Some Of the Pages are Teared and Damage

AN INTRODUCTION TO THE STUDY OF THE NERVOUS SYSTEM

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PREFACE TO THE FIRST EDITION

THIS book, as its title indicates, has been written primarily for students. It is intended to stress particularly the points which we, as teachers, find are not sufficiently clearly expressed elsewhere. In a book intended for such readers no apology therefore is necessary for a certain amount of dogmatism. Brevity and clearness have been our objects. For these reasons controversial matter has been largely omitted, except where it has seemed to us that there is a real difference of opinion. When this occurs we have, as far as possible, stated the opposing points of view.

Minute structure and function have been considered together, but no description of gross structure has been given, as this can be found so admirably expressed in the many modern text-books. Some emphasis has been laid on clinical application, for the sake of hospital students, but neurology and pathology (as such) have been purposely omitted. In order to facilitate references to other books, alternative names have been given where such are in common use, as this book is meant only as an introduction to the study of the Nervous System.

Our thanks are due primarily to Professor Winifred Cullis, who has kindly written the Foreword and given us every encouragement throughout. For the account of recent work on the olfactory nerve connections we are indebted to Professor Elliot Smith and Dr. Una Fielding, and we are deeply grateful to Dr. Linnell, to Dr. Kathleen Sykes and to Mrs. McLellan for their valuable help in criticism and in compiling the Index.

Where other authors have been drawn upon acknowledgment as far as possible has been made in the text.

Finally, we greatly appreciate the helpful consideration given us throughout by our publishers.

E. E. H.
G. M. S.

1929.

PREFACE TO THE SECOND EDITION

SINCE the publication of the first edition of this book considerable advances have been made in the knowledge of the minute anatomy and physiology of the Nervous System.

For this reason we have enlarged the sections devoted to the corpus striatum and diencephalic nuclei, the cerebellum and particularly the autonomic nervous system—the latter in view of the increased interest of this system to surgeons.

In addition, the chapter on the cranial nerves has been considerably revised, and new sections have been added on the cerebrospinal blood vessels and neuroglia. Two tables are included, one showing the various components of the cranial nerves, and the other summarising the autonomic supply of certain structures in so far as it is at present known.

The number of diagrams has been increased ; some of those which have not been found helpful have been replaced, and several new ones added.

Our deepest thanks are offered to Dr. J. C. Greenfield, not only for his continued encouragement, but also for his invaluable assistance at every stage.

Very much help over the difficulties of the autonomic system has been most generously given by Professor J. S. B. Stopford, Mr. J. Paterson Ross and Mr. Leslie Paton. Professor Mary F. Lucas Keene has helped us greatly with various anatomical points, particularly in connection with the cranial nerves.

Our grateful thanks are also due to Sir Farquhar Buzzard, Professor J. Ernest Frazer, Professor Blair, Dr. E. A. Carmichael and Dr. F. E. Reynolds for many helpful suggestions.

We should like to mention the courtesy and able assistance so generously afforded by the Library Staff of the Royal Society of Medicine.

E. E. H.
G. M. S.

1933.

CONTENTS

PART I

PART II

DIAGRAMS

PART I

AN INTRODUCTION TO THE STUDY OF THE NERVOUS SYSTEM

CHAPTER I

NEURONES AND SUPPORTING TISSUES

THE structure of the nervous system is complex, and in order to understand its functions it is of importance to grasp both the minute and the gross anatomy of its various parts.

All nervous tissue arises from the ectoderm of the early embryo, the primitive neural tube giving rise to the brain and spinal cord, and neural crests giving rise to the cranial and spinal ganglia. The primitive epithelium of the neural tube is differentiated at a later stage into neuroglial tissues (ependyma and true neuroglia) and the neurones of the brain and spinal cord, while the cells of the neural crests similarly give rise to neurones and to satellite cells which encapsulate the nerve cells and are continued as cells of Schwann (or neurolemma) of the peripheral nerve fibres. The sympathetic ganglia are formed from embryonic cells that migrate ventralward from the neural crests, and from others that pass out from the neural tube with the anterior spinal root fibres : some of the cells become neuroblasts of the sympathetic ganglia, and others become sheath cells for the neurones, while yet others are transformed into chromaphil tissue.

It appears logical to consider first the elements of which the neurones are composed, namely cells and fibres, and to deal secondly with the supporting tissues including the neuroglia.

I. NEURONES

A. Nerve Cells.

The various types of nerve cells are usually distinguished according to their form, being subdivided into unipolar, bipolar, and multipolar (see Diagram 1).

(*a*) *Unipolar Nerve Cells.*

This type is found chiefly during embryonic development, most neuroblasts assuming this form at some stage of their growth. In the human adult these cells are only sparsely distributed, being found in the retina and in the mesencephalic nucleus of the fifth cranial nerve.

The cell body is more or less spherical, but with a prolongation at one pole

that continues into the single process of the cell: this process usually divides not far from its origin.

(*b*) *Bipolar Nerve Cells.*

The typical bipolar cell, with a spherical cell body prolonged at opposite poles into a process, is somewhat rare, being found only in the peripheral nervous system in certain ganglia, such as Scarpa's ganglion and the spiral ganglion of the cochlea, in the retina, and in the olfactory epithelium.

In mammals the bipolar cells of the posterior root ganglia and of the ganglia on the course of many of the cranial sensory nerves (*e.g.*, Gasserian ganglion) acquire a unipolar appearance, the single process having a T-shaped branching close to the cell; this is due to the growing round of one process to approximate to and fuse with the other process for a short distance.

(*c*) *Multipolar Nerve Cells.*

This type of nerve cell is the most common and the most important, nearly

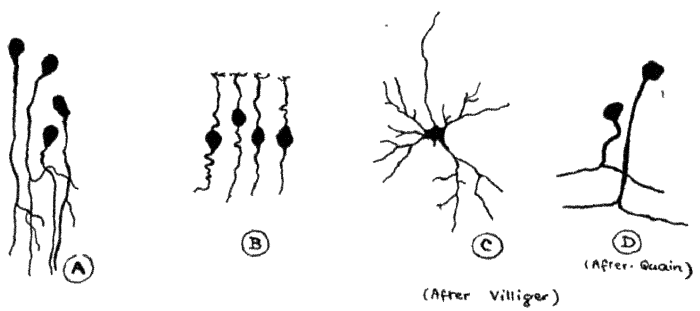

DIAGRAM 1.—Nerve cells of different types.

A. Unipolar cells.
B. Bipolar cells.
C. Multipolar cell.
D. Posterior root ganglion cells.

all cells of the central nervous system and of the sympathetic ganglia being of this form.

The shape of the cell body varies greatly, but in every case there are numerous processes; one of these processes is usually long and unbranched until its termination, although it may give off collaterals at right angles to its axis, and is known as the axon: the other processes are usually shorter and branch frequently in all planes; these are known as the dendrites.

The nucleus of the nerve cell is relatively large, and contains at least one nucleolus and not much chromatin. The cytoplasm contains granules which are large, strongly basophil, and arranged concentrically round the nucleus and passing into the dendrites; these are known as Nissl granules. The part of the cell giving rise to the axon is clear of these granules, but frequently contains yellow pigment (especially in the sympathetic ganglion cells and in old age); this region is known as the "axon hillock." The whole cell is pervaded by exceedingly fine neurofibrils, which extend the whole length of all the cell processes.

B. Nerve Fibres.

The processes of the nerve cells are known as nerve fibres; in the peripheral nervous system the fibres run together in definite bundles known as nerves. The nerve fibres are usually classified, according to their structure, into medullated and non-medullated fibres (see Diagram 2).

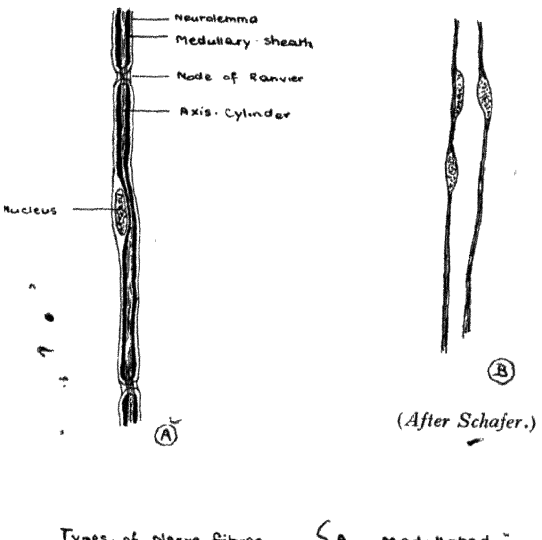

DIAGRAM 2.—Types of Nerve fibres.

(*a*) *Medullated Nerve Fibres.*

The medullated or white fibres consist of a central core—the axis cylinder—which is a direct prolongation of the substance of the cell that gives rise to the fibre. The axis cylinder is enclosed in a fatty sheath (the medullary or myelin sheath); this sheath gives the fibre its white appearance, and is interrupted at regular intervals, producing the nodes of Ranvier. Surrounding the myelin sheath is a thin, nucleated, continuous sheath, known as the neurolemma (primitive sheath or sheath of Schwann); this covering is continuous with the nucleated capsule that encloses each nerve cell in the spinal, cranial and sympathetic ganglia and belongs, with these capsule cells, to the oligodendroglial tissue; it is, however, absent from all nerve fibres actually within the central nervous system, a fact of great importance in connection with the recovery of nerve fibres after injury (see Chapter II.). The neurolemmal sheath possesses one nucleus to every internode.

Medullated nerve fibres vary greatly in size, but have all the same structure, whether axons or dendrites, this latter distinction being fundamentally one of function rather than of structure.

(*b*) *Non-medullated Nerve Fibres.*

The non-medullated or grey fibres consist of a central core—the axis cylinder—a prolongation of the cell of origin of the fibre. There is no myelin sheath, but the axis cylinder is directly enclosed in the neurolemmal sheath; in these fibres the nuclei of this sheath appear to be much more numerous than in the case of the white fibres.

THE NEURONE THEORY

The nervous system consists not merely of cells and fibres, but is built up of definite units known as "neurones." A neurone is a nerve cell with all its

processes, and this conception of the structure of nervous tissue emphasises the fact that a nerve fibre is merely a part of a nerve cell and cannot function or even exist if separated from its cell.

The actual formulation of this theory is due to Waldeyer (1891), but it is based upon previous researches of His, and of Cajal and Golgi. The former showed that embryologically each neurone develops from one neuroblast cell, the processes being outgrowths from the cell and developing into the nerve fibres. To Cajal and Golgi is due the elaboration of the newer histological methods, including the silver chromate technique, whereby it has become possible to investigate accurately the minute structure and distribution of nerve cells and fibres. By this means it has been shown that degenerative changes following injury are con-

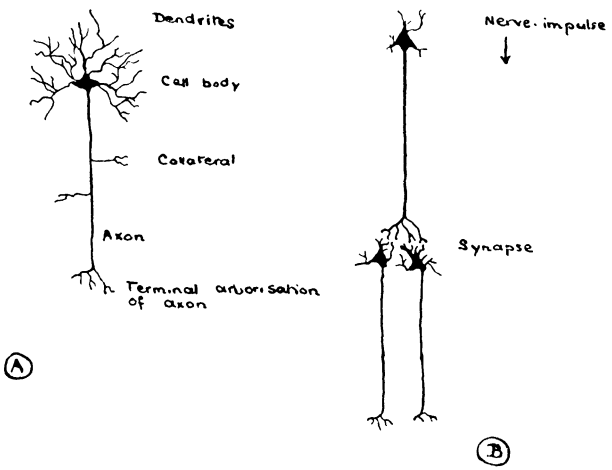

DIAGRAM 3.

A. Schematic representation of a neurone.
B. Schematic representation of junction between neurones.

fined to the neurone involved, with no spreading to adjacent cells or fibres. Thus the nervous unit, or neurone, is to be regarded anatomically and physiologically as a single nerve cell.

Connection is established between neurones by contiguity, and not by continuity, and it is important to distinguish between the types of cell process. The dendrites are those processes conveying the nervous impulse *into* the cell from which they are derived, the axon being the process carrying the nervous impulse *away from* the cell. Thus the linkage of neurones is brought about by the mingling of the terminal arborisation of one axon with the dendrites of the next neurone (see Diagram 3). The surface of separation between two neurones is known as the *synapse* (Sherrington), and it is the variations of physico-chemical conditions at the synapse that explain the characteristics of the reflex arc (see Part II., Chapter VIII.).

A point of extreme importance in
of the nervous system is that conductio
is always in one direction only, namel
from it by the axon. The nerve im
reverse direction, although it can p
direction (see p. 68). This is kno
follows as a necessary corollary to t
dendrites.

II. SU

True connective tissue i n the
meninges, is only present in s mall amo
the function of supporting t he neurones
carried out by the neurogl ia : in the peri
tissue is the main suppo ting substance and
capsular sa[illegible]ite cells surrounding the ganglionic
ath of Schwann of the nerve fibre.

In early embryological stages the neural tube is li
these cells arise the neuroblasts, and in addition there a
their inner surface the *ependyma* cells which line the whole ca
and (*b*) from their outer surface the *true neuroglia*, permeating
of the neural wall and comprising the astrocytes and oligo
structures are, therefore, all ectodermal in origin. Just before
an immigration of cells that are differentiated from the embryo
meninges : these cells rapidly permeate the whole framework of the ner
and are known as *microglia*. They are therefore mesodermal in origin,
although lying within the supporting plexus of true neuroglial tissue they are
one of its constituents.

A. True Neuroglia (or Macroglia).

1. ASTROCYTES (astroglia).

These cells begin to appear in the third month fœtus, and are still imma
at birth : they differentiate in large numbers at the time of myelination.

The cells have processes that branch in all directions, and are provided
expansional attachments or feet to small blood vessels. In the grey matter
cells are usually of the protoplasmic type, with no fibres, while in the fibre t
the processes are straighter and longer, the cells being known as fibrous astrocy
fibrils are present in the fibres and feet.

The astroglia is the real supporting structure of the nervous system ;
suggested, also, that these cells nourish and insulate the neurones, and pos
that by the contraction of their expansions they may make and break syn
contacts (Cajal) ; pathologically they help in cicatrix formation.

It is likely that the cells share with the oligodendrocytes the *rôle* of mainta
myelin.

processes, and this conception of the stru
fact that a nerve fibre is merely a part of a n early embryo but appears with the onset
exist if separated from its cell. astrocytes but have no perivascular feet,

The actual formulation of this theory is du he expansions are small and delicate.
upon previous researches of His, and of Cajal, e medullary sheaths of nerve fibres
that embryologically each neurone develops from or as satellite cells round the nerve
being outgrowths from the cell and developing i
and Golgi is due the elaboration of the newer k is probably the formation and
the silver chromate technique, whereby it has b t they may enable the neurone to
accurately the minute structure and dist ion o e length.
this means it has been shown that dege chan

are round a
Dendrites, and the cell bo nd have pseudopodia: when
spiny twigs that enc dy is small with numerous
c: nervous system, being more d freely. Microglia cell
resent as satellites to nerve cells and their process at in gre
oglia cells.
nts the reticulo-endothelial tissue of the central nervous
s and phagocytosing erythrocytes and cellular debris, thus
of katabolic activity.

CTIONS OF THE SUPPORTING TISSUE.

esponds to injury or to toxic conditions either by rapidly perishing
or g stimulated to hypertrophy, in which case the astrocytes in particular
help to make scar tissue; it is unaffected by a degree of anæmia sufficient to
destroy nerve cells. Microglia is resistant to anæmia and to many conditions that
y neuroglia, but it is stimulated by a sufficient amount of the products of
ounding destruction, *i.e.*, when the condition is either prolonged or severe.
such circumstances, the microgliocytes adjacent to the seat of the destructive
process intervene first, and then distant ones are also attracted by chemiotactic
influence. The cell form may change, giving rise to lamellar cells, fat granule
cells and rod cells.

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For further details of structure, of cell types, and of nerve endings, reference should be made to Quain's "Anatomy" (Schafer), Vol. II., Part I.

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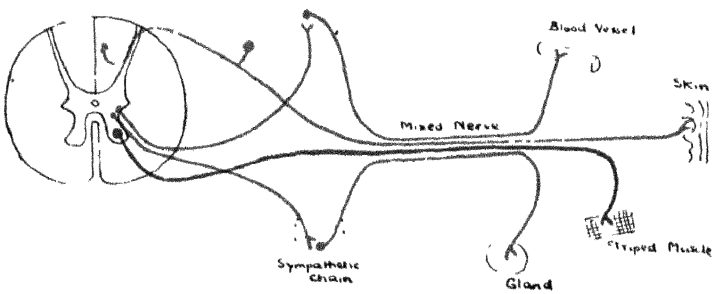

DIAGRAM 4.—Diagram representing the more important Fibres present in a Mixed Nerve

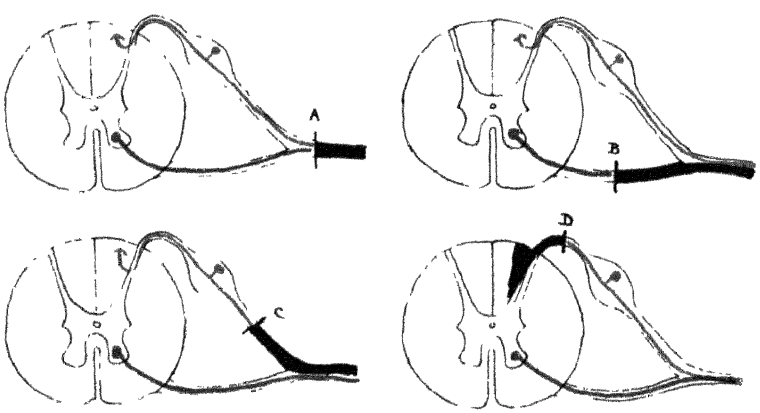

DIAGRAM 5.—Degenerative effects following section of Nerve Roots in various positions. The letter shows the position of the section.

CHAPTER II

CHANGES FOLLOWING SECTION OF NERVES

SECTION of a nerve will produce results varying according to the type of the fibres cut. A mixed nerve usually contains the following fibres :—

(*a*) Motor, arising from anterior horn cells of the spinal cord (somatic efferent).

(*b*) Sensory, consisting of long dendrites coming from a sensory surface or from the muscles and the viscera to their cells in the posterior root ganglion (somatic and visceral afferent).

(*c*) Pre-ganglionic (white) fibres belonging to the autonomic system, arising from lateral horn cells of the spinal cord (visceral efferent).

(*d*) Post-ganglionic (grey) fibres of the autonomic system, arising from one of the sympathetic ganglia (visceral efferent).

Thus the mixed nerve carries motor, sensory, secretomotor, vasomotor, trophic and possibly other special nerve fibres (see Diagram 4).

Section of a nerve fibre is invariably followed by degeneration of that portion which is cut off from its cell. This is well seen in the fibres of the spinal nerve roots (see Diagram 5). Section of the nerve distal to the fusion of the roots (*i.e.*, at A) is followed by degeneration of the nerve, all the motor and sensory fibres being cut off from their cells of origin. Section of the anterior root (*i.e.*, at B) is followed by degeneration of the motor fibres only of the nerve. Section of the posterior root distal to the ganglion (*i.e.*, at C) produces degeneration of the sensory fibres only of the nerve, while section of the posterior root between the ganglion and the cord (*i.e.*, at D) is followed by degeneration of the entering posterior root fibres involving their upward passage in the posterior columns of the cord.

A. Degenerative Changes.

The degenerative changes that take place may conveniently be considered as those occurring in the nerve trunk, both peripheral and central to the lesion, in the nerve cells belonging to the fibres involved, and in the organs supplied by the nerve fibres.

1. DEGENERATIVE CHANGES IN THE NERVE TRUNK (see Diagram 6).

(*a*) *Peripheral Part.*

Within twenty-four hours of the injury marked changes begin in the fibres cut off from their cells. Simultaneously the myelin sheath fragments, the axis cylinder breaks up into small portions, and the neurolemmal nuclei increase in number. Very shortly the protoplasm round these nuclei becomes more definite, and the sheath breaks up into numerous separate cells. Some of these neurolemmal

cells then become phagocytic, engulf the droplets of myelin and fragments of axis cylinder, and pass, full of fat, into the lymph stream. The remainder of the neurolemmal cells then arrange themselves in a row down the middle of the empty sheath, becoming known as the " band fibre," which structure is essential for regeneration of the nerve fibres (see below).

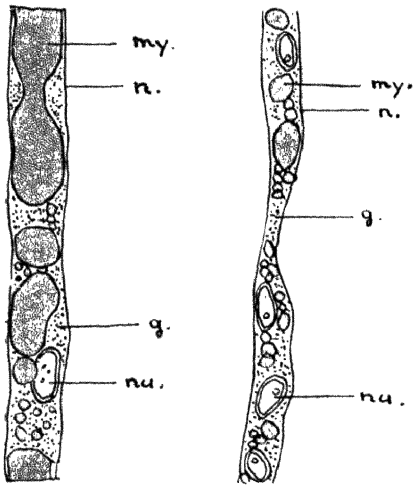

DIAGRAM 6.—Degeneration of Nerve Fibres.
A. Section 50 hours previously.
B. Section 4 days previously.
my. Medullary sheath breaking up into drops of myelin.
n. Neurolemmal sheath.
g. Granular protoplasm replacing myelin.
nu. Nuclei multiplying by division.
Axis cylinder is not shown.
(*After Ranvier.*)

Chemical changes occur in the myelin at the same time as these alterations in appearance. The myelin gives rise to lecithin and kephalin, the latter breaking down into glycerophosphoric acid, choline, and some very unsaturated fatty acids; on the presence of these latter depends the Marchi staining reaction (see Appendix). At the same time the phosphorus content of the tissue diminishes.

(*b*) *Central Part.*

Similar degenerative changes occur also in the fibres central to the lesion, the breakdown spreading up to the next node. At this node the end of the axis cylinder frequently swells, the neurolemma bulging round it.

2. DEGENERATIVE CHANGES IN THE NERVE CELLS (see Diagram 7).

The nerve cells whose fibres have been cut show degenerative changes which are most marked when the lesion is near the cells of origin. The cell becomes globular, and the nucleus takes up an excentric position. At the same time the Nissl granules disorganise and the staining reaction is lost. Later the cell becomes shrunken in appearance, and if no regeneration of the fibres occurs the cell ultimately disappears.

3. CHANGES IN THE ORGANS SUPPLIED.

(*a*) *Muscle.*

The muscles supplied are paralysed, and lose their tone. The muscle substance wastes rapidly, much more quickly than is the case in disuse atrophy. If no regeneration of the nerve fibres occurs, the muscle is ultimately largely replaced by fibrous tissue. The response of the muscle to direct electrical stimulation is altered. A muscle with its nerve supply intact responds to faradic or to galvanic stimulation by a sharp contraction and relaxation, the response at

"make" of the constant current being greater at the kathode than at the anode—*i.e.*, KCC > ACC. When the nerve supply is destroyed the muscle gradually ceases to respond to faradic stimulation, but it reacts to galvanic stimulation with a slow, slug-like contraction, the response at the anode being now greater than that at the kathode—*i.e.*, ACC > KCC. This alteration of response is known as the "reaction of degeneration," or RD, its rate of appearance and its persistence depending on the nutrition of the parts involved.

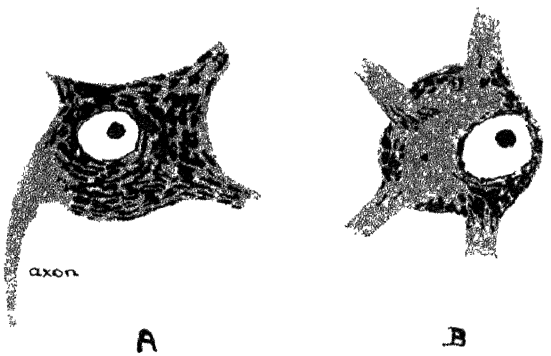

DIAGRAM 7.—Nerve Cells.
A. Normal. B. Showing Nissl Degeneration.
(*After Schafer.*)

(*b*) *Skin.*

There is complete anæsthesia of the part supplied by the nerve, due to interference with the sensory fibres. The skin becomes smooth and shiny, the nails tend to atrophy, and any injury is followed by very slow healing. These changes are in reality trophic, and are due to malnutrition following on disturbance of the vascular supply (see below).

(*c*) *Blood Vessels.*

There is loss of vasomotor control of the blood vessels supplied by these nerve fibres, and consequently loss of tone in the arterioles, and persistent vasodilatation. This leads to a relative stasis, and hence to nutritional changes in the parts supplied, such as the skin.

(*d*) *Glands.*

If the nerve cut contains secretomotor fibres, there is interference with the secretory activity of the gland, which may lead to atrophy of the secreting cells.

(*e*) *Bones.*

If the nerve cut contains fibres supplying bone, the bone substance tends to become rarefied. In the case of a child the growth of the bone is delayed, and the osseous tissue is unusually fragile.

β. Regenerative Changes.

Regeneration of nerve fibres is impossible after the death of the cells of origin of the fibres cut. It is also impossible within the central nervous system, due to the absence of neurolemmal covering to the fibres, this structure being essential for regeneration.

Regeneration occurs by downgrowth of the axis cylinder from the central end. The degenerative changes spread back from the lesion on the central side as far as the next node, the fibre thus terminating in a somewhat swollen axis

cylinder covered with neurolemma. This swollen end then puts out pseudopodial-like processes in the direction of the " band fibre." This structure has been shown to exert a chemiotactic influence on the growing axis cylinder, and one of the processes grows down among the neurolemmal cells of the band fibre, ultimately linking up with the original specialised end organ (*e.g.*, myoneural substance, tactile corpuscle, etc.). The neurolemma thus acts as a guide for the growing axis cylinder, at the same time restraining its progress to the correct path. The myelin sheath of the new fibre is then acquired, and the neurolemmal covering is probably formed by growth from the band fibre.

The way in which regeneration takes place explains why recovery of function is so extraordinarily complete, as this depends on the re-establishment of connection between the nerve cell and the end organ. It also explains why suture of the cut ends of a nerve soon after injury will assist in regeneration of the fibres, the growing ends of the axis cylinders being thus in contact with the " band fibres." There is never any joining of cut fibres, regeneration being always by downgrowth from the central end. Clearly, regeneration is most likely to be complete if the cut fibres are joined at once ; also, the more remote from the cell that the lesion occurs the better will be the chance of complete recovery.

If the growing end of the axis cylinder is prevented by scar tissue from establishing connection with the band fibre, then regeneration is arrested. If the scar tissue is removed and the two freshened stumps sutured together, regeneration then occurs. This has been known to occur as long as two years after the injury.

Non-medullated Nerve Fibres.

After section, these degenerate much more slowly than do the medullated fibres, very little change being apparent for two or three days. Then the neurolemmal cells proliferate, and the axon becomes pale and granular, being finally resorbed without phagocytosis.

Regeneration occurs by downgrowth of processes from the central stump as in the case of medullated fibres : the process is rapid, but the result not usually complete.

Nerve Fibres of the Central Nervous System.

After trauma, the axis cylinder and myelin sheath of severed fibres fragment in the usual way, the debris being removed partly by microglial cells and partly by invading leukocytes that have entered at the wound. Attempts at regeneration are made by outgrowth from the cut axis cylinders in the usual way, but such efforts are abortive, and functional repair does not occur.

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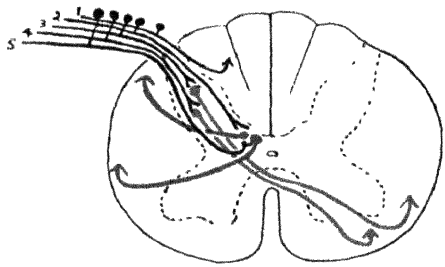

DIAGRAM 8.—Termination within Spinal Cord of Fibres entering by Posterior Root.

1. Passes up by posterior columns to nucleus gracilis or nucleus cuneatus.
2. Ends in Clarke's cells } Relay by direct and indirect cerebellar tracts to cerebellar
5. Ends in Clarke's cells } cortex of same side
3. Ends in posterior horn cells } Relay by spinothalamic and spinotectal tracts of
4. Ends in posterior horn cells } opposite side to thalamus or to corpora quadrigemina and thence to cerebral cortex.

(*After Herrick.*)

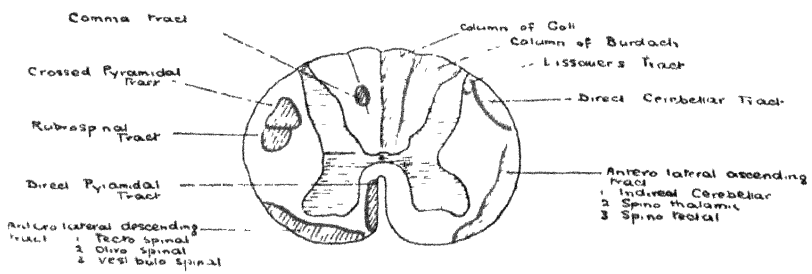

DIAGRAM 9.—Diagram of Cross-Section of Spinal Cord, showing position of Fibre Tracts.
Right : Ascending fibres.
Left : Descending fibres.

CHAPTER III

THE SPINAL CORD: ASCENDING TRACTS

THE long fibres ascending in the spinal cord carry impulses from the periphery. There is only one path of entry into the cord, namely, by the posterior root fibres that enter at the posterior horn; some of these fibres run upwards in the cord, such tracts being part of the first neurone on the particular path; other fibres make a cell station in the cord immediately, and for these paths the tract in the cord is the second neurone (see Diagrams 8 and 9).

Sensory fibres on entering the central nervous system branch into at least two branches, usually an ascending and a descending one. In the cord the descending branch is generally short.

In the following description the tracts are traced up to the cortex of either cerebellum or cerebrum; the interconnections and reflex paths are considered later. (See Diagram 10.)

1. COLUMNS OF GOLL AND OF BURDACH (also known as posterior columns).

Fibres enter by the posterior roots, and at once turn upwards, passing in the posterior columns to the lower part of the medulla, where they end. The tract of Goll is derived from the nerve roots of the lower half of the trunk and lower limbs. As they pass upwards they become displaced nearer to the middle line by the fibres from the upper half of the trunk and upper limbs that constitute the tract of Burdach. The fibres of the tract of Goll terminate in the nucleus gracilis, and those of the tract of Burdach in the nucleus cuneatus; these nuclei appear as outgrowths of the central grey matter into the fibre columns, just below the level of the lower border of the olives.

The second neurone arises from the cells of the nuclei gracilis and cuneatus, the fibres crossing at once anteriorly to the central canal as the sensory decussation (or internal arcuate fibres); the crossed fibres take up a position between the olives, and pass upwards as the medial fillet to end in the optic thalamus (lateral nucleus), gradually becoming more posterior in position as they ascend.

The third neurone arises in the thalamus, passes out by the anterior and posterior limbs of the internal capsule, and proceeds as part of the corona radiata to end in the post-Rolandic cortex of the cerebrum.

This path from periphery to cerebral cortex thus consists of three neurones, and gives a crossed relation. (Some medial fillet fibres end in the subthalamic and hypothalamic nuclei.)

There is a further connection with the cerebellum. Some fibres arising in the nuclei gracilis and cuneatus pass as external arcuate fibres (some crossed, but mostly uncrossed) to the cortex of the cerebellum by the inferior peduncles.

2. LISSAUER'S BUNDLE (also known as marginal bundle).

Incoming posterior root fibres give off a small branch which runs upwards in a position just anterior to the tip of the posterior horns. These fibres, many of them unmyelinated, run up for a few segments, and then turn into the central grey matter, and end by arborising round cells in this position.

These fibres are connector, and do not carry impulses to higher centres.

3. DIRECT CEREBELLAR TRACT (also known as dorso-spino-cerebellar, or tract of Flechsig).

This tract lies on the lateral surface of the cord. Entering fibres pass to Clarke's column of cells of the same side at the root of the posterior horn ; here they end. The second neurone arises from these cells, the fibres passing out to the lateral position, where they run upwards, entering the cerebellum of the same side by the inferior peduncle and ending by arborisation in the cerebellar cortex.

4. GOWERS' TRACT (also known as antero-lateral ascending).

The ascending fibres running in the antero-lateral region of the cord are known collectively as Gowers' tract. This tract comprises three groups of fibres—the spinothalamic, the spinotectal and the indirect cerebellar.

(*a*) *Spinothalamic Fibres.*

Fibres entering by the posterior roots pass in to arborise round cells in the posterior horns of the same side. The axons of these cells, making the second neurone on the path, cross in the anterior commissure, and run up in the antero-lateral position to end in the lateral nucleus of the optic thalamus of that side. The third neurone passes from the thalamus by the anterior limb of the internal capsule to the post-Rolandic cerebral cortex. (According to Cajal this path is always broken at or below the medulla.)

(*b*) *Spinotectal Fibres.*

The first neurone of this path also consists of the posterior root fibres that end in connection with posterior horn cells of the same side. The second neurone crosses to the opposite side and runs up in the antero-lateral position to end round the cells of the inferior corpora quadrigemina. The third neurone passes up through the internal capsule to end in the post-Rolandic cerebral cortex.

(*c*) *Indirect Cerebellar Fibres* (also known as ventro-spino-cerebellar).

Entering posterior root fibres arborise round cells of Clarke's column on the same side. From these cells fibres pass out to the antero-lateral position on the same side, and run up to pass to the cerebellar cortex by the superior peduncle.

It will be seen, therefore, that the connection between the periphery and the cerebral cortex is a contralateral or crossed one, and that between the periphery and the cerebellar cortex is ipsolateral or uncrossed.

2. LISSAUER'S BUNDLE (also known as marginal bundle).

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(*c*) *Indirect Cerebellar Fibres* (also known as ventro-spino-cerebellar).

Entering posterior root fibres arborise round cells of Clarke's column on the same side. From these cells fibres pass out to the antero-lateral position on the same side, and run up to pass to the cerebellar cortex by the superior peduncle.

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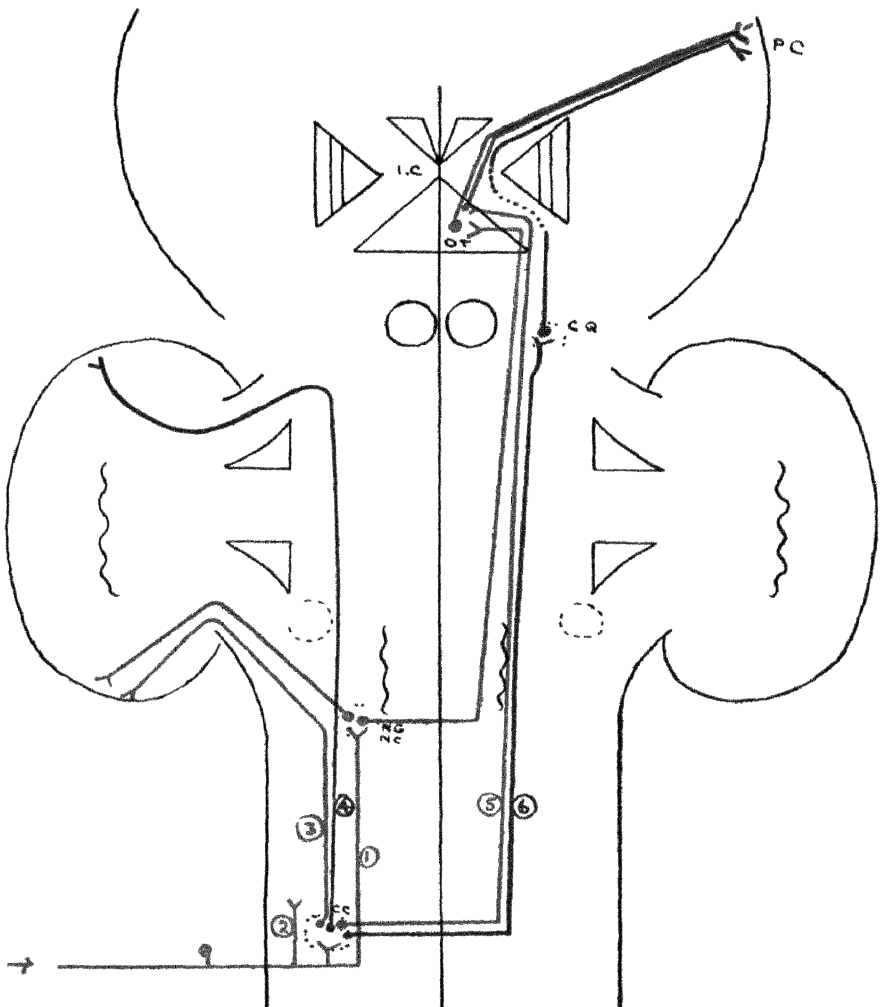


DIAGRAM 10.—Ascending Tracts of the Spinal Cord.

P.C. Post-Rolandic cerebral cortex.
O.T. Optic thalamus.
C.Q. Corpora quadrigemina.
N.G., N.C. Nuclei gracilis and cuneatus.
C.C. Clarke's cells, and posterior horn cells.
I.C. Internal Capsule.

1. Columns of Goll and Burdach
2. Tract of Lissauer.
3. Direct cerebellar tract.
4. Indirect cerebellar tract.
5. Spino-thalamic tract.
6. Spino-tectal tract.

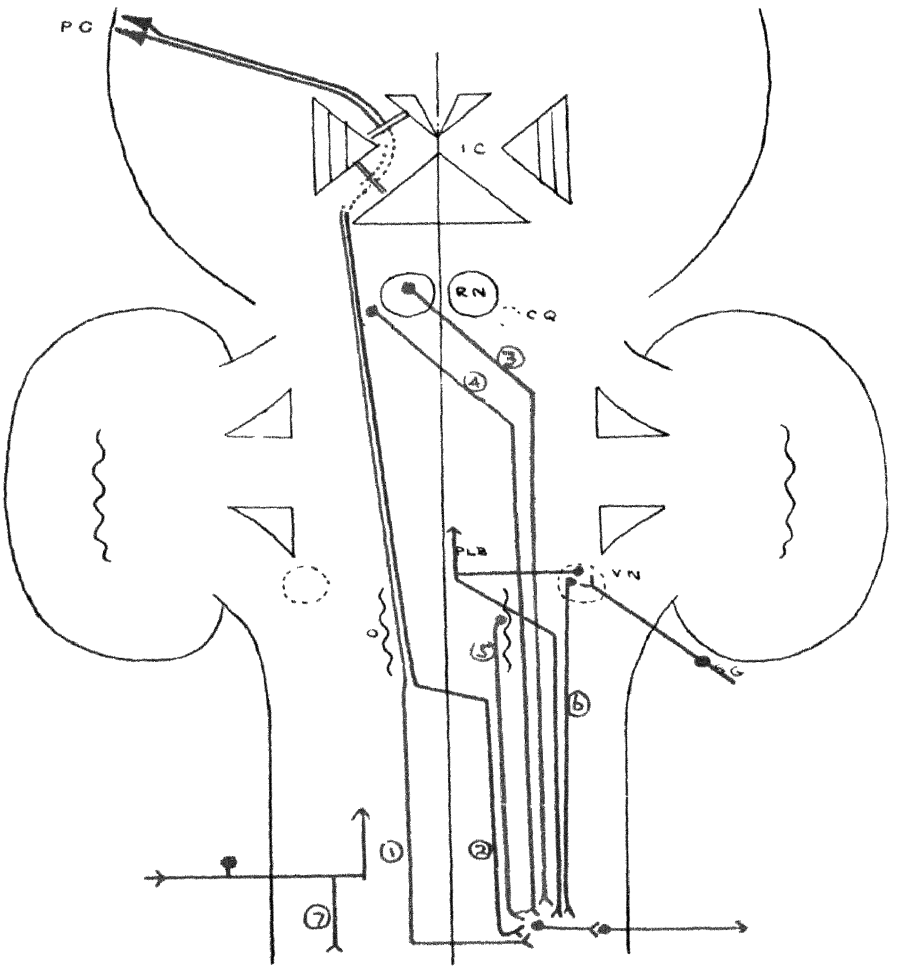


DIAGRAM 11.—Descending Tracts of the Spinal Cord.

P.C. Pre-Rolandic cerebral cortex.
I C. Internal capsule.
R.N. Red nucleus.
C.Q Corpora quadrigemina.
V.N. Vestibular nuclei.
S.G. Scarpa's ganglion.
P.L.B. Posterior longitudinal bundle.
O. Olive

1. Direct pyramidal tract.
2. Crossed pyramidal tract
3. Rubrospinal tract.
4. Tectospinal tract.
5. Olivospinal tract.
6. Vestibulospinal tract.
7. Comma tract.

CHAPTER IV

THE SPINAL CORD: DESCENDING TRACTS

THE long fibres found descending in the spinal cord all terminate by turning into the central grey matter and arborising round cells there. A connector neurone carries the impulse to a cell in the anterior horn, and the axon of an anterior horn cell then passes out as an anterior root fibre to join a spinal nerve. These descending fibres originate in various higher centres, and run in definite groups or tracts in the cord (see Diagram 11).

1. DIRECT PYRAMIDAL TRACT.

Pyramidal cells in the pre-Rolandic cerebral cortex (ascending frontal convolution) give rise to axons which pass down in the corona radiata, through the genu and anterior two-thirds of the posterior limb of the internal capsule, through the middle three-fifths of the crusta, through the pons whose crossing fibres split up the pyramidal tracts into small bundles, through the medulla, where they appear as the pyramids on the anterior surface, to the cord; in the cord these fibres are found at the side of the anterior fissure. The fibres then cross in the anterior white commissure to end round cells of the opposite anterior horn. This tract does not extend below the thoracic region. (The pyramidal fibres give off collaterals to the basal ganglia, pontine nuclei, and reticular formation (Cajal).)

2. CROSSED PYRAMIDAL TRACT (also known as lateral pyramidal).

Fibres arise as axons of the pyramidal cells of the pre-Rolandic cerebral cortex, and follow the same path as the direct pyramidal fibres, running with them as far as the lower border of the medulla; here they cross over from the anterior position to the lateral position on the opposite side, cutting off the anterior horn of grey matter in so doing. (This part of the grey matter gives rise to the nucleus ambiguus and other nuclei of cranial nerves.) The fibres then run down the cord in the lateral position, ultimately turning in to connect with cells of the grey matter at various levels.

(*Aberrant Pyramidal Fibres.*—Some corticospinal fibres leave the main bundle below the internal capsule, and run, some with the medial fillet and some more laterally, ultimately rejoining the bundle in the medulla.)

3. RUBROSPINAL TRACT (also known as pre-pyramidal or von Monakow's bundle).

Fibres arise as axons of cells in the red nucleus; they cross immediately to the opposite side anteriorly to the central canal as the decussation of Forel. They

then pass down as a distinct tract to the spinal cord, where they are found immediately anterior to the crossed pyramidal tract. Ultimately the fibres turn in to connect with cells of the grey matter of the same side. This tract is relatively more developed in animals than in man, where it probably ends in the olives, the path being carried on by the olivospinal tract.

4. Tract of Lowenthal (also known as antero-lateral descending).

The fibres found descending in the antero-lateral region of the cord can be divided into four groups—thalamospinal, tectospinal, olivospinal and vestibulospinal.

(*a*) *Thalamospinal Fibres.*

Fibres arise in the thalamus, cross to the opposite side, and pass downwards to the cord, many of them having a cell station in the olives.

(*b*) *Tectospinal Fibres* (predorsal bundle of Held).

Fibres arise from the superior corpora quadrigemina, cross to the opposite side in the decussation of Meynert anteriorly to the central canal, and pass out to the antero-lateral position; they then run down into the cord, and turn in to connect with cells of the grey matter of the same side.

(*c*) *Olivospinal Fibres* (tract of Helweg).

Fibres from the cells of the olivary nuclei also pass down to the cord in the antero-lateral position; some are crossed, and some uncrossed.

(*d*) *Vestibulospinal Fibres.*

These fibres are derived from the various vestibular nuclei of the same side. The details of these connections will be found in Part I., Chapter VI.

5. Comma Tract (also known as the fasciculus interfascicularis or tract of Schultze).

The incoming fibres of the posterior roots give off short descending branches, which run downwards in the cord for several segments before turning in to connect with posterior horn cells of the same side. (This tract thus corresponds to Lissauer's tract, which passes upwards, and, like it, contains also fibres of intraspinal origin.) The position of this tract varies at different levels in the cord, and receives in consequence different names :—

C. 1 to T. 10.—Comma tract, lying deeply between columns of Goll and Burdach.

T. 10 to L. 3.—Septomarginal tract, lying next to the posterior septum.

L. 3 to S. 1.—Oval area of Flechsig, lying medially.

Sacral.—Posterior triangle of Gombault and Phillippe, lying most posteriorly.

Ground Bundles (or fasciculi proprii).

Immediately surrounding the grey matter of the cord are the ground bundles, which are composed of short ascending and descending fibres of intraspinal origin, that serve to connect different levels of the cord. The anterior ground bundle contains in addition descending fibres of the posterior longitudinal bundle.

Formatio Reticularis.

This consists of irregular collections of grey matter traversed by white fibres that are passing in all directions. In the spinal cord it is particularly well marked in the cervical region where it occupies a position in the lateral white columns opposite the base of the posterior horns. In the medulla it lies in part dorsal to the pyramids, medial to the hypoglossal nerve and extending up to the central canal, and in part dorsal to the olive and lateral to the hypoglossal nerve, this latter portion being more cellular than the former. In the pons it is scattered, and occupies that part not already filled by the central grey matter, named nuclei, and principal fibre tracts : it extends up into the lower part of the midbrain.

CHAPTER V

CEREBELLAR CONNECTIONS

THE cerebellum is composed of two large lateral hemispheres which are connected by the small median vermis. Within each hemisphere is the dentate nucleus, a mass of cells somewhat similar in appearance to the inferior olive. In close relation to the dentate nucleus are found the nuclei emboliformis and globosus. Near the mid-line and in the roof is found the nucleus fastigius.

The cerebellum receives impulses from all parts of the nervous system, the entering fibres passing straight to the cortex, where they arborise round the various cells present. The only exception to this rule is found in connection with the vestibular fibres, some of those that enter the cerebellum from Deiters' nucleus passing directly to the fastigial nucleus. All the fibres that leave the cerebellum arise in the various nuclei, of which the dentate is the largest. The connection between the cortex and these nuclei is provided by the Purkinje cells ; the dendrites of these cells arborise in the outer layer of the cerebellar cortex, and their axons pass to the cerebellar nuclei ; the axons of the Purkinje cells never leave the cerebellum.

It is convenient to consider the cerebellar connections under the headings of entering and leaving fibres as found in the various cerebellar peduncles (see Diagram 12). The following list includes the most important of these fibres.

I. INFERIOR CEREBELLAR PEDUNCLE (or restiform body).

A. **Entering Fibres**, passing to the vermis, except olivary fibres which pass to the lateral hemispheres.

1. Direct cerebellar tract, from same side of cord.
2. External arcuate fibres, from nuclei gracilis, cuneatus, and arcuatus, of same side.
3. Vestibular fibres, from nuclei Deiters, Bechterew, and vestibularis, of same side.
4. Olivary fibres, from olivary nuclei of both sides, chiefly crossed.

B. **Leaving Fibres**, arising from nucleus fastigius.

5. To nuclei of Bechterew and Deiters of same side, and thence relayed by
   (*a*) Vestibulo-spinal tract down cord.
   (*b*) Posterior longitudinal bundle up to nuclei of cranial nerves 6, 4, and 3, and down cord in anterior ground bundle.
6. To olives of both sides, and thence relayed by olivospinal tract down cord.
7. To formatio reticularis of medulla, thus connecting with motor nuclei of cranial nerves.

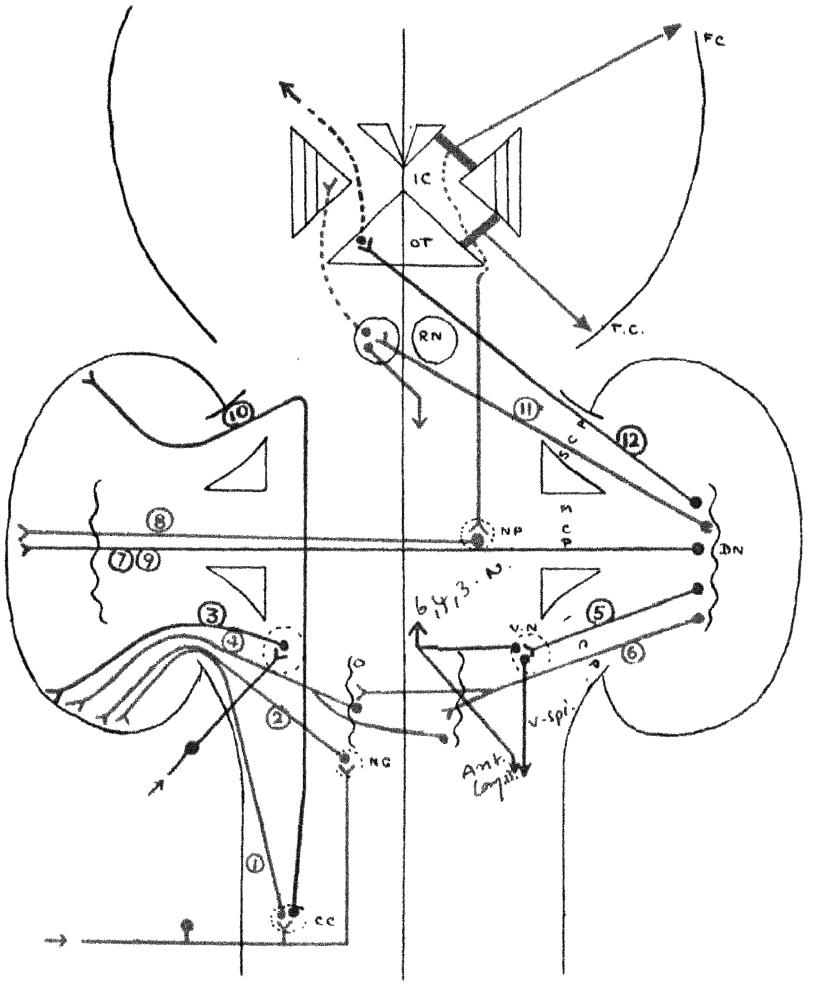


DIAGRAM 12.—Important Cerebellar Connections.

I.C. Internal capsule.
O.T. Optic thalamus.
F.C. Frontal cerebral cortex.
T.C. Temporal cortex.
R.N. Red nucleus.
S.C.P. Superior cerebellar peduncle.
M.C.P. Middle cerebellar peduncle.
I.C.P. Inferior cerebellar peduncle.
N.P. Nuclei pontis.
D.N. Dentate nucleus.
V.N. Vestibular nuclei.
O. Olive.
N.G. Nuclei gracilis and cuneatus.
C.C. Clarke's cells.

1. Direct cerebellar fibres.
2. External arcuate fibres.
3. Vestibular fibres.
4. Fibres from olives.
5. Fibres to vestibular nuclei.
6. Fibres to olives.
7, 9. Fibres from cerebellar nuclei of one side to opposite cerebellar cortex.
8. Fibres from nuclei pontis (cortica-pontine cerebellar).
10. Indirect cerebellar fibres.
11. Fibres to red nucleus.
12. Fibres to optic thalamus.

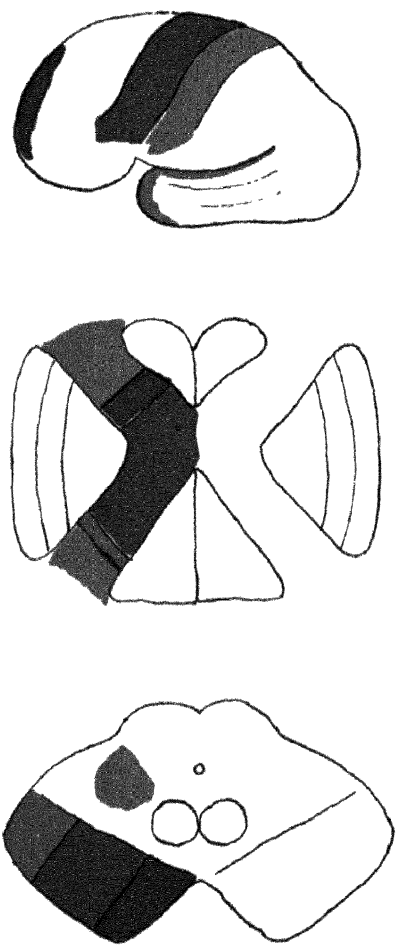


DIAGRAM 13.—Diagram to show Relative Positions of Important Fibres in Internal Capsule and Mid-brain.

Blue : Motor (pyramidal).
Green : Sensory (fillet group).
Red : Temporo-pontine cerebellar
Purple : Fronto-pontine cerebellar.

II. Middle Cerebellar Peduncle.

A. **Entering Fibres,** passing to the lateral hemispheres.

8. From cerebellar nuclei of opposite side.

9. From pontine nuclei of opposite side (temporo-pontine-cerebellar tract or bundle of Türck, and (?) fronto-pontine-cerebellar tract). Collaterals of pyramidal fibres also connect with pontine nuclei.

B. **Leaving Fibres.**

10. To opposite cerebellar cortex.

(The crossing fibres of these three groups 8, 9, 10, cross ventrally in the pons.)

III. Superior Cerebellar Peduncle.

A. **Entering Fibres,** passing to the vermis.

11. Indirect cerebellar tract, from same side of cord.

[11A. From tectum, for visual reflexes : tract not actually demonstrated in man.]

B. **Leaving Fibres,** arising from all nuclei except nucleus fastigius.

12. To opposite red nucleus, and thence relayed—

(*a*) To globus pallidus and lateral nucleus of optic thalamus of same side.

(*b*) By rubrospinal tract to opposite side of cord.

(*c*) To reticular formation of pons and medulla.

13. To opposite optic thalamus (lateral nucleus), and thence relayed to cerebral cortex.

Thus the cerebellum is connected on both afferent and efferent sides with the same side of the cord, and with the opposite side of the cerebrum. It should be noticed also that in the superior cerebellar peduncles fibres entering the cerebellum are uncrossed, and those fibres leaving the cerebellum (brachium conjunctivum) cross as the decussation of the superior peduncles anteriorly to the Sylvian aqueduct.

The connection between cerebellum and cerebrum is a crossed one, consisting, on both afferent and efferent paths, of two neurones (see Diagram 13).

The dentate nucleus receives its afferent fibres chiefly from the lateral hemispheres, which in their turn receive fibres from the nuclei pontis (the cell station on the descending path from the cerebral cortex), and from the olives. The nucleus fastigius is connected closely with the vestibular paths, and this nucleus together with the nuclei globosus and emboliformis receives its afferent fibres from the vermis. The efferent cerebellar fibres pass out in the inferior peduncles from the nucleus fastigius, and in the superior peduncles from the remaining three nuclei.

CHAPTER VI

DEEP CONNECTIONS OF THE CRANIAL NERVES

By deep connections of the cranial nerves are meant the connections of these nerves within the brain substance. In spite of similar nomenclature, it is essential to distinguish between a *motor* nucleus and a *sensory* nucleus.

The *motor* nucleus of a cranial nerve consists of a group of nerve cells the axons of which pass outwards from the brain as the fibres of the motor nerve.

The *sensory* nucleus of a cranial nerve is made up of a group of cells around which arborise the incoming axons of cells which are found in some outlying ganglion. This outlying ganglion is the *true* nucleus of the sensory nerve, and the intracerebral " nucleus " is only a relay station on the path of the nerve. This station may relay impulses up to the higher centres or downwards to the spinal cord.

The connection between the cerebral cortex and the motor nuclei is in most cases not definitely known, although it is usual for a motor nucleus of one side to receive impulses from the cortex of both sides. In the ensuing description mention is made only of the cortical connections where there is definite evidence of such paths.

It should be pointed out that the principal named nerve trunks and their branches are collections of a very great number of nerve fibres, and that it is possible for one " nerve " to contain fibres which have entirely different functions. In the process of branching the fibres devoted to a specialised function may leave the parent trunk, and pursue their path along another named nerve, while the rest of the fibres continue in the main pathway. Furthermore, certain specialised fibres may use a nerve pathway for a short distance and then pass on in the collection of fibres which compose another named nerve. This is well shown by the complicated course pursued by the fibres conveying taste from the anterior part of the tongue. These fibres use a series of pathways during their course from the tongue to the brain, and yet their function remains distinct throughout.

This shows clearly that a " physiological " nerve and an " anatomical " nerve are not by any means the same.

(See Diagram 14.)

The position of the various nuclei of the cranial nerves within the brain stem will be made clearer by a consideration of the various components of the nerves, both spinal and cranial. These are usually divided into somatic and visceral (or splanchnic).

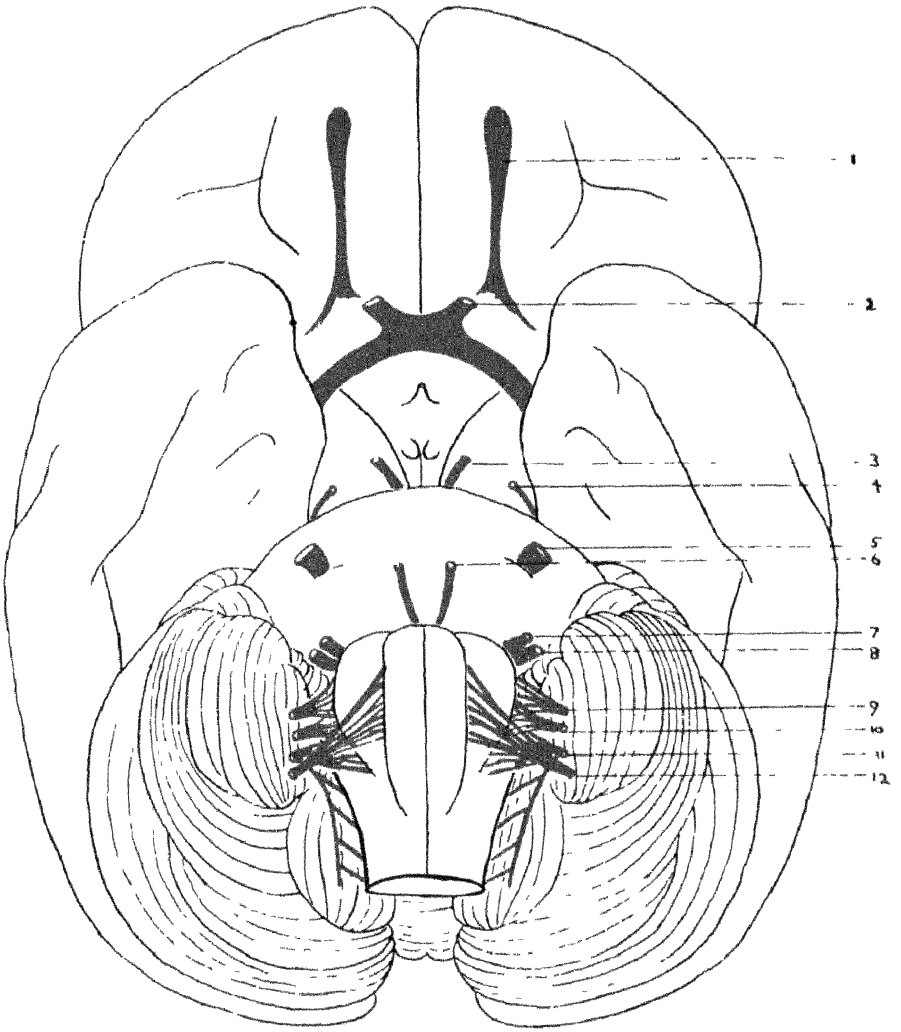
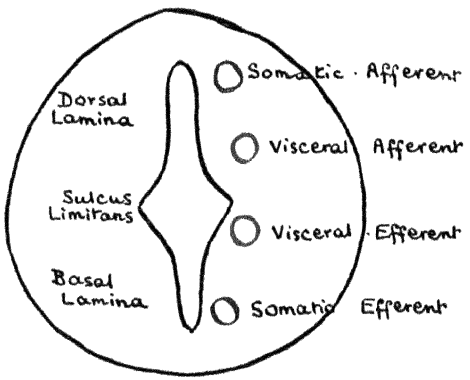
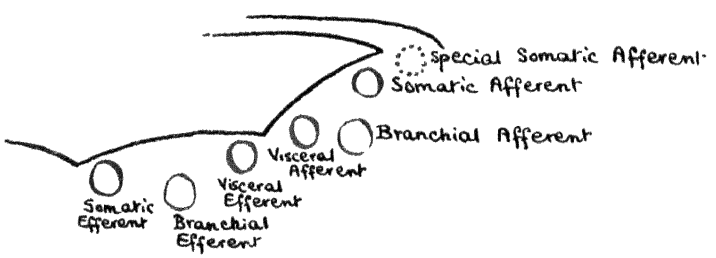


DIAGRAM 14 - Basal Aspect of Brain, showing Cranial Nerves



Hypothetical localisation of primitive nuclei. (After Frazer)



Localisation in the brain-stem of the nuclei of the special components (See Table, p 33)

The *somatic* fibres innervate the skeletal muscles and body surface, the afferent fibres conveying exteroceptive impulses received from the surface and sense organs, and proprioceptive impulses from within the body, *i.e.*, muscles, joints, tendons and vestibular part of the ear.

The *visceral* fibres innervate the visceral and vascular systems, including all involuntary muscle and glandular tissue, the afferent fibres conveying interoceptive impulses from these structures.

In addition to these groups of fibres, in the cranial nerves are found *special visceral efferent* (sometimes called lateral somatic), or branchial, fibres supplying the striped muscle derived from the branchial arches, *special visceral afferent* or branchial fibres conveying impulses from the special visceral sense organs (*i.e.*, olfactory mucous membrane and taste buds), and *special somatic afferent* fibres from the special somatic sense organs, the eye and the ear. The nuclei of these fibres in the brain stem are usually found lying between the true somatic and visceral nuclei. (See Diagram 15.)

It has been shown that embryologically the dorsal lamina of the spinal cord and brain stem is concerned particularly with receiving afferent impulses, while the basal lamina is concerned with efferent functions.

CRANIAL NERVES

* 1. OLFACTORY (sensory).

Cells of Origin.—Special bipolar cells in the nasal mucous membrane.

Axons.—Pierce the cribriform plate of the ethmoid in twelve to fifteen bundles and enter the olfactory bulb, arborising round mitral cells in the bulb.

Secondary Neurone.—Arises in the bulb. The axons of the mitral cells pass in the olfactory tract along the under-surface of the orbital portion of the frontal lobe in the olfactory sulcus to the olfactory trigone, which is in front of and in surface continuity with the anterior perforated spot. Some fibres (a) have a cell station here; others (b) pass on in the *lateral root* of the olfactory tract to reach the pyriform area. This root passes directly outwards, curves medially again (over the Island of Reil) and enters the pyriform lobe.

Tertiary Neurone.

(*a*) Axons of cells in the olfactory trigone pass in the *medial root* to reach the hippocampal formation.

(*b*) Axons of cells in the pyriform area pass as short fibres to the hippocampus portion of the hippocampal formation. *The hippocampal formation* in man includes in addition to the hippocampus, the sub-callosal gyrus, the induseum griseum, the gyrus dentatus, the supra-callosal gyrus, the fasciola cinerea, and the white fibres in the striæ of Lancisii.

* It is customary to include the olfactory and the optic among the cranial nerves although these are morphologically part of the brain itself.

Further connections.—From the hippocampus of one side, *viâ* the fornix—

(1) To the hippocampus of the opposite side.
(2) To the corpora mammillaria, and thence to
  (*a*) the optic thalamus (anterior nucleus) in the bundle of Vicq d'Azyr, with further relay to the corpus striatum and subthalamic nucleus. (See p. 39.)
  (*b*) the tegmentum in the bundle of Gudden, with further relay to the lower motor centres.
(3) To the habenular region of both sides *viâ* the striæ medullares. Efferent fibres from the habenular ganglion pass ventrally forming the fasciculus retroflexus of Meynert and end in the interpeduncular ganglion of the posterior perforated spot.
(4) To the pyriform area by a few fibres of the anterior pillars of the fornix which run down in front of the anterior commissure and pass in the diagonal band of Broca. In addition to these fibres, the diagonal band of Broca also contains fibres of the striæ of Lancisii (white matter of the hippocampal formation).

(See Diagram 16.)

2. OPTIC (sensory).

Cells of Origin.—Ganglion cells of the retina (see Diagram 17).

Axons.—Pass out of the eyeball as the optic nerve: these fibres have no neurolemma.

Fibres from the inner half of the retina cross in the optic chiasma, while those from the outer half continue on the same side. Thus the optic tract of one side contains—

(*a*) Fibres from the temporal half of the retina of that side.
(*b*) Fibres from the nasal half of the opposite retina.
(*c*) Fibres of Gudden's commissure.

(Gudden's commissure consists of fibres passing from the internal geniculate body of one side to the inferior corpus quadrigeminum and internal geniculate body of the other. According to some authorities, the fibres only link up the internal geniculate bodies of both sides. These fibres have nothing to do with the normal visual path.)

Visual fibres of the optic tract pass to—

(*a*) External geniculate body.

Fibres from the upper half of the retina pass to the medial part of the geniculate body, and from the lower half of the retina to the lateral part. The macula fibres occupy a large central zone of the geniculate body, and those from the nasal side of the retina for monocular vision pass to a narrow strip in the ventral part (Brouwer and Zeeman).

(*b*) Superior corpus quadrigeminum (for visual reflexes only).

These are known as the lower visual centres.

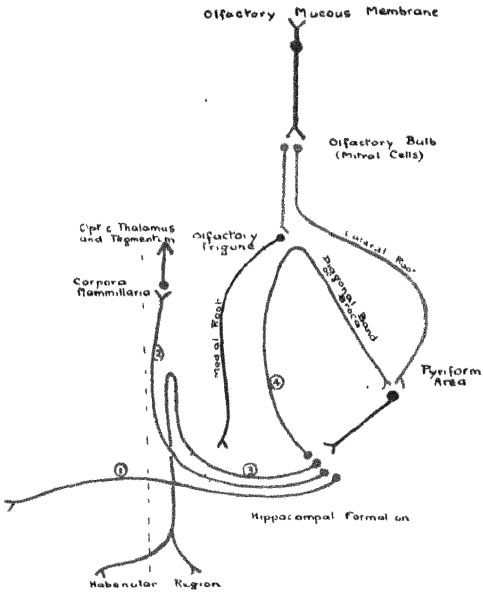


DIAGRAM 16.--Diagram of Olfactory Path.

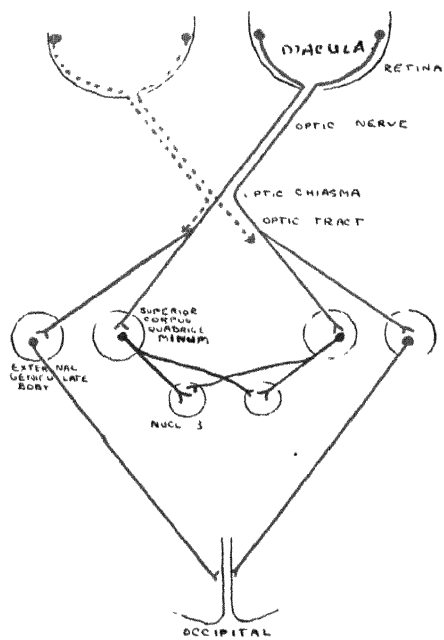


DIAGRAM 18.—Diagram to show the Optic Path.

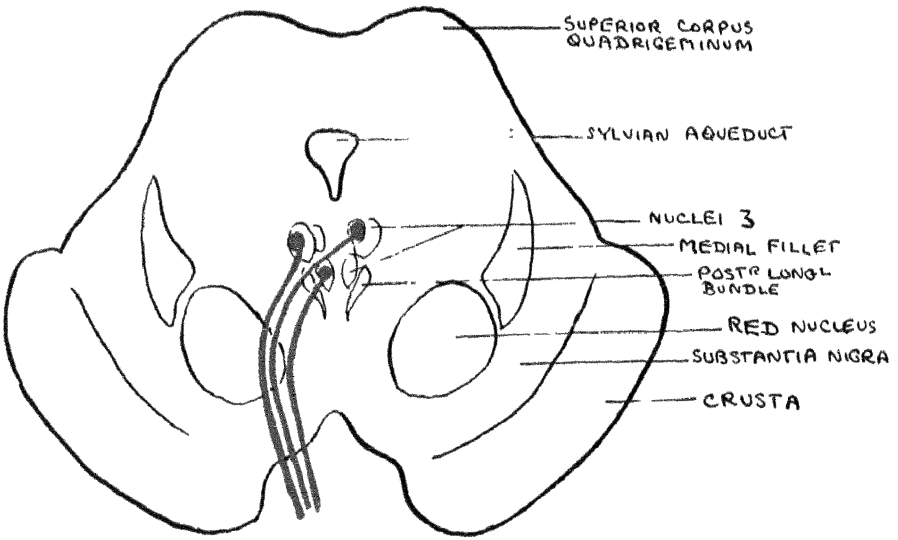


DIAGRAM 19 -Diagram to show Origin of Third Nerve

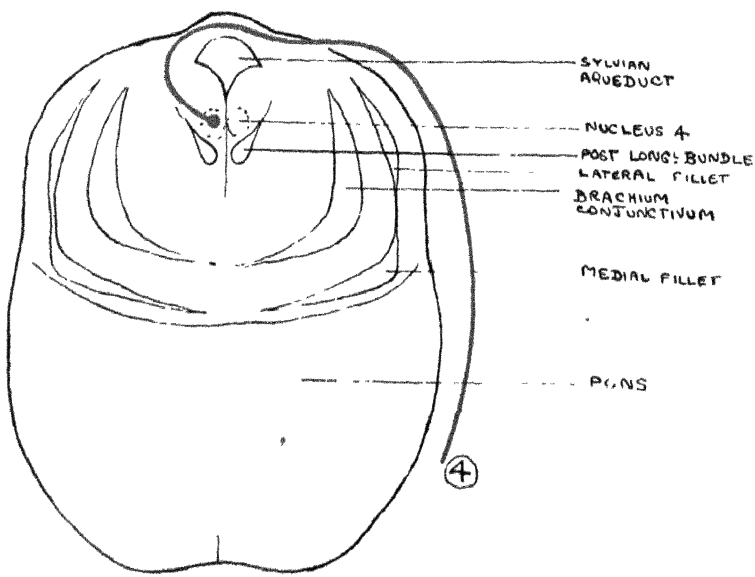


DIAGRAM 20.—Diagram to show Origin of Fourth Nerve.

Secondary Neurone.—From the external geniculate body to the occipital lobe of the cerebral cortex of the same side by means of the optic radiation (see pp. 38, 92). (The macula is said by some to be bilaterally represented

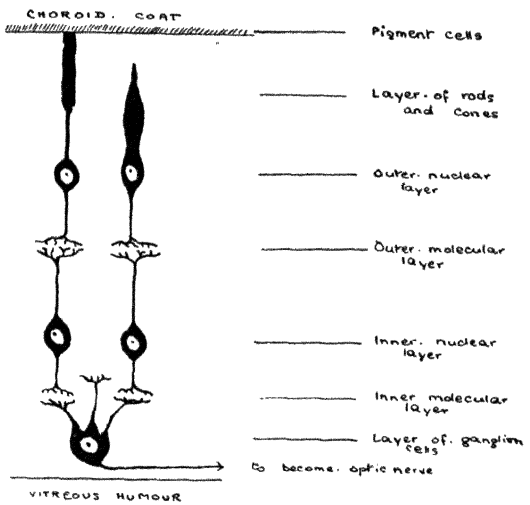


DIAGRAM 17.—Diagram showing neurone components of retina.

in the occipital cortex.) Some fibres pass from the external geniculate body to the pulvinar and lateral nucleus of the thalamus.

(See Diagram 18.)

The superior corpus quadrigeminum is connected with the third nerve nucleus and thence to the ciliary ganglion (see "Interconnections of Cranial Nerves").

3. OCULOMOTOR (motor).

Cells of Origin.—Nucleus ventral to the Sylvian aqueduct, at level of the superior corpora quadrigemina. The nucleus consists of an unpaired median cell group, small paired lateral groups (Edinger-Westphal) in the rostral region of the nucleus, and elongated paired lateral groups in the caudal region.

Axons.—Emerge ventrally on the medial surface of the crura, some passing through the red nucleus on the way. The fibres from the lateral nuclei are partly crossed close to their origin.

(See Diagram 19.)

In addition many afferent fibres (proprioceptive from eye muscles) are found in the nerve, and their cells appear to lie on the trunk of the third nerve.

(*Autonomic Fibres.*—See p. 64.)

4. TROCHLEAR (motor).

Cells of Origin.—Nucleus ventral to the Sylvian aqueduct, at level of the inferior corpora quadrigemina.

Axons.—Cross in the valve of Vieussens, emerge posteriorly, and curve round the crus of the opposite side.

(See Diagram 20.)

5. TRIGEMINAL (mixed motor and sensory).

A. **Motor Part.**

Cells of Origin.—Main motor nucleus. Upper pons.

Axons.—Emerge at the side of the pons where the sensory fibres enter, and passing deep to the Gasserian ganglion, join the third (mandibular or inferior) division of the fifth nerve.

B. **Sensory Part.** (Two subdivisions.)

1. *Cells of Origin.*—Gasserian (semilunar) ganglion.

Axons.—Enter laterally at mid-pons and divide into an ascending and a descending branch.

(*a*) *Ascending Branch.*—Fibres arborise round cells constituting the sensory nucleus of the fifth nerve, lateral to the main motor nucleus.

(*b*) *Descending Branch.*—Fibres pass down as spinal (descending) root of the fifth nerve, giving off collaterals arborising round cells of the substantia gelatinosa of Rolando.

The substantia gelatinosa extends from this level to the level of the upper cervical cord (C_2), where it makes a cap of cells on the tip of the posterior horn.

Secondary Neurone.—Fibres from both these nuclei cross and run up as the trigeminal fillet (found postero-lateral to the medial fillet) to the lateral nucleus of the optic thalamus.

Tertiary Neurone.—Fibres from cells of the optic thalamus pass through the internal capsule to the post-Rolandic cortex.

(See Diagram 21.)

2. *Mesencephalic Division.*—There is a long narrow nucleus of unipolar cells in the lateral portion of the central grey matter extending from the level of the main motor nucleus up to the upper limit of the mid-brain. The fibres of these cells are afferent (entering with the other sensory fibres), having passed straight through the Gasserian ganglion. The cells have probably migrated into the brain at a very early stage, and correspond to the outlying sensory ganglion of other sensory nerves.

(*Autonomic Fibres.*—See p. 64.)

6. ABDUCENS (motor).

Cells of Origin.—Nucleus in floor of fourth ventricle near the mid-line, directly deep to the arching fibres of the seventh nerve, which make the

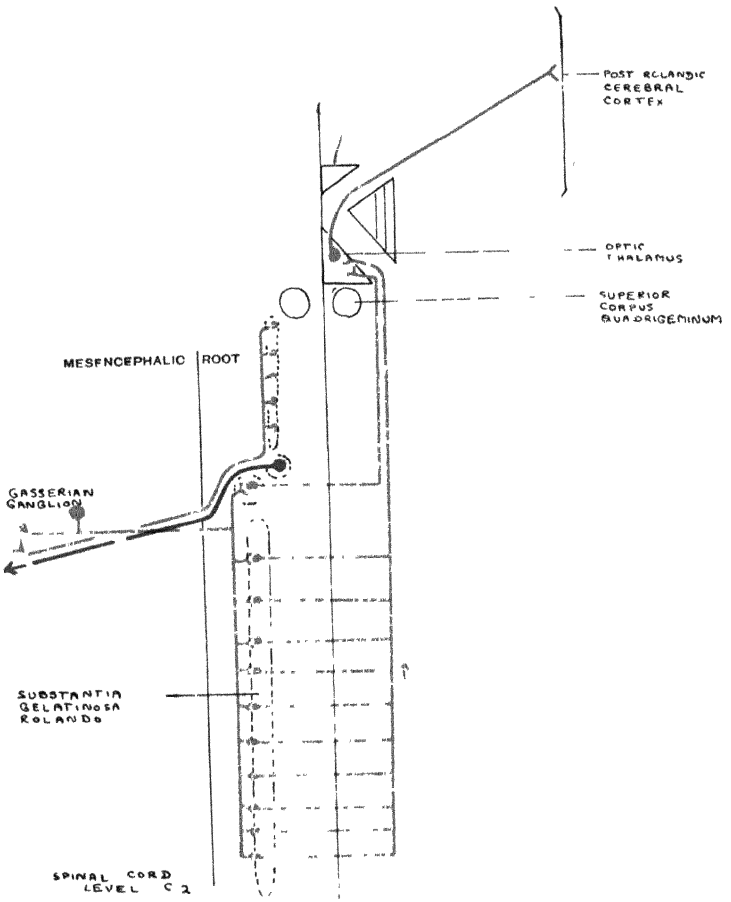


DIAGRAM 21.—Diagram of Path of Fifth Nerve Fibres in the Brain.
Red: Sensory. Blue: Motor.

2. Vestibular.

elevation in the floor of the ventricle known as the eminentia teres (colliculus facialis).

Axons.—Pass out to emerge near the mid-line on the ventral surface at the lower border of the pons.

(See Diagram 22.)

7. FACIAL (motor and sensory). (Sensory part is the nervus intermedius of Wrisberg.)

A. **Motor Part.**

Cells of Origin.—Ventro-lateral in lower pons.

Axons.—Pass backwards towards the mid-line and arch over the nucleus of the sixth nerve, making the rounded elevation on the floor of the fourth ventricle (eminentia teres or colliculus facialis). The fibres then emerge ventrally, passing between the nucleus of the seventh nerve and the substantia gelatinosa and appearing at the inferior border of the pons.

B. **Sensory Part.**

Cells of Origin.—Geniculate ganglion.

Dendrites. Arise (1) From taste buds of anterior two-thirds of tongue, passing *viâ* lingual nerve and chorda tympani, to main trunk of facial.

(2) From superficial muscles of face and scalp, *viâ* main trunk of facial.

Axons.—Pass as the nervus intermedius of Wrisberg to enter the pons at the same point at which the motor part of the seventh nerve emerges and the eighth nerve enters the brain; they then pass to the dorsal (principal) sensory nucleus, and to the superior part of the column of grey matter in connection with the tractus solitarius: "taste fibres" pass to the latter.

Secondary Neurone.—Fibres cross, and join the medial fillet running to the optic thalamus.

Tertiary Neurone.—From the thalamus the fibres pass to the hippocampal gyrus.

The *Glossopalatine* nerve is the name given to the nervus intermedius (sensory 7), the geniculate ganglion, and the great superficial petrosal and chorda tympani nerves, which are both sensory and motor. This is quite apart from the motor fibres of 7 which supply the facial muscles. The central connections and peripheral distribution of this nerve resemble those of the ninth nerve, and suggest it being considered as an aberrant part of the latter.

(See Diagram 23.)

(*Autonomic Fibres.*—See p. 64.)

8. AUDITORY OR ACOUSTIC (sensory).

This consists of two parts:—

1. Cochlear.
2. Vestibular.

Cochlear Nerve.

Cells of Origin.—Bipolar cells in the spiral ganglion of the cochlea.

Dendrites.—Arborise among the hair cells of the organ of Corti.

Axons.—Enter at the lower border of the pons. The fibres then divide and pass to—

(*a*) Ventral cochlear nucleus.

(*b*) Dorsal cochlear nucleus or tuberculum acousticum.

(See Diagram 24.)

Secondary Neurone.

(*a*) From the ventral nucleus some fibres cross as the trapezoid fibres and then turn up as the lateral fillet of the opposite side (some having a cell station in the nucleus of the lateral fillet), passing to the inferior corpus quadrigeminum and internal (medial) geniculate body of the thalamic region, while other fibres join the lateral fillet on the same side. Some lateral fillet fibres end in the substantia nigra.

(Some fibres connect with superior olives on *both* sides.)

(*b*) From the dorsal nucleus some fibres cross as the striæ acousticæ (striæ medullares) in the floor of the fourth ventricle, and in the mid-line turn deeply, and join the fibres from the ventral nucleus in the lateral fillet. Other fibres join the lateral fillet on the same side.

Tertiary Neurone.—Fibres pass from the internal geniculate body and the inferior corpus quadrigeminum through the auditory radiation to the superior surface of the temporal lobe (Heschl's convolution).

(Some American writers consider that the last auditory neurone is from the internal geniculate body only to the cortex, thus making the internal geniculate body into a lower auditory centre. The inferior corpus quadrigeminum is regarded merely as a reflex centre for co-ordinating eye and body movements with auditory impressions, while the optic thalamus is not regarded as a cell station on the auditory path.)

Vestibular Nerve.

Cells of Origin.—In Scarpa's ganglion.

Dendrites.—Come from cristæ and maculæ of vestibular part of the inner ear.

Axons.—Enter at the lower border of the pons and divide into an ascending and a descending branch.

Descending Branch (Roller's bundle).—These fibres end within the nucleus nervi vestibularis spinalis, which extends as far as the posterior column nuclei.

Ascending Branch.—Divides into three, passing to—

(*a*) Principal vestibular nucleus (dorsal nucleus).

(*b*) Deiters' nucleus (lateral nucleus).

(*c*) Bechterew's nucleus (superior nucleus).

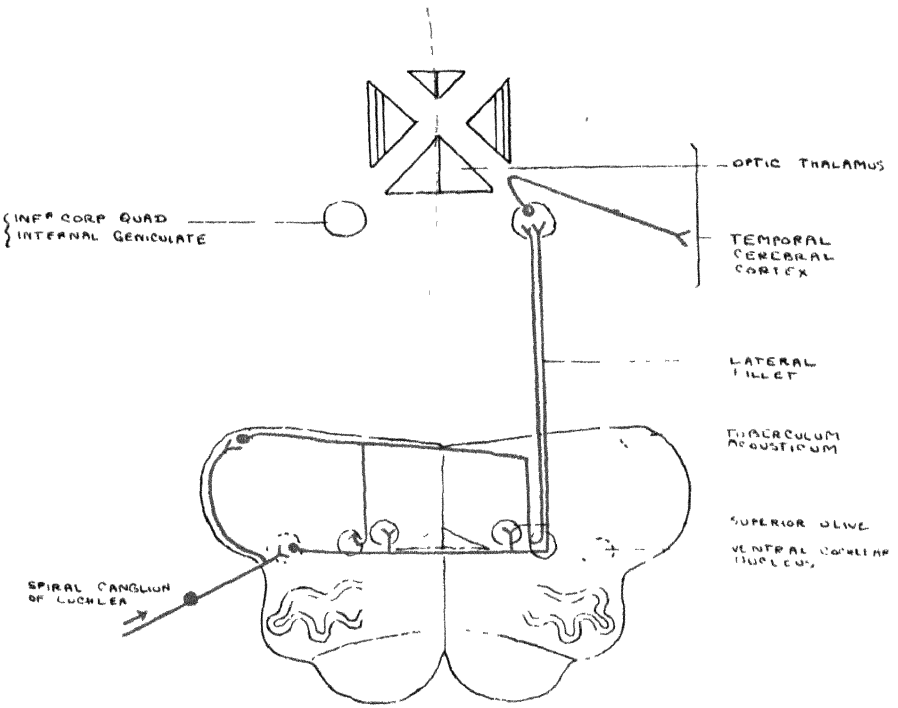


DIAGRAM 24.—Diagram to show Path of Fibres of Cochlear Division of Eighth Nerve.

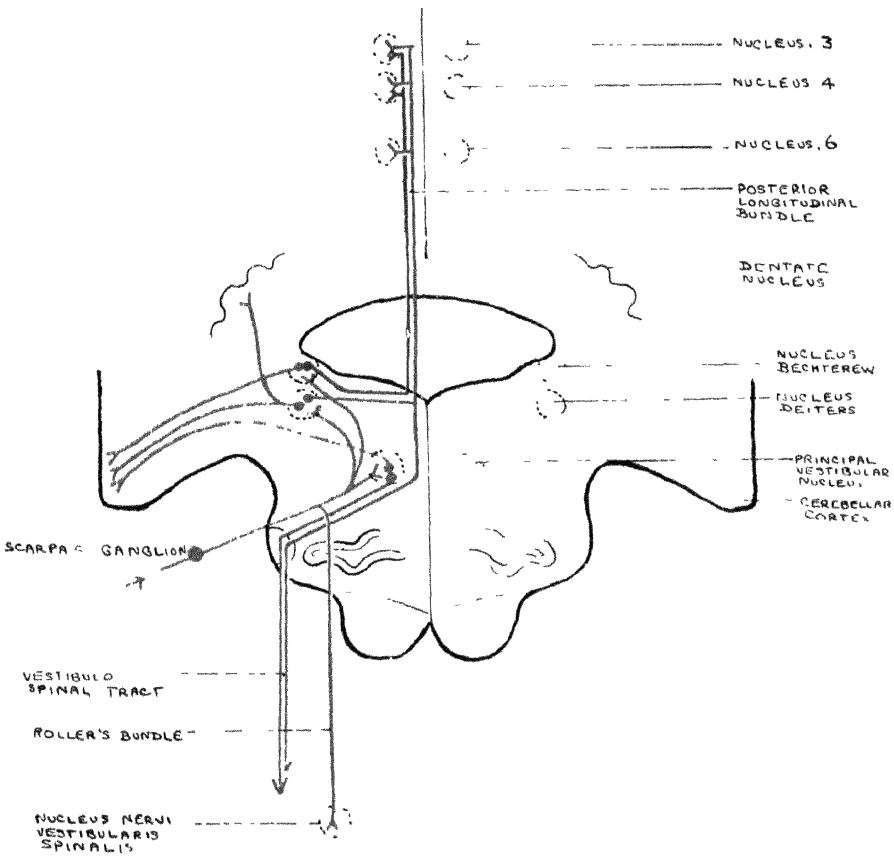


DIAGRAM 25.—Diagram to show Path of Vestibular Fibres of Eighth Nerve.

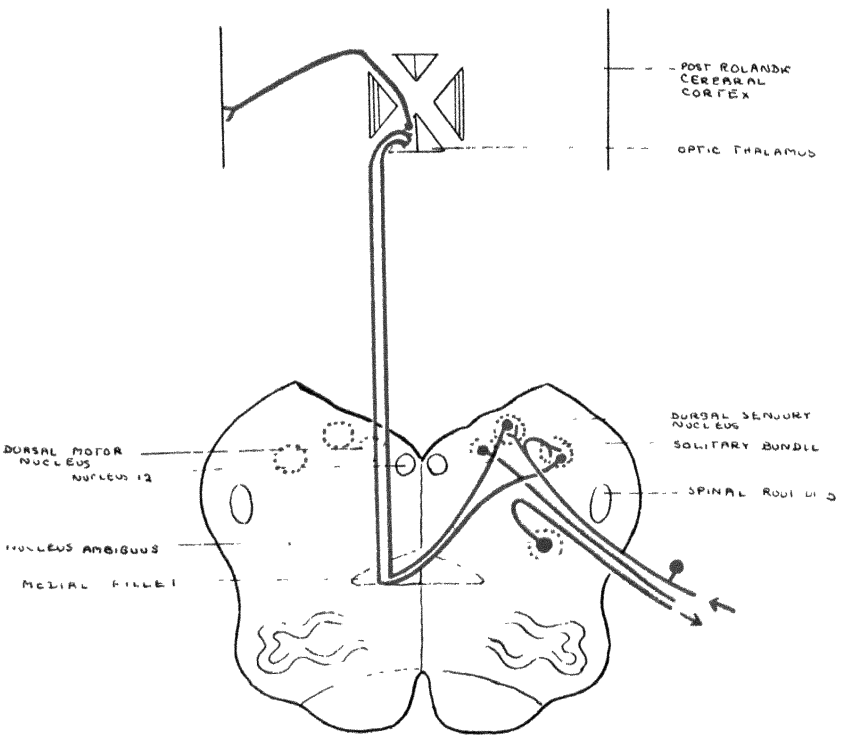


DIAGRAM 26.—Diagram to show Cranial Path of Nerves 9 and 10

Red : Sensory. Blue : Motor.

Secondary Neurone.—From these three nuclei fibres pass to the cerebellar cortex by the inferior cerebellar peduncles. A few pass direct to the cerebellar nuclei.

(See Diagram 25.)

Further Connections.

(1) From the principal vestibular nucleus fibres pass antero-laterally and then down the cord as part of the vestibulospinal tract.

(2) From Deiters' nucleus fibres pass to the mid-line and divide into descending and ascending branches.

(*a*) The descending branch passes antero-laterally, and joins the vestibulospinal tract of the cord.

(*b*) The ascending branch passes upwards as part of the posterior longitudinal bundle, giving off collaterals to the nuclei of cranial nerves 6, 4, and 3.

(3) From Deiters' nucleus to the lateral fillet.

(4) From Bechterew's nucleus fibres pass to the nuclei of cranial nerves 4 and 3 through the posterior longitudinal bundle.

(According to Muskens, the vestibular nuclei are also connected with the corpus striatum by fibres that cross in the posterior commissure.)

9. GLOSSOPHARYNGEAL (motor and sensory).

Motor.

Cells of Origin.—Nucleus ambiguus (ventral), lying anterior to the principal (dorsal) autonomic nucleus. (This ventral nucleus supplies fibres to stylopharyngeus muscle.)

Axons.—Emerge between the olive and the restiform body.

Sensory.

Cells of Origin.—Jugular and petrosal ganglia.

Axons.—Enter between restiform body and olive and divide into ascending and descending branches.

Ascending branches end in the dorsal or principal sensory nucleus (which is common to it and the vagus).

Descending branches join the solitary bundle, and end round these cells. (These fibres carry taste sense from posterior one-third of tongue.)

Secondary Neurone.—Fibres arising in these two nuclei cross the middle line, and pass up with the medial fillet to the optic thalamus.

Tertiary Neurone.—From the optic thalamus to the cerebral cortex (" taste fibres " to hippocampal gyrus).

(See Diagram 26.)

(*Autonomic Fibres.*—See p. 64.)

10. VAGUS (motor and sensory).

Motor.

Cells of Origin.—Nucleus ambiguus (ventral) lying anterior to the principal (dorsal) autonomic nucleus. (The nucleus ambiguus supplies fibres to cricothyroid muscle, and the three constrictors of the pharynx.)

Axons.—Emerge between the olive and the restiform body.

Sensory.

Cells of Origin.—Ganglia of the root and trunk of the vagus.

Axons.—Enter between the restiform body and the olive and divide into ascending and descending branches.

Ascending branches end in the dorsal or principal sensory nucleus (a small part of which nucleus belongs to the glossopharyngeal).

Descending branches join the solitary bundle, ending round cells in that region. (These fibres carry taste sense from epiglottis.)

Secondary neurone and *tertiary neurones* are the same as for the glossopharyngeal nerve; *i.e.*, the fibres cross the middle line and pass up with the medial fillet to the thalamus, and thence to the cerebral cortex.

(See Diagram 26.)

Arnold's nerve (auricular branch of vagus), consisting of afferent fibres from skin of external ear, ends round cells of the spinal nucleus of the trigeminal nerve.

(*Autonomic Fibres.*—See p. 64.)

11. SPINAL ACCESSORY (motor).

This nerve consists of two parts :—

(1) Spinal part, which is motor.

(2) Accessory part, which is motor and is so called because it is "accessory" to the vagus. (See p. 32.)

Spinal Part.

Cells of Origin.—Anterior horn cells of the first six cervical segments.

Axons.—Emerge laterally from the cord, and joining together run up in the spinal canal and then join the accessory part of the eleventh nerve, supplying the sternomastoid and trapezius muscles.

Accessory Part.

Cells of Origin.—The same column of cells which higher up constitutes the nucleus ambiguus.

Axons.—Emerge between the olive and the restiform body and join the vagus trunk, supplying fibres to striped muscle of pharynx, and intrinsic muscles of larynx except cricothyroid.

(See Diagram 27.)

(*Autonomic Fibres.*—See p. 64.)

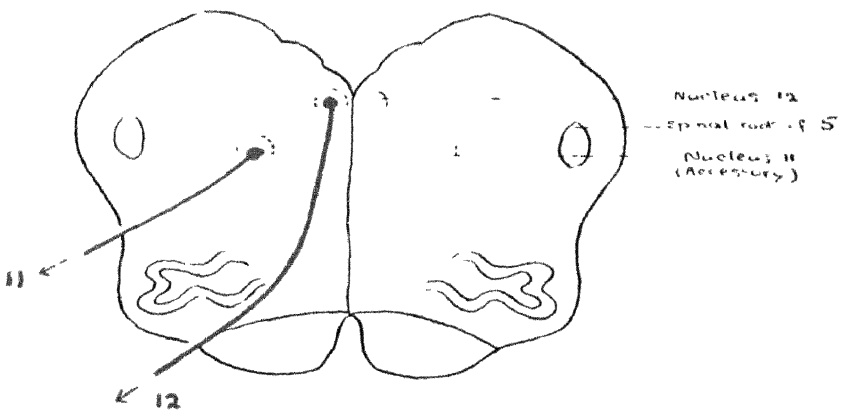


DIAGRAM 27.—Diagram to show Origin of Nerves 11 (accessory part) and 12.

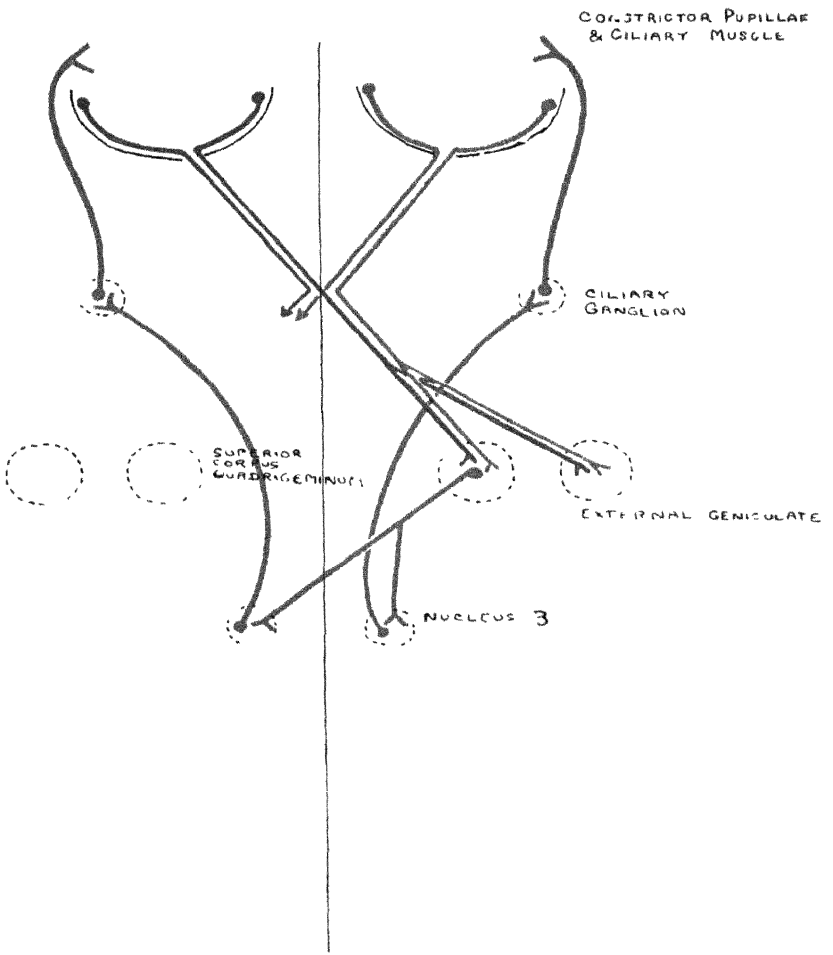


DIAGRAM 28 —Diagram to show Connection of Optic Nerve with the Oculomotor Nerve

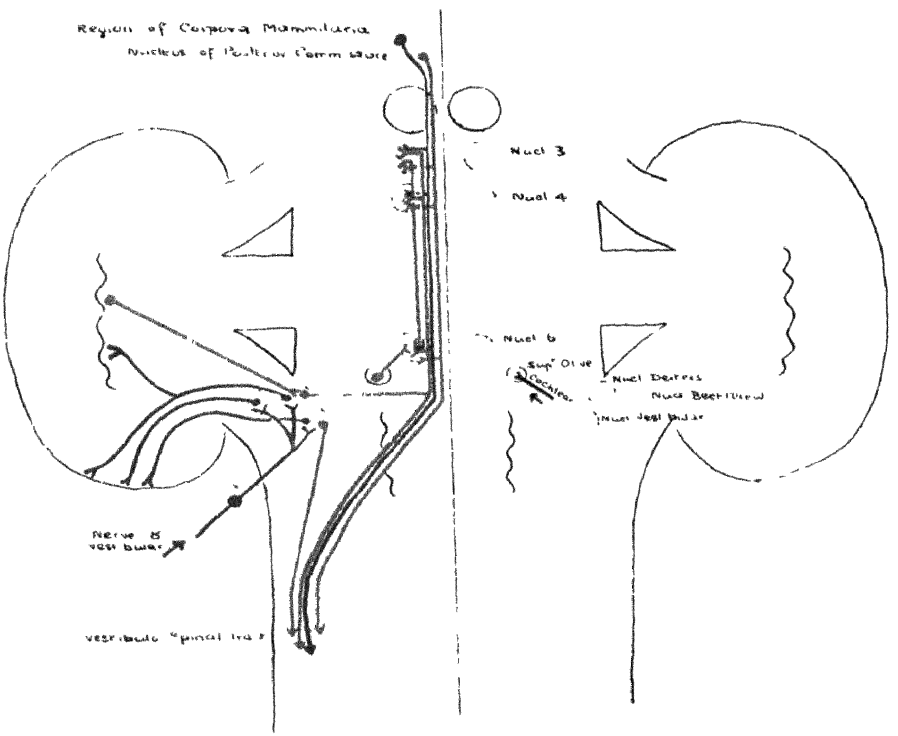


DIAGRAM 29.—Diagram to show Fibres of Posterior Longitudinal Bundle

12. HYPOGLOSSAL (motor).

Cells of Origin.—Nucleus near the mid-line in the floor of the fourth ventricle, extending throughout the medulla. The upper part is subjacent to the trigonum hypoglossi.

Axons.—Emerge between the pyramid and the olive.

(See Diagram 27.)

INTERCONNECTIONS OF THE CRANIAL NERVES

Certain of the cranial nerves make connections with other cranial nerve nuclei within the substance of the brain itself. It is essential for the clear understanding of the effect of local and multiple lesions that the more important of these connections should be noted. (Reference should also be made to Chapter XI. for connections with the autonomic nervous system.)

A. Connections of the Optic Nerve with the Oculomotor Nerve.

Fibres from the optic tract, containing fibres from both eyes, relay through the superior corpus quadrigeminum to the nuclei of the oculomotor nerves, crossing both anterior and posterior to the Sylvian aqueduct. From this oculomotor nucleus fibres pass to the ciliary ganglion and thence (as post-ganglionic fibres) to the constrictor pupillæ and ciliary muscles *viâ* the short ciliary nerves.

(See Diagram 28.)

B. Connections of the Oculomotor Nerve with the Trochlear, Abducens, Vestibular and Cochlear Nerves. (Posterior longitudinal bundle.)

The most important band of fibres in this connection is the posterior longitudinal bundle (also known as the medial longitudinal bundle and the fasciculus longitudinalis medialis). This band consists of the following fibres.

(*a*) Fibres from Deiters' nucleus (vestibular 8) which run to the mid-line where some cross; they then divide into—

1. A descending branch that joins the vestibulospinal tract in the cord, and the anterior ground bundle.
2. An ascending branch that gives off collaterals to the nuclei of the abducens, trochlear and oculomotor nerves.

(*b*) Fibres from the abducens nucleus to the oculomotor nucleus.

(*c*) Fibres connecting with the mammillary region, and with the nucleus of the posterior commissure, some passing down giving off collaterals to the nuclei of the oculomotor, trochlear and abducens nerves.

(See Diagram 29.)

In addition there are fibres from the superior olive (which itself receives fibres from cochlear 8) that pass to the abducens nucleus, and thence connect with the nucleus of the third nerve by the posterior longitudinal bundle.

C. Inter-relations of the Facial Nerve with the Trigeminal and the Glossopharyngeal Nerves.

(*a*) WITH THE TRIGEMINAL NERVE.

(i.) *Sensory Division of the Fifth Nerve.*

(*α*) Fibres from Meckel's (spheno-palatine) ganglion pass *viâ* the superior maxillary nerve and the Gasserian ganglion to the nucleus of the sensory part of the fifth nerve.

(*β*) Fibres of the fifth nerve, carrying sensory fibres from the anterior two-thirds of the tongue, run in the lingual nerve with taste fibres of the facial. The latter join the chorda tympani nerve, passing *viâ* the geniculate ganglion and the nervus intermedius of Wrisberg to the sensory nucleus (solitary bundle) of the facial nerve. The fibres of the trigeminal then pass on to the Gasserian ganglion *viâ* the mandibular division, and thence to the sensory nucleus of the fifth nerve.

(*γ*) Fibres from the spinal (sensory) root of the fifth nerve make connection with the motor nucleus of the facial.

(ii.) *Motor Division of the Fifth Nerve.*

Fibres from the motor nucleus of the fifth nerve pass out along the third or mandibular division of the fifth through the otic ganglion.

(*b*) WITH THE GLOSSOPHARYNGEAL NERVE.

(i.) *Sensory Division of the Ninth Nerve.*

Fibres from the posterior third of the tongue, carrying taste, pass in the main ninth nerve trunk *viâ* the petrous ganglion to the solitary bundle.

(ii.) *Motor Division of the Ninth Nerve.*

Fibres from the inferior salivatory nucleus of the glossopharyngeal nerve pass to the otic ganglion by the tympanic nerve and the lesser superficial petrosal nerves, which must therefore be regarded as mixed nerves. (See Diagram 31.)

(*c*) WITH THE SUBMAXILLARY GANGLION. (See p. 32.)

(*d*) THE MOTOR NUCLEUS OF THE FACIAL NERVE.

This has further connections with—

(i.) The spinal root of the fifth nerve (sensory), receiving from thence most of its afferent impulses.

(ii.) The corpus trapezoideum.

(iii.) The pyramidal tract of the opposite side.

D. Cranial Autonomic Ganglia.

(*a*) SPHENOPALATINE (MECKEL'S) GANGLION. (Parasympathetic ganglion of 7. See Diagram 30.)

(i.) *Parasympathetic Cell Station.*

7. Fibres arise from superior salivatory nucleus, pass *viâ* nervus

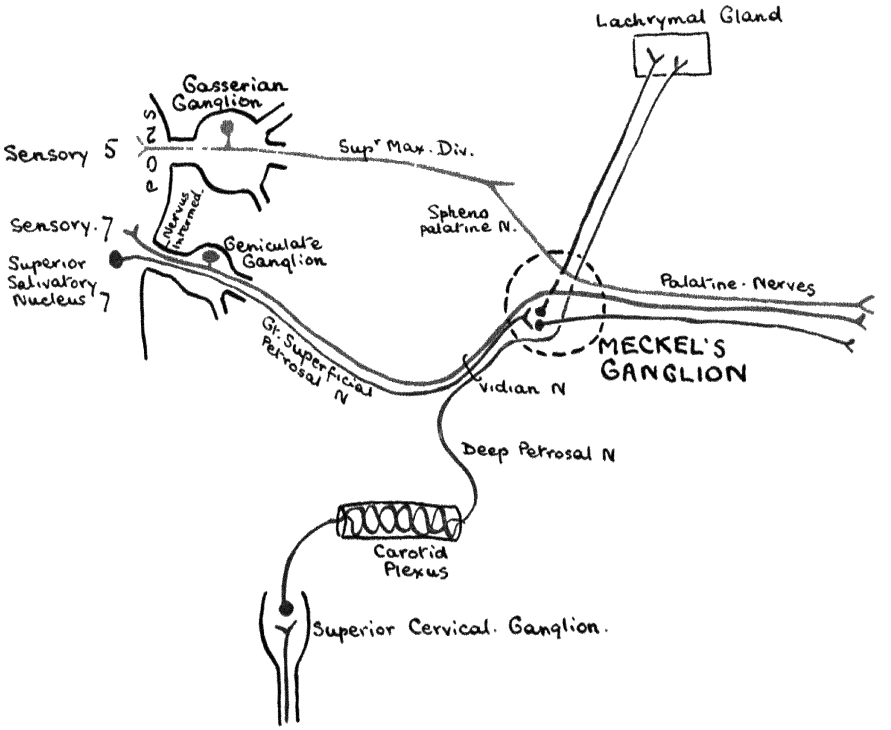


DIAGRAM 30—The Sphenopalatine (Meckel's) Ganglion

Sensory (Autonomic) 5 Green
Sensory (Autonomic) 7. Red
Parasympathetic 7. Violet
Sympathetic Blue

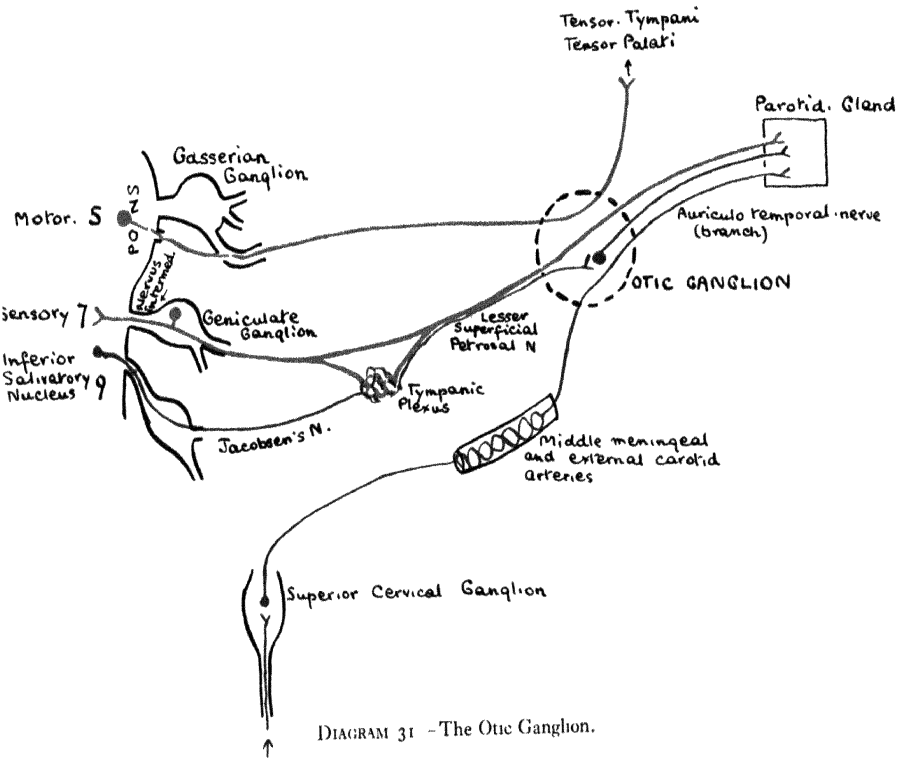


DIAGRAM 31 – The Otic Ganglion.

Sensory (Autonomic) 7. Red
Motor 5. Green.
Parasympathetic 9 Violet
Sympathetic Blue.

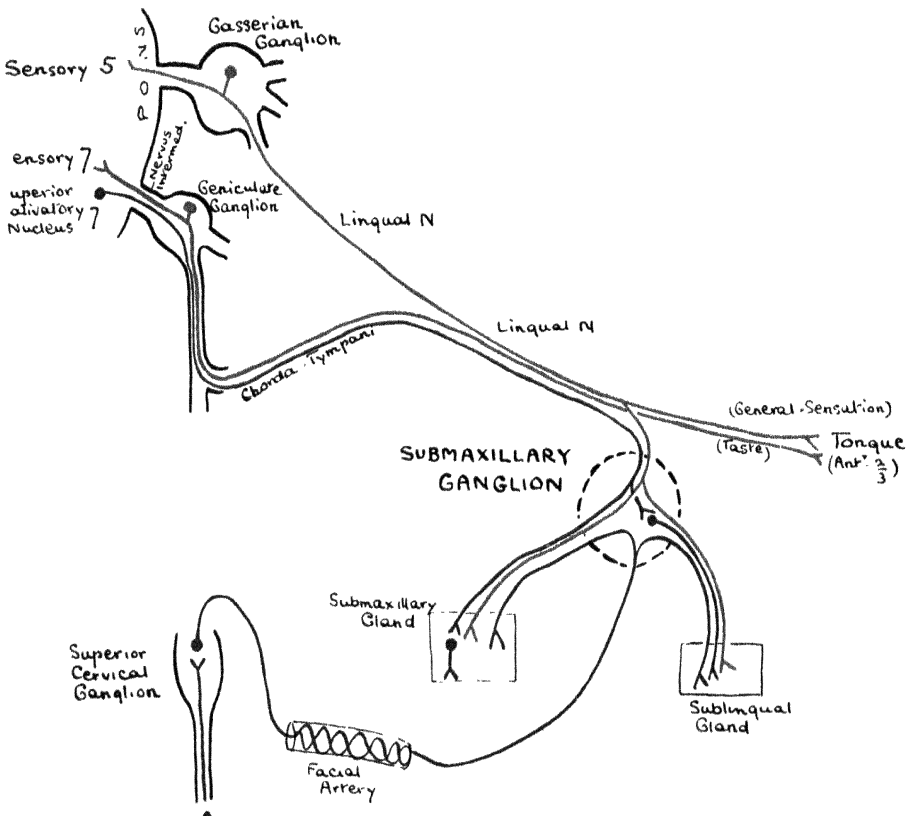


DIAGRAM 32.– The Submaxillary Ganglion

Sensory (Autonomic) 5 Green
Sensory (Autonomic) 7. Red
Parasympathetic 7. Violet
Sympathetic . Blue

intermedius, through geniculate ganglion, by greater superficial petrosal and Vidian nerve to Meckel's ganglion.

Post-ganglionic, *viâ* temporomalar nerve to lachrymal gland, and *viâ* palatine nerves to palatal glands.

(ii.) *Sensory Autonomic Fibres passing through.*

5. Fibres come from palate, *viâ* palatine nerves through ganglion (some do not go through ganglion) by short connection (sphenopalatine nerve) to superior maxillary division to Gasserian ganglion (cells of origin), and thence to sensory nucleus of 5.

7. Fibres come from palate, *viâ* palatine nerves, through ganglion, *viâ* Vidian nerve and then greater superficial petrosal nerve to geniculate ganglion (cells of origin), and thence by nervus intermedius to sensory nucleus of 7.

(iii.) *Sympathetic Fibres passing through.*

Post-ganglionic fibres arise from superior cervical ganglion, pass *viâ* carotid plexus, thence by deep petrosal nerve to join the Vidian nerve, then passing through the ganglion and in the temporomalar nerve to lachrymal gland.

b) OTIC GANGLION. (Parasympathetic ganglion of 9. See Diagram 31.)

(i.) *Parasympathetic Cell Station.*

9. Fibres arise from inferior salivatory nucleus, pass *viâ* Jacobsen's nerve through tympanic plexus, *viâ* lesser superficial petrosal nerve to otic ganglion.

Post-ganglionic, *viâ* auriculo-temporal nerve to parotid gland.

(ii.) *Sensory Autonomic Fibres passing through.*

7. Fibres come from parotid gland, *viâ* auriculo-temporal nerve through ganglion, *viâ* lesser superficial petrosal nerve (some then through tympanic plexus) to geniculate ganglion (cells of origin) and thence *viâ* nervus intermedius to sensory nucleus of 7.

(iii.) *Motor Fibres passing through.*

5. Fibres arise from motor nucleus of 5, pass through ganglion to supply tensor tympani and tensor palati muscles.

(iv.) *Sympathetic Fibres passing through.*

Post-ganglionic fibres arise from superior cervical ganglion, pass *viâ* plexus on middle meningeal and external carotid arteries, through ganglion, then *viâ* auriculo-temporal nerve to parotid gland.

c) SUBMAXILLARY GANGLION. (Parasympathetic ganglion of 7. See Diagram 32.)

(i.) *Parasympathetic Cell Station.*

7. Fibres arise from superior salivatory nucleus, pass by nervus intermedius through geniculate ganglion and then by chorda tympani and lingual nerve to submaxillary ganglion.

Post-ganglionic, to sublingual gland.

(ii.) *Parasympathetic Fibres passing through.*

7. As above, but some pass through submaxillary ganglion to end in submaxillary gland or round cells on the submaxillary duct: short post-ganglionic fibres to gland cells.

(iii.) *Sensory Autonomic Fibres passing through.*

5. Fibres from sublingual and submaxillary glands pass through ganglion, joining others from anterior two-thirds of tongue, in lingual nerve *viâ* inferior division to Gasserian ganglion (cells of origin) and thence to sensory nucleus of 5.

(iv.) *Sympathetic Fibres passing through.*

Post-ganglionic fibres arise from superior cervical ganglion, pass *viâ* plexus on facial (external maxillary) artery, through ganglion to sublingual and submaxillary glands.

(*d*) CILIARY GANGLION. (Parasympathetic ganglion of 3. See Diagram 33.)

(i.) *Parasympathetic Cell Station.*

3. Fibres arise in nucleus of 3 (probably Edinger-Westphal division), pass by branch of 3 supplying inferior oblique muscle to ciliary ganglion. Post-ganglionic, *viâ* short ciliary nerves, to ciliary muscle and sphincter pupillæ.

(ii.) *Sensory Autonomic Fibres passing through.*

5. From all parts of eyeball *viâ* naso-ciliary nerve (ophthalmic division of 5) to Gasserian ganglion (cells of origin) and thence to sensory nucleus of 5. Some fibres pass by long ciliary nerves and do not pass through the ciliary ganglion.

(iii.) *Sympathetic Fibres passing through.*

Post-ganglionic fibres arise from superior cervical ganglion, pass *viâ* carvernous plexus on internal carotid artery through ganglion, *viâ* short ciliary nerves to dilator pupillæ, and blood vessels of eyeball; some fibres pass by long ciliary nerves and do not pass through the ciliary ganglion.

E. **Relations between the Tenth and the Eleventh Nerves.**

The *accessory* (cerebral) part of the eleventh nerve joins the vagus, and supplies the muscles of the larynx through the external and recurrent laryngeal nerves, and the muscles of the soft palate (except tensor palati) through its pharyngeal branch. The greater part of the motor fibres of the vagus are in reality derived from this accessory part of the eleventh nerve (" accessory " signifying accessory to the vagus); these include the pre-ganglionic inhibitor fibres to the heart and motor fibres to the alimentary canal. The *spinal* part of the eleventh nerve supplies the sternomastoid and trapezius muscles.

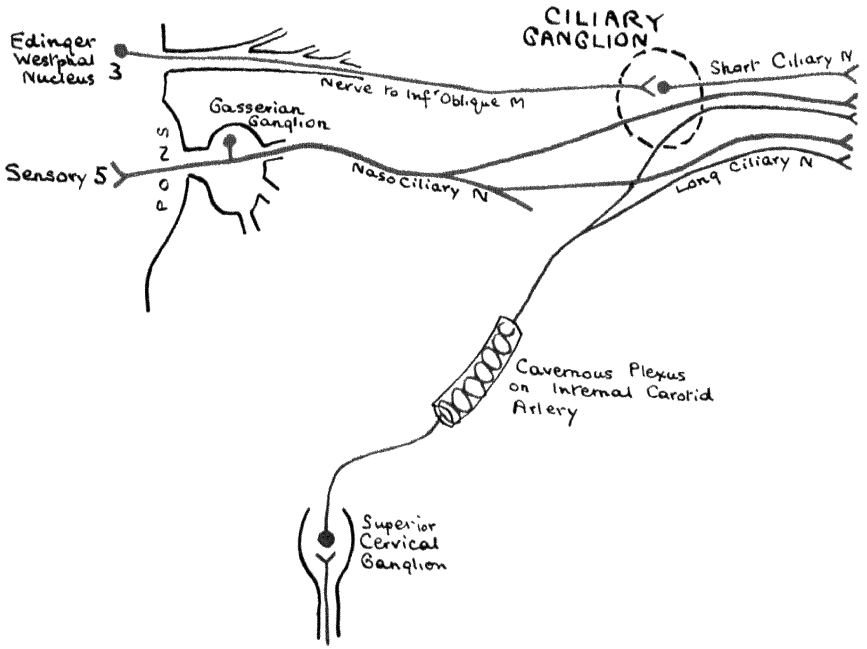


DIAGRAM 33 - The Ciliary Ganglion.

F. **Summary of the Tracts conveyed in the Fillets** (or Lemnisci).

I. *Medial Fillet.*

1. Fibres from the opposite nucleus gracilis and nucleus cuneatus, passing up to the optic thalamus.
2. Fibres of the spinothalamic and spinotectal tracts join the fillet.
3. Fibres from the nuclei of the sensory cranial nerves (10, 9 and 7).

II. *Lateral Fillet.*

Fibres from both cochlear nuclei and from the superior olives, chiefly of the opposite side, passing up to the inferior corpus quadrigeminum and the internal geniculate body. (Some fibres give collaterals to a nucleus on the lateral aspect of the brachium conjunctivum.)

III. *Trigeminal Fillet.*

Fibres from both sensory nuclei of the fifth nerve of the opposite side. In the mid-brain this fillet is indistinguishable from the medial fillet.

G. **Components of the Cranial Nerves**

A table is appended showing the various components of the cranial nerves. As there is doubt about the morphological value of the laminæ in the mid-brain region, nerves 3 and 4 cannot be said to be definitely somatic (Frazer), although classed as such in the table.

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CHAPTER VII

THE CONNECTIONS OF THE CORPUS STRIATUM AND OF THE DIENCEPHALIC NUCLEI

THE primitive neural tube gives rise to the brain and the spinal cord ; the subdivisions of the brain include the following parts :—

I. PROSENCEPHALON.

(*a*) *Telencephalon*
- Cerebral cortex.
- Corpora striata.
- Rhinencephalon.
- Pars optica hypothalami.

(*b*) *Diencephalon*
- Epithalamus.
- Metathalamus (geniculate bodies).
- Thalamus.
- Hypothalamus.
  - Hypophysis.
  - Tuber cinereum.
  - Mammillary bodies.

II. MESENCEPHALON.
- Corpora quadrigemina.
- Crura cerebri.

III. RHOMBENCEPHALON.

(*a*) *Metencephalon.*
- Cerebellum.
- Pons.

(*b*) *Myelencephalon* Medulla oblongata.

This chapter deals with the more important of the connections of the corpus striatum and the diencephalic nuclei : the functional significance of these masses will be considered on p. 76.

The Corpus Striatum.

The term " corpus striatum " is usually taken to include the caudate nucleus, the lenticular nucleus and the internal capsule : the amygdaloid nucleus and the claustrum belong to the same group of structures, which are sometimes linked together as the " basal ganglia." (See Diagrams 34 and 35.)

The lenticular nucleus consists of two parts, the globus pallidus and the putamen : the former contains large multipolar cells of typical motor form, while the putamen like the caudate nucleus consists chiefly of smaller cells with short axons.

The developmental significance and functions of the nuclei of this region will be discussed later, but the meaning of their various connections will be understood

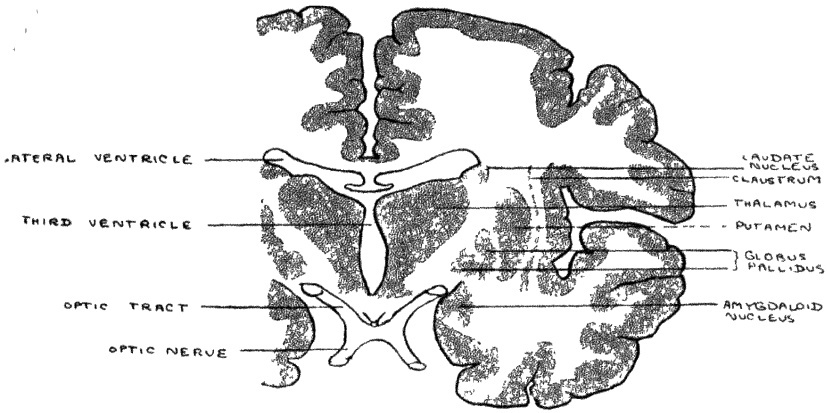

DIAGRAM 34.—Diagram to show basal ganglia. (*After Cunningham.*)

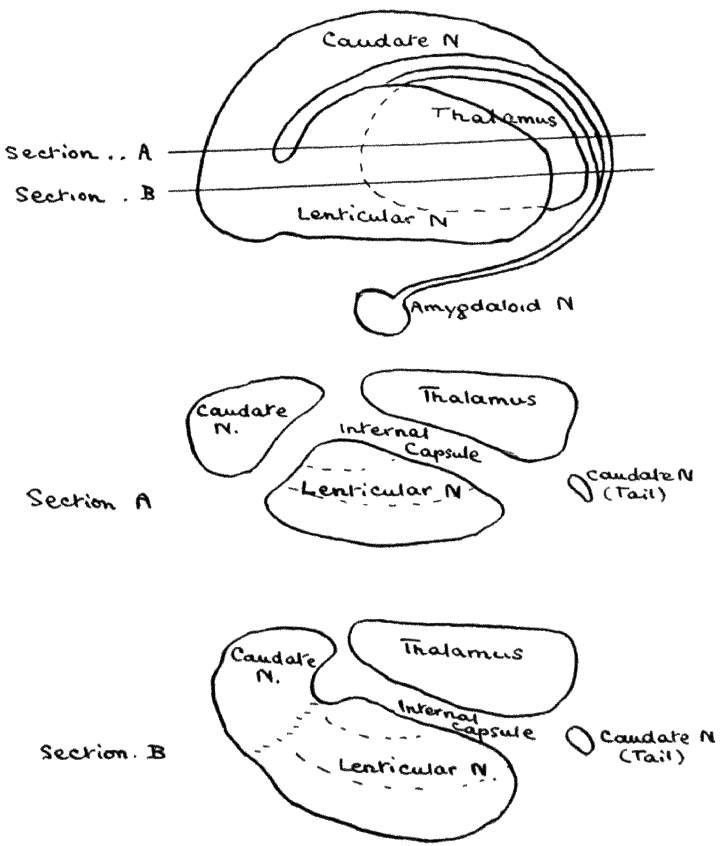

DIAGRAM 35.—Lateral view and sections of the nuclei of the corpus striatum.
(*From Ranson, after Jackson-Morris.*)

more readily if it be remembered that the optic thalamus is the most important receiving station on the sensory path, that the globus pallidus is developed from the palæostriatum and probably represents the oldest motor cortex, and that most of the caudate nucleus and the putamen are developed later and represent a refining influence exerted on the motor activities of the globus pallidus by modifying the impulses that this nucleus receives from the thalamus. The amygdaloid nucleus is olfactory in function.

The connections of the corpus striatum and thalamus.

(See Diagram 36.)

A. Fibres coming from elsewhere and ending in these nuclei.
- (i.) To thalamus by all general sensory paths (see p. 39).
- (ii.) To thalamus from contralateral cerebellar nuclei.
- (iii.) To thalamus from ipsolateral cerebral cortex.
- (iv.) To thalamus from corpora mammillaria.
- (v.) To globus pallidus from ipsolateral red nucleus (and thus from contralateral cerebellum).

B. Fibres arising and ending within these nuclei.
- (i.) From thalamus to caudate nucleus.
- (ii.) From thalamus to globus pallidus.
- (iii.) From caudate nucleus to putamen.
- (iv.) From caudate nucleus to globus pallidus.
- (v.) From putamen to globus pallidus.
- (vi.) From globus pallidus to thalamus.
- (vii.) Commissural fibres between the two thalami and the two lenticular nuclei, crossing in the commissure of Forel.

C. Fibres arising in these nuclei and ending elsewhere.
- (i.) From thalamus to ipsolateral cerebral cortex.
- (ii.) From thalamus to olives (thalamo-olivary tract).
- (iii.) From thalamus to subthalamic nucleus.
- (iv.) From thalamus to spinal cord (thalamo-spinal tract).
- (v.) From globus pallidus to ipsolateral red nucleus and thence by rubrospinal tract to contralateral cord.
- (vi.) From globus pallidus to ipsolateral substantia nigra, and thence probably to lower motor centres.
- (vii.) From globus pallidus to subthalamic nucleus.
- (viii.) From caudate nucleus to ipsolateral red nucleus.

(The centrifugal fibres from the globus pallidus are collected into a bundle known as the ansa lenticularis, which is distributed to the thalamus, subthalamic nucleus, red nucleus and substantia nigra.)

The Internal Capsule.

This consists of a band of white matter semilunar in shape with its convexity directed medially. The anterior division (or limb) lies between the caudate and

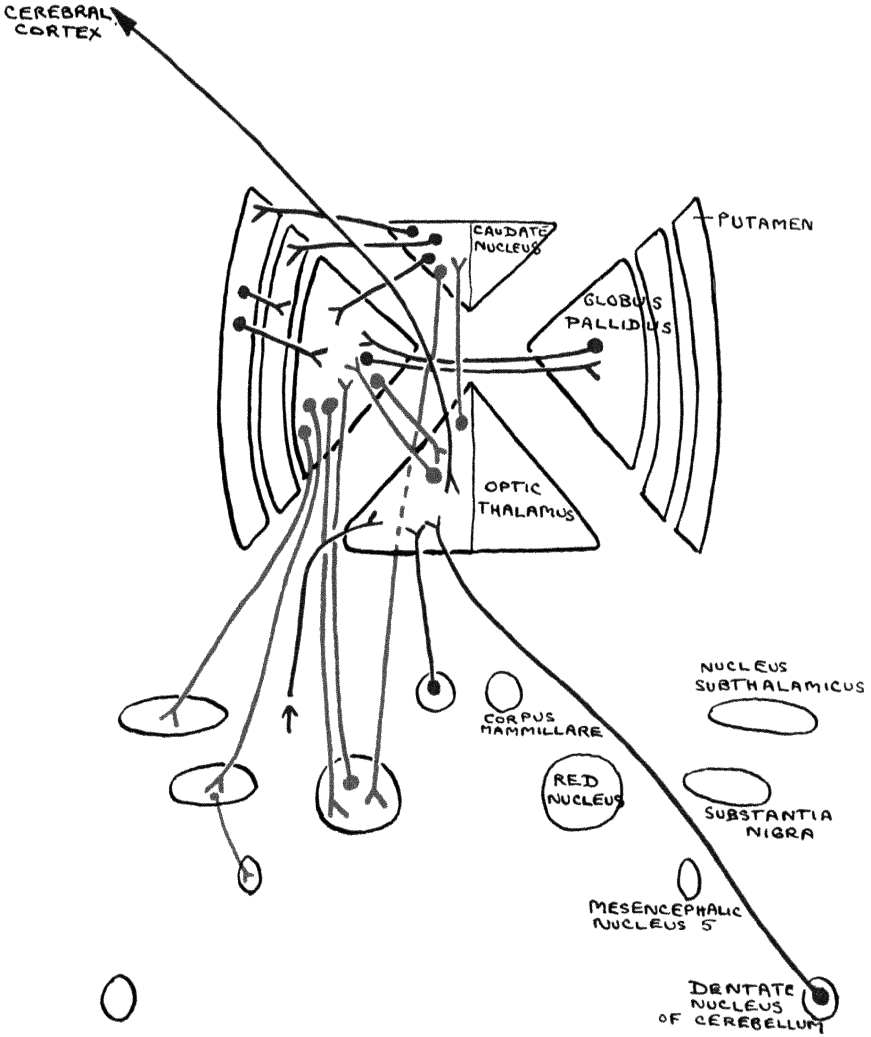

DIAGRAM 36 Diagram to show chief Basic Ganglia Connections

Mauve. Fibres . to. thalamus.
Green. Fibres . to basal ganglia
Blue. Interconnecting. fibres
Red. Outgoing fibres.

lenticular nuclei, the posterior division lying between the optic thalamus and the lenticular nucleus : the two limbs together form a knee-shaped bend, which is known as the middle division or genu.

(See Diagram 37.)

The fibres found passing through the internal capsule are as follows :—

(*a*) *Anterior Limb.*

(i.) Thalamo-cortical fibres, from thalamus (lateral nucleus) to frontal cerebral cortex.

(ii.) Fronto-pontine fibres, from frontal cortex to nuclei pontis, and thence relayed to opposite cerebellar cortex.

(iii.) Cortico-thalamic fibres, from cerebral cortex to thalamus (lateral nucleus).

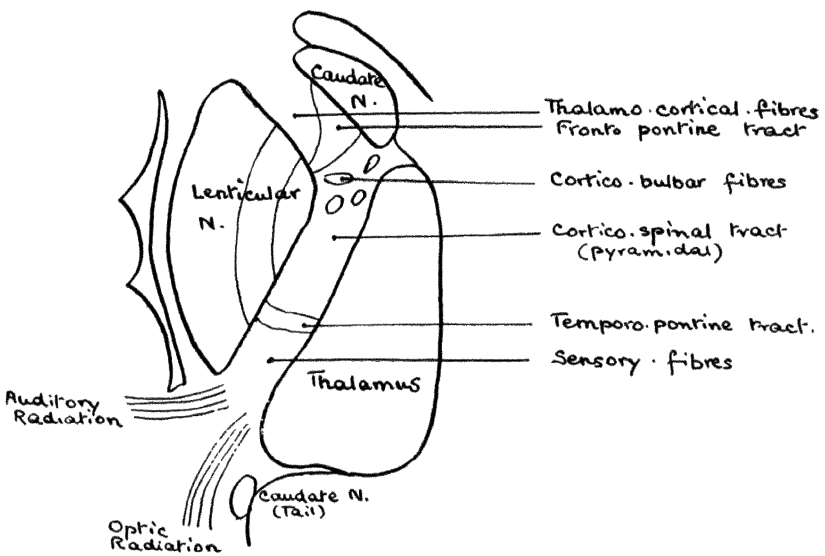

DIAGRAM 37.—Diagram showing fibres of internal capsule.

(*b*) *Genu and Posterior Limb.*

(i.) Cortico-bulbar fibres, from pre-Rolandic cerebral cortex to motor nuclei of cranial nerves (occupying the genu).

(ii.) Cortico-spinal fibres, from pre-Rolandic cerebral cortex to spinal cord (occupying the anterior two-thirds of the posterior limb). Fibres for the arm are nearer the genu than those for the leg.

(iii.) Cortico-rubral fibres, from pre-Rolandic cerebral cortex to red nucleus (Monakow).

(iv.) Temporo-pontine fibres, from temporal cortex (and ? occipito-pontine fibres from occipital cortex) to nuclei pontis, and thence relayed to opposite cerebellar cortex.

(v.) Thalamo-cortical fibres, from thalamus (lateral nucleus) to post-Rolandic cerebral cortex (last neurone on sensory path).

(vi.) Cortico-thalamic fibres, from cerebral cortex to thalamus (lateral nucleus).

(vii.) Fibres of optic radiation, from lateral geniculate body to occipital cortex.

(viii.) Fibres of auditory radiation, from medial geniculate body to temporal cortex.

Thus the anterior part of the anterior limb and the posterior part of the posterior limb contain chiefly corticopetal (sensory) fibres, the genu and the anterior two-thirds of the posterior limb containing mostly corticofugal (motor) fibres. Between the ascending and the descending fibres in both anterior and posterior limbs are found the fibres of the cortico-pontine-cerebellar path. It should be noted that the sensory fibres have a cell-station at this level, whereas most of the motor fibres pass through with no connection.

In addition to the fibre tracts that pass through the internal capsule there are many fibres that pass across this band of white matter linking up the basal ganglia and the thalamus (see above) and passing from the former to the subthalamic nucleus.

The Epithalamus.

The epithalamus includes the pineal body, the striæ medullares, the habenular trigone, and the posterior commissure.

1. *Pineal Body.*—This is a small glandular structure that probably passes its secretion into the pineal recess of the third ventricle. It is not composed of nervous elements, but is attached by a short stalk which divides into a ventral lamina continuous with the posterior commissure and a dorsal lamina continuous with the habenular commissure.

2. *Habenular Ganglion.*—This is a nuclear mass within the habenular trigone that receives afferent fibres by the *stria medullaris* from the olfactory centres (see p. 22). Some of these afferent fibres cross to the ganglion of the opposite side as the habenular commissure. Efferent fibres pass from the habenular ganglion as the fasciculus retroflexus of Meynert which ends in the interpeduncular ganglion. These connections thus provide a path for olfactory reflexes.

3. *Posterior Commissure.*—This is a band of fibres crossing on the dorsal surface of the upper end of the Sylvian aqueduct. It consists of a *dorsal part* carrying chiefly commissural fibres between the two thalami, and between the superior corpora quadrigemina and lateral geniculate bodies, and a *ventral part* carrying chiefly fibres from the nucleus of Darkschewitsch, the locus niger and the capsule of the red nucleus to the opposite thalamus and hypothalamus.

The Metathalamus.

The methalamus comprises the geniculate bodies, two on each side.

(*a*) *Medial* (internal or inferior) geniculate body.

Receives acoustic fibres from the lateral fillet, the inferior corpus quadrigeminum, and the opposite medial geniculate body.

Sends fibres by the auditory radiation to the temporal cerebral cortex (Heschl's convolution), to the opposite medial geniculate body, and to the thalamus (lateral nucleus).

Gudden's commissure links the medial geniculate body of one side with that of the opposite side and with the opposite inferior corpus quadrigeminum. The fibres cross in the posterior part of the optic chiasma.

(*b*) *Lateral* (external or superior) geniculate body.

Receives optic fibres from the optic tract.

Sends fibres by the optic radiation to the occipital cerebral cortex, and also possibly to the thalamus (pulvinar and lateral nucleus).

The retinal fibres have been localised in definite areas of the lateral geniculate body (Brouwer) (see p. 23).

The Thalamus.

The dorsal surface of the thalamus is covered by a thin layer of white matter, the stratum zonale, from which a vertical plate of white matter penetrates into the thalamus (as the internal medullary lamina) dividing it into three parts—the anterior, medial and lateral nuclei. (See Diagram 38.)

1. ANTERIOR NUCLEUS.—This lies in the dorsal part of the rostral extremity, penetrating like a wedge between the medial and lateral nuclei, and protruding as the anterior tubercle of the thalamus.

   Afferent fibres—from the mammillo-thalamic tract of Vicq d'Azyr.

   Efferent fibres—to the medial nucleus of the thalamus, to the caudate nucleus, and possibly to the mammillary body and the cingular cortex.

2. MEDIAL NUCLEUS.—This lies between the central grey matter of the third ventricle and the internal medullary lamina.

   Afferent fibres—from olfactory centres through anterior nucleus, and possibly from the medial and trigeminal fillets (Kappers).

   Efferent fibres—to the caudate nucleus and to the subthalamic nucleus.

3. LATERAL NUCLEUS.—This is the largest of the thalamic nuclei, and contains more myelinated fibres than do the others. It can be divided into a lateral and a ventral part and the pulvinar.

(*a*) *Lateral part.*

Afferent fibres—from medial fillet, superior cerebellar peduncles and red nucleus : also from the temporal and occipital cortex.

Efferent fibres to the frontal cortex (through anterior limb of internal capsule), to the temporal and parietal cortex (through posterior limb).

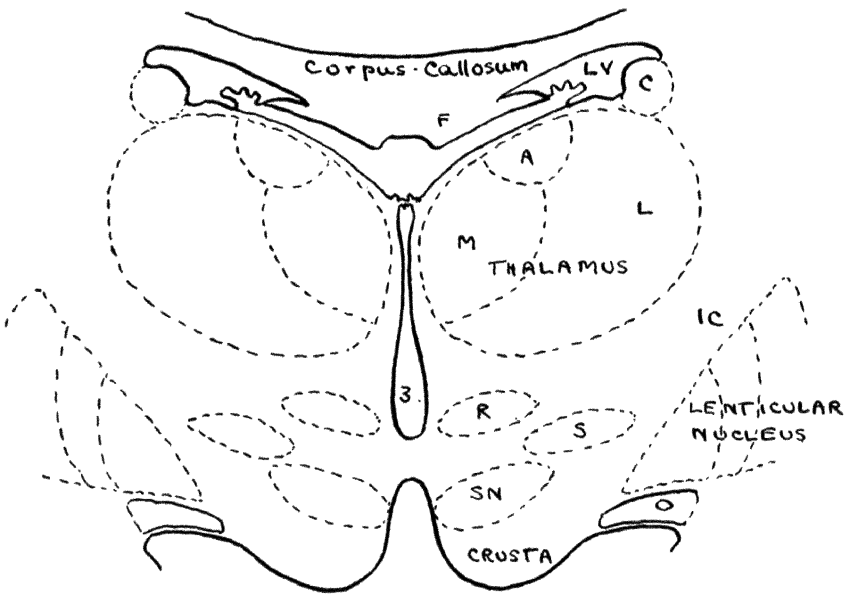

DIAGRAM 38.—Coronal section through the thalamus. (Diagrammatic.)

F. Fornix.
C. Caudate nucleus.
A. Anterior nucleus } of thalamus.
M. Medial nucleus }
L. Lateral nucleus. }
IC. Internal capsule.
R. Red nucleus.
S. Subthalamic nucleus.
SN. Substantia nigra.
O. Optic tract.
3. Third ventricle.
LV. Lateral ventricle.

(*b*) *Ventral part*, within which are two nuclear masses, the centre-median nucleus of Luys lying medially, and the semilunar (arcuate) nucleus of Flechsig lying ventro-laterally.

Afferent fibres—from medial fillet, trigeminal fillet, and spino-thalamic tract, superior cerebellar peduncles and red nucleus : also from the temporal and occipital cortex, and from the medial and lateral geniculate bodies, and from the globus pallidus.

Efferent fibres—to the post-Rolandic cortex (through posterior limb of internal capsule) : also to the globus pallidus.

(*c*) *Pulvinar*, the most caudal part of the thalamus.

Afferent fibres—source doubtful, but probably from the lateral geniculate bodies.

Efferent fibres—to the parietal cortex.

4. DESCENDING TRACTS ARISING IN THE THALAMUS.

The thalamo-olivary and thalamo-spinal tracts pass downwards from the thalamus, but it is not known from which nucleus they arise.

The Hypothalamic Region.

The " hypothalamus " includes that part of the tegmental region that lies inferior to the thalamus, together with the structures forming the floor of the

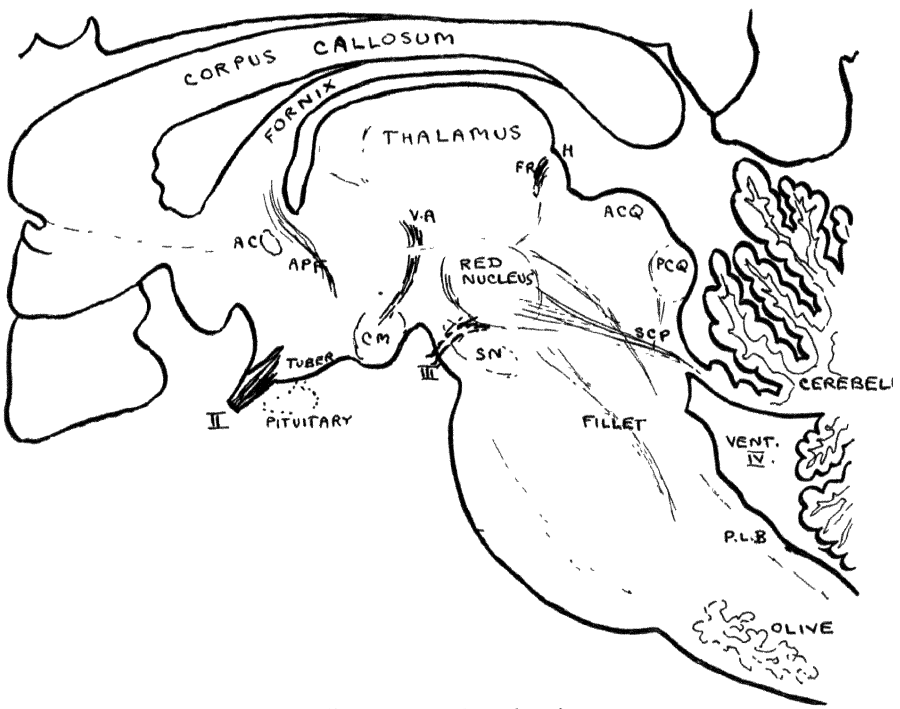

DIAGRAM 39.—Sagittal section

AC.	Anterior commissure.	FR.	Fasciculus retroflexus of Meynert.
APF.	Anterior pillar of fornix.	H.	Habenula.
CM.	Corpus mammillare	SCP.	Superior cerebellar peduncle.
VA.	Bundle of Vicq d'Azyr.	PLB	Posterior longitudinal bundle.
SN.	Substantia nigra.	ACQ.	Anterior corpus quadrigeminum.
		PCQ.	Posterior corpus quadrigeminum.

third ventricle—*i.e.*, the so-called hypothalamus lying medially, with the nuclei in the walls and floor of the third ventricle, and the subthalamus lying laterally. Thus each hypothalamic region can be regarded as bounded *medially* by the wall of the third ventricle, *laterally* by the internal capsule (and to a small extent the substantia nigra), *inferiorly* by the tegmentum of the midbrain which projects rostrally into it, and *anteriorly* (if the pars supra-optica is included) by the lamina terminalis. (See Diagram 39)

(See also the Integration Centres of the Autonomic System, p. 61.)

A. Hypothalamus.

This consists of two parts :—

(1) Pars optica hypothalami, which belongs to the telencephalon, and which includes the supra-optic nuclei (see below).

(2) Pars mammillaris hypothalami, which includes the corpora mammillaria, the tuber cinereum, the infundibulum and the hypophysis, and the ventricular nuclei (see below).

Corpora Mammillaria.

Two small spherical masses, close together in the interpeduncular space. Each consists of a larger medial group of small cells commonly known as the mammillary body, and of a smaller accessory (lateral) group of large cells.

(i.) Medial group.

Lateral part receives the fornix (from hippocampus).

Medial part gives rise to the principal mammillary bundle, which divides into—

(*a*) The bundle of Vicq d'Azyr, going to the anterior nucleus of the thalamus.

(*b*) Gudden's bundle, going to the tegmentum.

(ii.) Accessory group.

Receives the peduncle of the mammillary body from the tegmentum.

Tuber Cinereum.

A ventral hollow mass of grey matter, rostral to the mammillary bodies, and behind the optic chiasma. To it is attached the infundibulum or stalk of the hypophysis.

Hypophysis.

The pars posterior of the pituitary gland, developed from the floor of the third ventricle.

B. Nuclei of the Third Ventricle.

A very large number of cell groups has been described as lying in the floor and walls of the third ventricle. These may be grouped into two (Beattie).

(*a*) Supra-optic and tuber nuclei, lying in the floor and anterior wall of the third ventricle, with important afferent connections from the olfactory area and the thalamus, and efferent connections to the posterior lobe of the pituitary, tegmentum, posterior hypothalamic nuclei, and probably the medulla.

(*b*) Paraventricular nuclei, lying in the walls of the third ventricle in the posterior hypothalamus and receiving afferent fibres from the supra-optic and tuber nuclei, and from the thalamus, and sending efferent connections downwards by the posterior longitudinal bundle (Beattie) or by the crossed pyramidal bundle (Brincker) to link up with the thoracic lateral horn cells that give rise to sympathetic fibres.

C. Subthalamus.

This is the lateral region lying between the posterior part of the thalamus and the tegmentum of the mesencephalon. The long ascending tracts of the tegmentum pass through it on their way to the lateral nucleus of the thalamus, and the red nucleus and the substantia nigra project upward into it from the mesencephalon. A well-marked mass of grey matter is found in this region, known as the *subthalamic nucleus*, or corps de Luys. It lies dorsi-lateral to the upper end of the substantia nigra, lateral to the red nucleus, and ventral to the lateral nucleus of the thalamus. The subthalamic nucleus—

(*a*) Receives fibres from the lenticular nuclei of both sides, the substantia nigra, the cerebral cortex, the opposite subthalamic nucleus, and the thalamus (medial nucleus);

(*b*) Sends fibres to the lenticular nuclei of both sides, the red nucleus, the opposite subthalamic nucleus, and the stratum intermedium for further relay downwards.

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CHAPTER VIII

MICROSCOPIC STRUCTURE OF CORTEX OF CEREBELLUM AND OF CEREBRUM

A. Structure of Cerebellar Cortex.

The grey matter of the cerebellar cortex has the same general structure throughout ; it is arranged to form three layers, the middle being incomplete :—

(*a*) *Outer molecular layer*, containing—

1. Dendrites of Purkinje cells.
2. Axons of cells of inner granular layer.

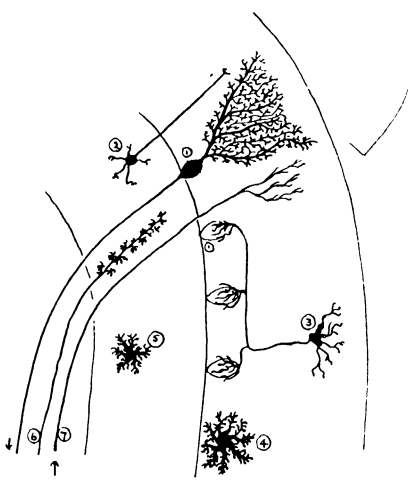

DIAGRAM 40.—Diagram of Cells and Fibres of Cerebellar Cortex.

1. Purkinje Cell.
2. Granule Cell.
3. Basket Cell.
4. Neuroglia Cell.
5. Golgi Cell.
6. Moss Fibre.
7. Tendril Fibre.

(*After Schafer.*)

3. Tendril or climbing fibres, or axons of incoming fibres.
4. Star-shaped cells, with axons running parallel to the surface, making a " basket " network round the bodies of the Purkinje cells.
5. Neuroglia cells of various types.

(*b*) *Layer of Purkinje cells*, consisting of large flask-shaped cells, of which

the dendrites arborise in the outer molecular layer, and the axons pass inwards through the inner granular layer to connect with the cerebellar nuclei.

(*c*) *Inner granular* (*or nuclear*) *layer*, containing—

1. Axons of Purkinje cells passing through.
2. Granule cells, whose unmyelinated axons run into the molecular layer, and bifurcate at right angles to the plane of arborisation of the Purkinje dendrites.
3. Golgi cells of various types.
4. Moss fibres, or axons of incoming fibres.

Thus the medullary part of the cerebellum contains—

(*a*) Afferent fibres { Moss fibres ending in granule layer. / Tendril fibres ending in molecular layer.

(*b*) Efferent fibres, the axons of the Purkinje cells.

(See Diagram 40.)

B. **Structure of Cerebral Cortex.**

Many layers have been distinguished in the grey matter of the cerebral cortex by different workers, but the following classification (Brodmann and Vogt) is the most convenient.

Six layers can be distinguished in all parts of the cortex with the exception of the hippocampus and pyriform lobe (which are archipallium and not neopallium) : in addition, in most parts of the cerebral cortex two well-defined white bands can be seen, the inner and outer lines of Baillarger : these consist of myelinated fibres running parallel to the surface.

1. Outer molecular layer (plexiform lamina of Campbell) : end branches of dendrites of pyramidal cells and of axons, and some small fusiform cells of Cajal. Also contains many neuroglia cells.
2. External granule layer : small, round cells, densely packed together, and some small pyramidal cells.
3. Outer pyramidal cell layer : large, well-formed pyramidal cells. The outer line of Baillarger lies in the deepest part of this layer.
4. Inner granule layer : small stellate cells, densely packed together.
5. Internal pyramidal or ganglionic layer : pyramidal cells, chiefly large. The inner line of Baillarger lies in this layer.
6. Inner polymorphic cell layer : fusiform or stellate cells.

Certain variations in these layers occur in different parts (not necessarily lobes) of the cerebral cortex, the following being the most important :—

(*a*) *Pre-Rolandic* (*or pre-central*) *area* (motor area).

Includes the pre-central gyrus, and posterior portions of the superior, middle and inferior frontal gyri.

The molecular layer is very dense, the internal pyramidal layer contains Betz cells (or giant pyramidal cells) in the posterior part, and the granule cells are almost absent.

(*b*) *Post-Rolandic* (*or post-central*) *area* (for general sensation).

Includes all the post-central gyrus except the lowest part, and extends to the paracentral lobule on the medial side.

The granule layers are very dense, and the outer band of Baillarger well marked.

(*c*) *Frontal Area.*

Includes all the cortex anterior to the precentral area, and the portion of the frontal lobe that appears on the medial surface. The pyramidal cell layers are especially well formed with the exception of the ganglion layer. The layer of polymorphic cells is thin.

(*d*) *Parietal Area.*

Includes the cortex lying between the visual area behind and the post-central area in front.

The granule layers are well-developed, and the inner band of Baillarger is large. There is an absence of large cells from the ganglionic and pyramidal layers.

(*e*) *Occipital Area* (visual area).

Includes the greater part of the occipital lobe.

(i.) Visuo-sensory area (deep in the anterior limb and in the walls of the posterior limb of the calcarine fissure, extending on to the surface of the cuneus above and the lingual gyrus below, and posteriorly to the occipital pole).

The outer band of Baillarger is broad and known as the line of Gennari, the inner band is absent. Both granule layers are very conspicuous, the inner one being duplicated. The deeper part of the pyramidal layer has some large stellate cells (Cajal's visual cells) instead of large pyramidal cells.

(ii.) Visuo-psychic area (surrounding the visuo-sensory area, and extending considerably on to the external surface).

The two bands of Baillarger are present, and the outer granule cell layer is extremely thick.

(*f*) *Temporal area* (auditory area).

Includes the superior temporal gyrus and the transverse temporal gyrus of Heschl (part of temporal operculum).

(i.) Auditory sensory area (whole of Heschl's gyrus and some of the lateral surface of the superior temporal gyri).

The granule cell layers are very thick, and the whole cortex contains large numbers of nerve fibres.

(ii.) Auditory psychic area (remainder of superior temporal gyrus). Similar to auditory sensory area, but the granule layers are not so thick and the pyramidal layer is deeper.

(*g*) *Cortex of the Rhinencephalon.*

The structure of the cortex is considerably modified.

(i.) Olfactory bulb—five layers can be made out, including a considerable amount of neuroglia.

(ii.) Pyriform area—the six layers are similar to those of the neopallium, but the outer molecular layer is unusually deep.

(iii.) Hippocampus—the structure is primitive and consists of three layers : (1) a deep outer molecular layer, (2) a thick layer of large pyramidal cells, and (3) a layer of polymorphous cells. The axons of the pyramidal cells pass through the polymorphous layer and stream out on the surface of the hippocampus as the alveus going to form the posterior pillar (fimbria) of the fornix.

The significance of these structural variations will be considered in Part II., Chapter V.

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CHAPTER IX

THE CEREBROSPINAL BLOOD VESSELS

THE blood vessels of the brain are extremely complex in their course and distribution, and in spite of investigations carried out by injection methods, and by post-mortem observations on cases known to have suffered from occlusion of one or more vessels before death, there still remains much work to be done before our knowledge is complete.

Arterial blood is carried into the rigid skull by the two internal carotid vessels and by the two vertebral arteries (one vertebral vessel usually being larger than the other).

The Circle of Willis is formed at the base of the brain by the anterior and posterior cerebral branches of the carotid, and by the posterior cerebral arteries from the basilar, which has itself been formed by the union of the two vertebral vessels. The anterior and posterior communicating arteries join the two anterior cerebrals, and the middle and posterior cerebrals respectively—so as to make the circle complete.

From this region groups of branches are given off evenly to—

1. The basal ganglia (basal branches).
2. The choroid plexus.
3. Most of the deep white matter.
4. The surface of the cortex and the pia-arachnoid (cortical branches).

For the general anatomy of these vessels, the reader is referred to text-books of anatomy, while the more peripheral distribution is given in the Table on p. 50.

The following account of the meninges and the blood vessels of the brain and spinal cord is intended to supplement the usual anatomical descriptions, and should be read in conjunction with a current text-book.

The Meninges.

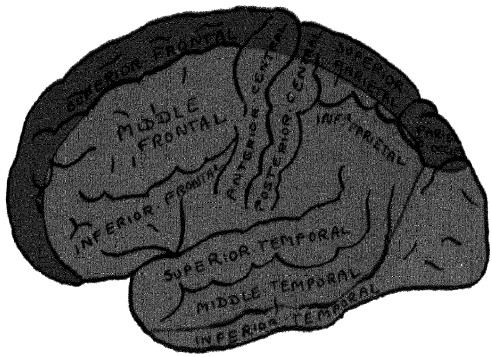
There are three meninges surrounding the brain and spinal cord.

1. DURA MATER.

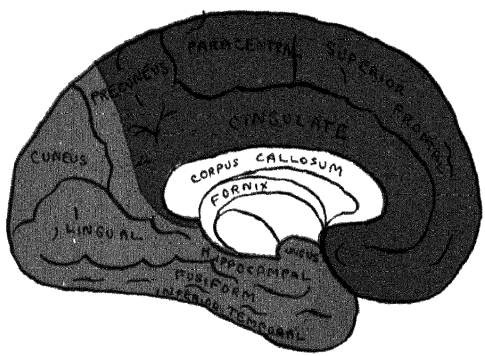
This is the outermost membrane, and is strong, thick and dense in structure.

The cranial portion consists of two layers, and these split to enclose the large venous sinuses and certain other structures.

The outer dura forms the internal periosteum of the skull, and over the vault the membrane may be stripped away easily, but in the base it is more resistant and fixed. There are no lymphatics within the dura mater.



Lateral Surface



Medial Surface

Areas supplied by Anterior Cerebral Artery - Blue
Areas supplied by Middle Cerebral Artery - Red
Areas supplied by Posterior Cerebral Artery - Green

(After Gray's

DIAGRAM 41 Arterial Blood Supply of Brain

In the spinal region, the two portions are not in approximation, for the outer layer is identical with the periosteum of the vertebral canal, while the inner part becomes the true spinal dura.

Between the two layers is found the epidural space, which is filled with fatty areolar tissue and an extensive thin-walled venous plexus.

2. ARACHNOID MATER.

This membrane has a delicate fibrous matrix consisting of white fibres with an admixture of elastic elements. It projects inwards as irregular cores for the arachnoid trabeculæ.

3. PIA MATER.

This is not a continuous membrane as is the arachnoid, for the pia is pierced by the perivascular cuffs of the entering and emerging blood vessels, and also by the foramina of Luschka and Majendie.

In the brain, branches from the Circle of Willis pass upwards in the pia mater and these smaller vessels dip into the brain substance, while in the spinal cord, the peripheral arteries (pial arterial network) penetrate the white substance of the cord along its entire circumference.

Fusion of the dura and the arachnoid occurs where the arachnoid villi, which are continuations of the arachnoid mesh, project into the lateral walls of the great dural sinuses, so that the arachnoid mesothelium comes to lie directly beneath the vascular endothelium ; it also occurs where arachnoid cell columns (representing prolongations of the arachnoid mesothelium) push their way into the dura at sites other than those along the great dural sinuses.

Schaltenbrand and Bailey consider the pia-arachnoid as one membrane, and believe that it not only covers the surface of the brain, but also the blood vessels that enter and leave the subarachnoid space.

Basal Arteries of the Brain.

These were considered by Beevor and Duret to be " end-arteries," and at the present time there is no further evidence to dispute this view, so that it must be held that these branches are more strictly " end-arteries " than are the cortical ones.

Cortical Arteries of the Brain.

It has been stated that " the cortical arteries of the cortex have no intercommunication when they have penetrated the cortex, so that the arterioles after they enter the cortex are ' end-arteries ' and do not anastomose with their neighbouring arterioles " (Beevor). This observer considered that there is an anastomosis between the cortical arteries at the borders of the different areas, and that this communication is more free than that between the contiguous branches of the same artery. Henbaer disagreed with this and maintained that there is an anastomotic network in the pia mater. Beevor and Duret both agreed that the cortical

arteries give off medullary branches which pass through the grey matter of the cortex and supply the medullary white matter. These branches extend through the whole depth of the centrum ovale as far as the upper surface of the caudate and lenticular nuclei and the internal capsule, but do not supply these latter structures.

The misconception of these cortical arteries being " end-arteries " has arisen entirely from the study of infarcts in this region—and this erroneous statement has been copied from book to book. It is known that infarcts occur in the spleen and in heart muscle, and yet these tissues have no " end-arteries." In the brain an infarct produces œdema, contraction of the arterioles, capillary diapedesis of the red cells and necrosis, but this condition is due to a lack of normal oxygen supply to the tissues, and not to an " anæmia " (as previously thought), for plenty of blood remains in the infarcted area.

General Plan of the Cerebral and Spinal Cord Blood Supply.

In accordance with modern views the following sequence occurs :—

A. In the Brain.

The cortical arteries give off perforating arterioles which pass down into the cortex and subcortical white matter, become smaller and reach the capillary bed. These arterioles and capillaries have a rich anastomosis with branches from a few deep arteries which come upwards through the white matter and the basal ganglia.

The venous limbs of the capillaries flow into venules, drain out to the cortex and are collected by the surface veins and empty into the dural sinuses. These sinuses have no valves, and so they join up and make an open system of blood channels which drain mainly through the jugular bulbs into the jugular veins of the neck.

It should be noted that these venous sinuses are less compressed than would be expected, because of the toughness of the dura, and because of their triangular shape. As previously mentioned, the skull is an almost " closed box," so that any changes in venous pressure will quickly alter the relative volumes of arterial, capillary and venous blood as well as the amount of intracellular and extracellular fluid.

The blood supply of the various parts of the brain is summarised in the accompanying tables.

I.	Area supplied.	Basal Branch of Artery.
Anterior commissure.	Median part	Ant. cerebral.
	External part	Mid. cerebral.
	Postero-external	Ant. choroidal.
Caudate nucleus.	Head, lower half	Ant. cerebral.
	upper half	Mid. cerebral.
	Tail	Ant. choroidal (mainly).
	Body	Mid. and post. cerebral.
Corpus mammillare		Post. cerebral.

Area supplied.		Basal Branch of Artery.
Corpus callosum	Body	Ant. cerebral.
	Genu and Rostrum	Ant. cerebral.
	Splenium	Post. cerebral.
	Tapetum, medial part	Ant. or mid. cerebral.
	external part	Mid. cerebral.
	post. part	Mid. or post. cerebral.
	forceps major	Post cerebral.
Crusta pedunculi,	dorsal third	Post. communicating or ant. choroidal
	ventral two-thirds	Post. cerebral or ant. choroidal.
Fascia dentata		Post. cerebral.
Fimbria		Ant. choroidal or post. cerebral.
Fornix.	Body	Post. cerebral.
	Columns, inf. part	Post. cerebral.
	sup. part	Ant. cerebral.
Geniculate bodies		Post. cerebral.
Hippocampus major		Ant. choroidal or post. cerebral.
Internal capsule.	Ant. limb	Ant. cerebral and mid. cerebral.
	Post. limb	Post. communicating and ant. choroidal and mid. cerebral.
Lenticular nucleus.	Putamen	Mid. cerebral.
	Ant. inf. part	Ant. cerebral.
	Post. inf. part	Ant. choroidal.
	Mid. segment	Mid. cerebral.
	Int. segment	Ant. choroidal (occasionally post. communicating and ant. cerebral).
Optic radiations and retro-lenticular fibres		Ant. choroidal (at commencement), mid. and post. cerebral.
Optic thalamus.	Ant. nucleus	Post. cerebral.
	Lat. nucleus	Post. communicating and post. cerebral.
	Med. nucleus, ant. half	Post. communicating or post. cerebral.
	post. half	Post. cerebral.
	Pulvinar	Post. cerebral.
Optic tracts		Ant. choroidal
Septum lucidum		Ant. cerebral.
Subthalamic nucleus and Forel's field		Post. communicating.
Uncus		Ant. choroidal.

II. Artery.	Summary of Areas Supplied.
Anterior choroidal (*Ant. or Paleostriate part*)	Amygdaloid nucleus (postero-medial part) (*remainder by mid. cerebral*). Caudate nucleus, head (part of), tail (two-thirds of), globus pallidus (*remainder of corpus striatum by mid. cerebral*), optic tract (post. two-thirds).
(*Posterior or post. cerebral part.*)	Acoustic radiation (commencement of), cerebral peduncle (mid. third), external geniculate body (ant. and lateral aspects) (*remainder by posterior cerebral*), internal capsule, post. limb (including retrolenticular part), optic radiation, commencement of, *i.e.*, as far as lateral aspect of inferior horn of lateral ventricle (*remainder by post. cerebral*). ? red nucleus (superior part) and substantia nigra, ? thalamus (lateral part of lateral nucleus).

ABBIE.

Artery.	Summary of Areas Supplied.
Posterior communicating.	Internal capsule, post. limb (ant. third or fifth), optic chiasma, optic thalamus (ant. external part and ant. half sometimes), pes pedunculi (dorsal third), regio subthalamica, tuber cinereum.
Ant. choroidal . *Basal branches.*	Amygdaloid nucleus, ant. commissure (outer part), caudate nucleus (tail), choroid plexus in descending and post. horns, internal capsule, post. limb (post. four-fifths or two-thirds), lenticular nucleus, internal segment, lenticular nucleus, external segment (sometimes), optic radiations at origin, optic tract, pes pedunculi (ant. third and posteroexternal two-thirds sometimes), retrolenticular fibres, post. to ext. capsule.
Cortical branch .	Uncinate gyrus.
Ant. cerebral . . *Basal branches.*	Ant. commissure (median part), caudate nucleus (inferior half of head), fornix (superior part of ant. column), internal capsule (inferior half of ant. limb), lamina terminalis, lenticular nucleus (external and mid. part), septum lucidum.
Cortical branches .	Corpus callosum, *gyri* fornicatus (median surface), frontalis superior, frontalis ascendens (superior quarter), marginalis (external surface), parietalis ascendens (superior quarter), parietalis superior (ant. half), rectus orbitalis (inferior surface), lobulus quadratus (ant. three-quarters).
Middle cerebral . *Basal branches.*	Ant. Commissure (outer part), caudate nucleus (superior part of head and body), internal capsule (superior part of ant. limb, post. limb above middle part of lenticular nucleus), lenticular nucleus (external and middle parts).
Cortical branches .	*Gyri* angularis, frontalis ascendens (inf. three-quarters), orbitalis internus, medius and externus, parietalis superior (post. half), parietalis ascendens (inferior three-quarters), supramarginalis, temporalis superior and medius, temporalis inferior (superior half), lobus temporalis (ant. end).
Posterior cerebral . *Basal branches.*	Choroid membrane, choroid plexus of body of lateral ventricle, corpus mammillare, fornix (body, post. crus, inf. part. of descending columns), geniculate bodies, internal and external, optic thalamus (ant. and ext. nuclei, internal nucleus post. third), pes pedunculi (ventral two-thirds), red nucleus.
Cortical branches .	*Gyri* cuneus, fusiformis, lingualis, quadratus (post. half inch), temporalis inferior (inferior half).

BEEVOR.

Anterior spinal . *Cord branches.*	Grey matter around central canal, posterior cornua (ant. and base), white matter of ventral columns and around anterior roots.
Medullary branches.	Dorsal longitudinal bundle, Gowers' tract, hypoglossal nucleus (except cephalically), internal and ventral external arcuate fibres with nucleus, medial lemniscus, nucleus and tractus solitarius (at decussation), olivo-cerebellar fibres (crossing the mid-line), pyramids and pyramidal decussation, tecto-spinal tract, dorsal vagus nucleus (at calamus region).
Vertebral . .	Dorsal accessory olive, hypoglossal nucleus (cephalic part), inferior olive (ventral part and cephalic portion of dorsal part), nucleus and tractus solitarius (at calamus), nucleus and tractus spinalis nervi trigemini (at decussation), pyramids (most of), tegmento-olivary tract, and olivo-cerebellar fibres in formatio reticularis, vago-glossopharyngeal nucleus dorsal part (above calamus).

Artery.	Summary of Areas Supplied.
Posterior inferior cerebellar.	Vago-glossopharyngeal nucleus or emerging fibres of X. and IX. nerves, nucleus ambiguus, nucleus and tractus spinalis of V. nerve, olivo-cerebellar fibres (as they pass to inferior cerebellar peduncle), rubro-spinal tract, spino-thalamic tract, ventral part of inf. cerebellar peduncle.
Posterior spinal .	Descending root of the vestibular nerve (part of), funiculi and nuclei gracilis and cuneatus, inferior cerebellar peduncle (caudal and more dorsal part).
Basilar . . .	Corpus trapezoidum (medial part), medial leminscus, medial
Medial branches.	longitudinal bundle, nuclei of IV. and VI. nerves, and of III. nerve (caudal part), tecto-spinal tract, thalamo-olivary tract, transverse pontine fibres.
Transverse branches.	Brachium pontis, corpus trapezoidum (lateral part), nuclei of VII. nerve, VIII. nerve (remaining fibres), V. nerve (remaining fibres including motor nucleus), superior olive.
Anterior inferior cerebellar.	Brachium pontis (most caudal part), cerebellum (inferior surface), internal ear and VIII. nerve, medulla (upper and dorso-lateral parts).
Superior cerebellar .	Brachium pontis (most cephalic part), cerebellum (superior surface and dentate nucleus), hind-brain (dorsal third), inferior corpora quadrigemina, spino-thalamic tract. (Critchley.)

STOPFORD.

B. IN THE SPINAL CORD.

The blood flow in this region is analogous to that in the brain, but as in the cord the white matter lies outside the grey there is a reversal of the arterial arrangement, because it is essential for the grey matter to have a richer blood supply than the white. The three large arteries lie in the subarachnoid space and send branches through the white matter to the grey matter beneath. The anterior spinal artery, for example, divides at the bottom of the anterior fissure into a right and left branch: each branch passes through the white matter and supplies a grey ventral horn.

In the spinal cord all the blood vessels appear to come by way of the surface arteries and their perforating branches, *i.e.*, there are no central vessels and there is a much less complete anastomosis between different segments of the cord than between different parts of the brain.

The external white matter is supplied by numerous short perforating branches mostly derived from the two posterior spinal vessels. The capillaries drain into venules, and these pass outwards to the surface veins as in the cerebral cortex.

The arrangement of the veins differs from that of the arteries, for the venous branches emerge from the periphery of the cord and from the anterior median fissure and pass to a diffuse plexus in the pia mater. From the pia the venous blood drains to the veins around the anterior and posterior nerve roots.

Lymphatics.

There are no lymphatics within the central nervous system. Blood fluids, which pass out from the capillaries, seep through tissues and are not collected in

lymphatic vessels as in most other parts of the body. Blood vessels which penetrate from the pia mater are surrounded by perivascular " lymph channels " which open freely on the brain surface into the subarachnoid spaces. (These are further considered later on.)

Structure of the Arteries.

The cerebral arteries change markedly with increasing age. They all have a thick internal elastic lamina, and in the larger arteries this is usually doubled or multiple. Beneath the elastic layer there is a weakly-staining interstitial substance ; the cerebral arteries are unique in the absence of an external elastic lamina and have only a weakly developed adventitia.

Structure of the Veins.

The veins are extremely thin in relation to the large lumen and the walls are composed largely of connective tissue. The smaller veins that run out of the capillaries are indistinguishable in their structure from the arterioles. The larger veins show a thin elastic membrane, and as the veins increase in size there is relatively less and less elastic tissue in their walls. In the pia mater the elastic layer only exists as a very thin ring external to the endothelium.

Structure of the Capillaries.

The capillaries appear to be much like those in other parts of the body and there is a sharp demarcation between the muscular arterioles and the capillaries with their large extent of free endothelial surface.

Observations show that there is more closeness of the capillary network and increased metabolism in areas of grey matter than in white, and also that sensory nuclei and correlation centres have a greater blood supply than motor ones. The parietal lobe is more vascular than any other, while the blood supply to the rest of the cerebral and cerebellar cortex is approximately the same. It is concluded that the capillary supply to any region is directly related to its functional activity, and it is of interest to note that a greater blood supply is required for metabolism than is needed merely for growth.

Structure of the Perivascular Spaces.

These spaces are also known as Virchow-Robin spaces, and much controversy has arisen as to their exact anatomical relationships.

There is slight doubt as to whether or not the Virchow-Robin spaces connect with the subarachnoid space on one hand, and with the perineuronal space on the other. From the arachnoid spaces the fluid drains into the general cerebral circulation.

The perivascular space is lined with endothelium on both sides, and on the vessel side this endothelium lies over thick connective tissue, *i.e.*, the adventitia of the vessel wall. On the other side the endothelium lies close to the parenchyma of the brain (largely macroglia cells which encircle the vessel and send out the processes known as " sucker feet "). The perivascular space thus enfolds large

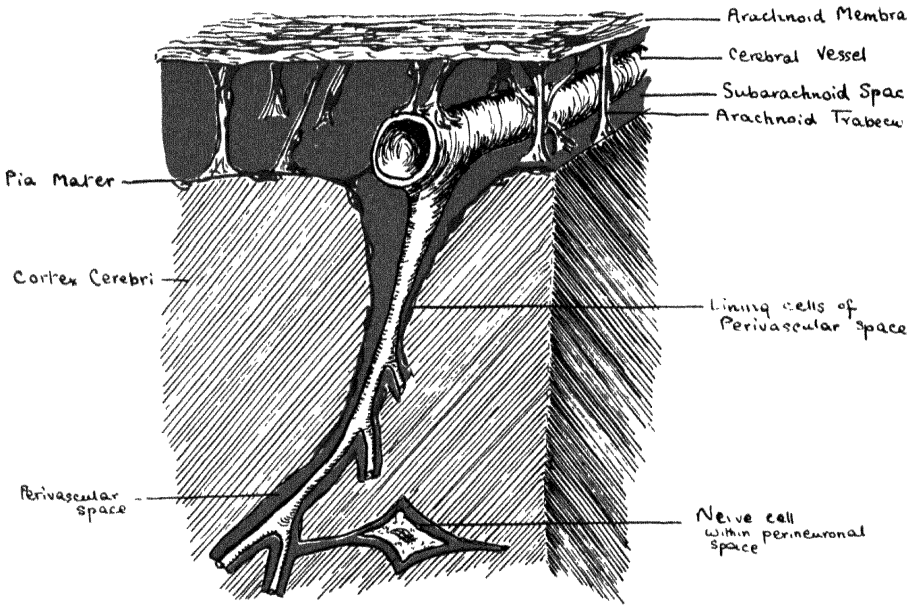


DIAGRAM 42 Diagram to show relation of subarachnoid space, perivascular channels, and nerve cells The lining cells of the pia mater are reflected inwards for a short distance to form a lining for the perivascular space

(*After Weed*)

and small arteries and veins within the nervous tissue, but a well-defined space is not discernible about the smallest arterioles, venules and capillaries. The capillaries run close to the nerve cells and there is a perineuronal space which often appears to join the pericapillary space (see Diagram 42). This therefore affords an ideal arrangement for the exchange of fluid between the capillary and the nerve cell.

The transition from the ill-defined intercellular fluid spaces, the pericapillary and perineuronal spaces to the clearly defined perivascular spaces is a gradual one ; probably this latter is nowhere clear and wide, but it is a variable and potential space with many arachnoidal trabeculæ.

The cerebrospinal fluid moves slowly through the perivascular space and empties into the subarachnoid space, where a layer of pia mater has to be pierced, so that a strong ring is formed around the mouth of the vessel, and this resists dilatation and keeps the opening of the perivascular space small even though the area behind may be dilated. To summarise, fluid flows downwards from the perineuronal space to the perivascular space and thence to the subarachnoid along both veins and arteries, so that any exudates from the subarachnoid space are unlikely to enter the Virchow-Robin spaces (Kubie and Weed).

The Choroid Plexus.

A choroid plexus is found in the third and fourth ventricles, and in the body and descending horns of the lateral ventricle. Each plexus has an afferent and an efferent vessel and the arterial supply is mainly derived from the anterior and posterior choroidal arteries. The choroid plexus is a highly vascular pial membrane consisting of tufts of blood vessels, both arteries and veins, with walls which are of varying thickness ; there are also arterioles and many capillaries. The walls of the venous sinuses are much thinner than those of the veins and contain no muscle fibres but have elastic fibres which curl in wide spirals about them.

The epithelial cells of the plexus are concerned with secretion.

Stohr found nerve fibres and nervous corpuscles and ganglion cells in the pial tissues of the choroid plexus, and he considered that the nerves may regulate the intra-cranial blood circulation and also the intra-cerebral pressure.

In the embryo the epithelial cells show a large amount of glycogen and are rich in fats, but these disappear by birth. During the second half of pregnancy the lipoids increase in the epithelium and in the subepithelial and perivascular tissue of the choroid plexus.

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CHAPTER X

CEREBROSPINAL FLUID

(A.) Distribution.

The cerebrospinal fluid is found in the lateral ventricles which communicate by the foramina of Monro with the third ventricle; this in turn communicates by the Sylvian aqueduct with the fourth ventricle and thence to the central canal of the spinal cord. The fluid is thus found in the whole of the cerebrospinal canal. In addition it fills the subarachnoid space, communication being established with the fourth ventricle by the medial foramen of Majendie and the two lateral foramina of Luschka; this subarachnoid space is enlarged in places into intercommunicating cisternæ of which the most important is the cisterna magna above the medulla and below the posterior border of the cerebellum.

Every blood vessel perforating into nervous tissue is surrounded by a covering of cells of the arachnoid and pia mater, which turn in with it; it lies therefore in a cell-enclosed channel which communicates directly with the subarachnoid space and is continued to connect with the spaces round the nerve cells, the fluid thus bathing all the neurones. (See also p. 55.)

(B.) Source.

The cerebrospinal fluid is produced from the blood by the choroid plexuses, by secretion, or by selective filtration: this power is exercised by the choroid plexus and, to a very slight degree, by the capillaries of the brain, spinal cord and meninges, the flow being outwards into the subarachnoid spaces from the latter, and inwards into the ventricles from the former.

Evidence.

(i.) Histological.—Changes can be observed in the cells of the choroid plexus of the type usually associated with secretory activity. Further, the position of the Golgi apparatus in these cells favours the view that they are producing a secretion on their free surface.

(ii.) Direct observation.—The exposed choroid plexus "sweats" on the free surface.

(iii.) Embryological.—Congenital internal hydrocephalus is frequently associated with hypertrophied choroid plexus.

(iv.) Experimental.

(*a*) Internal hydrocephalus follows occlusion of the Sylvian aqueduct, or of the foramina of Magendie and Luschka.

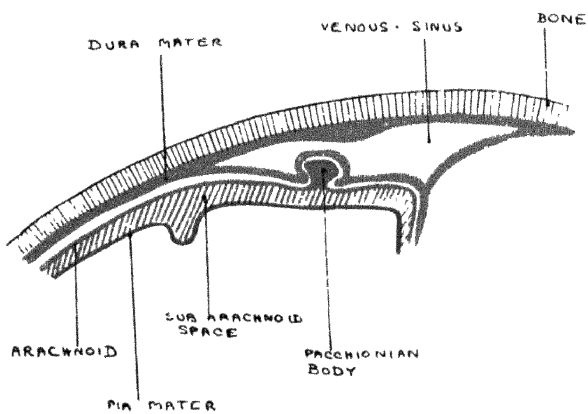
DURA MATER
VENOUS SINUS
BONE
ARACHNOID
SUB ARACHNOID SPACE
PACHIONIAN BODY
PIA MATER

DIAGRAM 43

(*b*) Unilateral internal hydrocephalus follows occlusion of one foramen of Monro, but this is prevented by extirpation of the choroid plexus of that side.

(*c*) Destruction of the choroid plexus and ependyma cells causes diminution in the amount of fluid formed.

(C.) Circulation and Absorption.

The fluid is slowly but continuously formed, and consequently it must be continually removed. It circulates slowly through the brain ventricles and the meshes of the subarachnoid spaces, and passes away by three routes :—

(i.) The arachnoid villi, which include the Pacchionian bodies, and thence into the venous sinuses, especially the superior longitudinal sinus ; also directly through the arachnoid into the cortical cerebral vessels wherever there is a large surface of contact. This path accounts for most of the fluid.

(ii.) The venous plexus round the foramen magnum and into the meningeal and spinal veins.

(iii.) Along the perineural sheath of the cranial nerves, into the extracranial lymphatics outside the dura, and along the spinal nerve roots into the veins.

The method of absorption has been fully investigated by Weed, to whose work reference should be made.

(See Diagram 43.)

The presence of sensory nerve endings in the choroid plexus suggests the possibility of a nervous control of secretion dependent on movements of the fluid. (Stöhr.)

(D.) Pressure.

The pressure of the cerebrospinal fluid is normally about 60 — 150 mm. water.

The pressure varies, as a rule, directly as the capillary pressure, but it is possible to vary the blood pressure (*e.g.*, by vagus stimulation) without affecting that of the cerebrospinal fluid. The venous pressure is normally consistently below that of the cerebrospinal fluid, and consequently diffusion occurs into the veins. The reverse can, however, occur : if distilled water is injected intravenously, the occipital headache due to removal of cerebrospinal fluid by puncture is relieved because fluid then diffuses from the veins into the cisterna basalis.

(E.) Normal Composition.

Normal cerebrospinal fluid is a clear colourless liquid, of specific gravity 1004 to 1006. The cells usually number less than ten per cubic millimetre. The *p*H is between 7·4 and 7·6 (blood = 7·4), but on standing it may rise to 8.

It contains the following :—

Glucose : varying from 0·05 to 0·08 gm. per 100 c.c.
Protein : trace, about 0·02 gm. per 100 c.c.
Inorganic salts, as in blood plasma.
(Chlorides = 0·73 to 0·75 gm. NaCl per 100 c.c.)
Urea : the same as in plasma.
Active principles from pituitary gland (in the ventricular fluid).
CO_2, in excess of that in the blood.

It contains no antibodies and no opsonins, and does not clot on standing.

The amount of the fluid is variable, estimated as 80 to 100 c.c., or even as much as 150 c.c.

(F.) Functions.

The more important functions of the cerebrospinal fluid are as follows :—

(i.) Acts as a mechanical support for nervous tissues, being protective by equalising the pressure within and without, and by providing a pressure independent of the arterial blood pressure.

(ii.) Helps to balance the amount of blood in the cranium.

(iii.) Acts possibly as intermediary for O_2, nutriment, CO_2, and waste, between the blood and nervous tissues, as it bathes all the neurones.

(iv.) Is protective to nervous tissues in that the choroid plexus does not allow of the passage of blood poisons into the cerebrospinal fluid.

(G.) Variations in Composition.

(i.) *Physical Changes.*

The fluid may be turbid (as in septic meningitis) or bloodstained. It may be clear, but clot on standing (as in tubercular meningitis). It is sometimes straw-coloured.

(ii.) *Cell Content.*

The number of cells is increased in inflammation.

Lymphocytes are increased in many acute infections, especially tubercular meningitis, encephalitis lethargica, anterior poliomyelitis, and all syphilitic affections of the nervous system.

Polymorphonuclear leucocytes are increased in all pyogenic infections.

Large mononuclear cells are increased in syphilis and in cases of tumours involving the meninges.

(iii.) *Glucose Content.*

As determined by Fehling's method, this is increased in diabetes and decreased in septic meningitis, and usually decreased in tubercular meningitis.

(iv.) *Protein Content.*

An excess of protein is due to inflammation, to œdema or to damage to capillary walls ; it also occurs frequently in tumours of the brain and spinal cord. As a rule the albumin is much in excess of the globulin, but in certain pathological conditions, such as general paralysis of the insane, the two are usually approximately equal. As a direct result of this increase of globulin the cerebrospinal fluid in these cases precipitates colloidal suspensions : this is the basis of the well-known gold test.

(v.) *Chloride Content.*

This apparently varies with the blood chlorides, and is in the proportion of 120 in the cerebrospinal fluid to 100 in the blood. Consequently it is reduced in tubercular meningitis and in other septic conditions.

(vi.) *Abnormal Constituents.*

Cholesterol is present in general paralysis of the insane and in meningitis, and choline may appear in conditions of excessive breakdown of nervous tissue.

(H.) **Diagnostic Applications.**

(i.) *Lumbar Puncture.*

The most valuable method for investigation of pathological conditions of the central nervous system is the examination of the cerebrospinal fluid : this is most usually withdrawn from the subarachnoid space between the fourth and fifth lumbar vertebræ. (The fluid may also be withdrawn from the cisternæ and the ventricles.)

(ii.) *Lipiodol Injection.*

This substance, which is opaque to X-rays, may be used in the light and in the heavy form by injection into the spinal subarachnoid space for the exact localisation of spinal tumours.

(iii.) *Ventriculography.*

X-ray examination of the ventricular system after the replacement of cerebrospinal fluid with air is sometimes of value in detecting and localising intracranial tumours when other and less hazardous lines of investigation have failed.

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CHAPTER XI

AUTONOMIC NERVOUS SYSTEM

THE autonomic (or vegetative) nervous system is sometimes defined as that part of the nervous system which is independent of the control of the will. This definition is not strictly correct as certain reflexes carried out by the central nervous system (*e.g.*, knee jerk) cannot be voluntarily prevented. Langley described the autonomic nervous system as consisting of " the nerve cells and nerve fibres by means of which efferent impulses pass to tissues other than multinuclear striated muscle." This conception must, however, be enlarged in view of more recent investigations.

The autonomic system is the fundamental nervous system, on to which has been added the cerebrospinal system. Each must be regarded as a whole, consisting of afferent, central, and efferent paths, the central path and integration centres for both systems lying within the cerebrospinal axis.

A. Afferent Part of the Autonomic System.

The subdivision of the autonomic system into parasympathetic and sympathetic systems rests very largely on the results of the study of the efferent autonomic fibres from anatomical, physiological and pharmacological aspects. It seems best, therefore, to group all afferent fibres of the system together simply as autonomic fibres.

These afferent fibres are the dendrites of autonomic cells in the sensory ganglia of the various cranial and spinal nerves (Kölliker); the fibres have come in these nerves from the viscera, and frequently pass through the autonomic ganglia reaching the sensory ganglia by the white rami communicantes where such are present. They pass into the brain stem, and by posterior root fibres into the spinal cord, at levels corresponding to the outflow of the efferent autonomic fibres. Thus, afferent fibres of this system are found in the fifth, seventh, ninth and tenth cranial nerves (see p. 64) and may be present in any or all of the spinal nerves. The distribution of these fibres for some of the more important structures of the body is given in Table II. Their function is chiefly that of producing reflex responses in regulating the activity of the various " involuntary " structures such as unstriped muscle and glands (see p. 120); they also carry the impulses underlying " visceral sensation."

B. Central Paths and Integration Centres.

(i.) ASCENDING PATH.

The afferent fibres passing in by the posterior roots may enter the central grey matter at once; the impulse may then be relayed by connector neurones to

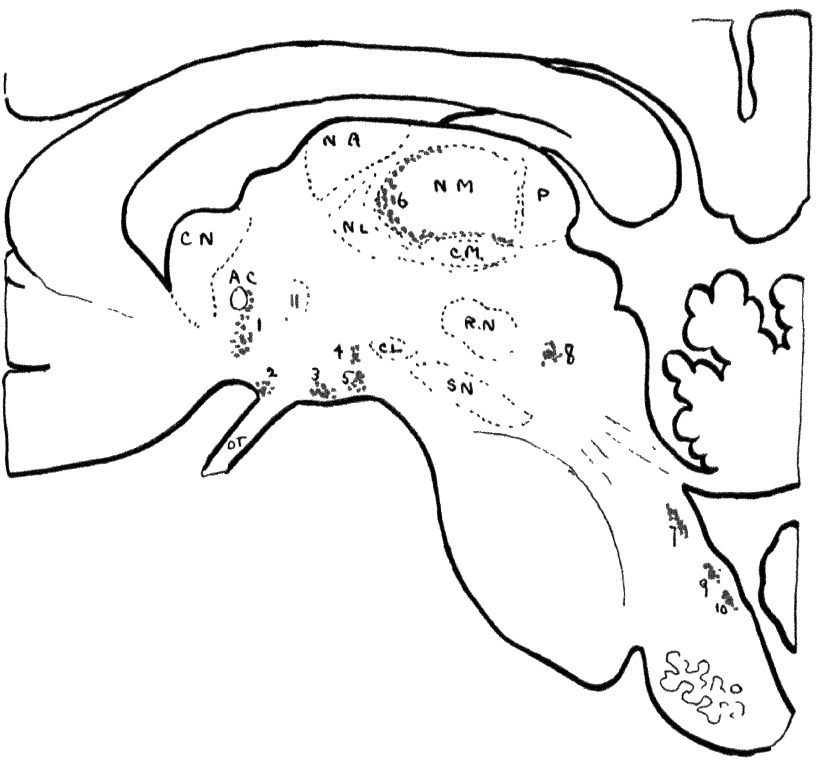

DIAGRAM 44 --Diagram of Sagittal Section, showing position of chief Autonomic Centres

C.N. Caudate nucleus.
A C Anterior commissure.
N A Anterior nucleus of thalamus
N.L. Lateral nucleus of thalamus
N M Medial nucleus of thalamus
C M Centre median nucleus of Luys
P. Pulvinar of thalamus.
C L Subthalamic nucleus (corps de Luys).
R N. Red nucleus.
S N Substantia nigra
O. Olive.
O T. Optic tract.

1 Innominate substance of Reichert
2 Nuclei of optic tract
3 Ventral nucleus of tuber.
4 Nuclei of field of Forel.
5 Accessory mamillary nucleus.
6. Thalamic cell groups.
7. Autonomic nucleus of nerve 7.
8. Autonomic nucleus of nerve 3.
9 Autonomic nucleus of nerve 9.
10 Autonomic nucleus of nerve 10
11. Periventricular nuclei surrounding anterior pillar of fornix. [Not in the plane of the section.]

the cells of origin of efferent autonomic fibres, and a reflex visceral response evoked. More frequently the afferent autonomic fibres pass up with the " sensory" fibres of the cerebrospinal system to the thalamus, which represents the highest integration level for the autonomic system. Some of the afferent fibres may relay through Clarke's cells to reach the cerebellum : others terminate in relation with any of the integration centres (see below).

(ii.) INTEGRATION CENTRES.

The autonomic centres are found throughout the cerebrospinal axis : they have been identified experimentally (and in some cases clinically) and are all developed from the intermediate band of grey matter lying between the dorsal and basal laminæ and adjacent to the sulcus limitans. The cells are usually oval, often bipolar, and nearly always pigmented ; they are arranged either in well-defined masses or in streams connecting with the masses.

The following centres have been described (Delmas and Laux) :—

(See Diagram 44.)

1. SUB-CORTICAL CENTRES.

(*a*) *Thalamo-striate Region.*

(i.) Thalamus. Cells surrounding the medial nucleus, a mass of cells near the centre median nucleus (Luys), a group near the grey commissure, and a juxtaventricular mass, all joined together.

(ii.) Striate body. Centres not identified, but probably present from clinical evidence, for control of sweat, temperature, etc.

(*b*) *Sub-optic Region.*

Nuclei of the Field of Forel, the cells continuing to the tuber region, to the vegetative nucleus of the oculomotor nerve, to the medial nucleus of the thalamus and to the corpora mammillaria.

(*c*) *Sub-lenticular Region.*

Groups of cells in a horizontal plane in the innominate substance of Reichert.

(*d*) *Infundibulo-tuber Region* (between the anterior commissure and the posterior perforated spot).

(i.) Periventricular nuclei, surrounding anterior pillar of fornix.

(ii.) Ventral nucleus of tuber.

(iii.) Nuclei of optic tract.

(iv.) Accessory supra-optic nuclei.

(v.) Accessory mammillary body.

These five groups are linked by chains of cells, and probably play a part in fat metabolism, sugar regulation, control of temperature, of water content of body, and of sleep. Possibly the substantia nigra belongs to this group. (See also p. 42.)

Commissural connections between these subcortical centres are provided by the commissure of Meynert, and by the bundle of the tuber.

2. Brain-stem Centres.
   (*a*) *In Cerebral Peduncles.*
   Vegetative (Edinger-Westphal) nucleus of oculomotor nerve.
   (*b*) *In Pons.*
   Lachrymo-muco-nasal nucleus, adjacent to motor nucleus of facial nerve. (Exact position not determined.)
   (*c*) *In Medulla.*
   Superior salivatory nucleus. Fibres join facial nerve.
   Inferior salivatory nucleus. Fibres join glossopharyngeal nerve.
   Nucleus of Staderini. Fibres join vagus nerve.

3. Spinal Cord Centres.
   (*a*) Clarke's column of cells. (Thoracic and lumbar.)
   (*b*) Lateral column of cells. (i.) C. 3 and 4.
   (ii.) C. 8—L. 2.
   (iii.) L. 4—S. 5.
   (*c*) Medio-ventral column of cells (Sacral).

(iii.) Descending Path.

It is difficult to identify the actual paths taken by the descending autonomic impulses. The thalamus sends fibres to the striate body, and the globus pallidus in its turn sends fibres to the red nucleus, hypothalamus, and infundibular region ; further details of these connections will be found on p. 42. The actual descending path in the spinal cord is known to lie in the lateral columns, the fibres passing through the formatio reticularis as they turn in to the grey matter.

C. Efferent Part of the Autonomic System.

The peripheral efferent fibres arise from cell groups in the midbrain, medulla and spinal cord : they emerge as medullated fibres and end round the dendrites of a " sympathetic " cell in some ganglion ; the axon of this cell then passes to the peripheral tissue. Thus the peripheral efferent autonomic path always consists of two neurones, the fibres coming out from the central nervous system being medullated and constituting the white rami communicantes (pre-ganglionic fibres), while the fibres passing from the ganglion (post-ganglionic) are usually non-medullated, and run in the grey rami communicantes. This anatomical arrangement for relaying the efferent impulse after its emergence from the central nervous system is related to the special functions of the autonomic system as contrasted with those of the cerebrospinal mechanism.

As the autonomic ganglia are formed of cells that have migrated during development (see p. 3) it is unlikely that there will be a constant anatomical pattern for the cell-stations on the autonomic paths. This probably accounts for the variability in the results obtained after sympathetic ganglionectomy.

These pre-ganglionic fibres are given off from three distinct regions of the central nervous system, and can be grouped in the following way, the groups being distinguished from one another on physiological and anatomical grounds.

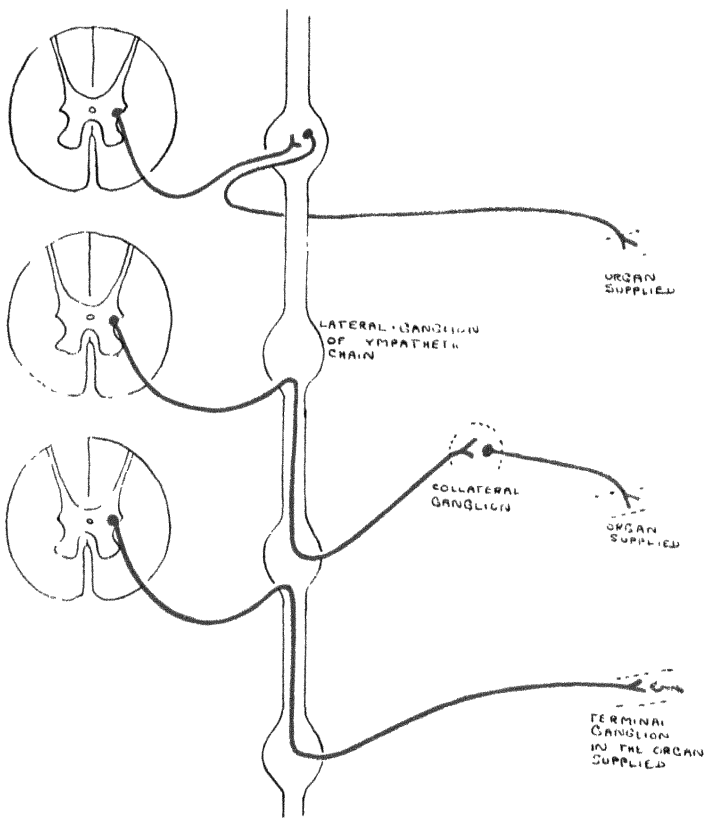

DIAGRAM 45.—Diagram to show Ganglion Connections of the Autonomic System.

Red : Pre-ganglionic fibre. Blue : Post-ganglionic fibre.

1. Parasympathetic, or cranio-sacral outflow.
   Fibres emerge :—
   (i.) In cranial nerves 3, 7, 9, 10, 11 (cranial outflow).
   (ii.) In sacral nerves 2, 3 4 (sacral outflow).
   (According to Danielopolu, parasympathetic fibres emerge by all the posterior roots of the spinal cord.)
2. Sympathetic, or thoracico-lumbar outflow.
   Fibres emerge from the spinal cord between the first thoracic and third lumbar segments.

Position of the Autonomic Ganglia.

We owe our knowledge of the position of the cell stations of the autonomic paths to Langley, who devised the nicotine method for tracing fibres. Nicotine paralyses the synapse between pre-ganglionic fibre and nerve cell, but does not affect the actual nerve fibres. If, therefore, an appropriate ganglion is painted with nicotine, stimulation of pre-ganglionic fibres will produce no response, whereas stimulation of post-ganglionic fibres will do so. By this means it is possible to pick out the ganglion in which definite nerve fibres have their cell-station.

The autonomic ganglia fall into three groups (see Diagram 45) :—

(i.) *Lateral ganglia*, or sympathetic chain, consisting of paired chains of ganglia extending through the thoracic and lumbar region and forward into the cervical region. In the neck the ganglia are reduced to three by fusion of adjoining ganglia (the superior, middle and inferior cervical ganglia). In the thorax there are usually eleven (10–12) ganglia, in the lumbar region four, and in the sacral region four or five.

(ii.) *Collateral or intermediate ganglia*, comprising the ciliary, spheno-palatine, submaxillary, otic, cœliac, superior and inferior mesenteric ganglia.

(iii.) *Distal or terminal ganglia*, consisting of groups of ganglion cells in the walls of the organs supplied, *e.g.*, in the heart and intestine.

The parasympathetic pre-ganglionic fibres usually terminate in the distal ganglia, whereas the sympathetic pre-ganglionic fibres have cell stations in either the lateral or the collateral ganglia. The ganglia act as the distributing stations, so that this arrangement is clearly bound up with the differing functions of the two groups of fibres (see p. 117).

1. PARASYMPATHETIC SYSTEM

(*a*) *Cranial Parasympathetic Fibres.*

Parasympathetic fibres are found in the cranial nerves 3, 5, 7, 9, 10 and 11, some being afferent and some efferent.

1. THIRD NERVE.

(*b*) *Efferent fibres.* Cells of origin—anterior end of nucleus 3 (probably Edinger-Westphal).

Pre-ganglionic fibres pass to ciliary ganglion.

Post-ganglionic fibres pass in short ciliary nerves to ciliary muscle and sphincter pupillæ.

2. FIFTH NERVE.

(*a*) *Afferent fibres.* From anterior two-thirds of tongue (not taste), salivary and lachrymal glands, from eyeball, and from palatal glands.

3. SEVENTH NERVE.

(*a*) *Afferent fibres.* From palate, uvula, and nasal fossæ, and from parotid gland.

(*b*) *Efferent fibres.* Cells of origin—superior salivatory nucleus.

(i.) Pre-ganglionic fibres pass to submaxillary ganglion and gland.

Post-ganglionic fibres pass to sublingual and submaxillary glands.

(ii.) Pre-ganglionic fibres pass to Meckel's ganglion.

Post-ganglionic fibres pass to lachrymal and palatal glands.

4. NINTH NERVE.

(*a*) *Afferent fibres.* From posterior third of tongue (not taste) and mucous membrane of mouth and pharynx.

(*b*) *Efferent fibres.* Cells of origin—inferior salivatory nucleus.

Pre-ganglionic fibres pass to otic ganglion.

Post-ganglionic fibres pass to parotid gland and glands of mucous membrane of mouth.

5. TENTH AND ACCESSORY PART OF ELEVENTH NERVES.

(*a*) *Afferent fibres.* From pharynx, larynx, trachea, œsophagus, thoracic and abdominal viscera.

(*b*) *Efferent fibres.* Cells of origin—dorsal nucleus.

Pre-ganglionic fibres pass to parasympathetic ganglia of plexus for thoracic and abdominal viscera.

Post-ganglionic fibres pass to thoracic and abdominal viscera.

(*b*) *Sacral Parasympathetic Fibres.*

The white rami carrying fibres from cells of the lateral part of the grey matter of the cord to the second, third and possibly fourth sacral nerves, give off branches that unite as the pelvic (splanchnic) nerves or nervi erigentes.

They join with branches of the sympathetic pelvic plexus and supply the rectum, bladder, kidney, uterus, erectile tissue and prostate. The cell stations of these fibres are in ganglia in the walls of the organs supplied.

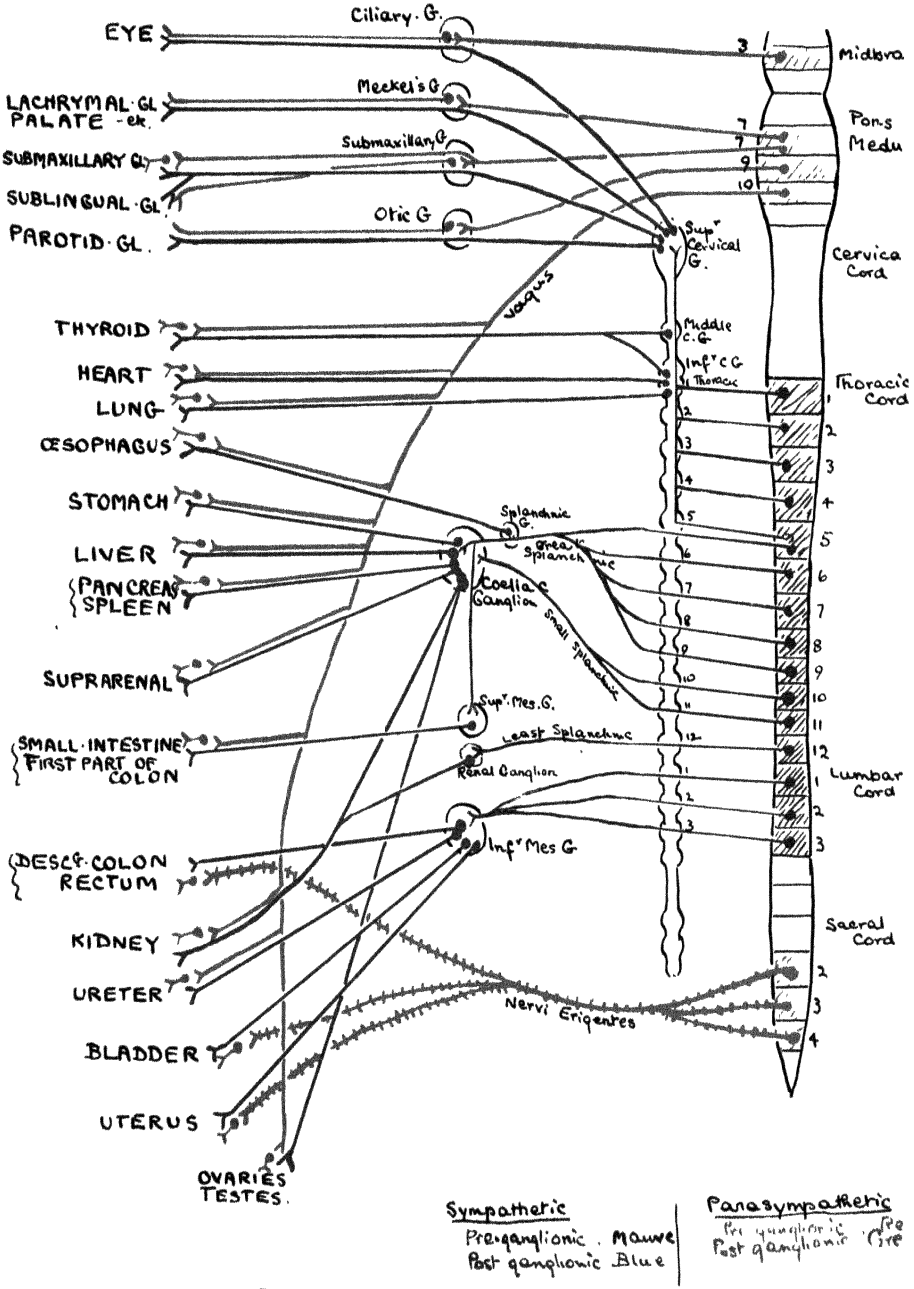

DIAGRAM 46.—Autonomic Supply of Certain Organs.

2. SYMPATHETIC SYSTEM

Axons of lateral horn cells of the spinal cord segments T. 1 to L. 3 pass out in the white rami communicantes to the sympathetic chain of ganglia : they then run either up or down in the chain, some connecting with cells of one or other of these ganglia, and others passing through the chain and running out to connect with cells of the outlying ganglia. The chain, or sympathetic trunk, consists of cervical, thoracic, lumbar and sacral portions.

Cervical Sympathetic.

This consists of three ganglia (superior, middle and inferior) connected to one another by nerve cords. The superior ganglion is probably formed by the coalescence of the first four cervical ganglia, the middle ganglion corresponds to the fifth and sixth cervical, and the inferior to the seventh and eighth cervical ganglia. The inferior ganglion is frequently fused with the first thoracic ganglion, the mass being then known as the stellate ganglion : sometimes the second thoracic ganglion is also included.

The fibres for the cervical sympathetic arise chiefly from segments T. 1–5 ; most of them pass up through the inferior cervical ganglion then travel to the middle ganglion, and end in the superior cervical ganglion. The post-ganglionic fibres run usually as follows.

A. **Superior Cervical Ganglion.**

(i.) Internal carotid nerve. Arises from upper end of ganglion, passing up into cranial cavity, and dividing to form the internal carotid and cavernous plexuses.

(ii.) Lateral branches. Grey rami to nerves C. 1–4, to vagus (ganglion nodosum and jugular), to hypoglossal nerve, to glossopharyngeal nerve (petrous ganglion).

(iii.) Medial branches.

(*a*) Laryngopharyngeal branches to join fibres of glossopharyngeal and vagus nerves in pharyngeal plexus : thence to muscles and mucous membrane of pharynx, and muscles of soft palate except tensor palati.

(*b*) Superior cardiac nerve (several branches). Probably efferent only. Right nerve joins deep cardiac plexus, receiving branches from external laryngeal, vagus and recurrent nerves. Left nerve joins superficial part of cardiac plexus.

(iv.) Anterior branches. Ramify as plexuses on the common carotid and external carotid arteries and branches.

B. **Middle Cervical Ganglion** (Sometimes absent).

Grey rami to nerves C. 5, 6 (sometimes 4 and 7). Supplies fibres to thyroid. Gives rise to middle cardiac nerve, which receives fibres from recurrent nerve, and joins deep part of cardiac plexus.

C. **Inferior Cervical Ganglion.**

Grey rami to nerves C. 7, 8. Gives rise to inferior cardiac nerve (sometimes

from first thoracic ganglion): this communicates with recurrent and middle cardiac nerves, and joins deep part of cardiac plexus. Sends branches to form plexuses on subclavian artery and its branches. Sometimes sends branch to vagus.

Thoracic Sympathetic.

The thoracic part of the sympathetic chain consists of a series of ganglia corresponding in number to that of the thoracic spinal nerves, although adjacent ganglia sometimes fuse with one another. Each thoracic spinal nerve is connected with the sympathetic chain by a white ramus communicans. In addition to the afferent autonomic fibres previously mentioned the white rami contain efferent pre-ganglionic fibres arising from the lateral horn cells. The fibres from T. 1–5 run for the most part upwards in the chain to be distributed through the cervical sympathetic (see above): the fibres from T. 6–12 pass mostly downwards to be distributed in the abdomen, while some of them supply the thoracic viscera. Grey rami communicantes (post-ganglionic fibres from the ganglia) join the spinal thoracic nerves, and are distributed with them; they supply vasomotor, pilomotor, and sudomotor fibres, and fibres for the thoracic and abdominal viscera.

In addition to the grey rami communicantes, the ganglia give off other branches. Post-ganglionic fibres are distributed from the ganglia of T. 1–5 to the thoracic aorta and its branches, from those of T. 2–4 to the posterior pulmonary plexus, and from those of T. 2–5 to the deep cardiac plexus. Pre-ganglionic fibres emerge from the ganglia of T. 5–12, and unite to form the splanchnic nerves.

(i.) *Greater Splanchnic.* Arises from the sympathetic chain between T. 5 and T. 9 or 10; the emerging fibres join to make the great splanchnic nerve. Opposite T. 11 or T. 12 the splanchnic ganglion is found on this nerve, and from this arise branches for the supply of the œsophagus. The nerve then passes to the anterior end of the cœliac ganglion. From here post-ganglionic fibres pass to supply the stomach, liver, pancreas, suprarenals and abdominal blood vessels. Some fibres pass through the cœliac ganglion to end in the superior mesenteric ganglion, whence post-ganglionic fibres are relayed to the small intestine, ascending and transverse colon.

(ii.) *Lesser (or small) Splanchnic.* Arises from the sympathetic chain opposite T. 10 and 11, and passes to the lower end of the cœliac ganglion.

(iii.) *Least (or lowest) Splanchnic.* Arises from the sympathetic chain opposite T. 12, and passes to the renal plexus.

Lumbar Sympathetic.

There are usually four ganglia, but their number and the degree to which they fuse with one another vary greatly. The white rami to the chain emerge with the fibres of the first and second or sometimes the third lumbar spinal nerves: this represents the lower limit of the sympathetic outflow from the spinal cord. Post-ganglionic fibres pass from all the ganglia as grey rami to join the lumbar spinal nerves. In addition, pre-ganglionic fibres pass out through the upper three

lumbar sympathetic ganglia as irregular branches with a cell station in the inferior mesenteric ganglion : post-ganglionic fibres pass from thence to supply the rectum, the urinary and the genital organs.

Sacral Sympathetic.

This comprises four or five small ganglia with the intervening portions of the sympathetic trunk. It receives no white rami, but the ganglia send (post-ganglionic) grey rami to the sacral and coccygeal spinal nerves.

In addition, post-ganglionic fibres from the first two ganglia of both sides pass to join the pelvic plexuses, and from the remaining ganglia to join the plexus on the middle sacral artery, and to supply the coccygeal body.

3. AUTONOMIC SUPPLY OF CERTAIN SPECIAL STRUCTURES

Many structures have both a sympathetic and a parasympathetic nerve supply : some of the more important are summarised in the table at the end of this chapter. (In the table, Cs stands for cell-station.)

Vasodilator Nerve Fibres.

Fibres which on stimulation give rise to active vasodilatation are found in certain mixed nerves.

1. In peripheral *sensory* nerves.

The cells of origin are in the posterior root ganglia. (Possibly these are post-ganglionic parasympathetic fibres, arising from the lumbar-sacral region passing out by *posterior* roots, and relaying in the posterior root ganglia (Ken-Kuré).) It has been suggested that these fibres produce dilatation by liberation of a histamine-like substance, and not by direct action on the cutaneous vessels (Lewis).

2. In sympathetic nerves.

These nerves also contain constrictor fibres which are in tonic activity. The two kinds of fibres can be differentiated by :—

(*a*) Paralysis of the constrictors by ergotoxin and subsequent stimulation by adrenin : this then produces dilatation instead of constriction.

(*b*) Stimulation of the peripheral cut end of the nerve with slow shocks ; this results in dilatation instead of the usual constrictor response to a rapid stimulation.

(*c*) Section of the nerve and subsequent stimulation after some days ; this results in dilatation as the constrictor fibres degenerate very rapidly.

3. In parasympathetic nerves.

Such fibres have been demonstrated in the fifth, seventh and ninth cranial nerves and in the nervi erigentes.

Distribution of Vasodilator Fibres.

(*a*) Upper limb. By posterior root fibres of the lower cervical cord.
(*b*) Lower limb. By posterior root fibres of the sacral cord.
(*c*) Abdominal viscera. (i.) By posterior root fibres (T. 6–12).
(ii.) By splanchnic nerves.
(*d*) Erectile tissue of external genitalia. By nervi erigentes.
(*e*) Submaxillary and sublingual glands and anterior two-thirds of tongue. By chorda tympani from facial nerve.
(*f*) Glands of palate and nasopharynx and lachrymal gland. From facial nerve, through Meckel's ganglion.
(*g*) Parotid gland and posterior third of tongue. From glossopharyngeal nerve, through otic ganglion.
(*h*) Mucous membrane of inside of cheeks and nares. From cervical sympathetic, distributed in branches of trigeminal nerve.

There is some evidence that vasodilator fibres have a cell station somewhere on their course and probably near their destination : this would suggest that they may perhaps form part of the parasympathetic system. Such cell stations have been demonstrated in the case of the vasodilator fibres of the chorda tympani in the hilus of the submaxillary gland, and of those of the nervi erigentes in the hypogastric plexus.

The *axon reflex*. If mustard is applied to the surface of the skin, a local vasodilatation of the cutaneous blood-vessels occurs even after section of the posterior nerve roots. It does not occur after degeneration of the sensory fibres, and is explained as dependent on a branching of the peripheral end of the sensory nerve to give collaterals to the blood-vessels : the impulses pass from the skin up the fibre to these collaterals and then down to the blood vessels.

Capillary Dilatation.

Capillaries can constrict and dilate independently of the arterioles. This dilatation may be due to hormone action, or to nervous impulses ; the latter are in part the vasodilator impulses also affecting the arterioles, and are in part due to local axon reflexes from neighbouring small blood vessels.

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PART II

CHAPTER I

THE NORMAL PHYSIOLOGY OF THE SENSORY PATH

THE sensory path is frequently taken as synonymous with the ascending path, although the " sensory " impulses are, strictly speaking, only those which reach consciousness and evoke a sensation ; it is, therefore, more correct to speak of the afferent or ascending impulses if the term is to include those which reach higher centres other than the cortex of the cerebrum.

The sensory path is an extremely complex one, but nearly all the fibres relay through the optic thalamus ; one would, therefore, expect to find that this region plays an important part in the interpretation of the afferent impulses. The type of sensation evoked depends always on the type of end organ stimulated, and this explains why stimulation of the sensory cerebral cortex does not produce a sensation that is related to the stimulus. The special sensations of sight, hearing smell and taste will be considered separately ; the following description applies only to general or ordinary sensation. " Referred pain " will be considered later. (See p. 119.)

Ordinary sensation is usually grouped into two divisions : deep sensibility and superficial or cutaneous sensibility.

(*a*) *Deep Sensibility.*—This includes afferent impulses coming from the deep structures, such as muscles, joints, and tendons. The sensations produced are those of " muscle sense," stereognosis, vibratory sense, and a sense of pressure-pain. The fibres conveying these afferent impulses pass in the so-called motor nerves of the muscles.

(*b*) *Cutaneous Sensibility.*—This includes afferent impulses coming from the skin, the fibres passing in the cutaneous branches of the nerves. According to Head's account of the loss of sensation following section of the sensory branch of his radial nerve and the subsequent recovery, cutaneous sensibility is of two kinds, protopathic and epicritic : as a result of his observations he formulated the theory of two separate systems corresponding to his two types of sensibility.

Protopathic Sensibility.—This is a somewhat crude, primitive type of sensation, not localised to the spot stimulated, but of a radiating nature. It includes—

(i.) Recognition of gross differences of temperature, *i.e.*, a sensation of cold below 25° C., and of heat above 38° C., but no sensation of " temperature " between 25° C. and 38° C.

(ii.) Recognition of pain, but with a high threshold and excessive reaction, and no localisation.

Epicritic Sensibility.—This is a more highly differentiated type of sensation accurately localised to the spot stimulated. It includes—

(i.) Recognition of light touch (tactile sensation).

(ii.) Recognition of variations in temperature, including those between 25° C. and 38° C.

(iii.) Recognition of pain, with a low threshold and normal reaction, the sensation being accurately localised.

(iv.) Recognition of simultaneous stimulation of two points—tactile discrimination.

This classification of the types of sensation depends on the experiments originally carried out by Head and Rivers. According to them division of a cutaneous nerve is followed by complete loss of epicritic sensation in the area supplied by the nerve cut, and loss of protopathic sensation over a somewhat smaller area within this ; deep sensation is not interfered with. As regeneration of the nerve occurs protopathic sensation returns first and is complete in about thirty weeks. Epicritic sensation returns much more slowly, and not always completely, there being no further improvement in function after the lapse of two years.

Later workers have not confirmed these results in full. Deep sensation is interfered with if the correct nerve is cut, and the loss of sensation and its return after nerve suture does not always follow the distribution and the time intervals stated by Head. All forms of sensibility tend to reappear together, and the surface with returning sensation is at first hypoæsthetic, and gradually approaches normal sensibility (Trotter and Davies).

More recently Sharpey-Shafer has recorded the results of division of the branch of the ulnar nerve supplying the radial side of his little finger, and compared them with the effects of squeezing the branch of the nerve to the ulnar side of the same finger, the two operations being performed at an interval of nine weeks.

This observer criticises Head's deductions (but not his observations) in the light of his own results : he considers that " protopathic " sensation is merely hyperalgesia (peculiar in character) which is referred peripherally owing to the fact that the nerves involved are being stimulated not at their natural endings but in their course ; further, that the particular intensification of pain that is experienced is due to the abnormal environment in which the newly growing nerve fibres are found. The growing axis cylinders have no neurolemmal sheaths, which appear to be essential for the proper protection of the fibres, and since they are slow in acquiring these sheaths the increase of sensitivity (or according to Trotter and Davies " the intensification of reaction to stimuli ") may last for an indefinite time. Sharpey-Shafer considers that this theory gains additional support from his observations on a crushed nerve. In this case the neurolemmal sheaths are present from the first, but as a result of the severance of the axis cylinders the lemmal cells have undergone proliferation, and the relationship of the growing axis cylinder to its sheath is only at first abnormal : after a time the normal relationship is recovered and the increased sensibility disappears.

It would appear from these and other observations that it is unnecessary to

assume that special nerve fibres subserve the particular kind of sensation manifested during the process of recovery, as has been concluded by Head.

Many observers have also drawn attention to the necessity of choosing a suitable nerve on which to operate and conduct series of observations during recovery. Sufficient consideration has not been taken of the material fact of the existence of accessory fibres from neighbouring nerves passing to the affected area : this probably accounts for the many discrepancies in the results of some observers.

Stopford is of the opinion that it is rare for " epicritic " sensibility to recover as completely after division of a cutaneous nerve as it did in Head's experiment, as he finds that in the majority of cases there is some permanent loss of " epicritic " sensibility, and that this loss is very considerable when a piece of nerve has to be resected before suture. He divides sensation into thalamic and cortical (rather than into " protopathic " and " epicritic "). Thalamic sensation is protective and affective, and includes recognition of pain, of extreme temperatures, and of tactile pressure. Cortical sensation is discriminative and includes the power of localisation, of discrimination, of recognising position and passive movements, and recognition of fine differences of temperature and light touch. Normally the cortex " damps down " the thalamus, and the first stage of recovery after injury is to be explained as due to the release of the thalamus from cortical control. These two systems are present in both cutaneous and deep sensibility.

It is probable therefore in the future that the terms " epicritic and protopathic " will gradually disappear from the literature.

THE PATH OF THE SENSORY IMPULSES

A. Receptors.*

The receptors are the specialised nerve endings that respond to the various sensory stimuli, but the particular receptors subserving particular sensations are not in all cases known. The chief sensory nerve endings are the following :—

(i.) Deep.	(*a*) Muscle spindles in striped muscle.
	(*b*) Organs of Golgi in tendon.
(ii.) Superficial.	(*a*) Pacinian corpuscles.
	(*b*) Tactile corpuscles.
	(*c*) End bulbs.
	(*d*) Free terminal branchings.

The cutaneous sensations are not distributed evenly over the whole skin, but in discrete spots, corresponding, no doubt, to the distribution of the specialised nerve endings. This can be demonstrated by mapping out in a certain area those spots of which stimulation of various kinds gives rise to the different kinds of sensation.

Nerve endings consisting of varicose arborescences subserving the sense of light touch are found in the epidermis, while the dermis is the organ for superficial

* It was felt that any discussion on the actual nature and passage of the nervous impulse would be out of place in an introductory book of this nature.

pain (Waterston). The brush endings of Ruffini are probably concerned with an appreciation of heat, and Krause's end bulbs with that of cold.

B. Path in the Spinal Cord.

All the impulses enter by the posterior root fibres. (See Diagram 47.)

(i.) *Columns of Goll and Burdach.*

The column of Goll carries impulses from the lower limbs and lower half of the trunk, and that of Burdach from the upper limbs and upper half of the trunk, the column of Goll being pushed medially by the fibres of Burdach. The fibres pass straight up to the nucleus gracilis (Goll) and the nucleus cuneatus (Burdach). The next neurone passes by—

(*a*) External arcuate fibres to the cerebellum or

(*b*) Internal arcuate fibres (sensory decussation) and medial fillet to the optic thalamus.

The third neurone passes to the post-Rolandic cerebral cortex. (Some workers postulate an extra connecting neurone in the thalamus.)

The impulses carried are those underlying the sensations of—

(*a*) Vibration.

(*b*) Stereognosis.

(*c*) Passive movement and of position, including " muscle sense " (see below).

(*d*) Some touch and tactile discrimination.

(ii.) *Direct and Indirect Cerebellar Tracts.*

The entering fibres arborise round Clarke's cells of the same side at a level some segments higher than that at which they enter. The next neurone carries the impulses by—

(*a*) The direct cerebellar tract to the cerebellar cortex of the same side by the inferior peduncle,

(*b*) The indirect cerebellar tract to the cerebellar cortex of the same side by the superior peduncle.

The impulses carried are those from the muscles, joints, and tendons, and arise as a *result* of the contraction of the muscles. These are the " secondary afferent impulses " underlying " unconscious muscle sense," the impulses reaching the cerebellum and producing " reflex " movements which do not arouse consciousness : they also modify and control muscular contractions and inhibitions that are already taking place.

(iii.) *Spinotectal and Spinothalamic Tracts.*

The entering fibres arborise round posterior horn cells of the same side. The next neurone fibres cross in the anterior commissure (some run up for several segments before crossing) and then pass up in the antero-lateral ascending tract, the spinotectal to the inferior corpora quadrigemina and the spinothalamic to the lateral nucleus of the optic thalamus.

The next neurone carries the impulses to the post-Rolandic cerebral cortex.

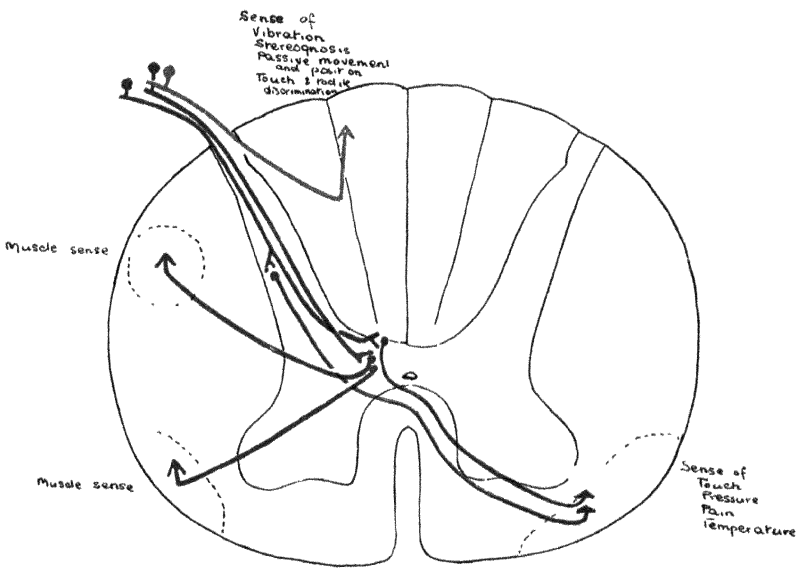

DIAGRAM 47.—Diagram of Paths of Various Sensory Impulses.

The impulses carried are those underlying the sensations of touch, pressure, pain, and temperature, all impulses of one kind, both " protopathic and epicritic," passing up together in the spinal cord. Low down in the cord the crossing of all fibres is nearly transverse, but as the cord is ascended the fibres cross more obliquely. Fibres for pain cross most transversely, and those for touch most obliquely. Fibres for pain, heat and cold travel by the spinothalamic tract (dorsal spinothalamic), and those for touch and pressure by the spinotectal tract (ventral spinothalamic).

C. Part played by the Optic Thalamus and Cortex Cerebri respectively.

Most of the general sensory impulses are relayed in the optic thalamus, and this nucleus plays an important part in the appreciation of these impulses. The last neurone on the sensory path carries the impulse to the sensory cortex, *i.e.*, for general sensation to the post-Rolandic area, for sensation of sight to the occipital region, of hearing to the temporal region, and of smell to the olfactory lobe. In these areas of the cortex are stored the memories of previous afferent impulses of similar nature, and by interaction with these the cortex is able to interpret and appreciate the precise nature of the stimulus and to localise its origin. But the thalamus itself also responds to all these stimuli that can provoke a sensation, although in a more crude way.

Our knowledge of the part played by the thalamus is due largely to the work of Head. All sensory impulses possess a " feeling tone " component that gives rise to an emotional response ; in other words, all impulses give rise in a certain degree to a painful or a pleasurable impression. The painful or pleasurable component of the impulse is spoken of as " feeling tone," and it is this that is appreciated by the thalamus. Normally an impulse arousing thalamic activity passes on to the cerebral cortex, and this " modifies the crude sensation of the thalamus by giving it a discriminating and intellectual stamp," the thalamic response being controlled by the corticothalamic fibres.

This distinction is perhaps best seen under conditions where there is interference with the corticothalamic path. The thalamus, released from cortical control, then overacts to the feeling tone stimulus. If a patient in this condition is stimulated by a pin-prick on the finger, he will say, " Something is happening to me ; I am being hurt," whereas a normal individual would say, " You are sticking a pin into my finger." There is no localisation of the stimulus and no discrimination as to the type of stimulus, but an over-reaction to its painful component. Similarly, if a glass of hot water is placed in the patient's hand, he will merely recognise the contact of the object and will know that it is unpleasantly hot ; he will not realise the shape, size or texture of the vessel, nor will he know what part of his hand is holding it, nor will he appreciate how hot it is.

The uncontrolled thalamic response thus gives rise to crude sensation with no discrimination. There is also a high threshold value for the stimulus, a long latent period, and a persistence of the sensation after removal of the stimulus. The characteristics of the cortical response are a discrimination of the stimulus

brought about by comparison (similarity and difference) with memories of previous impulses reaching the same part of the cortex, and in addition there is spatial perception in three directions, or stereognostic sense. An afferent stimulus capable of provoking a sensation will thus receive full interpretation of all its components because it will arouse the activity both of the thalamus and of the appropriate sensory area of the cortex cerebri ; but the kind of sensation produced depends entirely upon the nerve ending stimulated.

The Functional Significance of the Corpus Striatum and the Diencephalic Nuclei.

1. Corpus Striatum.

In primitive vertebrates the anterior part of the cerebrum is largely olfactory in function : in the basal part of each hemisphere is a large nucleus termed the *palæostriatum* which receives its afferent fibres from the olfactory region and from the thalamus, and sends efferent motor fibres to the brain stem and medulla : this corresponds to the globus pallidus of man. In the reptile brain the *neostriatum* appears, as new fibres appear growing in from the thalamus to the telencephalon and carrying visual, tactile, gustatory and other sensory impulses ; the neostriatum inhibits and regulates the activities of the palæostriatum that result from these new sensory impressions. Already in the reptile brain the primitive striatum possesses a lateral afferent part (putamen) and a medial efferent part (globus pallidus), which are intimately connected with the thalamus : the caudate nucleus is derived partly from the olfactory part of this primordial striatum and partly in relation to the neostriatum. The globus pallidus, together with the subthalamic nucleus, at first carries out the motor responses evoked by the afferent impulses reaching the thalamus, and at a later stage the caudate nucleus and putamen exert a modifying influence on these responses. The later appearance of new sensory centres requires the establishing of higher motor centres for the control of the body movements, and the mammalian cerebral cortex and pyramidal system are evolved, the corpus striatum remaining, however, entirely independent of the cerebral cortex.

Thus in the higher vertebrates the function of the corpus striatum has become relatively subsidiary to that of the cerebral cortex. Investigation of lesions of this area suggest that the corpus striatum exerts a steadying influence on muscular activity, because if it is removed tremor develops during voluntary movement (see p. 98).

2. The Thalamus.

The thalamus is the chief receiving station on the sensory path. The *medial* and *anterior nuclei* represent the oldest part, both receiving impulses from the olfactory centres and both sending impulses to the older part of the caudate nucleus, whence they are passed to the globus pallidus. These nuclei are thus primitive correlation centres for lower vertebrates, and are probably associated with a crude form of consciousness, or " awareness without discrimination." The *lateral nuclei* are of more recent development, and represent relay stations on the

somatic sensory paths to the cerebral cortex. The ventral group of these nuclei is connected with the post-central region of the cortex, while the lateral group connects with the frontal, temporal and parietal regions, the parietal cortex being associational in function, and the frontal cortex representing the highest functional level of the brain. It is suggested further that as the grey matter covering the medial surface of the thalamus is continued downwards through the brain-stem as the dorsal longitudinal bundle of Schütz, this portion of the thalamus may form a centre for vasomotor and visceral reflexes, being thus brought into connection with the visceral efferent nuclei of the brain.

The thalamus and epithalamus, constituting the dorsal part of the diencephalon, can be regarded as a sensory correlation station for somatic impulses.

3. THE EPITHALAMUS.

This region is clearly concerned with olfactory reflexes. Edinger suggests also that as the cells of origin of the striæ medullares are intimately related to ascending fibres from the sensory nuclei of the fifth cranial nerve, there is a possibility of afferent impulses from the nose, mouth and tongue being concerned in feeding reflexes.

4. THE HYPOTHALAMIC REGION.

The ventral part of the diencephalon, comprising hypothalamus and subthalamus, can be regarded as a visceral correlation station closely linked with the pituitary.

The visceral activities can be subdivided into sympathetic and parasympathetic (see p. 117).

(*a*) *Sympathetic Representation.*

There can be no doubt that the higher centres exert a definite influence over the sympathetic nervous system. The pre-ganglionic neurones of similar groups arising in the lateral horn cells of the cord are normally under the control of medulla mechanisms, but superimposed on this mechanism is a higher control arising from the base of the diencephalon capable of causing simultaneous discharge over the whole series of neurones. Karplus (1909) showed that electrical stimulation of the hypothalamus caused dilatation of the pupils, vasoconstriction and excessive secretions, all of which are manifestations of sympathetic activity.

This control is localised by Bard in the area comprising the caudal half of the hypothalamus and the most ventral and caudal part of the corresponding segment of the thalamus (the corpora striata and cranial half of the diencephalon not being involved). Beattie localises the centre in the paraventricular nuclei (see p. 42) and states that the subthalamic nucleus is not involved. From this "centre" the efferent path is described by Beattie as through the posterior longitudinal bundle, some fibres ending in the medulla and others passing down to end in the cord in connection with the lateral cell columns of the upper thoracic region. Brincker, who regards the impulses as passing down with the

crossed pyramidal fibres, postulates a still higher control, from the cerebral cortex to the thalamus and hypothalamus, describing the path from these latter levels as the second neurone.

(*b*) *Parasympathetic Representation.*

The central control of parasympathetic activity is probably connected with the pituitary, the posterior and intermediate parts of which are innervated from the tuber and supra-optic nuclei. It is suggested that the active principles secreted by this part of the pituitary may pass into the cerebrospinal fluid (Cushing) or by the " pituitary portal " circulation (Poppa and Fielding), and thus act on the diencephalic centres adjacent to the ventricles : in this way the neuro-hypophysis mechanism (*i.e.*, posterior pituitary, tuber and supra-optic nuclei) may bear the same relation to the parasympathetic division of the autonomic system as does the adrenal medulla to the sympathetic division (Cushing). Experimental work carried out on this region of the diencephalon in cats (Hess) indicates that sleep may be regarded as a parasympathetic reflex, possibly connected with a shifting of bromhormone from the pituitary to the medulla (Zondek and Bier).

(*c*) *The Subthalamus.*

The nuclei of this region can be regarded as forming links in the chain which connects the corpus striatum with the red nucleus and substantia nigra.

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CHAPTER II

RESULTS OF INTERFERENCE WITH THE GENERAL SENSORY PATH AT VARIOUS LEVELS

THIS chapter should be read in conjunction with the previous chapter, which deals with the normal physiology of the sensory path. Interference with this path may be due to :—

1. Irritation.
2. Partial destruction.
3. Complete destruction.

The resulting effects will vary in each case.

An *irritative* lesion always produces intense pain, which may be referred to the distribution of a single nerve, as, for example, in sciatic neuralgia.

Partial destruction produces altered conduction, so that there is delay, and a stronger stimulus is required to produce a characteristic reaction. There is sometimes also a sensation of tingling, numbness or pricking in the affected area, and hyperæsthesia.

Complete destruction of a conducting path leads to the complete loss of all forms of sensation resulting from afferent impulses normally passing along that route.

The results of destructive lesions at different levels in the sensory path are considered below, beginning at the periphery and working upwards.

1. Peripheral Receptors.

Destruction, either primary or secondary, of nerve endings produces anæsthesia of the part involved. Hyposensitivity of any cutaneous area due to any pathological condition when limited to one side of the body results in the reference of sensations from that area to the corresponding part of the opposite side of the body : if both sides are hyposensitive, the reference is to the next segment above or below. This phenomenon is known as *allocheiria*.

2. Cutaneous Nerves.

Section of a cutaneous nerve causes anæsthesia of the area innervated.

The loss of sensation to pinprick is usually less than that to cotton-wool.

3. Posterior Root Fibres.

Section of these fibres leads to—

(*a*) Anæsthesia due to division of the primary afferent fibres coming from the skin, etc.

(*b*) A lack of muscular control (ataxia), due to section of the secondary afferent fibres from muscles which " correct " the degree of muscular response.

(*c*) Loss of muscle tone and disuse atrophy of the muscles innervated. There is no reaction of degeneration.

(*d*) Interference with local reflexes both spinal and visceral.

(*e*) Trophic lesions of the skin in the area innervated.

(*f*) Degeneration of the columns of Goll, Burdach and Lissauer, and of the comma tract, for a short distance, and a consequent interference with the local tendon reflexes.

(See Part II., Chapter VIII.)

If the lesion involves irritation, there will also be " lightning pains " (characteristic of tabes), and " herpes zoster " if the ganglia are affected.

4. Conducting Paths in the Cord.

(*a*) *Goll and Burdach.*

(These are destroyed, for example, in tabes dorsalis and in postero-lateral sclerosis of the spinal cord.)

Interference with these columns produces—

(i.) Loss of spatial discrimination and postural sense.

(ii.) Interference with the local tendon reflexes.

(iii.) Loss of vibration sense.

(*b*) *Cerebellar Tracts.*

Such interference may affect the cerebellar maintenance of posture and so lead to ataxy.

(*c*) *Spinothalamic and Spinotectal Tracts.*

Complete destruction leads to the loss of all ordinary sensation except that due to impulses which travel in the columns of Goll and Burdach.

Partial destruction produces a dissociation between the different types of sensation. Thus there may be loss of sensation of pain, heat and cold, with retention of the sense of touch over a segmental sensory area.

5. Sensory Path in the Brain.

It is most unusual for the sensory fibres alone to be involved.

(*a*) *Thalamus.*

(Usually the internal capsule is also affected.) There is complete anæsthesia and loss of emotional control.

(*b*) *Internal Capsule.*

A posterior limb lesion produces the same effects as (*a*) but not so marked, and in addition there is interference with the optic and auditory radiations (if

the lesion extends sufficiently far back), so that sight and hearing may be affected. There is blindness of the homolateral half of each retina.

6. **Sensory Cortex.**

The sensory cortex is more extensive than the postero-Rolandic convolution, and is concerned with intensity, localisation, discrimination, similarity and difference of stimuli, and also with stereognosis. Consequently the loss of function will correspond with the situation and the extent of the lesion concerned.

CHAPTER III

VISUAL PATH AND INTERFERENCE THEREWITH

FOR the anatomical course of the visual fibres the student is referred to p. 22.

(See Diagram 18, *facing* p. 22.)

It is important to emphasise that the image of any object situated on the temporal side of an eye falls on the nasal half of the retina of that eye. Similarly, an object situated on the nasal side of the eye produces an image on the temporal half of the retina of that eye. This, of course, only holds good if the object is not obscured from view by the nose. Consequently it is obvious that a distinction must always be made between the temporal half of the retina and the temporal field of vision. Images in the temporal field of vision will fall on the nasal half of the retina.

(See Diagram 48.)

Lesions of the Path.

The results of interference with the visual path at different levels between the periphery and the cortex are here considered, no distinction being made between the different pathological conditions which may cause the lesion ; a few of these only are mentioned to serve as illustrations.

(*a*) *Ganglion Cells of the Retina.*

There is loss of the field of vision corresponding to the area involved.

(*b*) *Optic Nerve.*

There is—

1. Blindness of the eye on the same side.
2. Diminution of the field of vision on the same side.

(See Diagram 49.)

(*c*) *Optic Chiasma.*

1. A transverse lesion of the chiasma leads to complete blindness.
2. Pressure on the crossing fibres in the chiasma, such as occurs in a progressive pituitary tumour, causes bilateral diminution of the outer fields of vision. This is known as bitemporal hemianopia.

(See Diagram 50.)

3. Pressure on the outer fibres of the chiasma on both sides causes a bilateral loss of the nasal fields of vision.

(See Diagram 51.)

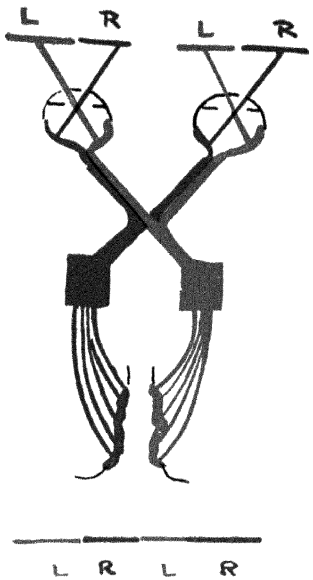

DIAGRAM 48.—Diagram of Field of Vision.

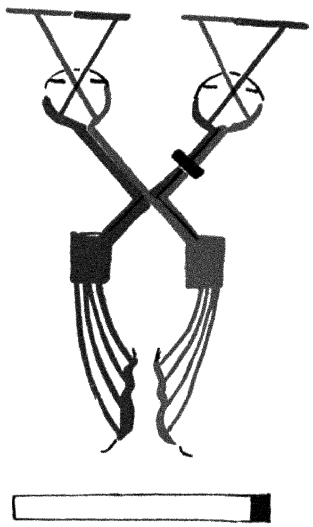

DIAGRAM 49 —Lesion of one Optic Nerve.

Effect on field of vision. Some diminution on side of lesion.

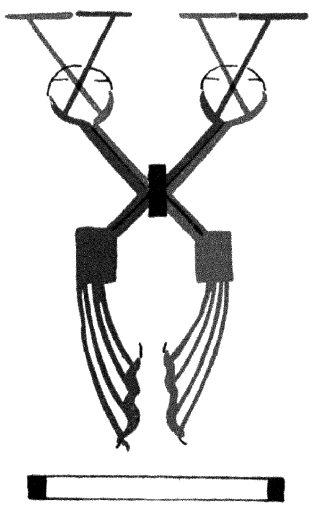

DIAGRAM 50.—Lesion of Crossing Fibres of Optic Chiasma.

Effect on field of vision. Bilateral diminution of peripheral field of vision.

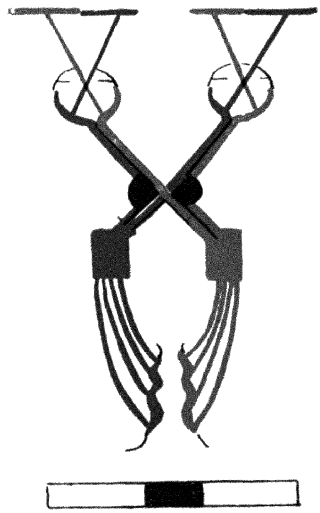

DIAGRAM 51.—Lesion of Outer Fibres of Optic Chiasma.

Effect on field of vision. Bilateral loss of nasal fields of vision.

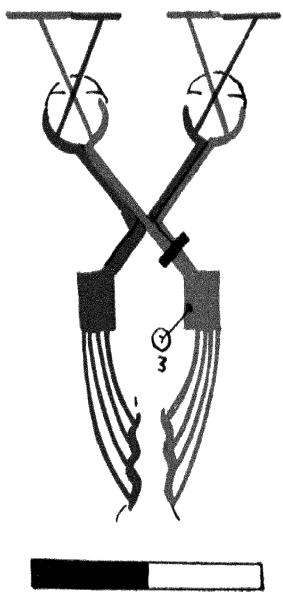

DIAGRAM 52.—Lesion of Optic Tract.

Effect on field of vision Loss of field of vision on opposite side.

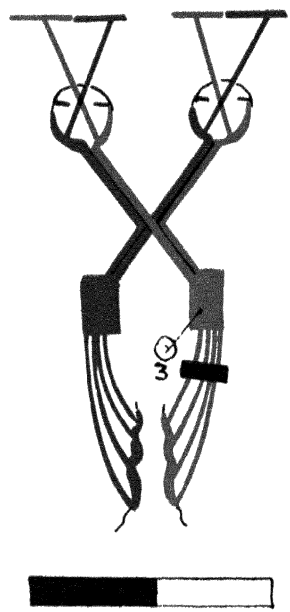

DIAGRAM 53.—Lesion of Optic Radiation.

Effect on field of vision. Loss of field of vision on opposite side. Light reflex unaffected.

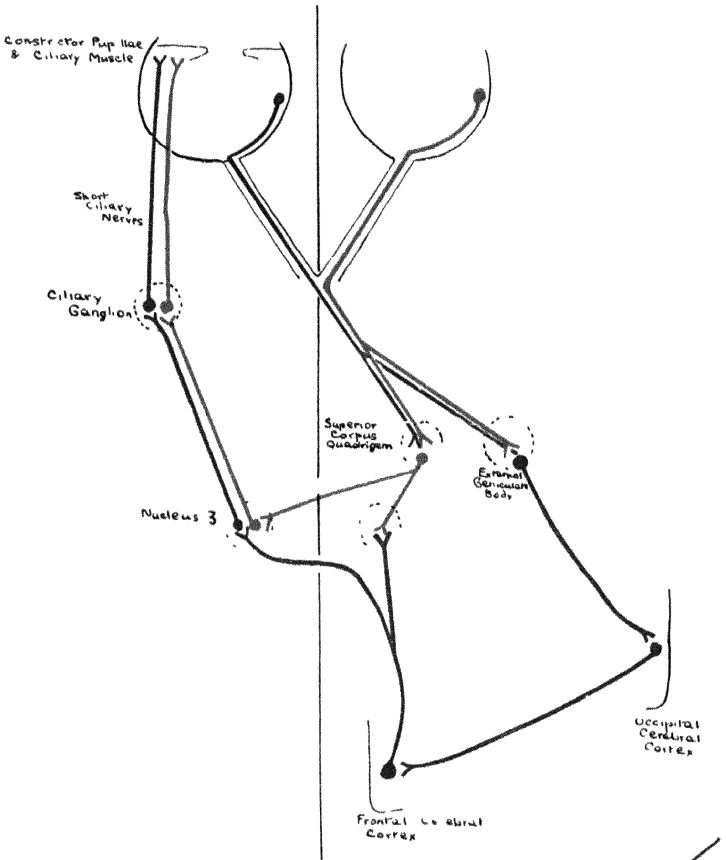

DIAGRAM 54.—Diagram to show Paths for the Light Reflex and for Accommodation.
Blue : Accommodation path. Red : Light reflex path.

(*d*) *Optic Tract.*

There is loss of the opposite field of vision, blindness of the nasal half of the opposite retina and of the temporal half of the retina of the same side.

(See Diagram 52.)

(*e*) *Optic Radiation or Occipital Lobe.*

The result is the same as that occurring in a lesion of the optic tract, except that the light reflex is intact.

(See Diagram 53.)

[NOTE.—As there is some ambiguity in the use of certain terms in connection with vision, the following list of terms, with their meaning, is given :—

Hemiopsia	Presence of half the field of vision.
Hemianopsia	Loss of half the field of vision.
Hemiopia	Half-sight.
Hemianopia	Half-blindness.]

Accommodation Reaction.

The pathway of accommodation is from the occipital lobe, which receives the afferent impulses from the retina, to the frontal cortex. From this cortex the fibres run through the genu of the internal capsule and the medial part of the crusta to the nuclei of both third nerves. Axons from the third nerve nucleus pass to the constrictor pupillæ muscle and the ciliary muscle through the ciliary ganglion. It will be noted that the superior corpus quadrigeminum does not lie on this pathway.

(See Diagram 54.)

Light Reflex.

The pathway of the light reflex passes from the retina by specially thick fibres (Monakow) in the optic tracts to the superior corpus quadrigeminum. The next relay arises in the corpus, and crossing the mid-line by fibres both anterior and posterior to the Sylvian aqueduct, reaches the front part of the nucleus of the third nerve : some fibres pass to the nucleus of the third nerve of the same side. From this nucleus fibres are relayed in the ciliary ganglion, and so reach the eye *viâ* the short ciliary nerves. It will be noted that fibres from each retina reach both optic tracts and also both superior corpora quadrigemina, so that light shining on one eye causes constriction of both pupils. This constitutes the " consensual light reflex."

There are many other pupillary reflexes, for the details of which the reader is referred to a text-book of ophthalmology.

The following reactions are used so commonly that a short description of the anatomical pathway taken by them is given :—

I. *The Argyll-Robertson Pupil.*

In this the light reflex is lost, but the accommodation reflex is intact. It is due to a lesion in the neighbourhood of the Sylvian aqueduct, or to a lesion of the pathway between the superior corpora quadrigemina and the third nerve nucleus, or of the ciliary ganglion.

II. *Wernicke's Pupillary Reaction.*

In this the light reflex remains, although sight is lost, due to a lesion in the optic radiation, or in the higher visual centres in the cortex, or in the external geniculate bodies, thus not affecting the superior corpus quadrigeminum.

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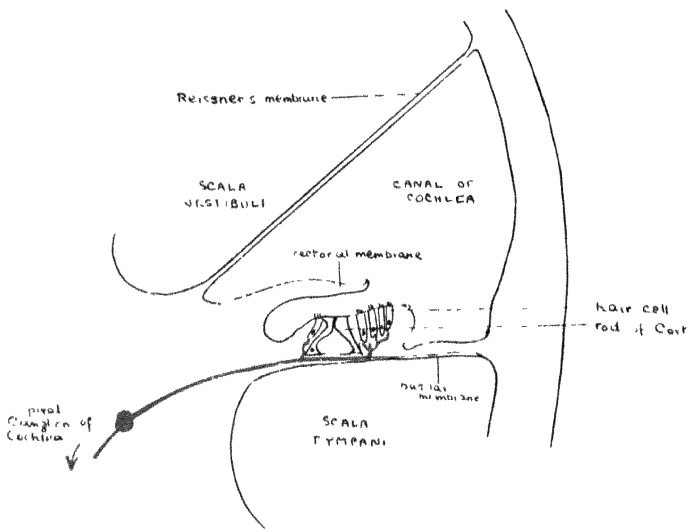

DIAGRAM 55 —Diagram to show Origin of Cochlear Nerve Fibres among Hair Cells of Organ of Corti.

CHAPTER IV

THE COCHLEAR PATH AND THE OLFACTORY PATH AND INTERFERENCE THEREWITH

Interference with the Cochlear Path.

For the anatomical course of the cochlear division of the eighth nerve reference may be made to p. 26.

(See Diagram 24, *facing* p. 26.)

1. Destruction of the cells of the upper part of the cochlea produces deafness to low notes, while destruction of the cells of the lower part of the cochlea produces deafness to high notes.

(See Diagram 55.)

2. (*a*) An irritative lesion on the peripheral path of the cochlear nerve causes tinnitus on that side.
   (*b*) A destructive lesion of the peripheral path causes complete deafness on that side.
3. Unilateral destruction of the temporal lobe does not cause deafness, as both cochleæ are represented in both temporal lobes.

The effects of interference with the connections of the auditory centre are further discussed in connection with the condition of " Aphasia," p. 128.

Interference with the Olfactory Path.

As the sense of smell subserves the needs of the human organism to such a small extent in comparison with the importance of this function in some animals, the results of interference with the olfactory path are relatively few and unimportant. It must also be remembered that it is difficult in man to dissociate smell from taste, and *vice versâ*, the two senses being intimately associated.

1. Destruction of the cells of the olfactory epithelium leads to loss of smell.
2. Lesions of the pyriform area sometimes lead to subjective sensations of smell.

(See Diagram 16, *facing* p. 22.)

CHAPTER V

THE CEREBRAL CORTEX

THE structure of the cerebral cortex has been described in Part I., Chapter VIII.

Significance of the Cortical Layers.

1. Outer pyramidal cell lamina.
   (*a*) This layer is the last to develop in man, and is the first to be affected by disease.
   (*b*) The degree of development of this layer is increased as the animal scale is ascended.
   (*c*) Its thickness varies directly with the mental capacity of the individual.
   (*d*) If this layer is congenitally deficient, amentia results.
   (*e*) Degenerative changes in this layer are associated with dementias.
2. Granule cell laminæ.
   (*a*) These layers are thickest in the post-Rolandic area and part of the occipital and temporal lobes.
3. Internal pyramidal lamina.
   (*a*) This layer contains the giant motor cells (Betz cells) in the pre-Rolandic area only.
4. Inner cell lamina, of polymorphic cells.
   (*a*) This layer is the first to develop in man.
   (*b*) It does not increase in thickness in man after birth, and is of constant depth throughout the cerebral cortex.
   (*c*) It is relatively thick and well developed in lower animals.
   (*d*) It is the last layer to be affected in disease. It shows marked decrease in aments, and also in gross dements who cannot carry on the ordinary functions of life.

From the foregoing observations it is concluded that these cell layers have the following functions :—

1. The outer pyramidal cell layer subserves the higher functions of memory and the higher intellectual and moral qualities.
2. The granule cell layers are concerned with receiving afferent impressions from the lower sensory neurones or from other regions of the cerebrum.
3. The inner cell layer carries out the lower voluntary and instinctive activities involved in the maintenance of life and species.

The Localisation of Function in the Cerebral Cortex.

Historical.

One of the first attempts to localise any particular function in any special area of the brain was due to a phrenologist, Gall, in 1810. He ascribed consciousness to the cerebral hemispheres, and endeavoured to correlate the appearance of the inside of the skull with the appearance of the brain that originally occupied it and the characteristics of the individual to whom it had belonged. As a result he drew up elaborate brain maps ascribing various characters to different parts of the brain. In 1824 Flourens carried out some experiments in dogs, removing the cerebral hemispheres in small portions, and he found that at first there was no change; then the animal became dull and stupid, and then unintelligent all at once. He found no difference for different parts of the brain, the result depending only on the amount of tissue removed. He concluded that there was no localisation, but that the brain was functionally equivalent in all its parts.

This doctrine was undisputed until in 1861 Broca made the observation that loss of speech is frequently associated with a lesion of a definite spot. This area, known as Broca's area, was consequently for many years regarded as the seat of the function of speech. In 1864 Hughlings Jackson observed that localised muscle spasms are connected with lesions of certain parts of the central convolutions, to which were therefore ascribed motor functions.

Another and very promising method of investigation was introduced in 1870 by Hitzig and Fritsch, who made use of dogs. They observed the effects of weak faradic excitation of different parts of the exposed cortex; definite co-ordinated movements of muscle groups were produced by pre-central stimulation, and these workers drew up plans of the brain ascribing definite functions to various regions. This work was repeated in 1873 by Ferrier, and he confirmed the results in monkeys. He showed also that removal of these motor areas resulted in loss of volitional initiation of movement.

Since this time the work has been frequently repeated and extended to the higher apes, and even to man, by Horsley, Schafer, Sherrington, and others. Head has made confirmatory observations on men in whom part of the cortex had been exposed by gunshot wounds.

Evidence as to the Localisation of Function in the Cerebral Cortex.

The information obtained from all methods of investigation must be considered together. There are five methods that yield contributory evidence :—

1. Structure.
   - (*a*) Gross, comparing different animals.
   - (*b*) Minute, comparing different parts of the cortex.
2. Stimulation.
   - (*a*) Experimental.
   - (*b*) Pathological—*i.e.*, an irritative lesion, such as a tumour producing over-action of the part pressed on.

3. Destruction.
   (*a*) Experimental.
   (*b*) Pathological—*i.e.*, a destructive lesion, causing replacement of tissue by a pathological process such as a tumour.
4. Flechsig's myelination method.
5. Investigation of conditioned reflexes. (See p. 105.)

Considering the evidence of each of these methods in turn, the following information is obtained :—

1. STRUCTURE.
   (*a*) *Gross.*—The gross structure of the brain varies greatly in different animals, the relative development of the olfactory lobes, optic lobes, cerebellum, and cerebral hemispheres varying with the relative degree of development in the animal of that function which (from other sources of evidence) is ascribed to that particular part. Thus in fishes the olfactory lobes are enormously developed, and are much more highly differentiated in animals low in the vertebrate scale than in those higher up. The optic lobes are exceedingly prominent in birds, in which the sense of sight is greatly specialised. Many other examples of this principle can be found.
   (*b*) *Minute.*—The minute structure of the cortex has already been described, including the variations in different parts of the brain. These variations, considered in conjunction with the functions of the different layers just described, throw considerable light on the localisation of function in the different parts of the cortex.

2. STIMULATION.
   (*a*) *Experimental.*—The unipolar method of electrical stimulation is used, because by this means it is possible to localise the stimulus very precisely, and also to use a stimulus of known strength which can be varied or repeated as required. Weak stimulation of a motor area always gives an immediate motor response, stimulation of any one particular part producing always the same movement, but a certain amount of irradiation always occurs, so that the motor response is out of proportion to the area to which the stimulus is applied. Stimulation of the sensory areas is unsatisfactory, as in animals sensory effects cannot be detected by the observer, and an intense stimulus is necessary to produce even a slight response of the corresponding motor region. Stimulation of other areas of the cortex gives rise to no obvious response, and these are consequently known as "silent areas."
   (*b*) *Pathological.*—Irritation of the motor cortex caused by some pathological process produces the Jacksonian type of epilepsy. This is characterised by a definite sequence of movements which are "fired off" by the cortical stimulus that causes the initial movement. Thus the movements always begin in the same part of the body, and this

corresponds to the cortical area that is being stimulated ; the movements then spread always in a definite sequence. It should be noted that movements rather than muscles are represented in the cortex. The evidence so obtained was confirmed and extended by the observations of Head and Riddoch on the effects of gunshot wounds.

3. DESTRUCTION.

(*a*) *Experimental.*—Removal of a motor area causes loss of voluntary movement in the area represented. Similarly, removal of a sensory area involves loss of the sensation concerned. The degree of recovery depends on the capacity of other parts of the brain to take on the

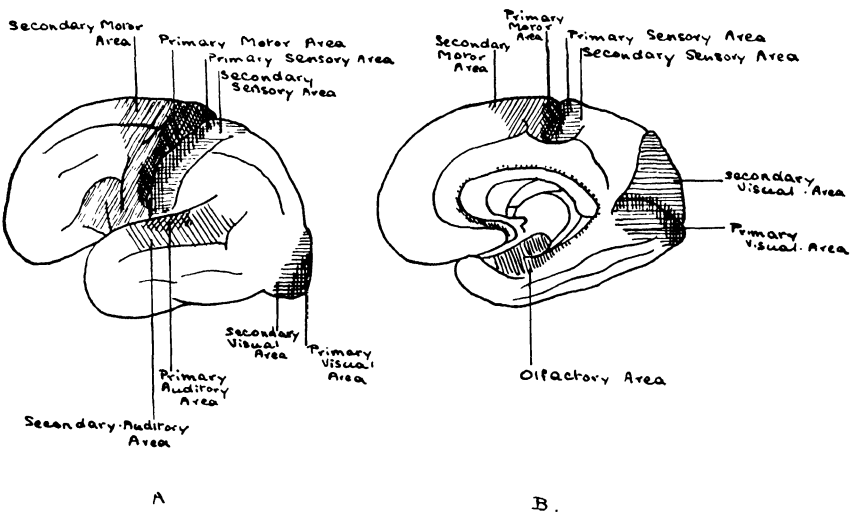

DIAGRAM 56.—Campbell's cortical projection areas.

A. Lateral aspect of cerebral hemisphere. B. Medial aspect of cerebral hemisphere. (*After Ranson.*)

function of the part removed ; there is no regeneration of cerebral nervous tissue. Further confirmation is afforded by war injuries.

(*b*) *Pathological.*—The results of some pathological conditions are difficult of interpretation because a tumour may cause destruction of one part and simultaneous irritation of another, so that the results are not usually very localised.

4. MYELINATION.

The date of myelination of nerve fibres is usually said to bear some relation to the time at which they first function. Thus the sensory paths myelinate early, the column of Goll at five to five and a half months of fœtal life, and the column of Burdach at the beginning of the fourth month of fœtal development. The

motor tracts myelinate later, the pyramidal tracts being fully developed only two years after birth. The association tracts myelinate last of all.

Evaluation of Evidence.

Evidence obtained by the foregoing methods shows clearly that certain functions are associated with certain areas of the cerebral cortex, and it is possible to distinguish definite motor and sensory areas, the remaining cortical tissue being designated as silent or association areas. Since volitional motor impulses never arise spontaneously in the pyramidal cells, but activity is determined by afferent impressions, there must be a close relation between the afferent and efferent neurones.

A motor area is controlled by and closely associated with the region in which are stored the memories of its previous activities, such an area being spoken of as a kinæsthetic area (κινέω (I move) and αἴσθησις (sensation)). Similarly, a

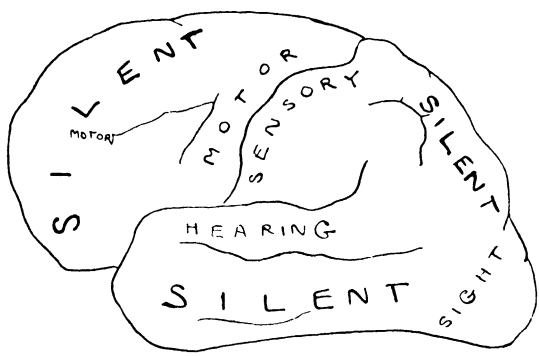

DIAGRAM 57.—Diagram to show " silent " or " association " areas of cerebral cortex.

sensory area is closely associated with the region in which are stored the memories of previous impressions reaching this sensory area, this being known as a sensory-psychic area. The part played by these kinæsthetic and psychic areas is well illustrated in the various types of aphasia (see p. 128).

(See Diagrams 56 and 57.)

A. **Region in Front of the Rolandic Fissure.**

(*a*) *Motor.*

(i.) Area for eye movements.

Stimulation of this area on the right side leads to conjugate deviation of both eyes to the left; hence these movements are bilaterally represented in the cortex. A further analysis of these movements will be found on p. 112.

(ii.) Pre-Rolandic area.

This area extends further than was originally described and includes primary and secondary voluntary motor centres,

the pyramidal fibres arising here from the Betz cells of the posterior part. In these centres the limbs are contralaterally represented, but movements involving both sides, such as those of the head and trunk, are bilaterally represented. The bilaterality of response is not altered by extirpation of the cortex of the hemisphere opposite to that being stimulated, so that interconnection must be at the lower motor levels. It should be emphasised that movements are represented in the cerebral cortex and not muscles : the movements affecting the various muscle groups are precisely localised in the pre-Rolandic area, those concerned with the lower limb being represented at the upper end of the gyrus, and below, in the order given, those for the trunk, upper limb, mouth, lips, tongue and larynx. It has been suggested that the posterior part is responsible for individual movements, and the anterior part for the control of the series of movements which constitute an act.

(*b*) *Association or Silent.*

The function of this area has been elucidated by observation in cases of congenital deficiency, degenerative disease, and accidental destruction. The higher moral and intellectual qualities are usually assigned to this area, and this is exemplified by the well-known case of the crowbar accident to the American miner. The fronto-pontine-cerebellar fibres arise here.

B. **Region Posterior to the Rolandic Fissure** (as in diagram).

(*a*) *Sensory.*

This area includes primary and secondary sensory centres ; it receives in its anterior part most of the afferent fibres from the thalamus that represent the last neurone on the sensory path from the cord and brain-stem. The localisation of function is not very accurate. The more anterior part can be regarded as the actual receiving area, while the posterior part relates these impulses to past experience.

(*b*) *Association or Silent.*

These regions are of a lower type than those described above. They probably correlate the afferent impulses reaching the great sensory areas, *i.e.*, the post-Rolandic sensory area, the visual area and the auditory area.

C. Occipital Region.

(*a*) *Sensory.*

(i.) Visuosensory.

In this area are received optic impulses from the lateral geniculate body, but they can only be interpreted by co-operation of the adjoining visuo-psychic area. Owing to the partial crossing of optic fibres the visuo-sensory cortex of one side receives impulses from the temporal part of the retina of that side and from the nasal part of the opposite retina. The macula is represented in the polar region occupying an area as extensive as the whole peripheral retina.

(ii.) Visuopsychic.

This is on the outer aspect of the occipital lobe, and is used for the storing of the memories of impulses reaching the visuosensory area. This area is consequently essential for the interpretation of such impulses.

(*b*) *Motor.*

There is a region at the occipital pole which on stimulation produces conjugate deviation of the eyes similar to that produced by stimulation of the eye area in the frontal region. (This is possibly explained by an inter-connection between these two areas.)

D. Temporal Region.

(*a*) *Sensory.*

(i.) Olfactory-sensory.—The uncus and pyriform area are concerned with smell.

(ii.) Auditory-sensory.—This area receives auditory impulses from the medial geniculate body. The actual elucidation of the impulses is dependent on the adjacent auditory-psychic area.

(iii.) Auditory-psychic.—The auditory impressions are stored in the posterior part of the superior temporal convolution, and are therefore available for the interpretation of the auditory sensory impulses.

(*b*) *Association or Silent.*

The temporo-pontine-cerebellar fibres arise here.

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CHAPTER VI

THE NORMAL PHYSIOLOGY OF THE MOTOR PATH

It is improbable that motor acts are ever initiated spontaneously by the nervous system ; they occur as a response to some stimulus which sends afferent impulses to the cord or to the brain or in response to stimulation by some hormone brought by the blood to the centres. The involuntary " fated " response that sometimes occurs is spoken of as a reflex response (see Part II., Chapter VIII.). But in many cases the response is determined by memories and associations of previous situations that are stored in the cerebral cortex, and in this case the response frequently appears quite unrelated to the stimulus ; such motor responses are usually spoken of as " voluntary." A " voluntary " movement, however, frequently includes components that are outside consciousness and might be termed involuntary. Many movements that are at first voluntary, requiring conscious attention, later become relegated to centres lower than the conscious " voluntary " cortex, and are carried out automatically. An example of such a movement is that of walking.

The impulses for voluntary movement are carried by the pyramidal paths arising in the pre-Rolandic cerebral cortex. These tracts are not completely myelinated until about two years after birth ; consequently the movements of the new-born baby are carried out by other motor paths, the extra-pyramidal system, which is developmentally an older path than is the pyramidal.

The Pyramidal Path.

The fibres of the pyramidal tracts are the axons of the Betz cells of the cerebral cortex, and are the longest nerve fibres in the body ; they pass straight down through the internal capsule, crusta, pons, and pyramids, to the cord giving off collaterals to the nuclei pontis, but with no cell station until they reach the level at which the impulse is to pass out. The fibres then arborise round cells of the grey matter, and connector neurones distribute the impulse to many anterior horn cells, the stimulus ultimately passing out by many nerve fibres supplying the groups of muscles. Thus it is brought about that an impulse passing down the pyramidal fibres will produce, not the contraction of a certain muscle, but a " movement " involving many muscles. This point will be considered more fully in subsequent chapters.

The impulses passing down the pyramidal fibres can also control impulses from other sources converging on a lower motor neurone, and these modify or inhibit the response that would otherwise occur.

The Extra-pyramidal Paths.

This system includes the corpus striatum (*i.e.*, caudate nucleus and the two divisions of the lenticular nucleus, *i.e.*, globus pallidus and putamen), the red nucleus, substantia nigra, subthalamic nuclei and other nuclei of the tectal region of the mid-brain, and the tracts arising directly from these or from nuclei receiving impulses from them, namely, the thalamospinal, rubrospinal, tectospinal, pontospinal, vestibulospinal, thalamo-olivary and olivo-spinal tracts.

Phylogenetically the globus pallidus (to which some would add the subthalamic nucleus and substantia nigra) is the oldest part of this sytem of nuclei (see p. 36), and its efferent fibres myelinate very early. The caudate nucleus and putamen are of more recent development and more highly specialised, and are both concerned with modifying the motor responses of the globus pallidus chiefly through the afferent thalamic impulses reaching them. Our knowledge of the functions of these nuclei is derived chiefly from a consideration of lesions involving the nuclei or their tracts, and may be briefly summarised here.

The caudate nucleus and the putamen regulate the motor responses of the globus pallidus. Afferent impulses are continually streaming up to the red nucleus and to the thalamus, many of which overflow into the efferent path through the globus pallidus giving rise to the forced involuntary movements. This overflow is prevented and controlled by the caudate nucleus and putamen.

The globus pallidus probably carries out many of the so-called automatic movements, which were originally mediated through the cerebral cortex, and from much use have become relegated to lower grade motor centres. It also exerts a controlling action on muscle tone. These muscle tone reflexes, which include the mechanism of neuromuscular rhythm, are normally carried out through the cerebellar—red nucleus—rubrospinal path, and these responses are controlled at the red nucleus level by impulses from the globus pallidus of the same side.

The extra pyramidal system is also intimately linked with the cerebellum (see p. 109).

The Effector Nerve Endings.

The efferent nerve fibres terminate in the organs supplied in a variety of ways.

1. Striped Muscle. Motor end plates beneath the sarcolemma.
2. Smooth Muscle. Small end knobs within the muscle cell.
3. Cardiac Muscle. Possibly a network, as actual endings have not been identified.
4. Glands. Fine varicose endings, possibly within the secreting cells.

(For details of structure the student is referred to histological textbooks.)

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CHAPTER VII

RESULTS OF INTERFERENCE WITH THE MOTOR PATH AT VARIOUS LEVELS

THIS chapter should be read in conjunction with the previous chapter which deals with the normal physiology of the motor path.

The results of unilateral destructive lesions at different levels in the motor path will be considered, beginning at the cortex and working towards the periphery; the central autonomic path is not here considered.

1. Cerebral Motor Cortex.

The effect of damage to the cerebral motor cortex is discussed in Part II., Chapter V., and varies according to the part of the motor area involved.

2. Internal Capsule.

Since all pyramidal fibres are concentrated into a narrow band passing through the internal capsule, any lesion (such as hæmorrhage) is likely to involve a large part of the path. It must be noted that sensory involvement from such a lesion is usually small and readily clears up. Particular results depend on the exact position of the lesion, and which fibres are involved, the effects being always on the opposite side of the trunk and limbs.

The most common lesion is due to hæmorrhage from the lenticulo-striate artery, and there is always some residual fibrosis from the clot. The occurrence is so frequent that a full account is given.

(*a*) The muscles of the opposite side are at first flaccid and toneless; the deep reflexes are lost, even though these depend on the integrity of the brain stem and spinal cord reflex arcs, because in any severe lesion of the central nervous system function is disturbed, even in regions remote from the structures directly affected. The paralysis varies in different regions of the body; for example, the eye, chest and abdomen muscles are very slightly affected, while muscles which act bilaterally usually escape, because of the commissural fibres connecting the nuclei of their nerves of supply.

(*b*) Recovery may occur and be nearly complete after the initial stage of shock is over, and this is probably due to the improvement in the general circulation and to the removal of pressure from the fibres, for if the fibres are actually destroyed function in them clearly cannot be restored.

(*c*) Emotional instability is marked, due to removal of inhibitory cortical control. The pathway for emotional expression is distinct from the pyramidal path.

(*d*) Certain reflexes can be aroused on the affected side by stimulation of the normal one, and these are concerned with " associated movements," such as clenching the fist.

It must be remembered that such a lesion may also involve the corpus striatum connections (see p. 97).

3. **Pyramidal Path in the Mid-brain.**

All pyramidal fibres are still uncrossed at this level; hence the lesion affects the opposite side of the trunk and limbs.

Intracranial cerebral fibres of the cranial nerves may also be involved on account of their position. The third nerve is especially liable to be affected in this way, and as this is a lower motor neurone lesion, the effect will be on the same side of the body, thus producing a " crossed motor paralysis."

(See Diagram 58.)

4. **Pyramidal Path in the Pons.**

(i.) *Upper Pons.*—The results are the same as for the mid-brain, but the cranial nerve involved is the fifth.

(ii.) *Lower Pons.*—The sixth and seventh cranial nerves are usually involved in this lesion, and there is a " crossed motor paralysis." Since some or most of the upper motor neurone fibres of the facial nerve cross, a lesion extending upwards may involve both sides of the face.

5. **Pyramidal Path in the Medulla.**

There is—

(*a*) An upper motor neurone paralysis of the opposite side of the trunk and limbs, but the head escapes.

(*b*) A lower motor neurone paralysis due to involvement of the hypoglossal nerve of the same side, so that there is complete paralysis of one side of the tongue.

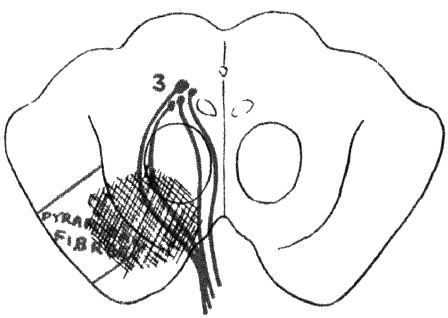
(*c*) Frequently some involvement of the eleventh nerve.

6. **Pyramidal Path in the Cord.**

Since all the direct pyramidal fibres cross by the mid-thoracic level, and all crossed pyramidal fibres cross in the medulla, it follows that a lesion involving half the cord above the mid-thoracic level will interfere with voluntary movement on both sides, and a lesion below this level will involve movement on the same side only.

7. **Motor Part of a Mixed Nerve.**

This is a lower motor neurone lesion; the reader is therefore referred to p. 9 for an account of degeneration of a nerve.



Pyramidal fibres supplying opposite side of body

Third nerve fibres supplying eye of same side.

DIAGRAM 58.—Diagram to illustrate "Crossed Paralysis" due to a Lesion involving Pyramidal Fibres and a Cranial Motor Nerve.

TABLE TO COMPARE THE EFFECTS OF A LOWER MOTOR NEURONE LESION WITH THOSE OF AN UPPER MOTOR NEURONE LESION

	Lower Motor Neurone (Anterior Horn Cells and Efferent Fibres).	Upper Motor Neurone (Betz Cells and Axons and Connector Neurones).
1. Wasting	Prominent feature.	Slight, and only in consequence of disuse.
2. Reflexes	Abolished in the affected segments, including "reflex tone."	Muscles are only flaccid during the period of shock. Tendon reflexes are always exaggerated. Plantar reflex usually gives an extensor response. Superficial abdominal reflexes often lost.
3. Rigidity	Limbs tend to become flaccid.	Limbs tend to become rigid.
4. Paralysis	Loss of all movements in the affected muscles.	No group is completely paralysed. Those devoted to skilled movements usually suffer most.
5. Electrical reactions.	Reaction to faradism and galvanism modified, or in complete lesions a typical "reaction of degeneration."	No obvious changes.
6. Contractures	Irregular deformities owing largely to the unopposed actions of non-paralysed muscles.	Rigidity accompanied by contractures in which the upper limb tends to become flexed and adducted, and the lower limb usually extended.

EXTRA-PYRAMIDAL SYSTEM

The functions of these paths have been almost entirely worked out by observing the results of disease (Parkinson's disease, encephalitis lethargica, and progressive lenticular degeneration). In these cases there is a varying degree of pathological change in the lenticular and caudate nuclei, and to a lesser extent in the associated nuclei. Simultaneous changes sometimes occurring in the substantia nigra have led some workers to include this cell mass in the extra-pyramidal system.

The reader is referred to p. 36 for an account of the basal ganglia connections.

Lesions of this system produce—

1. Rigidity.
2. Involuntary movement.
3. Disturbances of voluntary movement.

1. Rigidity.

This so-called "extra-pyramidal rigidity" must be differentiated from "pyramidal rigidity."

Pyramidal Rigidity.

(*a*) Is usually hemiplegic.

(*b*) Affects the flexor muscles to a greater extent than the extensors.

(*c*) Produces the so-called " clasp-knife " effect.

Extra-pyramidal Rigidity.

(*a*) Is usually segmental in its effect.

(*b*) Is more marked proximally than distally.

(*c*) Produces the so-called " leaden pipe " effect.

(*d*) Produces the " cogwheel " effect.

Extra-pyramidal rigidity can be abolished by the injection of cocaine into the rigid muscle. As cocaine abolishes the sensitivity of sensory nerve endings, this suggests that striate rigidity is reflex in origin.

This rigidity affects both the agonists and the antagonists, giving a fixed position of flexion, and it may be so marked that voluntary movement becomes impossible, although the pyramidal path is intact.

There is a mask-like condition of the face, but the reflexes are unaffected until the rigidity is sufficient to prevent any response.

2. Involuntary Movement.

Tremor is usually the most marked involuntary movement, and has been described by Kinnier Wilson as " a fairly regular rhythmical alternating contraction of a muscular group or groups and their antagonists." Striate tremor shows a fairly constant rate (*i.e.*, six per second), but the range varies from very fine to coarse wide movements. The movements most commonly affected are in the distal parts of the body, *i.e.*, the fingers, hand, lips, or tongue.

The law of reciprocal innervation holds good (see p. 112), and recent work seems to show that striate tremor may be due to the released activity of a centre, probably situated in the mid-brain.

3. Disturbances of Voluntary Movement.

There is—

(*a*) Weakness of muscles, so that fatigue sets in more rapidly than usual.

(*b*) Slowness, irregularity and limitation in extent of many movements, especially those made by the laryngeal and eye muscles: this latter effect produces a jerky movement of the eyes on looking to one side. The small muscles of the limbs are also affected.

(*c*) Inability to maintain a contraction.

(*d*) A lack of movements of co-operation, which, together with a general poverty of movement, is probably due to the rigidity, ease of fatigue, and need for extra effort on the part of the patient to carry out a movement. Hence there is a tendency to avoid these movements, although there is no actual interference with the pyramidal path.

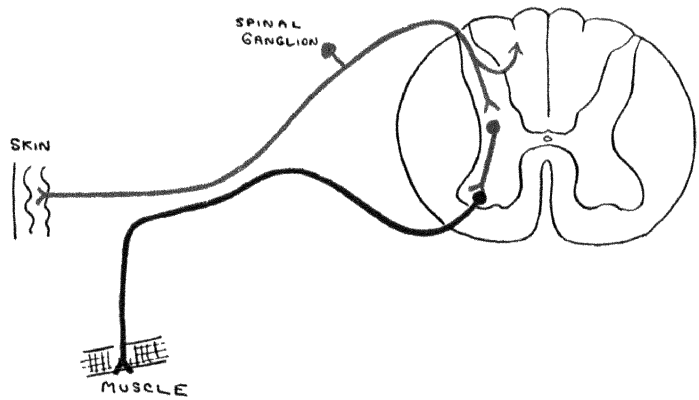


DIAGRAM 59.—Diagram of Simple Reflex Arc as present in the Spinal Cord.
Red : Receptor neurone. Green : Connector neurone. Mauve : Effector neurone.

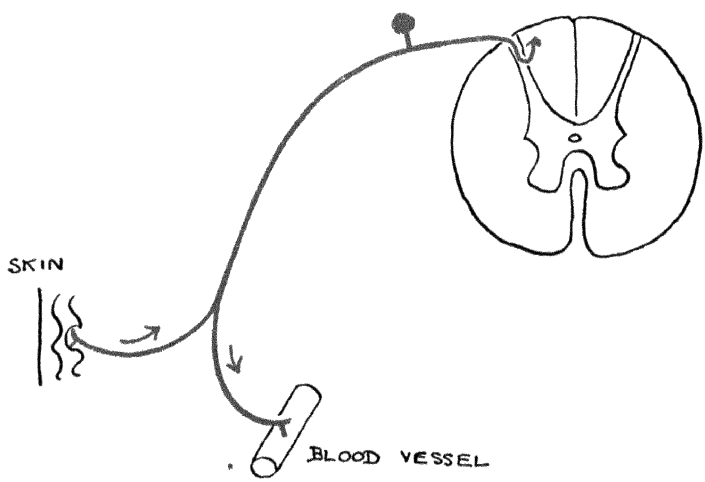


DIAGRAM 60.—Diagram to illustrate Axon Reflex of Skin.

CHAPTER VIII

REFLEX ACTION

THE term " reflex action " includes a stimulus, with its involuntary response. There is no essential difference between the voluntary response to an afferent impulse and the involuntary reflex response. In each case there must be an afferent impulse due to a stimulus (nervous or chemical) which is at some level brought into relation with the origin of efferent impulses. The reflex response in some cases arouses consciousness (*e.g.*, the watering of the eye due to the presence of a foreign body), but in many cases there is absolute unconsciousness of the reflex act in progress (*e.g.*, the opening of the ileocolic sphincter due to nervous impulses from the stomach).

The simplest anatomical arrangement whereby a stimulus may produce a definite motor response is known as the reflex arc, and in the nervous system of vertebrates the reflex arc consists of three neurones. There is—

1. The afferent or receptor neurone, consisting of the specialised ending of dendrites for receiving the stimulus, the nerve cell in the posterior root ganglion, and its axon passing into the cord by the posterior root and arborising in the grey matter.
2. The connector neurone in the grey matter, whose axon arborises round the dendrites of an anterior horn cell.
3. The efferent or effector neurone, consisting of the anterior horn cell, with its axon passing out to the organ of response (see Diagram 59).

The simplest reflex arc is the one involving posterior and anterior root fibres and cord connections at one level, but the integration of the afferent impulse with the efferent impulse can occur at many levels, such as the medulla, cerebellum and mid-brain. At every synapse it is possible for other nervous impulses to enter and modify the response, and consequently the real characteristics of a purely reflex act frequently become obscured. In order to study the pure reflex it is necessary to prevent impulses from higher centres from reaching the level at which the integration is occurring, and for this reason the " spinal " animal is used, *i.e.*, one in which the cord is severed from the medulla, and the spinal reflexes can be studied. As the animal scale is ascended the functions of the spinal cord become more and more subservient to those of the cerebral cortex, and consequently the range and degree of the purely spinal reflex become less.

A. Reflexes in the Spinal Frog.

If the cord is cut just below the medulla, the animal passes at once into the condition known as " spinal shock." It lies flat and motionless, with the limbs

completely flaccid, and gives no reaction to stimuli. After about ten minutes the condition of shock begins to pass off, the muscles resume their condition of tone, and the animal assumes the normal squatting posture. It will then respond to stimuli in the usual way, but will carry out no voluntary act. If placed at the foot of an inclined board, it will hop to the top and sit there ; if placed in water, it will swim. If a drop of weak acid is placed on the flank, the frog will try to wipe it off with the corresponding leg ; if this leg is held, it will use the opposite one. The stronger the stimulus used the more rapid is the response. These few examples serve to show the protective nature of these spinal reflexes, and also the purposeful character of the response. The response evoked is directly related in kind and in degree to the stimulus, and it is possible to predict what will be the response to any given stimulus. In the spinal animal the reflex response is a " fatal " one, *i.e.*, it must always be the same for any one stimulus ; in the intact animal the " fatal " response may be modified by impulses from higher centres.

By " reaction time " is meant the time that elapses between the giving of the stimulus and the response, and this will depend upon the synapse. A nerve impulse travels very rapidly along a nerve fibre, but much more slowly across a synapse ; thus the condition of the synapse can affect the reaction time to a marked degree. The passage of a nerve impulse is delayed by conditions that impede its passing across this junction ; for example, bromides, chloroform or fatigue increase the resistance at the synapse, and therefore increase the reaction time. On the other hand, the resistance at the synapse may be lowered ; if this occurs to any marked extent (as in strychnine poisoning), the nerve impulse will spread to adjacent neurones, and the response loses its local purposive character and becomes widespread. This " reflex spread," or irradiation, is the cause of strychnine convulsions.

B. **Reflexes in the Spinal Dog.**

The immediate effect of section of the cord just below the medulla is again one of " spinal shock," with complete loss of tone and loss of response to stimuli. After several days the condition of shock wears off and muscle tone returns. The animal can then take a few steps if raised and given a push forwards, and certain reflex movements are carried out. Reflex emptying of the bladder and rectum takes place, pregnancy with a normal parturition is possible, and the scratch reflex, flexor reflex and extensor or stepping reflex are easily elicited.

C. **Reflexes in Spinal Man.**

The immediate condition of spinal shock with complete flaccidity of muscles lasts for sixteen days or more ; if sepsis should supervene, the condition of shock lasts longer. Reflex (or automatic) emptying of the bladder and rectum then returns with the return of muscle tone, but other spinal reflexes below the level of the lesion tend to lose their local significance and become " mass reflexes." Thus any afferent stimulus below the lesion may provoke diffuse and widespread sweating and premature evacuation of the bladder. These mass reflex responses may result from such a stimulus as scratching the sole of the foot.

From a consideration of these examples it is seen that the chief characteristic of reflex actions is their protective nature; originally the response was one necessary for life. The reflex response is rapid and purposeful in nature, being limited to the needs of the stimulus. If impulses from other sources can be excluded, it is usually possible to predict the response that will occur to any given stimulus.

Inhibition of the Reflex Response.

The involuntary response of the reflex can be temporarily inhibited under certain conditions.

(*a*) *Chemical Inhibition.*

If a crystal of salt is placed on the distal cut end of the spinal cord, all spinal reflexes are inhibited.

(*b*) *Voluntary Inhibition.*

Within certain limits it is possible by an effort of will to inhibit the reflex responses to some stimuli.

(*c*) *Inhibition by a Stronger Sensory Stimulus.*

If a stronger sensory stimulus is applied simultaneously with the original stimulus, the reflex response to the original stimulus is frequently inhibited. For example, yawning or sneezing can be prevented by firm pressure or pinching of the skin of the bridge of the nose or upper lip.

(*d*) *Inhibition by a Hurtful Stimulus.*

If a hurtful stimulus is applied, any reflex response to another stimulus that may be in progress is inhibited, so that the protective response to the harmful stimulus may take place. For example, if the scratch reflex is elicited in a dog, and during its progress the foot is pricked, immediately there is a flexor reflex response and inhibition of the scratch reflex. A hurtful stimulus is always the preponderant one, this type of inhibition being spoken of as "inhibition by nociceptive stimuli." It is clear that two reflexes cannot occupy the same nerve path at the same time, and since there is only one "final common path" from the spinal cord to any one muscle, it is necessary that one impulse should receive preference; this preference is always accorded to the protective impulse which is the reflex response to the hurtful stimulus.

Facilitation of the Reflex Response.

It sometimes happens that a small stimulus produces an impulse which is insufficient to pass across the synapse and produce a response. In such a case repetition of such small stimuli will ultimately produce a response. The initial impulse is not strong enough to pass across the synapse, but it does nevertheless produce a physico-chemical change. The final result of a series of such impulses is to bring about physico-chemical changes sufficient to carry the impulse across the synapse to the next neurone, and so bring about a response. The reflex

response is also facilitated by frequency of elicitation; in other words, if a particular reflex arc is used frequently, the reaction time involved in its use is decreased. This is the basis of habit formation, and must be due again to some change at the synapses between the neurones involved.

The Axon Reflex.

This special type of reflex has been already mentioned (see p. 68). It is an example of a very rapid local protective mechanism, the impulse not passing through any nerve cells. (See Diagram 60.)

Visceral Reflexes.

These reflexes involving autonomic paths are discussed on p. 120.

Types of Reflexes in Man.

The reflexes are usually divided into three groups :—

(A) Superficial or skin reflexes—*e.g.*, the plantar and abdominal reflexes.

(B) Tendon reflexes—*e.g.*, the knee jerk.

(C) Deep or visceral reflexes—*e.g.*, micturition.

(A) *The Plantar Reflex.*

If the outer side of the sole of the foot is stimulated, the big toe moves downwards—*i.e.*, a flexor response. In children up to two years and in cases of disease of the pyramidal tracts, this stimulus causes an upward stretching of the big toe—*i.e.*, an extensor response. The extensor plantar reflex is a purely spinal one, the flexor response being due to cerebral activities through the pyramidal fibres. An extensor response after two years of age is known as the Babinski phenomenon, and hysterical paralysis with the flexor plantar reflex can thus be distinguished from pyramidal paralysis with the extensor response. The reflex depends upon the integrity of the spinal centres at the levels of L. 5, S. 1 and S. 2.

The Abdominal Reflex.

If the skin of the upper abdomen is stroked there is retraction of the body wall. This reflex is of most diagnostic importance in cases of hemiplegia where comparison can be made with the normal side; in bilateral lesions the reflex is uncertain. The abdominal reflex is lost in disease of the pyramidal tracts, and is therefore probably cerebral.

(B) *The Knee Jerk.*

If the patellar tendon is tapped with the hamstring muscles relaxed, there is contraction of the extensors and relaxation of the flexors, resulting in the upward kick of the leg. The normal response varies considerably, but certain conditions affect the movement in a very definite way. (See Diagram 61.)

(i.) *Loss of Knee Jerk.*—This may be due to—

(*a*) Interference with the reflex arc.

1. Division of anterior crural nerve.
2. Division of anterior or posterior (*e.g.*, locomotor ataxy) nerve roots, L. 3 or 4.

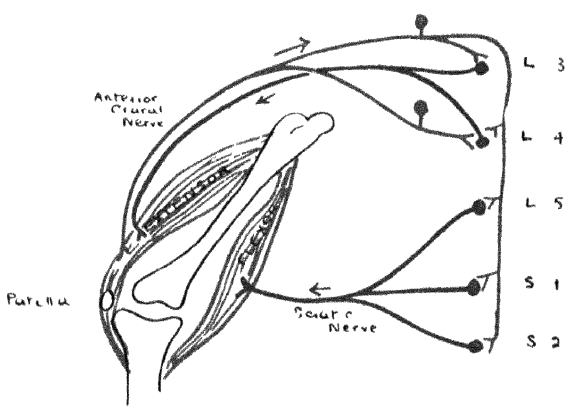


DIAGRAM 61 —Diagram to illustrate the Knee Jerk.

3. Destruction of anterior horn cells at level L. 3 or 4 (*e.g.*, anterior poliomyelitis).

(*b*) Shock from complete section of the spinal cord. (The reflex then seldom returns except in lower animals.)

(*c*) Increased inhibition of the antagonist muscles, due to stimulation through the sciatic nerve.

(*d*) Interference with the anatomical paths connected with the maintenance of muscle tone, particularly the posterior column fibres.

(*e*) Sleep.

(ii.) *Increase of Knee Jerk.*—This may be due to—

(*a*) Removal of impulses from the cerebrum and consequent increased reflex excitability of the lower spinal centres—*i.e.*, an upper motor neurone lesion, such as injury to cerebral cortex or pyramidal tracts. The reflex excitability may be so greatly increased that a single stimulus evokes a clonic response—*i.e.*, a series of contractions and relaxations. (This clonus is obtained in the case of the ankle jerk more readily than in the knee jerk.)

(*b*) Hyperexcitability of the nervous system, as in hysteria.

(*c*) Action of drugs, such as strychnine, which lower the resistance at the synapse.

(*d*) Voluntary reinforcement by a simultaneous strong voluntary contraction. This is due to the concentration of cerebral control into the distracting voluntary action and consequent diminution of cerebral inhibition of the reflex. (Some writers explain reinforcement as due to general increased motor irritability produced by overflow from the voluntary motor activity.)

(*e*) Division of the sciatic nerve and consequent removal of the action of the antagonist muscle.

(C) *Micturition.*

Micturition was originally a reflex carried out by a centre in the lumbar cord. The afferent path from the bladder is by the nervi erigentes and pudic nerve, and the efferent path to the bladder by these same nerves; the inhibitor path is by the hypogastric nerve. The normal stimulus for the reflex is a rise of pressure in the bladder due to the presence of urine. When cerebral control has been developed this reflex is subconsciously inhibited unless overriden by afferent stimuli; the cerebral control can also be voluntarily removed.

According to Barrington, there are many factors concerned in the mechanism of voluntary micturition, including a higher centre in the pons. He found that in a decerebrate animal the following sequence occurred :—

1. Distension of the bladder, which produced strong contraction of the bladder wall.
2. This caused the expulsion of fluid into the urethra.

3. This distension of the posterior urethra produced a feeble contraction of the bladder.
4. The passage of fluid through the urethra reflexly inhibited the sphincter.
5. The bladder contracted and caused reflex relaxation of the urethra.

In the spinal animal the contraction of the bladder (1 and 3) did not occur; these responses are therefore carried out by a long reflex arc, of which the centre is found to be in the pons. The spinal cord is concerned only with the inhibition of the sphincter. This is supported by the observation that in spinal man contraction of the bladder is produced by reflex relaxation of the sphincter and spasm of the abdominal muscles.

The following are the spinal levels for the reflexes most commonly used in clinical examination :—

Pupillary reflex (sympathetic). Dilatation of pupil by irritation of neck.	C. 4–D1
Biceps and supinator longus reflexes. Flexion of forearm by tapping of tendon.	C. 5, 6
Triceps reflex. Extension of forearm by tapping of tendon . .	C. 6
Extensor wrist reflex. Extension of hand by tapping of extensor tendons.	C. 6–8
Flexor wrist reflex. Flexion of hand by tapping of flexor tendons .	C. 7, 8
Abdominal reflex. Retraction of abdomen by stroking of skin . .	D. 9–12
Genital reflex. Contraction of abdominal muscles by compression of testis.	L. 1–3
Patellar reflex (knee jerk). Extension of leg by striking patellar tendon .	L. 3, 4
Ankle jerk. Flexion of ankle by tapping Achilles tendon . . .	S. 1–3
Plantar reflex. Flexion of great toe by striking sole of foot . .	L. 5–S. 2

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CHAPTER IX

CONDITIONED REFLEXES

In addition to the unconditioned reflexes or " instincts " described in the previous chapter, there is a series of reflexes which are not inborn, but are acquired, and to which Pavlov has given the name of " conditioned reflexes."

These conditioned reflexes only occur when the cerebral cortex is existent, and are subject to inhibition as the result of many extraneous circumstances. It is the intrusion of such a variety of inhibitory influences that makes the actions of the cerebral cortex so involved. These reflexes have only recently been scientifically investigated, and the method used has been to build up in normal animals reflexes which can be evoked with the same certainty and measured with the same accuracy as can the reflexes in a spinal animal.

Law governing the Formation of Acquired Reflexes.

" Stimulation of any receptor organ occurring simultaneously with reflex excitation of an effector organ leads to the formation of a new reflex." These acquired reflexes can only develop on the basis of another existent reflex, which may itself be either unconditioned or conditioned. Conditioned reflexes have been established with respect to the vasomotor system, glandular secretion, the heart, pupils, muscular movements, micturition, and so on. Their formation is due to the fact that " if a given receptor organ is stimulated during the occurrence of any original unconditioned or inborn reflex, a new link, a new nervous path, is formed between new receptors and the effector organ."

Most of Pavlov's investigations have been carried out by using the parotid salivary gland in the dog as the *effector* organ. An accurate quantitative measurement of the saliva secreted can be made, and sound has been used to form the conditioned reflex. Fundamentally there must be the simultaneous application of the original (unconditioned) stimulus and of any other stimulus which elicits ordinary reflex activity.

Consequently a conditioned reflex is built up in the dog by sounding a bell when food is brought into the animal's chamber. When the reflex is properly established the animal will salivate at the sound of the bell (conditioned stimulus), even though the food (representing the unconditioned stimulus) may not be brought in. There are three types of conditioned reflexes: simultaneous, delayed, and trace :—

(*a*) *Simultaneous*, *i.e.*, the conditioned and unconditioned stimuli are applied simultaneously. The response is immediate.

(*b*) *Delayed*, *i.e.*, the application of the conditioned stimulus precedes that of the unconditioned, and is maintained until the latter is applied. The

latent period of the response is the time elapsing between the application of the two stimuli.

(*c*) *Trace, i.e.*, the application of the conditioned stimulus precedes that of the unconditioned, and is maintained only for a short time, a pause occurring before the application of the unconditioned stimulus. The latent period is equal to this interval of time, and the response is due to the " trace " left in the central nervous system by the conditioned stimulus.

The rate of formation of these different types varies, simultaneous ones being formed much more quickly than are the delayed or the trace variety. The rate of formation is also dependent largely on the intensity of the conditioned stimulus employed, and there is an optimum intensity for every reflex, while discontinuous conditioned stimuli always produce a more rapid formation of acquired reflexes.

Properties of Conditioned Reflexes.

1. *Summation.*

   If two conditioned reflexes using the same effector path are simultaneously applied, the resulting reflex activity is increased. For example, if an animal stimulated with the smell of camphor produces sixty drops of saliva, and stimulated electrically yields thirty drops, it produces ninety drops when the two stimuli (camphor and electricity) are applied together.

2. *Specificity.*

   When a conditioned reflex is firmly established its specificity is increased.

3. *Stability.*

   To maintain the strength of any conditioned reflex, it must be regularly reinforced by the unconditioned stimulus.

4. *Experimental Extinction.*

   A conditioned reflex can quickly be extinguished if it is applied on several occasions without the accompaniment of the unconditioned stimulus.

5. *Irradiation.*

   (*a*) With simultaneous reflexes irradiation is only seen before the conditioned reflex is very firmly established. Once this has been accomplished, the area of irradiation is reduced to a small point round the original position ; consequently the reflex is nearly specific within the same receptor organ.

   (*b*) With delayed type reflexes, however long the latent period may be, they always culminate in strictly localised reflexes.

   (*c*) With trace reflexes of a long latent period irradiation is much more extensive.

6. *Discrimination.*

   This is the function of the central nervous system, and discrimination can be made between very closely related stimuli, dividing them into effective and ineffective.

Pavlov has given the name of " analyser " to the entire mechanism comprising those parts of the central nervous and peripheral nervous systems which are related to each particular receptor organ. Probably analysis is mainly carried out in the cerebral cortex, which region is therefore essential for the building up of conditioned reflexes. It must be noted that a single conditioned reflex can be extinguished without producing any effect on any other reflex, and also that the specificity of conditioned reflexes, even within *one* receptor, is not perfect.

Auditory, visual, cutaneous and other senses may be used as analysers of conditioned reflexes, and a varying range of appropriate stimuli serves the purpose of building up very complicated conditioned reflexes. Discrimination of rate of vibration and of pitch is more accurate in the dog than in man, but visual stimuli are more perfectly estimated by the latter. Tactile stimuli and those of smell, muscle sense and pain can also be used for the formation of widely varying conditioned reflexes.

Inhibition of Conditioned Reflexes.

Inhibition of a conditioned reflex is only of temporary duration, and if an extraneous stimulus is repeated, its inhibitory effect decreases markedly and eventually disappears. Inhibition can be produced by any kind of stimulus affecting the central nervous system, provided that this stimulus is applied during or shortly before the occurrence of a conditioned reflex. This type of inhibition is known as *external*, and does not require any development of adaptation on the part of the animal. *Internal* inhibition, however, causes a previously effective stimulus to become ineffective, and is apparently due to the development of an active inhibitory process in the animal. It is probable that the inhibition originates within the excitatory analyser.

Conditioned reflexes of higher orders may be established on the basis of other conditioned reflexes, and this includes both excitor and inhibitor types of response.

Localisation of Conditioned Reflexes.

The cerebral cortex is absolutely essential for the establishment of these reflexes. Local damage to the cortex has only a temporary effect on the reflexes, but more extensive injury leads to a permanent weakening of the inhibitory process, even though the reflexes themselves are still present. No single place in the cortex has been found which when extirpated leads to the abolition of all conditioned reflexes ; in most cases the centre for any given conditioned reflex corresponds practically with the anatomical cortical area associated with the particular analyser concerned. In higher animals localisation of the analysers is more precise than in lower animals, and the seat of inhibition is within the excitatory analyser, and not within the inhibiting one.

Sleep.

" This may be regarded as an accumulation of internal inhibitions, which is not concentrated merely within one analyser, but spreads over the whole

cortical and subcortical areas." Similarly a lack of adequate inhibition for any particular process leads to a state of widespread excitation, but unless the general conditions alter, both conditioned excitor and inhibitor reflexes are extremely stable (see also p. 78).

Effect of Altered Conditions.

(*a*) Digestive troubles lead to a temporary weakness and then to the abolition of the reflexes.

(*b*) Pregnancy and inanition cause a marked diminution of the reflexes, but they return to normal soon after parturition.

(*c*) Cretins show definite inability to develop any discrimination, and in them it is difficult to establish any kind of conditioned reflex.

(*d*) In the young conditioned reflexes are more quickly acquired than in the aged, but once the reflex is established in youth, it persists to the end of life.

(*e*) It is possible that heredity plays a part in the facility with which a particular conditioned reflex is acquired in successive generations.

(*f*) Drugs have a definite effect on these reflexes. Caffeine and strychnine augment the reflex and at the same time diminish every inhibitory process, while bromides increase the inhibitory power of the cortex : alcohol has a purely depressant effect.

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CHAPTER X

THE CEREBELLUM

Phylogenetic Development of the Cerebellum.

THE cerebellum of vertebrates is developed from the dorsal lamina of the brain-stem, *i.e.*, that part chiefly concerned with receiving afferent impulses. The fibres of the eighth nerve reach the dorsal edge of this lamina, in which occurs the subsequent development of the vestibular and cochlear nuclei. Other afferent impulses from the muscles pass to the same region which responds by increased growth. The two cerebellar plates thus formed increase in size and unite as a bar across the fourth ventricle, the later expansion of this arch giving rise to the cerebellum. In the human the arch is represented by the connection between the vestibular nuclei and the vermis. In the lower and aquatic vertebrates balance and postural changes depend largely on afferent impulses from the lateral line system and from the semicircular canals. In the cyclostomes special nuclei are developed for these systems, the nuclei receiving also impulses from the cerebrum and from the tectum ; thus a correlation centre is established which is the foundation for subsequent cerebellar development. In the amphibia, representing the transition from aquatic to terrestrial life, the lateral line system drops out, but the vestibular system increases and with the greater development of paired limbs the spinocerebellar tracts become more important : the tectal connection, bringing in optic impulses, persists at least to the lower mammals and possibly higher still. In mammals there is an increase in the transverse axis of the cerebellum due to development of the lateral hemispheres in connection with the cortico-pontine system : at the same time the connection with the inferior olive becomes more important, and the vestibular correlations become somewhat overshadowed by the importance of the spinocerebellar connection.

The oldest part of the cerebellum consists of the anterior and posterior lobes of the vermis which receive the spinocerebellar system, and of the fastigial nucleus with its vestibular connections : the median lobe with the emboliformis and globosus nuclei and part of the dentate nucleus is of later development, while the cerebellar hemispheres with the remainder of the dentate nucleus appear first in mammals in relation to the cortico-pontine system. Thus, in general, the middle older parts of the cerebellum receive the more direct proprioceptive impulses, while the lateral newer parts receive more olivary and cortico-pontine impulses.

Stimulation of the Cerebellum.

Stimulation of the cortex electrically inhibits decerebrate rigidity on the same side of the body, but gives rise to no positive reactions unless the current is strong

enough to spread to the underlying nuclei. A strong stimulation causes movements of the head and of the eyes towards the side stimulated.

A pathological condition causing irritation of the cerebellum produces giddiness, and forced movements of the head towards the side of the lesion.

Destruction of Cerebellar Tissue.

If part of the cerebellum is removed certain symptoms appear after a few days which are permanent except in so far as there may be a later improvement consequent on compensation by other parts of the nervous system. There is no loss of sensation : the effects are manifested in muscles on the same side of the body as the lesion, the most obvious alterations being atonia, asthenia, and astasia. In other words, there is a loss of tone in the muscles affected, so that the limbs tend to assume unnatural positions owing to the effect of gravity ; there is a weakness of the muscles on the affected side, but no paralysis ; and there is tremor of the muscles under sustained contraction.

In addition there is a disturbance in the voluntary movements of the body which is spoken of as asynergy, or lack of co-ordination. This is perhaps particularly well shown by the difficulty in carrying out rapidly alternating movements, such an inability being termed adiadokokinesia.

There is probably very little localisation of functions in different parts of the cerebellum beyond the correlation between each half of the cerebellar cortex and the regulation of tone and movement in the corresponding half of the body.

Most of the impulses from the vestibular part of the ear enter the cerebellum, and destruction of this organ on one side produces effects somewhat similar to those following ablation of one cerebellar hemisphere (see also p. 113).

The Functions of the Cerebellum.

The cerebellum cannot act alone but only with other motor integration levels either in the cerebral cortex, midbrain, medulla or spinal cord : in cerebellar deficiency, therefore, there is inability " to perform muscular movements in a co-ordinate synergic manner," such movements resulting from the activity of the other levels alone.

Developmentally the subcortical or extra-pyramidal systems appear first and are concerned with the normal involuntary and athetoid movements that are first made by a child ; with the later development of the pyramidal system there are definite voluntary movements, but these are uncertain and poorly co-ordinated ; lastly the cortico-pontine-cerebellar path is established and the co-ordination of movement becomes perfected through the agency of the cerebellum.

The cerebellum, however, plays an important part not only in co-ordination of movement of all kinds, but also in the maintenance of posture which is a necessary adjunct to the balance of muscle activities. This relationship is perhaps most clearly explained according to Ramsay Hunt's analysis, on which the following account is based.

In the motor activities of the body there can be recognised a *kinetic* (active) system, or function of movement, and a *static* (passive) system, or function of

posture. Each of these systems may further be divided into three, each subdivision corresponding with a stage of development. Thus in the kinetic system can be recognised :—

(*a*) Archeokinetic system, or spinal cord reflexes.

(*b*) Palæokinetic system, or automatic associated movements of striate-spinal (extrapyramidal) origin.

(*c*) Neokinetic system, or voluntary dissociated movements of cortico-spinal (pyramidal) origin.

Similarly in the static system can be recognised :—

(*a*) Archeostatic system, or segmental mechanism of spinal cord and brain-stem.

(*b*) Palæostatic system
(*c*) Neostatic system

} or cortico-cerebellar and cerebellar spinal mechanisms, the cortico-pontine-cerebellar path corresponding to the pyramidal tract.

All the posture systems pass to the cerebellum for their complete and final integration ; although the higher forms of movement are conscious voluntary processes, yet the corresponding postures which are secondary and follow automatically in the path of the movement are maintained by cerebellar activity.

The afferent impulses underlying these responses are those of the proprioceptive system, *i.e.*, those from the muscles and tendons, and those from the vestibular part of the ear, and in this system also there is a static and a kinetic element. The *kinæsthetic* system is the sensory component that underlies the twitch, the contractile tone and the reflexes of *movement*, while the *statæsthetic* system is the sensory component that underlies the plastic tone, the " lengthening and shortening reactions " of muscles and the reflexes of *posture* (see also p. 113).

Pathologically these two systems are usually involved together : they are nevertheless distinct from one another. A dog without a cerebellum cannot stand or walk, but it can swim easily ; this is because the integration of the posture systems in the cerebellum is lacking, but in water the support afforded to the body makes this of secondary importance, and as the kinetic systems are intact the dog can swim.

Thus cerebellar function resolves itself into the regulation of posture and postural tone. In cerebellar deficiency there is a decomposition of the movement during any co-ordinated act, because the disorder in the mechanism for posture co-ordination prevents the posture and movement systems from acting together. " In any co-ordinated act posture patterns are a necessary complement of motion patterns, to give stability and direction, and to initiate and check the movements." Any defect in the postural component, either in the afferent proprioceptive path (as in locomotor ataxia) or in the integrating mechanism (as in cerebellar destruction), produces of necessity a disorder of movement which is strictly secondary. The deficiency becomes most marked at the end of the movement when an attempt is made to fix the posture—*e.g.*, cerebellar intention tremor, and cerebellar nystagmus.

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CHAPTER XI

LEVELS OF INTEGRATION AND MECHANISM OF CO-ORDINATED MUSCULAR MOVEMENT

ANY voluntary movement must involve the contraction of one group of muscles and the inhibition of the antagonists.

In considering any simple voluntary movement, muscles can be grouped into—

1. Agonists, or prime movers.
2. Antagonists, or muscles tending to interfere with the desired joint displacement.
3. Synergists, or muscles facilitating the precise movement.

In considering such a simple movement as clenching the fist, for example, the *agonists* are the *flexors* of the fingers and thumb, the *antagonists* are the *extensors* of the fingers and thumb, while the *synergists* are represented by the *extensors* of the wrist.

It will thus be seen that some mechanism is necessary for the integration of nerve impulses to these different muscles, and this mechanism is supplied by the process of " reciprocal innervation " as described by Sherrington.

Reciprocal Innervation.

Muscles are innervated in such a way that the contraction of one or more muscles is accompanied by the simultaneous relaxation of the antagonistic ones, so that voluntary movement becomes possible.

Sherrington demonstrated this quality in an experiment on the eye muscles of the monkey. He cut the third and fourth nerves of the left eye, leaving the sixth nerve intact, so that the left external rectus was acting unopposed, and consequently rotated the eye outwards. Normally, if the left frontal lobe of the brain is exposed and stimulated, there is contraction of the right external rectus and of the left internal rectus. In Sherrington's experiment he exposed the left frontal lobe and stimulated it, but as the left third nerve had been cut, the left internal rectus muscle could not contract. The internal and external rectus muscles are antagonistic to each other, so that stimulation of one should lead to inhibition of the other; consequently in this experiment, when the cortex is stimulated as described, the internal rectus cannot contract, but the external rectus can be inhibited. This actually occurs, so that the external rectus relaxes and the left eye moves back again to the mid-line.

(See Diagram 62.)

The same phenomenon can be shown in connection with the muscles of the thigh, and the reader is referred to the diagram for necessary details.

(See Diagram 63.)

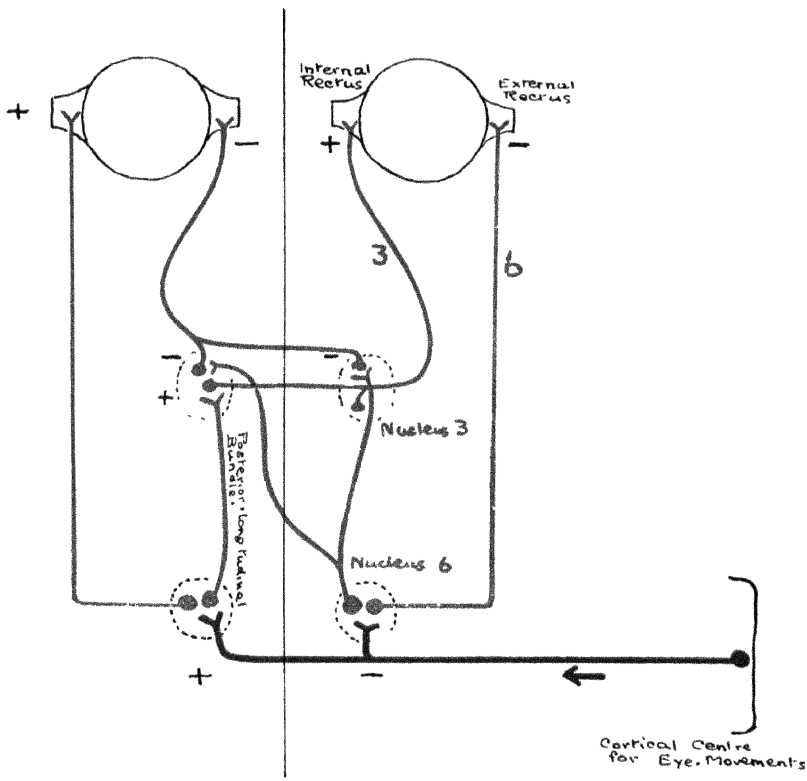

DIAGRAM 62.—Diagram to illustrate Sherrington's Experiment on the Reciprocal Innervation of Eye Muscles.

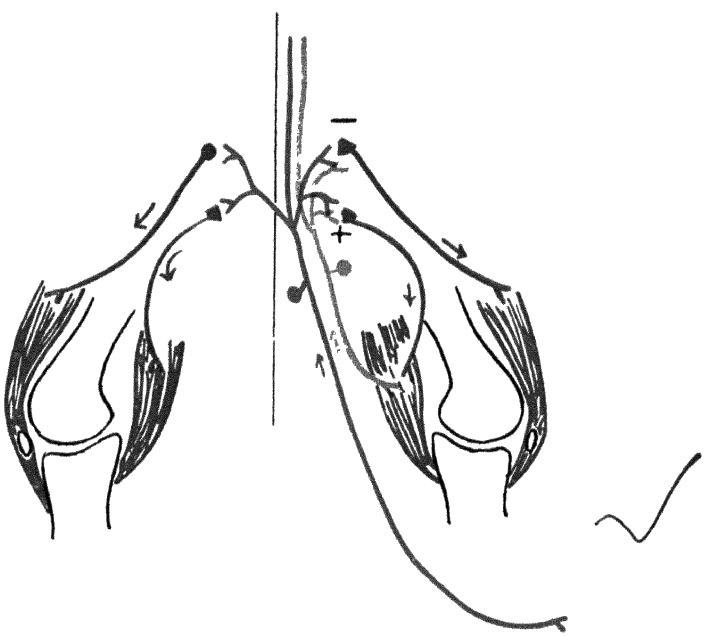

DIAGRAM 63.—Diagram to illustrate the Reciprocal Innervation of Antagonistic Muscles.

(After Sherrington.)

Maintenance of Posture.

Posture, according to Sherrington, may be—

(*a*) Passive, or

(*b*) Active.

In the first case, it may be demonstrated by the position which a dead body takes up through the force of gravity, but active posture denotes a " reaction in which the configuration of the body and of its parts (in spite of forces tending to disturb them) is preserved by the activity of contractile tissues, these tissues then functioning statically."

Muscle tone has been described as " a beautifully graded series of proprioceptive reflexes, continuously and unconsciously playing its part in our every motor act." It is the " raw material of posture," and efforts have recently been made to divide tone into—

1. Contractile tone.
2. Plastic tone.

This latter is responsible for the maintenance of position. Plastic tone is considered to hold the muscle at rest, and to maintain the intermediate postures through which muscles pass during the execution of movements, so that every advance made by contractile fibres is at once consolidated by the plastic elements. It has been suggested (Hunter and Royle) that plastic tone depends on the integrity of the sympathetic supply to striated muscle, but as these fibres appear to end in the neighbourhood of the muscle fibres, but not actually within them, it seems probable that the sympathetic influence on these muscles is exerted through the liberation of some hormone in their vicinity. It is important to note that a static pose can be maintained for long periods without fatigue, whereas prolonged voluntary contraction of the same muscles is very fatiguing. Smooth muscle has tonus even when isolated from the central nervous system, whereas striated muscle has no such intrinsic tonus.

Maintenance of Tone.

This is governed by two reflex systems; in the case of skeletal muscle, these are played upon by the cerebral cortex in the production of the voluntary action of the intact organism.

I. *The first reflex system*, which extends to a considerable degree up into the brain stem, maintains and regulates a steady tone, or " tonus," in the muscle, which is the basis of posture. This reflex tone arises in the muscles themselves, under the influence of that state of tension which obtains in them in varying degrees. This stimulus is known as the " stretch stimulus."

Variations in tone, and therefore in posture, are produced by continual reactions which arise in—

(*a*) The otolith organs.

(*b*) The proprioceptors throughout the body musculature.

(*c*) Receptors on the body surface, which subserve the sense of pressure.

Such reflexes are known as the " tonic standing and righting reflexes " of Magnus and De Kleijn, and may be secondary to phasic or movement reactions which are elicited from the exteroceptors. These reflexes of Magnus and De Kleijn have a very long latent period, and they continue unchanged so long as the stimulus which evokes them persists. This stimulus may be a variation in plane of the otolith membrane in the case of the labyrinths, or " stretch " in the case of proprioceptors.

Postural reactions of the body when at rest are called *static reflexes*, and are divided into :—

(1) Stance reflexes or reflexes of pose (" tonic standing ").

(2) Righting reflexes, by means of which pose is restored after disturbance.

In other words : (1) " keep you right way up when you are," and (2) " put you right way up when you are not."

When the body is in movement the postural reactions are known as *statokinetic*, and these reactions are produced by the initiation, cessation and variation of a movement.

II. *The second reflex system* consists of short-lived movements, and its reflex arc does not extend above the spinal cord.

All these types of stimuli are analysed and compounded, so that the phasic and the tonic elements co-operate, balance is maintained, and a beautifully co-ordinated movement is produced. It must be observed that all reactions of both systems use one peripheral effector organ, which is the striated muscle, and one efferent pathway, *i.e.*, the motor neurone from the ventral horn of the cord, which is known as " the final common path."

Most of the work on the classification of these reflexes has been done on animals in which a state of *decerebrate rigidity* has been produced. This condition results when a trans-section of the brain stem is made between the level of the inferior corpora quadrigemina and the entry of the eighth cranial nerve. Decerebrate rigidity is not abolished by removal of the cerebellum, but it disappears after section of the afferent nerve fibres from the muscles : the labyrinths are apparently not necessary for the production of the extreme tonus. Study of this condition has shown " that many different sense organs are involved, that very different centres integrate their stimuli, that the muscles concerned act in many different combinations in the production of the reactions, and that a whole series of diverse reflex groups are balanced together." Recent work suggests that the maintenance of decerebrate rigidity may be due in part to a peripheral mechanism under humoral control.

Magnus' Classification of Postural Reflexes.

I. STATIC REFLEXES.

(i.) Local static reactions, *e.g.*, those confined to one limb.

(ii.) Segmental static reactions, those involving one segment, *e.g.*, both hind limbs, both fore limbs, or the neck.

(iii.) General static reactions, those involving more than one segment. These may be divided into—

(*a*) Reflex pose—responses of head, trunk and limbs to afferent impulses from neck muscles and labyrinth.

(*b*) Compensatory pose of eyes—responses of eyes to afferent impulses from neck muscles and labyrinth.

(*c*) Righting reflexes—responses of body and head to afferent impulses from neck muscles, labyrinth and body itself.

II. Stato-kinetic Reflexes.

A. Reactions to Rotation.

These reactions include responses made by head, eyes and body. Movement of the head, for example, produces motion of the vestibular endolymph, with resulting afferent impulses to the vestibular nuclei. The efferent response may produce movements of the body (vestibulo-spinal path), and of the eyes (posterior longitudinal bundle).

B. Reactions to Progressive Movement.

These reactions include responses made by the head and extremities.

C. Reactions to Partial Body Movements.

This table serves to show how varied and widespread are these reactions, and a detailed account of these will be found in Lovatt Evans' " Recent Advances in Physiology " ; a few points may, however, be stressed.

The *head* is markedly the predominant feature determining body posture. *Righting reflexes* only take control when a trans-section is made cephalic to the thalamus, *i.e.*, when the whole of the mid-brain is left in continuity with the pons, medulla and cord. The centre for these reflexes is in the red nucleus. The grey matter of these long reflex arcs all lies within the brain stem, mid-brain, pons and medulla, while it should be noted that the efferent and afferent nerves never traverse the cerebellum. *Phasic reflexes* arise from the semicircular canals, and both phasic and tonic reflexes are present in an animal (from which the cerebral hemispheres have been removed but the thalamus left intact), even after removal of the cerebellum ; therefore neither the cerebellum nor the corpus striatum is essential to the *reflex* co-ordination of movement and posture. It would appear, however, that the cerebellum is essential to *voluntary* co-ordinated movement. Removal of the cerebral hemispheres has but little effect on normal posture, or on the righting reactions by which that posture is resumed after disturbance.

Levels of Integration

Magnus and Sherrington differ as to where the integration of co-ordinated movement actually occurs, but it is helpful to summarise briefly the possible levels which have both an anatomical and physiological basis for the part which they may play in this complex mechanism.

1. *Spinal cord—e.g.*, a simple spinal reflex.
2. *Upper part of the spinal cord*, where the nerves concerned with neck muscles derive their supply.
3. *Vestibular nuclei.*
4. *Cerebellum* (see Part II., Chapter X.).
5. *Between the entry of the eighth cranial nerve and the inferior corpora quadrigemina—e.g.*, Magnus' reflexes from the head and neck.
6. *Red nucleus.*
7. *Thalamus* and *basal ganglia.*
8. *Cerebral cortex.*

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CHAPTER XII

THE FUNCTIONS OF THE AUTONOMIC NERVOUS SYSTEM

THE autonomic nervous system must be considered as a part of the general nervous system with which it acts in close co-operation. It regulates the activity of structures not dependent on voluntary control and which can carry out their functions when isolated from the central nervous system : such structures include the smooth muscle and glands throughout the body.

The anatomical peculiarity of this part of the nervous system lies in the arrangement of the efferent fibres, all of which after emerging from the central nervous system relay in some ganglion before passing to their destination. The relation of the different fibres to the various ganglia is described on p. 63.

Fibres arising from anterior horn cells of the spinal cord pass, without relay, direct to the striped muscle fibres that they supply ; the nerve impulse passing out from the cord cannot be modified by any other nerve impulses, nor can it pass to any other muscle fibres ; in other words, the impulse is strictly limited in its effects. But the autonomic fibres arising from the lateral horn cells of the spinal cord, on the other hand, pass first of all to some ganglion where they make synaptic connection with post-ganglionic neurones that may pass on to supply structures in various parts of the body : in addition, the original nerve impulse reaching the ganglion may be modified by other impulses simultaneously arriving in the ganglion. In other words, the impulse may be very widespread in its effects. If the relay station is in or near to the organ supplied, the effects are not so widely spread throughout the body, *e.g.*, the parasympathetic fibres relaying in the terminal ganglia. If, on the other hand, the synapse is in the sympathetic chain or collateral ganglia, as for the sympathetic fibres, the resulting effects may be manifest all over the body, *e.g.*, vasoconstriction, sweating, etc.

Sympathetic and Parasympathetic Systems.

The subdivision of the autonomic nervous system into sympathetic and parasympathetic groups depends partly on the anatomical arrangement of the fibres with respect to their origin and to their relay stations, partly on the functional differences of the fibres, and partly on their response to various drugs.

(*a*) Sympathetic System.

The pre-ganglionic fibres emerge from the spinal cord between the first thoracic and third lumbar segments, and have their cell station either in the sympathetic chain or in the collateral ganglia (cœliac and mesenteric). From these ganglia the post-ganglionic fibres are distributed to all parts of the body.

Stimulation of the sympathetic system produces effects in the various structures innervated similar to those produced by the action of adrenin, and adrenin itself

stimulates the sympathetic nerve endings. This close relation between the adrenal medulla and the sympathetic system is not surprising when it is remembered that the former is developed from the same neuroblast masses as those giving origin to the sympathetic ganglia, and is itself stimulated by sympathetic impulses. Adrenin appears to sensitise the nerve endings of sympathetic fibres, thus reinforcing the effect of the nerve impulse.

The effects produced by sympathetic stimulation are those which serve to activate the body for a struggle and to increase its powers of defence. A few examples will make this clear :—

(i.) The pupil dilates—*i.e.*, there is an increased perception of light.

(ii.) The heart beats more quickly and more forcibly—*i.e.*, there is an increased blood supply to the muscles.

(iii.) There is vaso-constriction in the splanchnic area, *i.e.*, there is a rise of blood pressure, and blood is driven from the digestive area to the skeletal and cardiac muscles, lungs and brain.

(iv.) There is stimulation of the sweat glands—*i.e.*, the body is cooled, so getting rid of the heat produced by muscular effort.

(v.) The hairs are erected—*i.e.*, the animal assumes a more alarming appearance.

(vi.) There is a mobilisation of sugar from the liver glycogen, *i.e.*, food is provided for the extra muscular work.

These effects are all of the katabolic and emergency type, produced by or causing a utilisation of energy and a breakdown of material. They are brought about by a discharge of nervous impulses over the entire sympathetic outflow from the thoracico-lumbar cord, and this simultaneous discharge is controlled by higher centres. Subsidiary centres presiding over certain activities are found in the medulla (*e.g.*, vasomotor, respiratory, cardiac centres), but the dominating control comes from the paraventricular (or posterior hypothalamic) nuclei (see p. 77) ; some workers have postulated a further control of the paraventricular nuclei by the cerebral cortex itself.

(*b*) **Parasympathetic System.**

The pre-ganglionic fibres emerge from the brain stem in certain cranial nerves, and from the sacral region of the spinal cord ; they have their cell stations in the outlying ganglia which are either close to or actually within the organs supplied.

The effects produced by parasympathetic stimulation are comparatively localised because of the proximity of the cell stations to the ultimate destination of the fibres. The nerves belonging to the cranial outflow produce effects that lead to fortifying against a time of strain or special need and a building up of the necessary body reserves, whereas the sacral outflow is " of internal service to the body in the performance of acts leading immediately to greater comfort " (Cannon). A few examples will make this clear :—

(i.) The pupil contracts, *i.e.*, the retina is shielded.

(ii.) The heart-beat is slowed, *i.e.*, there is a longer rest period for the muscle.

(iii.) The flow of saliva and of gastric juice is increased, and the tone of the alimentary muscle is raised—*i.e.*, conditions are produced that favour digestion of food and its absorption.

(iv.) The bladder and the rectum are emptied, *i.e.*, waste material is removed from the body.

These effects are mostly of the anabolic type, producing a conservation or building up of material; by some writers sleep is regarded as a parasympathetic function. Pilocarpine, by stimulating these nerve endings, produces similar effects, whereas the nerve endings are paralysed by atropine: these drugs do not have such effects on the sympathetic fibres, nor does adrenin stimulate parasympathetic nerve endings; thus the two systems respond differently to the action of drugs.

The central control of parasympathetic activity is probably to be found in connection with the posterior pituitary (see p. 42), whose secretion reaches and stimulates the tuber and supra-optic nuclei. The relation of the posterior pituitary to this system, through these nuclei, is comparable to that obtaining between the adrenal medulla and the sympathetic system, and analogously it has been shown that stimulation of these nuclei increases the outpouring of posterior pituitary secretions.

In connection with the cerebral control of the autonomic system it should be noted that afferent nerve paths to the hypothalamic region are very scarce, particularly from lower centres, and these nuclei are probably also stimulated directly by changes in the blood, which is a primitive mechanism.

Significance of Double Innervation.

Gaskell has shown that where both sympathetic and parasympathetic fibres are distributed to the same structure, the effects of stimulation of the nerves are antagonistic.

	Sympathetic Stimulation.	Parasympathetic Stimulation.
Pupil	Dilated	Constricted
Heart	Accelerated	Slowed
Intestinal peristalsis	Inhibited	Increased
Bladder sphincter	Constricted	Relaxed

Thus in pain, fear, rage and excitement the sympathetic neurones are rapidly stimulated, the effects being increased by consequent and accompanying outpouring of adrenin; simultaneously the parasympathetics are inhibited so that the defensive katabolic activities can be carried on.

Referred Pain.

Afferent autonomic fibres from the viscera carrying impulses from these structures pass into the brain stem and by posterior root fibres into the spinal cord

at levels corresponding to the outflow of the autonomic fibres. The healthy viscera are insensitive to the usual stimuli which produce sensation when applied to the outer body wall, such as heat, touch, prick, etc., but violent pressure changes occurring in a hollow viscus produce a sensation of pain. In the case of stationary organs such as the heart, the pain is sometimes referred to the correct internal region, but in the case of movable organs like the intestine, the sensation is usually referred to some remote but definite area on the surface of the body. This phenomenon is known as " referred pain," and is explained by the fact that the afferent nerve fibres from the viscera (splanchnic or visceral afferents) terminate in the cord in close association with the afferent nerve fibres from certain skin areas (somatic afferents) which enter the cord by the same posterior root. Thus the sensation from the viscus is referred to the peripheral distribution of the cutaneous fibres which is of a definitely segmental arrangement.

By investigating the cutaneous areas of " referred pain " due to impulses from the viscera it is possible to determine the probable course of the afferent autonomic fibres from these organs (see p. 60).

Visceral Reflexes

The close relationship that exists between the autonomic and the central nervous system is well seen in the various types of reflex action that may involve both. There is the typical reflex action in which only somatic paths are involved, and there is the purely visceral reflex in which only autonomic paths are concerned. In addition, a stimulus from the surface of the body may produce a visceral response such as the pupillary reflex resulting from pinching the neck, in which case the afferent path is a somatic one, and the efferent path is autonomic. And again, afferent impulses from the viscera passing by autonomic paths can bring about a response that may involve somatic paths, as in the case of impulses from the lungs or the stomach affecting the contractions of the voluntary muscles of respiration. The purely visceral reflexes are therefore those in which afferent impulses passing by autonomic paths affect the activity of various " involuntary " structures, such as unstriped muscle and glands. The following are some of the more important of these reflexes.

(1) Cardiac Reflexes.

Afferent impulses pass from the heart to the medulla and reflexly affect the rate of the beat and the blood pressure. From the left ventricle and the arch of the aorta impulses pass up in the depressor fibres, and from the carotid sinus in the carotid sinus nerves, which inhibit the vasomotor centre (causing fall of blood pressure) and stimulate the vagus centre (slowing the heart). From the great veins and the right auricle impulses pass up the vagus to depress the vagus centre, and to stimulate the sympathetic accelerator fibres (quickening the heart beat) and the vasomotor centre (causing a rise of blood pressure): a low carotid sinus pressure reflexly produces the same result.

Impulses from other viscera can also reflexly affect the heart. Thus dilatation

of the stomach causes acceleration of the beat: stimulation of afferent nerve endings in the lungs by irritating vapours may reflexly slow the heart rate.

(2) Respiratory Reflexes.

Afferent impulses pass from the lungs in the vagus to the respiratory centre, regulating its rate of response. Reflex respiratory effects are produced by irritation of the nerve endings in the lungs and in the pleura. In addition, a low carotid sinus pressure reflexly stimulates the respiratory centre, while a high pressure depresses it.

(3) Local Reflexes in Abdominal Viscera.

It is probable that a large degree of correlation is effected between the abdominal viscera by local nerve reflexes through the various abdominal nerve plexuses, without necessarily involving paths within the central nervous system itself.

(4) Vascular Reflexes.

Control of the activity of the vasomotor fibres is carried out by a vasomotor centre in the medulla and by subsidiary centres in the lateral horns of the thoracic spinal cord. Both vasoconstrictor and vasodilator centres probably exist, but knowledge of the latter is scanty: the former is situated near the vagus centres. The subsidiary centres usually serve only to relay impulses coming from the vasoconstrictor centre in the medulla, but if the path for these impulses is interrupted, the subsidiary centres, after a short interval, take on the function of reflex centres.

The vasomotor centre in the medulla can react to hormones: thus it is stimulated by a rise of hydrogen-ion concentration or of CO_2 tension in the arterial blood, or by lack of oxygen or by adrenin. The subsidiary centres are much less sensitive to such stimulation than is the centre in the medulla. The more usual means of stimulation is however by afferent nervous impulses, chiefly from the aorta and carotid sinus, those causing a rise of blood pressure being called pressor, and those causing a fall being called depressor. Most of the sensory nerves of the body appear to contain both kinds of fibres. The tonus of the arterial vasoconstrictor centre is normally in a state of reflex inhibition because of the normal blood pressure acting on the nerve endings of the aortic and carotid sinus areas, the tonus of the centre being then maintained by the arterial CO_2 tension.

But changes occurring in the size of blood vessels in one area do not necessarily take place all over the body; a reciprocal relationship is found to hold between the blood supplies of various parts. Thus during digestion there is dilatation of the vessels in the splanchnic region, and constriction of those elsewhere; hence the feeling of cold after a heavy meal. Again, in muscular exercise there is dilatation of the vessels of the working muscles, and compensatory constriction elsewhere. These reflexes ensure that the distribution of the blood in the body will be adapted to the varying needs of the different areas. There may be some form of reciprocal innervation of such areas corresponding to that obtaining for antagonistic skeletal muscles (see p. 112). A purely local vasoconstriction or vasodilatation may even

occur due to an axon reflex, and the balance of the vasomotor response is maintained by the local response of the muscle to the two-fold stimulation or inhibition by hormones and by nervous impulses. This dual control is found not only in the arterioles, but also in the capillaries. These, like the arterioles, are normally in a state of tonic constriction ; section of the nerves causes dilatation, which is only temporary, and the constriction reappears in response to the adrenin or pituitrin hormones in the blood.

The fact that sensory nerve endings are present in the walls of all arteries and veins, being most abundant in the arterioles, suggests that afferent impulses from the vessels themselves probably play an important part in the reflex responses resulting in vasoconstriction of one area and simultaneous vasodilatation in another region.

Visceral Reflexes in Abnormal Conditions

Visceral disease may sometimes result from abnormal autonomic activity, and it may give rise to abnormal visceral afferent impulses.

Under such conditions the afferent nervous impulses may provoke responses also in structures that are not " involuntary." For example, coronary thrombosis gives rise to vomiting and may increase salivation, both visceral responses ; but it also gives rise to reflex spasm of the intercostal muscles, with consequent feeling of intense chest constriction, which is a spinal motor response. Again, afferent impulses from diseased viscera frequently produce strong and lasting contraction of abdominal muscles. The vomiting of pregnancy may be another example of a visceral reflex.

It is also said that abnormal or unusual visceral afferent impulses may produce " depression " in the central nervous system. This may be the explanation of the depressed feelings sometimes associated with constipation, and sometimes preceding menstruation.

Surgery and the Autonomic System

During recent years considerable attention has been paid to the surgery of the autonomic system, and it is of interest to note that, even as the progress of cranial surgery in the early part of this century contributed to our knowledge of the physiology of the brain, so the surgery of the autonomic nervous system at the present time is adding its quota to our still meagre cognisance of the normal physiology and anatomy of this system. Certain physiological premises have been disproved, others confirmed : but anyone surveying the large amount of literature that has been produced recently on this vast subject is bewildered by the variability of the post-operative results. This may largely be accounted for as suggested on p. 62 by the great possibility of variation in ultimate anatomical localisation of these groups of primitive cells during development : consequently it may never be possible to determine exact paths in this system.

The operation of sympathetic ganglionectomy has been carried out in many types of disease, frequently in cases where a knowledge of normal physiology should have prevented the subsequent failures.

According to Telford, Lake and others, the most promising results, however, have been obtained in cases of :—

1. Diseases affecting the Blood Vessels.
   E.g., Raynaud's disease, thrombo-angeitis obliterans, cervical ribs, retinitis pigmentosa, and sometimes anterior polio-myelitis.
2. Diseases affecting Smooth Muscle.
   E.g., Hirschprung's disease, and some cases of " rheumatoid arthritis " (with vasospastic phenomena).
3. Profuse Sweating.
4. Severe Visceral Pain.
   E.g., carcinoma of bladder.

Certain puzzling facts, considered in the light of our previous physiological and anatomical knowledge, have emerged as the result of these operations, which must however still be regarded largely as experimental.

(*a*) After removal of the stellate ganglion, Hörner's syndrome necessarily follows, *i.e.*, enophthalmos, ptosis, narrowing of the palpebral fissure, and absence of sweating on the affected side. In young persons this appears to be only transitory, varying in duration from three months to several years. In the older subject the syndrome is slower in disappearing, and may persist indefinitely, though the signs tend to improve in the course of a few years. There is apparently no known explanation for this.

(*b*) In cases of vascular occlusion the immediate effects of operation are very striking: vaso-dilatation is marked, a rise of surface temperature of 8–10° occurs, and pain is completely abolished. Unfortunately these good results are not usually maintained, though both observers and patients agree that with the recurrence of symptoms, these are never so severe, and consequently operation appears to be justifiable, although too optimistic a prognosis should not be given.

Lewis and his co-workers maintain that in Raynaud's disease, for example, sympathectomy will fail to cure symptoms, however wide the excision of nerves, because the real cause of the spasm is peripheral and not central, *i.e.*, a local fault of the vessels themselves. He postulates that there are structural changes in the arteries such as intimal thickening, or else a more powerful response of these vessels to such a local stimulus as cold.

Simpson, Brown and Adson, however, maintain that the disease is primarily neurogenic, and that the local changes in the vessel walls are secondary. Leriche and Fontaine consider that the presence of sensory nerve fibres in the vessels is proved, and they postulate the existence of certain vascular reflexes. The more important of these are :—

1. Peripheral vascular reflexes having their centre in the intramural plexuses.
2. Vascular changes through axon reflexes.

3. Intrasympathetic reflexes having their centre in the ganglia of the sympathetic trunk.
4. Medullary vascular reflexes.
5. Cerebral vascular reflexes.

For these reasons, these workers advocate periarterial sympathectomy in preference to ganglionectomy for the relief of uncomplicated cases of vasospasm.

Furthermore, in any attempt to account for the variation in the results of operation, it should be remembered that there is, as yet, no conclusive knowledge of the exact distribution of the arterial branches of the peripheral nerves in the extremities. There is, apparently, a significant difference in the anatomical arrangement of the proximal sympathetic supply to the blood vessels of the upper and lower limbs (Sheehan).

Todd, Telford and Stopford among others, in their survey of cases of vascular occlusion due to cervical ribs, consider that the sympathetic fibres destined to innervate the peripheral vessels of the arm enter *viâ* the lowest cords of the brachial plexus, while the subclavian and axillary arteries are innervated from a different source. Stopford considers that the proximal supply comes from the lower part of the cervical portion of the sympathetic ganglionated cord, and accompanies the subclavian and axillary arteries to the arm as a perivascular plexus, while in the lower limb there is an extension of the aortic sympathetic plexus along the common iliac, external iliac, and femoral arteries; the more distal supply in each limb (consisting of fine filaments arising from neighbouring peripheral nerves) reaches the vessels at intervals. Woollard confirms this, and emphasises the fact that there is a change in the method of nerve distribution at the junction of the axillary and brachial arteries in the arm, and at the bifurcation of the femoral artery in the lower limb.

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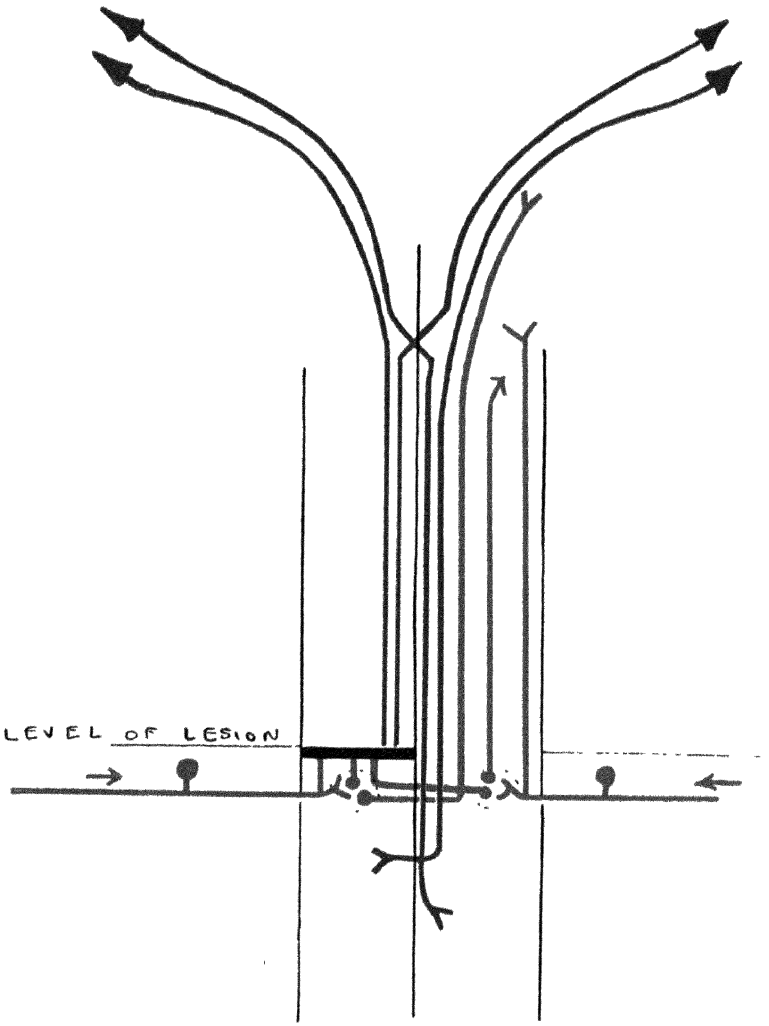

DIAGRAM 64 —Diagram illustrating Functional Effects of Hemisection of Cord.

CHAPTER XIII

NOTES ON CERTAIN PATHOLOGICAL CONDITIONS

In this chapter some account is given of certain pathological conditions which are considered to be of importance in the study of the physiology of the nervous system. They are as follows :—

1. Hemisection of the Cord.
2. Complete Section of the Cord.
3. Aphasia.
4. Nystagmus.

1. Hemisection of the Cord.

Hemisection, or a unilateral transverse lesion, of the cord by trauma or disease results in morbid phenomena, to which the name of " Brown-Sequard's symptom complex " has been given. Obviously it is relatively rare to find a typical classical " Brown-Sequard condition," for disease usually does not cause a complete unilateral division ; more frequently the lesion is incomplete or else extends in addition partly over on to the opposite side of the cord. The classical description will be given, but the student must bear in mind that it will have to be modified in most cases. The reader is referred to Part I., Chapter II., for the effects of nerve section.

The sequelæ of a hemisection occur in those parts of the body distal to the site of the lesion, and they may be divided into—

(*a*) Changes on the same side as the lesion.
(*b*) Changes on the side opposite to the lesion.

(See Diagram 64.)

(*a*) On the Same Side.

(1) *Motor paralysis* of the same side occurs below the level of the lesion. This paralysis is " spastic " in nature, because there is interference with the cortico-spinal path.

(2) *Vasomotor paralysis* of the same side occurs, the skin in the early stages being reddened and warm, but later a chronic condition of cold and cyanosis supervenes. This is due to interruption of the vasoconstrictor fibres of the lateral column of the same side.

(3) *Disturbance of deep sensibility* occurs distal to and on the same side as the lesion ; consequently, even when motility is restored to these parts, ataxia (incoordinated gait) is a prominent feature, and is due to interference with the posterior columns and the spinocerebellar tracts.

(4) *Superficial hyperæsthesia* is found, and is not readily explained, but may

be due to the fact that, as tactile impressions are partly crossed and partly uncrossed at any given level, only the crossed fibres can convey impressions upwards from the same side as the lesion. This means that extra work is thrown on these fibres, and the cells of the dorsal horn pass on " summated " stimuli, so that until adaptation of the organism to the new condition has occurred painful impressions are received. It should be noted that this phenomenon is transitory.

(5) *Flaccid paralysis* occurs in groups of muscles corresponding with the half-segment affected, due to a lower motor neurone type of paralysis.

(6) *Complete anæsthesia* of all forms is present for the affected half-segment, due to a lesion of the lowest sensory neurone.

There is usually a zone of cutaneous hyperæsthesia in the skin area corresponding to the peripheral distribution of the posterior nerve root entering the cord just above the level of the lesion.

(*b*) On the Opposite Side.

Superficial anæsthesia occurs on the side opposite to the lesion, so that there is loss of sensation of pain, heat and cold, due to interference with the spinothalamic and spinotectal tracts after the decussation of their constituents.

The reader is reminded that if the lesion is below the upper thoracic region all the fibres of the direct pyramidal tract will have crossed, so that those injured will be supplying the same side of the body as the lesion. Also, with a lesion in the thoracic region the intercostal muscles of the same side are paralysed, and with an upper cervical lesion the same side of the diaphragm is paralysed.

There are in addition certain *reflex changes* which may be summarised.

(1) At first there is loss of muscle tone at the level of the lesion, due to destruction of the spinal arc. After the stage of shock is over tone returns to the muscles below the level of the lesion, and consequently reflex response reappears.

(2) When the lesion is above the lumbar region, defæcation, micturition and parturition still occur as usual, as central control is bilaterally represented.

(3) The vascular dilatation and dryness of the skin on the side of the lesion are most marked when the hemisection is in the thoracic region, because of interference with the path from the medulla to the accessory vasomotor centres in the cord.

(4) The knee jerk is increased on the side of the lesion, due to the cutting off of controlling impulses from the higher centres.

(5) The plantar reflex becomes " extensor " on the side of the lesion, due again to the general law of " release of function in the nervous system," by which when a higher centre is cut off lower centres are released and exhibit their independent and more primitive activities.

2. Complete Section of the Cord.

This condition may occur as a result of trauma or of disease, and investigation has been very completely undertaken by Head and by Riddoch in connection with war injuries.

In civil life section of the cord is usually slowly progressive, and then the

initial stage of shock does not occur. In cases of acute trans-section there is always an initial stage of shock which varies in its duration, sometimes lasting up to sixteen days or more, and which exists only in the part of the body distal to the lesion. The intensity varies with the position of the organism in the animal scale, and is therefore most extreme in man. After a varying period, if the patient survives, reflex action begins to return. The level of the lesion is responsible for a varied series of signs, and these may be briefly summarised :—

(*a*) In the *upper cervical* region a simultaneous paralysis and anæsthesia affect the four extremities and the trunk.

(*b*) In the *dorsal* region the lower extremities and the lower half of the trunk are affected.

(*c*) In the *lumbar* region only the lower limbs are involved, producing a paraplegia.

At whatever level, however, the lesion occurs, there is complete abolition of sensation and of movement below that level.

The loss of sensory function is complete, as all the ascending tracts are interrupted, while there is an absolute paralysis due to interference with the pyramidal tracts and also of every link between the brain and the spinal motor centres.

MOTOR CHANGES.

(1) In complete division of the cord in its upper region, during the early stages there is complete muscular atony and abolition of reflexes in the paralysed regions. This is expressed in " Bastian's law," and there are many theories to account for its occurrence, none of which appear to be adequate.

(2) Muscles of the bladder and rectum are involved, so that retention of fæces and urine occurs. When, however, the distension of the bladder reaches a certain point, overflow incontinence ensues. If, as rarely happens, the patient survives, reflex micturition and defæcation become re-established.

(3) There is vascular dilatation, due to vasomotor paralysis in the paralysed region, followed later by cold and cyanosis due to chronic vascular relaxation. Similarly, the marked engorgement of the corpora cavernosa is due to vasomotor disturbance.

(4) General flexion spasms occur as part of the " mass reflex."

(5) Erection, micturition and profuse sweating (known as mass reflexes) may be elicited by pinching the skin anywhere below the lesion, except in a narrow band corresponding to the lesion itself where the spinal arc is interrupted. The sweat fibres to the head and neck arise from the first and second thoracic segments, so that with a lesion at the level of the first thoracic segment the whole body would sweat when the mass reflex was elicited.

SENSORY CHANGES.

(1) Complete loss of all sensation below the level of the lesion.

(2) Temporary hyperæsthesia in an area above the anæsthetic zone and sometimes a corresponding area of muscular tonic spasm from heightened reflex irritability.

3. Aphasia.

By this term is meant " the loss of intelligent speech," the word " speech " being taken to include the appreciation and the production of both the written and the spoken word. True aphasia should be distinguished from the condition known as dysarthria: the latter is due to a pure motor breakdown, either local or central, which causes a difficulty in the actual motor performance, and which may occur in the course of many diseases.

Speech is the most highly evolved and the most complicated function of the brain, and any analysis of the mechanism involved must of necessity be somewhat crude. The many varying views on the subject will be found set forth in Head's monograph on aphasia, but a working hypothesis can be deduced from a survey of certain fundamental facts.

It is essential to regard the mechanism of speech as a whole. There seems to be no doubt that certain regions of the brain are closely connected with definite elements of the speech mechanism, although interference with any part of the mechanism may be due to a lesion on the connecting paths rather than to a definitely localised cortical condition. There are five areas of the brain that appear to be more particularly concerned with speech (see Diagram 65):—

A. *Post-Rolandic Area*, concerned with appreciation of general sensation.

B. *Spoken Speech.*

(i.) Sensory aspect: auditory-psychic area, concerned with the interpretation of afferent impulses reaching the adjacent auditory sensory area.

(ii.) Motor aspect: glossokinæsthetic area, concerned with the production of spoken speech through the adjacent labio-glossomotor area.

C. *Written Speech.*

(i.) Sensory aspect: visuopsychic area, concerned with the interpretation of afferent impulses reaching the adjacent visuosensory area.

(ii.) Motor aspect: cheirokinæsthetic area, concerned with the production of written speech through the adjacent cheiromotor area.

Although these regions are especially concerned, it is probable that the simplest act of " speech " involves the activity of all parts of the cerebral cortex, and if one element of the mechanism is interfered with the whole function of speech becomes abnormal. Interference may occur with a cortical area, but more frequently a lesion involves the association paths between the areas or the afferent or efferent paths connecting with the areas, and consequently the resulting functional disturbance becomes complex.

To take a simple example, a lesion involving the cheirokinæsthetic area only, or isolating this area, leads to inability to write what is desired. The individual can write because the motor area is not involved, but he is unable to call up memories of previous similar movements and so cannot write what he wishes to. Similarly, a lesion of only the glossokinæsthetic area renders an individual unable

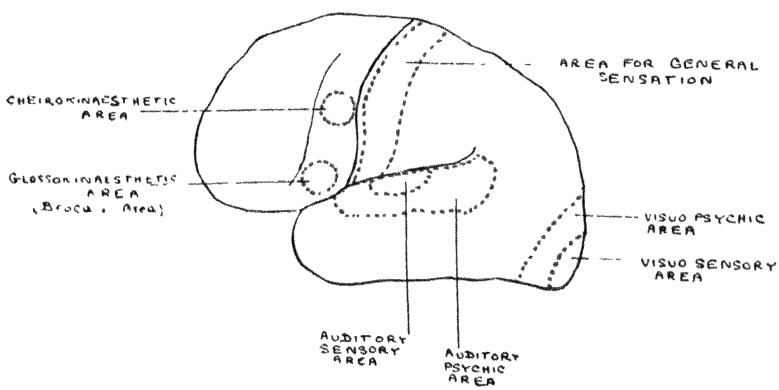

DIAGRAM 65.—Diagram to illustrate Position of Centres chiefly concerned in Mechanism of Speech.

to say what he wants to, although he can speak; but he hears himself say the wrong thing and knows that it is wrong. This illustrates the way in which motor speech is kept at a high level of accuracy by correction through sensory paths. Again, a lesion isolating the visuopsychic area leads to inability to understand what is seen : a man cannot read, although he can see, because he cannot compare his visual impressions with memories in the visuopsychic area, and so he does not interpret what he sees. Similarly, a lesion involving the auditory-psychic region produces inability to understand spoken speech, although the man can hear.

The intimate connection between the various parts of the cortex in respect of this function of speech is shown in the case of a man who becomes blind, *i.e.*, his visuosensory area is no longer being stimulated. The visuopsychic area, with its stored memories, can still, however, be aroused to activity by sensory paths other than the usual visual one ; for example, the feel or the sound of a cat will still call up an image of the appearance of the animal and of other visual memories therewith connected.

Speech functions which are more recently acquired tend to drop out before those learnt in early life ; similarly, a man who is a good linguist loses the power of speaking the last-learnt foreign language rather than one he acquired early in his career. A child learns speech in its elements, whether spoken or written, but when once this faculty is developed we receive speech in a " running pattern " of which the individual elements are disregarded. The breakdown of some association path may then lead to inability to produce a particular word of command, although that word can be used in the run of a pattern. This is exemplified by the patient who, after many attempts to produce the word " No," said : " I am very sorry, sir, but I can't say ' No,' sir."

Head divides aphasia into four types :—

(*a*) *Verbal.*—There is defective word formation, either written or spoken, or both ; this is usually associated with a lesion in the posterior end of the inferior frontal convolution.

(*b*) *Nominal.*—There is defective naming of letters, words, or objects ; this is found associated with a lesion of the angular gyrus.

(*c*) *Syntactical or Jargon.*— Speech is voluble and rapid, but entirely senseless, because there is loss of correction by other sensory paths ; this occurs with lesions of the superior and middle temporal convolutions.

(*d*) *Semantic.*—There is inability to retain a complete conception in the mind ; this is associated with a lesion of the supramarginal gyrus.

The following terms are used in connection with the subject of aphasia :—

Alexia. Word-blindness, inability to appreciate the written word.

Anarthria. Impairment of the motor powers of expression (Head's verbal aphasia).

Apraxia. Inability to do as desired.

Agnosia. Inability to appreciate meaning.

Agraphia. Inability to write.

4. Nystagmus.

Normally the eye is kept at rest in the central position by the postural mechanism ; this produces a steady gaze.

In abnormal conditions, however, deviation of 10° to 30° away from the central point occurs, so that on looking fixedly at an object elsewhere in the visual field jerking movements are produced, the condition being known as nystagmus. This occurs whenever there is any lesion affecting the maintenance of postural mechanism of eye movements, and is the endeavour of the eyes to compensate for the lesion (see p. 111).

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APPENDIX

HISTOLOGICAL METHODS

THE following simple methods of investigating nervous structures give reliable results. Further details can be found under the given references.

A. NERVE CELLS.

1. *Film Preparation.*

Spread a thin film evenly ; dry in air.
Fix in 80 per cent. alcohol for fifteen minutes.
Stain in Löffler's methylene blue (or 1% aqueous toluidine blue) for ten to twenty minutes.
Wash in methylated spirit.
Differentiate if necessary in 75 per cent. alcohol, or in acid alcohol (HCl, 1 c.c. ; alcohol, 70 c.c. ; water, 30 c.c.).
Dehydrate in absolute alcohol.
Mount in Gurr's neutral mounting medium or cedar-wood oil.
(N.B.—Nissl granules dark blue, nuclei paler blue.)

(Hall and Herxheimer, p. 221.)

2. *In Tissues.*

(*a*) Picrocarmine method.

Fix in 10 per cent. formol for forty-eight hours.
Transfer to Müller's solution for any period up to six months.

(Potassium bichromate	2·5 gm.
Sodium sulphate	1 gm.
Water	100 c.c.)

Embed and section in usual way.
Stain from water with Stöhr's (or Ranvier's) picrocarmine for at least twenty-four hours.
Wash in methylated spirit (not water).
Dehydrate and mount in usual way.

(Stirling, p. 66.)

(*b*) Nissl method.

Fix in 10 per cent. formol saline (neutral) for two to three days.
Wash, embed slowly in paraffin and section in usual way, cutting at least 10 μ thick.
Stain from distilled water with 1 per cent. aqueous toluidine blue for twenty minutes at 50° C.
Wash in water.
Differentiate in absolute alcohol, controlling under the microscope.
Clear in xylol.
Mount in thick cedar-wood oil.

(Anderson, p. 42.)

B. Myelinated Nerve Fibres.

1. *Osmic Acid Method* (Robertson-Heller).

Fix in 10 per cent. formol (or in Weigert's gliabeize) for eight to ten days.
Wash, embed, and section in usual way.
Stain from water in 1 per cent. osmic acid for at least thirty minutes in the dark.
Transfer to 5 per cent. pyrogallic acid, thirty minutes.
Differentiate in 0·25 per cent. $K_2Mn_2O_8$, thirty + minutes.
Wash, dehydrate, and mount as usual.

(Hall and Herxheimer, p. 183.)
(Bolles Lee, pp. 595, 627.)

2. *Hæmatoxylin Method* (Weigert-Pal).

Fix thin pieces in 10 per cent. formalin for one week
Transfer to Müller's fluid for one week.
Mordant for one week in—

Potassium bichromate	5 gm.
Fluorchrome	2·5 gm.
Water	100 c.c.

boiled and filtered.

Take through spirits, dehydrate, clear and embed as usual.
Sections at least 30 μ thick.
Mordant from water for thirty minutes in—

Neutral copper acetate	5 gm.
Fluorchrome	2·5 gm.
Water	100 c.c.

boiled and 5 c.c. acetic acid 36 per cent. added.

Transfer to Kulschitsky's hæmatoxylin for twenty-four to forty-eight hours in incubator at 37° C.

(10 per cent. hæmatoxylin in absolute alcohol, ripened for some weeks . . . . . 10 c.c.
Distilled water . . . . . 90 c.c.
Acetic acid glacial . . . . . 2 c.c.)

Transfer to Müller's fluid for ten minutes.
Wash in tap water very thoroughly.
Differentiate in 0·25 per cent. $K_2Mn_2O_8$, thirty seconds.
Wash in water.
Transfer to Pal's solution

(Oxalic acid . . . . . 0·5 gm.
Potassium sulphite . . . . . 0·5 gm.
Water . . . . . 100 c.c.)

for some seconds; wash in water.

If necessary, repeat treatment with $K_2Mn_2O_8$ and Pal's solution until "grey" substance is colourless and "white" substance is dark blue. Wash in distilled water for one hour: transfer to tap water for several hours. Dehydrate and mount as usual.

(Hall and Herxheimer, pp. 178–180.)

C. Axis Cylinders of all Nerve Fibres.

Some one of the modifications of the Bielschowsky silver methods should be used. The technique must be followed exactly. Details will be found in Bolles Lee, pp. 573–582. Da Fano's modifications are the best.

Ranson's method also gives good results for axis cylinders and for nerve endings.

Fix for forty-eight hours in—

Absolute alcohol . . . . . 99 c.c.
Concentrated ammonia . . . . . 1 c.c.

[Fixation in 10 per cent. formalin can be used if followed by washing in running tap-water for about twelve hours.]

Rinse in distilled water.
Place in pyridine for at least twenty-four hours.
Wash in repeated changes of distilled water for twenty-four hours.
Place in 2 per cent. $AgNO_3$ in the dark at 35° C for three days.
Rinse in distilled water.
Reduce for several hours (not less than six) in—

Pyrogallol . . . . . 4 gm.
5 per cent. formol in distilled water . . 100 c.c.

Wash in water.
Dehydrate, clear, and embed in the usual way.
Cut sections about 10 μ thick. Axis cylinders appear black.

(Carleton, p. 275.)

D. NEUROGLIA.

1. *Cajal's Method.*

Fix immediately after death in formol bromide for two to eight days, not longer.

(Ammonium bromide . . . . . 2 gm.
Formalin . . . . . 14 c.c.
Distilled water . . . . . 86 c.c.)

Cut frozen sections 20 μ and transfer to formol bromide.
Wash in distilled water.
Transfer to gold-sublimate for four to eight hours in the dark at 22° C.

(A. Gold chloride, 1 per cent. . . . . 6 c.c.
B. Mercuric chloride. 0·3 gm. in 40 c.c. dist. water.
Mix immediately before use.)

(Not more than 7 sections to 30 c.c. of stain.)

When dark purple, wash in distilled water.
Transfer to 5 per cent. sodium hyposulphite containing 10 per cent. absolute alcohol for ten minutes.
Wash in distilled water.
Transfer to a slide ; blot ; dehydrate, clear, and mount in Canada balsam.

(Anderson, p. 87.)

2. *Mallory's Method.*

Staining with phosphotungstic acid hæmatoxylin.

(Anderson, p. 48.)

E. MICROGLIA.

Hortega's Method (Cone and Penfield's modification).

Fix fresh material in 10 per cent. formalin, and cut frozen sections 20 μ thick
Place sections in weak ammonia (in distilled water) overnight.
Transfer to 5 per cent. hydrobromic acid at 37° C. for one hour.
Wash in three changes of water.
Place in 5 per cent. sodium carbonate for one to five hours.
Transfer without washing to—

10 per cent. silver nitrate . . . . . 5 c.c.
5 per cent. sodium carbonate . . . . 20 c.c.
Ammonia to dissolve precipitate.
Distilled water to . . . . . 75 c.c.

for five minutes or longer until light brown.

Place in 1 per cent. formalin, and agitate.
Wash in distilled water.
Tone in 0·2 per cent. gold chloride till grey.
Fix in 5 per cent. sodium hyposulphite.
Wash, dehydrate, clear and mount.

(Anderson, p. 90.)

F. Nerve Endings.

1. *Gold Chloride Method* (Ranvier's method—Fischer's modification).

Place small pieces of fresh tissue in 25 per cent. formic acid, ten to fifteen minutes.
Absorb fluid from pieces by a clean duster.
Transfer to 1 per cent. $AuCl_3$ twenty minutes in dark.
Absorb fluid from pieces by a clean duster.
Place in 25 per cent. formic acid in dark, twenty-four hours.
Absorb fluid from pieces by a clean duster.
Transfer to glycerine for examination.
If not sufficiently reduced, add formic acid to the glycerine.
Mount in pure glycerine, and ring coverslip with cement.
(Nerve endings dark purple.)

(Stirling, p. 78.)

2. *Vital Methylene Blue Method.*

Remove tissue with as little injury as possible and spread on slide.
Treat with 0·05 per cent. methylene blue in isotonic saline (0·6 per cent. NaCl for frog, 0·85 per cent. NaCl for mammal) for twenty minutes, covered with watch-glass lined with moist filter paper.
Drain off stain ; examine in isotonic saline.
Various methods are available for fixation of the stain. (See Carleton, p. 277.)
(Nerve endings dark blue, not permanent.)
The dye can be used also by injection.

(Langley, pp. 125 and 321.)

G. Degenerating Nerve Fibres (Marchi's method, Busch's modification).

Fix in 10 per cent. formalin at least one week.
Wash pieces not more than 2 mm. thick for several hours.
Transfer to Busch's fluid for seven days in daylight.

(1·5 per cent. potassium iodate . . . . . 2 parts
1 per cent. osmic acid . . . . . 1 part.)

Wash in running water for three hours.
Transfer to chromo-hypochlorite for seven days at 37° C.

(5 per cent. potassium bichromate . . . 15 c.c.
2 per cent. calcium hypochlorite . . . . 5 c.c.)

Wash in running water for twenty-four hours.
Transfer to methylated spirit for one hour, then absolute alcohol one hour, then equal parts alcohol and ether two to three hours.
Embed in celloidin as usual. Cut sections 20–30 μ thick.
Mount from 90 per cent. alcohol in Gurr's neutral mounting medium.

(Anderson, p. 68.)

NOTES

1. When dealing with blocks of tissue that are brittle or that will give large sections, it is better to embed in celloidin rather than in wax, as the celloidin prevents the tissues from breaking in subsequent manipulations, and also allows of the cutting of thick sections. (See Anderson.)

2. *Weigert-Pal Method for Myelin.*—The principle of this method is that all the structures are intensely stained with hæmatoxylin after double mordanting. The $K_2Mn_2O_8$ oxidises the hæmatoxylin to a colourless substance, and itself gives rise to MnO_2; the MnO_2 is then converted into $MnSo_4$, which is colourless and soluble, and this is then washed away. This process will naturally take place most readily in the open grey matter, and should be interrupted when this appears light; the dense myelin keeps the stain more tenaciously.

3. *Marchi's Method for Degenerating Myelin.*—Osmic acid blackens normal myelin because of the presence of oleic acid, which reduces it to the black OsO_2. Treatment with the potassium iodate oxidises the oleic acid, and the myelin does not blacken on subsequent treatment with osmic acid. Degenerating myelin contains large quantities of very unsaturated fatty acids greatly in excess of what is oxidised by the treatment with potassium iodate; in this case, therefore, the degenerating fibres still blacken on treatment with osmic acid. The reaction can be obtained about forty hours after the lesion, increases in intensity up to fourteen days, and after about forty-four days is usually absent owing to the removal of the broken-down material.

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INDEX

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