usual in the anthropoid apes, the parieto-occipital fissure does not reach the calcarine, being separated from it by a superficial annectent gyrus.

Orang (Simia satyrus) (figs. 286 and 287).—With this brain we enter upon the examination of the cerebral hemispheres of the larger anthropoid apes, a group which includes the orang, chimpanzee, and gorilla. In all of these the brain is very much larger and the secondary sulci more numerous than in the gibbon.[1]

As in the gibbon, the *superior limiting* sulcus of the insula appears in front of the Sylvian fissure, but it is longer in the orang and bifurcates anteriorly. The *fronto-orbital* fissure is also very distinct. The *inferior precentral* runs parallel with the lower part of the central fissure, but is well in front of it, so that the *anterior central* convolution is unusually broad, and is broken up by two independent fissures as well as by a branch extending backwards from near the upper end of the precentral fissure. The *superior precentral* is bifid at both

[1] The functions of the cerebral cortex of the orang and chimpanzee have been experimentally investigated by Sherrington and Grünbaum (Proc. Royal Soc. 1901), and mapped out into areas according to their histological structure by A. W. Campbell (The Localisation of Cerebral Function, Cambridge, 1905).

extremities, and the *superior frontal* is represented by several fissures running more or less parallel with the median plane. The *inferior frontal* is separated

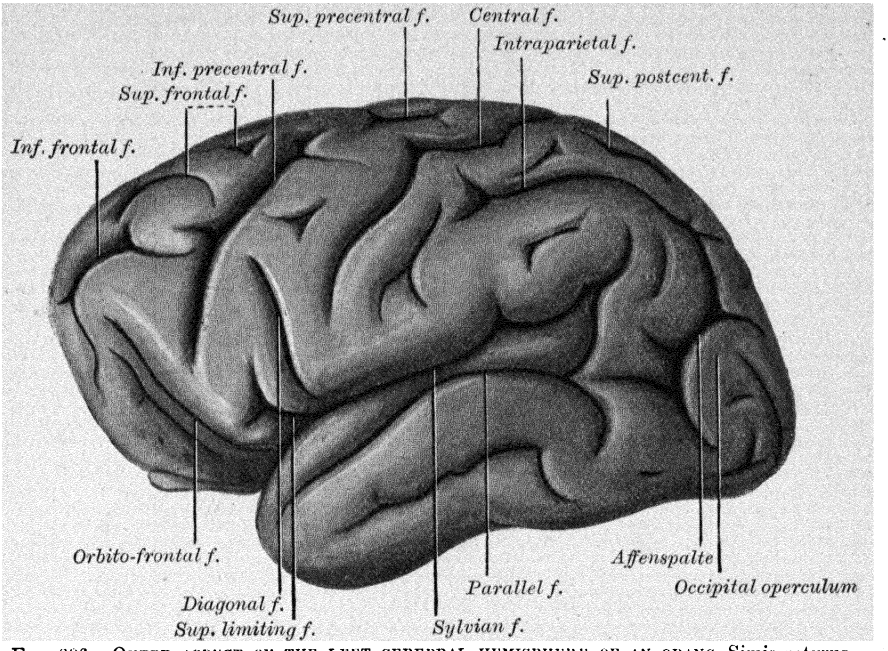


FIG. 286.—OUTER ASPECT OF THE LEFT CEREBRAL HEMISPHERE OF AN ORANG, Simia satyrus. Natural size. (J. Symington.)

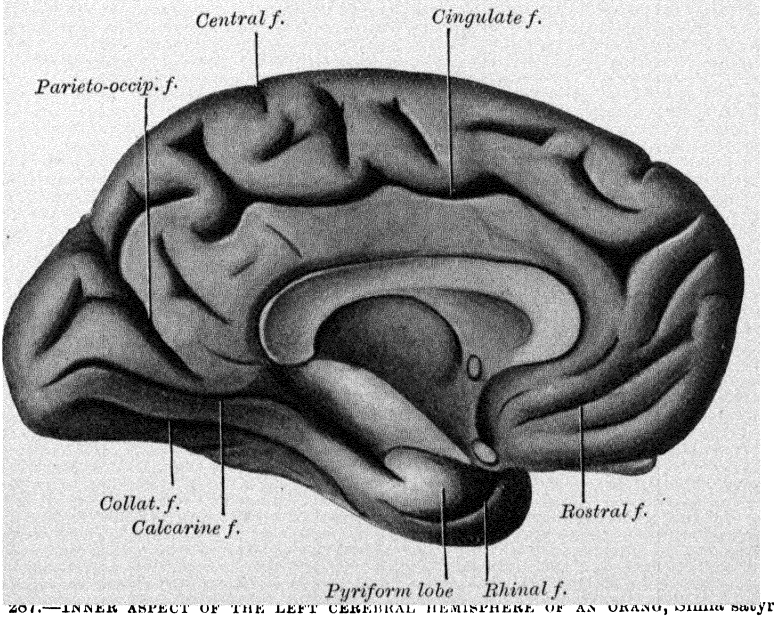


FIG. 287.—INNER ASPECT OF THE LEFT CEREBRAL HEMISPHERE OF AN ORANG, Simia satyrus. Natural size. (J. Symington.)

posteriorly from the inferior precentral by a narrow gyrus, and anteriorly reaches on to the orbital aspect of the frontal lobe. The *intraparietal* system of fissures is decidedly complicated. Thus the *postcentral* fissure is represented by four

sulci, of which the third, counting from above downwards, is continuous with the ramus horizontalis of the intraparietal. (In the left cerebral hemisphere of a man, shown in figs. 255 and 256, the postcentral fissure is broken up into four pieces, but it is the second one that passes backwards into the ramus horizontalis.) The intraparietal fissure joins the 'Affenspalte' posteriorly, and on opening up the latter it is seen to end in a concealed transverse occipital sulcus. The 'Affenspalte' is bounded by a distinct occipital operculum and is markedly curved, with the convexity forwards.

The inner aspect is much more richly convoluted than in the gibbon. There are several *rostral* sulci, and the marginal convolution is partially subdivided into an upper and a lower portion by a series of short sulci. The *internal*

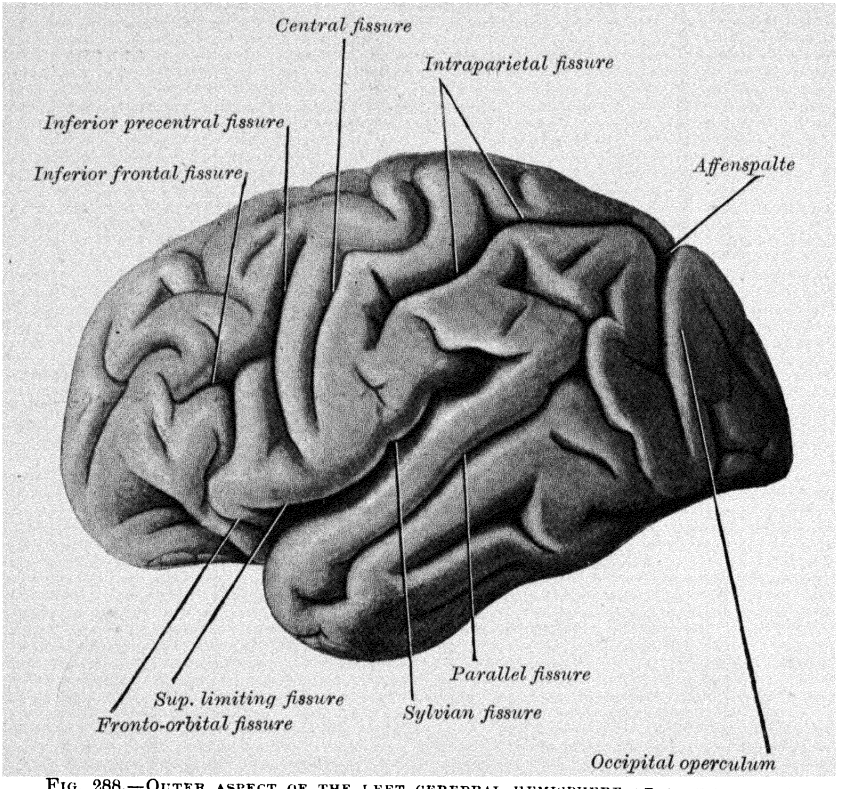


FIG. 288.—OUTER ASPECT OF THE LEFT CEREBRAL HEMISPHERE OF A CHIMPANZEE, Anthropopithecus troglodytes. Natural size. (J. Symington.)

parieto-occipital is separated by a narrow gyrus from the *calcarine* fissure, and the latter does not bifurcate posteriorly.

Chimpanzee (Anthropithecus troglodytes).—The brain of the chimpanzee is about the same size as that of the orang, and its convolutionary pattern is of about the same complexity (figs. 288 and 289).

On the outer aspect the *superior limiting* sulcus extends in front of the Sylvian fissure, but does not bifurcate anteriorly. The left *central* fissure in the brain figured reaches nearly to the mesial border of the hemisphere, and its inferior genu forms a deep bay, in which a process of the anterior central convolution is lodged. The *superior* and *inferior precentral* sulci are well developed, and are joined respectively with the *superior* and *inferior frontal* sulci. There are two depressions on the superior frontal gyrus which may represent the *sulcus frontalis*

mesialis, a fissure either absent or very feebly marked in the anthropoid apes. There is a typical *intraparietal* fissure, but the well-marked superior postcentral element does not join it. The 'Affenspalte' is very distinct, and runs from the mesial border of the hemisphere, where it appears to join the internal parieto-occipital, transversely across the external surface of the hemisphere nearly as far as its lateral border.

The parietal and temporal opercula do not present any special peculiarity in the apes as compared with man, but it is quite otherwise with the frontal operculum. According to Cunningham, the orbital and intermediate (frontal of Cunningham) portions of the frontal operculum are entirely undeveloped, and the anterior portion of the insula is uncovered and bounded anteriorly by the orbito-frontal sulcus, a fissure corresponding to the anterior limiting sulcus of the insula

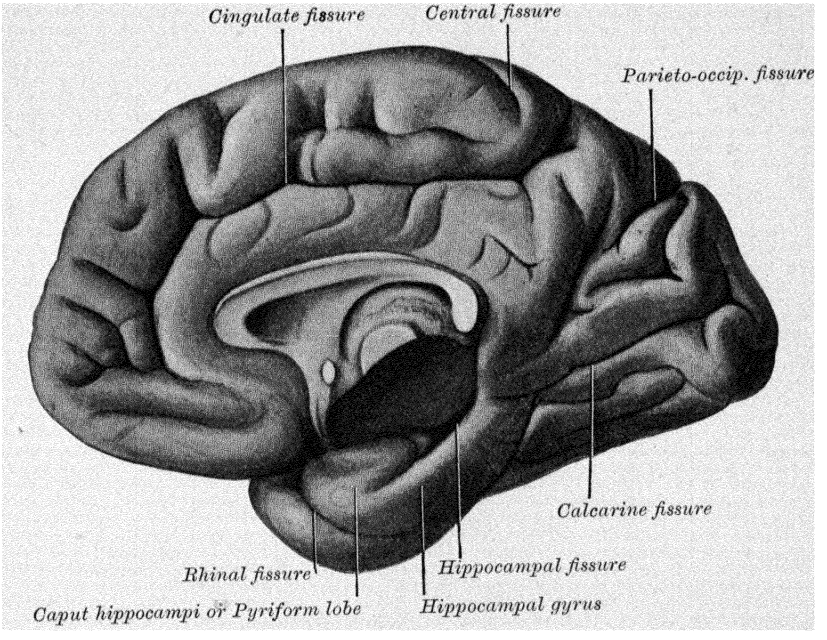


FIG. 289.—INNER ASPECT OF THE RIGHT CEREBRAL HEMISPHERE OF A CHIMPANZEE, Anthropopithecus troglodytes. Natural size. (J. Symington.)

in the apes. The insula in many of the lower apes is quite smooth, and even in the chimpanzee it is only slightly subdivided by fissures.

The inner aspect of this brain does not differ in any important points from that of the orang. The *rostral* sulci and the depressions on the marginal convolution are about as well developed, and the *central fissure* appears in front of the upturned end of the cingulate gyrus. The *internal parieto-occipital* is not so sharply defined, but the posterior end of the *calcarine* fissure is better developed.

Gorilla (G. savagei).—The brain of the gorilla is the largest of all the anthropoid brains, and probably approaches the human brain more nearly than that of any of the other apes. It is, however, much more nearly allied to the brain of the orang and chimpanzee than to that of man. Figs. 290 and 291 are from an extremely well-preserved specimen in the Hunterian Museum in London.[1]

[1] According to Elliot Smith, it 'is probably by far the best specimen of its kind to be found anywhere.' See Catalogue of the Physiological Series of Comparative Anatomy in the Museum of the Royal College of Surgeons of England, ii. (2nd ed. 1902), where it is fully described.

The hemispheres appear in this specimen more elongated in form than those of the orang and chimpanzee already figured, but this is probably due to the fact

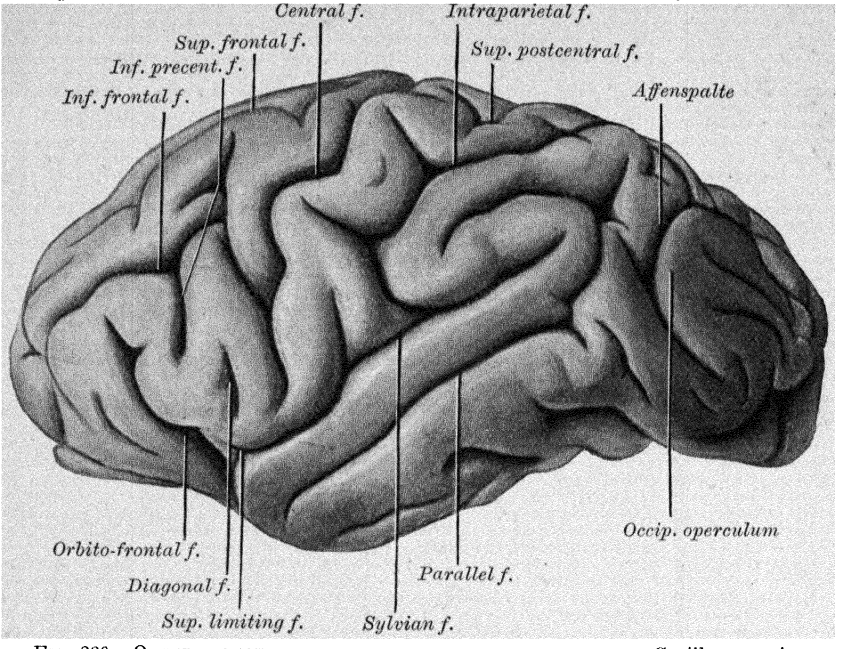


FIG. 290.—OUTER ASPECT OF THE LEFT HEMISPHERE OF A GORILLA, Gorilla savagei. Natural size. (J. Symington.)

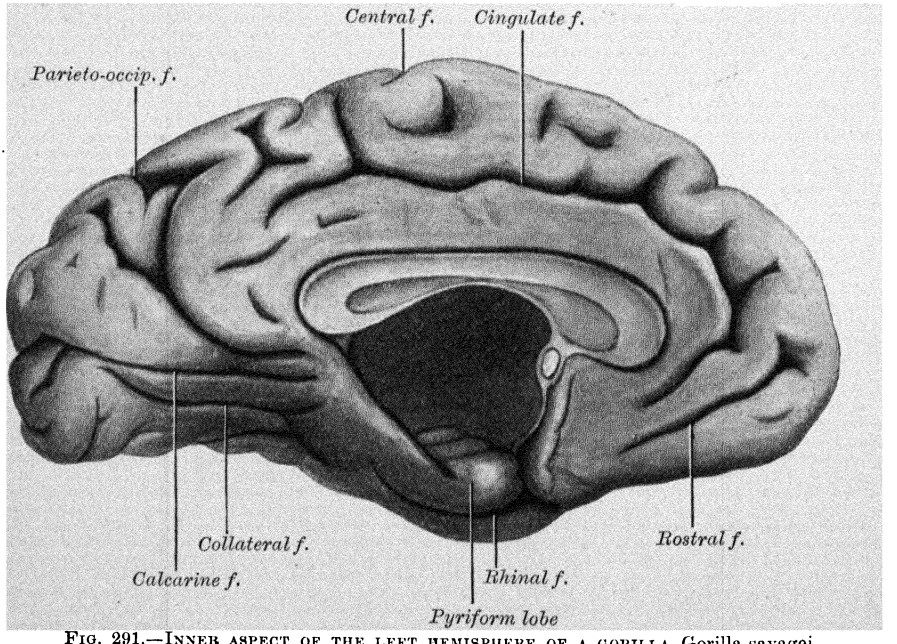


FIG. 291.—INNER ASPECT OF THE LEFT HEMISPHERE OF A GORILLA, Gorilla savagei. Natural size. (J. Symington.)

that the specimen was not hardened *in situ*. On its outer aspect (fig. 290) two fissures are seen to cut into the upper border of the *Sylvian* fissure,

which however ends without bifurcating. Elliot Smith has shown that in this specimen nearly the whole of the insula is concealed within the Sylvian fissure, and the *superior limiting* sulcus is separated from the orbito-frontal simply by a concealed gyrus, so that the insula is almost completely shut off from the frontal lobe. This approximation to the condition found in man is only an individual variation, the usual arrangement in the gorilla being similar to that met with in the orang and chimpanzee. The *intraparietal* fissure ends posteriorly in the 'Affenspalte,' and the latter fissure, as in the orang, is markedly curved; moreover its inner limb does not reach the mesial border of the hemisphere, and is quite distinct, even superficially, from the parieto-occipital fissure.

The inner aspect (fig. 291) of this gorilla's brain does not differ in any important point from that of the orang or chimpanzee, as can be readily seen by a comparison with figs. 287 and 289. The precuneate lobule is occupied by a *triradiate* sulcus, the upper limb of which extends to the upper border of the hemisphere, but does not pass outwards for some distance on the cranial surface, as it usually does in man. The *parieto-occipital* fissure is evidently complex, as is so frequently the case in the human subject. The *parieto-occipital* and *calcarine* fissures are still separated by a superficial annectent gyrus, but this is crossed by a shallow sulcus. The *rhinal* fissure presents the characteristic simian type—viz. a simple curved sulcus separating the pyriform from the temporal lobe.

Comparison between the human and anthropoid brains.—The most important differences between the brain of man and that of the higher apes are in size and weight; the cerebrum being two and a-half to three times larger and heavier in man than in the largest anthropoid. The hemispheres are also more richly convoluted. The enlargement and increase of complexity involve all the lobes except the olfactory. In the frontal lobe there is not only a general increase in complexity, but the orbital and usually also the intermediate portion of the frontal operculum are developed, and, concealing the anterior portion of the insula, give rise to an anterior limb of the Sylvian fissure. There is a marked increase in the size and complexity of the parietal lobe, involving the inferior parietal lobule more than the superior. The great development of the parietal lobe is associated with a displacement backwards and inwards of the visuo-sensory centre (A. W. Campbell), so that this area, which in the apes extends forwards and outwards nearly to the posterior lip of the 'Affenspalte,' in man barely reaches the occipital pole, and is only visible to a very slight extent, if at all, in a view of the hemisphere from the lateral aspect.[1]

The human brain may be said to exhibit simian or ape-like characters when it has a narrow frontal region, feebly developed orbital and intermediate frontal opercula, so that part of the insula is uncovered, a prominent sulcus lunatus ('Affenspalte') appearing on the lateral aspect and bounded behind by a distinct occipital operculum, and a small inferior parietal lobule.

[1] It should be noted that, according to Elliot Smith, this area has a greater lateral extension in many Egyptian brains.

For further information regarding the Primate brain the following works, among others, may be consulted:

Gratiolet, Mémoire sur les plis cérébraux de l'Homme et des Primates, Paris 1854; W. Turner, 'The Convolutions of the Brain,' Journ. Anat. and Phys. xxv. 1890; D. J. Cunningham, 'Contributions to the Surface Anatomy of the Cerebral Hemispheres,' Cunningham Memoirs of the Royal Irish Academy, 1892; Elliot Smith, Catalogue of the Physiological Series of Comparative Anatomy contained in the Museum of the Royal College of Surgeons of England, ii. (2nd ed. 1902); A. W. Campbell, Histological Studies on the Localisation of Cerebral Function, 1905.

THE CENTRAL PARTS AND BASE OF THE CEREBRUM.

THE LATERAL VENTRICLES; VENTRICLES OF THE CEREBRAL HEMISPHERES.

An aperture (interventricular foramen, or foramen of Monro) which has been already mentioned as opening out of the anterior part of the third ventricle (see p. 223) leads on each side into the corresponding ventricle of the cerebral hemisphere or lateral ventricle (figs. 292, 293). Each lateral ventricle is an irregularly curved cavity, extending in the substance of the corresponding hemisphere for about two-thirds of its entire length, and lined by a prolongation of the ciliated epithelium which characterises the inner surface of the true brain-ventricles. It may be described as consisting of a *body* (pars centralis), an *anterior horn*, a *posterior horn*, and an *inferior horn*. The anterior horn lies in front of the foramen of Monro and extends from opposite this opening forwards, downwards, and a little outwards into the frontal lobe; the body passes backwards, and then curves downwards and outwards, and ends at the trigonum collateralis by dividing into a posterior and an inferior horn; the posterior horn passes backwards, with a bold curve convex outwards, into the occipital lobe; and the inferior horn passes forwards and slightly downwards also in a bold curve with its convexity outwards, into the temporal lobe, and extends to within an inch or rather more of the apex of that lobe.

The **anterior horn of the ventricle** is about an inch long, and rather more than half an inch broad, reaching from opposite the foramen of Monro nearly as far forwards as the level of the anterior extremity of the genu of the corpus callosum, and terminating externally at the outer border of the upper surface of the caudate nucleus. The cavity is sometimes reduced in its outer and anterior portions to a mere slit, but more usually the walls are separated from one another by distinct intervals (see fig. 260). The horn is bounded above and in front by fibres passing from the anterior part of the corpus callosum into the frontal lobe. Its floor is convex, looks upwards, forwards, and inwards, and is formed by the expanded anterior end (caput) of the caudate nucleus. A well-marked curved groove bounds the head of the caudate nucleus in front and on the inner side. The most internal portion of this groove is deepened to form a small fossa (anterior median recess of Retzius) which is bounded posteriorly by a slightly raised area—the trigonum striæ terminalis—continuous posteriorly with the stria terminalis. The vertical inner wall consists of the two layers of the septum pellucidum, with the cavum septi pellucidi between them (see fig. 294).

The *body*, or pars centralis, is directly continuous in front, opposite the foramen of Monro, with the anterior horn. The upper and anterior portion of the body is prolonged backwards in a slightly arched manner for about one and a-half inch; beyond this the cavity turns outwards and downwards behind the tail of the caudate nucleus and bifurcates opposite the eminentia collateralis into the posterior and inferior horns. This descending part always possesses a well-marked lumen which reaches within about one and a-half inch of the lateral surface of the hemisphere in the region of the posterior part of the first temporal convolution. The body, like the anterior horn, is roofed over by the corpus callosum, with its lateral extension into the substance of the hemisphere, and presents a ribbed appearance (see fig. 134). In examining the ventricle from above it is usual to slice the brain horizontally down to the level of the callosum, and then to cut through this commissure a short distance on each side of the middle line, and remove it sufficiently to expose

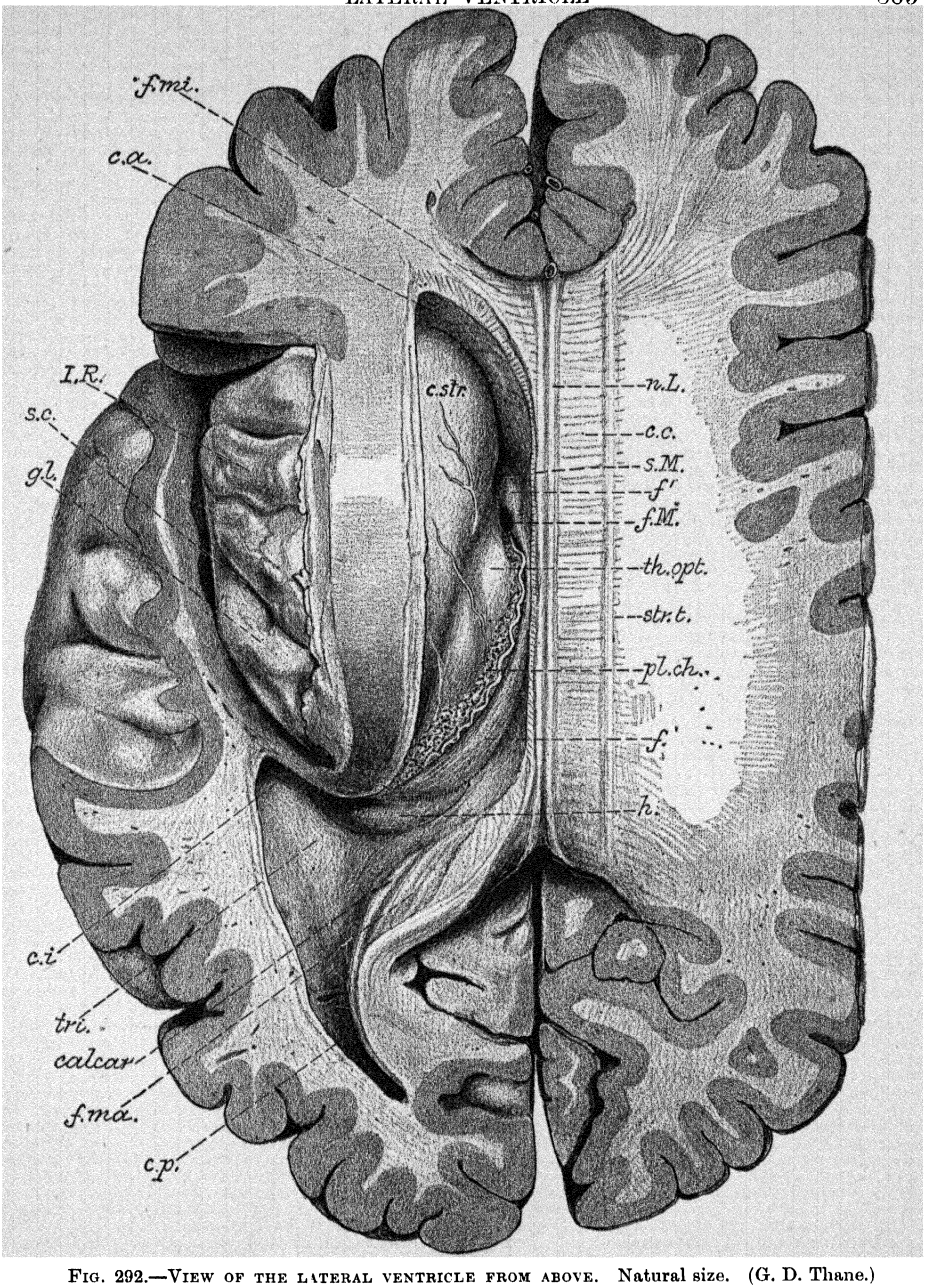


FIG. 292.—VIEW OF THE LATERAL VENTRICLE FROM ABOVE. Natural size. (G. D. Thane.)

The preparation was made with the brain *in situ* (hardened). The skull cap and membranes having been removed, the brain was sliced down to the level of the corpus callosum. The left lateral ventricle was then opened by cutting away its roof, and the island exposed by slicing away the opercula. The drawing is made from a photograph.

I.R., insula Reilii (the line points to the middle of the three gyri breves); *s.c.*, sulcus centralis insulæ; *g.l.*, gyrus longus insulæ; *c.c.*, corpus callosum; *n.L.*, nerves of Lancisi; *str.t.*, stria tecta; *f.mi.*, forceps minor; *f.ma.*, forceps major; *c.a.*, cornu anterius of ventricle; *c.p.*, cornu posterius; *c.i.*, entrance to cornu inferius; *f.M.*, foramen Monroi; *s.M.*, sulcus leading backwards to the foramen Monroi; *c.str.*, nucleus caudatus of corpus striatum; *th.opt.*, thalamus, anterior tubercle; *pl.ch.*, plexus choroides; *f.*, fornix; *f'*, its column; *h.*, posterior end of hippocampus; *tri.*, trigonum ventriculi; *calcar*, calcar.

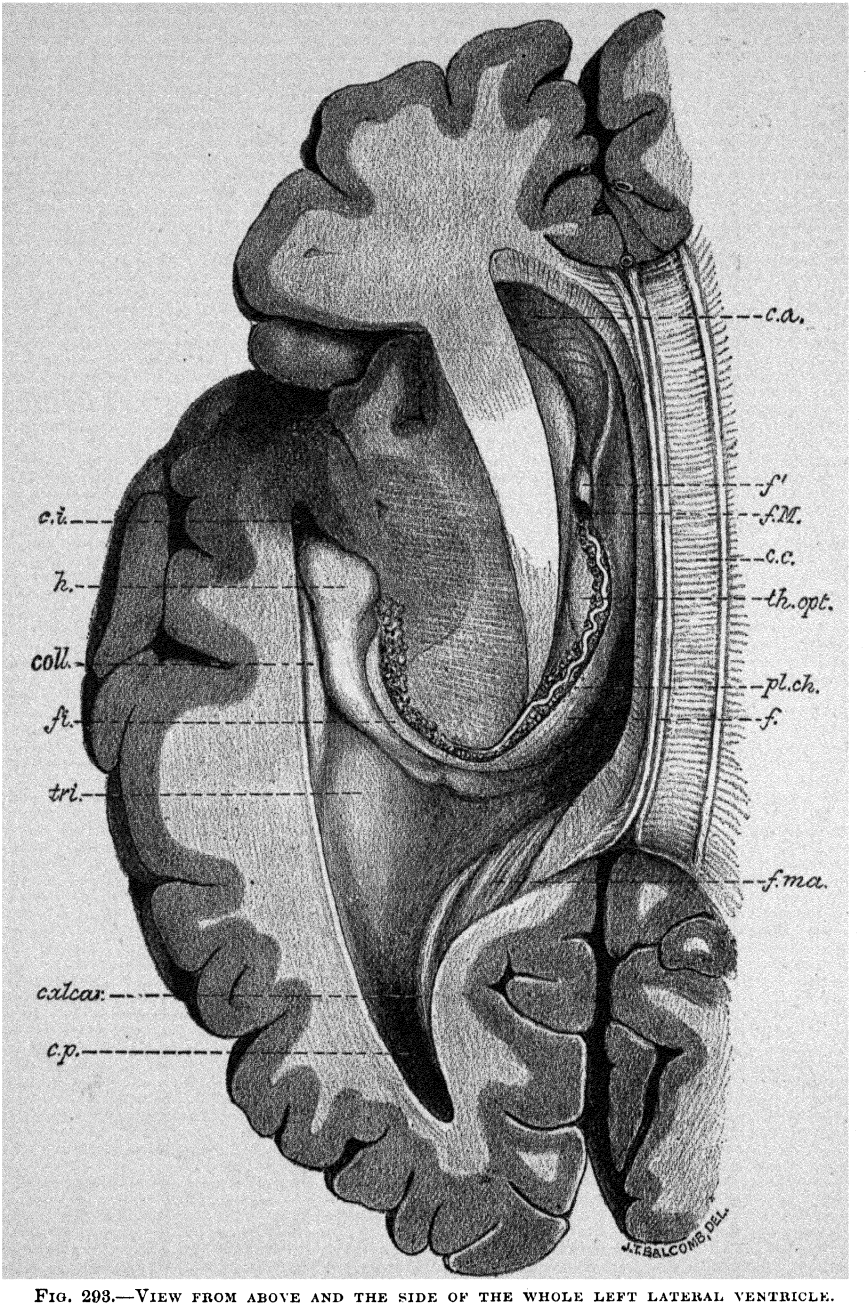


FIG. 293.—VIEW FROM ABOVE AND THE SIDE OF THE WHOLE LEFT LATERAL VENTRICLE. Natural size. (G. D. Thane.)

This is a further dissection of the preparation shown in fig. 292. The insula has been sliced away and the inferior cornu, *c.i.*, exposed. Within this are seen the following parts: *fi.*, fimbria, continued from the fornix; *h.*, the hippocampus; *coll.*, the eminentia collateralis. The other lettering as in fig. 292.

the interior of the ventricle. The following parts, which form its floor, are then brought into view from within outwards:

(*a*) The edge of the body of the **fornix** (figs. 292, 293, *f*), a flattened tract of white matter with longitudinal fibres, which lies immediately under the callosum, broadening behind as it passes under the splenium, and bifurcating in front into two cylindrical bundles, each of which passes over and in front of the foramen of Monro, and then sinks into the mesial part of the subthalamic tegmentum.

(*b*) If the callosum and fornix are removed, a layer of pia mater is seen underneath. This is the tela choroidea of the third ventricle (fig. 294), and its

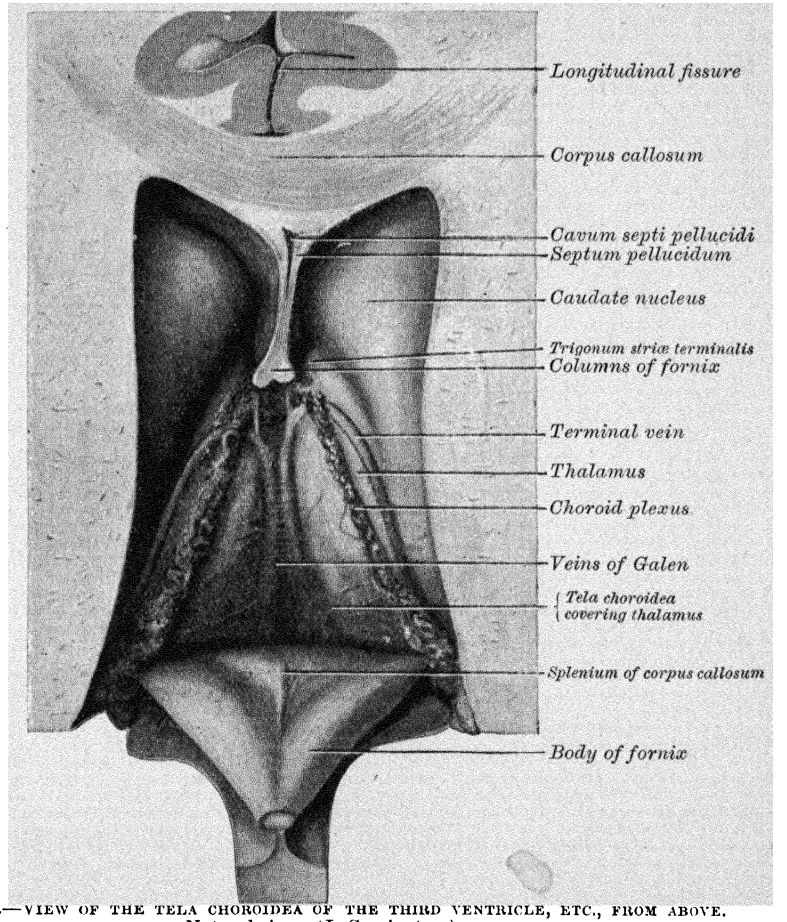


FIG. 294.—VIEW OF THE TELA CHOROIDEA OF THE THIRD VENTRICLE, ETC., FROM ABOVE. Natural size. (J. Symington.)
The columns of the fornix were divided and its body separated from the tela choroidea and turned backwards.

edge projects as the *choroid plexus of the lateral ventricle* from beneath the margin of the fornix in the form of a vascular fringe (figs. 292, 293, *pl.ch.*), which extends from the foramen of Monro (at the back of which it is continuous with the corresponding plexus of the opposite side as well as with those of the third ventricle) over the surface of the thalamus, as far as the inferior cornu, into which it projects along the whole length of the horn (mesial border).

(*c*) Lateral to the choroid plexus two masses of grey matter, separated by an obliquely placed white stria, form the floor. The mesial of these is a part of the

dorsal surface of the thalamus (fig. 292, *th.opt.*), covered with a thin layer of white matter. This area of the thalamus, which thus appears to form part of the floor of the lateral ventricle, is covered by a layer of cells continuous with that on the choroid plexus. This layer is the persistent primitive wall of the cerebral hemisphere between the choroid plexus and the caudate nucleus, and, although very thin and adherent, really shuts off the thalamus from the lateral ventricle.

The white stria, *stria terminalis* (fig. 228), gradually increases in breadth from behind forwards, and in front of the foramen of Monro expands into the *trigonum striæ terminalis*. A vein (vena terminalis) runs forwards superficial to the stria, and opposite the foramen of Monro turns inwards and joins the vein of the septum pellucidum to form the vein of Galen (see fig. 294). Close to the ependyma, and lying over the terminal vein, is a small greyish band containing longitudinally running nerve-fibres ; this has been named the lamina cornea. The lateral mass of the grey matter is a continuation backwards of the nucleus caudatus, which gradually narrows from before backwards into a long slender tail curving downwards and forwards along the dorsal part of the inferior horn. On the inner side of the upper part of the body of the ventricle is a narrow groove between the corpus callosum and the fornix. This groove is bounded internally by the narrow posterior part of the septum pellucidum, and behind this by a direct union of the corpus callosum with the fornix. On the inner and anterior wall of the descending part of the body the convex eminence known as the hippocampus or cornu Ammonis begins, while lower down and farther backwards between the posterior and inferior horns is a triangular area, the trigonum ventriculi, the greater part of which is occupied by a smooth raised surface known as the eminentia collateralis, on account of its correspondence with the collateral fissure externally.

The *posterior horn* (figs. 292, 293, *c.p.*), which is curved around the lower end of the parieto-occipital fissure, its concavity therefore being directed inwards, passes, as before said, into the occipital lobe. It is surrounded by the fibres of the corpus callosum which are passing to the temporal and occipital lobes. At the upper part of its mesial wall there is a bundle of fibres (forceps major) sweeping round from the splenium of the callosum to enter the occipital lobe. This produces a projection into the cavity of the horn which is known as the *bulb of the posterior horn*; frequently there are several projections in place of one. Below it is another curved eminence which extends from the base of the horn backwards for a variable distance, to end in a pointed extremity. It corresponds with the anterior calcarine fissure on the mesial surface of the hemisphere, and is known as the calcar.

The calcar is not peculiar to the human brain, as was at one time thought, but is found in the brains of many Primates (Huxley). In the human subject the posterior horn varies greatly in size, and the calcar is still more variable in its development, being sometimes scarcely to be recognised, and at others proportionally large. It is usually most developed where the posterior horn is longest; but the length of the posterior horn, and prominence of the calcar, are by no means in proportion to the dimensions of the hemisphere.

The *inferior horn* (fig. 293) is directed forwards and downwards from the lower end of the body of the ventricle, finally curving inwards, and ending about an inch to an inch and a-half from the apex of the temporal lobe, where it abuts against the amygdala. The dorso-lateral boundary (roof) is formed by the fibres of the callosum, which are arching over it into the temporal lobe, forming a part of the so-called *tapetum*. The tail of the nucleus caudatus and the stria terminalis are prolonged into the roof. Extending along the floor of the

horn is an eminence known as the *hippocampus* or *cornu Ammonis* (fig. 295), which becomes enlarged as it descends, and, being notched, its edge here presents a certain resemblance to an animal's paw (*pes hippocampi*). This eminence corresponds with the hippocampal fissure externally, which thus indents the floor of the cornu, and the grey matter at the bottom of the fissure being separated from the cavity of the ventricle by a thin layer of white substance (covered with ependyma), shows through and gives a bluish-white appearance to the hippo-

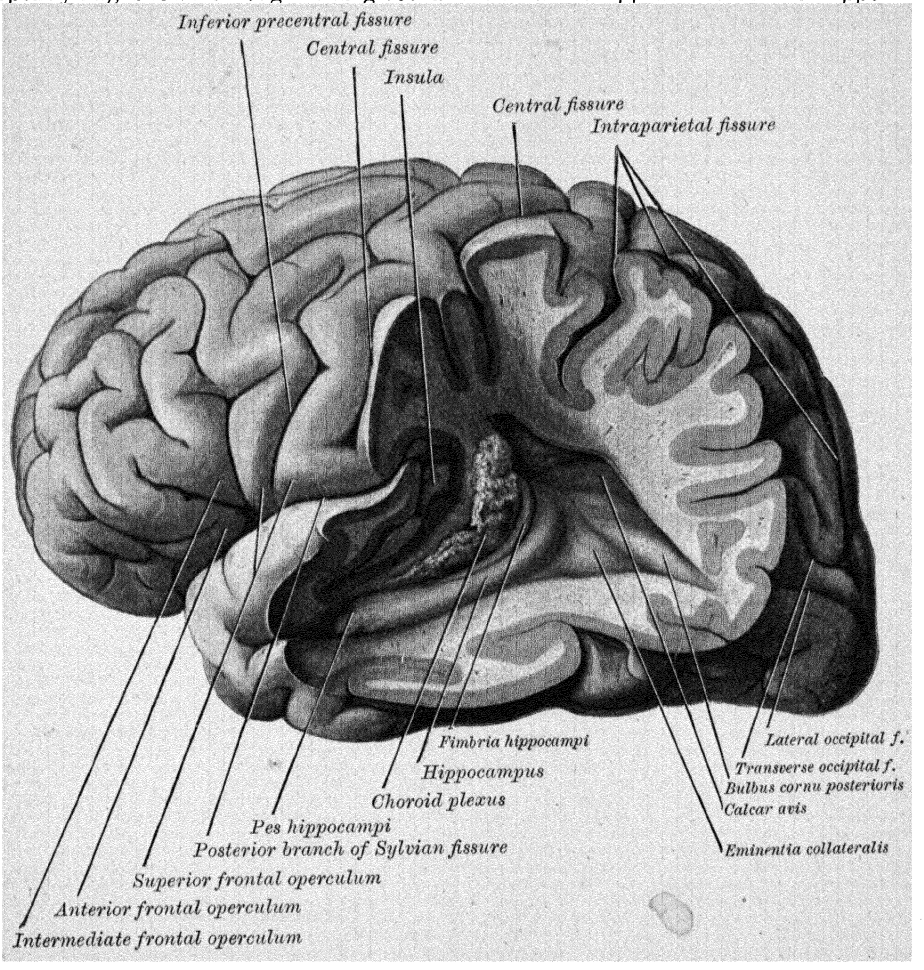


FIG. 295.—OUTER ASPECT OF LEFT CEREBRAL HEMISPHERE WITH PART OF CEREBRAL WALL REMOVED TO EXPOSE POSTERIOR PORTION OF THE BODY OF THE LATERAL VENTRICLE AND ITS INFERIOR AND POSTERIOR HORNS. (J. Symington.)

campus. Mesial to the hippocampus is the white band known as the fimbria (fig. 295), prolonged from the crus of the fornix; and over the fimbria, at the angle which the floor of the horn here forms with its roof, the choroid plexus projects into the cavity from the external pia mater; the plexus is, however, covered by the epithelial lining of the cavity, which extends over it in passing from roof to floor. If the pia mater is pulled away it drags along with it this covering layer of epithelium, and the cornu is made to open on the surface of the brain. A cleft-like opening is thus produced, which has been called the

inferior fissure of the cerebrum, being the lower part of the so-called great *transverse fissure*, which follows the plane of the tela choroidea over the thalamus and third ventricle, and emerges posteriorly between the splenium of the corpus callosum and the corpora quadrigemina. It is along this fissure that the choroid plexuses of the pia mater are invaginated into the ventricles, covered by the ventricular epithelium, which is pushed in before them. It is only when the choroid plexuses are dragged away that an actual fissure is formed in the hemisphere-wall between the fornix and fimbria on the one side and the thalamus on the other; but with the plexus *in situ* it is a deep sulcus—*i.e.* an invagination only—of the thin hemisphere-wall (here formed of the ventricular epithelium alone). It is known as the *choroidal fissure*, and appears at an early

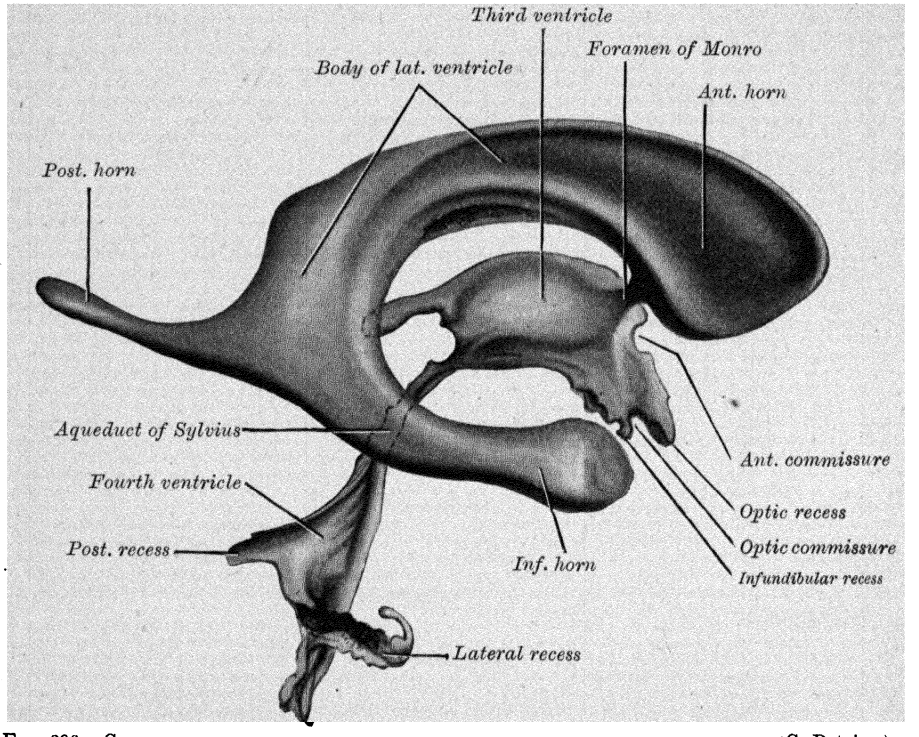


FIG. 296.—CAST OF THE VENTRICLES OF THE BRAIN VIEWED FROM THE RIGHT SIDE. (G. Retzius.)

period of embryonic development. Except near its extremities, the lumen of this horn is seldom more than a narrow curved slit.

Merkel and Mierzejewsky described an actual cleft in the pia mater along the inferior horn which effects a communication between the ventricle and the subarachnoid space, analogous to the foramen of Magendie and the lateral apertures in the fourth ventricle. This observation has not been confirmed by the more recent researches of G. Retzius.

The shape of the ventricles is best shown in a cast of the cavities, which can be made in plaster of Paris, wax, or gelatin, but the best results are obtained by the use of fusible metals (figs. 296 and 297).[1]

The **corpus callosum** or **great transverse commissure** (figs. 227, 260, 292) is a white structure which connects the two hemispheres with one another.

[1] G. Retzius, 'Die Gestalt der Hirnventrikel des Menschen, nach Metallausgüssen dargestellt,' Biologische Untersuchungen, ix. 1900.

Where it crosses the median plane it is about half the length of the hemispheres and approaches nearer their anterior than their posterior extremities. Its upper free surface lies at the bottom of the great longitudinal fissure and extends outwards on each side, forming the lower boundary of the callosal fissure. This surface is about 2 cm. broad behind, but somewhat narrower in front. The distance in a straight line between its anterior and posterior ends is about 8 cm., but when measured along its upper convex surface it is fully 10 cm. long.

It is distinctly marked by transverse furrows, which indicate the direction of the greater number of its fibres. It is also marked in the middle by a longitudinal furrow (*raphe*), which is bounded by two white tracts, placed close to each other,

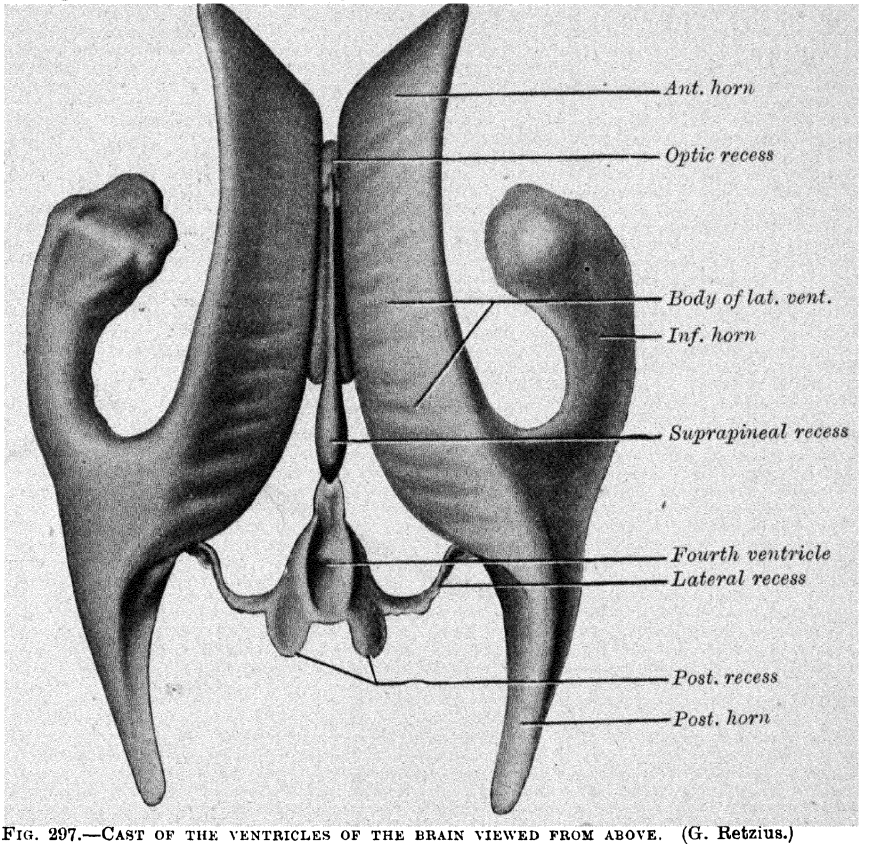


FIG. 297.—CAST OF THE VENTRICLES OF THE BRAIN VIEWED FROM ABOVE. (G. Retzius.)

named the *mesial longitudinal striæ* or *nerves of Lancisi* (fig. 292). On each side, near the margin, are seen other longitudinal lines (*grey* or *lateral longitudinal striæ*). The lateral striæ lie within a fissure (*callosal fissure*) which separates the upper surface of the commissure from the gyrus fornicatus (by which convolution they are entirely covered in: hence the name, *tæniæ tectæ*, which is often applied to them). Both the mesial and lateral longitudinal striæ are traceable, when well developed, into the gyrus dentatus posteriorly. The morphological value of these structures will be afterwards referred to.

The thickness of the corpus callosum is greater at the ends than towards the centre, being about 10 mm. in front, 6 to 8 mm. in the middle, and increasing to 15 mm. behind.

In front, the corpus callosum is reflected downwards and backwards, forming a bend named the *genu* (fig. 298). The inferior or reflected portion, which is named the *rostrum*, becomes gradually narrower as it descends, and is connected with the lamina cinerea by a thin white layer, the *commissura baseos alba* of Henle. It is described also as giving off two bands of white substance, the *peduncles of the corpus callosum*, which, diverging from one another, run backwards across the posterior margin of the anterior perforated space on each side to the uncus of the temporal lobe, where they meet the outer olfactory roots. These peduncles traced upwards around the genu are said to be continued into the mesial longitudinal striæ.

Behind, the corpus callosum terminates in a free thickened border, often turned directly downwards, named the *splenium*, but this term is sometimes restricted to the under part of this thickened border, which appears as if rolled round under the rest (*splenium proper*, Beevor).

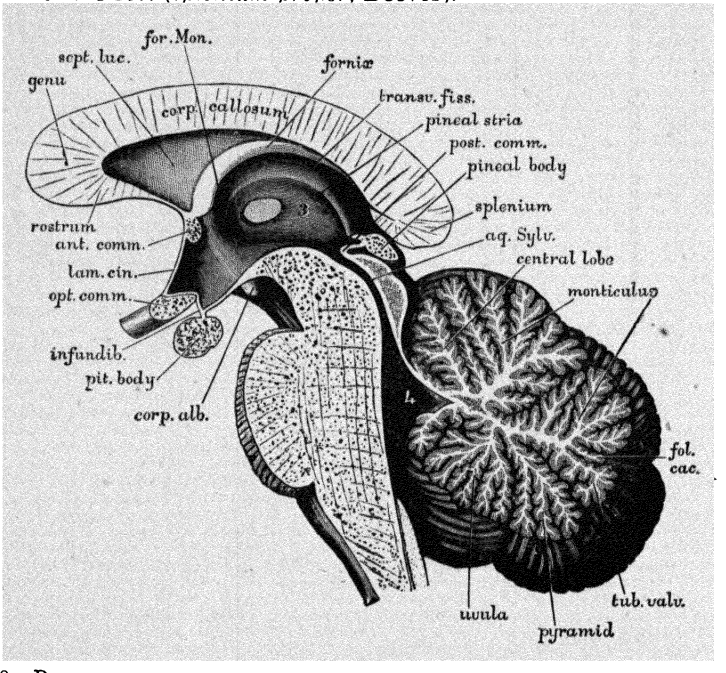


FIG. 298.—PORTION OF A MEDIAN SECTION OF THE BRAIN, SHOWING THE CORPUS CALLOSUM, THIRD VENTRICLE, AQUEDUCT AND FOURTH VENTRICLE, PONS, CEREBELLUM, ETC. ¾. (G. D. Thane.)

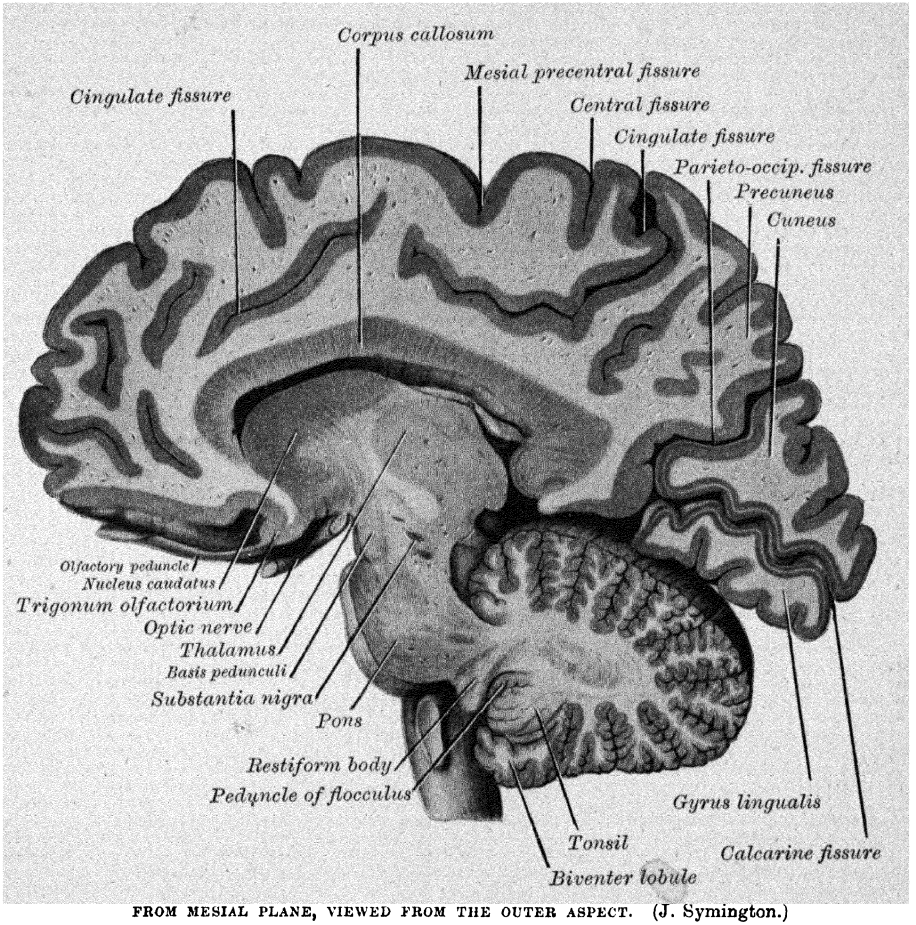
The mesial part of the under surface of the corpus callosum is connected behind with the fornix, and in the rest of its length with the septum pellucidum, a vertical partition between the two lateral ventricles, which is included in the anterior bend of the corpus callosum. The enlarged posterior part or splenium lies above and behind the mesencephalon, with pia mater, the veins of Galen, and the pineal gland between.

At the sides the free, usually ridged, under surface of the corpus callosum is much more extensive than the upper surface, since it roofs in the lateral ventricles.

The transverse fibres of the corpus callosum pass in a radiating manner, interlacing with those of the internal capsule, through the medullary centre to the cortex of each hemisphere. Those in front which sweep round into the

prefrontal region form the so-called *forceps minor*. Those from the body and the upper part of the splenium which curve over the lateral ventricle form the *tapetum*, whilst a large mass of fibres from the splenium proper curves round into each occipital lobe and is known as the *forceps major*.

The **septum pellucidum** (fig. 298, *sept. luc.*), a thin double partition, separates the anterior part of the two lateral ventricles. It is composed of two distinct laminæ, having an interval between them (*cavum septi pellucidi*) which contains fluid probably of the nature of lymph. It occupies the interval between the corpus callosum above and in front, and the anterior part of the fornix



FROM MESIAL PLANE, VIEWED FROM THE OUTER ASPECT. (J. Symington.)

behind; and gradually tapers backwards to end over the middle of the third ventricle, from which it is separated by the fornix and choroid tela. Antero-inferiorly it extends downwards in an angle which reaches the anterior commissure.

The laminæ of the septum are formed of a part of the mesial wall of the hemispheres which has remained free, while the surrounding parts have become united by the development of the corpus callosum above and in front and the fornix below and behind. The ventricle of the septum was therefore originally a part of the great longitudinal fissure, and has no connection with the internal

ventricular cavity of the brain. Accordingly we find that it is not lined by ciliated epithelium, but each lamina consists of a thin layer of grey matter next to the cavity and homologous with the grey matter of the cerebral cortex, and a thicker layer of white matter continuous below on either side with the general white matter of the hemisphere. Externally, next to the lateral ventricle, is a layer of ependyma, and covering this the epithelium which lines the lateral ventricle; internally is a layer of connective tissue, homologous with the pia mater.

The **fornix** (fig. 305, *f*) is an arched longitudinal white tract consisting of two lateral halves, which are separated from each other in front and behind, but in the intermediate part are joined together in the median plane. The two parts in front form the *columnæ fornicis*; the middle conjoined part is named the *body*; and the hind parts, which are again separated from each other, form the *crura fornicis*; further, the lateral edge of each crus, where it comes into relation with the concave margin of the corresponding hippocampus, is termed the *fimbria hippocampi*.

The *body* of the fornix is triangular in shape, being broad and flattened behind, and narrower and more rounded in front where it divides to form the columns. The median part of its upper surface is attached to the posterior-inferior border of the septum pellucidum, while on each side it appears in the floor of the body of the lateral ventricle. Its under surface rests upon the tela choroidea, which separates it from the thalami and the third ventricle (fig. 294).

The *columnæ fornicis* (*anterior pillars*) (fig. 294), cylindrical in form, can be traced downwards, slightly separated from each other, in front of the foramina of Monro, of which they form the anterior boundaries, and through the grey matter on the sides of the third ventricle, curving backwards to the corpora mamillaria. There each column turns upon itself, making a twisted loop which forms the white portion of the corpus mamillare; its destination will be subsequently noticed. It is sufficient here to mention that the fibres of the columns find a termination in the grey matter of the corpora mamillaria, and are not directly continuous, as in dissected preparations they seem to be, with the bundle of Vicq d'Azyr (see p. 230). Each column is connected near the foramen of Monro with the stria medullaris and with the stria terminalis, and it gives fibres to the septum pellucidum.

The *crura fornicis* (*posterior pillars*) (fig. 293) are the diverging posterior prolongations of the two flat lateral bands composing the body. Their origin is best seen by examining the ventral surface of the fornix. In such a view the two halves of the body of the fornix are found to be partially separated by a narrow median groove. At the posterior end of the body this groove widens out into a triangular space known as the lyra or psalterium, the lateral boundaries of which are formed by the diverging halves of the fornix. The crura have a free under surface resting upon the posterior part of the thalamus, the tela choroidea intervening; their upper surfaces are attached internally to the corpus callosum, but in the greater part of their extent appear in the floor of the lateral ventricle. The outer part of each crus becomes continuous with the fimbria hippocampi, and the inner part is lost upon the surface of the hippocampus. The *fimbria hippocampi* diminishes in size as it curves downwards towards the low extremity of the descending horn, and ends by joining the tip of the uncus (gyrus intralimbicus, Retzius). It is separated on its ventricular aspect by a shallow groove from the hippocampus, in the concavity of which it lies, and on its outer aspect by the fimbrio-dentate sulcus from the gyrus dentatus.

The free edge of the fornix from just behind the foramen of Monro to the lower part of the inferior horn of the lateral ventricle forms one of the boundaries of the choroidal fissure through which the pia mater projects towards the cavity of the ventricle, and becomes fringed to form the choroid plexus. The edge of the fornix (*tænia fornicis*) is continuous with a layer of cells covering this ingrowth of pia mater, and these cells thus separate the pia mater from the ventricular space.

The fornix in the human subject appears to be essentially a longitudinal commissure uniting structures on the same side of the brain. Thus the fibres of the fimbria arise from the cells of the hippocampus and the gyrus dentatus, and pass through the crus, body, and column of the fornix to the grey matter of the corpus mamillare. Some of the fibres of the column, however, pass through the septum pellucidum to the grey matter of the anterior perforated spot and the uncus, thus establishing a connexion with the roots of the olfactory nerve. It is probable that some fibres of the column cross to the opposite side through the anterior commissure. It is also maintained by some that a considerable number of fibres pass from the inner part of the crus of the fornix in the psalterium to the opposite crus, fimbria, and hippocampus, thus forming a transverse commissure between the two hippocampal formations. Such transverse commissural fibres are easily demonstrated in certain mammals (rabbit, rat) in which the hippocampi are highly developed, but they are difficult to demonstrate in man, and Beevor denies their existence in the monkey.

The **stria terminalis** is a band of white matter which lies in the groove separating the ventricular surface of the nucleus caudatus from that of the thalamus. It extends from the extremity of the inferior horn of the lateral ventricle, where it passes into the nucleus amygdalæ, to the anterior part of the body of the ventricle, as far as the foramen of Monro, having a curved course corresponding with that of the ventricle. Its anterior connexions are somewhat obscure, but, according to Schwalbe and Testut, it divides anteriorly into two parts, one of which is continued into the column of the fornix, and the other passes over and in front of the anterior commissure to become lost in the grey matter which intervenes between the septum pellucidum and the anterior end of the nucleus caudatus, some fibres perhaps penetrating into that nucleus. According to Foville, each extremity is ultimately traceable into the anterior perforated space.

The **corpora striata** (*ganglia of the cerebral hemispheres*), situated in front and to the outer side of the thalami, are two large ovoid masses of grey matter, the greater part of each of which is imbedded in the white substance of the hemisphere (extraventricular portion), while a part becomes visible in the body and anterior horn of the lateral ventricle (intraventricular portion). The corpus striatum derives its name from the streaked appearance it presents, especially in its anterior part, when cut into, an appearance which is due to the passage through it of bundles of white fibres of the internal capsule to the frontal lobe of the hemisphere.

The **nucleus caudatus** (*intraventricular portion of the corpus striatum*) (fig. 294; fig. 292, *c.str.*) is of pyriform shape, its larger end being turned forwards and appearing in the floor and partly in the lateral wall of the anterior horn. This enlarged anterior extremity projects into the white matter of the frontal lobe, where it is bounded by the fibres which pass from the genu of the callosum. Its narrow end is prolonged backwards and outwards along the body of the ventricle and into the roof of the inferior horn, passing nearly to the extremity of the latter. The caudate nucleus is separated from the thalamus on its ventricular aspect by a groove, in the floor of which are found the vena

terminalis and the stria terminalis, and below these some white matter continuous with the internal capsule. Opposite the anterior perforated space the caudate nucleus joins the putamen of the lenticular nucleus, and the combined mass is continuous below with the grey matter of that space. Above and behind its union with the lenticular nucleus the caudate nucleus is bounded externally by the anterior limb of the internal capsule. Where it lies in the lateral ventricle (superior surface) the nucleus caudatus is covered by a layer of ependyma, and over this by the ciliated ventricular epithelium. The ganglion is itself composed of a reddish-grey substance like that of the outer zone of the lenticular nucleus (see below). On the deeper side, that turned towards the internal capsule, the nucleus receives from this a number of bundles of medullated fibres which are traceable from the crusta. According to Wernicke it is doubtful if any of these pass on to the white matter of the hemispheres, nor do

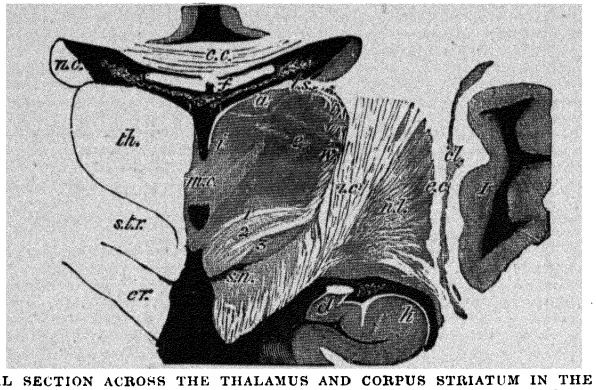


FIG. 300.—CORONAL SECTION ACROSS THE THALAMUS AND CORPUS STRIATUM IN THE REGION OF THE MASSA INTERMEDIA. Natural size. (From a preparation by S. G. Shattock.)

th, thalamus; *a*, *e*, *i*, its anterior, external, and internal nuclei respectively; *w*, its latticed layer; *m.c.*, massa intermedia; above and below it is the cavity of the third ventricle; *c.c.*, corpus callosum; *f*, fornix, separated from the third ventricle and thalamus by the tela choroidea. In the middle of this are seen the two veins of Galen and the choroid plexuses of the third ventricle; and at its edges the choroid plexuses of the lateral ventricles; *t.s.*, stria terminalis; *cr.*, forward prolongation of the crusta passing laterally into the internal capsule, *i.c.*; *s.t.r.*, subthalamic prolongation of the tegmentum, consisting of (1) the dorsal layer, (2) the zona incerta, and (3) the nucleus of Luys; *s.n.*, substantia nigra; *n.c.*, nucleus caudatus of the corpus striatum; *n.l.*, nucleus lenticularis; *e.c.*, external capsule; *cl.*, claustrum; *I*, insula.

they come from the crusta directly, but only after traversing the medullary laminæ of the lenticular nucleus.

The nerve-cells of the nucleus caudatus are multipolar, and, in the adult, pigmented. Some are very large, rich in Nissl bodies, and with long axis-cylinder processes; but most are medium-sized and small, belonging to Golgi's second type, with short axis-cylinder processes (Marchi). The nerve-processes pass in various directions, some especially from the large cells into the internal capsule, from which the nucleus caudatus also receives fibres. In addition, peculiar spheroidal cells containing two or more nuclei were described by Henle.

The **nucleus lenticularis** (*extraventricular portion of the corpus striatum*) is almost entirely surrounded by white matter and does not appear on the surface of the brain, so that it is only seen in sections of the hemisphere. Its horizontal section (fig. 301, *n.l*) somewhat resembles that of a biconvex lens, being wider in the centre than at either end, but larger anteriorly than posteriorly. It is less extensive than the caudate nucleus, which projects beyond it at either end. The antero-posterior diameter corresponds closely with that of the insula,

or island of Reil, and the greatest width is opposite the anterior edge of the thalamus. On a transverse vertical section about the middle this nucleus appears triangular, having a *lateral*, a *mesial*, and an *inferior surface*, facing respectively the external capsule, the internal capsule, and the base of the brain. Two white lines (*medullary laminæ*), parallel to the lateral border, divide it into three zones, of which the outer (*putamen*, Burdach) is the largest and of a dark reddish colour marked with fine radiating white striæ, while the inner two, known conjointly as the *globus pallidus* (*gl.p.*), are yellowish in tint. On its outer side is a grey lamina, termed the *claustrum* (*cl.*), which is separated from the lenticular nucleus by the stratum of white substance named the *external capsule* (*c.e.*). The internal capsule (continuation of the crusta) separates it in the greater part of its extent from the caudate nucleus and thalamus, but anteriorly, as already mentioned, the two nuclei of the corpus striatum are united at their bases, and farther back it comes in contact below with the nucleus amygdalæ; through these structures it is continuous with the grey cortex of the hemisphere.

All three zones of the nucleus lenticularis are pervaded by bundles of white fibres, but they are most conspicuous in the outer zone. The grey matter between the fibres contains many cells with yellow pigment in them. The cells (fig. 302) on the whole resemble those of the caudate nucleus, but there are more in proportion belonging to the first type of Golgi (cells with a long nerve-process). Fibres pass directly from the inner zone into the adjacent part of the inner capsule (*i.e.* into the peduncle of the cerebrum), while others from the substantia innominata below the thalamus curve outwards around the mesial edge of the peduncle and enter the lower part of the lenticular nucleus as a distinct bundle (ansa lenticularis), and passing into its medullary laminæ are distributed in the middle and outer zones.

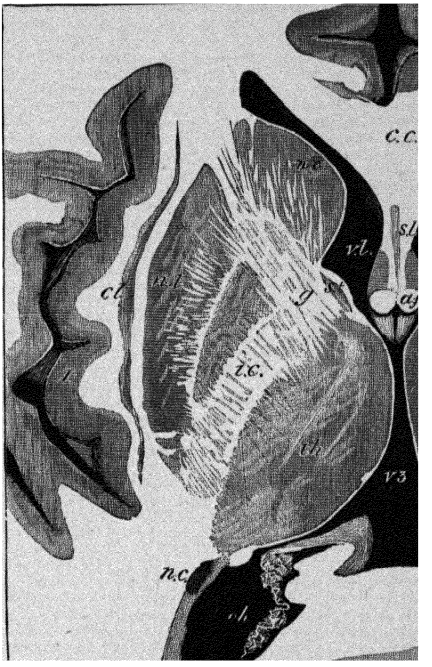


FIG. 301.—HORIZONTAL SECTION THROUGH PART OF THE CEREBRAL HEMISPHERE. Natural size. (From a preparation by S. G. Shattock.)

The section is viewed from below; *v.l.*, lateral ventricle, anterior cornu; *c.c.*, corpus callosum; *s.l.*, septum pellucidum; *a.f.*, columns of the fornix; *v3*, third ventricle; *th*, thalamus; *s.t*, stria terminalis; *n.c.*, nucleus caudatus, and *n.l*, nucleus lenticularis of the corpus striatum; *i.c.*, internal capsule; *g*, its angle or genu; *n.c*, tail of the nucleus caudatus appearing in the inferior cornu of the lateral ventricle; *cl.*, claustrum; *I*, insula.

Other fibres connect the caudate with the lenticular nucleus, and others again pass from this nucleus into the corona radiata or white substance of the hemispheres and thence to the cortex, but few fibres emerge from or enter the lateral surface of the lenticular nucleus, which is sharply marked off from the external capsule.

The **external capsule** is formed of fibres which are not directly connected with the lenticular nucleus, but are derived partly from the anterior commissure, and in part from a portion of the ansa lenticularis.

The **claustrum** (figs. 300, 301, *cl.*) is a thin lamina of grey matter which is smooth next to the outer capsule, but ridged and furrowed externally, the ridges and furrows corresponding to the gyri and sulci of the insula, with the white substance of which the claustrum is in immediate relation. According to Meynert, the claustrum is to be looked upon as a separated part of the grey cortex of the insula; but this is denied by Cajal, who regards it as a separated portion of the lenticular nucleus. In transverse sections of the hemisphere the

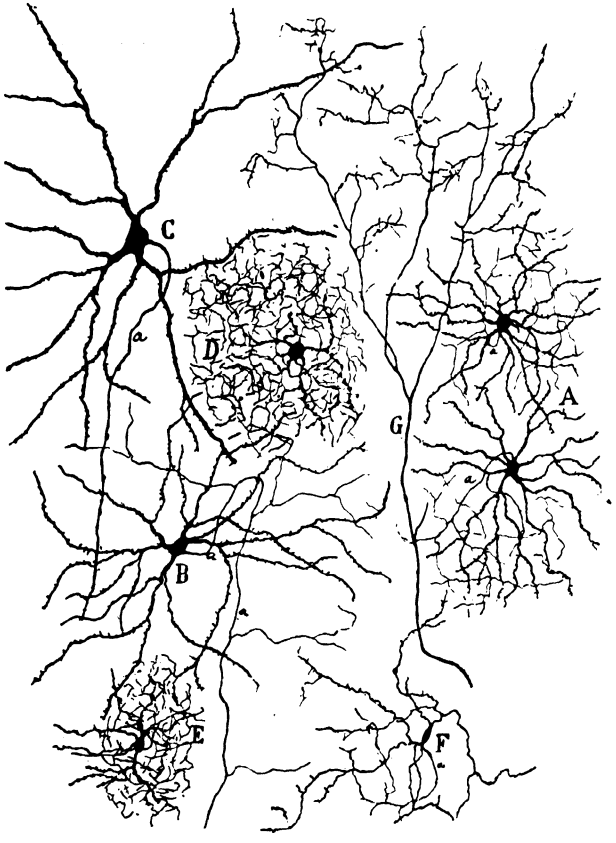


FIG. 302.—TYPES OF CELLS FROM THE CORPUS STRIATUM OF A CHILD, FROM THE NEIGHBOURHOOD OF THE CLAUSTRUM. (Cajal.)

A, short-axoned cells of small size; B, a long-axoned cell with ventrally directed axon; C, a giant-cell with long ventrally directed axon; D, E, compact short-axoned cells; G, an afferent fibre arborising within the nucleus.

claustrum is seen to taper to a fine thread superiorly (apex) and to expand below (base), having the shape of an elongated triangle.

In the claustrum the cells are for the most part small and spindle-shaped, and arranged parallel with the surface. Most of the cells contain yellow pigment.

The **internal capsule** (Burdach) (fig. 301, *i.c.*) is a lamellated tract of white fibres which lies between the nucleus lenticularis laterally and the nucleus caudatus, stria terminalis, and thalamus mesially. The white matter which lies external to the thalamus and behind the level of the lenticular nucleus

is sometimes termed the retro-lenticular part of the internal capsule. It is somewhat interrupted, especially in front, by strands of grey matter which unite the caudate and lenticular nuclei. In front, behind, and above it is continuous with the white substance of the hemispheres, its fibres diverging in a fan-like manner towards the cortex (*corona radiata* of Reil). Below it passes directly into the crusta, of which it is the immediate continuation. In horizontal sections (fig. 301) the internal capsule shows a bend (genu) opposite the stria terminalis, the anterior third forming an angle of about 120° with the posterior two-thirds; these two parts are known as the *anterior* and *posterior limbs* respectively. In vertical sections (fig. 300) it appears to take a straight course upwards and outwards from the pedunculus cerebri to the corona radiata. It has been determined as the result of experimental observations in animals, and from pathological and clinical observations in man, that most of the fibres which course in the posterior two-thirds of the internal capsule (*i.e.* which are opposite the globus pallidus of the lenticular nucleus) are connected with the part of the cerebral cortex, excitation of which gives rise to movements in the various parts of the body, whilst those of the anterior third are connected with the prefrontal region. Those of the posterior third are intermingled with fibres coming from and passing to the occipito-temporal region.

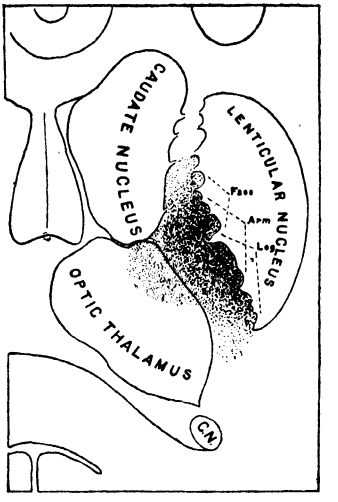


FIG. 303.—HORIZONTAL SECTION THROUGH INTERNAL CAPSULE OF MONKEY, SHOWING BY SHADING THE AREA WHICH IS INVADED BY DEGENERATION WHEN THE WHOLE OF THE MOTOR CORTEX OF THE HEMISPHERE OF THE SAME SIDE IS DESTROYED. (Simpson and Jolly.)

The parts which are invaded by degeneration when the face, arm, and leg regions of the motor cortex respectively are destroyed are indicated. It will be seen that these show considerable overlap. Notice also the invasion of the thalamus (but not of the corpus striatum) by the degeneration.

Besides these fibres which connect the cortex of the hemisphere with the crusta, the internal capsule contains others derived from various sources—viz. from the caudate and lenticular nuclei, the thalamus, and hypothalamus, and also, through the corpus callosum, from the cortex of the opposite hemisphere (Hamilton). The exact localisation within the internal capsule of most of these fibres has not as yet been determined.

The **nucleus amygdalæ** is a collection of grey matter situated above and in front of the anterior end of the inferior cornu of the lateral ventricle, in the roof of which it forms a prominence. It is continuous below and on its side with the anterior end of the hippocampus and the uncus. Its upper surface is partly in relation with the base of the lenticular nucleus and partly free where it forms the lower boundary of the vallecula Sylvii and shows the elevations described by Retzius as the *gyrus semilunaris* and the *gyrus ambiens*. The tail of the caudate nucleus passes into it.

THE MEMBRANES OF THE BRAIN AND SPINAL CORD.

The cerebrospinal axis is covered by three *membranes*, named also *meninges*. They are: (1) An external fibrous membrane, named the *dura mater*, which lines the interior of the skull and forms a loose sheath in the spinal canal; (2) An internal areolar and vascular tunic, the *pia mater*, which closely covers the brain and spinal cord; and (3) An intermediate non-vascular membrane, the *arachnoid*, which lies over the pia mater, the two being in some places in close connexion, in others separated by a considerable space.

Some authors describe only two meninges, considering the arachnoid and pia mater to constitute one (*leptomeninx*), and the dura mater the other (*pachymeninx*).

THE DURA MATER.

The dura mater is a very strong dense inelastic fibrous tunic of considerable thickness (·5 mm. or more in the cranium, less in the spinal canal). Its inner surface, turned towards the brain and spinal cord, is smooth and lined with epithelium (endothelium), which was formerly regarded as the outer or parietal portion of a serous sac. It is here described as a part of the dura mater. The space between the dura mater and arachnoid was formerly in like manner regarded as the sac of the arachnoid, but is now termed the *subdural space*. The arrangement of the dura mater in the cranium differs in several respects from that in the spinal canal.

CRANIAL OR ENCEPHALIC DURA MATER.—In the cranium the dura mater adheres to the inner surface of the bones, and forms their internal periosteum. The connexion between the two depends, in a great measure, on blood-vessels and small fibrous processes, which pass from one to the other; and the membrane, when detached and allowed to float in water, presents a flocculent appearance on its outer surface, in consequence of the torn parts projecting from it. The adhesion between the dura mater and the bone is more intimate opposite the sutures and at the base of the skull than at the other parts of the cranial wall. During infancy this adhesion is very firm at the sutures and fontanelles. At the sutures on the vault it is continuous through the sutural ligaments with the pericranium, opposite the sphenoidal fissure it joins the periosteum of the orbit, and while the petro-squamous suture persists it is united with the lining membrane of the tympanum. At the base it presents apertures for the cerebral nerves and sends outwards upon them tubular processes which blend with the areolar coat of the nerves. The two roots of the fifth cerebral nerve are enclosed along with the semilunar (Gasserian) ganglion in a common tube (cavum Meckelii) which subsequently divides to invest the main divisions of the nerve. The relation of the dura mater to the optic nerve differs from that to the other nerves as the dural sheath remains separate from the nerve and joins in front the sclerotic coat of the eyeball. At various places the fibrous tissue of the dura mater separates into two distinct layers, leaving intervening channels called sinuses. These sinuses, which are elsewhere described, are channels for venous blood, and are lined with a continuation of the endothelium of the veins. Between the two cavernous sinuses the pituitary body is received into a depression of the membrane, which closely surrounds the organ in question except where the infundibulum enters it. There is further a fissure immediately over the orifice of the aquæductus vestibuli, and here the prolongation of the membranous labyrinth of the ear, known as the saccus endolymphaticus, is received between the two layers.

The dura mater also sends inwards into the cavity of the skull three strong membranous processes or partitions. Of these, one descends vertically in the

median plane, and is received into the longitudinal fissure between the two hemispheres of the cerebrum. This is the *falx cerebri*. The second is a sloping vaulted partition, stretched across the back part of the skull, between the cerebrum and the cerebellum, named the *tentorium cerebelli*. Below this, another vertical partition, named the *falx cerebelli*, of small extent, passes down between the hemispheres of the cerebellum. Lastly, the portion of dura mater which stretches over the sella turcica, and, pierced by a small hole for the infundibulum,

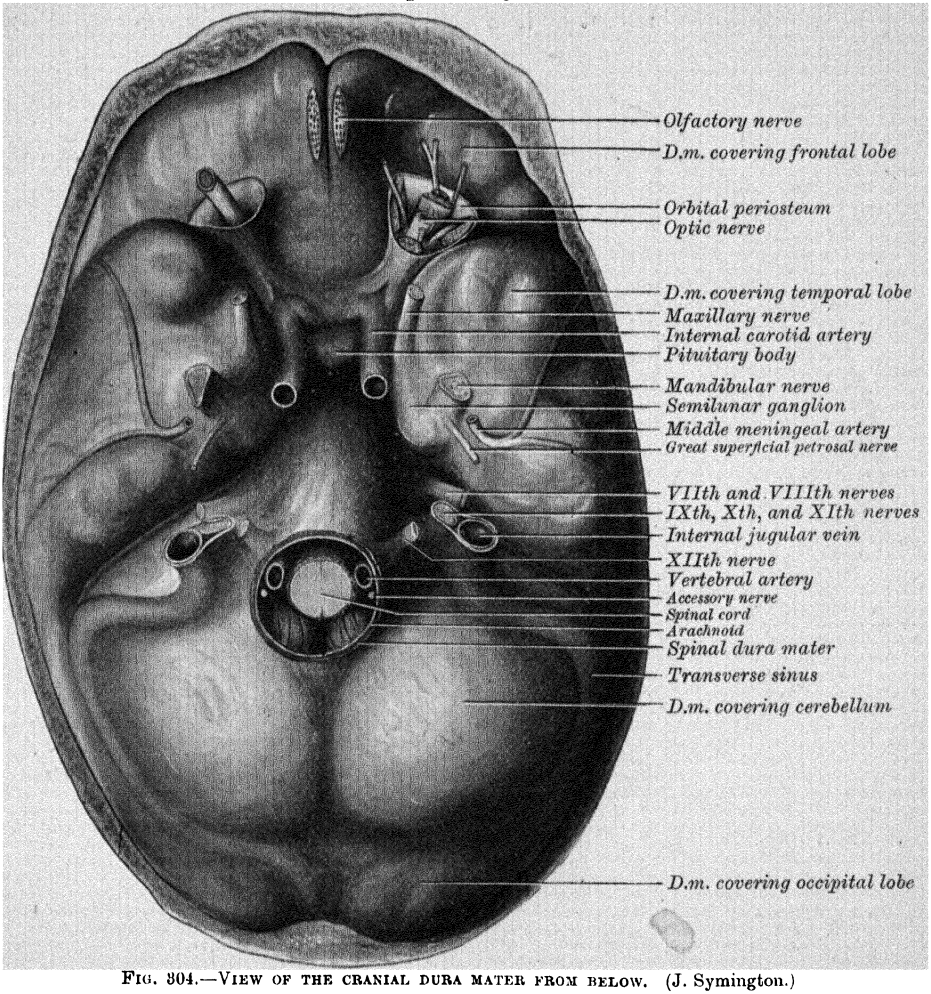


FIG. 304.—VIEW OF THE CRANIAL DURA MATER FROM BELOW. (J. Symington.)

The specimen was prepared by breaking up the bones forming the floor of the cranium and removing them in pieces, so as to preserve the tubular sheaths of the dura mater investing the nerves and the continuity of the dura mater with the periosteum of the orbit. The internal carotid arteries were divided after their exit from the carotid canals. The deep groove behind the pituitary body was occupied by the dorsum sellæ of the sphenoid bone and the depression on each side passing from this groove outwards and backwards contained the petrous part of the temporal bone.

covers the pituitary body, is sometimes spoken of as the *diaphragma sellæ* or *tentorium hypophysis*.

The **falx cerebri** (fig. 306, 1) is narrow in front, where it is fixed to the crista galli, and broader behind, where it is attached to the middle of the upper surface of the tentorium, along which line of attachment the straight sinus is

attached. Along its upper convex border, which is attached to the middle line of the inner surface of the cranium, runs the superior sagittal (superior longitudinal) sinus. Its under edge is free, and reaches to within a short distance of the corpus callosum, approaching nearer to it behind. This border contains the inferior sagittal (inferior longitudinal) sinus.

The **tentorium cerebelli** or **tent** (fig. 306, 8) is elevated in the middle, and declines downwards in all directions towards its circumference, thus following the form of the upper surface of the cerebellum. Its inner border is free and concave, and leaves in front of it a shield-shaped opening (*incisura tentorii*)

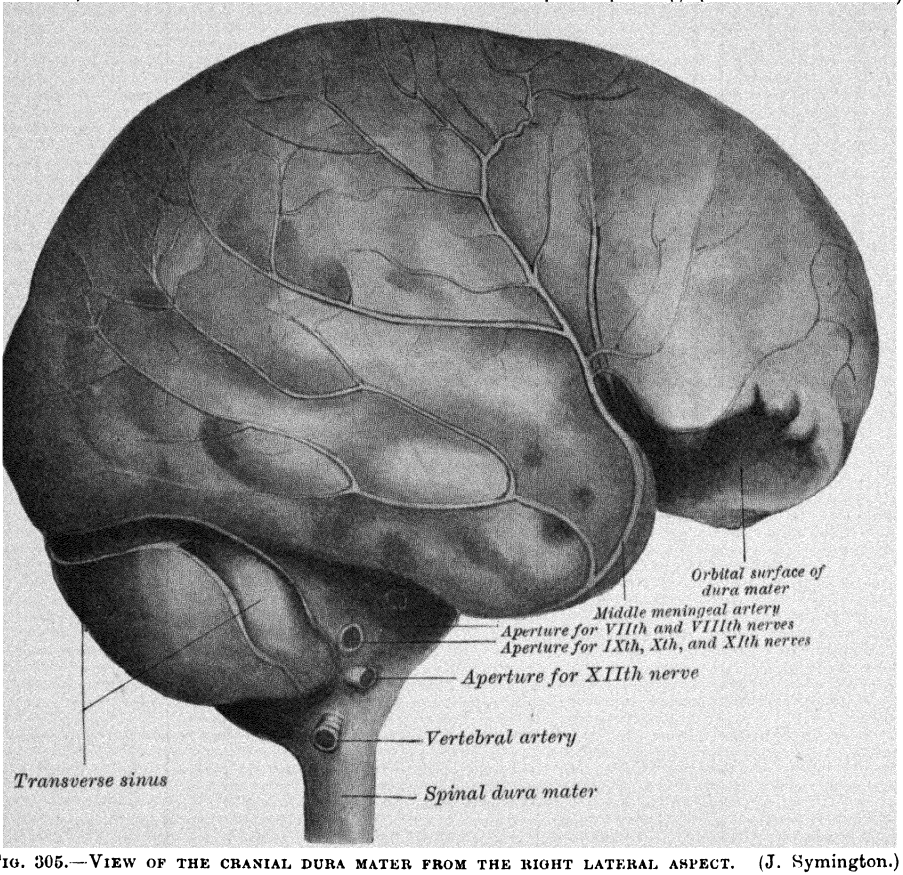


FIG. 305.—VIEW OF THE CRANIAL DURA MATER FROM THE RIGHT LATERAL ASPECT. (J. Symington.)

The specimen was prepared by making a median section of the head, removing the right half of the brain, and then separating the dura mater from the inner surface of the skull and dividing the tubular prolongations of the dura mater on to the nerves. The transverse sinus was subsequently laid open.

through which the isthmus encephali extends. It is attached behind and at the sides by its convex border to the horizontal part of the crucial ridges of the occipital bone and to the posterior inferior angles of the parietal bones, and there encloses the transverse (lateral) sinuses. Farther forward it is connected with the upper edge of the petrous portion of the temporal bone, the superior petrosal sinus running along this line of attachment. At the point of the pars petrosa the external and internal borders meet, and may be said to intersect each other, the former being then continued inwards to the posterior, and the latter forwards to the anterior clinoid process.

The **falx cerebelli** (falx minor, fig. 306, 13) descends from the middle of the posterior border of the tentorium, with which it is connected, along the vertical ridge named the internal occipital crest towards the foramen magnum, bifurcating there into two smaller folds. Its attachment to the bony ridge marks the course of the occipital sinus or sinuses.

SPINAL DURA MATER.—In leaving the skull the dura mater is intimately attached to the margin of the foramen magnum, and within the vertebral canal it forms a loose sheath (theca) round the cord and is not adherent directly to the bones, which have an independent periosteum. The theca ends opposite the second sacral vertebra; below this the dura mater is prolonged downwards as a fibrous band (filum terminale externum) which spreads out below and is attached

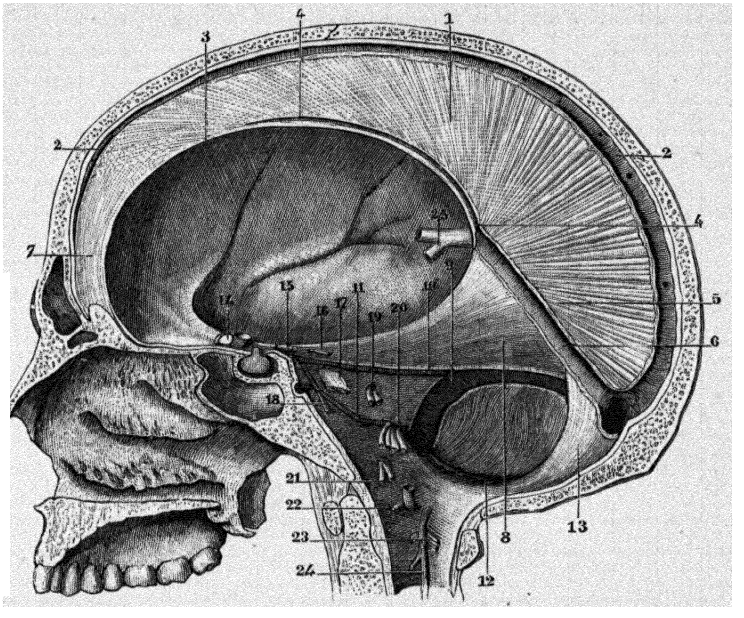


FIG. 306.—THE CRANIUM OPENED TO SHOW THE FALX OF THE CEREBRUM AND TENTORIUM OF THE CEREBELLUM, AND THE PLACES OF EXIT OF THE CEREBRAL NERVES. ½. (Sappey.)

1, falx; 2, superior sagittal sinus; 3, concave border of the falx; 4 inferior sagittal sinus; 5, base of the falx; 6, straight sinus; 7, anterior part of the falx; 8, right side of the tentorium cerebelli, seen from below; 9, transverse sinus; 10, superior petrosal sinus; 11, inferior petrosal sinus; 12, occipital sinus; 13, falx cerebelli; 14, 15, 16, 17, 18, second, third, fourth, fifth, and sixth cerebral nerves; 19, seventh and eighth nerves; 20, ninth, tenth, and eleventh nerves; 21, twelfth nerve; 22, 23, first and second cervical nerves; 24, upper end of the ligamentum denticulatum; 25, veins of Galen.

to the periosteum of the lower end of the sacral canal or to the back of the coccyx.

Opposite each intervertebral foramen the dura-matral theca has two openings, placed side by side, which give passage to the two roots of the corresponding spinal nerve. It is continued as a tubular prolongation on each nerve (fig. 307), and is lost in its sheath. Besides this, it is connected with the circumference of the foramen by areolar tissue.

The spinal dura mater is fixed in position mainly by its lateral prolongations on to the spinal nerve-roots, but also by various ligamentous bands passing from it to the wall of the spinal canal.[1] The most important of these connect the

[1] Max Hofmann, Archiv für Anatomie, 1898.

anterior part of the dura mater with the posterior common (longitudinal) ligament. The union is firmest opposite the axis, where the posterior common ligament is continued upwards as the posterior occipito-axoid ligament. Below this, as far down as the third or fourth lumbar, rather loose fibres pass on each side from the dura mater downwards and outwards to be connected with the posterior common ligament near its lateral borders. From this point downwards the fibres form a median septum between the dura mater and the lower part of the posterior common ligament and the anterior wall of the sacral canal. In addition to this ventral median septum there are several dorso-lateral ligaments in the sacral canal, the best marked of which arises from the hinder part of the lateral aspect of the dural sac opposite the sheaths of the second and third sacral nerves and passes to the neural arch of the third sacral vertebra. In the neck the sheaths of the cervical nerves are united together by longitudinal fibres. Except where

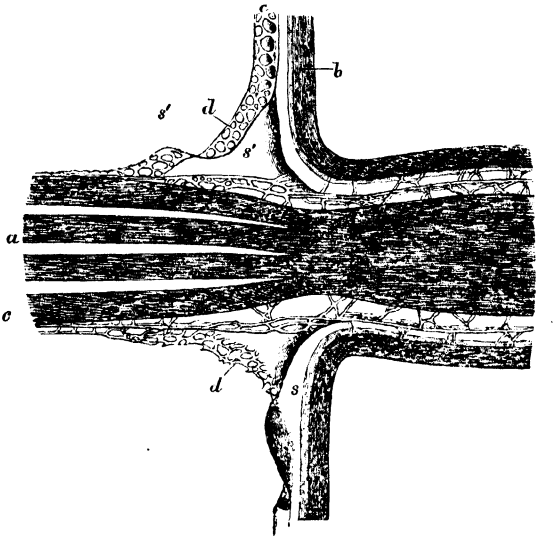


FIG. 307.—SECTION THROUGH THE PLACE OF EXIT OF A SPINAL NERVE-ROOT THROUGH THE DURA MATER. (Key and Retzius.)

a, bundles of the nerve-root becoming collected into a single bundle as they emerge; *b*, dura mater; *c*, arachnoid; *d*, a reticular lamella of the arachnoid reflected along the nerve-root; *s*, subdural space; *s'*, *s'*, subarachnoid space.

it is traversed by ligaments the circumdural space is occupied by areolar tissue, by loose fat, and by a plexus of spinal veins. Above the atlas the theca has an orifice on each side for the passage of the vertebral artery, while a number of small spinal arteries reach the cord along the sheaths of the nerve-roots.

Structure.—The dura mater consists of fibrous and elastic tissue, arranged in bands and laminæ, those of the two layers crossing each other obliquely for the most part in the cranial dura mater. In the falx and tentorium the bundles are arranged radially. It is not uncommon to find the cranial dura mater ossified in parts: most commonly in the falx cerebri. In the spinal dura mater the bundles have a nearly longitudinal arrangement. A layer of flattened endothelial cells covers its inner surface, and also its outer surface between the places of adherence to the bones and sutures. A similar layer of cells also covers both sides of the spinal dura mater. The cranial membrane is traversed by numerous blood-vessels which are chiefly destined for the bones, but there is a

wide-meshed capillary network with peculiar ampullary enlargements, distributed near the inner surface of the cranial dura mater, and another network near the outer surface. The spaces between the fibrous trabeculæ contain flattened connective-tissue corpuscles which frequently have an epithelioid arrangement: these spaces, like those of connective tissue generally, doubtless serve for the passage of lymph. They can be injected from the circumdural space where this exists, and the injecting fluid can be forced along them through the thickness of the dura mater into the subdural space. They can also be filled by inserting the injecting cannula into the substance of the membrane. Minute nervous filaments, derived from the fifth (Luschka) and tenth (Arnold) and twelfth (Luschka, Rüdinger) cerebral nerves, and from the sympathetic, enter the dura mater of the brain to be distributed chiefly to the blood-vessels and to the bone, but partly perhaps to the membrane itself. Nervous filaments have likewise been traced into the dura mater of the spinal cord.

The arteries of the cranial dura mater are derived from various sources. The principal are three in number—viz. the anterior meningeal, derived from the ethmoidal branch of the ophthalmic; the middle meningeal, by far the largest, a branch of the internal maxillary; and the posterior meningeal, a branch of the vertebral. There are also others derived from the ascending pharyngeal and occipital arteries. Veins accompany these arteries, but others, mostly small ones, run independently and open into the venous sinuses. One sinus-like vein which accompanies the anterior branch of the middle meningeal artery communicates superiorly with the superior sagittal sinus, and passes inferiorly either into the veins of the orbit, or into the diploic veins, or through the spheno-parietal sinus into the sinus cavernosus (Merkel). Communicating with the superior sagittal sinus from its anterior end as far back as the beginning of the occipital region are a number of diverticula, from 0·5 to 3 cm. long, which form a series of venous *lacunæ laterales*.[1] These receive the independent meningeal veins, and some veins from the diploë, communicate by small branches with the cerebral veins, and are invaginated by Pacchionian granulations (see fig. 311). These venous lacunæ are not entirely confined to the region of the superior sinus, but some may occur in the neighbourhood of other sinuses, especially the transverse and straight sinus.

Subdural space.—The space between the dura mater and the arachnoid, which was formerly, when the latter was considered to be a serous membrane, known as the cavity of the arachnoid, is now, as already stated, more usually known under the above title. It is in most parts a narrow capillary cleft, containing but very little fluid, which is probably of the nature of lymph. Its contained fluid finds exit chiefly around the arachnoid villi (Pacchionian granulations) into the sinuses of the dura mater, but partly by way of the lymph-clefts in the sheaths of the issuing nerves, cerebral and spinal (Key and Retzius). In animals it has been shown (by Schwalbe) that the space is also in communication with the deep lymphatic vessels and glands of the neck and loin. Coloured fluids injected into the subdural space are never found to pass into the subarachnoid space, the arachnoidal limiting membrane being everywhere a closed one. Nevertheless, coloured fluids can be made to pass from the subarachnoid space through the arachnoid villi into the prolongations of the subdural space which surround those villi within the venous sinuses and lacunæ, and thence into the sinuses themselves. This passage may, however, take place by filtration.

[1] Key and Retzius, Studien in der Anatomie des Nervensystems und des Bindegewebes, 1875. Trolard, 'Les lacunes veineuses de la dure-mère,' Journal de l'Anatomie et de la Physiologie, 1892.

THE PIA MATER.

The pia mater is a delicate fibrous and highly vascular membrane, which immediately invests the brain and spinal cord.

ENCEPHALIC PIA MATER.—Upon the hemispheres of the brain it is applied to the entire cortical surface of the convolutions, and dips into all the sulci, most of which thus contain a double layer. From its internal surface numerous small vessels pass into the substance of the brain, and hence this inner surface is very flocculent, and is named *tomentum cerebri.* On the cerebellum a similar arrangement exists, but the membrane is finer, and the double fold only distinct in the larger sulci. The pia mater also at the transverse fissure is invaginated into the lateral ventricles and over the third ventricle (covered however by the epithelium of those cavities), and there forms the tela choroidea (velum interpositum) of the third ventricle and the choroid plexuses of the third and two lateral ventricles. It is also prolonged over the posterior wall or roof of the fourth ventricle, where it forms the tela choroidea and choroid plexuses of that ventricle.

The **tela choroidea ventriculi tertii** or **velum interpositum** is a triangular fold of pia mater, between the two layers of which arachnoidal tissue and blood-vessels are contained. It lies immediately underneath the fornix, and can therefore only be properly seen when this structure is cut through and raised (as in fig. 308). The velum interpositum is then seen to cover-in the third ventricle and to extend over the adjacent upper surface of the thalamus on each side as far as the oblique groove which marks that surface (p. 225, and fig. 228). The base of the triangle is continuous with the general pia mater below the splenium of the corpus callosum; the apex ends just behind the columns of the fornix (at the foramen of Monro). Each side of the triangle is bordered by a choroidal plexus which projects from under the edge of the fornix into the respective lateral ventricle; behind, these plexuses are continued along the mesial border of the inferior cornu of the ventricle, where they are invaginated into the choroidal fissure, projecting over the fimbria; in front they converge, becoming gradually smaller, to the foramina of Monro, between which they become united. From this united part two other smaller plexuses pass backwards along the under surface of the velum interpositum, close to the middle line in front, but diverging behind (choroid plexuses of the third ventricle).

The choroid plexuses are covered where they project into the cavities by the ependymal epithelium of the ventricles, as is also that part of the velum interpositum which roofs-in the third ventricle. Along the choroid plexuses a prominent vein, the choroid vein, courses from behind forwards to join the terminal vein and form the corresponding vein of Galen at the foramen of Monro: the two veins of Galen pass backwards from this point in the middle of the choroid tela, diverging somewhat behind, but again converging and ultimately becoming united into a common trunk which ascends behind the splenium of the corpus callosum to open into the straight sinus. In this course they receive several tributaries from the thalami and other parts.

Tela choroidea ventriculi quarti.—This name has been given to the layer of pia mater which, prolonged from the medulla oblongata, overlies the inferior half of the fourth ventricle and is reflected at the margin of the velum medullare inferius on to the under surface of the cerebellum. Like the choroid tela of the third ventricle, this also has two sets of choroid plexuses, mesial and lateral, which are continuous with one another in front. The mesial plexus extends upwards along either side of the middle line from the foramen of Magendie to where the tela is reflected along the edge of the inferior medullary

velum; here the mesial plexuses are continued into the lateral plexuses on either side, and these extend to the apertures (in the pia mater) of the lateral recesses of the ventricle and appear at the base of the brain below and in front of the flocculus.

SPINAL PIA MATER.—On the spinal cord the pia mater has a very different character from that which it presents on the encephalon, so that it has been described by some as a different membrane under the name *neurilemma of the cord*. It is thicker, firmer, less vascular, and more adherent to the subjacent

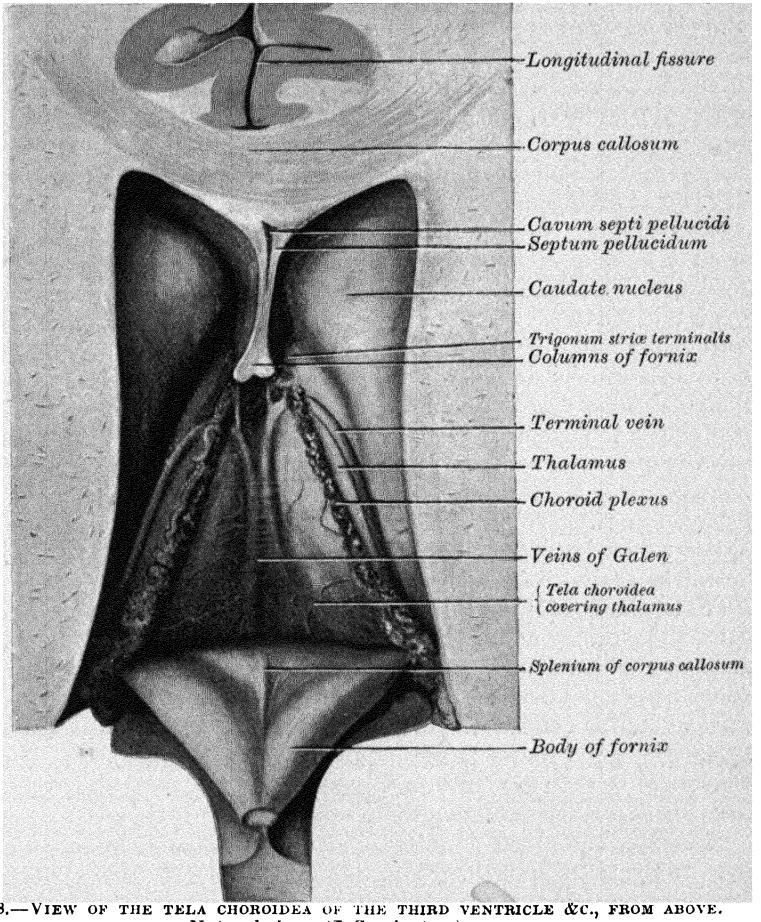


FIG. 308.—VIEW OF THE TELA CHOROIDEA OF THE THIRD VENTRICLE &C., FROM ABOVE. Natural size. (J. Symington.)

The columns of the fornix were divided and its body separated from the tela choroidea and turned backwards.

nervous matter: its greater strength is owing to an external fibrous layer, which is arranged in longitudinal glistening bundles. A fold of this membrane dips down into the anterior fissure of the cord, and serves to conduct blood-vessels into that part. A thinner process passes into the greater part of the posterior fissure. At the roots of the nerves, both in the spine and in the cranium, the pia mater becomes continuous with their connective-tissue sheaths.

The pia mater of the cord is thickened by a conspicuous fibrous band, running down in front over the anterior median fissure. This was named *linea splendens* by Haller

Structure.—The pia mater of the cord consists of two layers, the outer one being composed of interlaced bundles of connective tissue, which are for the most part parallel and longitudinal, and the inner or intima of peculiar stiff bundles bending suddenly and enclosing somewhat angular interspaces. Both surfaces of this inner layer are covered with endothelial cells, and there is a network of fine elastic fibres near the surfaces. The outer and inner layers are separated here and there by cleft-like lymphatic spaces communicating on the one hand with the subarachnoid space and on the other with the perivascular canals immediately to be mentioned. In the pia mater of the brain only the inner of the two layers of the pia mater of the cord is represented.

The pia mater is sometimes pigmented in certain situations at the base of the brain, such as the orbital surfaces of the frontal lobes, the optic chiasma, the cerebral peduncles, and the pons and medulla oblongata, while on the spinal cord the pigmentation is best marked at the cervical and lumbar enlargements. The degree and frequency of this pigmentation varies in different races.[1]

The choroid plexuses are beset with a large number of highly vascular villous prolongations of the pia mater (choroidal villi), the larger of which are from 1 mm. to 2 mm. long, but are subdivided into smaller secondary or even tertiary villi. Each larger villus has an afferent artery and efferent vein which open into a capillary network lying close to the surface. The free surface of the villi and of the depressions between them is covered everywhere by a simple flattened or cubical epithelium, which is ciliated in lower vertebrates, but in mammals is said to possess cilia only in embryonic life. Each cell very commonly contains a yellowish fat-globule.

The pia mater contains great numbers of blood-vessels, which subdivide in it before they enter the nervous substance. In the pia mater of the cord they lie between its two layers, but in that of the brain on the surface of the membrane, either projecting freely or covered by subarachnoid trabeculæ. Further, each vessel is enclosed by a sheath composed of a more dense arrangement of the fibres of the membrane (perivascular sheath). The diameter of the (lymphatic) canal thus formed may be considerably larger than that of the contained vessel. A similar sheath, derived from the pia mater, accompanies the vessel into the substance of the brain. At its commencement it is loose and funnel-shaped and can be injected from the subarachnoid cavity. On the cerebrum the inner layer of the pia mater is more closely adherent to the cortical substance of the convolutions than on the cerebellum, where a distinct space traversed by fibres exists between the two.

Purkinje described a retiform arrangement of fine nerve-fibres in the pia mater; these are derived, according to Kölliker and others, from the sympathetic and from the third, fifth, sixth, facial, vagus, glossopharyngeal, and accessory nerves. Most of the fibres are destined in all probability for the blood-vessels.

The spinal pia mater is supplied by nerves from the grey rami communicantes of the sympathetic.

THE ARACHNOID MEMBRANE.

The arachnoid is a delicate transparent membrane which is outside the pia mater and invests the brain and spinal cord much less closely than that membrane. It is bounded on its outer surface by the subdural space, and between it and the pia mater is a space (subarachnoid). This space is traversed by trabeculæ and thin membranes of delicate connective tissue (subarachnoid), by the cerebral and

[1] W. St. C. Symmers, Journal of Anatomy and Physiology, xl.

spinal nerves, and by the larger blood-vessels of the brain and spinal cord, and contains the cerebrospinal or subarachnoid fluid, which differs in many respects from ordinary lymph.[1]

The nerve-roots as they pass from the brain and spinal cord receive their perineural covering from the pia mater, and, after crossing the subarachnoid space to reach the apertures in the dura mater, two looser sheaths, an outer from the dura mater, and an inner from the arachnoid. Upon the optic nerve these sheaths remain distinct and separate, so that the space which each encloses may be injected, the outer from the subdural, the inner from the subarachnoid space. On the other nerves the arachnoidal sheath soon ceases, and the single sheath eventually blends with both the epineurium and perineurium of the nerves. It is found that injection driven into either the subdural or the subarachnoid space passes readily along the nerves even as far as the limbs. There thus exists a continuity between the subarachnoid space and the lymphatic spaces within the nerve-sheaths.

SPINAL ARACHNOID MEMBRANE AND SUBARACHNOID SPACE.—In the spinal canal the arachnoid forms a loose sheath for the spinal cord, being separated from the pia mater by a large subarachnoid space (fig. 309) which is divided by an imperfect fibrous septum on either side termed the ligamentum denticulatum (*g*) into anterior and posterior portions. As was pointed out by Magendie, there also exists a sort of septum dividing the subarachnoid space at the back of the cord (*septum posticum*) (fig. 309, *c*), the relations of which have been studied by Axel Key and G. Retzius. It is a thin membranous partition, which passes in the median plane from the pia mater covering the osterior median fissure of the cord to the opposite part of the loose portion of the arachnoid membrane. It is most perfect in the cervical region, being incomplete below. It consists of numerous fine lamellæ, enclosing between them small spaces, within which run the larger blood-vessels. Subarachnoid trabeculæ also connect the nerve-roots with the inner surface of the arachnoid, and in the dorsal region fine membranous trabeculæ extend between the posterior nerve-roots and the posterior septum. In most parts however the subarachnoid trabeculæ are far less developed in the spinal canal than in the cranium.

Below the cord the arachnoid forms a common tubular investment for the nerve-roots of the cauda equina and bounds a large reservoir for the cerebro-spinal fluid. Opposite the second and third lumbar vertebræ this arachnoid sheath is about 2 cm. to 2·5 cm. in breadth; below this it gradually diminishes in size until it reaches the sacral canal, where it decreases more rapidly and ends at the level of the second sacral vertebra.

Ligamentum denticulatum.—This is a narrow fibrous band which runs along each side of the spinal cord in the subarachnoid space, between the anterior and posterior roots of the nerves, commencing above at the foramen magnum, and reaching down to the lower pointed end of the cord. By its inner edge this band is connected with the pia mater of the cord, while its outer margin is widely denticulated; its denticulations are attached by their points to the inner surface of the dura mater, and thus serve to support the cord along the sides, and to maintain it in the middle of the cavity. The first or highest denticulation is fixed opposite the margin of the foramen magnum, between the vertebral artery and the hypoglossal nerve; the others follow in order, alternating with the successive pairs of spinal nerves. In all, there are about twenty-one of these points of insertion, but the lower six or seven are less regular. The points of the lower denticulations are prolonged into threads, and ascend slightly to their attachments. At the lower end, the ligamentum

[1] Halliburton, 'Cerebrospinal fluid,' Journal of Physiology, x.

denticulatum may be regarded as continued into the terminal filament of the spinal cord, which thus connects it to the dura mater at the extremity of the sheath. The free edge, in the intervals between the denticulations, is slightly thickened, and in many parts is closely applied to the inner surface of the arachnoid, with which it is often directly connected by fine trabeculæ. The denticulations do not perforate the arachnoid, but receive from it funnel-shaped sheaths which accompany them to the inner surface of the dura mater (Axel Key and Retzius).

In structure the ligament consists of fibrous tissue, mixed with many exceedingly fine elastic fibres. Several layers of fine connective-tissue trabeculæ may be traced; they are surrounded by sheaths, which are composed of delicate nucleated cells, and here and there expand into membranes. Its tissue is continuous on the one hand with that of the pia mater, and at the apices of the denticulations with that of the dura mater.

ENCEPHALIC ARACHNOID MEMBRANE AND SUBARACHNOID SPACES.—The encephalic arachnoid differs from the spinal arachnoid in being closely applied to the

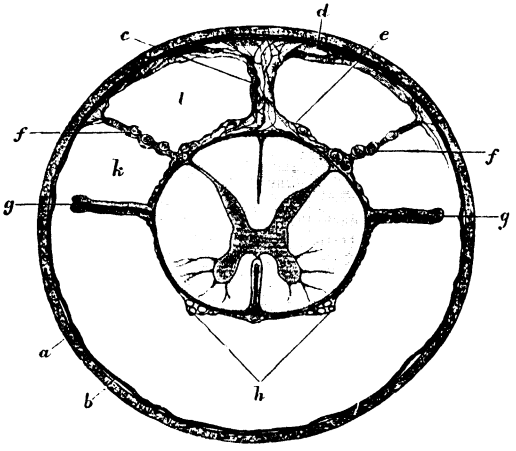


FIG. 309.—SECTION OF THE SPINAL CORD WITHIN ITS MEMBRANES (UPPER THORACIC REGION). Magnified. (Key and Retzius.)

a, dura mater; *b*, arachnoid; *c*, septum posticum; *d*, *e*, *f*, subarachnoid trabeculæ, those at *f*, *f*, supporting bundles of a posterior nerve-root; *g*, ligamentum denticulatum; *h*, sections of bundles of an anterior nerve-root; *k*, *l*, subarachnoid space.

pia mater in some places, whereas in others it is separated by distinct intervals termed cisternæ arachnoidales: the most important of these are found at the base of the brain. The subarachnoid tissue is most abundant where the space between the two membranes is least. It is dense in the neighbourhood of the vessels, and is continuous with the tissue of their walls.

The arrangement of the arachnoid at the base of the brain and of the neighbouring cisternæ cannot be satisfactorily demonstrated on brains removed in the usual way from the cranial cavity, because during this procedure the arachnoid is extensively torn. It can, however, be displayed by cutting away the base of the skull piecemeal and then carefully reflecting the dura mater with or without previous injection of the subarachnoid cavity.

The arachnoid passes upwards from the spinal canal through the foramen magnum and immediately expands to enclose the medulla oblongata. Behind the medulla oblongata and below the cerebellum it forms the *cisterna cerebello-*

medullaris or *cisterna magna*. This cisterna has a considerable transverse diameter (5 cm. to 6 cm.), as it lies not only below the inferior vermis, but also extends outwards on the under surface of the cerebellar hemispheres beyond the tonsils. This line of separation of arachnoid and pia mater passes forwards to the outer side of the flocculus, where the cisterna magna communicates with the lateral recess of the fourth ventricle by means of the foramen of Luschka. This cisterna also communicates in the median line with the lower end of the fourth ventricle through the foramen of Magendie. In front and at the sides of the medulla oblongata and pons the arachnoid is separated from the pia mater by the basilar and two vertebral arteries, and passes outwards to the openings in the dura mater for the fifth to the twelfth cranial nerves. The subarachnoid space is here divided into a median and two lateral parts, a *cisterna media pontis* containing

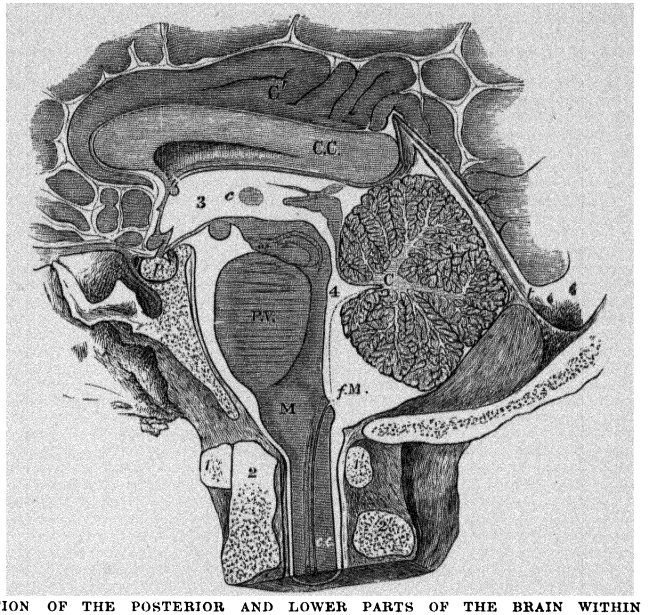


FIG. 310.—SECTION OF THE POSTERIOR AND LOWER PARTS OF THE BRAIN WITHIN THE SKULL, TO EXHIBIT THE SUBARACHNOID SPACE AND ITS RELATION TO THE VENTRICLES. (After Key and Retzius.)

The section was made in the frozen state, the cavities having been previously filled with injection.

1, 1', atlas vertebra; 2, odontoid process of the axis, 2'; 3, third ventricle; 4, fourth ventricle; *C.C.*, corpus callosum; *C'*, gyrus fornicatus; *C*, cerebellum; *t*, tentorium; *p*, pituitary body; *c.c.*, central canal of the cord; *f.M.*, in the cerebello-medullary part of the subarachnoid space, is close to the foramen of Magendie by which that space communicates with the fourth ventricle.

the basilar artery and the *cisternæ laterales pontis* the two vertebral arteries and the cerebral nerves just mentioned. Between the pons and the optic commissure the arachnoid stretches across from one temporal lobe to the other, forming the lower boundary of the *cisterna basilaris*. This cisterna contains the third nerves and the terminations of the basilar and internal carotid arteries. On each side it communicates behind with the subarachnoid spaces around the posterior cerebral and superior cerebellar arteries and in front with the *cisterna fossæ Sylvii* along the middle cerebral artery. The *cisterna terminalis* is in front of the optic commissure and the lamina terminalis. It contains the anterior cerebral arteries, and is continuous, as is also the *cisterna basilaris*, with the subarachnoid space around the optic nerve. On the exposed surface of the cerebral convolutions the arachnoid membrane is closely adherent to the pia

mater, but instead of following the pia mater into the various fissures it bridges across them, leaving subarachnoid clefts (flumina) which follow the course of the great fissures (Sylvian, central, &c.), and these flumina receive the clefts which follow the course of the secondary and tertiary fissures (rivi and rivuli of Duret). In the longitudinal fissure the arachnoid crosses immediately below the edge of the falx cerebri, and in the interval thus left between the arachnoid and the corpus callosum are found the callosal branches of the anterior cerebral arteries. There is also a distinct subarachnoid space (*cisterna venæ magnæ cerebri*) between the splenium of the corpus callosum and the cerebellum which contains the posterior portion of the veins of Galen. All the various subarachnoid spaces form a series of intercommunicating channels, and the fluid they contain is continuous with that of the ventricular cavities by the foramen of Magendie and the foramina of Luschka.[1]

Structure.—When examined under the microscope, the arachnoid membrane is found to consist of distinct riband-like bundles of fine fibrous tissue interlaced with one another. The intervals between these bundles are filled up by delicate membranes, composed of expanded cells, the nuclei of which persist and are

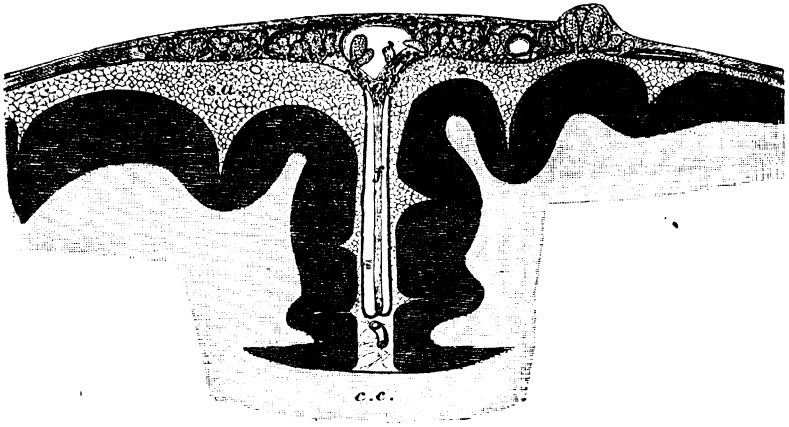


FIG. 311.—SECTION OF THE UPPER PART OF THE BRAIN AND MENINGES TO SHOW THE RELATIONS OF THE ARACHNOIDAL VILLI. Magnified. (Key and Retzius.)

c.c., corpus callosum; *f*, falx cerebri; *s.a.*, subarachnoid space, pervaded by a network of fine trabeculæ; from it the fungiform villi are seen projecting into the lateral lacunæ of the dura mater. Some are projecting into the superior sagittal sinus.

scattered over the structure. Several layers of this tissue, arranged in a complex way, constitute the arachnoid membrane proper. The subarachnoid trabeculæ consist of bundles of similar fine fibrillar tissue, each of which is surrounded by a delicate nucleated sheath, also composed of cells and continuous with the intertrabecular cell-membranes of the arachnoid itself. The finer trabeculæ when swollen by acetic acid very frequently show the well-known ring-like constrictions. The subarachnoid membranous expansions have a similar structure. In the spinal arachnoid the fibril-bundles have for the most part a longitudinal direction.

Pacchionian granulations. — These are small, pale, pulpy-looking elevations, generally collected into clusters, the great majority of which are

[1] For full particulars regarding the subarachnoid spaces see Key and Retzius, Studien in der Anatomie des Nervensystems und des Bindegewebes, 1875; and Duret, Archives de Physiologie, 1873 and 1874.

situated in the neighbourhood of the longitudinal sinus, but some are occasionally found in relation to the lateral, superior petrosal, and cavernous sinuses. They are either absent or very few in number at birth, and are small and inconspicuous until about puberty. After this they gradually increase in number and size as age advances. They first appear as very small projections of the arachnoid, attached to the membrane by a narrow peduncle and having their outer portion expanded into balloon-shaped masses. They are covered by the arachnoid and contain in their interior a spongy network of subarachnoid tissue, the meshes of which are occupied by subarachnoid fluid. Some of them may retain this simple form, but generally they become complex by the growth of numerous secondary processes, which may be attached to a common peduncle or be seated upon the primary dilatation. These bodies form clusters which vary greatly in size. As they grow they press against, become adherent to, and partly erode the dura mater, so that when the latter is torn off the granulations, its under surface presents a fasciculated appearance. The granulations covered by a thin layer of dura mater project into an adjacent venous sinus, or into the venous *lacunæ laterales*. Those which protrude into the lateral lacunæ almost obliterate the cavity, and pushing thin portions of the dura mater before them become lodged in pits on the inner side of the cranial wall.

Fluid injected into the subarachnoid space passes freely into the Pacchionian bodies, and is found after a time to filter through their walls and thus to get into the subdural space, although there does not appear to be any open communication between the interior of these bodies and the prolongation of the subdural space which surrounds them. Moreover, if the injection is continued it can be driven even into the interior of the venous sinuses and lacunæ which are found in connexion with them, especially into the superior longitudinal sinus, into which the arachnoidal villi project. So that these villi seem to afford a means of passage of the cerebrospinal fluid from the subarachnoid space into the venous sinuses, when the fluid pressure in the subarachnoid space becomes from any cause increased above the normal.

BLOOD-VESSELS OF THE BRAIN AND SPINAL CORD.

Blood-supply of the spinal cord.—The arteries of the spinal cord are (1) the *anterior spinal*, double above where it is derived from the vertebrals but single and median below where it is reinforced by a series of small vessels derived from the vertebral, intercostal, lumbar, and other arteries, and passing to the cord along the anterior roots, and (2) the paired *posterior spinal arteries*, similarly derived from the vertebrals, intercostals, and other arteries, and running just in front of the line of attachment of the posterior roots. Another small longitudinal anastomotic chain formed by branches of the posterior spinal runs along just behind the line of the posterior roots. The branches of these vessels ramify in the pia mater investing the cord, communicating with one another to form transverse anastomoses, and from the main vessels and their ramifications vessels pass in to supply both the grey and white substance.

The small entering branches may be described as forming two systems, a centrifugal and a centripetal. The first is composed of a series of arterioles (*central arterioles*, Ross), 200 to 300 in number, which pass from the anterior spinal artery into the anterior median fissure, penetrating to the anterior commissure. Here each one passes either to the right or left, and divides into smaller arteries and capillaries for the central parts of the corresponding crescent

of grey matter; but a considerable ascending and descending ramuscule is also given off, and these overlap in their distribution the corresponding longitudinal branches of the adjacent central arterioles. Although mainly distributed to the central parts of the grey matter, the central arterioles may also send branches to join the capillaries of the white matter.

The second or centripetal set, better developed than the centrifugal, has a converging or radial arrangement, passing in from the periphery. Some of these simply form capillary loops, which supply the superficial layers of the cord. Others are distributed to the white matter, where they form comparatively large-meshed longitudinal plexuses. But the most considerable of the centripetal arteries penetrate to the grey matter and pour their blood into the close

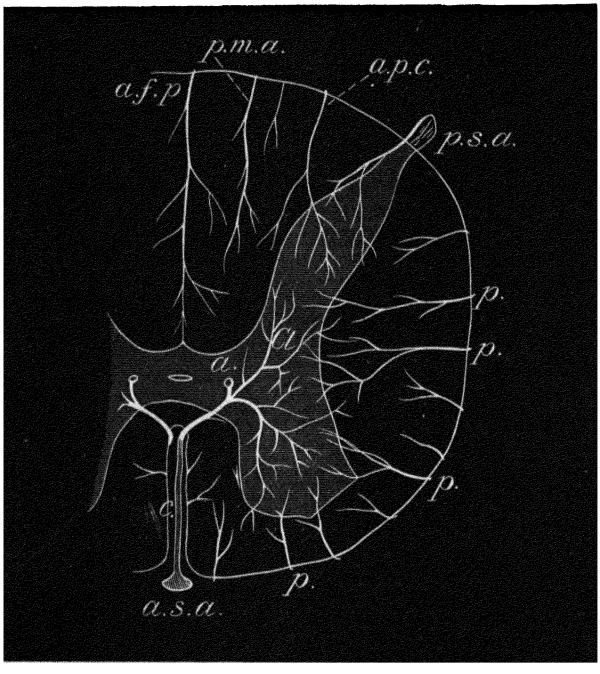


FIG. 312.—SEMI-DIAGRAMMATIC REPRESENTATION OF THE ARTERIES IN THE INTERIOR OF A SEGMENT OF THE SPINAL CORD. (Obersteiner.)

a.s.a., anterior spinal artery; *c.*, a central arteriole; *a.*, an anastomotic branch uniting it with another arteriole of an adjacent segment; *Cl.*, branch to Clarke's column; *a.f.p.*, artery of posterior fissure; *p.m.a.*, posterior mesial artery; *a.p.c.*, artery of posterior cornu; *p.s.a.*, branch of posterior spinal artery passing into gelatinous substance; *p.*, other peripheral or centripetal arterioles passing through white substance of cord.

capillary network which pervades it, supplying the parts not served by the centrifugal vessels. The capillaries of the substantia gelatinosa are less numerous than in the rest of the grey matter, and their meshes are mostly longitudinal.

Special mention may be made of a series of small median arterial branches which enter the posterior fissure, penetrating in it to the posterior commissure, and giving off branches which supply the adjacent parts of the posterior white columns and Clarke's column, where this is found; and of the vessels which enter the grey matter with the bundles of the anterior and posterior nerve-roots, and are distributed to the corresponding cornua. It would appear however that

no one part is supplied by only one set of arterioles, nor is any one set of arterioles confined in its distribution to any one white column or group of cells in the grey matter. At the same time it should be noted that within the cord itself (as within the brain) all the arteries are 'terminal arteries,' in Cohnheim's sense—that is to say, they do not anastomose with other arteries, but each one terminates in its own capillary area, and supplies no other. There is however much variation in the extent of the capillary area supplied by any of the arterial branches, and no definite statement can be made concerning the exact region supplied by any set of arterioles (Kadyi).

The most considerable veins of the spinal cord are two longitudinal median vessels, one running along the anterior median fissure along with the anterior spinal artery, and another over the posterior median fissure unaccompanied by any considerable artery. Both of these median veins have a tortuous course, and the posterior one is frequently broken up into a kind of venous plexus, with longitudinal meshes, which extends over the whole posterior surface of the cord. There is also a less perfect lateral anastomotic chain lying behind the line of exit of the anterior nerve-roots. All these vessels communicate freely with one another by lateral offsets. They receive the venous blood from the cord on the one hand, and on the other hand carry it away by veins which accompany, at frequent intervals, the nerve-roots. In the upper part they join the veins of the cerebellum and pons, and the venous sinuses around the foramen magnum. Within the cord their branches anastomose frequently. The vein accompanying the anterior spinal artery receives, like that vessel, very numerous tributaries from the anterior median fissure (*central venules*): these carry away a large part of the blood from the grey matter; the *peripheral venules*, which enter the veins of the pia mater which covers the general surface of the cord, chiefly carry away the blood from the capillaries of the white matter.[1]

Blood-supply of the brain.—The origin and course of the vessels which supply the brain are described in the section Angeiology. In passing to their distribution the several arteries divide and subdivide in the subarachnoid space into branches, which, in their further ramification on the nervous centres, are supported by the pia mater, and, it may be remarked, are more deeply placed in the various fissures and sulci than the small veins, which do not accompany the arteries, but pursue a different course and are chiefly seen upon the surface of the pia mater. Huebner[2] divided those passing to the cerebral hemispheres into basal and cortical. The basal are small vessels which pass directly into the brain at its base and do not anastomose with one another or with other cerebral arteries. The cortical vessels ramify on the surface of the brain and divide in the pia mater into fine twigs from which very numerous small branches pass vertically into the grey matter of the convolutions. Most of these (*cortical arteries*) at once break up into a close plexus of capillaries for the grey matter; but others (*medullary arteries*), larger but less numerous, pass through the grey matter, giving off only a few small branches to it, and penetrate for some distance into the medullary centre, where they divide into a long-meshed capillary network. The smaller branches of arteries anastomose together to a certain extent in the pia mater (Huebner), but the branches which pass into the superficial grey matter and subjacent white matter do not anastomose with one another.[3]

[1] A. Adamkiewicz, Sitzungsber. d. k. Akad. d. Wiss. in Wien, 1881 and 1882; H. Kadyi, Ueber die Blutgefässe des Menschlichen Rückenmarkes, Lemberg, 1889; J. Ross, Brain, ix. 1880; G. Sterzi, Anatomische Hefte, xxiv. 1904.

[2] Die luetische Erkrankung der Hirnarterien, Leipzig, 1874.

[3] C. E. Beevor, Phil. Trans. 1908.

Moreover, it is to be observed that, while the main branches of the arteries are situated at the base of the brain, the principal veins tend towards the upper

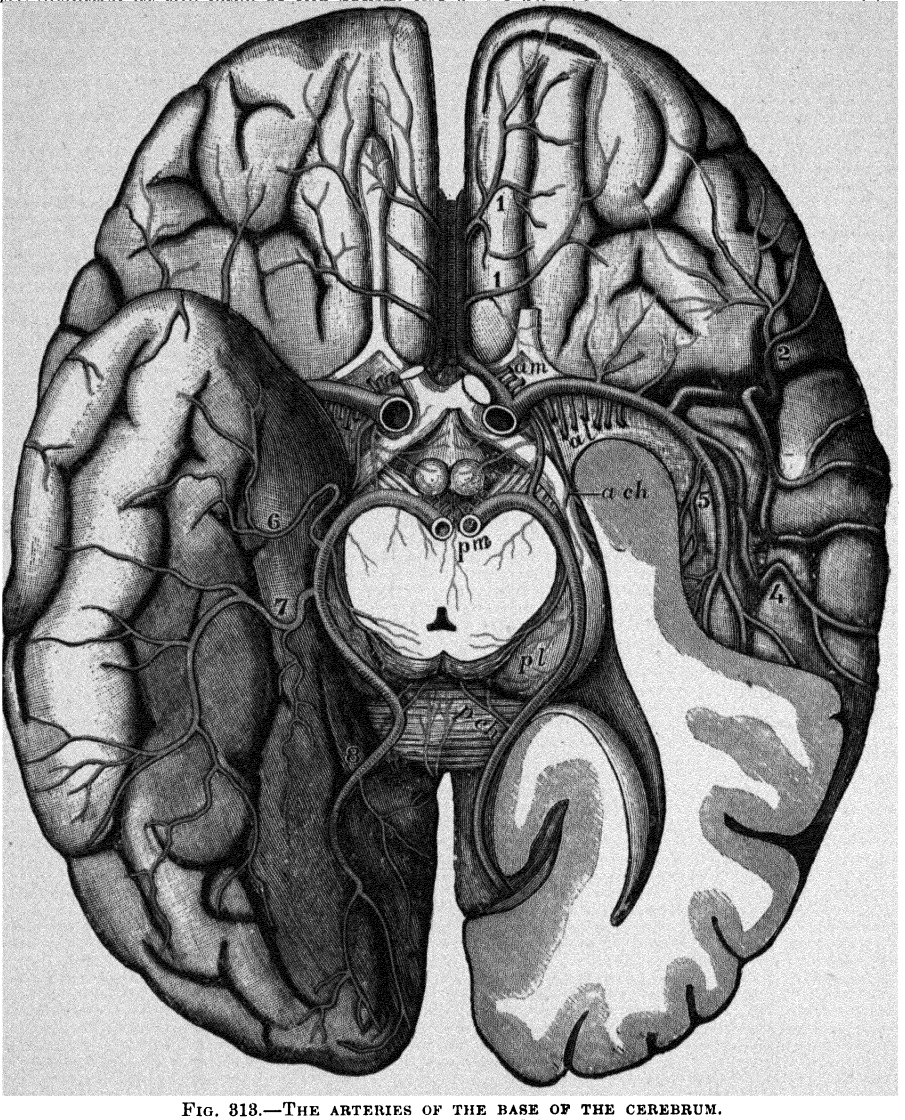


FIG. 313.—THE ARTERIES OF THE BASE OF THE CEREBRUM.
(G. D. Thane, after Duret, and from nature.)

On the left side of the brain the temporal lobe is cut away so as to open the inferior and posterior horns of the lateral ventricle. The mid-brain is divided close above the pons, and the posterior cerebral arteries are cut at their origin from the basilar.

Central arteries (to the basal ganglia): *am*, antero-mesial group arising from the anterior cerebral; *al*, antero-lateral group, from the middle cerebral; *pm*, *pl* (on the optic thalamus), postero-mesial and postero-lateral groups, from the posterior cerebral.

Choroidal arteries: a ch, anterior from the internal carotid; *p ch* (on the splenium), posterior, from the posterior cerebral.

Cortical arteries: 1, 1, inferior internal frontal, from the anterior cerebral; 2, inferior external frontal; 3, ascending frontal; 4, ascending parietal, and 5, temporo-parietal, from the middle cerebral; 6, anterior temporal, 7, posterior temporal, and 8, occipital, from the posterior cerebral.

surface of the hemispheres, where they enter the superior longitudinal sinus, most of them looping forwards as they pass into the sinus, and often entering

the dura mater a short distance from the sinus, but more usually having a free course, sometimes of considerable length, through the subarachnoid space in passing from the pia into the dura mater. The veins of Galen, coming from the lateral ventricles and choroid plexuses, run backwards to the straight sinus, in the subarachnoid tissue which lies between the two layers of the velum interpositum.

It may be convenient here to recapitulate the sources of the blood-supply to the several parts of the encephalon.

The **medulla oblongata** and **pons** are supplied by branches from the anterior spinal, the vertebral, the basilar, and the posterior cerebral arteries. The branches enter the pons and medulla oblongata in two sets, lateral or radicular (following the roots of the nerves), and median—the latter passing in the raphe to the grey matter on the posterior surface. The superior medullary velum and the superior peduncle of the cerebellum receive twigs from the

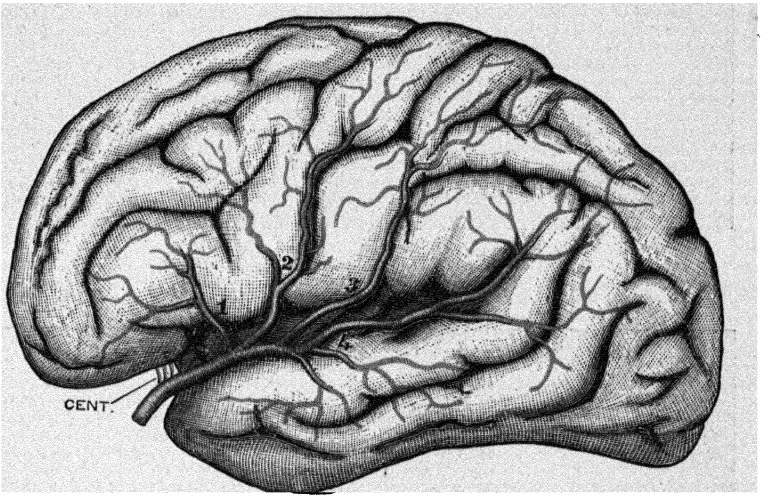


FIG. 314.—CORTICAL DISTRIBUTION OF THE MIDDLE CEREBRAL ARTERY. Diagrammatic. (G. D. Thane, after Charcot.)

CENT., antero-lateral group of central arteries; 1, inferior external frontal artery; 2, ascending frontal artery; 3, ascending parietal artery; 4, parieto-temporal artery.

superior cerebellar arteries. The choroid plexuses of the fourth ventricle are supplied by the inferior cerebellar arteries.

Cerebellum.—The under surface is supplied by the inferior cerebellar arteries from the vertebral, and the anterior from the basilar. The upper surface is supplied chiefly by the superior cerebellar arteries from the basilar: its posterior portion from the inferior cerebellar.

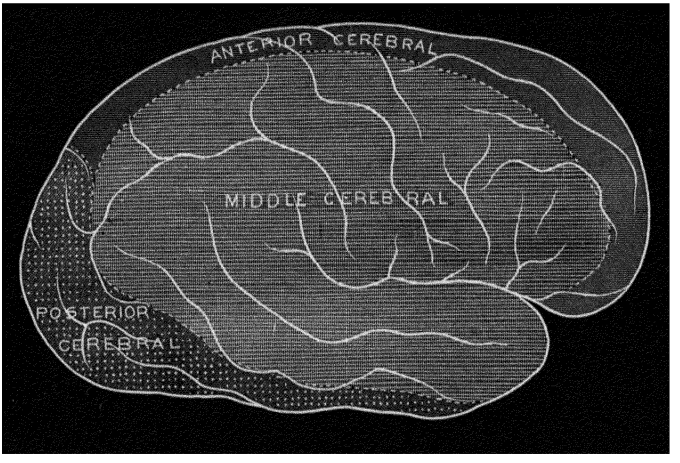
The **pedunculi cerebri** derive their blood-supply from the posterior communicating and the posterior cerebral arteries. Branches of the latter, and also others from the end of the basilar, enter the posterior perforated space.

The **corpora quadrigemina** and **corpora geniculata** are both supplied by the posterior cerebral artery, but branches of the superior cerebellar arteries pass to the inferior corpora quadrigemina.

The **thalamus** is supplied above and on the outer, inner, and posterior sides by branches of the posterior cerebral artery, but its anterior and inner portion receives twigs from the posterior communicating artery.

Cerebral hemispheres.—*Frontal lobe.*—The superior frontal and anterior two-thirds of the middle frontal convolution, with the upper extremity of the anterior central, are supplied by the anterior cerebral. The inferior and middle

A



B

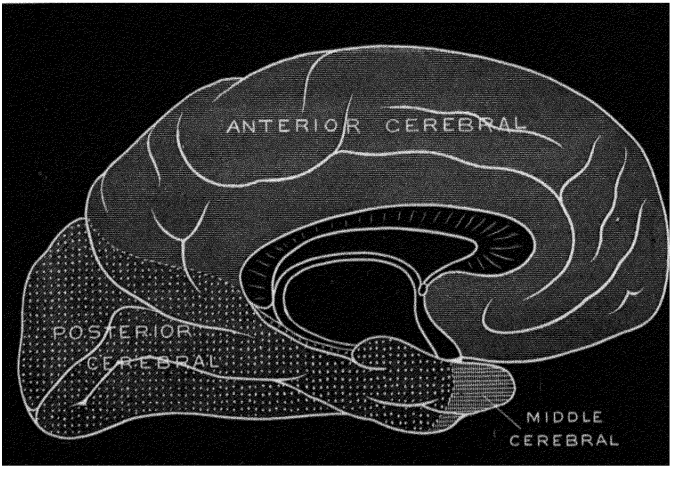


FIG. 315.—DIAGRAMS SHOWING THE AREAS OF CORTICAL DISTRIBUTION OF THE ANTERIOR, MIDDLE, AND POSTERIOR CEREBRAL ARTERIES RESPECTIVELY. (E. A. Schäfer.)

A, lateral aspect; B, mesial aspect.

The area supplied by the middle cerebral frequently extends to the upper border of the hemisphere in the region of the parietal lobe, and therefore somewhat farther than is represented in A.

frontal convolutions and the greater part of the anterior central convolutions are supplied by the middle cerebral. The orbital surface is supplied, outside the orbital sulcus, by the middle cerebral: within that sulcus (including the olfactory bulb) by the anterior cerebral.

Parietal lobe.—The convolutions of the parietal lobe are supplied by the middle cerebral artery, except those on the inner surface and those along the inner part of the external surface as far back as the anterior half of the postero-superior lobule, which are supplied by the anterior cerebral.

Occipital lobe.—This lobe is supplied entirely by the posterior cerebral artery.

Temporal lobe.—The superior and middle temporal convolutions are supplied by the middle cerebral artery; the lower portion of the lobe by the posterior cerebral.

Inner surface of the hemispheres.—The whole anterior and upper portion, as far back as the middle of the lobulus quadratus, is supplied by the anterior cerebral artery; the posterior half of the quadrate lobule, cuneate lobule, and the occipito-temporal region by the posterior cerebral.

The most common distribution of arteries to the several parts of the cerebral cortex is illustrated in the accompanying diagrams (fig. 315), which are compiled from various sources. They correspond closely with those given by Beevor (*op. cit.*).

The *corpus callosum* is chiefly supplied by the anterior cerebral.

The *grey substance at the base* of the cerebrum is supplied by small twigs from the adjacent vessels of the circle of Willis, or from the roots of the cerebral vessels which pass off from that anastomosis.

Corpus striatum.—Both nucleus caudatus and nucleus lenticularis are supplied almost exclusively by the middle cerebral artery, the numerous branches to these parts entering through the foramina in the anterior perforated space (fig. 313). They are divided by Duret into *lenticular, lenticulo-striate,* and *lenticulo-optic* (lenticulo-thalamic). These pass directly to their destination without anastomosing with one another, and traverse the zones of the lenticular nucleus and the internal capsule, to terminate finally in the caudate nucleus and optic thalamus. One in particular of the lenticulo-striate arteries which passes through the outer part of the putamen is very frequently the seat of hæmorrhage, and it has accordingly been termed by Charcot the 'artery of cerebral hæmorrhage.'

The anterior part of the caudate nucleus is also supplied by the anterior cerebral, and its upper surface receives fine twigs from the lateral choroidal branch of the posterior cerebral.

Internal capsule.—The anterior limb is supplied in its upper half by the middle cerebral and in its lower half by the anterior cerebral, and the posterior limb by the posterior communicating, the anterior choroidal, the middle cerebral, and in some cases, to a slight degree, by the posterior cerebral (Beevor).

The *choroid plexuses of the lateral ventricles* are supplied (1) by the anterior choroid branch of the internal carotid which passes obliquely backwards and outwards, and enters the choroid plexus at the anterior end of the descending cornu, supplying two-thirds of the plexus of the lateral ventricle; (2) by the postero-lateral choroid artery, a branch of the posterior cerebral, which supplies the remaining third of the plexus. The *choroid plexus of the third ventricle* is supplied by a branch (postero-mesial) of the posterior cerebral. The tela choroidea of the third ventricle is also supplied by the two last-named branches of the posterior cerebral. The *parts in the quadrilateral space* at the base of the brain including the chiasma, the infundibulum, and the corpora mamillaria receive branches directly from the circle of Willis.

Lymph-paths of the brain and spinal cord.—Neither the brain nor the spinal cord possesses true lymphatic vessels. The lymph finds its way out of these organs by means of perivascular spaces in the tunica adventitia of the blood-vessels; these perivascular spaces communicate with the subarachnoid space at the surface of the brain and cord (Key and Retzius).

MEASUREMENTS OF THE BRAIN.

Dimensions.—The length of the cerebral hemispheres, measured from the frontal to the occipital pole, varies in the larger proportion of cases between 160 mm. and 170 mm. for the male brain; and between 150 mm. and 160 mm. for the female brain. The greatest transverse diameter of the whole brain for both sexes is about 140 mm. and the greatest vertical measurement of each hemisphere about 125 mm. (Huschke). The brains of dolichocephalic individuals are naturally longer than those of brachycephalic; in the latter there is a tendency to a breaking up of the longitudinal gyri by transverse fissures, thereby increasing the amount of surface and hence of grey cortex in proportion to the whole brain.

Extent of grey cortex.—The attempts hitherto made to measure or estimate the relative proportions of the different convoluted parts of the cerebrum to each other and to the degree of intelligence, either more directly or by cranioscopic methods, have been attended with little success. Such investigations were first systematically carried out by Rudolph Wagner.[1] His researches had for their object to institute an accurate comparison between the brains of certain persons of known intelligence, cultivation, and mental power, and those of persons of an ordinary or lower grade. As examples of brains of men of superior intellect he selected those of Professor Gauss, a well-known mathematician of eminence (æt. 78), and Professor Fuchs, a clinical teacher (æt. 52); and as examples of brains of ordinary persons, those of a woman of 29 and a workman.

The careful measurement of all the convolutions and the intervening grooves in the four brains above-mentioned was carried out by H. Wagner,[2] by covering the cortex everywhere with gold-leaf, and determining the extent of surface by the amount employed. The result of these measurements is partly given in the accompanying table, the numbers indicating square millimetres of surface.

It is found that although there seem to be certain differences in the brains examined, these are by no means so striking as might have been expected. Indeed, it may be stated that the general result of these and similar observations has been inconclusive; for although there have been observed several notable instances in which superiority of intellect has been found to be accompanied by increased size or complexity of the cerebral surface, in many other cases no such relation has been noticed.

Comparative measurement of the extent of surface of the cerebral convolutions.

	Surface of each Lobe separately.					Free and Deep Surfaces of Convolutions.		Whole surface of cerebrum.
	Frontal.	Parietal.	Occipital.	Temporal.	Central.	Free surface.	Deep surface, including surface of insula.	
1. Gauss	89,545	45,493	38,286	44,062	2,252	72,650	146,988	219,638
2. Fuchs	92,380	44,783	37,927	43,468	2,447	72,100	148,905	221,005
3. Woman ...	84,318	41,838	32,851	42,982	2,126	68,900	135,215	204,115
4. Workman .	72,890	40,142	32,490	39,880	2,270	62,750	124,922	187,672

It will be seen from the above that the total surface, exposed and sunken, is about 200,000 sq. mm., and that there is about twice as much sunken as exposed surface. With this estimate the determinations made by subsequent

[1] Vorstudien zu einer wissenschaftlichen Morphologie und Physiologie des menschlichen Gehirns als Seelenorgan, 1860.

[2] Maassbestimmungen der Oberfläche des grossen Gehirns; Göttingen, 1864.

observers mostly agree. Baillarger, who dissected off and unfolded the cortex, and then measured its whole extent, obtained only an area of 170,000 sq. mm. as the mean of the brains thus treated. Paulier,[1] by a modification of the method of Wagner, obtained a result similar to that of Baillarger for the whole surface, and further found the sunken surface to measure but little more than the exposed surface, and the extent of surface to bear no relation to the weight of the brain. Calori measured forty-one brains (Italians), and obtained the following average results (in sq. mm.) for the total surface: Male, brachycephalic, 243,773. Male, dolichocephalic, 230,212. Female, brachycephalic, 211,701. Female, dolichocephalic, 198,210.

Danilewsky [2] attempted to determine the area of the whole cortex by a comparison of the weight of the brain, its specific gravity (1,038), the specific gravity of the grey matter (1,033), and white matter (1,041), and the average thickness of the grey matter, which he estimated at 2·5 mm. He obtained in this way a result which showed the weight of the cortex to be 33 per cent. of the total weight of the brain, and giving for a brain weighing 1,324 grm. a total surface of 169,200 sq. mm. De Regibus made similar calculations from estimation not of the specific gravity, but of the amount of water in the whole brain and in its two component substances. His estimates of the total area of the cortex of both hemispheres are higher than those of Danilewsky, varying from about 217,472 to 278,940 sq. mm. Donaldson [3] calculated that the cortex forms about 50 per cent. of the weight of the brain.

Thickness of cortex.—It is clear that a measurement of surface alone, without taking into account the thickness of the cortex, may be entirely misleading as to the amount of grey matter in the brain. This has been recognised by various observers, who have accordingly endeavoured to form an estimate both of the average thickness of the cortex generally, and also its thickness in special localities. The results have been tabulated by Donaldson, and from them it would appear that the thickness may vary from 1·55 mm. to 3·5 mm., or even somewhat more than this, the average in normal brains being 2·9 mm. If a section be made across a gyrus it will be found that the cortex is thickest at the summit of the gyrus and thinnest at the bottom of the bounding sulci, so that it is necessary to take a mean between these two measurements in order to arrive at the average thickness for any locality. But beyond the fact that the cortex is somewhat thinner near the hemisphere-poles, and especially the occipital pole, than in the intermediate parts, no definite statement regarding the relative thickness of different parts can at present be made. Females have a very slightly less thickness of cortex than males (less than 1 per cent.), and the right hemisphere less than the left (Donaldson).

Weight.—The results obtained by Sims, Clendinning, Tiedemann, and J. Reid showed the maximum weight of the adult male brain, in a series of 278 cases, to be about 1,810 grammes (64 oz.), and the minimum weight about 960 grammes (34 oz.). In a series of 191 cases, the maximum weight of the adult female brain was 1,585 grammes (56 oz.), and the minimum 880 grammes (31 oz.). In a very large proportion the weight of the male brain ranges between 46 oz. and 53 oz., and that of the female brain between 40 oz. and 47 oz. Similar statistics have been published by Peacock, R. Wagner, Bischoff, Huschke, Boyd, Weisbach, and others. The mean weight at from 20 to 40 years of age was found by Boyd to be 48 oz. (1,360 grammes) for the male, and 43½ oz. (1,230 grammes) for the female brain. Although many female brains exceed in

[1] Détermination de la Surface du Cerveau, &c.; Paris, 1892.
[2] Centralblatt f. d. med. Wissensch. 1880.
[3] American Journal of Psychology, iii. and iv.

weight particular male brains, as a general fact it may therefore be affirmed that the adult male encephalon is on an average heavier by 4 oz. or 5 oz. than that of the female (or about 9 per cent.).

The appended table, compiled from the observations of R. Boyd (Phil. Trans. 1860), shows in grammes the mean weights at different ages in the two sexes.

	Males.	Females.		Males.	Females.
Children stillborn at term...	393 ...	347	From 14 to 20 years	1,374 ...	1,244
Children born alive at term.	330 ...	283	From 20 to 30 years	1,333 ...	1,237
Under 3 months	493 ...	451	From 30 to 40 years	1,364 ...	1,220
From 3 to 6 months	602 ...	560	From 40 to 50 years	1,351 ...	1,212
From 6 to 12 months.....	776 ...	727	From 50 to 60 years	1,343 ...	1,220
From 1 to 2 years	941 ...	843	From 60 to 70 years	1,313 ...	1,208
From 2 to 4 years	1,095 ...	990	From 70 to 80 years	1,288 ...	1,168
From 4 to 7 years	1,138 ...	1,135	Over 80 years	1,283 ...	1,125
From 7 to 14 years.....	1,301 ...	1,154			

It would appear from the above that the brain is absolutely heavier between 14 and 20 years of age than at any other period of life, and that at the age of 80 it has lost about 90 grammes, or rather more than 3 oz.—*i.e.* about $\frac{1}{15}$ of its whole weight.

The figures obtained by Broca are somewhat higher than these—*e.g.* between the ages of 30 and 35, in the male, an average of 1,421 grammes (50 oz.); in the female, 1,269 grammes (45 oz.). According to the same statistics, the weight of the brain attains its maximum, not before the age of 20, as found by Boyd, but between 25 and 35 in the male, and a little earlier in the female. This agrees with the results of Peacock.

The difference between the weight of the brain in newly born male and female infants is not always so great as given by Boyd. Mies [1] determined the weight of 203 full-time fœtuses and found the average for the males to be 339·25 grammes and for the females 329·99 grammes. After birth the male brain increases more rapidly in weight than the female. Pfister [2] ascertained the weight of the brain in 156 children. His results do not differ materially from Boyd's. At the end of the first year the brain is about two and a-half times heavier than at birth, and at the end of the sixth year its weight is not unfrequently equal to that of the adult.

E. A. Spitzka [3] collected the records of the brain-weights of 100 distinguished men, and found the average weight to be 1469·65 grammes or fully 100 grammes above the average for Europeans. He further showed that the senile decrease in weight was delayed about ten years in the 'distinguished' as compared with the 'ordinary' series.

The two hemispheres of the same brain, although hardly ever of exactly the same weight, show no constant difference, the one-half preponderating just about as often as the other, and the average difference being only about 5 grammes (Braune). There is no evidence that the right hemisphere is the heavier in left-handed people.

The *relative weight of the encephalon to the body* is liable to great variation; nevertheless, the facts to be gathered from the observations of Clendinning, Tiedemann, and Reid furnish the following general result. In a series of 81 males, the average proportion between the weight of brain and that of the body at the ages of 20 years and upwards was found to be as 1 to 36·5; and in a series of 82 females, to be as 1 to 36·46. The results of Bischoff's observations gave 1 to 35·2 in the female. In these cases the deaths were

[1] Wiener klin. Wochenschrift, 1889. [2] Arch. f. Kinderheil. xxiii.
[3] American Anthropologist, v. 1906.

the result of more or less prolonged disease; but in six healthy individuals dying suddenly from acute disease or accident the average proportion was 1 to 41.

The proportionate weight of the brain to that of the body is much greater at birth than at any other period of extra-uterine life, being, according to Tiedemann, about 1 to 5·85 in the male, and about 1 to 6·5 in the female. From various observations, it further appears that the proportion diminishes gradually up to the tenth year, being then about 1 to 14. From the tenth to the twentieth year the relative increase of the body is most striking, the ratio of the two being at the end of that period about 1 to 30. After the twentieth year the general average of 1 to 36·5 prevails, with a further trifling decrease in advanced life.

Influence of stature on brain-weight.—According to J. Marshall, the proportion of entire brain (in ounces) to each inch of stature is for the male sex 0·708; in the female 0·688. This relative preponderance in the male is due entirely to preponderance of *cerebral* development; the average stature-ratio for cerebrum alone being 0·0619 oz. in the male per inch of stature, and 0·599 oz. in the female, while the stature-ratios of cerebellum, pons, and medulla oblongata are similar in the two sexes.

The following tables were compiled by Marshall from the data furnished by the observations of R. Boyd upon the brains of 1,150 sane persons—viz. 598 males and 552 females. They show the average weights in ounces of the encephalon and its several parts at certain periods of life and in individuals having certain differences of stature:

MALES.

Total number of cases.	Ages.	Stature 69 inches and upwards.				Stature 68–66 inches.				Stature 65 inches and under.			
		Whole Brain.	Cerebrum.	Cerebellum.	Pons and Med. Obl.	Whole Brain.	Cerebrum.	Cerebellum.	Pons and Med. Obl.	Whole Brain.	Cerebrum.	Cerebellum.	Pons and Med. Obl.
146	20—40	49·72	43·43	5·29	1	47·99	41·9	5·09	1	46·95	41·15	4·9	·9
337	40—70	48·15	42·1	5·09	·96	47·08	41·01	5·1	·97	45·74	39·88	4·96	·9
115	70—90	46·92	41·19	4·8	·93	46·	40·1	4·9	1	44·15	38·6	4·65	·9
598	20—90	48·40	42·34	5·09	·97	47·13	41·08	50·6	·99	45·61	39·84	4·87	·9

FEMALES.

Total number of cases.	Ages.	Stature 64 inches and upwards.				Stature 63—61 inches.				Stature 60 inches and under.			
		Whole Brain.	Cerebrum.	Cerebellum.	Pons and Med. Obl.	Whole Brain.	Cerebrum.	Cerebellum.	Pons and Med. Obl.	Whole Brain.	Cerebrum.	Cerebellum.	Pons and Med. Obl.
133	20—40	44·64	39·14	4·7	·8	42·98	37·23	4·85	·9	42·26	36·78	4·64	·84
299	40—70	42·67	37·21	4·63	·83	42·75	37·29	4·56	·9	42·49	37·08	4·54	·87
120	70—90	41·13	35·77	4·52	·84	39·84	34·45	4·55	·84	39·59	34·36	4·36	·87
552	20—90	42·76	37·32	4·62	·82	42·37	36·84	4·64	·89	41·53	36·17	4·5	·86

It will be seen from these that although there is an increase of brain-weight with body-stature, this increase does not keep pace *pari passu* with the stature. That is to say, taller persons, although they have absolutely more brain substance, have relatively less than shorter persons. This is true for both sexes. Nevertheless the proportion of brain to the stature remains larger in the male both at the mean height of both sexes, and at nearly corresponding heights.

Marshall further found from a minute analysis of these results of R. Boyd, that in the case of males of mean height the weight in ounces of the cerebrum may be obtained by simply dividing the number of inches of height by 1·6, or in grammes by multiplying the number of centimetres of height by 7.

For females, the same formula as that employed for the male can be used, but the result must be multiplied by $\frac{30}{31}$.

Thus—

Weight in ounces of the mean male cerebrum $= \frac{\text{Height in inches}}{1{\cdot}6}$

" " " female cerebrum $= \frac{\text{Height in inches}}{1{\cdot}6} \times \frac{30}{31}$

Weight in grammes of the mean male cerebrum = Height in centimetres × 7

" " " female cerebrum = Height in centimetres × 7 × $\frac{30}{31}$.

The weights as calculated from these formulæ are found by Marshall to correspond very nearly with the observed weights for definite statures as recorded in Boyd's tables. The correspondence is most complete for statures near the mean, the observed weights being slightly defective at the higher, and excessive at the lower statures.[1]

Most of the estimates of brain-weight in different races have been obtained as the result of measuring the cubic contents of the skull-cavity. In this way it is estimated (Davis[2]) that the Chinese have an average brain-weight of about 1,330 grammes (approaching that of the European); the Sandwich islanders one of 1,300 grammes; the Malays and North American Indians one of 1,265 grammes; the negro 1,245 grammes; the native Australians 1,185 grammes. The Hindus have also a small brain-weight (probably in relation to the small prevailing stature)—viz. 1,190 grammes. Amongst Europeans the Latin races have a somewhat less brain-weight than the Teutonic and Sclavonic races; here also in all probability the influence of stature is apparent.

An estimate of the weight of the brain in prehistoric races depends entirely upon the determination of the cranial capacity, and in some of the most important of the prehistoric skulls such as the 'Neanderthal' and 'Trinil' the measurements cannot be more than a rough approximation, since only the upper parts of the crania are preserved. The weight of the 'Neanderthal' brain was probably fully 1,000 grammes and that of the 'Trinil' not more than 800 grammes.

Weight of the several parts of the encephalon.—The proportionate weight of the cerebellum (inclusive of the pons and the medulla oblongata) to that of the cerebrum is, in the adult, as 13 to 87 (Huschke). The cerebellum is both absolutely and relatively somewhat heavier in the male than in the female.

In the new-born infant the ratio of the weight of the cerebellum to that of the whole brain is strikingly different from that observed in the adult. Huschke found the weight of the cerebellum, medulla oblongata, and pons together in the new-born infant, as compared with that of the cerebrum, to be in the proportion of 7 to 93.

Meynert found the proportions between the frontal, parietal, and conjoined occipital and temporal lobes to be 41·5 : 23·4 : and 35·1 (in both the male and female).

According to Donaldson,[3] the weight of all the nerve-cell bodies in the human encephalon is less than 27 grammes. He also estimated the cortical cell-bodies and their dendrons to form only 2 per cent. of the weight of the cortex, the greater part of the cortex being composed of axis-cylinder processes and their branches. Hammerberg[4] found that a comparatively small diminution in the development of the cortical cells was sufficient to reduce the intelligence to moderate imbecility. As the total weight of these cells is relatively so small, their moderate diminution would not reduce the brain-weight beyond a very moderate range of variation.

[1] For further discussion of the proportion of stature to brain-weight, the reader is referred to a paper by Le Bon in the Revue d'Anthropol. 1879, and to one by J. Marshall in the Jour. of Anat. and Phys. July, 1892.

[2] Phil. Trans. 1868.

[3] Journ. Comp. Neurology, ix. 1899.

[4] Studien über Klinik und Pathologie der Idiotie nebst Untersuchungen über die normale Anatomie der Hirnrinde; Upsala, 1895.

CRANIO-CEREBRAL TOPOGRAPHY.

A. RELATION OF THE BRAIN TO THE INNER SURFACE OF THE CRANIUM.

The parts of the brain which, covered by the meninges, lie in more or less intimate relation with the inner surface of the cranium are the medulla oblongata, the pons, the cerebellum, and the cerebral hemispheres.

The anterior surface of the medulla oblongata and pons lies behind the occipital and sphenoid bones from the foramen magnum to the upper border of the dorsum sellæ, separated, however, by the vertebral and basilar arteries, portions of the hinder eight cerebral nerves and a variable amount of cerebrospinal fluid. At the sides and behind, the medulla oblongata and pons are separated from the cranial wall by the cerebellum.

The convex portion of the inferior aspect of the lateral lobe of the cerebellum lies in the cerebellar fossa formed mainly by the occipital bone, but completed externally by the mastoid portion of the temporal. Internal to this fossa the cerebellum is grooved by the ridge of bone separating the posterior half of the foramen magnum from the cerebellar fossa, and internal to this groove the lateral lobe projects downwards into the foramen magnum. Each lateral lobe of the cerebellum is in close proximity anteriorly with the skull over an area on the posterior aspect of the petrous portion of the temporal bone bounded above by the superior petrosal sinus, below by the transverse sinus, and internally by the internal auditory meatus and jugular foramen.

As a rule the convolutions and fissures of the basal portions of the cerebral hemispheres are more closely moulded to the inner surface of the cranial wall than is the case at the vault, so that the juga cerebralia and impressiones digitatæ are very distinct in the anterior and middle cranial fossæ, while on the roof they are feebly developed and the convolutions are separated from the bone and dura mater by numerous veins, the Pacchionian bodies, and a much larger amount of cerebrospinal fluid than at the base.

In the anterior fossa the concave orbital surface of the frontal lobe is closely applied to the convex aspect of the orbital plate of the frontal bone; the digital impressions are always well marked and correspond generally to the convolutions in relation to the orbital sulcus. Internal to the roof of the orbit the frontal lobe dips down towards the cribriform plate of the ethmoid and is separated merely by thin plates of bone from the subjacent frontal, ethmoidal, and sphenoidal air-sinuses. The pole of the superior frontal convolution, the gyrus rectus, and a strip of the cortex external to it and of about the same breadth are the portions of the frontal lobe in relation with the upper accessory nasal sinuses (G. Killian).

The lateral portion of the squama of the frontal bone which enters into the formation of the temporal fossa shows on its inner aspect a well-marked depression lodging part of the inferior frontal convolution.

The free border of the lesser wing of the sphenoid dips into the deep groove between the frontal and temporal lobes and occasionally indents the under surface of the frontal lobe so as to form the anterior boundary of the so-called post-orbital limbus.[1] The external part of this border is continuous with a ridge on the lateral wall of the skull termed by Schwalbe[2] the crista Sylvii, since it projects into the lateral aspect of the stem of the Sylvian fissure and the commencement of its posterior branch. Below the crista Sylvii the middle fossa of the skull usually exhibits well-marked depressions for the lodgment of

[1] Spitzka, E. A., Philadelphia Medical Journal, April 1903.

[2] Deutsches Archiv für klinische Medicin, Bd. lxxiii. 1902, and Zeitschrift für Morphologie und Anthropologie, Bd. x. 1906.

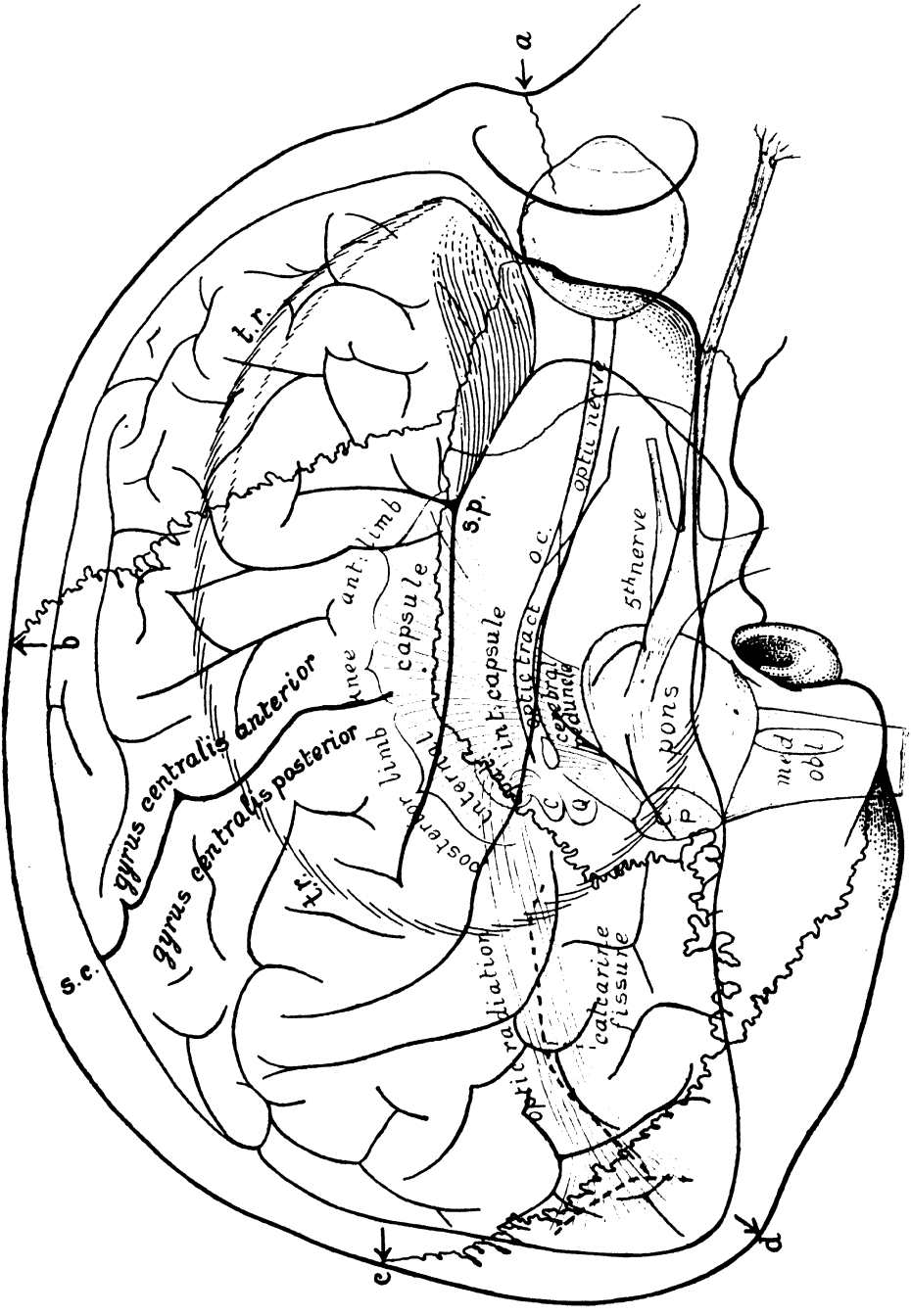


FIG. 316.—RIGHT LATERAL ASPECT OF THE SKULL AND CEREBRAL HEMISPHERE OUTLINED IN BLACK, WITH ORTHOGONAL PROJECTION OF THE MEDULLA OBLONGATA, PONS, MID-BRAIN, INTERNAL CAPSULE, VISUAL TRACTS, AND FIFTH CEREBRAL NERVE IN RED. MAN AGED FIFTY-SIX YEARS. Cephalic index, 70. (J. Symington.)

a, nasion; *b*, bregma; *c*, lambda; *d*, inion; *t.r.*, temporal ridge; *s.c.*, sulcus centralis; *s.p.*, Sylvian point.

the temporal convolutions. The groove for the first temporal convolution lies mainly on the parietal bone, and that for the second temporal is bounded above by a ridge along the inner part of the squamous suture. A small part of the third temporal looks outwards, but the greater portion is on the inferior aspect of the temporal lobe and is closely related to the ear. It rests on the inner part of the roof of the external auditory meatus and the thin tegmentum tympani and is grooved by the prominence on the petrous bone due to the superior semicircular canal. Between this eminence and the groove for the fifth nerve the fourth temporal convolution is found on the pars petrosa. The cerebral convolutions cease to be in close relation to the bones forming the middle fossa of the base of the skull internal to a line uniting the inner end of the sphenoid fissure with the external border of the foramen ovale. This separation of skull and brain is due to the presence of the cavernous sinus and the various structures in its walls. The hippocampal gyrus is in contact with the dura mater forming the lateral wall of this sinus. Behind the upper border of the petrous bone the under surface of the temporal lobe rests on the tentorium cerebelli, and the brain is here much smoother than in front, where it is moulded to the inequalities of the middle cranial fossa.

There are several more or less well-marked depressions on the inner surface of the cranial wall which receive prominent parts of the cerebral hemispheres. Thus the frontal, temporal, and occipital poles lie against the frontal, sphenoidal, and occipital bones, and the most prominent part of the parietal lobe is opposite the parietal fossa on the inner surface of the parietal bone. The cerebral fossæ of the occipital bone are unequal in size, and as the superior sagittal sinus usually inclines to the right to end in the right transverse sinus, the left cerebral fossa is generally larger than the right one. With the exception of the Sylvian, none of the interlobular fissures are associated with corresponding prominences of the cranial wall, but on the inner aspects of the coronal and lambdoidal sutures there are slight ridges which may groove the cerebral hemispheres.

B. RELATION OF THE BRAIN TO THE OUTER SURFACE OF THE CRANIUM.

The cranial wall corresponds in its general form to that of the contained brain, but in various situations the shape of the outer aspect of the skull has been modified by the development of special-sense capsules, of air-sinuses and of prominences for the attachment of muscles, producing a want of congruity between the two surfaces of the skull. In a few places, however, there is a close congruity between the skull and brain, so that depressions or elevations of the brain are associated with corresponding depressions and elevations on the external surface of the skull. The best examples of this condition are found in the temporal fossa, where the skull is covered by the temporal muscle. On the outer surface of the great wing of the sphenoid there is always a distinct depression, which is prolonged upwards and backwards across the pterion on to the lateral part of the parietal bone. This groove marks the anterior limit of the temporal lobe, the stem and the anterior part of the posterior limb of the Sylvian fissure, and is termed by Schwalbe the *sulcus spheno-parietalis*. Below this groove the squamous portion of the temporal is more or less distinctly marked by prominences opposite the first, second, and third temporal convolutions, and above it on the temporal aspect of the frontal bone there is almost invariably a rounded prominence which is directly superficial to the inferior frontal convolution.

The *medulla oblongata* is situated about two inches internal to the external surface of the mastoid portion of the temporal bone. It lies just behind the

plane of the external auditory meatus, and its upper border is on about the same level as the roof of the meatus. The pons extends upwards for about an inch above the level of the external meatus and bulges forwards so that it reaches the plane of the anterior wall of the meatus. Its upper three-fourths is separated from the lateral wall of the skull by the temporal lobes.

The upper part of the *cerebellum* is separated from the cranial wall by the tentorium cerebelli, the posterior part of the cerebral hemispheres, and the transverse sinus. Below the sinus its inferior aspect lying in the cerebellar fossa is close to the skull-wall over an area which looks to a considerable extent downwards, gives attachment to numerous muscles, and is pierced by the mastoid vein and crossed by the occipital artery. The transverse sinus may occasionally have a lower position than normal, and it is advisable, therefore, in operations upon the cerebellum that the opening in the bone should be kept at least 1 cm. (half an inch) below the level of a line drawn from the external occipital protuberance to the centre of the external auditory meatus, while at the same time it should not extend farther forwards than a vertical line (one and a-half inches) behind the latter spot (G. D. Thane).

Extent of the cerebral hemisphere.—The superior mesial border of the cerebral hemisphere extends from the nasion, or fronto-nasial suture, backwards nearly to the external occipital protuberance.

It does not quite reach the middle line, being separated from its fellow by an interval which corresponds to the superior sagittal (longitudinal) sinus, and, like that, increases in breadth posteriorly, where it measures fully 1 cm. Owing to the lateral deviation of the sinus, the margin of the hemisphere commonly approaches nearer to the middle line on the left side than on the right. Below the sinus the mesial surfaces of the two hemispheres are nearly in contact, being separated only by the thickness of the falx cerebri. Inferiorly, the cerebral hemisphere reaches in front nearly to the eyebrow, at the side to the upper margin of the zygoma, and behind to the superior curved line of the occipital bone. The lower limit of the hemisphere is more precisely indicated by marking out its lateral margin, which consists of two parts—frontal and occipito-temporal. The frontal part begins internally at the nasion (which is felt at the bottom of the depression below the glabella), and about 1 cm. from the median plane it rises rapidly in an arch as it passes outwards, being about 8 mm. above the centre of the supra-orbital margin of the frontal bone. External to this point it descends slightly and crosses the temporal line just below the deepest part of the hollow formed by the frontal bone immediately above the external angular process. From the temporal line the frontal margin passes backwards and slightly downwards along the fore part of the temporal fossa to a spot 25 mm. to 30 mm. behind the external angular process, where it meets the temporal margin in a receding angle which corresponds to the stem of the Sylvian fissure. It is at first separated from the lateral margin of the temporal lobe by a broad groove, which gradually narrows as the margins approach one another. The occipito-temporal division of the lateral margin begins posteriorly at the occipital pole of the hemisphere, which is placed 5 mm. to 15 mm. above and outside the external occipital protuberance, and passes forwards in a nearly horizontal direction, but having a slight curve with its convexity upwards, towards the back of the ear. It then crosses the supramastoid ridge and is continued forwards about 6 mm. (varying from 3 mm. to 9 mm.) above the roof of the external auditory meatus, and then on a level with or a little below the upper border of the zygomatic arch for about the posterior half of its length. Then curving gradually upwards, the border reaches its foremost point, corresponding to the temporal pole of the hemisphere, about 20 mm. above the zygoma and 15 mm. behind the external

angular process, and finally turns backwards and upwards to meet the end of the frontal margin somewhat anterior to the Sylvian point.

Relations of the cerebral fissures and convolutions to the cranial wall.—The division of the stem of the Sylvian fissure is situated in the region of the pterion, usually near the posterior end of the spheno-parietal suture. From this, the Sylvian point, the posterior limb of the fissure runs backwards and somewhat upwards, at first following the line of the squamous suture, and then crossing the temporal area of the parietal bone, to end near the temporal ridge and beneath the parietal eminence. In the child the posterior limb of the fissure is distinctly above the line of the squamous suture. The position in relation to the skull of the anterior branches of the Sylvian fissure will vary according to the development of the intermediate frontal operculum. If this extends downwards so as almost entirely to separate the two branches, the horizontal branch will pass forwards close to the spheno-parietal suture and the ascending upwards about 1 cm. behind the coronal suture. The parieto-occipital fissure is placed opposite the lambda, or often rather above that point, especially in young subjects. The central fissure is wholly beneath the parietal bone, its upper end being from 4 to 5 cm., and its lower end about 3 cm., behind the coronal suture. The superior precentral sulcus is from 2 to 3 cm. behind the upper part of the coronal suture; and the inferior precentral sulcus is a short distance (1 to 2 cm.) behind the lower part of the same suture. The inferior frontal sulcus about corresponds to the stephanion and the temporal crest of the frontal bone. The intra-parietal fissure is very variable in position: its ascending or postcentral portions are approximately parallel to and about 15 mm. behind the central fissure; while its longitudinal portion runs backwards, with a slight inclination inwards, just above the parietal eminence, and at an average distance of 45 mm. from the median line anteriorly, 35 mm. posteriorly, opposite the lambda. The parallel fissure lies mainly beneath the upper part of the squamous and the hinder part of the temporal area of the parietal bone, but its posterior end crosses the temporal lines and runs upwards for a short distance in the parietal lobe of the hemisphere under the superior division of the parietal bone; its position in the temporal part of its extent is indicated approximately by a line drawn from the marginal tubercle of the malar bone to the lambda. In the child, owing in great measure to the relatively small size of the squamous part of the temporal bone, the parallel fissure appears to be placed much higher, often reaching the level of the squamous suture.

From the foregoing determination of the situation of the central fissure and precentral sulci, it follows that the anterior central and the bases of the upper, middle, and lower frontal convolutions are placed beneath the anterior third of the parietal bone. The main parts of the superior and middle frontal convolutions correspond to the frontal region of the frontal bone, and of this area the superior frontal convolution may be said to occupy rather less than the inner half, and the middle frontal convolution rather more than the outer half. The centre of the frontal eminence is commonly over the middle convolution. The apex of the pars triangularis of the inferior frontal convolution corresponds to the antero-inferior angle of the parietal bone; and the pars orbitalis is covered by the temporal division of the frontal bone and the upper end of the great wing of the sphenoid. The whole of the parietal lobe is under cover of the parietal bone, the parietal eminence corresponding to some part of the supramarginal convolution; while the occipital lobe occupies the cerebral division of the occipital bone, and sometimes extends slightly beneath the adjacent part of the parietal bone. The temporal lobe lies for the most part beneath the squamous division of the temporal bone and the postero-inferior fourth of the parietal bone, its superior

convolution being marked off from the rest by the line given above for the parallel fissure; but the anterior extremity of this lobe projects under the great wing of the sphenoid, while posteriorly the third temporal convolution is prolonged beneath the occipital bone to the occipital pole of the hemisphere.

Determination of the principal fissures on the surface of the head.—If a median line be drawn over the head from the nasion (centre of the naso-frontal suture) to the inion (external occipital protuberance), a point 1 cm. (or half an inch) behind the centre of this line will indicate with sufficient accuracy the spot where the fissure of Rolando meets the upper border of the hemisphere, and may be termed the *superior Rolandic point.* From 8 to 10 cm. farther back the lambda may be felt, or, if that is not possible, a point should be taken on the nasio-inial line 6·5 cm. (or $2\frac{1}{2}$ inches) above the inion, and a line carried transversely outwards for a distance of 2 cm. from this spot will mark the parieto-occipital fissure.

On the side of the head, a line from the lowest point of the infra-orbital margin to the upper border of the external auditory meatus is taken as the horizontal. This line is about parallel with the upper border of the zygomatic arch; and vertical lines are perpendicular to it. A spot on the base-line in the hollow between the tragus of the ear and the condyle of the lower jaw is known as the *pre-auricular point.* From the fronto-malar junction let a line be carried horizontally backwards for 35 mm., and from the end of this a vertical line for 12 mm. upwards; the upper end of the latter line marks the spot where the anterior branches are given off from the Sylvian fissure, and may be termed the *Sylvian point.* A line drawn from the fronto-malar junction through the Sylvian point to the lower part of the parietal eminence will about lie over the posterior limb of the Sylvian fissure, and may be called the *Sylvian line.* The anterior ascending and horizontal branches of the fissure may be marked by lines 2 cm. long, starting from the Sylvian point, the one directed upwards and forwards at right-angles with the Sylvian line, and the other horizontally forwards.

On the Sylvian line, 25 mm. behind the Sylvian point, is the *lower Rolandic point,* the spot where the fissure of Rolando, if prolonged, would meet the Sylvian line. The lower Rolandic point is about 5·5 cm. (varying from 4 to 7) above the upper border of the zygomatic arch, on or slightly in front of a vertical line passing through the pre-auricular point. The *Rolandic line* may now be drawn between the upper and lower Rolandic points, and gives the general direction of the fissure of Rolando. The line forms an angle (the *Rolandic angle*) anteriorly with the median line of about 70° (varying in individual cases from 64° to 75°); and if prolonged downwards it crosses the zygomatic arch about the middle (Le Fort). The fissure of Rolando is not quite so long as the Rolandic line, since the margin of the hemisphere does not quite reach the median line above; while below, the fissure of Rolando usually ends about 1 cm. above the Sylvian fissure or lower Rolandic point. The Rolandic line coincides most nearly with the upper part of the fissure, the inferior genu of which projects somewhat in front of the line, a little below its centre, a spot which is placed from 5 to 15 mm. above the lower temporal line on the parietal bone.

The precentral sulci are situated about 15 mm. in front of the fissure of Rolando, with which they are nearly parallel; from the lower of these the inferior frontal sulcus arches forwards and downwards beneath the temporal crest of the frontal bone, which can be felt through the skin; and the position of the superior frontal sulcus may be indicated approximately by a line running forwards from the superior precentral sulcus slightly internal to the centre of the interval between the temporal crest and the median line of the forehead.

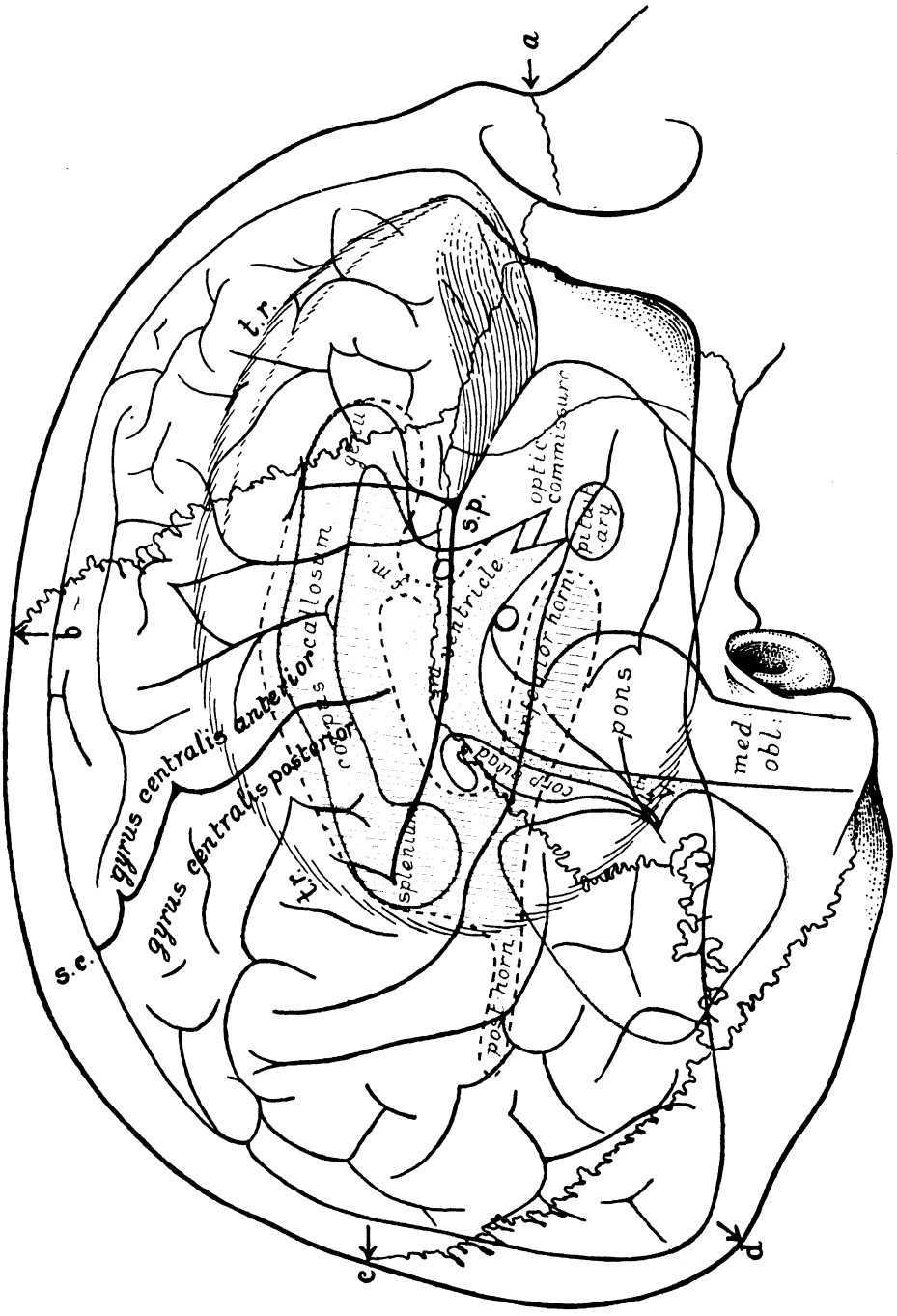


FIG. 317.—RIGHT LATERAL ASPECT OF THE SKULL AND CEREBRAL HEMISPHERE OUTLINED IN BLACK, WITH ORTHOGONAL PROJECTION OF THE STRUCTURES IN THE MEDIAN PLANE AND OF THE RIGHT LATERAL, THE THIRD AND THE FOURTH VENTRICLES IN RED. MAN AGED FIFTY-SIX YEARS. Lettering as in fig. 316. (J. Symington.)

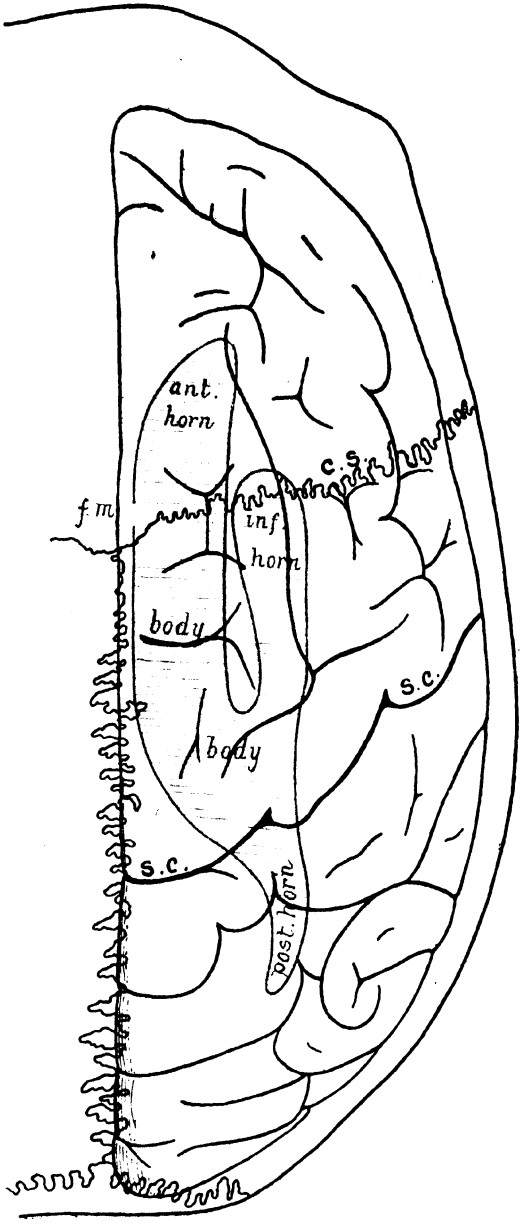


FIG. 318.—VIEW FROM ABOVE OF THE RIGHT HALF OF THE SKULL AND OF THE RIGHT CEREBRAL HEMISPHERE OUTLINED IN BLACK, WITH ORTHOGONAL PROJECTION OF THE RIGHT LATERAL VENTRICLE IN RED. From same subject as figs. 316, 317. (J. Symington.)

The postcentral sulci being also nearly parallel to, and about 15 mm. distant from, the fissure of Rolando, the average position of the longitudinal portion of the intraparietal sulcus may be marked by a line drawn from the centre of the Rolandic line to a spot 35 mm. external to the lambda, or 15 mm. from the end of the parieto-occipital line.

Lastly, the seat of the parallel fissure may be determined by the above-mentioned line from the marginal tubercle of the malar bone to the lambda.

The insula.—The pole of the insula is situated about 15 mm. internal to the Sylvian point. The insula extends forwards 10 mm. to 15 mm. in front of this point, and backwards about 35 mm. along the line of the posterior branch of the Sylvian fissure. When the insula is traced backwards from its pole it is found to recede gradually from the lateral surface of the brain, so that at its posterior angle it lies at a depth of about 25 mm. The superior surface of the insula is overlapped by the frontal and parietal lobes and its postero-inferior surface by the temporal lobe. The vertical extent of the insula in the region of its pole is about 25 mm., but behind this point it gradually diminishes.

The lateral ventricle (fig. 317).—The whole of this cavity except the posterior horn, when viewed from the lateral aspect, is situated within the area of the temporal fossa. The foramen of Monro lies a few millimètres above the level of the horizontal branch of the Sylvian fissure and above 15 mm. from its commencement. Above this opening the anterior horn reaches forwards to a little beyond the coronal suture and the body backwards to the temporal ridge, in front of which it turns downwards and ends in the inferior and posterior horns. The inferior horn follows the direction of the middle temporal convolution and ends about 30 mm. behind the temporal pole. Under normal conditions the cavity of the lateral ventricle, with the exception of the descending part of the body, is so small that on section it forms little more than a mere slit. The descending part of the body always possesses a distinct cavity. It lies internal to the superior and upper part of the middle temporal convolutions and is about 35 mm. from the surface. It might be punctured at a point 25 mm. behind and 40 mm. above the external auditory meatus.

The corpora striata, thalamus, and internal capsule are situated mainly between the insula externally and the anterior horn and anterior part of the body of the lateral ventricle and the third ventricle internally, but the thalamus and internal capsule extend farther back than the insula and the caudate nucleus higher up.

INTIMATE STRUCTURE OF THE CEREBRAL HEMISPHERES.

STRUCTURE OF THE WHITE MATTER.

The cerebral hemispheres, like the rest of the encephalon, are composed of white and grey substance, the white pervading nearly the whole of the middle of each hemisphere, where it forms what is known as the *medullary centre*, and extending into the convolutions; the grey forming a covering of some thickness over the whole surface of the convolutions (*cortex*), and occurring also at the base of the hemisphere in the form of the *corpus striatum*.

The white matter consists of medullated fibres, varying in size in different parts, but in general smaller than those of the cord and bulb. They are arranged in flattened bundles separated by neuroglia; the bundles have a somewhat rod-like appearance in transverse section.

The fibres of the medullary centre, though forming many different groups, may be referred to three principal systems (see diagram, fig. 322), according to the general course which they take—viz. 1. *Projection-fibres*, which pass from the basal ganglia and isthmus encephali to the cortex of the hemispheres, or *vice versâ*. 2. *Commissural fibres*, which pass from one hemisphere to the other. 3. *Association-fibres*, which, keeping on the same side of the middle line, pass between near or distant parts of the same hemisphere.

The **projection-fibres** in each hemisphere are continuous in part with the fibres of the pedunculus cerebri, but many extend only between the cortex and the corpus striatum and thalamus. They are of two kinds—viz. *corticifugal* or *efferent* and *corticipetal* or *afferent*. The former are direct prolongations of the axis-cylinder processes of cells of the cortex.

The efferent fibres which are continuous with those of the crusta pass through the internal capsule, between the thalamus and nucleus caudatus mesially, and the nucleus lenticularis laterally, giving off collateral fibres to those ganglia. As they pass towards the internal capsule the fibres converge from the general white matter of the hemispheres (fig. 319), forming part of the system of radiating fibres known from its fan-like arrangement as the *corona radiata* (Reil) or *fibrous cone* (Mayo), the latter term being derived from the way in which the assemblage of radiating fibres is curved round in the form of an incomplete hollow cone which follows the curve of the lateral ventricle.

Although many of the fibres of the crusta pass directly from the medullary centre and through this from the grey cortex, without entering the basal ganglia of the hemispheres, others arise in those ganglia, especially in the corpus striatum, and become in the crusta more or less intermingled with the projection-fibres from the cortex. The latter form the *pyramid-tract*, which is traceable through the internal capsule (opposite the middle of the lenticular nucleus) and corona radiata from the grey cortex of the anterior central and adjoining part of the marginal convolution, which gyri both physiological experiment and anatomical structure indicate as the source of nerve-impulses governing the action of the chief groups of muscles of the body (motor area of the cortex).

Another group of projection-fibres (afferent) is the *direct sensory tract*, which passes in the lateral part of the crusta and through the posterior part of the internal capsule towards the white matter of the occipital and temporal lobes of the hemisphere, where are situated the centres for some of the special senses.

The projection-fibres from the prefrontal region pass downwards in the anterior part of the internal capsule: they are not traceable beyond the pons. According to Horsley and Beevor[1] they cannot be traced even to the mid-brain. These

[1] Brain, 1902, p. 486.

observers further state that few fibres are traceable into the crus cerebri from the temporo-sphenoidal region, but more from the occipital region.

A few of the fibres of the crusta (those nearest the inner or mesial side) do not pass into the inner capsule and corona radiata, but are collected into the bundle known as *ansa lenticularis* (see p. 250).

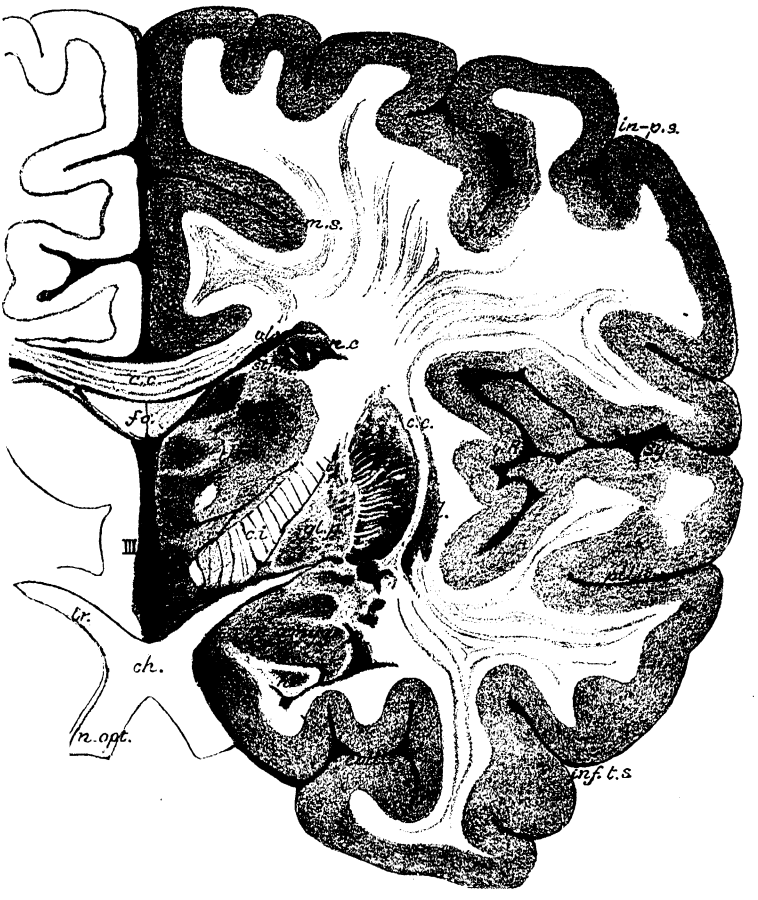


FIG. 319.—VIEW FROM BEHIND OF A CORONAL SECTION THROUGH THE RIGHT HEMISPHERE TAKEN JUST BEHIND THE OPTIC CHIASMA. (E. A. Schäfer.)

The figure shows the grey cortex and white matter (corona radiata); the internal capsule bounded by the basal ganglia; the corpus callosum; fornix; third ventricle, &c.

c.c., corpus callosum; *fo.*, body of fornix; *III.*, third ventricle; *v.l.*, lateral ventricle; *n.c.*, nucleus caudatus; *str.m.*, stria terminalis; *th.*, thalamus; *c.i.*, internal capsule; *gl.p.*, globus pallidus; *pu.*, putamen; *c.e.*, external capsule; *cl.*, claustrum; *i.R.*, insula; *n.amyg.*, nucleus amygdalæ; *h*, anterior end of hippocampus projecting into the inferior cornu of the lateral ventricle; *tr.*, optic tract; *ch.*, optic chiasma; *n.opt.*, optic nerve; *c.m.s.*, cingulate sulcus; *Ro.s.*, central sulcus; *in-p.s.*, intra-parietal sulcus; *Sy.*, Sylvian fissure; *pll.s.*, parallel fissure; *inf.t.s.*, second temporal sulcus; *coll.s.*, collateral sulcus.

The fibres which pass towards the cerebrum in the tegmentum are originally constituted by the longitudinal bundles of the formatio reticularis of the medulla oblongata (upper fillet and ascending fibres of cerebral nerves), reinforced as they pass upwards by other fibres of various origin. They become lost for the most part in the subthalamic tegmental region and in the thalamus. Other fibres

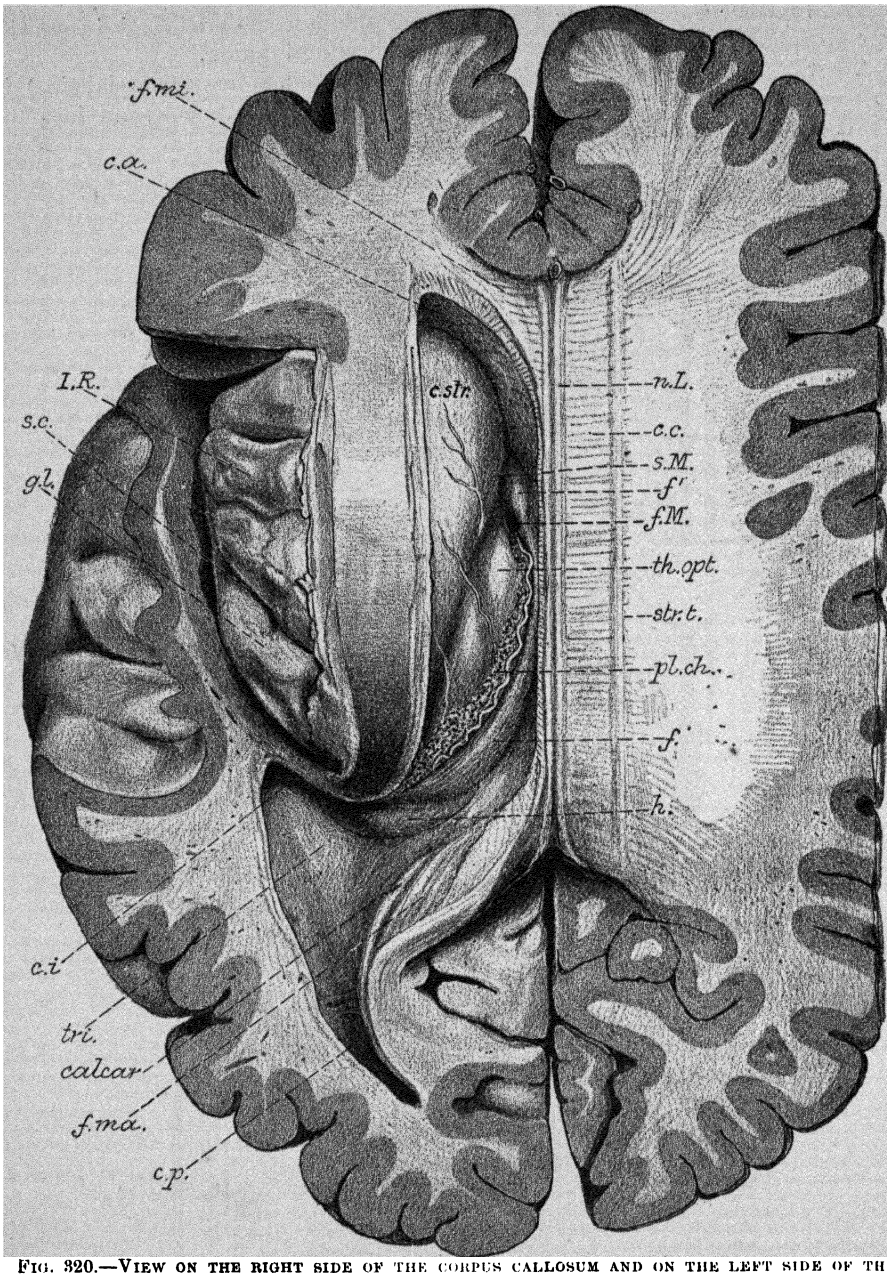


FIG. 320.—VIEW ON THE RIGHT SIDE OF THE CORPUS CALLOSUM AND ON THE LEFT SIDE OF THE LATERAL VENTRICLE FROM ABOVE. Natural size. (G. D. Thane.)

The preparation was made with the brain *in situ* (hardened). The skull cap and membranes having been removed, the brain was sliced down to the level of the corpus callosum. The left lateral ventricle was then opened by cutting away its roof, and the island exposed by slicing away the opercula. The drawing is made from a photograph.

I.R., insula (the line points to the middle of the three gyri breves); *s.c.*, sulcus centralis insulæ; *g.l.*, gyrus longus insulæ; *c.c.*, corpus callosum; *n.L.*, nerves of Lancisi; *str.t.*, stria tecta; *f.mi.*, forceps minor; *f.ma.*, forceps major; *c.a.*, cornu anterius of ventricle; *c.p.*, cornu posterius; *c.i.*, entrance to cornu inferius; *f.M.*, foramen of Monro; *s.M.*, sulcus leading backwards to the foramen of Monro; *c.str.*, corpus striatum; *th.opt.*, thalamus, anterior tubercle; *pl.ch.*, plexus choroides; *f*, fornix; *f'*, its column; *h.*, posterior end of hippocampus major; *tri.*, trigonum ventriculi; *calcar*, calcar.

pass into the posterior part of the thalamus from the optic tract. On the other hand, from the outer side of the thalamus fibres stream outwards and, joining the general system of the corona radiata, diverge to nearly every part of the hemisphere.

The **commissural fibres** which connect the hemispheres together include—(*a*) *The fibres of the corpus callosum.* (*b*) *The fibres of the anterior commissure.* (*c*) *The fibres of the psalterium.* (*d*) *The fibres of the fornix.*

The fibres of the *corpus callosum* are derived from the cells of the grey cortex, being either the direct prolongations of their axis-cylinder processes or collaterals

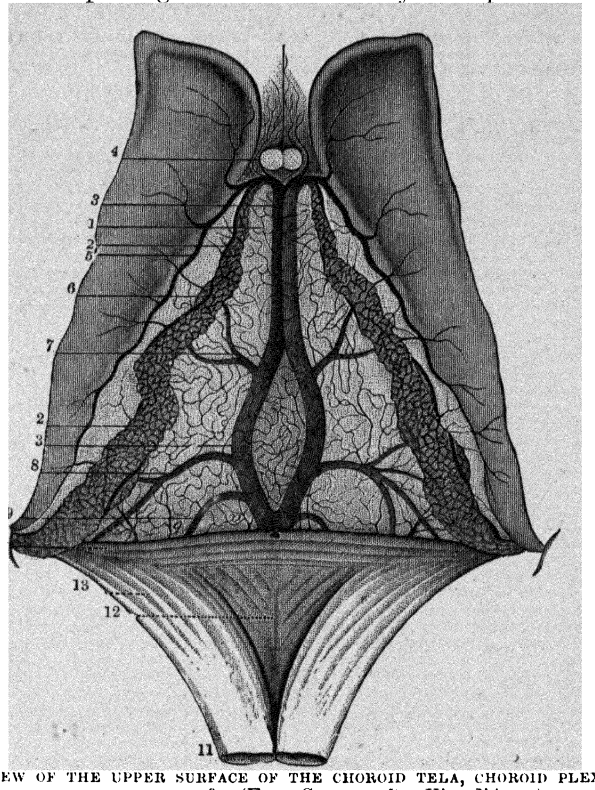


FIG. 321.—VIEW OF THE UPPER SURFACE OF THE CHOROID TELA, CHOROID PLEXUSES, AND CORPORA STRIATA. $\frac{3}{4}$. (From Sappey, after Vicq d'Azyr.)

1, fore-part of the tela choroidea or velum interpositum; 2, 2, choroid plexus; 3, 3, left vein of Galen partly covered by the right; 4, columns of the fornix divided in front of the foramen of Monro: on either side are seen small veins from the front of the corpus callosum and the septum pellucidum; 5, vein of the corpus striatum; 6, convoluted marginal vein of the choroid plexus; 7, vein rising from the thalamus and corpus striatum; 8, vein proceeding from the inferior cornu and hippocampus; 9, one from the posterior cornu; 11, fornix divided near its middle and turned backwards; 12, lyra; 13, crura of the fornix; 14, the splenium of the corpus callosum.

passing off from the projection-fibres before mentioned (fig. 322, *c*.). When, therefore, a portion of cortex is removed or destroyed, certain fibres in the corpus callosum undergo degeneration. By this means it may be determined that the anterior portions of the callosum contain chiefly fibres derived from the frontal lobes, the posterior chiefly fibres from the occipital lobes, and the middle portion from the intermediate parts of the mantle. The fibres from a localised part of the cortex are not, however, entirely limited to one part of the callosum, but show a tendency to scatter, so that not only similar but also dissimilar parts of the two hemispheres are connected through this commissure (Sherrington). A certain

number of projection-fibres also pass across the callosum to the other hemisphere, and then turn downwards in the internal capsule (Hamilton). Their presence accounts for the few fibres which are seen degenerated in the internal capsule and supra-bulbar pyramid-bundles on the side opposite to a lesion of the motor cortex of one hemisphere.[1]

The *anterior commissure* is a bundle of transverse fibres, which passes between the anterior part of the temporal lobes of the two hemispheres. The bundle is most compact in the middle line, which it crosses at the front of the third ventricle just in front of the columns of the fornix; in a median section of the brain it shows an oval section of 5 mm. long diameter, with its long axis from above down. From this point it passes laterally as a twisted bundle of fibres curving backwards and somewhat downwards through the ventral part of the globus pallidus, and below the putamen of the lenticular nucleus. Its fibres then diverge in a fan-like manner into the temporal region of the cortex.

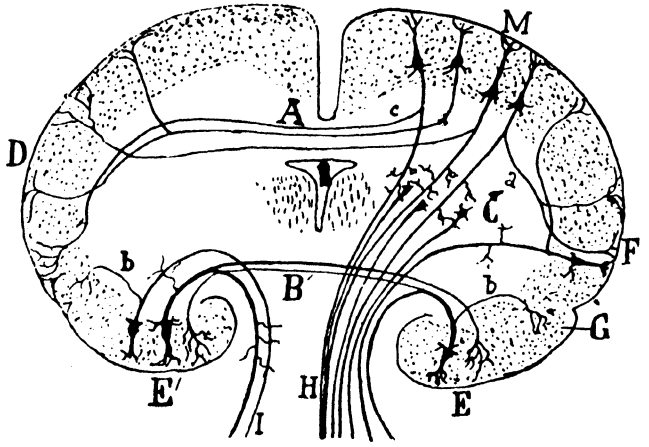


FIG. 322.—DIAGRAM OF ASSOCIATION, COMMISSURAL, AND PROJECTION FIBRES OF BRAIN. (Adapted from Cajal.)

A, corpus callosum; B, anterior commissure; C, basal ganglia; D, endings of commissural fibres; E, sensory cortex; M, motor cortex; F, endings of association-fibres from motor cortex (collaterals of projection-fibres); G, ending of association-fibres from sensory centre; H, projection-fibres from motor cortex passing to spinal centres; I, projection-fibres from sensory cortex; *a*, *b*, *c*, collaterals.

The anterior commissure not only contains many fibres which pass between the two hippocampal regions constituting what has been termed by Ganser the *pars temporalis*, but also others which are derived from the lobus olfactorius, and which connect the olfactory tract of one side with the hippocampal region of the opposite side. These form the *pars olfactoria* of Ganser: this part is very slightly developed in man.

The anterior commissure forms the segment of a circle, with the convexity directed forwards.

The rope-like twist of the anterior commissure is associated by A. Hill with a rotation of the cerebrum, which has occurred in the course of its development (Appendix A to English translation of Obersteiner's 'Anatomy of the Central Nervous Organs').

The *psalterium* contains transversely disposed fibres which belong to the same system as those of the pars temporalis of the anterior commissure. They pass between the hippocampi of opposite sides.

[1] See Sutherland Simpson Int. Monthly Journ. Anat. and Physiol. 1902.

The *fornix* is also composed of fibres which arise in the hippocampal region, and after pursuing a more or less antero-posterior course enter the nuclei of the corpus mamillare. In many animals the majority cross the middle line and end in the corpus mamillare of the opposite side. These last three commissural tracts (anterior commissure, psalterium, and fornix) belong mainly to the olfactory region of the hemisphere (rhinencephalon), and will be further noticed in dealing with that part.

The **association-fibres** which pass between different parts of the same hemisphere are either short or long. The *short association-fibres* (*fibræ propriæ*, Meynert; *laminæ arcuatæ gyrorum*, Arnold) (fig. 322, *a*, *b*; fig. 323, *s.*) serve to connect adjacent convolutions, passing round below the grey matter at the bottom of the fissures. The *long association-fibres* are mostly collected into

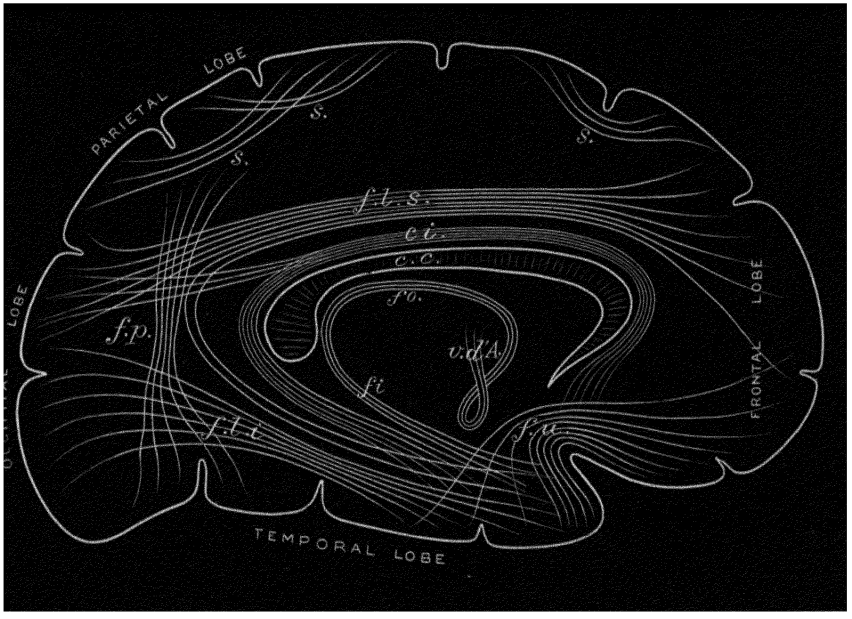


FIG. 323.—DIAGRAM TO SHOW THE GENERAL COURSE OF THE ASSOCIATION-FIBRES OF THE CEREBRAL HEMISPHERE. (E. A. Schäfer, after Meynert.)

s., short association-fibres, connecting adjacent gyri; *f.l.s.*, fasciculus longitudinalis superior; *ci.*, cingulum; *f.p.*, fasciculus perpendicularis; *f.l.i.*, fasciculus longitudinalis inferior; *f.u.*, fasciculus uncinatus; *fo.*, fornix; *fi.*, fimbria; *v.d'A.*, bundle of Vicq d'Azyr.

definite bundles, which can be traced for a considerable distance between the bundles of commissural and projection fibres, or which run free for a certain part of their course. The principal bundles or tracts of long association-fibres are the following:

(*a*) *Superior association-bundle* (*superior longitudinal fasciculus*, *fasciculus arcuatus*, Burdach).—This consists of sagittal fibres which run below the grey matter of the convex surface of the hemisphere, between the frontal and occipital lobes, and between the external part of the temporal lobe and frontal lobe (fig. 323, *f.l.s.*).

Mott states[1] that these fibres, without doubt, arise from the large pyramidal cells of the visuo-psychic area of the occipital lobe.

[1] Archives of Neurology, vol. i. p. 41.

(*b*) *Inferior association-bundle* (*temporo-occipital bundle, inferior longitudinal fasciculus*).—This is a bundle of fibres which lies close to the outer wall of the posterior and inferior cornua of the lateral ventricle and is usually stated to connect the temporal and occipital lobes (*f.l.i.*). But according to Redlich [1] and La Salle-Archambault [2] its fibres are projection-fibres and not association-fibres.

(*c*) *Anterior association-bundle* (*uncinate fasciculus*).—Under this name is described a white bundle, seen on the lower aspect of the hemisphere, passing across the bottom of the Sylvian fissure at the limen insulæ, and connecting the frontal with the temporal lobe (*f.u.*). The fibres of this bundle expand at each extremity, and the more superficial of them are curved or hooked sharply between the contiguous parts of the two lobes—from which circumstance it has derived the name uncinate. Its fibres appear especially to connect the third frontal gyrus with the temporal lobe and with the anterior part of the limbic lobe.

(*d*) *Cingulum* (*ci.*).—This forms the principal association-bundle of the gyrus fornicatus, its fibres coursing immediately above the transverse fibres of the corpus callosum, from the anterior perforated space in front, round the splenium of the callosum behind, and in the gyrus hippocampi as far as its anterior extremity. Some of the fibres diverge, as they pass backwards, into the white matter of the hemisphere; these may be projection-fibres. The constitution of this bundle and its connexions have already been dealt with and will again be referred to (see p. 398).

(*e*) The *perpendicular fasciculus* (Wernicke), which runs vertically immediately in front of the occipital lobe and connects the inferior parietal lobule with the fusiform lobule (*f.p.*). According to La Salle-Archambault,[3] some of its fibres pass also to the temporal lobe.

In most cases it is not yet possible to say at which end of an association-bundle is to be found the origin and at which the termination of its fibres, and it may be that some of the bundles which have been described as composed of association-fibres really contain projection-fibres, not continuous throughout, but turning towards the basal ganglia (see above, 'inferior association bundle').

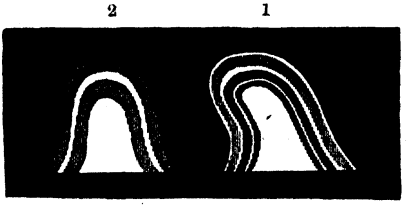


FIG. 324. — SECTIONS OF CEREBRAL CONVOLUTIONS. (After Baillarger.)

The parts are nearly of the natural size. 1, shows the layers seen in many parts of the cerebral cortex when carefully examined with the naked eye; 2, the appearance of a section of a convolution from the neighbourhood of the calcarine fissure, with the conspicuous white line of Gennari.

STRUCTURE OF THE CORTEX CEREBRI.

The grey matter on the convoluted surface of the cerebrum forms a continuous layer indistinctly divided into strata by interposed thin layers of paler substance.

On examining a section macroscopically (fig. 324, 1; fig. 335) we meet from without inwards—1. A thin coating of white matter, which in section appears as a faint white line, bounding the grey surface externally: it may be indistinct. This *superficial white layer* is not equally thick over all parts of the cortical substance, but becomes thicker as it approaches the borders of the convoluted surface; it is accordingly less conspicuous, or even indistinguishable, on some parts of the lateral convex aspect of the hemispheres, but is plainly visible on

[1] Arb. a. d. Neur. Instit. Wien, x. 1905. [2] Nouv. Iconogr. d. l. Salpêtrière, 1906.
[3] *Op. cit.*

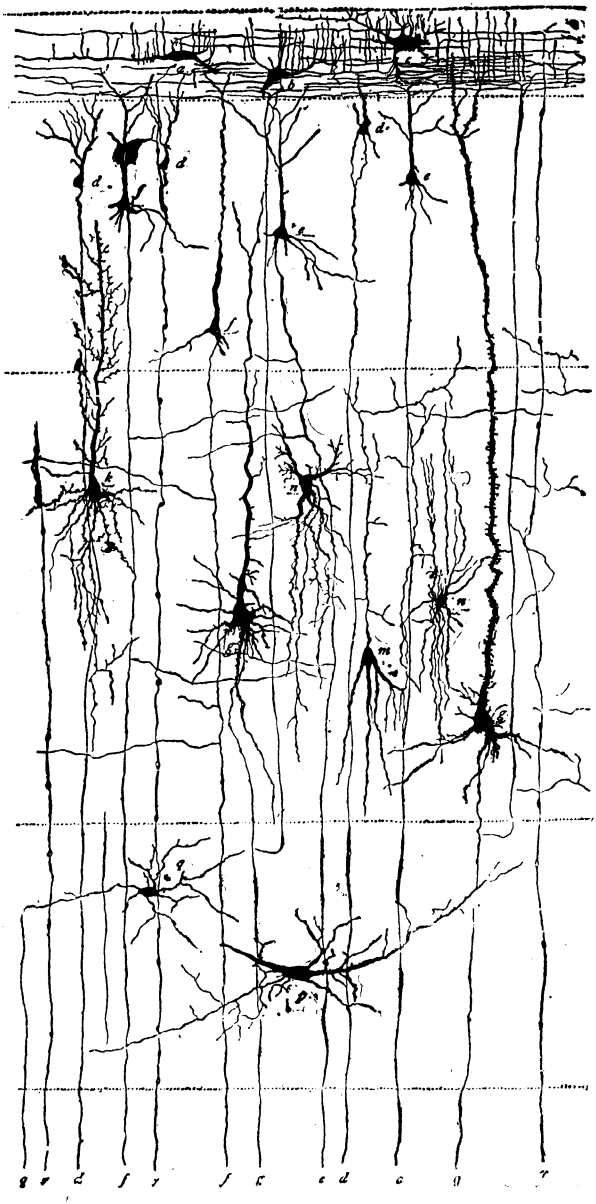


FIG. 325.—DIAGRAM SHOWING THE MOST COMMON TYPES OF CELLS OF THE CEREBRAL CORTEX. (From Barker's 'Nervous System,' after Starr, Strong, and Leaming.)

a, *b*, *c*, cells of Cajal in plexiform layer; *d*, *e*, small pyramids; *f*, medium pyramids; *g*, *g*, large pyramids, with axons passing to white matter but sending collaterals towards surface; *k*, *m*, *n*, cells of Golgi's type ii., with short axons; *m*, a cell sending its axon towards the more superficial layers; *p*, *q*, polymorph cells with descending axons; *r*, *r*, afferent fibres passing into cortex from white matter.

the convolutions situated in the longitudinal fissure which approach the white surface of the corpus callosum, and on those of the under surface of the brain. It is especially well marked on the hippocampal gyrus and subiculum, and it has been there described under the name of the *reticulated white substance*. 2. Immediately beneath the white layer just described is found a layer of grey or reddish-grey matter (*superficial grey layer*), the colour of which, as indeed of the grey substance generally, is deeper or lighter according as its very numerous vessels contain much or little blood. 3. A layer, appearing in section as a thin whitish line (*outer line of Baillarger*). 4. A second grey stratum (*middle grey layer*). 5. A second thin whitish layer (*inner layer of Baillarger*). 6. A yellowish-grey layer which lies next to the central white matter of the convolution (*deep grey layer*).

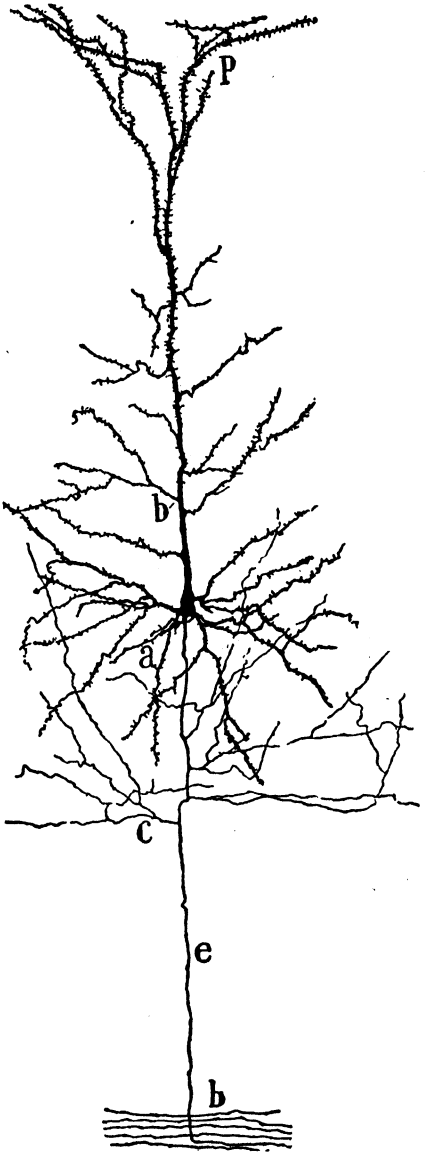


FIG. 326.—A PYRAMIDAL CELL OF THE CORTEX CEREBRI OF THE MOUSE. (Cajal.)

a, basal dendrons; *p*, apical dendron ramifying near surface; *e*, axon; *c*, its collaterals; *b*, fibres of white matter of brain.

In the convolutions bordering on the calcarine fissure the outer line of Baillarger (here known as the *line of Gennari*) is very distinct, but the inner line of Baillarger is not visible (fig. 324, 2). In certain other situations also only a single white line is visible (see fig. 335).

Medullated fibres radiate from the white centre of each convolution in all directions into the grey cortex, having a course for the most part perpendicular to the free surface. In passing through the grey substance they are arranged in bundles, and separate the nerve-cells into elongated groups, giving the section a streaked appearance (figs. 338, 341). The direction of the fibres varies according to the part of the convolution in which they occur, whether near the summit or the base, and the radiating direction is somewhat lost in the sulci between the convolutions, where arched fibres which connect the adjacent convolutions tend to obscure the radiating bundles.

Cells.—The cells of the cortex may be grouped under several heads:

1. Most numerous are the *pyramids* (figs. 325, 326), which are classified according to relative size as small, medium, large, and 'giant.' They have a conical or pyramidal cell-body, from the base of which a single axon, provided with several collaterals which ramify in the adjacent grey matter, extends towards the white matter. The dendrons are

of two kinds—viz. those which pass off from the base and sides of the pyramid, and the single large apical dendron. The former are relatively simple, ending in the grey matter not far from the cell-body. The apical dendron is large

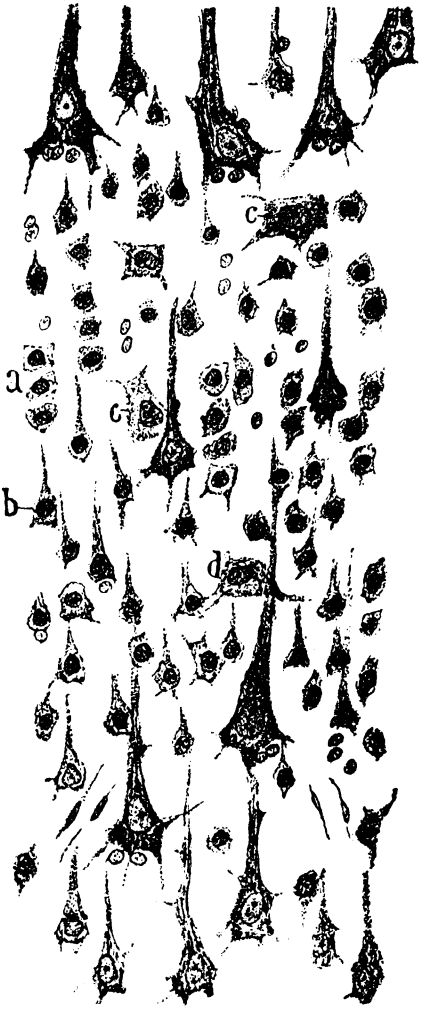


FIG. 328.—SECTION OF PART OF THE THICKNESS OF THE POST-CENTRAL GYRUS OF MAN, SHOWING THE LAYER OF GRANULES WHICH SEPARATES THE LARGE PYRAMIDS INTO TWO ZONES, SUPERFICIAL AND DEEP. (Cajal.)

a, *b*, *c*, *d*, granules (small nerve-cells) of various size and shape, mostly stellate, but some (*b*) pyramidal.

FIG. 327.—SECTION OF POSTCENTRAL GYRUS OF MAN. Stained by Nissl's method. (Cajal.)

1, plexiform layer; 2, small pyramids; 3, medium pyramids; 4, superficial large pyramids; 5, small stellate cells (granules); 6 and 7, deep large and medium pyramids; 8, fusiform cells.

and appears as a peripheral extension of the cell-body. It varies in length with the position of the cell-body in the depth of the grey matter. In all cases it extends nearly straight to the surface, giving off only a few lateral

branches on the way. But near the surface it breaks up into a more or less spreading ramification which interlaces in the superficial layer with the branches of similar dendrons of other cells. This apical dendron is furnished throughout its course with numerous very short clavate processes, the so-called 'spines.' These, which may also occur on the basal dendrons, have been supposed to effect contact with ramifications of the cortical cells or with terminal ramifications of afferent fibres, and have been regarded as retractile in nature; but the evidence for this is not conclusive.

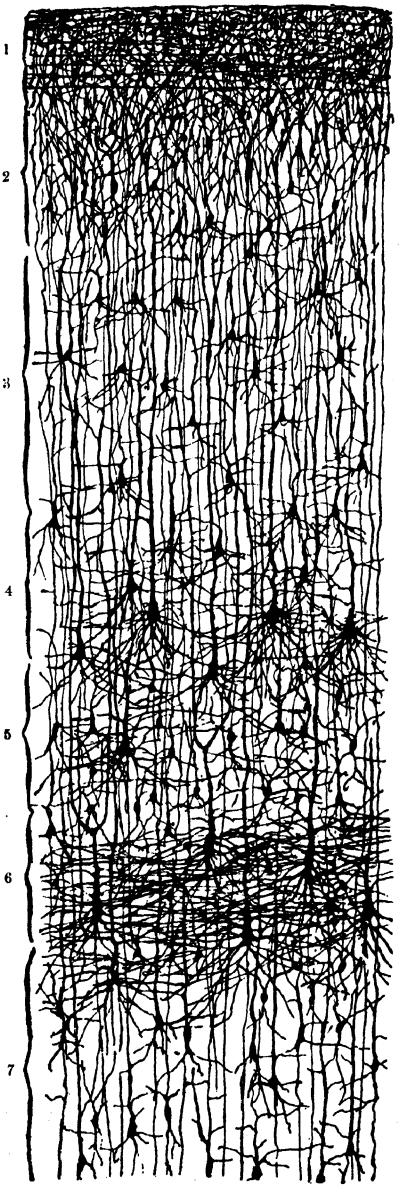


FIG. 329.—POSTCENTRAL CONVOLUTION. Golgi method. (Cajal.)

1, plexiform layer; 2, small pyramids; 3, medium pyramids; 4, superficial large pyramids; 5, granules; 6, deep large pyramids; 7, deep medium pyramids.

2. *Small stellate cells or 'granules.'*—These are short-axoned cells belonging to Golgi's type ii. (fig. 325, *k*, *m*, *n*; fig. 331, D to K). They occur in most of the strata and are very abundant in certain parts of the cortex. All have their axons ramifying near the cell-body. In some the dendrons are not specially numerous; in others they are very numerous, so that the cells have a neuroglia-cell-like aspect. In others, again, they are massed together into bunches at either end of the vertically disposed cell (brush-cells, *n*).

3. *Large stellate cells*, also short-axoned, and therefore belonging to Golgi's type ii., but with a much more voluminous cell-body, and with spreading axons and dendrons.

4. *Cells of Martinotti.*—These occur in most of the layers intermingled with the pyramid-cells, but differ from them in the fact that their axons, in place of passing downwards to the white substance, turn towards the surface and end by ramifying horizontally in the superficial layer, sending collaterals on their way into the layers they pass through.

5. *Horizontal cells of Cajal.*—These are found only in the superficial layer (figs. 325, 331). They are small and fusiform, and have long dendrons arborising horizontally and very long and large axons which form medullated fibres within the superficial layer.

6. *Polymorphous cells*, chiefly occurring in the deepest part of the grey matter They are of a fusiform or angular shape. Their axons are directed into the white matter of the hemisphere (fig. 325, *p*, *q*).

The form and arrangement of the cells met with in the cortex vary at different depths of the grey matter, and partly by these differences, partly by the strata of white fibres, several layers are differentiated, having more or less definite characters, but not sharply marked off from one another. Their relation to the stratification distinguishable by the naked eye is not everywhere obvious. A common type is that which is seen in the posterior central convolution of the parietal lobe. In this Cajal[1] distinguishes eight layers[2] as follows (figs. 327, 329):

I. *Molecular layer; plexiform layer* of Cajal.—This, the most external layer, is thin: on an average it perhaps forms about one-tenth of the thickness of the cortex. It contains many neuroglia-cells and some nerve-cells. Its medullated fibres chiefly run horizontally, and the most superficial form a thin white stratum immediately underneath the pia mater; but there are others running horizontally in the deeper parts of the layer.

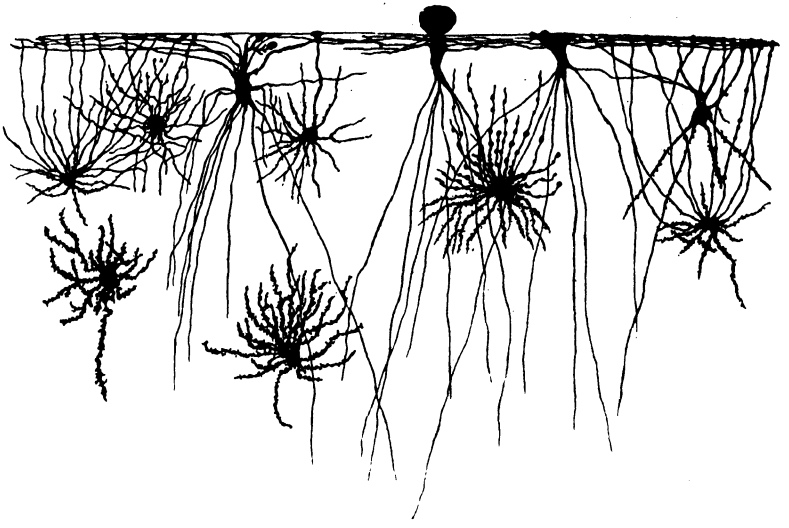


FIG. 330.—NEUROGLIA-CELLS OF CORTEX CEREBRI. Golgi method. (G. Retzius.)

The layer also contains innumerable interlacing branching fibres, which are derived from the peripherally directed processes of the pyramid-cells of the deeper layers.

The *neuroglia-cells* of the superficial layer are numerous, and many are set perpendicularly to the surface, where a principal process of each cell usually terminates in a foot or enlargement (fig. 330).

The *nerve-cells* of the layer (fig. 331) are mostly small. They are of two kinds—(*a*) with short and (*b*) with long axis-cylinder processes. The latter are for the most part fusiform and set parallel with the surface, and are hence termed *horizontal cells* by Cajal. Both their dendrons and their axis-cylinder processes, which give off numerous collateral branches, are for the most part confined to

[1] La Cellule, 1891; Textura del sistema nervioso, 1904.

[2] Vogt (Verh. d. Anat. Gesch. 1906) considers the primitive type to be six-layered, the strata being multiplied by subdivision and intercalation of other cell- and fibre-layers, or diminished by omission of certain strata. But although a six-layered cortex may be the most common, it can hardly be regarded as primitive, for in many of the lower vertebrata the layers do not exceed three in number, and a somewhat similar simple type occurs in man in the hippocampus, which has retained a more primitive type of structure than the rest of the cortex.

the layer; both dendrons and axons extend horizontally within it. The axons of these cells of Cajal are large and single—not multiple, as was at one time supposed—and extend a very considerable distance within the layer as horizontal medullated fibres, giving off vertical collaterals (fig. 325).[1]

The other cells of the plexiform layer are short-axoned cells, mostly small and with the axon ramifying near the cell-body; but others occur of somewhat larger size. They vary in shape and in the number and disposition of their dendrons.

The horizontal cells are supposed by Cajal to receive impulses from the afferent nerve-fibres of the cortex either directly or indirectly through the short-axoned cells of Golgi's type ii., and

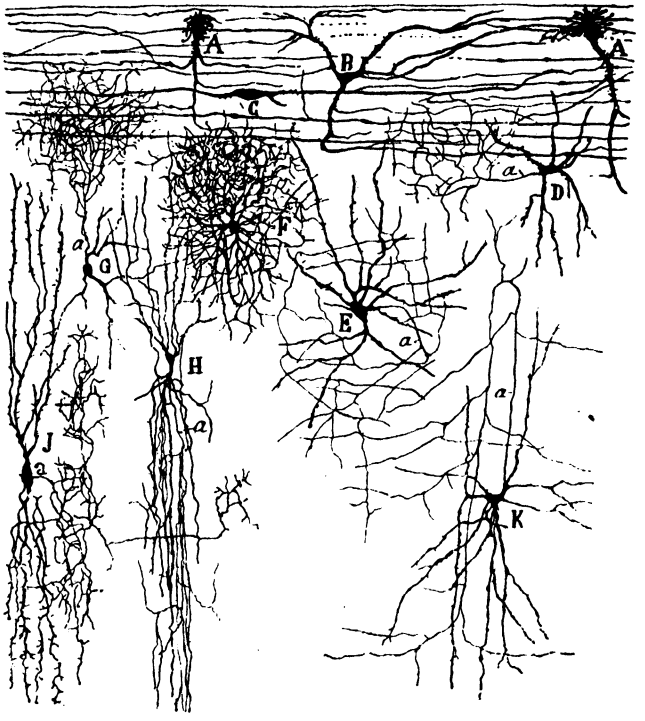


FIG. 331.—SUPERFICIAL LAYERS OF MOTOR CORTEX OF CHILD. Golgi method. (Cajal.)
A, B, C, cells of Cajal in plexiform layer; D to K, cells of type ii. of Golgi (with axons ramifying near cell-body); H, J, 'double-brush' types of cell.

to pass them on to the dendritic processes of the pyramid-cells which ramify within the layer.

The plexiform layer also has horizontal fibres which are derived from cells deeper in the cortex, which send their axons recurrently into the surface-layer (cells of Martinotti).

II. *Layer of small pyramids.*—This layer, of nearly the same thickness as the last, is characterised by containing a large number of small nerve-cells, mostly pyramidal, with dendrons extending mainly into the superficial layer, and an axis-cylinder process which starts from the base of the cell and, after giving off a few collaterals, passes downwards to the white centre, possibly to the corpus striatum, as a projection-fibre. But besides these small pyramids, which give

[1] G. Retzius, Biol. Unters. 1893.

the name to the layer, there are other types of cells, mostly of small size, but others somewhat larger, having their axis-cylinder processes ramifying near the cell-body (short-axoned cells, cells of Golgi's type ii.), and others which also belong to that type, having their dendrons prolonged vertically from either end of the somewhat elongated cell-body and breaking up into pencil-like masses, constituting the so-called 'double brush-cells' of Cajal. A few Martinotti cells are also met with in this layer.

III. *Layer of superficial medium-sized pyramids.*—This layer passes almost imperceptibly into those adjacent to it. It is characterised not only by the relative size of its pyramids (12 μ to 16 μ), but also by the fact that it contains very many small angular cells ('granules') with short and much-branched axons belonging to Golgi's type ii. and including many 'double-brush' cells. It is also the seat of the close horizontal interlacement of medullated fibres (fig. 332, B) which produces in section to the naked eye the appearance which is known as the *outer line of Baillarger.* Within it terminate many of the afferent fibres of the cortex. Its pyramid-cells send their axons into the white matter as projection or association fibres. There are also Martinotti cells, the axons of which proceed peripherally, and reaching the plexiform layer join within it the horizontally disposed medullated fibres which are characteristic of that layer. The main or apical dendrons of the cells of this layer all pass towards and into the plexiform layer.

IV. *Layer of superficial large pyramids.*—The fourth layer is of greater thickness. It contains large pyramidal cells, arranged as usual with the pointed extremities towards the surface of the cortex, and separated into groups by bundles of radiating nerve-fibres passing to and from the white matter of the hemisphere. In the innermost portion of the layer the cells are largest and the separation into groups more distinct. The axis-cylinder processes of these cells give off seven or eight collaterals, which become medullated and end by ramifying in the adjacent grey substance. The axis-cylinder is then continued on into the white matter as a medullated fibre. Like the other layers, this also has short-axoned cells of different types and also Martinotti cells scattered among the pyramids.

V. *Layer of small stellate cells or granules* (fig. 328).—The layer of superficial large pyramids is immediately succeeded by a stratum containing a large number of small multipolar short-axoned cells (*stellate cells*) belonging to Golgi's type ii., as well as small pyramids of the ordinary type, with axon passing to white layer. A few large pyramids are usually scattered in this layer also. Among the stellate cells, and also extending into the layer of superficial large pyramids, are many interlacing horizontally disposed fibres constituting the *inner line of Baillarger.* The axons of the stellate cells end either in the same layer or ascend into the third or even into the second layer. Cells of the double-brush type are not uncommon.

VI. *Layer of deep large pyramids.*—Below the last layer the large pyramids reappear. This layer seems as if separated off from the fourth layer by the interpolation of the granules. The apical dendrons of these cells are very long and stout, and extend to the plexiform layer. The basal dendrons are also spread out over a considerable area. The axon is large and passes down into the white substance, giving off several recurrent collaterals. There are also some medium-sized pyramids of the ordinary type and a number of short-axoned cells of varying character—arachniform, double-brush—as well as Martinotti cells.

VII. *Layer of deep medium-sized pyramids.*—The next layer is narrower and contains many moderately large irregular pyramids, with numerous dendrons

and a single axis-cylinder process. The axis-cylinder processes of most tend towards the white centre, but some (cells of Martinotti) pass peripherally to reach the molecular layer; here they become continuous with some of the nerve-fibres of that layer. Short-axoned cells of varying type are also met with among the pyramids.

VIII. *Layer of fusiform and angular (polymorphous) cells.*—The eighth layer, of greater width than the last and blending more or less with it, is composed of fusiform and angular cells. The fusiform corpuscles are placed for the most part vertically at the summit of a gyrus, but parallel to the surface in the sulci, where they correspond in direction to the arcuate fibres passing from one convolution to another. The cell-axons pass down towards the white matter, but, as in the other layers, there are also some cells with ascending axons, and others with short axons ramifying within this and the immediately superjacent layer.

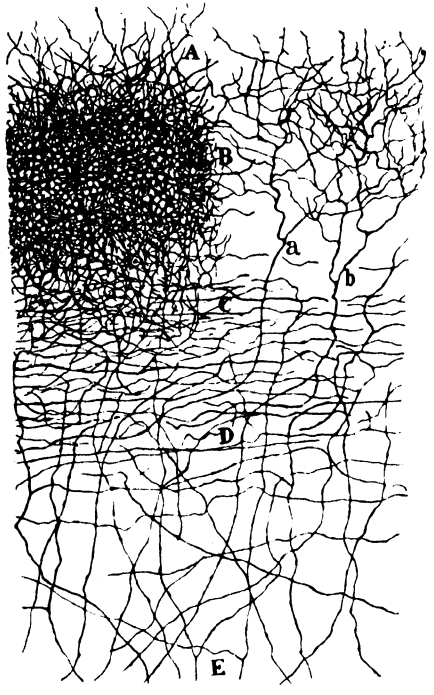


FIG. 332.—PREPARATION SHOWING SOME OF THE AFFERENT FIBRES OF THE PRECENTRAL GYRUS—HUMAN. (Cajal.)

A, part of second layer; B, layer of medium-sized pyramids with close terminal plexus; C to D, intermediate plexus of horizontal fibres; E, deep plexus of large oblique afferent fibres; *a*, *b*, afferent fibres arborising in the layer of middle pyramids, among which they form, along with fibres derived from cells in the cortex itself, the dense plexus which is shown in the left half of the figure. The efferent fibres are not shown in this figure.

Beneath the layer of polymorphous cells is the medullary centre, with which it gradually blends. The fibres of the white substance pass in bundles from and into the grey matter. The corticifugal fibres are mostly continuous with the axis-cylinder processes of the pyramidal and fusiform cells, the nerve-processes of which, when they reach the medullary centre, pass either as association-fibres to other parts of the cortex of the same hemisphere, or as commissural fibres to the corpus callosum and through this to the opposite hemisphere, or as projection-fibres to the corpus striatum and thalamus, or by way of the internal capsule to the mid-brain, bulb, and spinal cord. The junction with fibres of the association-bundles may be T-shaped; in other words, they may bifurcate and pass in opposite directions underneath the cortex. Eventually the association-fibres turn into the cortex again and end by free arborisation among its cells. Moreover, in their longitudinal course they give off collaterals here and there to intermediate parts of the cortex. The commissural fibres, after passing through the corpus callosum, course through the white matter of the opposite hemisphere, and end by collaterals and terminal arborisations in its cortex. Some of the commissural fibres are themselves collateral branches of the projection-fibres (fig. 322).

The cortex also receives a very large number of afferent corticipetal fibres, which for the most part course obliquely through the deeper layers of grey matter and end by arborising in the layers of stellate cells and large pyramids

(fifth and sixth layers), where they take part in the formation of the inner line of Baillarger; some extend into the layer of superficial medium-sized pyramids (third layer), where they form a very dense plexus around the cells, which is also contributed to by the axons of cells of Golgi's type ii. belonging to this and to adjacent layers, and by collaterals from the ascending axons of the cells of Martinotti from the deeper layers. The total effect of this mass of fibres is, as already stated, to produce the whitish line in the macroscopic appearance of the section of the fresh cortex which is known as the outer line of Baillarger (or the line of Gennari of the visual cortex). The corticipetal fibres probably originate mainly in the thalamus, but some come from other parts of the cortex itself.

In the brain of man, as compared with the lower mammals, there is a large preponderance of small nerve-cells of Golgi's type ii., especially in certain parts of the cortex.

STRUCTURE OF SPECIAL PARTS OF THE CEREBRAL CORTEX.

The results of recent researches have shown that there is a large amount of variation in the structure of the cortex in different regions. The variations manifest themselves (1) in the thickness of the grey matter, (2) in the relative number of medullated fibres passing into and away from the cortex, (3) in the number, breadth, and distinctness of the white striæ, (4) in the character of the nerve-cells, (5) in the relative time at which the medullation of the fibres occurs after birth. All these features have been employed by different observers to map out the various areas of the cortical surface, and it is found that some of the areas so mapped out correspond to areas which, on experimental grounds, have been considered to be concerned with definite functions. Adjacent areas of different structure do not, as a rule, pass by a gradual transition into one another, but the change is more or less abrupt. In many cases the line of demarcation is coincident with a cerebral fissure; but this is by no means constant, and it may, indeed, happen that the junction occurs at the convexity of a gyrus.

It is impossible within the limits of this work to give an account of the differences of structure of all the areas which have been thus variously mapped out, nor do all observers agree precisely as to the number of separate areas and as to their exact limits. It will suffice for the present to exhibit, in the form of diagrams, the results which have been obtained by three different methods, leaving it to the reader to notice the points of variation and of correspondence which are brought out in them. Figs. 333 A, and 333 B, show the areas into which Flechsig finds it possible to subdivide the surface according to the relative date of myelination of the fibres. It will be seen that altogether thirty-six areas are marked out, arranged chronologically. They form three main groups: a *primary*, which includes the areas numbered from 1 to 10; an *intermediate* group, from 11 to 31, and a *late* or *final* group, from 32 to 36. The primary areas are myelinated at or soon after birth; the intermediate do not begin to myelinate until a month after birth; and the final even later; these may not be fully myelinated eight months after birth. According to Flechsig, projection-fibres are confined almost entirely to the areas of the primary group, which includes the so-called motor cortex (precentral gyrus) and the portions of cortex which are believed to be receptive of the impressions of special sense, such as the visual (visuo-sensory, Bolton), the acoustic (audito-sensory), and the olfactory; the areas which are receptive of the impressions derived from the other special senses are not yet ascertained. The intermediate areas lie, for the most part, adjacent to the receptive; they include the areas around the visual receptive cortex corresponding with the visuo-psychic area of Bolton, those adjacent to the auditory receptive cortex (audito-psychic), and so on. The late myelinating, final or terminal, areas lie between the intermediate zones, and these two occupy the greater part of the surface of the human brain, but a much smaller proportion of the brain of lower mammals, even of Primates (except the anthropoid apes). They are regarded as being concerned with the higher functions of the brain and as being linked to the motor

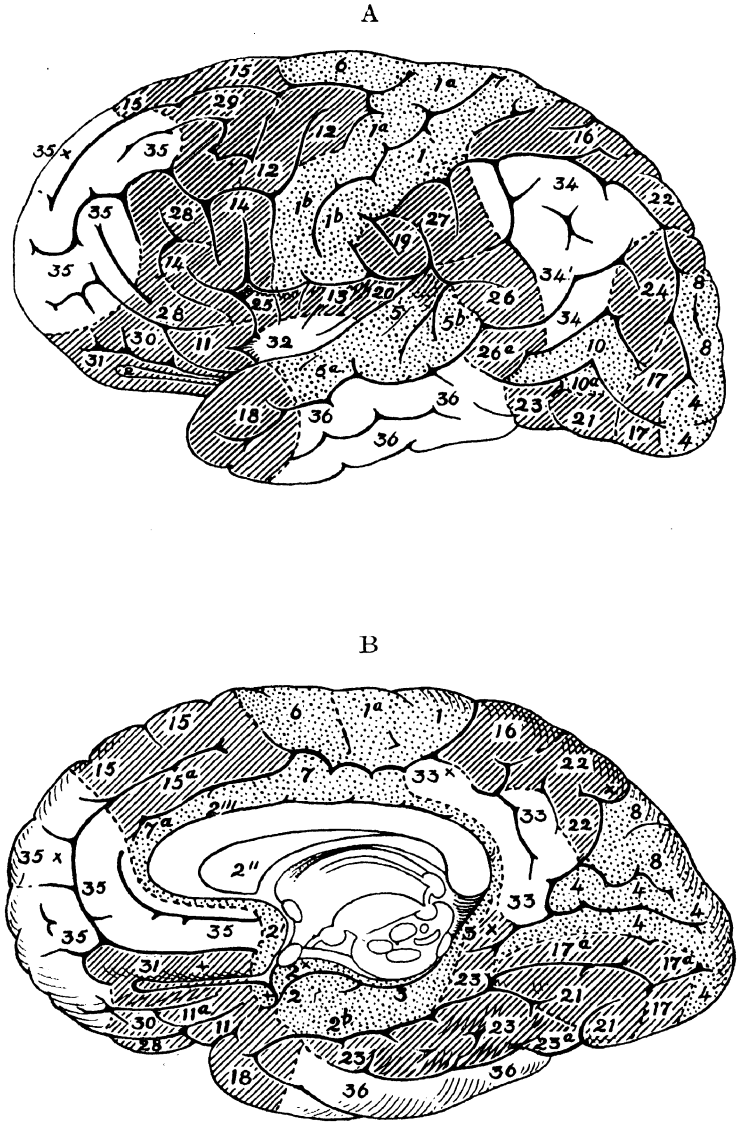


FIG. 333.—DIAGRAMS OF CORTICAL AREAS AS DETERMINED BY THE MYELOGENETIC METHOD. (Flechsig.)

A, external surface; B, mesial surface.

The numerals indicate, in a general manner, the order of myelination.

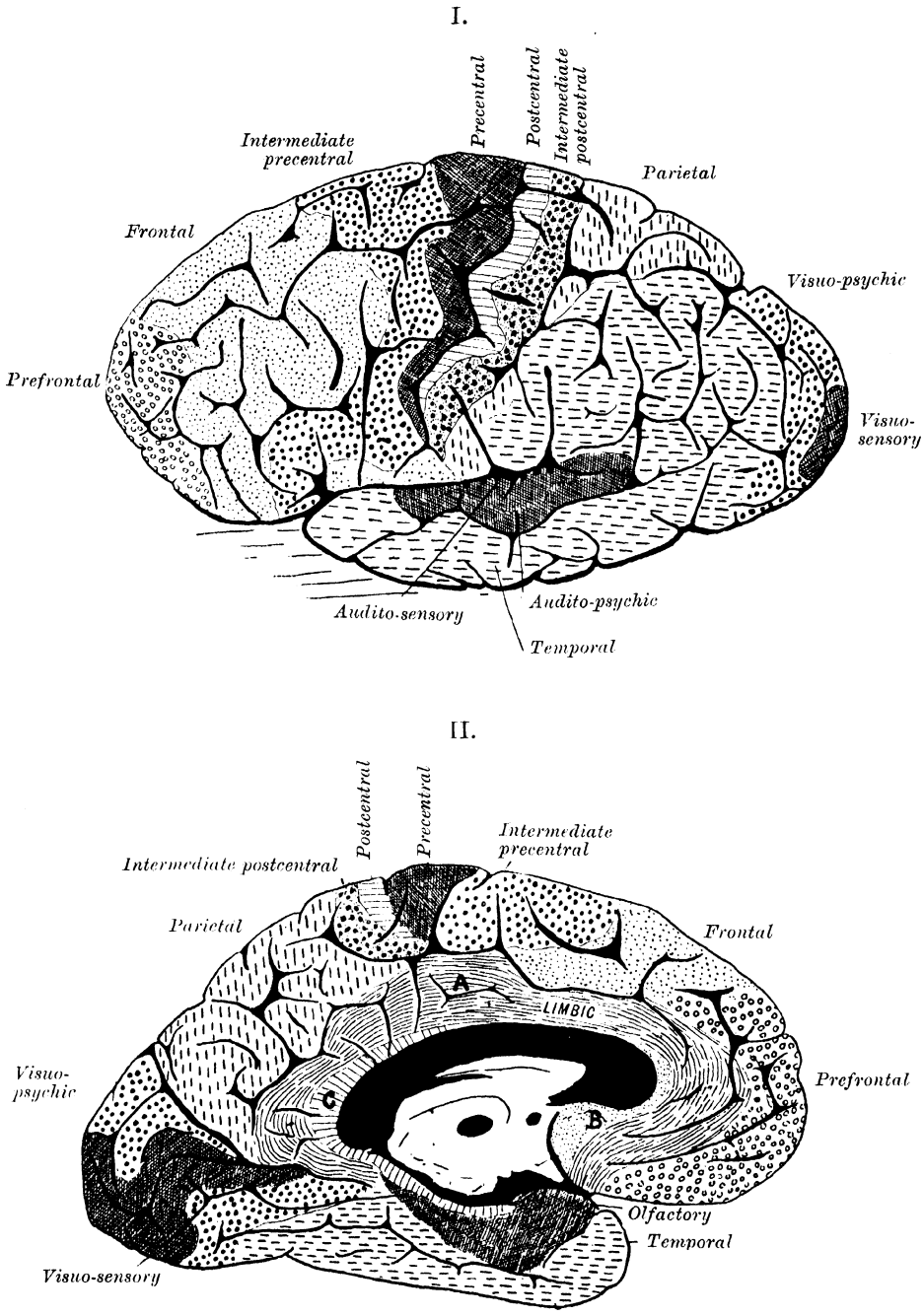


FIG. 334.—DIAGRAMS (ORTHOGONAL) OF CORTICAL AREAS AS DETERMINED BY THE DISTRIBUTION AND ARRANGEMENT OF FIBRES AND CELLS. (A. W. Campbell.)

I., lateral surface; II., mesial surface.

(Where a fissure appears to bound adjacent areas the real boundary is in the depth of the fissure.)
A, B, C (in II.), parts of the limbic lobe.

and receptive areas by association-fibres; hence the name 'associated areas,' which was originally applied to them by Flechsig.

Several observers have employed the characters of the cell-layers for the topographical analysis of the cortex (cyto-architectonic method). This method is the one which promises, in the long run, to yield the most accurate results, and which will have to be used ultimately to check the results obtained by other methods. But up to the present it has not been worked out in sufficient detail to enable us to map out every different portion with accuracy, although in the hands of Vogt and his collaborators considerable progress has been made in this direction. With regard to certain of the cortical areas, a mass of accurate information relating to the form of the cells and their arrangement is already accumulated, thanks to the labours of Bevan Lewis, Bolton, Mott, Vogt, Brodmann, Campbell, and Cajal.

It has proved more easy to obtain evidences of structural differences of the several areas by a study of the relative coarseness and fineness and the number of vertically running medullated fibres entering and issuing from the grey matter. With this is combined the observation of the manner in which they are distributed in the planes, parallel to the surface, which are known in section as the lines of Baillarger and of Gennari. This method has been employed by Kaes and by Campbell, in conjunction with the study of the cell-layers. The areas which Campbell has thus succeeded in defining are shown in fig. 334.

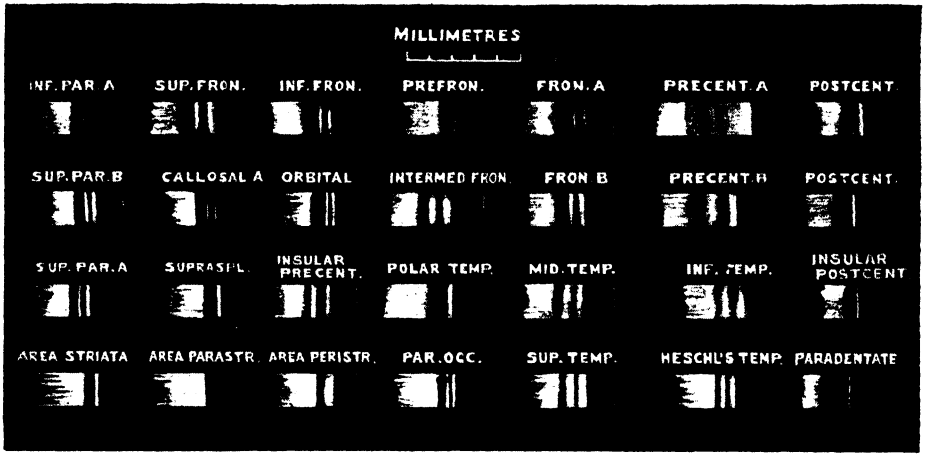
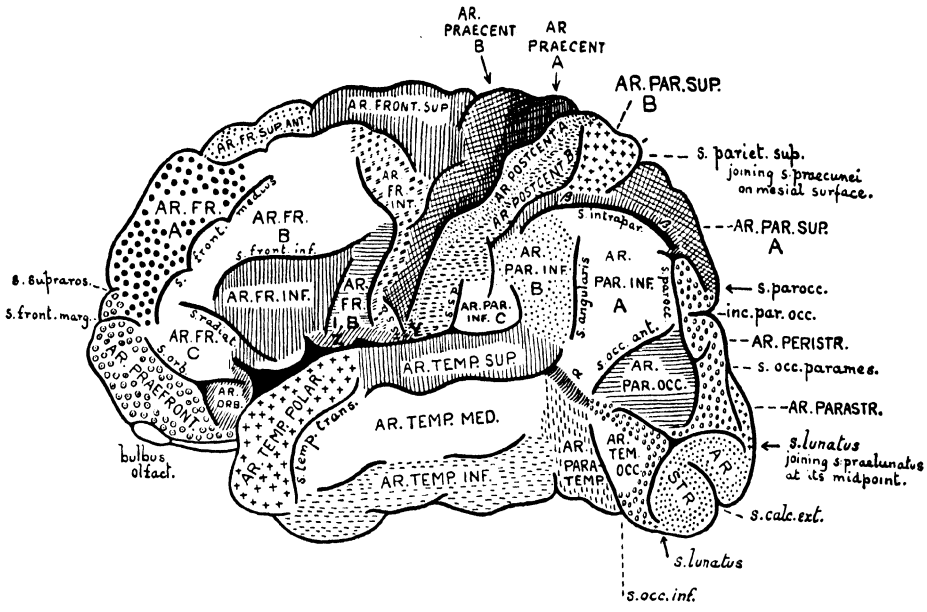


FIG. 335.—DRAWINGS SHOWING THE NAKED-EYE APPEARANCES OF SECTIONS OF THE FRESH CEREBRAL CORTEX IN DIFFERENT REGIONS. (Elliot Smith.)

(The regions from which the several sections are taken are shown in fig. 336.)

But even this method—for which Weigert-Pal preparations of the cortex are almost exclusively employed, assisted in the study of the cell-layers by sections stained by the methylene-blue method of Nissl—necessitates the preparation of an enormous number of microscopic sections and the expenditure of a prodigious amount of time and labour. These objections apply to all methods requiring histological investigation, owing to the great extent of surface which the brain presents. They are, however, largely obviated by a mode of examination which has been described by Elliot Smith. This observer, in place of using microscopic sections of fixed and stained brain-tissue, examines and measures the extent of the thickness of the grey matter and the character of the lines of Baillarger in the perfectly fresh or, failing this, in the formalin-injected cortex. The accompanying diagram (fig. 335) exhibits no fewer than twenty-eight different types of cortex, all, according to Elliot Smith, recognisable with the naked eye. The topographical diagrams, which are also here reproduced (fig. 336, I. and II.), serve to show the manner in which this method can be employed to map out the several areas. In illustration of its value the structural appearances of sections of the mesial occipital cortex may be taken. In this region the area striata, or visual cortex proper, characterised by the very distinct line of Gennari (see diagram, fig. 335), is found to be confined to the lips of the calcarine fissure. Immediately outside it is an area, the area parastriata, which no longer has the single white line of Gennari, but exhibits a double-lined

I.



II.

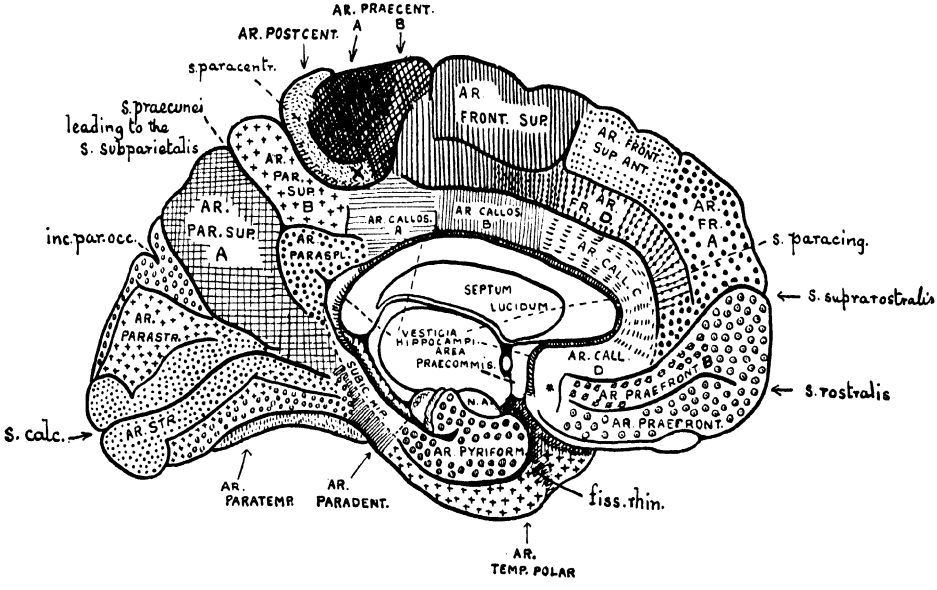


FIG. 386.—TOPOGRAPHICAL PLANS OF CORTICAL AREAS AS DETERMINED BY THE MACROSCOPIC EXAMINATION OF SECTIONS OF THE FRESH CORTEX. (Elliot Smith.)

I., external surface; II., mesial surface.

type, of a specific character, and quite clearly recognisable as distinct from that of the next area of the occipital lobe—the area peristriata, which forms a zone outside it again. From this we

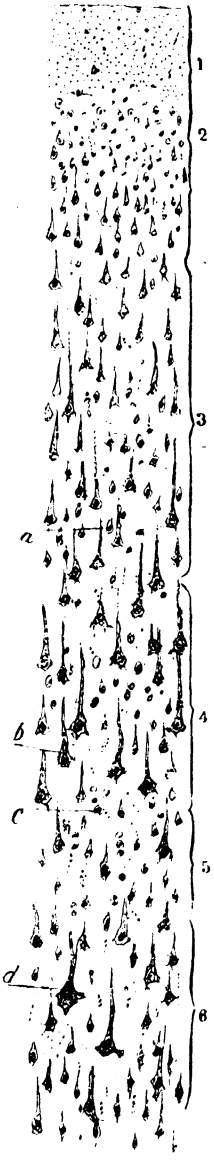


FIG. 337.

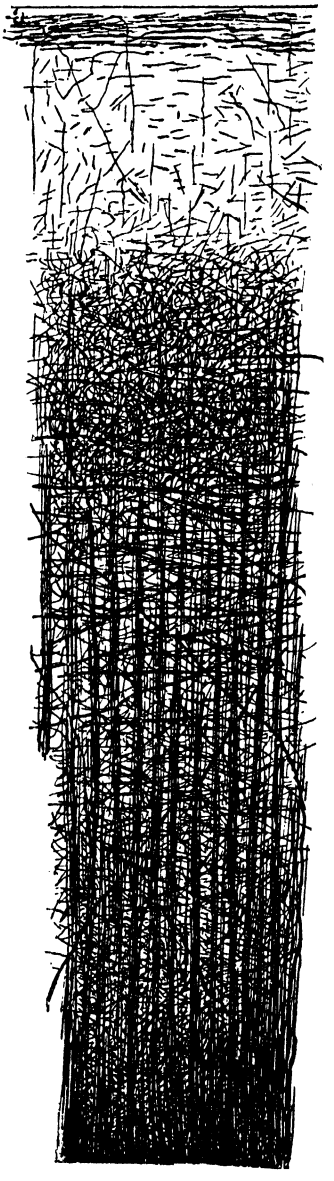


FIG. 338.

FIG. 337.—SECTION OF PRECENTRAL GYRUS (MOTOR CORTEX). Stained by Nissl's method. (Cajal.)
1 to 6, layers of the cortex; *a*, *c*, small cells among the pyramids; *b*, a large pyramid; *d*, a giant-cell of Betz.

FIG. 338.—SECTION OF MOTOR CORTEX (MAN). Stained by Weigert's method. (Cajal.)

pass to other types characterising the adjacent portions of the temporal and parietal lobes, all of which show specific features in the sectional appearance of their grey cortex.

For further details regarding the topography of the cerebral cortex the reader must consult the original memoirs, several of which are of a voluminous character, being stored with a great multiplicity of observations.[1] All that can here be attempted is to set forth the chief structural differences which have been found to obtain in certain types of cortex, and to compare these with the type which has already been described—that, namely, which is found in the post-central gyrus.

In the **anterior central gyrus** and the adjacent portion of the **marginal gyrus** the grey matter is thick and the lines of Baillarger broad and diffuse (fig. 335). Cytologically these gyri differ from the post-central mainly in two particulars—viz.: (1) The comparatively small number of 'granules' or stellate cells, which are insufficient in amount to constitute a distinct layer, so that the large pyramids constitute a single, and not a double, layer. (2) The presence in the deeper part of the layer of large pyramids of a certain number of very large cells—the giant pyramids—which are for the most part grouped into small batches (Betz, Bevan Lewis), and which are undoubtedly the cells of origin of the pyramid-tract fibres of the medulla oblongata and spinal cord. This is shown by the Nissl degeneration which supervenes in these cells if the pyramid-tract be cut, as well as by the Wallerian degeneration of the fibres of the pyramid-tract which follows destruction of this part of the cortex (motor cortex). As a result of the absence of the layer of granules, six layers only are obvious in the grey matter of the motor cortex (figs. 337, 338, 339). These are as follows, from without in:

1. The *plexiform layer*. This is somewhat thicker than in the post-central gyrus.
2. The *layer of small pyramids*.
3. The *first or more superficial layer of medium pyramids*. As in the post-central, this layer is characterised by the presence of a close plexus of medullated fibres, forming the outer line of Baillarger.
4. The *layer of large pyramids*, including the giant-cells of Betz, the largest of which are found in the anterior border and in the depth of the fissure of Rolando. In the deeper part of this layer there is another close plexus of nerve-fibres (inner line of Baillarger), but less marked than in the posterior central.
5. The *second or deeper layer of medium-sized pyramids*. Some of the Betz cells may extend down among these.
6. The *layer of fusiform and polymorphous cells*.

Short-axoned cells and cells of Martinotti are most numerous in the fourth layer, but are altogether much fewer in number than in the posterior central.

In the **superior temporal gyri** (figs. 340, 341, 342) and in the **gyri of the insula**, an eight-layered type is again met with, due to the presence of a well-marked granule-layer separating the layer of large pyramid-cells into two. The layers are as follows:

1. A *plexiform layer*, not specially characteristic.
2. A *layer of small pyramids* which also includes many short-axoned cells.
3. A first or *superficial layer of medium-sized pyramids*.

[1] The following list comprises some of the more recent works on the subject: J. S. Bolton, Phil. Trans. 1900; Brodmann, Allgem. Zeitschr. f. Psych. 1904; Neurol. Centr. 1903 and 1904; Journ. f. Psych. u. Neurol. ii. iv. vi. and vii. 1903–6; Cajal, Studien ü. d. Hirnrinde des Menschen, 1900–1905; A. W. Campbell, Histological Studies on the Localisation of Cerebral Function, 1905; Flechsig, Neurol. Centr. 1898 and 1903; Proc. Physiol. Congr. Turin, 1901 (Report in Brit. Med. Journ. Oct. 1901); Ber. d. k. Sächs. Ak. d. Wiss. 1904; Hösel, Arch. f. Psych. 1904; Kaes, Die Grosshirnrinde des Menschen, 1907 (with figures of sections of the various regions at all ages); C. K. Mills, Univ. of Pennsyl. Med. Bull. 1904; Mott, Archives of Neurology, vols. i. and ii.; Elliot Smith, Journ. Anat. and Phys. xli. 1907; O. Vogt, Journ. f. Psych. u. Neur. 1903; *ibid.* Bd. viii.; Verhandl. d. Anat. Gesel. in Anat. Anz. xxix. 1906; O. and C. Vogt, Neurobiologische Arbeiten, 1902.

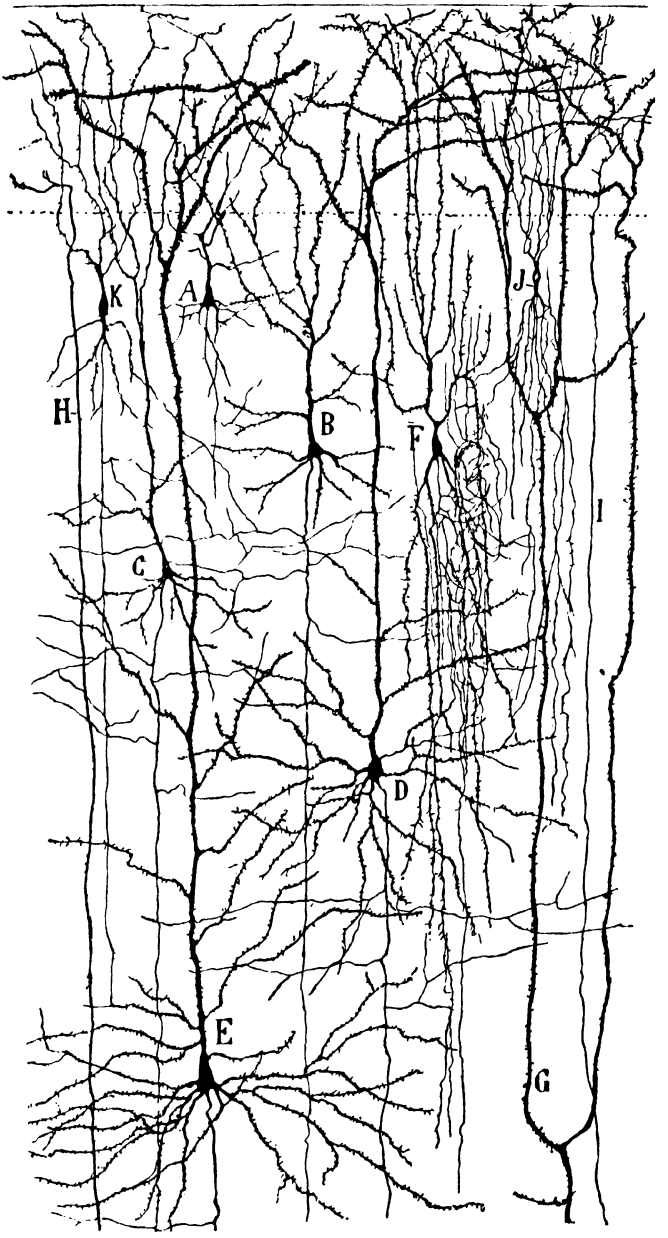


FIG. 389.—FIRST, SECOND, AND THIRD LAYERS OF THE PRECENTRAL GYRUS OF CHILD ONE MONTH OLD. (Cajal.)

A, B, C, small pyramids; D, E, medium pyramids; F, J, bipennate cells; G, dendron of a large pyramid from a deeper layer; H, I, fibres from cells in a deeper layer passing to end in the plexiform layer; K, small fusiform cell with long descending axon.

FIG. 340.

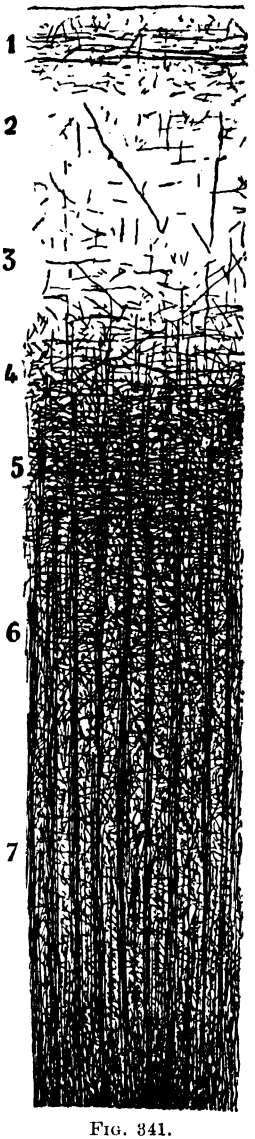


FIG. 341.

FIG. 340.—SECTION OF FIRST TEMPORAL GYRUS (ACOUSTIC CORTEX OF MAN). Stained by Nissl's method. (Cajal.)

1, plexiform layer; 2, layer of small pyramids; 3, superficial medium pyramids; 4, large pyramids; 5, small stellate cells (granules); 6, deep medium pyramids; 7, fusiform cells.

FIG. 341.—SECTION OF FIRST TEMPORAL GYRUS (MAN). Stained by Weigert's method. (Cajal.)

4. A first or *superficial layer of large pyramids.*

5. A well-marked *stratum of granules or stellate cells.*

6. A second or *deep layer of large pyramids.* Most of the cells of this layer are of the ordinary kind, but others (fig. 342, K, L) are highly characteristic of this

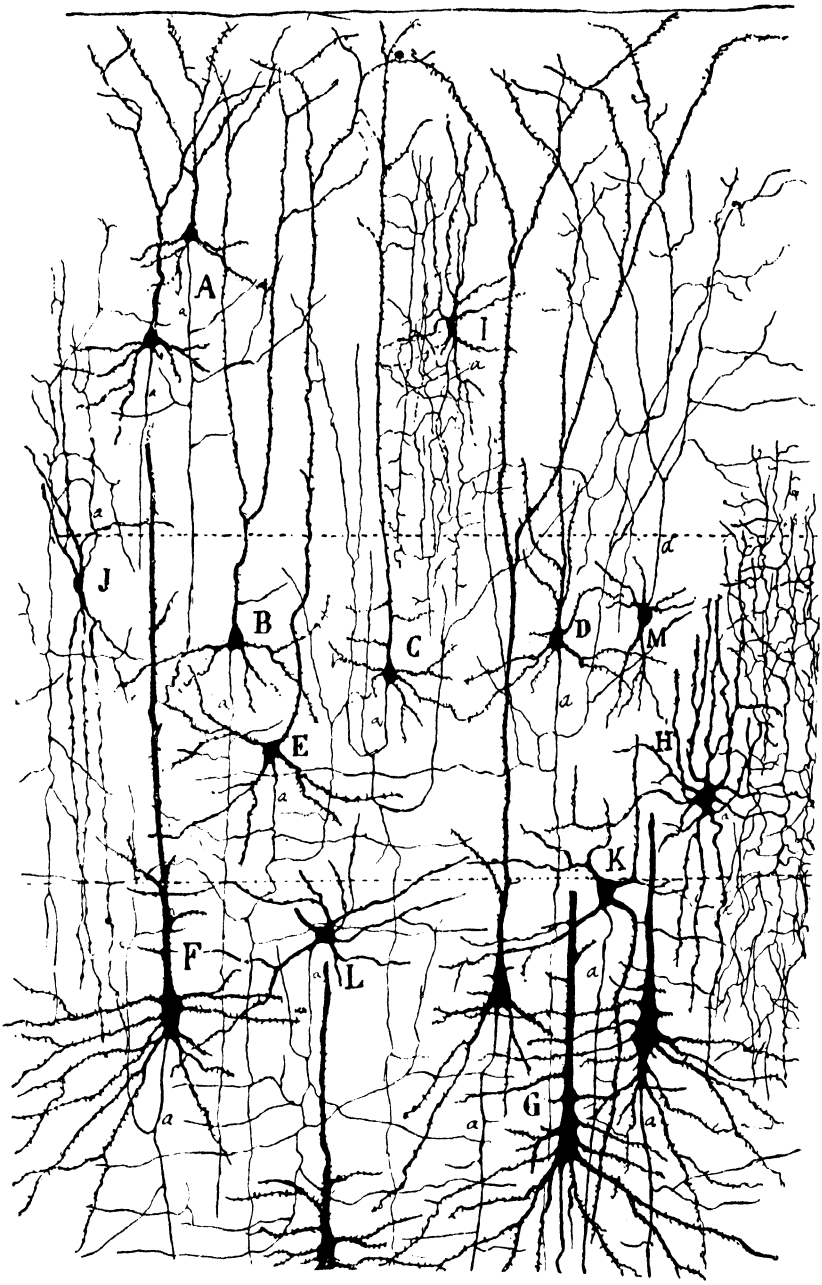


FIG. 342.—TYPES OF CELLS FROM THE ACOUSTIC CORTEX OF A KITTEN OF TWENTY-FOUR DAYS. (Cajal.)

A, small and medium pyramids; B, ordinary medium-sized pyramid of the fourth layer; C, D, small cells of fourth layer with recurved axons; E, stellate cell of fourth layer; F, G, large pyramids; H, cell of Golgi's type ii.; I, J, other smaller ones of a bipennate character; K, L, stellate cells of fifth layer ('acoustic cells' of Cajal); M, stellate cell of fourth layer with ascending axon.

part of the cortex and are regarded by Cajal as specific for the auditory cortex. They are fusiform or triangular rather than pyramidal in shape, large (40 μ to 60 μ), although not attaining the dimensions of the Betz cells of the motor area, they have no special apical dendron as have the pyramid-cells, and their other dendrons are axon-like in general appearance and tend to spread out horizontally, giving off vertical branches. Their axons pass obliquely to the white substance of the hemisphere, first giving off many collaterals which are distributed to the grey matter. Cells of this character are not entirely confined to this layer, but may also be found in other strata, but they are much more numerous in the sixth layer.

7. A second or *deep layer of medium-sized pyramids*. This is less distinct from the preceding layer than in other parts of the cortex, and the two are in fact described by Cajal as a single layer.

8. A *polymorph layer* of fusiform and triangular cells—not specially characterised.

As in other parts of the cortex, there are in all the layers below the plexiform large numbers of short-axoned cells, and, especially in the deeper layers, also cells of Martinotti, with axons ascending to the plexiform layer. The short-axoned cells include a large number of the bipennate cells (fig. 342, I, J), which were indeed first observed by Cajal in the temporal cortex, and were at first supposed to be special to this region.

The cortex of the insula agrees on the whole in structure with that of the adjacent temporal surface, but the pyramids have a tendency to assume a more fusiform shape, and their basal dendrons are less horizontally disposed and frequently pass almost vertically downwards in the grey matter. The special 'acoustic cells' of Cajal are seen here as in the temporal region, and all the layers described for that region are also present.

Meynert supposed the claustrum to represent the lowest layer of the cortex of the insula detached from the rest, and he accordingly termed the polymorph layer of the cortex generally the 'claustral formation.' But according to Cajal this is not the case, for the cortex of the insula possesses the usual deep layer of fusiform and polymorphous cells. He therefore regards it as more probable that the claustrum belongs to the formation of the lenticular nucleus and is not specifically related to the insula.

Many afferent fibres—the place of origin of which is unknown, but is supposed to be the mesial geniculate body—pass to this region of the cortex, and penetrating the deeper layers obliquely end for the most part in a fine plexus in the fifth or granule layer. Some extend to the fourth and third layers.

The cortex of the **occipital lobe in the immediate neighbourhood of the calcarine fissure** (visuo-sensory cortex, figs. 342, 343) also has a special structure. Even to the naked eye it is characteristic by reason of the well-marked white line (*line of Gennari*) which has been already referred to. The presence of this distinct line may be looked upon as specific for the visual cortex, and the extent of that cortex may be determined anatomically by mapping out the region in which the line of Gennari is visible. The area of cortex which shows this line is known as the *area striata* (Henschen); its limits in man are shown in figs. 334 and 336. The line itself is due to the interpolation into the middle of the cortex of a thick granule-layer with a dense plexus of medullated fibres among its cells. This mode of causation of the appearance is well seen, as shown by Mott, in sections through the margin of the visual area where this area abuts against the adjacent regions of the cortex. The visuo-sensory cortex

possesses large pyramid-cells of characteristic form and appearance. It may be subdivided into eight or nine strata (fig. 343):

1. A *plexiform* or *molecular layer* of the ordinary type.

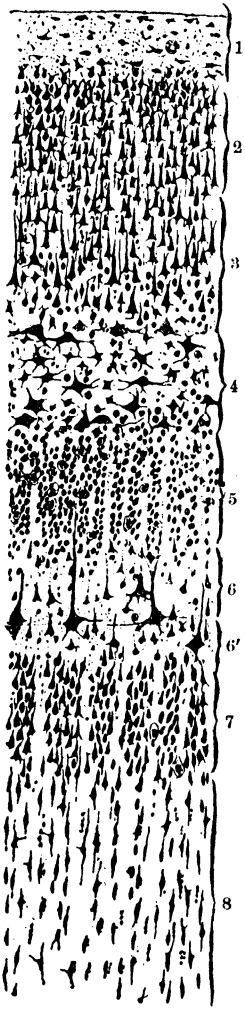


FIG. 343.—CALCARINE (VISUAL) CORTEX OF MAN. Nissl's method. (Cajal.)

1, plexiform layer; 2, small pyramids; 3, medium pyramids; 4, large stellate cells (characteristic of this part of the cortex); 5, small stellate cells; 6, a deep plexiform layer, containing some small pyramids and forming part of the layer which contains the large pyramids, 6'; 7, layer of small and medium pyramids; 8, fusiform cells.

2. A second layer or *layer of small pyramids*, composed of small densely accumulated cells, mostly of the pyramid type, but with not a few short-axoned cells among the pyramids.

3. A first or *superficial layer of medium-sized pyramids*, generally similar to the same stratum in other parts of the cortex, but of relatively considerable thickness. Many of the interpolated short-axoned cells have a double-brush character.

4. Partly imbedded in the deepest part of the third layer are seen a number of *large stellate pyramids*, forming the chief constituents of a narrow stratum which intervenes between the medium-sized pyramids and the granule-layer. This layer corresponds with the first or superficial layer of large pyramids of the parietal cortex, but differs from that in the form of its characteristic elements. These, as already stated, are large and stellate, with spinous dendrons spreading out mainly in a horizontal direction, but also upwards and downwards, and devoid for the most part of the apical dendron extending to the plexiform layer, which is characteristic of the pyramid-cell, although a certain number of the cells of the layer exhibit such a dendron and have the typical characters of pyramids. The axon descends through the deeper layers to the white substance, giving off collaterals on its way. Between these large stellate cells, which appear to be specific for the visual cortex, are a certain number of small stellate short-axoned cells (granules), and also cells of Martinotti with ascending axons. The layer is characterised by the presence of a very rich interstitial nervous plexus.

5. '*Granule*'*-layer*.—This forms a thick layer of closely arranged small stellate and pyramidal cells intervening between the large stellate cells and the large pyramids. It is described by Cajal as two layers, since the short-axoned granules are more abundant in the superficial part and the small pyramidal cells in the deeper part; but both kinds of elements occur throughout, and the subdivision may therefore, for simplicity of description, be dispensed with.

The granules or small stellate cells are short-axoned cells, with the axons either ramifying in the layer itself or passing up to end in the fourth and third layers. The dendrons are relatively large and spreading, and have a spinous

character. A considerable number of arachniform or neuroglia-like cells are also seen among the ordinary granules.

The small pyramids are of two kinds—viz. (*a*) ordinary pyramids with descending axon, and (*b*) pyramid-shaped cells with an axon which comes off from the base of the cell, and after descending a short distance turns round and passes upwards into the upper part of the fifth layer and into the fourth layer.

It is in this fifth layer that the dense plexus of medullated fibres which forms the line of Gennari is found, and the presence of this line causes the granule-layer to appear double when seen under a low power of the microscope.

6. *Deep layer of large pyramids.*—The cells which give the character to this layer are large cells of the pyramidal type (solitary cells of Meynert), with their

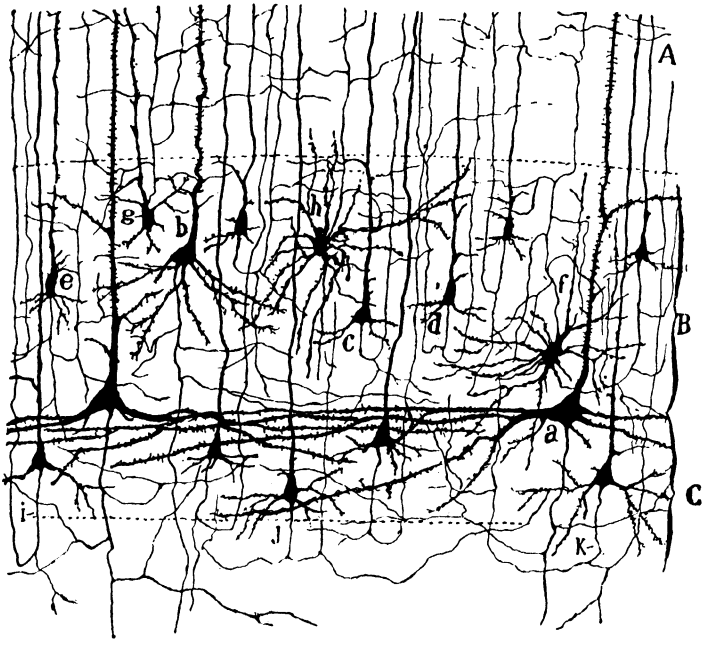


FIG. 344.—CELLS OF THE SIXTH AND SEVENTH LAYERS OF THE VISUAL CORTEX OF CHILD OF FIFTEEN DAYS.

A, fifth, B, sixth, C, seventh layer; *a*, large pyramid; *b*, medium pyramid; *c*, small pyramid with recurved axon; *d*, another with bifurcated recurved axon; *e*, another with recurved axon; *f*, *g*, *h*, stellate cells with ascending axons ramifying in the sixth and fifth layers; *i*, *j*, *k*, pyramids with recurved axons ramifying in the seventh and sixth layers.

basal dendrons enormously extended in a tangential direction (fig. 344). The apical dendron is thick, spiny, and extends to the molecular layer. The axon is also of considerable thickness, and extends down into the white matter, giving off several collaterals to the grey matter through which it passes. The layer contains also a certain number of smaller cells, some with descending and others with ascending axons.

7. *Deep layer of medium-sized pyramids.*—This layer is thick and well-marked, but otherwise shows nothing specially characteristic, unless it be the presence along with the ordinary pyramid-cells with descending axons of a considerable number of pyramidal and other forms with ascending axons, many of which, after at first descending, bend round and pass through the cortex to reach the plexiform layer (Martinotti cells).

8. *Polymorph. layer.*—The layer of triangular and fusiform (or polymorphous) cells is of the ordinary type.

The afferent fibres to the visuo-sensory cortex originate partly in the cells of the external geniculate body (projection-fibres), partly in the visual cortex of the opposite side passing across in the splenium of the corpus callosum (commissural fibres), partly in other portions of the cortex of the same side (association-fibres). They are large medullated fibres which pass to the occipital cortex in the optic radiation of Gratiolet, and, after traversing the deeper layers obliquely, become tangential in the granule-layer, and break up into a fine arborisation among the cells of this layer. Some pass on to the fourth layer and form an interlacement among its cells, and a few even reach the third layer and end there. These interlacements also include numerous collaterals from the ascending axons of cells in the deeper layers and from descending axons of cells in the more superficial layers.

According to Mott, the commissural fibres from the opposite occipital lobe pass mainly or entirely to the more superficial granules, and the afferent projection-fibres to those more deeply seated. Bolton found in a case of anophthalamos that one-half of the fibres of the line of Gennari had alone disappeared, the other half persisting: it may be assumed that the latter were the commissural fibres.

The efferent fibres from the visual cortex are derived from the axons of the pyramids, and pass downwards and backwards in the optic radiations towards the brain-stem. Eventually many of them are collected, along with those which pass from the auditory cortex, into the lateral part of the crusta (basis pedunculi), whence they are most probably ultimately distributed to the lower motor nuclei. But the mode and path of distribution have not as yet been elucidated.

Flechsig finds that the fibres of the optic radiations myelinate at three periods—viz. at birth (afferent, sensory), soon after birth (efferent, motor), and some time after birth (association and commissural).

In the remainder of the occipital lobe the plexus which in the calcarine cortex forms the line of Gennari and the granule-layer is less developed, and the large stellate cells become fewer in number as we pass away from the lips of the calcarine fissure. This is also the case with the cells with bent ascending axon and with the medium-sized pyramids (Cajal), while on the other hand the ordinary large pyramids which are superficial to the granules are increased in number.

Figs. 334 and 336 show the position with regard to the calcarine sulcus of the visual cortex (cortical retina) in the human brain. It will be seen that it is strictly confined to the sides of the calcarine fissure, including the extension of this backwards to the occipital pole; it is found also in the depth of the fissure. Anteriorly it is confined to the lower lip of the fissure (Bolton). Sometimes it covers a rather larger superficial area, but in such cases it will usually be found that the fissure is shallower. In lower Primates such as the macaque monkey it covers the whole of the occipital lobe.[1] But already in the anthropoid apes it is becoming restricted to the neighbourhood of the calcarine fissure; and the circumjacent part of the (relatively small) occipital lobe—termed visuo-psychic region by Bolton: the area parastriata, and area peristriata of Elliot Smith—has different histological characters, the line of Gennari and the lower layer of granules or small stellate cells having disappeared, and the large deep stellate cells being replaced by ordinary large pyramids.

[1] The results of physiological experiment have shown that the whole lobe in the monkey is directly excitable and that the excitation produces movements of the eyes such as would be caused by visual impressions.

Elliot Smith found as the result of measurement of one brain that the area striata occupies a superficial extent of about 3,000 sq. mm. on each side.

The arrangement of the fibres in the white matter of the occipital lobe has been studied by H. Sachs,[1] who finds the fibres arranged in four layers or series, from within out, as follows: 1. Those which are prolonged from the corpus callosum (forceps major), which occupy the central parts nearest the ventricle. 2. Next to these a layer composed of projection-fibres, passing to the internal capsule. They are finer than the callosal fibres. 3. Another layer of larger fibres which surrounds the projection-layer and is composed of long association-fibres. 4. A layer of short association-fibres, nearest the cortex. It will, of course, be understood that the peripheral layers are constantly pierced by the fibres which are passing from the cortex to join the more centrally situated layers.

THE RHINENCEPHALON.

Mammals are subdivided according to the relative development of their olfactory apparatus into *macrosmatics*, such as carnivores, ruminants, and rodents; *microsmatics*, such as Primates; and *anosmatics*, as in many Cetacea (Turner). This difference of development shows itself in certain corresponding parts of the brain—viz. the *olfactory bulb and tract*, the *olfactory tubercle* (anterior perforated space), the *pyriform lobule*, the *hippocampal gyrus* and *hippocampus*, the *dentate gyrus*, *fimbria*, and *fornix*, the *septum pellucidum*, the *fasciola cinerea*, the *indusium* and *nerves of Lancisi*, the *gyrus subcallosus*, and *area of Broca*. These constitute the **rhinencephalon.** Uniting certain parts of the rhinencephalon of the two sides are the *anterior commissure* and the *psalterium dorsale*; whilst forming a connexion with other parts which also probably belong to the olfactory part of the brain are the *habenula* passing from the fornix to the ganglion of the habenula, the *fasciculus retroflexus* passing from this to the *interpeduncular ganglion*, and the *corpus mamillare*, which is connected with the column of the fornix on the one hand and, through the bundle of Vicq d'Azyr and the bundle of Gudden, with the thalamus and tegmentum on the other. All these come into direct or indirect connexion with the olfactory apparatus proper, which itself essentially consists of bipolar nerve-cells (olfactory cells) in the olfactory epithelium of the nose. From these cells nerve-fibres pass to the olfactory bulb; from cells in the bulb other fibres carry the olfactory path through the olfactory tract to the spheno-hippocampal region and eventually

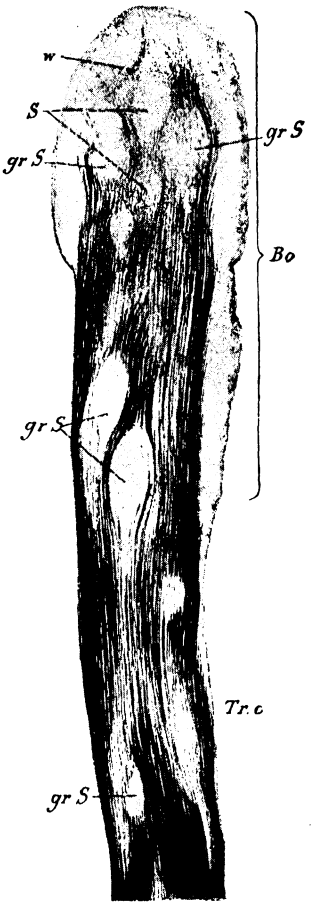


FIG. 345.—LONGITUDINAL HORIZONTAL SECTION OF OLFACTORY BULB AND TRACT OF MAN. Weigert method. $\frac{6}{1}$. (Kölliker.)

Bo, olfactory bulb; *Tr. o*, olfactory tract; *S*, septum-like layer of grey matter; *gr S*, islands of grey substance between the white bundles of the tract (the section does not pass through the central grey substance of the tract); *w*, bundles of white fibres prolonged into the anterior part of the bulb.

[1] Das Hemisphärenmark d. menschl. Grosshirns, 1892.

to the thalamic region; whilst from this it is again conducted towards the mid-brain and pons. The structure of some of the above parts has already been described: that of the hippocampal region of the cortex, the olfactory lobe (which includes the olfactory bulb and tract, the trigonum olfactorium, the area of Broca, and the anterior perforated space), the septum pellucidum and grey matter overlying the corpus callosum, and the commissures uniting these parts of the opposite hemisphere, may now be considered.

The **olfactory tract and bulb.**—The bulb is in man merely a solid greyish enlargement at the anterior end of the olfactory tract (fig. 345), whereas in osmatics it appears as the bulbous extremity of a well-marked projection of the hemisphere which is occupied by a prolongation of the ventricle. In the human subject it, as well as the tract, is also hollow in the first instance, but the cavity becomes obliterated in the course of development; its position is indicated by the central neuroglial or ependymal masses which are seen in section. Several strata may be distinguished in the bulb (figs. 346, 347):

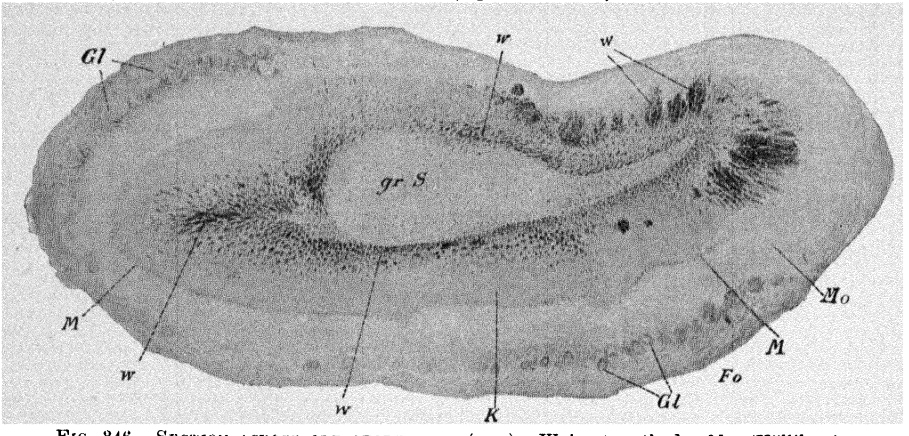


FIG. 346.—SECTION ACROSS OLFACTORY BULB (MAN). Weigert method. $\frac{25}{1}$. (Kölliker.)

Fo, layer of olfactory fibres; *Gl*, layer of glomeruli; *K*, granule-layer; *Mo*, molecular (external plexiform) layer; *M*, layer of mitral cells; *gr.S*, central grey substance (neuroglia); *w*, *w*, white fibres around central grey substance.

1. *Superficial nerve-fibre layer.*—The part of the bulb which rests on the cribriform plate of the ethmoid is formed of a layer of non-medullated nerve-fibres, which are derived from the bipolar olfactory cells of the nasal mucous membrane. These fibres, after passing in large bundles through the holes in the cribriform plate and dura mater, form a felted mass which underlies the rest of the bulb (fig. 347), and from this mass small bundles of the fibres pass, to end, one in each of the glomeruli of the next layer.

2. *Layer of olfactory glomeruli.*—Next to the nerve-fibre layer are seen in vertical sections of the bulb peculiar rounded nests of interlacing nerve-fibres with a few intercalated cells (figs. 347, 348). These are the olfactory glomeruli, and within them meet and interlace together (1) the ramified terminations of the olfactory fibres just mentioned, and (2) terminations of the dendrons of certain large helmet-shaped cells more deeply situated in the bulb, which are known as the 'mitral' cells, as well as others from certain cells, smaller in size and situated less deeply, termed by Cajal the 'tufted' cells. Besides these synapses, the glomeruli contain a certain number of small short-axoned nerve-cells and neuroglia-cells. The axon-processes of the former serve to bring neighbouring glomeruli into communication with one another (fig. 348).

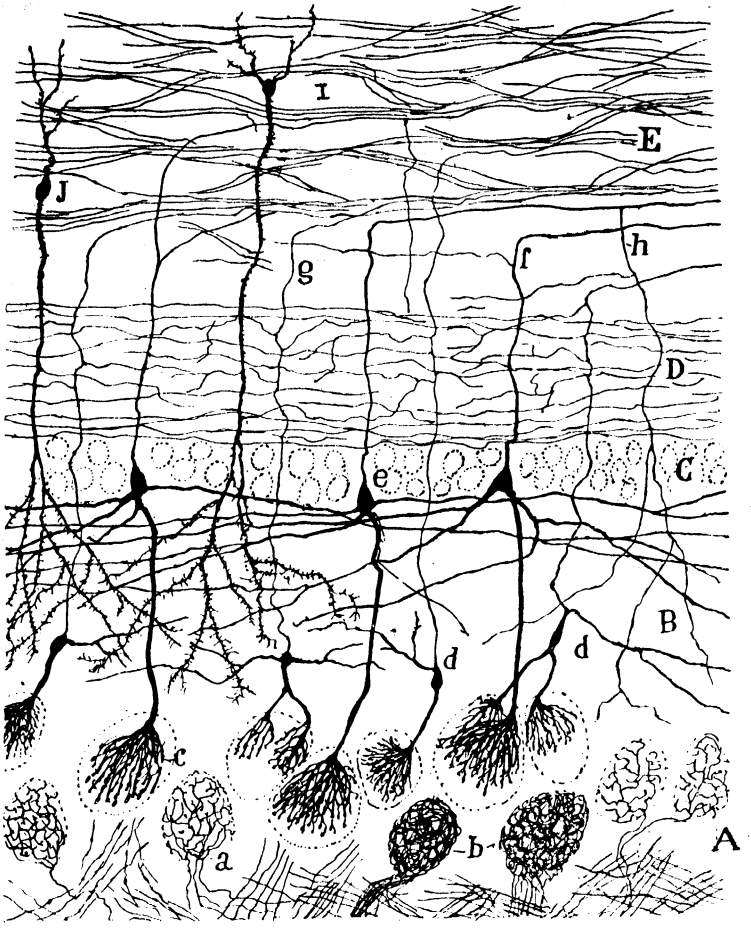


FIG. 347.—SECTION OF OLFACTORY BULB OF KITTEN A FEW DAYS OLD. (Cajal.)

A, layer of glomeruli; B, outer plexiform layer; C, layer of mitral cells; D, inner plexiform layer; E, white substance with interspersed groups of granules (I, J); *a*, terminal arborescence of olfactory fibre; *b*, glomeruli with endings of several olfactory fibres; *c*, brush-like ending of dendron of mitral cell; *d*, tufted cells of Cajal; *e*, body of mitral cell; *f*, axon of mitral cell; *g*, axon of tufted cell; *h*, collateral.

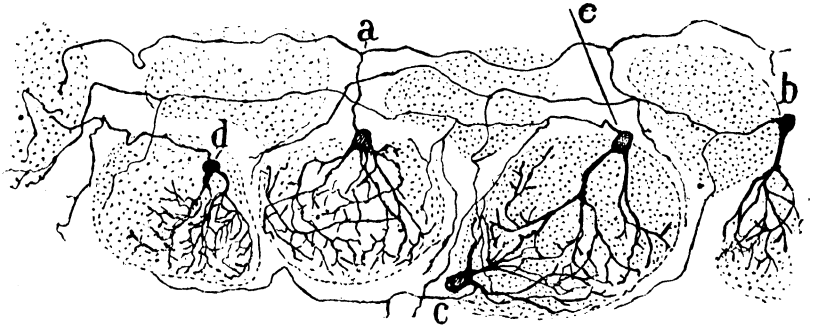


FIG. 348.—SMALL SHORT-AXONED CELLS OF THE OLFACTORY GLOMERULI OF THE CAT. (Cajal.)

a, axon of one of the cells, bifurcating and passing to other glomeruli; *b*, *c*, *d*, cell-bodies lying at edge of glomeruli, into which the dendrons penetrate while the axons pass to other glomeruli.

3. *First molecular (plexiform) layer.*—Next to the layer of glomeruli is a thick stratum containing, besides scattered short-axoned nerve-cells, a certain number of the tufted cells of Cajal and a rich interlacement of nerve-cell processes derived (*a*) from lateral arborisations of the dendrons of the mitral and tufted cells passing to the glomeruli, (*b*) from terminations of the axons of cells of the granule-layer, and (*c*) from collaterals descending from the axons of the mitral and tufted cells. The tufted cells resemble on the whole small mitral cells; the axon takes the same course as that of the mitral cell (see below), but is finer.

4. *Layer of mitral cells.*—These are characterised by their helmet shape and by their size; they are the largest cells in the olfactory bulb. The cell-body has well-marked Nissl granules and neuro-fibrils. The dendrons are large, long, and spreading. Some of them end in the plexiform layer, but the majority pass through this to enter the olfactory glomeruli and to interlace within these with the endings of the olfactory nerve-fibres. The axons pass at first vertically upwards; on reaching the nerve-fibre layer they turn backwards and run along the olfactory tract to the base of the brain. A few tufted cells occur here and there among the mitrals.

5. *Second molecular or deep plexiform layer.*—This is formed mainly of the ascending axons of the mitrals and tufted cells and their collaterals, but it includes a few small short-axoned cells (granules) sending their axons into the superficial plexiform layer, and here and there a dislocated mitral cell.

6. *Layer of granules.*—This is a fairly thick layer, passing more or less gradually into the white matter which surrounds the central ependymal mass. Its elements are small and fusiform or irregularly angular, and of two chief kinds. Those which are most numerous have descending axons, which pass through the deep plexiform and mitral layers and terminate by arborising in the superficial plexiform stratum. The others are short-axoned cells, the axons of which end in the granule-layer itself.

7. *Deep nerve-fibre layer.*—The nerve-fibres which are passing to and from the olfactory tract begin to collect in anastomosing bundles in the granule-layer, becoming more free from cells and antero-posterior in direction near the ependyma. They comprise both efferent and afferent fibres.

The *efferent* fibres are of two kinds—coarse and fine, derived respectively from the axons of the mitral and tufted cells. Both sets of fibres give off collaterals, which turn backwards into the deep plexiform layer. The fine fibres are traceable across the anterior commissure into the opposite olfactory tract and bulb (fig. 349, B).

The *afferent* fibres are also coarse and fine. The former come from cells in the hippocampal cortex; their arborisations end in the granule-layer. The fine fibres are those which have just been mentioned as coming from the opposite bulb. They pass through the granule and deep plexiform layers and form nests or basket-work around the bodies of the mitral cells.

The frontal and hippocampal olfactory cortex.—The greater mass of fibres of the olfactory tract are conducted by its lateral root across the vallecula Sylvii to the cortex of the hippocampal region (caput hippocampi). These fibres give off numerous collaterals into the plexiform layer of the part of the subfrontal cortex over which it passes. As we have just seen, the fibres in question originate for the most part, so far as they are efferent in character, in the axons of the mitral cells. Some of them leave the tract by the middle root and end directly in the grey matter of the olfactory tubercle. But the fine fibres of the tract pass by the mesial root to the anterior commissure.

The **frontal olfactory cortex,** which is subjacent to the fibres of the lateral root, like the olfactory region of the cortex generally, is of relatively simple structure (fig. 350). Its layers are reduced to three—viz.:

1. A *plexiform* or *molecular layer.*
2. A *pyramidal layer* containing small and medium-sized cells.
3. A *polymorph layer* containing also cells of Martinotti.

The plexiform layer is covered superficially by the fibres of the external olfactory root, which form a superficial white stratum over this part of the cortex, into which they send numerous collaterals. The rest of the plexiform layer has the usual characters and cells. The pyramid-layer is not clearly

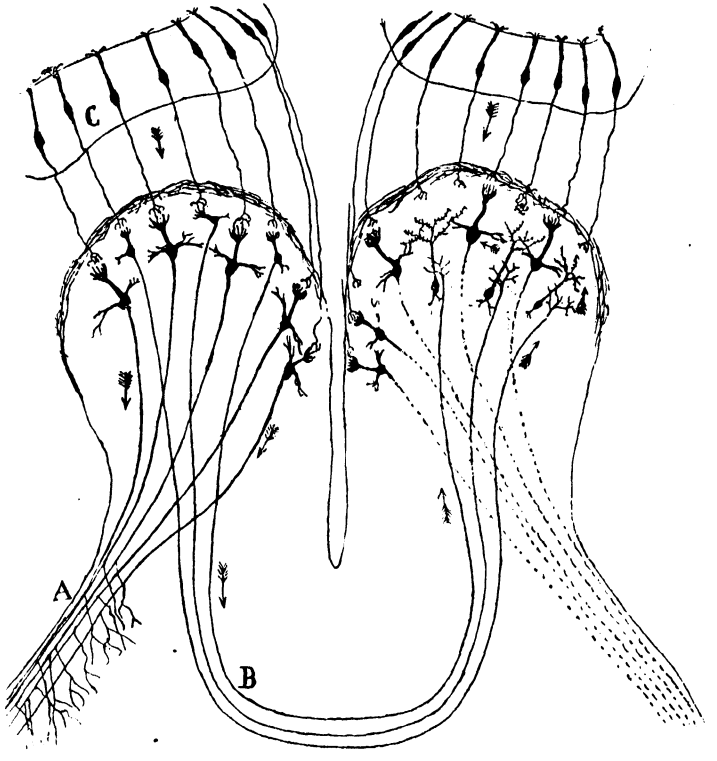


FIG. 349.—DIAGRAM INTENDED TO SHOW THE COURSE OF NERVE-IMPULSES IN THE OLFACTORY BULB AND TRACT. (Cajal.)

A, lateral root of olfactory tract; B, the part of anterior commissure which connects the olfactory lobes; C, olfactory cells in nasal mucous membrane.

distinguishable into strata, although as usual the more superficial cells are smaller than those which lie deeper. Many of the cells also are triangular and fusiform rather than of the usual pyramidal shape. Their axons pass down into the white substance and their apical dendrons up into the plexiform layer, where they commingle with the collaterals of the olfactory fibres and with the axon-endings of the cells of Martinotti. The polymorph layer has for the most part large cells with descending axons.

The fibres of the white matter of the frontal olfactory cortex are derived from the axons of the pyramids and polymorph cells. They give origin to projection-fibres, which take an antero-posterior direction to the subthalamic region sending

collaterals and terminal branches to the stria medullaris, and others towards the thalamus (Cajal). Some of the fibres extend farther back and are believed to reach the pons and medulla oblongata.

Hippocampal cortex (figs. 350 to 353) (including the *pyriform lobule*).—Most of the fibres of the lateral olfactory root pass to the hippocampal region of the cortex and especially to the gyrus hippocampi, which may be regarded

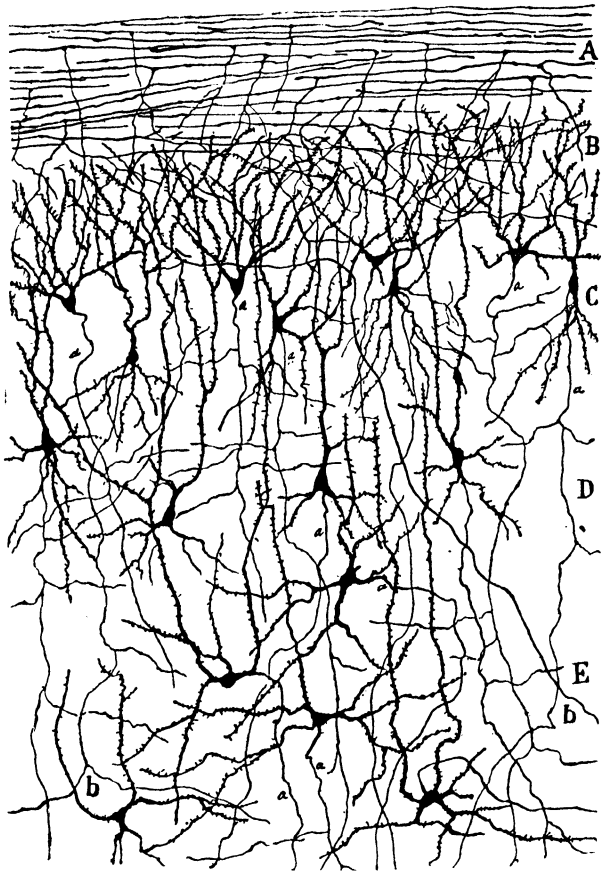


FIG. 350.—SECTION FROM THE PART OF THE FRONTAL (ORBITAL) CORTEX WHICH IS COVERED BY THE OUTER OLFACTORY ROOT. (Cajal.)

A, layer of olfactory fibres; B, plexiform layer; C, superficial polymorphous cells (corresponding to layer of small and medium pyramids); D, pyramids; E, deep polymorphous layer; *a*, *a*, axons; *b*, *b*, bifurcation of axons.

as the main place of ending of the secondary olfactory path, derived from the axons of the mitral cells. Cajal distinguishes five regions of the hippocampal cortex—viz.:

a. The *hippocampal gyrus proper* or principal olfactory region.

b. The *subiculum*, the part lying next to the dentate fissure.

c. The *presubiculum*, a transitional region between *a* and *b*.

d. The *external* or *fissural region*, comprising in animals the outer third of the pyriform lobule next to the limbic fissure, separating it from the visual region.

c. The *superior* or *caudal olfactory region* (*sphenoidal nucleus* of Cajal), situated at the postero-superior extremity of the pyriform lobule and next to the occipital lobule.

Hippocampal gyrus proper.—The grey matter of this shows four layers (fig. 351)—viz.: 1. A *molecular* or *plexiform layer*, fairly thick and covered superficially by a white stratum composed of the olfactory root-fibres. These give off branches (collaterals and terminals) which enter and ramify in the

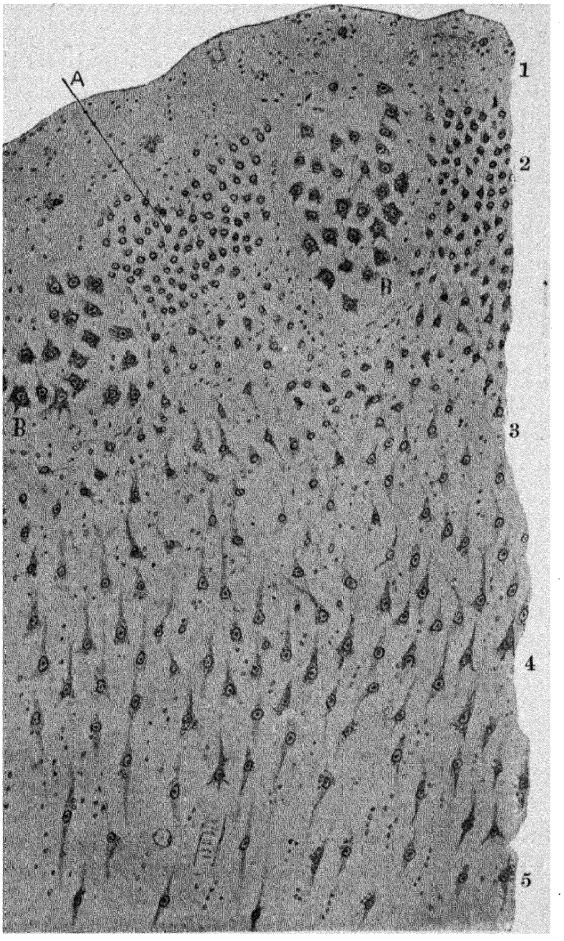


FIG. 351.—SECTION OF OLFACTORY PART OF HIPPOCAMPAL GYRUS (MAN). Nissl's method. (Cajal.)
A, islet of small pyramids; B, islet of large polymorph cells.

plexiform layer itself and in the second layer. Otherwise the plexiform layer shows the usual structures, containing the ramified terminations of the apical dendrons of the pyramids, the terminal arborisations of the cells of Martinotti, and the two kinds of nerve-cell found elsewhere in this layer—viz. the horizontal cells of Cajal and short-axoned cells belonging to Golgi's type ii.

2. *Superficial polymorph layer.*—A layer containing a large number of angular polymorphous cells, some large and others small. In the more central part of the gyrus these cells are in man collected into nests or islets, the islets containing

large and small cells alternately (Hammarberg, Calleja). The large cells, although not pyramidal in shape, appear to be of the nature of cortical pyramids; for each sends one or more strong dendrons into the plexiform layer, and the axon descends into the white matter of the gyrus, giving off collaterals on its way. The small cells of the islets have finer dendrons and their descending axons terminate in the subjacent layers of the grey matter. In most animals these polymorphous cells are not definitely collected into islets.

Besides these cells, which are characteristic of this layer, it also contains, as do all the layers, a certain number of scattered short-axoned cells with their ramifying axons, and many collaterals from the ascending axons of more deeply situated cells. These form a close plexus around the cells of the islets.

3. *Pyramid-layer.*—This contains pyramidal cells, smaller near the second layer but increasing somewhat in size in the deeper parts. They resemble the ordinary cortical pyramids with the exception that in most the basal dendrons are very numerous and come off as a kind of tassel or tuft from the deeper part of the cell-body. These 'tasselled pyramids' are also found in the subiculum and presubiculum and in the sphenoidal nucleus.

4. *Deep polymorph. layer.*—This consists mainly of triangular and fusiform cells with descending axons passing into the white substance.

The white substance is composed of medullated fibres of two kinds, coarse and fine; and between the fibres in man there are scattered many angular cells with ascending axons.

The hippocampal gyrus has no layer of large pyramids, and is relatively to other parts of the cerebral cortex, and especially parts which are related to special senses such as the visual and auditory regions, poor in short-axoned cells. There is no distinct granule-layer, nor are there seen any of the neuroglia-like and double-brush cells which are common in other special-sense regions.

The **subiculum** or part of the hippocampal gyrus which is next to the dentate fissure is characterised by the larger number of medullated nerve-fibres covering the plexiform layer, and by the presence within the plexiform layer of occasional islets of small and medium-sized pyramids. Otherwise it has the same simple structure—compared with the ordinary cortex—as the rest of the olfactory region.

The layers are:

1. *Plexiform* or *molecular*, the characters of which have just been mentioned. Its superficial white fibres, which form strong bundles, enter it from the white centre, piercing the rest of the grey matter (fig. 352). They are mostly passing on to the molecular layer of the hippocampus and fascia dentata, but give off some collaterals to the subiculum itself.

The cell-islets are composed of small pyramidal cells with descending axons. Between the islets run the apical dendrons of the pyramid-cells of the subjacent layer.

2. *Pyramid-layer.*—This contains medium-sized and large pyramids of the ordinary type, but the more superficial tend to be fusiform. The axons pass down into the white matter, where they turn in the direction of the hippocampus. There are also short-axoned and Martinotti cells among the pyramids.

3. *Polymorph layer.*—Many of the cells of this layer have ascending axons passing up to the molecular layer; others have descending axons.

The deep white substance of the subiculum of the hippocampus is thick. Mesially it is continuous with the alveus. Within it are fine and coarse fibres which in some animals tend to separate into two planes (Cajal). The finer fibres (in animals the more deeply situated) are commissural, passing to and from the psalterium dorsale, and are derived from the caudal region of the olfactory cortex.

At the junction of the subiculum with the hippocampus they are collected into a triangular bundle. The coarser fibres constitute the spheno-hippocampal path of Cajal (see below). They pierce the grey cortex of the subiculum in bundles, to reach the surface of the plexiform layer, where we have already met with them. Collaterals from both sets of fibres ramify in the grey substance.

Presubicular region.—This name is given by Cajal to the transitional region between the gyrus hippocampus proper and the subiculum just described.

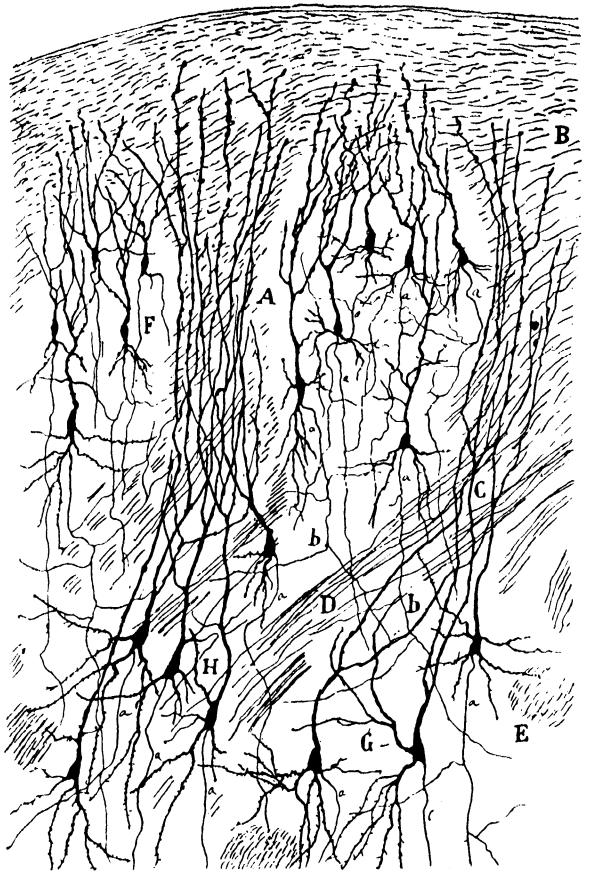


FIG. 352.—SECTION OF SUBICULAR REGION OF GYRUS HIPPOCAMPI OF CHILD FIFTEEN DAYS OLD. (Cajal.)

A, F, islands of small pyramids; B, superficial white layer; C, D, E, bundles of fibres passing down obliquely through the grey matter to the white centre; G, H, large pyramids; *a*, *a*, axons; *b*, a bifurcating axon.

It is characterised from them by the presence of a stratum of closely interlacing fibres with scattered granules (*deep plexiform layer* of Cajal) within the pyramid-layer, separating this into two parts. The plexus is formed by the ramifications of afferent fibres proceeding from the white substance. Some of these fibres ramify also in other layers, and some even reach the plexiform layer and pass towards the hippocampus. The small pyramids superficial to this layer are not disposed in islets.

The subicular and presubicular regions do not, according to Cajal, directly receive fibres from the olfactory root, but from the olfactory cortex proper, through the medium of secondary neurones. They represent, therefore, not a reception-centre, but rather an association-centre for olfaction (olfacto-psychic centre).

Outer or fissural hippocampal region.—As we trace the structure of the hippocampal gyrus outwardly towards the limbic fissure we find the cell-islets disappearing and the layer containing them acquiring the characters of the second layer of the ordinary associational cortex, such as that of the

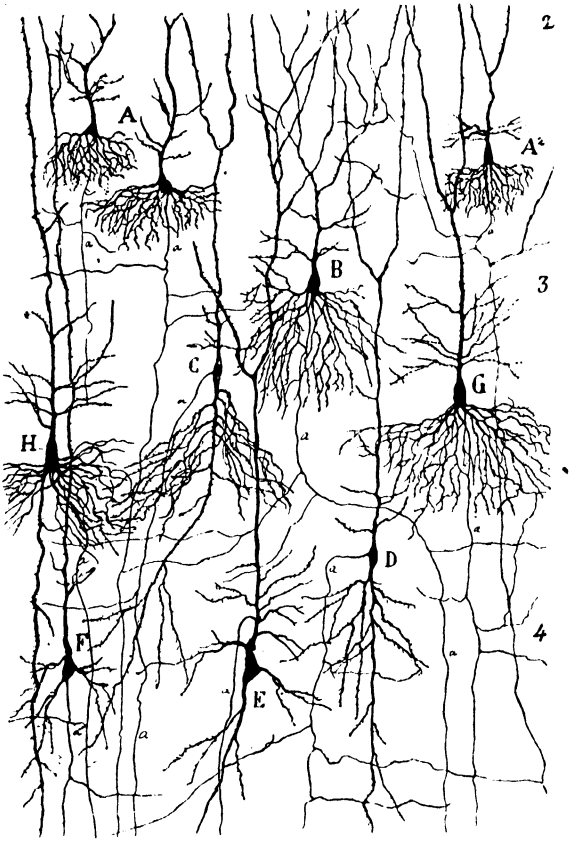


FIG. 353.—PART OF SECTION OF SPHENOIDAL CORTEX OF CHILD ONE MONTH OLD. (Cajal.)

The section including the layers of medium and large 'tasselled' pyramids (2 and 3) and the beginning of the layer of polymorph cells (4); A, A², medium-sized pyramids with tasselled dendrons; C, D, fusiform cells with similar dendrons and the axon springing from the side of the cell; E, F, cells of the polymorphous layer; B, G, H, large tasselled pyramids.

post-central gyrus. A stratum of granules also begins to appear in the large pyramid-layer, separating it into superficial and deep parts, so that the typical seven-layered cortex is produced.

Superior or caudal hippocampal region (sphenoidal cortex or sphenoidal nucleus).—This, also like the presubicular and subicular regions of the hippocampal gyrus, does not receive fibres direct from the olfactory tract, and must be looked upon as an association-centre (Cajal).

Its structure is more complex than that of the rest of the hippocampal region.

Cajal describes seven layers in its grey matter:

1. *Plexiform or molecular layer.*
2. *Layer of large stellate cells.*
3. *A thick layer of medium-sized* and *large pyramids.*
4. *A deep plexiform layer with numerous granules.*
5. *A layer of tangentially disposed cells.*
6. *A layer of granules* and *small pyramids.*
7. *A polymorph layer.*

There is a plexus of nerve-fibres of extraordinary richness in the second, third, and fourth layers, highly characteristic, and giving the region a special importance (Cajal). The fibres are derived partly from collaterals of the axons of the large stellate cells of the second layer and of the pyramids of the third layer; partly from short-axoned cells of the third layer and from axons and collaterals from the sixth layer; and lastly from afferent fibres and collaterals passing up from the white substance. The pyramids in man are characterised by their tasselled basal dendrons (fig. 353). Many of the cells of the sixth layer have their axons at first descending and then curving round and ascending to the more superficial layers, thus recalling the cells with recurrent axon, which are common in the deeper layers of the visual cortex. Moreover, most of the cells of the polymorph layer also have ascending axons.

The axons of the large stellate cells and of the pyramids pass down into the white substance. From this they are continued in three sets. One set forms a *crossed spheno-hippocampal bundle* and passes by the dorsal psalterium to the opposite hippocampus. Another set (*perforating spheno-hippocampal bundle*) passes to the subiculum, pierces its grey matter in the manner already seen (p. 391), and passes to the hippocampus and fascia dentata of the same side. A third set (forming the *spheno-alvear bundle*) also passes to the hippocampus; the fibres do not, however, penetrate the grey matter of the subiculum, but are continued directly into the alveus of the hippocampus.

Hippocampus and gyrus dentatus (figs. 354, 355).—The hippocampus forms a projection into the lateral ventricle corresponding to the depression of the hippocampal fissure on the external surface. Next to the cavity of the ventricle it is covered by ependyma, outside which is the white matter or *alveus*, and outside this again the grey matter of the hippocampus. The following layers occur in the grey matter from without in:

1. A *plexiform layer* which, as in other parts of the cortex, receives the endings of the pyramid-cells. This layer has in its superficial stratum a large number of tangential medullated fibres (*lamina medullaris involuta*) derived from the layer covering the subiculum belonging to the spheno-hippocampal bundles; there are also some derived from the ascending axons of Martinotti cells of the hippocampus. Below this is a molecular stratum resembling that of the cortex generally, and having two kinds of nerve-cells—viz. short-axoned small cells, ending within the layer in a close arborisation, and fusiform tangentially disposed cells of Cajal, which are, however, rarer than in other parts of the brain. Below this again, and still forming a part of what corresponds to the plexiform layer of the ordinary cortex, is the *stratum laciniosum*. This is characterised by an interlacement of nerve-fibres derived from collaterals and terminals of fibres of the alveus (afferent fibres), ascending collaterals of the pyramids, and axons of Martinotti cells. Between the fibres are numerous small stellate or angular nerve-cells (granules), with axons ending within the layer, and long dendrons having both an ascending and a descending direction.

2. *The pyramid-layer.*—There is no distinction seen of strata containing small, medium, and large cells, all being much of the same size and character.

They are moderately large and differ somewhat from the ordinary type in the fact that the cell-bodies are somewhat fusiform and the lateral dendrons few or lacking. The basal dendrons form a pencil descending to the next layer (stratum oriens), through which also the axon passes to reach the alveus. On its way it gives off collaterals, and not infrequently a strong collateral turns superficially to reach the stratum laciniosum. Besides the pyramids, the cell-bodies of which are chiefly confined to the deeper part of the layer, there are a

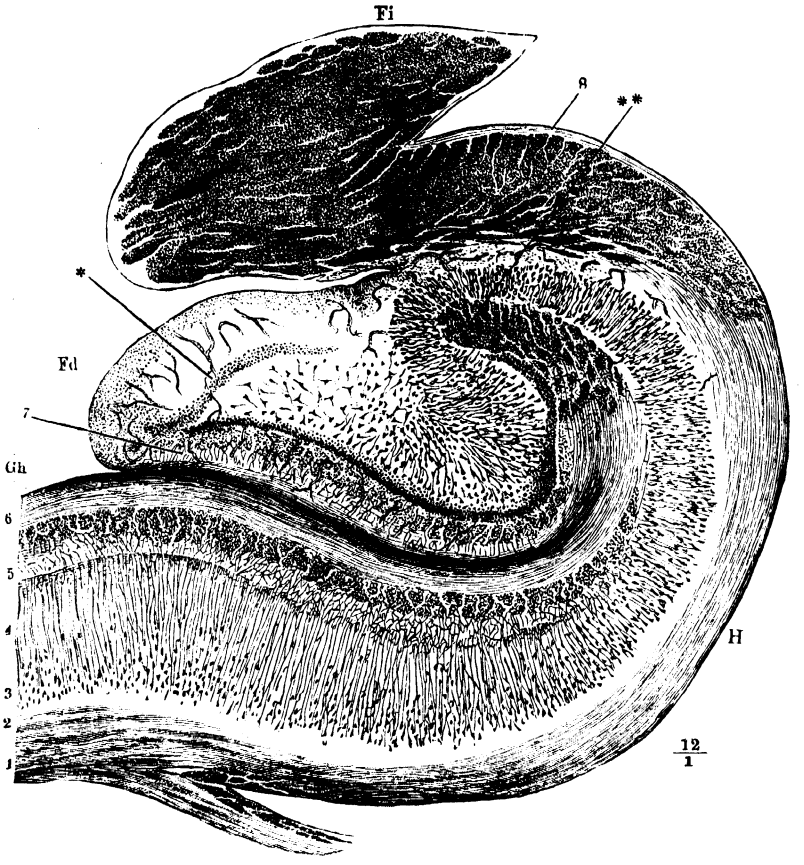


FIG. 354.—SECTION ACROSS THE HIPPOCAMPUS, DENTATE FISSURE, DENTATE GYRUS, AND FIMBRIA HIPPOCAMPI. (After Henle.)

Gh, subicular part of the gyrus hippocampi; *Fd*, gyrus dentatus or dentate convolution: between them is the dentate fissure; *Fi*, fimbria, composed of longitudinal fibres here cut across; 1, 2, medullary centre of the hippocampal gyrus prolonged around the hippocampus, *H*, as the so-called alveus, into the fimbria; 3, layer of large pyramidal cells; 4, stratum radiatum; 5, stratum laciniosum; 6, superficial medullary lamina, involuted around the dentate fissure; **, termination of this lamina, the fibres here running longitudinally; 7, superficial neuroglia of the fascia dentata; *, stratum granulosum.

few short-axoned small nerve-cells (granules) sending their axons, some upwards, others downwards. The superficial half or more of the layer is largely occupied by the apical dendrons of the pyramids proceeding to the stratum laciniosum and molecular layer, and has received the name of *stratum radiatum*. This is best marked in the part next to the subiculum. Within it short lateral ramuscules are here and there given off from the dendrons which appear to form moss-like synapses with the axons of some of the granules.

3. *Polymorph layer* (*stratum oriens*).—This contains cells with axons descending to the alveus, and others (cells of Martinotti) with axons ascending to the molecular layer, as well as short-axoned cells with their axons ramifying either in this or in the pyramid-layer. The more superficial part is marked off from the deeper part by the presence of the descending dendrons of the pyramid-cells, and the collaterals which come off from their axons and form an interlacement.

The *alveus*, which represents the white matter of the hippocampus, is composed of projection-fibres derived from the axons of the pyramids and of commissural (centripetal) fibres passing through the corpus callosum from and

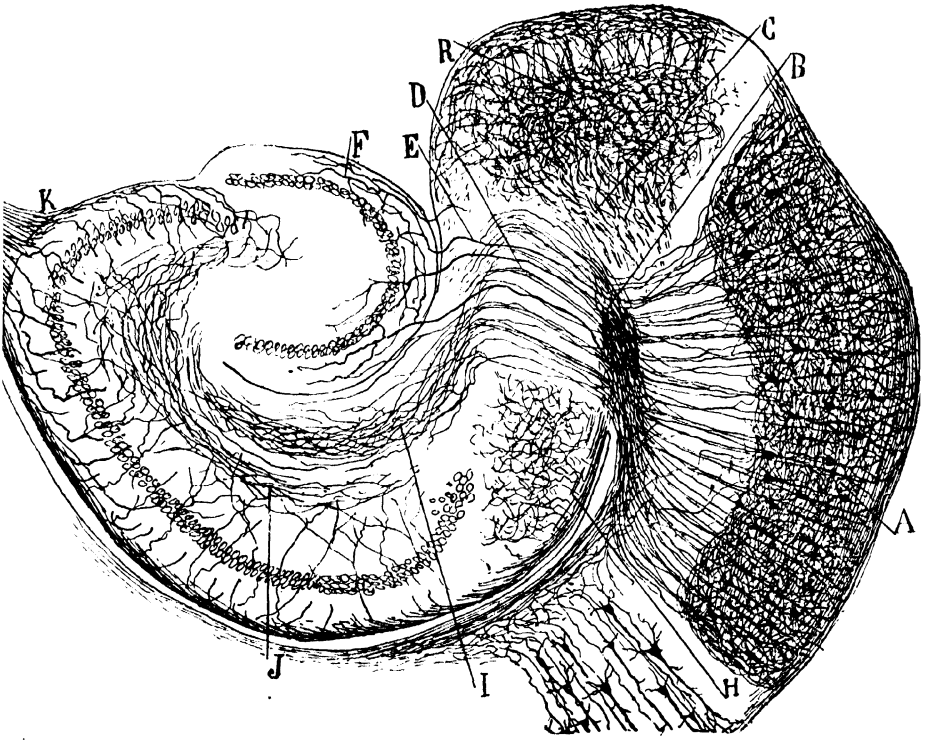


FIG. 355.—HORIZONTAL SECTION OF HIPPOCAMPAL GYRUS AND HIPPOCAMPUS JUST ABOVE THE PLANE OF THE ANGULAR BUNDLE. (Cajal.)

A, hippocampal gyrus; B, emergence of perforating fibres; C, fibres passing to subiculum and forming a close plexus in its deeper layers, R; D, perforating fibres passing to hippocampus; E, others passing to dentate gyrus, F; H, alveus; I, superficial layers of hippocampus with endings of perforating fibres; J, collaterals from alveus.

to the opposite side. These are finer than the projection-fibres and lie nearer the ventricle. Both sets of fibres give off collaterals into the grey matter.

The **gyrus dentatus** must be regarded as a modified part of the hippocampus. It is composed of three layers or zones:

1. The *molecular layer* contains (*a*) short-axoned cells, the axons of which ramify within the layer itself or extend down into the next layer; (*b*) angular cells which have the general characters of those of the next layer and are probably of a similar nature. It receives many medullated fibres from the cells of the fascia dentata itself and from the hippocampus (see below).

2. The *granule-layer* corresponds in position with the pyramid-layer of the hippocampus, and in Ornithorynchus is continuous with it (Elliot Smith),

although the continuity is lost in higher mammals. The cells of this layer are ovoid or fusiform in shape, and in place of a single apical dendron, as in the ordinary pyramids, two or three processes pass from the cell-body into the molecular layer and there end in arborisations. From the base no dendrons are given off, but only an axon which passes down into the succeeding layer and, becoming horizontal, enters the pyramid-layer of the hippocampus (which is continued round towards the middle of the fascia dentata) and terminates among the large cells of this layer in the moss-like synapses which have already been mentioned as occurring in connexion with their dendrons (p. 394). Many of the axons bifurcate and pass in two directions, and all in passing through the next layer give off collaterals which form a close plexus among its cells.

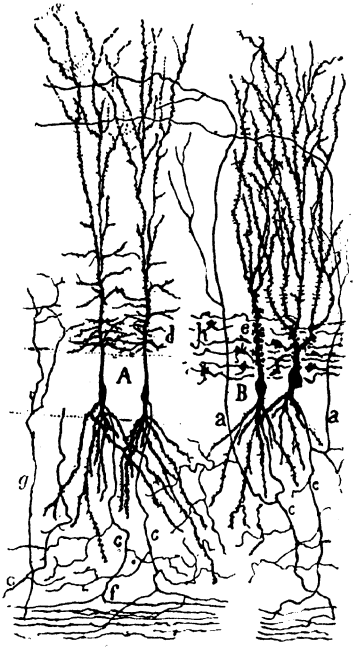


FIG. 356.—PYRAMIDAL CELLS OF HIPPOCAMPUS. (Cajal.)

A, smaller cells of upper part; B, larger cells of lower part; *a*, coarse peripherally directed collaterals; *c*, axons passing to alveus; *d*, *e*, spinous dendrons; *f*, bifurcation of axon; *g*, a collateral from alveus passing into cortex; *h*, moss-fibres among spinous dendrons of larger pyramids.

3. A *layer of polymorphs* which contains several kinds of cells, some with ascending, others with descending axons, and yet others with short axons terminating in the polymorph layer itself. The first named are chiefly found in the part next to the granule-layer and are partly separated from those with descending axons in the deeper part of the layer by a plexiform sub-zone formed mainly of the intricate arborisation of the cell-processes and collaterals.

The ascending fibres pass into the molecular layer, which also contains exogenous fibres derived from the sphenohippocampal fibres of the alveus.

The neuroglia of the fascia dentata contains many long cells resembling detached ependyma-cells, and a certain number of spider-cells.

Nerve-paths.—The hippocampus and fascia dentata have three nerve-paths in connexion with them—viz. one afferent, one efferent, and one commissural.

The *afferent* or *spheno-hippocampal* fibres have already been met with (p. 393). Those from the same side arise from the upper part of the pyriform lobule (superior sphenoidal cortex) and form a bundle or bundles which perforate the grey matter of the subiculum to end in the molecular layer of both hippocampus and fascia dentata. But some pass into the alveus (spheno-alvear) and do not perforate the grey matter.

In addition to the above fibres from the sphenoidal cortex of the same side, others from the corresponding cortex of the opposite side pass across the middle line in the dorsal psalterium. They are at first, in many mammals, gathered into a well-marked triangular bundle, close to the angle of the ventricle. Spreading out under the corpus callosum, they go, some to the presubiculum, some to the superior sphenoidal nucleus, while others, joining the direct or homolateral perforating fibres, pass with them through the subiculum to the molecular layer of the hippocampus.

The *efferent fibres of the hippocampus* are continued into the **fimbria**,

which is formed of the axons of the pyramids. But they also give off a strong collateral in the opposite direction which appears to end in the grey matter of the hippocampus. The efferent fibres are of two kinds, large and small. The large fibres are to be regarded as the *projection-fibres* of the hippocampus. From the fimbria they are continued into the crus of the fornix, but they do not comprise more than about one-fourth of all the fibres of the fimbria. They are continued in the fornix to the corpus mamillare of the opposite side (p. 232). As they pass down in the anterior column a bundle of fibres is given off to the tuber cinereum. The finer fibres, which comprise the majority of the fibres

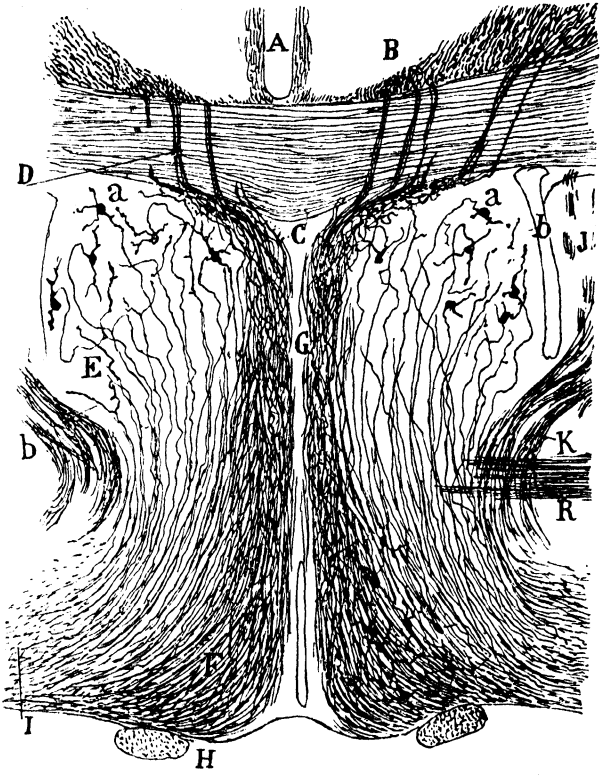


FIG. 357.—CORONAL SECTION OF SEPTUM PELLUCIDUM OF NEWLY BORN MOUSE. (Cajal.)

A, interhemispheric fissure; B, cingulum; C, placed below corpus callosum, has on each side the fornix longus, with which the radiation of Zuckerkandl (G, F) is incorporated; D, fibres of fornix perforating the corpus callosum and passing to cingulum; E, lateral nucleus of septum; H, optic nerve; I, place at which the arched coronal fibres are becoming sagittal; R, anterior commissure.

of the fimbria, are *commissural*. They pass in the ventral psalterium to the fimbria and hippocampus of the opposite side, where they are therefore seen as fine afferent fibres entering the grey matter. Their bundles are, in the psalterium, separated by islets of grey matter or interstitial nuclei (Katenki). The ultimate branches, on reaching the opposite hippocampus, traverse the stratum of pyramids and end chiefly in the stratum radiatum.

Lying between the ventral psalterium and the crura of the fornix, and partly prolonged along the fimbria, is a *triangular nucleus* which, as well as the interstitial nuclei, receives many collaterals from the fibres of the psalterium.

Others pass both from these fibres and from those of the fornix to the nuclei of the septum pellucidum.

According to Cajal, the connexion between the columns of the fornix and the stria thalami which has been affirmed by Honneger and others does not exist.

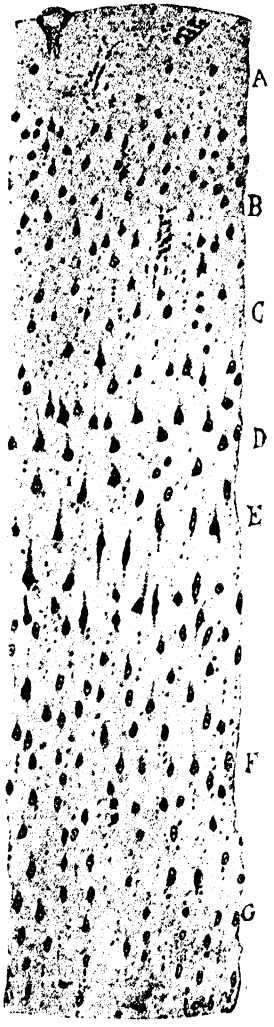


FIG. 358.—SECTION OF CORTEX OF THE INFERIOR PART OF THE GYRUS CINGULI OF MAN. (Cajal.)

A, plexiform layer; B, layer of small pyramids; C, deep plexiform layer; D, large pyramids; E, large spindle-cells; F, polymorph cells; G, white centre.

The nuclei of the septum pellucidum (fig. 357).—The septum pellucidum contains three nuclei—viz. (1) the principal or lateral; (2) the dorsal or triangular, already alluded to; and (3) a median, which is included between the bundles of fibres constituting the so-called olfactory radiation of Zuckerkandl.

The *lateral nucleus* is represented by the grey matter of the side of the septum, and contains chiefly ovoid and stellate cells of medium size. Their axons converge to the lower part of the septum and are continuous with the arciform fibres which were described by Kölliker. These are traceable backwards to the cerebral peduncle, where they become incorporated with the other fibres of the great olfactory stream.

The *triangular* and *median nuclei* contain chiefly small cells. The axons constitute a mesial efferent path, which mingles with the radiations of Zuckerkandl and passes to the superficial layer of the limbic cortex at the base of the brain. Another lateral path also issues from these nuclei and, passing more externally and at a deeper level than the mesial path, ends in the tuber cinereum. Other fine fibres are traceable to the subthalamic region.

The *olfactory radiations* described by Zuckerkandl (fig. 357, G, F) were supposed by that observer to connect the hippocampus with the septum pellucidum. According to Cajal, this is not the case, but the radiations contain fibres of two kinds, ascending and descending. The *ascending fibres* are derived from the cerebral peduncle, and, running over the surface of the subfrontal cortex (to which they give off collaterals), they end by ramifying in the nuclei of the septum pellucidum. The *descending fibres* are projection-fibres of the gyrus cinguli which have left the cingulum and have perforated the corpus callosum to join the fornix longus. Hence they pass downwards to the cerebral peduncle on both sides of the raphe, intermingled with the ascending fibres just described.

The septum also receives fibres from the tænia semicircularis, which arise from the part of the temporal cortex to which the fibres of the olfactory tract pass.

The gyrus cinguli and the cingulum (inter-hemispheric cortex of small mammals).—As compared with the cortex of most parts of the hemisphere, that of the gyrus cinguli is relatively simple. It tends, however,

to become more complex in the part farthest from the corpus callosum. The cingulum arises from it and represents its white matter, but in the higher mammals the white matter of the part farthest from the corpus callosum joins the corona radiata.

The following layers are enumerated in the grey matter (fig. 358)—viz.:

1. The *molecular* or *plexiform*, which contains cells of the usual character and dendron-ramifications from the more deeply lying cells, as well as a rich nerve-plexus derived from (*a*) the fibres of the cingulum, which sends collaterals

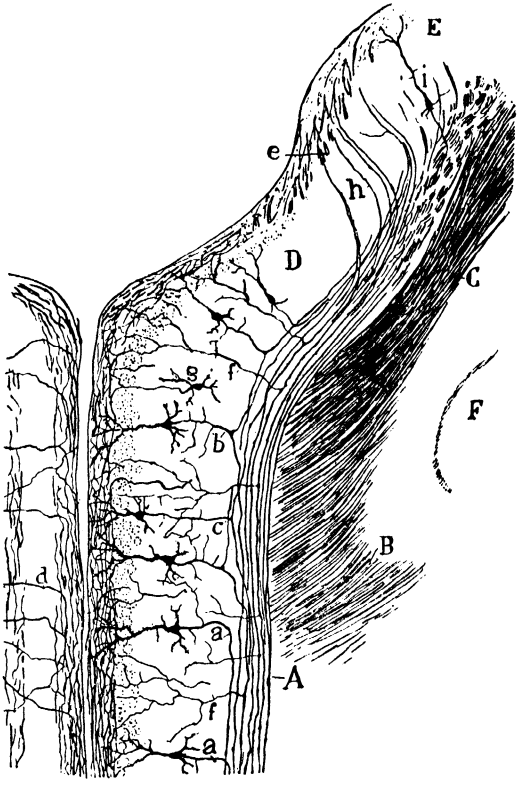


FIG. 359.—FROM HORIZONTAL SECTION OF BRAIN OF MOUSE EIGHT DAYS OLD. (Cajal.)

A, cingulum; B, corpus callosum; C, angular or crossed hippocampal bundle; D, occipital end of hippocampal region; E, subiculum; F, hippocampus; *a*, axons passing anteriorly; *b*, *c*, bifurcating axons; *d*, *e*, *f*, afferent fibres and collaterals ending in cortex; *g*, a cell with peripherally directed axon; *h*, perforating fibres of subiculum.

and terminals into it through the thickness of the grey matter, and (*b*) axons of its own cells and of cells of Martinotti from the deeper layers.

2. A *layer of angular and fusiform cells*, somewhat like the granules of the fascia dentata, with dendrons passing superficially and deeply, and axons passing down to the cingulum.

3. A *deep plexiform layer*, containing some small and medium-sized pyramids and short-axoned cells with ascending axons, and also a close nerve-plexus, formed mainly of collaterals from the cingulum and from the descending and ascending axons of cells of the adjacent layers and the short axons of those of the layer itself.

4. A *layer of large and medium-sized pyramids* of the usual character, with their axons passing down to the cingulum. This layer also has some Martinotti cells, with axons passing towards the surface.

5. A *layer of polymorph cells*, mostly with ascending axon. Among them are medium-sized pyramids.

The descending axons of the cells of the gyrus cinguli (and of the whole inter-hemispheric cortex in small mammals) pass into and form the *cingulum* (fig. 359). In it they turn saggitally, passing either forwards or backwards, and many of them bifurcating and sending a branch either way. The fibres and branches, which trend forwards, are traceable as far as the anterior part of the septum pellucidum to the head of the corpus striatum, where they become incorporated with the main mass of projection-fibres, passing towards the internal

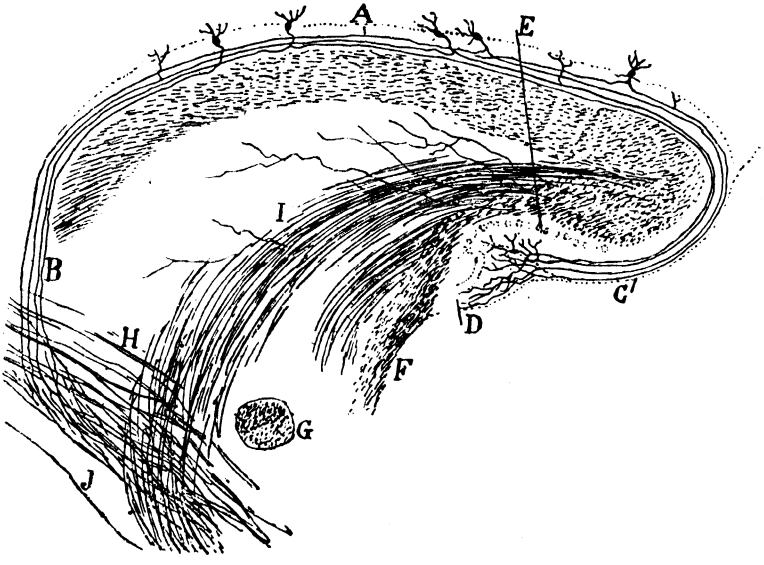


FIG. 360.—SEMI-DIAGRAMMATIC SAGGITAL SECTION OF CORPUS CALLOSUM, NERVES OF LANCISI, AND GYRUS DENTATUS OF MOUSE A FEW DAYS OLD. (Cajal.)

A, fibres of nerve of Lancisi, arising from cells of indusium and most of them bifurcating, the branches passing forwards and backwards; B, projection-fibres passing forwards; C, other branches passing backwards to gyrus dentatus, D; E, hippocampus; F, fimbria; G, anterior commissure; H, olfactory projection-fibres; I, olfactory radiations of Zuckerkandl; between B and I, the septum pellucidum.

capsule. Some may, however, end in the prefrontal cortex (association-fibres). Those which pass backwards end partly in the cortex of the subiculum, hippocampus, and fascia dentata, intermingling with the fibres of the sphenohippocampal tract, partly in the cortex of the occipital lobe, just behind the hippocampal region (occipital extremity of Cajal). Other fibres which are (in the rat) derived mainly from the posterior and middle regions of the inter-hemispheric cortex pierce the corpus callosum in bundles (joining the *fornix longus* of Forel) and pass down through the septum lucidum, intermingled with the olfactory radiations of Zuckerkandl and with fibres from the fornix, to reach the lower zone of the corpus striatum.[1]

[1] See, further, on the cingulum, Redlich, Arb. a. d. Neurol. Instit. Wien, 1904 Zuckerkandl, *ibid.*

Watson [1] describes a special (sensory) area occupying the posterior part of the gyrus cinguli lying behind the splenium of the corpus callosum next to the calcarine (visual) area but differentiated in structure both from this and from the remainder of the gyrus cinguli.

Connected closely with this region of the cortex are the nerves of Lancisi or mesial striæ, the lateral striæ, the indusium, and the fasciola cinerea (fig. 360).

Indusium.—The *nerves of Lancisi* represent the white matter of a rudimentary part of the inter-hemispheric cortex overlying the corpus callosum, termed the *indusium*, and they correspond with the cingulum of the gyrus cinguli. The *lateral striæ* are similar, but their corresponding grey matter is even more rudimentary than the indusium. The *fasciola cinerea*, lying above and behind the splenium of the corpus callosum, has been considered to be a part of the dentate gyrus, but belongs to the indusium (Cajal,[2] Zuckerkandl [3]), and the axons of its cells pass, like those of the indusium-cells, into the nerves of Lancisi, and eventually into the gyrus dentatus.

Like the corresponding fibres of the cingulum the fibres which form the nerves of Lancisi run partly forwards and partly backwards, while some pierce the corpus callosum and join the fornix longus. Those which pass forwards turn round the front of the corpus callosum and, in front of the anterior commissure, curve downwards to enter the corpus striatum, joining, according to Cajal, the olfactory projection-path. Those which pass backwards enter the gyrus dentatus.

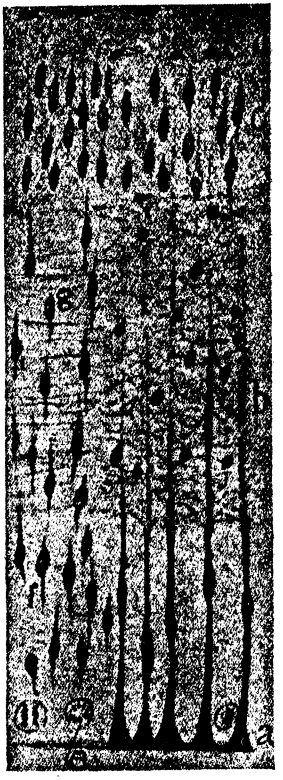


FIG. 361.—SECTION OF CORTEX OF EMBRYO AT COMMENCEMENT OF THIRD MONTH. (Cajal, modified from a diagram by His.)

a, germinal cap; *b*, rudimentary white matter; *c*, rudimentary grey matter; *d*, marginal stratum; *e*, germinal cells; *f*, *g*, uni- and bi-polar neuroblasts.

HISTOGENESIS OF THE CEREBRAL CORTEX.

The cortex cerebri is formed by a thickening of the superior and outer wall of the anterior cerebral vesicle.

As was shown by His, the cortex of the human fœtus of the second month consists of—

1. A *germinal layer*, next to the cavity of the vesicle, recognisable by the karyokinetic nuclei of its cells.
2. A *nuclear zone*, containing the nucleated bodies of the spongioblasts and neuroblasts.
3. An *intercalated zone*.
4. A *marginal zone*, next to the surface.

At the third month (fig. 361) the germinal cells are still recognisable by their dividing nuclei. Many of the neuroblasts of the second zone have altered their position and become superficial, lying immediately beneath the surface layer. A broad layer consisting of non-medullated fibres now separates the nuclear zone from the germinal layer: this is the beginning of the white substance.

Gradually the intercalated zone becomes occupied by the multiplying neuroblasts, which, however, at first show no special differentiation. According to Bolton,[4] who is confirmed by Watson,[5] this begins in the polymorph layer, which is the first of the layers to become distinct in the fœtus, while the (supragranular) pyramidal cells are the last to undergo differentiation, the 'granules' occupying an intermediate position. The differentiation of the pyramid-cells begins

[1] Arch. of Neur. 1907.
[2] Textura del sistema nervioso, 1904.
[3] Arb. a. d. Neurol. Instit. Wien, 1907.
[4] Arch. of Neurology, 1908.
[5] *Ibid.* 1907.

in the deeper layers (Cajal) and gradually extends towards those nearer the surface, so that at birth the largest (and deepest) pyramids are most developed. As with nerve-cells generally, the axon is the first process to appear; then an opposite dendron, so that the cell becomes bipolar; then the basilar dendrons and the branches of the apical dendron; and lastly the collaterals of the axon and the spines of the dendrons. Both Nissl granules and neurofibrils are present at birth.

As in the spinal cord, the neuroglia-cells are developed from the epithelial or ependymal cells, some of which become dislocated and modified in form by giving off numerous ramifying processes. But for a long time the radial fibres from the ependymal cells can be traced through the thickness of the developing grey matter, and in small animals may still, even at birth, reach the surface. In the human subject radially disposed neuroglia-cells are also not uncommon at birth (G. Retzius), but disappear later.

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