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AN INTRODUCTION TO THE THEORY OF PERCEPTION

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AN INTRODUCTION
TO
THE THEORY OF PERCEPTION

by

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PREFACE

An exhaustive treatise on perception would cover a large part of the whole field of psychology. This work makes no pretension to fill such a rôle, but is a mere attempt to gather together some prolegomena to such a treatise and at the same time to formulate a working hypothesis

For one who is convinced that progress in psychology depends upon the security of the biological foundations upon which it rests, and that these alone afford the crucial criteria of the truth of data derived from introspection and other methods of approach little amenable directly to scientific discipline, perception is of unique importance It is the bridge which spans the gap—if indeed it be more than an illusory gap—between nerve processes and consciousness

Viewed from the human standpoint, perception appears to be the result of the correlation and integration of many sensory factors of diverse modality and quality Viewed, however, from the phylogenetic standpoint, lack of differentiation of the receptive mechanisms in lower species points to the inevitable conclusion that such conscious responses as these animals are capable of are equally undifferentiated, and consist of "perceptions brutes" which we can only conceive of as "blooming, buzzing confusions," to use the picturesque phraseology of William James Yet it is certain that these relatively undifferentiated recepts give rise to responses which are of vital importance for the preservation of the individual and the species With the advance of differentiation certain modalities assume a preponderant rôle in certain species, as is shown by the lateral lines of fishes and the predominance of the olfactory apparatus in many lower animals The primates have attained their supremacy through the elaboration and predominance of their visual functions

The epoch-making researches of Sherrington on reflexes and their integration reveal principles which throw a flood of light on instinctive and other reactions, and are in many cases directly applicable to integrations of a higher order than those actually observed Lloyd Morgan's researches have demonstrated their profound significance in the physiological and psychological explanation of instinctive behaviour in animals. Head's researches on cutaneous sensations in man have elicited evidence of a dual mechanism at work—a more

primitive, protopathic mechanism upon which a more highly differentiated epicritic mechanism has been superposed: and Rivers has shown that the same principle is applicable to more complex integrations, instincts, subserved by lower neural centres, of which the optic thalamus is of most importance, being essentially "protopathic," whilst intelligent control of lower functions is essentially "epicritic."

Doubt has been cast upon the interpretation of Head's fundamental experiment on the regeneration of cutaneous nerves; but, although this is the basis of Head's theory, I do not think that the criticisms invalidate the theory of a dual mechanism, which rests upon a far wider evidential basis. In the present thesis I have modified the theory to the extent of hypothecating a primitive *dyscritic* mechanism, upon which an *epicritic* is superposed. At a still higher level I have hypothecated a *syncritic* mechanism, subserved by the cortex cerebri, having the function of integrating epicritic phenomena. When dealing with Head's researches I have retained the term "protopathic," as identically representing his views, with which I do not entirely agree. In the chapter on "The Evidence from Comparative Anatomy," I have given in some detail the anatomical evidence in favour of a dyscritic mechanism. For this I am much indebted to the writings of Prof. Ariëns Kappers, to whom I gratefully acknowledge the loan of illustrative figures.

Since perception is a phenomenon of consciousness, every inference must be derived from human experience: and since vision is the preponderant modality in the primates and has undergone the highest differentiation, it may be expected to afford specially valuable data. For that reason, and because it has been my own special study for many years, most of this thesis is devoted to that aspect of the subject, and I have incorporated in it the Bowman Lecture delivered before a Conference of English-speaking Ophthalmologists in 1925[1].

I am hopeful that others, better qualified than I, will elaborate the evidence derived from other "special senses" on similar lines, for I am convinced that psychology, *as a science*, can only be developed upon a sound biological basis. To that end the study of the "special senses," so much neglected in England, by students well equipped with a biological training, is of paramount importance.

J. H. P.

October 1926

[1] *Trans. Ophthalm. Soc.* XLV, 14, 1925.

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CHAPTER I

THE GENESIS OF PERCEPTION

THE status of perception in the scheme of animal existence—its origin and rôle—might be discussed from many points of view. As a factor in the conscious life of the animal, it is pre-eminently a psychological problem. As a factor in the behaviour of the animal, it is a physiological, neurological, biological problem, or at any rate has such concomitants. Whether it be studied and analysed purely and exclusively as a problem of psychology, or whether its biological concomitants—to use a non-committal term—be also studied and analysed, may be either a simple matter of method or may depend upon the philosophical creed of the investigator.

It is, therefore, desirable that I should state my creed briefly at the outset; premising, however, that the word 'creed' thus used carries no implication of dogma or infallibility, but implies merely a carefully selected assemblage of correlated hypotheses, endowed for the end in view with the status of postulates. It is chosen because it appears to me to be the most fruitful from the scientific point of view for this and other such problems. Its hypotheses are limited to the workable minimum, and its philosophical importance will depend solely upon whether it proves useful or not.

It is essentially the creed of Emergent Evolution as set forth by Lloyd Morgan[1], stripped of metaphysical implications, which, whatever their philosophical value, appear to me to be redundant to the more limited scientific universe of discourse.

"We live in a world in which there seems to be an orderly sequence of events.... But the orderly sequence, historically viewed, appears to present, from time to time, something genuinely new Under what I call here emergent evolution stress is laid on this incoming of the new. Salient examples are afforded in the advent of life, in the advent of mind, and in the advent of reflective thought. But in the physical world emergence is no less exemplified in the advent of each new kind of atom, and of each new kind of molecule. It is beyond the wit of man to number the instances of emergence. But if nothing new emerge—if there be only regrouping of pre-existing events *and nothing more*—then there is no emergent evolution."[2]

On the physical plane, when elements combine to form a new compound, some of the properties of which are quite different from those of either component; when a radio-active element changes into

[1] *Emergent Evolution*, London, 1923.
[2] *Ibid.* pp. 1–2.

the next product of the disintegration series; when crystallization occurs—in all such cases there is emergent evolution on the physical plane. Something new has occurred, which could not have been foretold, because it is not interpretable in terms of resultant effects calculable by algebraical summation. It is not to be attributed, in the scientific universe of discourse, to some "alien influx into nature" —force, entelechy, élan, God—but is to be accepted "with natural piety," as Alexander and Lloyd Morgan say, or as a legitimate hypothetical datum, as I should prefer to express it.

At a certain stage in evolution life emerged; at a later stage consciousness emerged. It may be that there is no life without consciousness; but, if so, consciousness at the lowest level must be very primitive

Lloyd Morgan, in 1896, distinguished two phases of organic development,

"first, that in which consciousness is either absent or inoperative; and secondly, that in which consciousness is a co-operating factor. The first may be termed the merely organic phase; the second, the conscious-organic phase. The latter may again be sub-divided into two phases. first, that in which mental evolution is subordinate to organic evolution, and secondly, that in which mental evolution is predominant."[1]

The distinguishing feature of the conscious-organic phase is the presence of "effective consciousness," *i.e.* consciousness which enables an animal to guide its actions in the light of previous experience, and the criterion of its presence is the exercise of choice.

"Whatever the physiological conditions of the process may be, it seems clear that consciousness, as choosing and controlling, stands in a sense outside that upon which it exercises control through its power of choice And, thus, on passing from the merely organic to the conscious-organic phase of evolution, we have to consider the development of an *imperium in imperio* "[2]

The further argument is based on conclusions drawn from the control of the involuntary and automatic activities of man by the *cortex cerebri*. But, in dealing with origins, we just either regard these functions of choice and control as absent in the amœba, or present only in the primitive form which we should expect associated with the primitive structure. If they are totally absent, the organism is the mere sport of circumstance, its sentience is a matter of interest to itself alone and is of unknown significance as a psychological germ of evolutionary value. This appears to correspond to the anoëtic sentience of Stout. There is evidence, however, that the activities of

[1] Lloyd Morgan, *Habit and Instinct*, p. 262, London, 1896.
[2] *Ibid.* p. 265.

Protozoa do exhibit traces of choice which fundamentally differs in type from the selective properties shown by a photographic plate or other inorganic material. In fact, it is scarcely possible to accept any other view in the light of the very exhaustive observations and experiments of H. S. Jennings[1].

There are many levels of emergent evolution, but these can be grouped, if only for methodological purposes, into three chief levels: *A*, the physical level; *B*, the level of life; and *C*, the level of consciousness. Events at each higher level involve and depend upon concurrent events at lower levels. Physico-chemical inter-relations govern events at the level of matter *A*. Physiological inter-relations govern events at the level of life *B*, but physiological events involve and depend upon physico-chemical events. Similarly, conscious events at level *C* (mind) involve and depend upon physiological events, themselves involving and dependent upon physico-chemical events. "No *C* without *B*, and no *B* without *A*. No mind without life, and no life without 'a physical basis.'"[2]

It would also appear that we must accept "with natural piety" that, when some new kind of relatedness is supervenient, the course of events at a lower level *may* be altered.

"Events of the kind we labelled *C involve* events of the kind we labelled *B*; and these in turn involve *A*-events. But in any given concrete case the specific way in which the *A*-events run their course, then and there, *depends on* the specific presence of some phase of vital *B*-relatedness; and similarly the specific way in which these *B*-events run their course—in behaviour for example—depends on such conscious *C*-relatedness as may be present"[3];

i.e. consciousness is "effective." So much for involvement (or, as Lloyd Morgan more ambiguously calls it, "involution"), dependence, and relatedness.

Similarly, there are levels of emergent evolution within the conscious level. Physical stimuli at level *A* arouse physiological responses at level *B*, by the effective inter-relatedness of which consciousness emerges (*C*). The dawn of consciousness is probably a sentiency with greater affective than cognitive tone—of which more in Chapter II. It is doubtful if a pure sensation is ever experienced in consciousness. Sensory presentations, as we experience them, invariably evolve perception, however naïve it may be, at the start: but there is no perception without sensory presentation. Similarly, there is no

[1] *Behaviour of the Lower Organisms*, Columbia University, Biological Series, No. 10, New York, 1906.

[2] Lloyd Morgan, *Emergent Evolution*, p. 15.

[3] *Ibid.* p. 16.

reflection, contemplative thought, or conception without perception. "At the level of contemplative thought, *how* perception runs its course depends on the guidance of reflective consciousness, so far as co-existent, and *how* what is given in sensory presentation takes form depends on the guidance of perception, if that level have been reached."[1]

Alexander's[2] lowest level is a Space—Time relatedness, independent of physical events. This is a metaphysical conjecture. It suffices for us, with Lloyd Morgan, to assume "that intrinsic to every minimal physical event, and extrinsic as between such events, there is (*a*) spatial here-there relatedness, and that there is (*b*) temporal now-then relatedness—always co-related as inseparably (*ab*)"[3]

Similarly, both Alexander and Lloyd Morgan conjecture that above consciousness there emerges deity, and that the nisus of all emergent evolution is towards deity. Over all and pervading all is Deity. Within the strict bounds of the *scientific* universe of discourse it does not appear to me to be necessary to accept this conjecture, even "under acknowledgment."

The chief value of emergent evolution is its function as a scientific method. Like agnosticism, it clearly segregates and labels what is known and what is unknown. It by no means follows that all emergents are unknowable, indeed, as knowledge increases, more and more emergents become known. But they are only knowable, as it were, from above. When sodium chloride dissolves in water something happens which could not have been foretold—a solution has emerged. Yet, with increased knowledge, we have learnt a great deal about solutions, and we can foretell much of what will happen when solution occurs again. Complete knowledge of an event seems to be attainable only by backstroke from a higher level, and this rule appears to hold good for every succeeding level. We can imagine a demon at each level who would know everything about every level below his own and nothing about higher levels except what was dependent directly upon the known processes of his own and lower levels. Above the top we can imagine a super-demon who would know everything.

[1] Lloyd Morgan, *Emergent Evolution*, p. 18.
[2] *Space, Time, and the Deity*, 1920.
[3] Lloyd Morgan, *Emergent Evolution*, p 24.

CHAPTER II

RECEPTORS

THE fundamental characteristic of all living organisms is irritability. As seen in the lowest unicellular organisms, this is manifested in the motor response to stimulation In the light of our own experience we conclude that irritability implies the possession of a receptor mechanism and a motor mechanism, however inextricably these may be combined in the apparently undifferentiated protoplasm of the amœba, for example In the cœlenterates the receptor and motor mechanisms, though differentiated, form a single receptor-muscular unit At a higher stage physiological experiment and observation have shown that differentiation leads to the structural and functional separation of the receptor mechanism from the motor mechanism, as shown in reflex action Structurally, we find that even in the simplest reflex arc an intermediate link is interposed between the receptor and the motor neurones, and to this link highly important functions are attributable Further evolution leads to specific differentiations of the receptor mechanism into receptors which respond only to specific types of stimuli, and these changes are accompanied by appropriate differentiations in the other links of the reflex chain

Consciousness involves a conscious subject and an object of which the subject is conscious The experience of the subject is primarily its consciousness of a sensory presentation The nature of the simplest form of consciousness is an inference derived from the analysis of our own highly complex consciousness, of which alone we have immediate knowledge In it we can discern the presence of re-presentations, attributable to the retention and recognition of previously experienced presentations, and so on So far as we can isolate a single "field of consciousness" in the continuous stream of consciousness, we find that it is characterized by cognition endowed with more or less affective tone, and that it eventuates in a motor response or a conation which implies motor activity From considerations of this kind we are led to the conclusion that the simplest form of consciousness, a mere sentiency, is of somewhat the following nature Stimulation of the receptor mechanism causes the emergence of an awareness of a *change* in the environment. This awareness is tinged with affective tone, with a minimum of cognition—the situation is pleasant or un-

pleasant, and so far possesses meaning, to which the organism responds by appropriate motor response, positive or negative, towards or away from the source of stimulation respectively. This is consciousness on the reflex plane As McDougall says· "it seems probable that the actions of even the lowest animals imply a vague awareness of something, together with some vague forward reference, some vague anticipation of a change in this something."[1] If so, these traces of controlled activity are the germ of conation, *i e.* striving towards an end. It is conation in a primitive form, panoramic and unfocussed, yet it is teleological, however minimal the objective signs may be, and however slight the subjective anticipated result or pre-sentience may be For such organisms do not cease their apparently random movements when they meet with obstacles, indeed, such opposition tends to augment the efforts. Even at this low stage there is also the germ of variation of striving in order the better to cope with the obstacle Whether there is any germ of learning by experience or improved efficiency in dealing with a similar situation on a subsequent occasion is less easy to prove. Since this depends upon retention and recognition, the germ of memory, we should only expect to find it in its liminal form Just as pre-sentience is minimal, so, too, we should expect recognition to be minimal

Awareness is the primitive form of attention, and by further differentiation and integration leads to interest This advanced evolution is the result of differentiation and integration of the sensory presentations and their accompanying complications from re-presentations, etc. The diverse simultaneous sensory presentations are integrated into perception, endowed with richer meaning than on the reflex plane. The corresponding integration of affective tones emerges in emotion This gives rise, by conation, to an integrated motor activity, which, by backstroke, contributes to the emotional affective tone. This is consciousness on the plane of instinct.

With further differentiations and integrations, assimilation of percepts into apperception-masses by means of memory and association, the higher stage of ideation and conceptual consciousness is reached. This is consciousness on the plane of intelligence, into the details of which it is unnecessary here to enter.

If, from the vantage point of the highest stage, which man alone has reached, we attempt, so far as we can, to analyse our experience, we note in the first place that perception plays a fundamental part. No matter how complicated the differentiations and integrations

[1] McDougall, *Social Psychology*, 8th ed. p. 360.

which take place, no matter how complex the co-ordinations and modifications of the percepts resulting in the emergence of higher states of consciousness, perception, though thus modified, persists in its essential characters as the foundation stone of the edifice.

At the lowest level of life organisms appear to react chiefly, if not solely, to stimulation by contact. If they are submissible at all to radiant energy, it is by physical contact with bodies emitting such energy, *e.g.* a body at a higher or lower temperature. From all the evidence available we conclude, with some degree of confidence, that primitive sentiency is essentially tactile. It is not to be regarded, however, as immediately comparable to our tactile experience. It is probably a vague, undifferentiated touch, in which awareness of a foreign body includes mechanical, thermal and chemical elements, to which, singly or combined, there is choice only of two responses, positive or negative, characterized sensorily as pleasant or unpleasant, motorially as movement towards or movement away.

At a somewhat higher level there is evidence of response to radiation of shorter wave-length—light, and perhaps ultra-violet radiation. As soon as this occurs the germ of projicience is found. The animal is sensitive to gradations of intensity of light and moves towards or away from the light—at first, as it would appear, by random movements attaining the desired positive or negative end by a process of trial and error. Very low down in the animal scale, however, specific organs responsive to light are found, and these at a very early stage appear to be adapted to directional sensitivity Often they are protected on one side by pigment cells

In due course a great array of specific receptor organs is evolved[1], of which the traditional five senses are but the most obvious According to C. J. Herrick[2], there are at least twenty sensory receptors in man.

The receptors which are found in animals may be classified into three groups according to the physical nature of the adequate stimuli, *viz.* chemo-receptors, mechano-receptors, and radio-receptors. The chemo-receptors include three classes, those of smell, the common chemical receptor, and those of taste. Those of smell include the olfactory apparatus and the vomero-nasal apparatus (Jacobson's organ) of lower animals. The common chemical sense in higher mammals is found only on mucous surfaces in close relationship

[1] See W. A. Nagel, "Die Phylogenese specifischer Sinnesorgane," *Bibliotheca zoologica*, pp. 1–42, 1894

[2] *An Introduction to Neurology*, Philadelphia and London, 1918.

with the apertures of the body—mouth, eye, anus, etc. Its receptors respond to irritating chemical agents, such as ammonia. In lower aquatic vertebrates, *e g.* fishes and amphibia, these receptors are scattered over the surface of the body. Phylogenetically they are very primitive, being in fact one of the earliest types of sensory receptors occurring in most invertebrates, *e.g* sea anemone, earthworm, etc. Taste receptors, limited in man to the tongue and neighbouring buccal and pharyngeal mucous membrane, are found scattered over the surface of the body in fishes We know little of their specific differentiation in these animals, but in man the four tastes which alone occur, *viz* sour, saline, sweet, and bitter, have attained an independence, anatomical and physiological, which authorize their being regarded as separate chemical "senses" or receptors. On the other hand, their teleological importance in the interests of nutrition, and hence of self-preservation of the animal, has suffered partial eclipse, for in fishes, for example, taste is endowed with local signature which is lost in man Thus, in the cat-fish, *Amiurus*, if a barbel, which is specially richly supplied with taste organs, is touched with a pledget of cotton-wool the fish turns, but does not snap at it But if the cotton-wool is soaked in meat juice and brought to the side of the fish, it turns and snaps. The former is a tactile reaction, the latter a true gustatory reaction, unaccompanied by touch, but obviously accompanied by a local sign[1] That these responses are really gustatory is proved by the fact that if the branch of the VIIth nerve which innervates the taste buds of the flank of *Amiurus* is cut, the responses no longer occur[2].

Phylogenetically, the common chemical sense must be regarded as the most primitive. As found in invertebrates, the neural structure is a sensory cell situated in the surface epithelium, with an axon which passes directly to the central nervous system It differs in vertebrates, in that, like other first sensory neurones, *e g.* those of pain, the cell body is transferred to the dorsal root ganglion, the end organ consisting of free nerve fibres amongst the superficial epithelial cells The very primitive nature of the olfactory and vomero-nasal receptors is shown by the persistence of the most primitive apparatus, a peripheral sensory cell in the epithelium, the axon of which passes directly into the central nervous system. The olfactory apparatus in

[1] C. J Herrick, *Bull United States Fish Commission*, 1902

[2] G H Parker, *Jl Acad Nat Sc* Philadelphia, xv, 221, 1912. See also *Smell, Taste and Allied Senses in the Vertebrates* (Monographs on Experimental Biology), Philadelphia and London, 1922.

the central nervous system of vertebrates is, however, so complicated that it may well be that the homologue of the dorsal root ganglion cell is intracerebral, a persistence of the very primitive condition exemplified by the intramedullary cells of *Amphioxus*, etc.[1] In any case the differentiation of the olfactory apparatus in higher mammals is along different lines from that of taste, for though we know little about olfaction, chiefly owing to its degraded position amongst the senses in man as compared with lower animals, it has certainly not become so specifically differentiated in man as has taste, itself somewhat similarly degraded. The less degraded position of taste is reflected in the anatomy of the apparatus, the taste buds being composed of neuro-epithelial receptor cells in synaptic relation with free nerve endings of axons which pass to unipolar cells in all respects comparable to dorsal root ganglion cells.

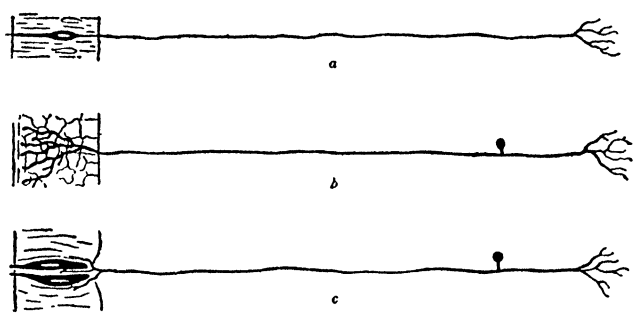


Fig 1 Receptor system of *a*, olfactory and vomero-nasal organs, *b*, organ of common chemical sense; *c*, gustatory organ (G H Parker)

Physiologically, all the adequate stimuli of the chemo-receptors are substances in solution; and, judged by the molar concentration of odorous and sapid substances necessary to arouse the liminal response to olfaction and taste respectively, in man olfaction is found to be vastly more efficient than taste, or the common chemical sense[2] The mechano-receptors can be divided into two classes, contact and distance receptors. The contact receptors include pain, touch or light pressure, temperature, and deep pressure The distance receptors include various forms of mechanical pressure transmitted by water or air Of these the lateral line organs of fishes and the vestibular apparatus of vertebrates are concerned in orientation, equilibration, and posture, and, therefore, belong to Sherrington's proprio-ceptive

[1] *Vide*, pp 75, 76, 77

[2] G H Parker and Stabler, *Amer Jl Physiol* XXXII, 230, 1913

group. Hearing must be regarded as a higher differentiation of this apparatus.

The radio-ceptors include temperature and vision, the adequate stimuli in each case being definite ranges of the radiant spectrum. Of them the receptors of vision are distance receptors *par excellence*. They possess the most highly developed local signature and the most accurate projicience of any receptors In these respects temperature receptors fall far below them, being on a par with touch as regards local signature, and possessing only a vague projicience. There is no evidence that other ranges of the radiant spectrum have any corresponding receptors in man; but, as regards ultra-violet radiation, we have no definite evidence that such do not occur in lower animals

Most of the receptors mentioned, with the exception of those of deep pressure—to which the so-called muscular and joint sense must be added—and the vestibular apparatus, which are proprio-ceptive, belong to Sherrington's group of extero-ceptors. The common chemical sense in man, olfaction and taste, belong to the intero-ceptors Probably all the receptors have not been included in the above list. It is probable that there are receptors for hunger, thirst, etc. belonging to the intero-ceptors, but our knowledge of these is very slight Phylogenetically, they must be very primitive, but their survival value must have been very great. Their responses in man have all the characteristics of the primitive—vague, ill-defined and undifferentiated, contributing little more than modifications of the general cœnæsthesis

From the vantage point of man's status it is permissible to enquire what confirmatory evidence as to the evolution of receptors is derived from teleological arguments. Biologically, the fundamental ends of animal conation are (1) self-preservation, and (2) the preservation of the species. The fundamental means to the end of self-preservation are nutrition and protection. In the amœba the responses to stimulation are reduced to the lowest terms, positive and negative, and we have inferred that the conscious responses are similarly dual, pleasant or unpleasant, and are scarcely at all differentiated It is probable that the earliest differentiation was into mechano- and chemo-receptors, of which the latter were most important for nutrition and survival. Hence the rudiments of taste and smell, probably as yet undifferentiated from each other, first arose. At a later stage smell became the distance receptor *par excellence* of nutrition, appearing first as a simple positive or negative chemotaxis. It initiated the appropriate motor response for taking

food, after which taste settled the question whether the material should be swallowed or rejected. In the former case the nutritional act was completed by the satisfaction of the conation, and pleasure was experienced. In the latter the conation failed and unpleasure was experienced, the primitive form of disgust.

Smell was also probably the great initiator of the reproductive act, after which the relatively undifferentiated tactile-temperature sensation led to the consummation of the conation There is reason to think that reproduction is itself derived from nutrition. In both, chemo- and intero-receptors probably play an important part, being stimulated specifically by hormones derived from the intestinal, reproductive and endocrine glands. In both, the result is an appetitive modification of the cœnæsthesis.

Thus, the fundamentally prepotent receptors of the living organism were intero-ceptors, to which the extero-ceptors became more and more accessory as they underwent higher differentiations, differentiations which were largely in the interests of protection

CHAPTER III

INSTINCT

1. Instinctive Behaviour

Since it is generally agreed that the highest levels of consciousness—ideation, conception, imagination—have not yet emerged in lower animals, or have only emerged to so slight a degree as to have relatively little influence in controlling lower levels, we may expect to obtain valuable data as to the nature, genesis and rôle of perception by studying their behaviour, and particularly their instinctive behaviour.

The instincts of lower animals afford the purest examples of consciousness on the perceptual plane It is true that they can be examined only objectively, and such conscious accompaniments as they possess can only be inferred from the motor responses, analysed in the light of our own experience and experiments Most of the vast literature on the instincts of lower animals is descriptive, dealing only with behaviour, or, if any psychological explanation is attempted, it is crudely anthropomorphic The work of Lloyd Morgan offers a conspicuous exception, and considered in the light of Sherrington's work on the integration of reflexes affords the most valuable data as to the genesis of perception. It will be briefly described, with only sufficient illustration to make it comprehensible, in the following chapter

Biologists are accustomed to view instincts chiefly from the motor aspect, *i e* from the point of view of behaviour Schneider[1] groups instinctive actions on a biological basis (1) those connected with the procuring of food, (2) those connected with self-preservation; (3) those connected with the care of offspring, (4) those connected with sexual relations Each of these groups is comprised of innumerable sub-groups Thus, that subserving nutrition often involves the search for prey, seizure of prey, and dealing with it when caught, all of which involve complex instinctive acts Crouching, flight, hiding, fighting, burrowing and mimicry are examples of protective instinctive behaviour. The hedgehog coils himself up, the tortoise withdraws his head and limbs under his carapace, the snail retreats within his shell. Mimicry is not only structural, as in many moths

[1] *Der thierische Wille*, Leipzig, 1880.

and butterflies, but also motor. A not uncommon beetle (*Clytus arietis*), which is mimetic of the wasp, has a fussy manner, unlike the usual staid demeanour of beetles, which serves to make the mimicry more effectual[1].

One of the most typical features of such behaviour is its stereotyped character, which is specially prominent in insects. Romanes[2] gives an instructive example.

"P. Huber has described a caterpillar which makes, by a succession of processes, a very complicated hammock for its metamorphosis, and he found that if he took a caterpillar which had completed its hammock up to, say, the sixth stage of construction, and put it into a hammock completed up only to the third stage, the caterpillar did not seem puzzled, but repeated the fourth, fifth and sixth stages of construction If, however, a caterpillar was taken out of a hammock made up, for instance, to the third stage, and put into one finished to the ninth stage, so that much of its work was done for it, far from feeling the benefit of this, it was much embarrassed, and even forced to go over the already finished work, starting from the third stage which it had left off before it could complete its hammock So, again, the hive-bee in the construction of its comb seems compelled to follow an invariable order of work"

Another feature is that instinctive activities are severally common to, and similarly performed by, all the members of the same sex of the same more or less restricted group of animals. Needless to say, there is the closest possible connection between the structure and organization of any animal and its instinctive activities. Flight of birds necessitates the possession of wings, spiders' webs spinnerets, and so forth. Instinctive activities are performed under special circumstances which are either of frequent occurrence, or are vitally essential to the welfare or continuance of the race. Some instinctive activities are performed seldom, or only once, and these are in all cases of vital importance to the continuance of the race. Of the many drones which follow the queen-bee in her nuptial flight, one only is successful in mating with her, and that but once in his life. Lloyd Morgan cites examples of exquisitely adaptive instinct in the behaviour of the yucca moth (*Pronuba yuccasella*). Another example may be quoted from the same source.

"A certain beetle of the genus *Sitaris* (one of the Meloidæ, to which belongs the common oil-beetle) lays its eggs at the entrance of the subterranean galleries excavated by a kind of mason bee (*Anthophora*) From these eggs the larvæ are hatched in autumn as active little insects very different from the ordinary type of beetle grub, having six legs, each armed with a sharp curved hook. In the winter they become sluggish, but resume their activity in the spring And when in April the drones of

[1] Lloyd Morgan, *Habit and Instinct*, p. 12. London, 1896.
[2] *Mental Evolution in Animals*, p. 179.

the bee emerge and pass out through the gallery, the *Sitaris* larvæ fasten upon them. There they remain till the nuptial flight of the bees, when, as the insects mate, they pass from the drone to the female bee. Then again they wait their chance. The moment a bee lays an egg, the *Sitaris* larva springs upon it, and at length breaks its prolonged fast Even while the poor mother is carefully fastening up her cell, her mortal enemy is beginning to devour her offspring; for the egg of the *Anthophora* serves not only as a raft, but as a repast The honey, which is enough for either, would be too little for both, and the *Sitaris*, therefore, at its first meal, relieves itself from its only rival. . . After eight days the egg is consumed, and on the empty shell the *Sitaris* undergoes its first transformation, and makes its appearance in a very different form. . . . It changes to a white fleshy grub, so organized as to float on the surface of the honey, with the mouth beneath and the spiracles above the surface. . . In this state it remains until the honey is consumed, and, after some further metamorphoses, develops into a perfect beetle in August."[1]

The following is a typical example of instinctive behaviour in a bird.

"Some years ago I had under observation two young moor-hens or water-hens which I had hatched in an incubator, and watched from day to day, almost from hour to hour, with some care One of these, about nine weeks old, was swimming in a pool at the bend of a stream in Yorkshire. A vigorous rough-haired puppy, highly charged with canine vitality, ran down from the neighbouring farm, barking and gambolling and from the bank he made an awkward feint towards the young bird. In a moment the moor-hen dived, disappeared from view, and soon partially reappeared, his head just peeping above the water beneath the overhanging bank Now this was the first time the bird had dived. I had repeatedly endeavoured to elicit this characteristic piece of behaviour, but had failed . . Under unnatural conditions, however, in a large bath, and under natural conditions in the Yorkshire stream, do what I would in my efforts to coax or frighten the young bird, I had never been able to make him dive. But now at last that blundering puppy succeeded, where I had so often failed. And when this characteristic piece of behaviour came upon my little friend—came upon him suddenly and without warning—his dive was absolutely true to type."[2]

Lloyd Morgan has exhaustively studied the pecking instinct of young birds. As an example that instinctive activity is subject to variation as the result of experience, the following may be quoted.

"A young chick two days old had learnt to pick out pieces of yolk from others of white of egg. I cut little bits of orange peel of about the same size as the pieces of yolk, and one of these was soon seized, but at once relinquished, the chick shaking its head. Seizing another, he held it for a moment in the bill, but then dropped it and scratched at the base of its beak That was enough; he could not again be induced to seize a piece of orange peel The obnoxious material was now removed, and pieces of yolk of egg substituted, but they were left untouched, being probably taken for orange peel. Subsequently he looked at the yolk with hesitation, but presently pecked doubtfully, not seizing, but merely touching. Then he pecked again, seized, and swallowed."[3]

[1] Lloyd Morgan, *Habit and Instinct*, p. 15.
[2] Lloyd Morgan, *Instinct and Experience*, p. 4, London, 1912.
[3] Lloyd Morgan, *Habit and Instinct*, pp. 40–41.

From the biological point of view, instinctive behaviour is best defined as "that which is, on its first occurrence, independent of prior experience; which tends to the well-being of the individual and the preservation of the race; which is similarly performed by all the members of the same more or less restricted group of animals; and which may be subject to subsequent modification under the guidance of experience."[1]

'From these and innumerable other examples which might be cited it is clear that many instinctive activities are exhibited in all their rich complexity at such an early period of life or under such conditions that it is impossible that they should have been learnt from experience. They spring into being fully fledged, like Athene from the head of Zeus. The example of the *Sitaris* beetle is a case in point. Here parental instruction is excluded, for the parent never sees her offspring Imitation is excluded, for each individual is isolated from others of its kind. Previous experience is excluded, for the larva has never before fastened upon a drone nor passed on to the female bee. If there be experience, it must be the inherited experience of ancestors that have each in turn carried out the same performance. So definitely is this absence of experience proved for many examples that it is justifiable to conclude that other examples of instinctive behaviour which are not manifested until later in life are, so far as they are instinctive, *i.e.* in their fundamental characteristics, independent of experience. The fledgling's first flight is a blundering performance, but it shows all the features of a true flight as distinguished from any other mode of behaviour. This is proved by the fact that it serves its purpose, and saves the infant bird from being dashed to destruction: it is serviceable at its first performance—serviceable for the preservation of the individual. It is true that the same muscles and nerves have often been exercised in apparently random exercises many times before the first flight; but they have never been co-ordinated into the specific complex sequence. The same remarks apply to instinctive behaviour of even later manifestation. Notable among such are the instinctive activities associated with sexual relations such as mating, nest-building, the sitting of a broody hen. Just as the winking reflex cannot be elicited in a kitten until the period after birth when it begins to see, so the sexual instincts cannot manifest themselves until the sexual organs have arrived at maturity. At the same time, as a general rule it may be stated that

[1] Lloyd Morgan, *Instinct and Experience*, p. 5.

the later the development of an instinctive reaction the less pure, *i.e.* the less unmixed with diverse products of experience, it is likely to be. The ontogeny of the instincts is, like that of structure, a modified recapitulation of their phylogeny. So we get the purest instinctive activities low down in the phylogenetic scale and early in the ontogenetic history, and of these two groups the primitive phylogenetic is the purer. The pure instinct is probably as much an abstraction as the pure reflex, but if it is difficult to find a pure instinct in the lower species, it is even more so in man, even in the child This is largely due to the immaturity of the new-born mammalian offspring Structural immaturity necessarily carries functional immaturity in its train, and the prolonged period of maternal nurture leads to modification of instinctive responses.

If, then, typical instinctive behaviour is, on its first occurrence, independent of prior experience, it follows that, from the objective point of view, it is dependent upon an inherited mechanism of, at any rate, effective adequacy, and from the subjective it implies an inherited disposition to act in a certain definite way in response to a definite situation. In contradistinction to the typical reflex act, the instinctive activity displays a relative plasticity, which, though scarcely distinguishable from the compound reflex act at the lower end of the scale, increases as the scale is ascended. This increasing plasticity is correlated with the increasing variability and complexity of the environmental situation with which the organism is confronted.

"Such behaviour is a more or less complex organic or biological response to a more or less complex group of stimuli of external and internal origin, and it is, as such, wholly dependent upon how the organism, and especially the nervous system and brain-centres, have been built through heredity, under that mode of racial preparation which we call biological evolution "[1]

It is scarcely necessary to emphasize the similarity of performance of instinctive activities by the individuals of restricted groups of animals. The larva of the great water beetle (*Hydrophilus piceus*) will, for example, as the period of pupation draws nigh, leave the pool and bury itself in the damp earth. It is an activity, as has been said, upon which you can safely bet.

Instinctive behaviour tends to the well-being of the individual and the preservation of the race. In the lower and most characteristic examples there can be no doubt about these points. So far, and from a strictly biological standpoint, the activities are teleological—

[1] Lloyd Morgan, *Instinct and Experience*, p. 5.

directed to well-defined ends. From the psychological point of view, where teleological activity is commonly held to imply some rudiment, at least, of a mental forecast of the end, in fact, some end *in view*, the teleology of instinct is a debatable proposition. Many examples in lower species can be adduced where any form of mental forecast of the ultimate end is patently absent. Thus, the mason wasp lays its eggs in a mud nest, fills up the space with caterpillars, which it paralyses by stings, then seals it up. Hence the wasp provides food for its young, whom it will never see and of whose needs it cannot have any possible forecast.

Though instinctive behaviour is on its first occurrence prior to experience, it is yet eminently characterized by being modifiable under the guidance of experience. The young bird soons learns to avoid pecking the delusive fragments of orange peel or cinnabar caterpillars, which are equally distasteful. In the higher species of animals, and above all in man, instinctive activities are so altered by experiential teaching that they are masked and have frequently been denied for that reason. Yet this learning by experience is manifested even in the most stereotyped examples. Thus, the solitary wasps instinctively close up the entrance to their nests, but the methods whereby they do it vary greatly and are undoubtedly modified by experience Nearly allied is the "persistence with varied effort" (Lloyd Morgan) of instinctive behaviour, the application of the method of trial and error. A dung beetle rolling its dung ball along the sand finds itself in a hollow the sides of which are too steep for pushing up the ball from below. It accordingly butts down the sand at one side so as to produce an inclined plane of much less angle[1]. The method of trial and error appears to spring from the fundamental property of living matter—irritability, with its concomitant response, movement. The movements of protozoal organisms are superficially described as "random" movements, but it is doubtful if this is literally accurate. There is evidence even thus low in the animal scale of trial and error. However this may be, there is no doubt about the fact in very early stages of animal evolution, and the method persists right up to and including man, ever increasing in objective richness of display and subjective fertility of resource. Trial and error is the experimental method, and it is the method of progress. Thus, the method of advance and progress throughout the animal kingdom is the inductive method.

[1] Lloyd Morgan, *Animal Life and Intelligence*, p. 458, London, 1890.

2. Data derived from Experimental Physiology

There is a large body of evidence which has accumulated in recent years tending to show that pure instinctive activities are carried out without any participation of the cortex of the cerebral hemispheres. Special attention may be directed to the differences which are observed in the behaviour of the animals when, on the one hand, only the cerebral hemispheres are removed, and, on the other hand, when in addition the lower centres (corpora striata, and especially optic thalami) are removed or seriously injured. It will generally be found that in the latter case the behaviour much more nearly approximates that of the spinal animal, *i. e.* a reflex automaton, than in the former In the purely decerebrate animal many instinctive activities are undoubtedly manifested.

Thus, in the decerebrate frog Desmoulins and Magendie (1825) showed that apparently spontaneous movements occur, and Schrader[1] has shown that such a frog will feed itself by catching flies, etc., will bury itself in the mud on the approach of winter in order to hibernate and resume activity with the advent of spring, and in breeding season will give evidence of possessing normal sexual instincts.

Similarly, in fishes, if only the hemispheres and corpora striata (which are much more nearly allied to the cortex than are the optic thalami) are cut away, the thalami and optic lobes being left intact, the behaviour of the animal is little, if at all, different from that of normal fishes, *e g.* it moves about and nibbles at passing objects, distinguishing edible from non-edible material

In the bird, too[2], if care be taken to avoid injury to the optic lobes, a decerebrate pigeon will in the light or in daytime walk about, avoiding all obstacles, even if transparent, like glass, but in the dark it will remain quiescent and apparently asleep

'It is able to maintain what appears to be a completely normal posture and can balance itself on one leg after the fashion of a bird which has in a natural way gone to sleep.. .Placed on its side or its back it will regain its feet; thrown into the air it flies with considerable precision for some distance before it returns to rest. It frequently tucks its head under its wings, and at times may be seen to clean its feathers, when its beak is plunged into corn it eats It may be induced to move not only by ordinary stimuli applied to the skin, but also by sudden loud sounds, or by flashes of light; in its flight it will, though imperfectly, avoid obstacles, and its various movements appear to be to a certain extent guided not only by touch but by visual impressions."

[1] *Arch f d ges. Physiol* XLI, 1887.
[2] Schrader, *Ibid.* XLIV, 1888.

Schrader says of these animals:

"They have no enemies and no friends They live like hermits, no matter in how large a company they find themselves. The languishing coo of the male makes as little impression on the female deprived of its cerebrum as the rattling of peas or the whistle which formerly made it hasten to its feeding place Neither does the female show interest in its young. The young ones that have just learned to fly pursue the mother, crying unceasingly for food, but they might as well beg food of a stone."

Here we see certain instinctive activities in abeyance, but it is to be noted that the corpora striata were also removed in these experiments.

Goltz[1] succeeded in removing both cerebral hemispheres from a dog, but the corpora striata and optic thalami were also partly involved in the lesion

"For the greater part of the day it walked restlessly up and down in its cage, but at night would go to sleep, rolled round in the manner usual with dogs It then required a loud sound such as that of a horn, or rough shaking to awaken it When awake it reacted to loud sounds by shaking its ears, to a glare of light by shutting its eyes, and by turning its head away It reacted promptly and consequentially to tactile impressions When its skin was pinched, it gave vent to its discomfort by snarling or barking just as a normal dog might do, and attempted to get away from the hand which was the cause of the discomfort, or failing to do this would turn round and bite at it, but in a clumsy manner and often without coming near it . The dog never showed any sign of recognition of persons or of any other dogs, showed no fear of threatening movements, never wagged his tail, or showed any sign of pleasure on being stroked or spoken to, when wetted, shook himself vigorously but never attempted to lick himself dry, as a normal dog does, never used his fore-paws to hold a bone or to dig a hole for one (although there was even less paralysis apparent than in animals from which only the sigmoid gyrus is removed), never gave any sign of spontaneous mental activity, unless an increased restlessness and other signs of impatience when food was withheld for longer than usual are to be in a measure so interpreted The animal showed absolutely no sign of memory Although its removal from the cage was the usual signal for feeding, it invariably resisted being taken hold of for this purpose, barking loudly and biting and struggling vigorously During sleep it never showed any indications, as dogs often do, of dreaming."[2]

It will be seen from these observations that the decerebrate animal is capable of expressing certain emotions, and particularly those which are associated with painful impressions. In the decerebrate cat Sherrington could never evoke any indications of pleasurable sensations. Snarling was easy to elicit, but the cat never purred.

It is necessary here to point out that, in the ordinary use of the words, pleasure and pain are not accurately antithetic. Pain usually means what is often called physical pain. "Physical pain is the

[1] *Ibid* LI, 1892.

[2] Schafer, *Text-Book of Physiology*, II, 702–3.

psychical adjunct of an imperative protective reflex."[1] It is associated with stimuli which threaten or actually commit damage to the tissues; which are in fact nocuous. Sensory nerves which, from the point of view of sensation, are cutaneous pain nerves, are from the point of view of reflex action conveniently termed nociceptive nerves[2]. Pleasure, on the other hand, in its ordinary meaning signifies the satisfaction which is derived from successful conation. Pleasure, meaning the opposite of physical pain, has been described as the absence of pain. Reflection will show that this statement, though embodying a great truth, is but a partial representation of the facts. Besides this negative form of physical pleasure, there is the positive physical pleasure which accompanies special modes of stimulation of sensory nerves. Thus, pleasant smells, tastes, sounds, and so on, possess a fundamental affective tone which is physical pleasure, and it is not wholly due to association. Certain methods of stimulating the skin arouse physical pleasure thus, tickling is eminently pleasurable to some people. There is no convenient word for the antithesis of physical pain, it might be called physical pleasure. Neither is there a convenient word for the antithesis of pleasure the best term is perhaps unpleasure (cf. "unpleasant," *Unlust*).

Physical pain, being associated with imperative protective reactions, is a stronger stimulus than physical pleasure, and it is, therefore, not surprising that the manifestations of the latter are submerged in the decerebrate animal whilst those of the former persist. It is a striking fact that "it is those areas, stimulation of which, as judged by analogy, are most fitted to excite pain which, as a general rule, excite in the spinal animal—where pain is of course non-existent—the prepotent reflexes"[3] From the physiological point of view no hard and fast line can be drawn between such reflexes and an instinctive reaction

"If various species of reflexes are arranged in their order of potency in regard to power to interrupt one another, the reflexes initiated in receptors which, considered as sense-organs, excite sensation of strong affective quality, lie at the upper end of the scale, and the reflexes that are answerable for the postural tonus of skeletal muscles lie at the lower end of the scale. One great function of the tonic reflexes is to maintain habitual attitudes and postures They form, therefore, a nervous background of active equilibrium It is of obvious advantage that this equilibrium should be easily upset, so that the animal may respond agilely to the passing events that break upon it as intercurrent stimuli."[4]

[1] Sherrington, *The Integrative Action of the Nervous System*, Yale University Press, 1920, p. 228.

[2] *Ibid.* p. 226.

[3] *Ibid.* p. 228.

[4] *Ibid.* p. 231.

"It is not usual for the organism to be exposed to the action of only one stimulus at a time. It is more usual for the organism to be acted on by many stimuli concurrently, and to be driven reflexly by some group of stimuli which is at any particular moment prepotent in action on it. Such a group often consists of some one pre-eminent stimulus, with others of harmonious relation reinforcing it, forming with it a constellation of stimuli, that in succession of time, will give way to another constellation which will in its turn become prepotent."[1]

The last quotation might be used without any alteration to describe the physiological substrata of an instinctive reaction. It seems justifiable to conclude that from the *physiological* point of view instinctive reactions are merely very highly complex compound reflexes. Of the lowest the anatomical basis may even be in the spinal cord, for Sherrington found that even in the spinal dog defæcation was invariably followed by a number of vigorous kicks with the hind-limbs

As Sherrington points out, reflexes are adapted reactions, and therefore, "in the light of the Darwinian theory every reflex *must* be purposive." He cites many examples of compound reflexes in various species which show the impossibility of drawing a line between them and instinctive reactions, at any rate in their physiological aspects. The brushing of irritants from the flank of the spinal frog he compares with the preening actions of the spinal fly, grasshopper, crayfish, etc., the nettoyage by the tortoise, and so on[2].

Thus, the headless bee stings in response to stimulation of the under surface pretty accurately at the site of irritation[3]. The yellow clover fly will, after decapitation, stand cleaning its wings with its hind legs, and clean its "three pairs of legs, rubbing them together in a determined manner, and raising its fore legs vainly in the air as if searching for its head to brush up"[4] In the grasshopper, after extirpation of the supra- and sub-œsophageal ganglia (entire brain), the front leg is protracted and in the normal way catches the antenna, and the usual movements of cleaning the antenna go on, although the antenna has entirely lost its innervation owing to the destruction of the brain[5]. The cleansing reflex of the spinal frog[6] and the scratch reflex in the dog[7] are accurately executed after severance of the afferent spinal roots of the limbs which carry out the movements.

[1] *Ibid.* pp. 177–8.
[2] Sherrington, *op. cit.* p. 238.
[3] Bethe, *Arch. f. mikr. Anat.* L, 629, 1897.
[4] Swinton, *Insect Variety*, London, 1880.
[5] Bethe, *Arch. f. d. ges. Physiol.* LXVIII, 1897.
[6] H. E. Hering, *Arch. f. exper. Path. u. Pharm.* XXXVIII, 1896.
[7] Sherrington, *op. cit.* p. 251.

"There is indeed one, rarely exemplified, group of reflexes in which the organ is sacrificed for the preservation of the rest of the individual In certain forms, *e.g. Asterias, Cometula, Ophiurus, Arachne, Carcinus*, a limb pulled upon violently or long suddenly ruptures itself and is shed These actions have been shown by Frederieq to be reflexes, employing muscular contraction "[1]

In the male frog sexual clasp is a spinal reflex[2]. The cord may be divided both in front and behind the brachial region without interrupting the reflex In the intact animal there is discrimination which is absent in the spinal animal[3].

For most, however, the anatomical basis of integration is to be sought in the basal ganglia or sub-cortical centres. "The instinctive vertebrate as such is a thalamencephalon—downwards animal."[4]

If the cortex cerebri is regarded as the highest level and the bulbo-spinal or reflex nervous mechanism as the lowest level, the sub-cortical centres of instinctive activities will occupy the middle level of the stages of evolution of the central nervous system This is but a slight modification of Hughlings Jackson's well-known three levels[5]—

"The lowest level (1) represents few *different* movements (little differentiation, little complexity), it (2) represents movements of little definiteness, movements for less particular ends (great generality, otherwise little specialization), (3) its centres represent in detail—that is, each centre represents some district of the body (little width of representation by each centre; that is, little integration), the centres of the level are (4) little connected (little association of centres, little co-operation)

Whilst saying that the lowest level is least complex, etc , and that the highest level is most complex, etc , we must bear in mind that the former is the most strongly organized, and therefore the least modifiable of all the levels, and that the latter is least strongly organized, and therefore the most modifiable of all the levels."[6]

3. The Psychology of Instinct

It is natural that biologists, being engaged upon a purely objective study, should have devoted most attention to the motor manifestations of instinctive behaviour As a result there has been a great tendency to ignore the subjective side Like reflex action, instinctive behaviour can be analysed into three parts—afferent, central, and efferent Each part is a synthesis of the receptor, conductor, and

[1] Sherrington, *op. cit.* p. 239

[2] Haller, *De partibus corporis humani sentientibus et non-sentientibus*, Gottingen, 1752

[3] Goltz, *Centralbl. f. d. med. Wissenschaft*, p. 705, 1865 See Sherrington, *op cit.* p. 230

[4] Lloyd Morgan, *Brit Jl. of Psychology*, III, 229, 1910.

[5] Hughlings Jackson, *British Medical Journal*, p. 65, 1889, *Lancet*, I, 394, 1895; *Neurological Fragments*, p. 125, London, 1925.

Cf. "dynamic plasticity," p 65.

effector parts of the complex compound reflexes which are the physiological basis of the instinct

The remarkable feature of the simplest types of instinctive behaviour is often the orderly sequence of events rather than their inherent complexity. Thus, in many insects the instincts are manifested by a series of reactions of the nature of reflexes. In the biological sense the activity is teleological in being directed to a definite end, in the psychological sense, it is teleological only in so far as each reaction is the result of an impulse towards a dimly perceived proximate end.

We know nothing of the conscious accompaniments of reflex acts, except that in man there are none It does not follow that there are none in those lowly organisms whose nervous systems consist only of a few ganglia and nerve fibres If the protozoon possesses sentience, we must assume that these organisms possess a more highly developed sentience—a consciousness which is on its way to become a percept When we reach the instinctive stage we are dealing with fully developed perception The component afferent impulses have become associated in consciousness and synthesized into a percept, which possesses "meaning."

Though we are unable to understand why a constellation of afferent impulses possesses meaning, it is possible to gain some knowledge of the integration of the nervous impulses themselves Sherrington divides afferent impulses into extero-ceptive, those derived from the cutaneous surface of the body, intero-ceptive, those derived from the visceral field, and proprio-ceptive, those derived from deep structures, such as muscles, tendons, joints, etc

The serial metamerism of the higher metazoa results in the development of a head, which takes the lead in active movements. The extero-receptors of the head "not only receive *more* stimuli, meet *more* 'objects' demanding pursuit or avoidance, but it is they which usually *first* encounter the agents beneficial or hurtful of the environment as related to the individual"[1] Hence these receptors undergo remarkable developments and predominate in the motor taxis of the animal Thus, photo-receptors, only slightly more potent in this part of the body in the earthworm than in other parts, become localized here in the retina in the highest vertebrates and undergo extraordinary development

"In like manner a certain group belonging to the system receptive of mechanical impacts attains such susceptibility for these as to react to the vibrations of water

[1] Sherrington, *op. cit* p 323.

and air that constitute physical sounds The retina is thus a group of glorified 'warm-spots,' the cochlea a group of glorified 'touch-spots.' Again, a group belonging to the system adapted to chemical stimuli reach in one of the leading segments such a pitch of delicacy that particles in quantity unweighable by the chemist, emanating from substances called odorous, excite reaction from them "[1]

Sherrington calls these *distance-receptors*, and they initiate sensations having the psychical quality termed *projicience*. In ourselves, sensations initiated through these receptors are forthwith "projected" to directions and distances in the environment fairly accurately corresponding with the "real" directions and distances of their actual sources. None of the sensations initiated in the proprio-ceptive or intero-ceptive fields possesses this property of projicience. *It is upon the distance-receptor organs that the brain is constructed and evolved.*

The distance-receptors initiate anticipatory, *i.e.* precurrent, reactions. In the processes of feeding and sexual conjugation, both primary requirements of an animal species, the non-distance-receptors play an essential part. Animal behaviour shows that these subserve differentiation of reaction, *e g.* swallowing, or rejection, of material already found and acquired, *e g* within the mouth The distance-receptor, *e.g.* smell, initiates and subserves far-reaching complex reactions of the animal anticipatory to swallowing, namely, all that train of reaction which may be comprehensively termed the quest for food.

"Just as a salient character of most of the reactions of the non-projicient receptors taken as sense organs is '*affective tone*,' *i e* physical pain or physical pleasure, so '*conative feeling*' is salient as a psychical character of the reactions which the projicient or distance-receptors, taken as sense organs, guide As initiators of reflex movements the action of these latter is characterized by tendency to work or control the musculature of the animal as a *whole*—as a single machine—to impel locomotion or to cut it short by the assumption of some *total* posture, some attitude which involves steady posture not of one limb or one appendage alone, but of all, so as to maintain an attitude of the body as a whole."[2]

Hence it is that these distance-receptors are the starting points of very widespread reflex arcs and are brought into relation with an immense number of final common paths, not directly, but by the intervention of shorter or longer internuncial paths. An example of such an internuncial path is the pyramidal tract of the higher vertebrates. Another is the Reissner fibre, linking the olfactory and visual receptors with the spinal motor common paths to the skeletal muscles.

The non-projicient receptors are most closely related to the final

[1] Sherrington, *op. cit.* pp. 323–4.
[2] *Ibid* p. 327.

or *consummatory* reactions; their reflex leads immediately to another which is consummatory. Thus, the tango-receptors of the lips and mouth initiate reflex movements which immediately precede the acts of swallowing. These reactions are all steps toward final adjustments and are not themselves end points. The distance-receptors initiate series of reactions which are much longer than those initiated by the non-projicient, and the projicient organs effect a continuous adaptive guidance.

"Thus in a positive phototropic reaction the eye continues to be the starting place of the excitation, and in many cases guides change in the direction not only of the eyeball but of the whole animal in locomotion as the reflex proceeds ..The reaction started by 'distance-receptors' where positive not only leads up to the consummatory reactions of the non-projicient, but on the way thither associates with it stimulation of other projicient receptors, as when, for instance, a phototropic reaction on the part of a Selachian brings the olfactory organs into range of the odorous prey, or conversely, when the beagle sees the hare after running it by scent....It is easy to see what copious opportunity for adjustment and of side connection such a reaction demands, consisting as it does of a number of events in serial chain, each link a modification of its predecessor."[1]

The importance of the distance-receptor in the integration of reflex activities is largely due to its greater *receptive range*, the slice of the external world from which it can receive stimuli. The receptive range of the eye, for example, is immeasurably greater than that of the touch-receptors of the skin. Since the distance-receptors are situated in the anterior segments or head, their respective receptive ranges overlap.

"The juxtaposition of groups of specially refined receptors in one set of segments, the leading or head segments, conduces towards their simultaneous stimulation by several agencies emanating from one and the same environmental object Thus, the property of brightness and the property of odour belonging to an object of prey may then better excite in unison a reaction in the distant reagent, or excite more potently than would either property alone And movements of the reagent itself are then more apt to intensify simultaneously the reactions of its two kinds of receptors. The collocation of the disparate receptors in one region will favour that which psychologists in describing sensation term 'complication,' a process which in reflex action has a counterpart in the conjunction of reflexes excited by receptors of separate species but of allied reaction. This alliance of reaction we have seen finds expression as mutual reinforcement in action upon a final common path. Thus a reaction is synthesized which deals with the environmental object not merely as a stimulus possessing one property but as a 'thing' built up of properties A reflex is attained which has its psychological analogue in a sense percept."[2]

Psychologists, for the most part, have refused to accept the view,

[1] Sherrington, *op. cit* p 330
[2] *Ibid.* p. 347.

originated by Herbert Spencer, that instincts are merely complex combinations of reflexes. On the hypothesis adopted in this thesis, the instinctive plane emerges from the reflex plane. Stout says[1]:

"Reflex action is of a nature fundamentally different from instinctive conduct The difference is that instinctive conduct does and reflex action does not presuppose the co-operation of intelligent consciousness, including under this head interest, attention, variation of behaviour according as its results are satisfactory or unsatisfactory, and the power of learning by experience"

It is clear that the argument here is derived from man, but if we assume, as psychologists now generally do, that mind has evolved just as structure has evolved, we must conclude that the conscious accompaniments of instinct are the products of evolution from the conscious accompaniments of the lower grades, *i.e.* the grades in which reflex action is supreme. The fact that in man the conscious accompaniments of reflex action are suppressed—or at any rate cannot be distinguished by introspective analysis—is no countervailing argument, for a selective submergence, partial or complete, of lower elements of consciousness appears to be the rule of progressive evolution[2].

The cognitive element of the emergent percept is meaning, and as evolution progresses percepts become more complex and meaning grows. The growth of meaning is twofold By the greater complexity of the perceptual synthesis it becomes fuller and richer in its content. By an ever-widening span of retentiveness and recognition and of pre-perception, dim pre-sentience develops into conscious pre-perception of proximate ends, and more and more remote ends are gradually gathered in. Thus, the germ of psychological teleology—consciousness of an end in view—grows from little more than a mechanical response into a motive force of behaviour, and ultimately, in the highest conceptual stage, into a motive force of conduct.

From the cognitive side, therefore, the instinctive process is of the nature of perception, suffused with significance or meaning for the animal That meaning carries with it an emotional state, at any rate in higher vertebrates, for we can clearly recognize signs of fear, anger, and tender feeling in dogs, cats and so on, associated with instinctive activities. This emotional state is the affective aspect of the instinctive mental process. It is hardly necessary to insist upon the conative aspect, for that is manifested in the motor response which has been the chief study of biologists.

[1] *Manual of Psychology*, p. 343.

[2] Cf. Lloyd Morgan, *Instinct and Experience*, p. 80

Hence McDougall defines an instinct from the psychological point of view as "an inherited or innate psycho-physical disposition which determines its possessor to perceive, and to pay attention to objects of a certain class, to experience an emotional excitement of a particular quality upon perceiving such an object, and to act in regard to it in a particular manner, or, at least, to experience an impulse to such action."[1]

A pure instinct is probably an abstract conception of psychological analysis; and this is chiefly because every instinct is modified by previous experience and it is almost impossible to define the moment of first experience. Thus, it may be said of the moor-hen's first dive that it had a long period of two months' experience behind it. It is true that it had never dived before, but it had run about and swum, thus using the same muscles and nerves, afferent and efferent, though never before in exactly the same manner.

If we consider the first peck of a newly hatched chick, the amount of previous experience is negligible. Here the visual impression of an object fires off a definite reaction which we call an instinctive activity It is not a "complicated reaction which is perfect the very first time,"[2] but it is sufficiently perfect to be practically serviceable. It may be, and probably is, accompanied by an emotional state; the sensations arouse an affective tone in consciousness. Now the chick possesses a cerebral cortex, and it is possible that the emotional state is due to stimulation of the cortex, but it is more probable that it is due to stimulation of sub-cortical centres[3], and this is the more likely to be the case the lower we descend in the vertebrate scale. The first peck must be regarded as an almost purely instinctive reaction, due to an inherited disposition acting through a nervous mechanism organized so to act "by centuries of racial preparation as the outcome of natural selection or of other factors in organic evolution "[4] In so far as it is accompanied by consciousness it is a specific form of experience. The second peck is not an exact replica of the first. The visual impression of a small object now arouses a re-presentation of the first peck. If the first peck had an inherited element of pre-perception[5], the second peck has this plus a pre-perception due to

[1] *Social Psychology*, p 29, 1914.

[2] Driesch, *Science and Philosophy of the Organism*, II, 110, 1908.

[3] *Vide infra.* Cf Pagano, *Archives Italiennes de Biologie*, 1906, see Mott in Allbutt and Rolleston's *System of Medicine*, VII, 258, 1911, Head and Holmes, *Brain*, XXXIV, 102, 1911; Pachon and Delmas-Marsalet, *C. R. de la Soc. de Biol.* XCI, 558, 1924.

[4] Lloyd Morgan, *Instinct and Experience*, p. 19.

[5] McDougall, *Social Psychology*, p. 28, Stout, *Brit. Jl. of Psychology*, II, 238, 1910.

experience. If the first object pecked up was a piece of yolk of egg, and the second a piece of orange peel, the emotional states aroused differ. The third peck at similar objects will be modified by the experience thus gained. The activity ceases to be purely instinctive, and in so far as it differs from the purely instinctive act, it is said to be intelligent.

To return to the moor-hen's first dive.

"If then I interpret the matter correctly in outline, there was, correlated with the cortical processes of the moor-hen as he swam in the pool, a certain amount of individual preparation of the cortex such as to afford the neural conditions of revived experience So much to begin with. Here we have the moor-hen as actual and potential experiencer. Then comes a new situation which the experiencer can assimilate. In this case, in so far as a new instinctive response is called forth, the conditions are largely supplied by the racial preparation of the lower brain-centres as the outcome of evolutionary process The new factors comprise (1) a specific presentation differing from previous presentations in what one may term initiating value, (2) a specific response, differing in certain ways from all previous responses and therefore affording new data to behaviour experience, and (3) a hitherto unfelt quality of emotional tone I do not think that the young bird had ever been really scared before But though we may analyse the newly experienced situation in some such way as this, the bird presumably gets the whole as a coalescent synthetic net result with a bearing on behaviour and some, perhaps much, reinstatement of the meaning which has qualified previous situations He just lives through one palpitating situation, assimilates its teachings, and emerges from the ordeal a new bird As experiencer he is never again what he was before."[1]

If we regard all consciousness in these animals as based on a cortical mechanism[2], then any pre-perception in the first instinctive act is due to an inherited cortical constitution, whilst the added pre-perception of the second and subsequent acts, due to experience, are caused by "backstroke" from the cortex. Thus, intelligence is based on the data of instinct, and reacts upon instinct by backstroke. "Instinctive behaviour, which has its roots in organic evolution, affords the rude outline sketch of that far less imperfect and far more fully serviceable behaviour, the finishing touches of which are supplied by practice under the guidance of intelligence."[3]

It will be seen that psychologists still tend to divorce the cognitive and emotional aspects of instinct, though not in the crude manner of their predecessors. For Lloyd Morgan the instinct-complex is (1) a specific presentation (cognition), (2) a specific response (conation), (3) a hitherto unfelt quality of emotional tone (affective state). McDougall adopts a more logical sequence—perception, emotional excitement, specific act or impulse to act. But all the changes in

[1] Lloyd Morgan, *Instinct and Experience*, p 13.
[2] *Ibid.* p. 29. [3] *Ibid.* p 26.

consciousness must be primarily the result of the afferent nervous impulses. If we return for a moment to the probable concomitants in consciousness of reflex action, where there is no cerebral cortex to complicate matters, we must conclude that, in the simplest reflex, the afferent impulse arouses a vague sentience. This sentience can be analysed into two parts. a part which is the germ of an affective state—rudimentary pleasure and pain; and a part which is the germ of a cognitive state—a dim consciousness of a change in state. Of these the former is the more primitive and of greater survival value, and therefore persists as the more deeply seated. With increase in complexity of reflexes many stimuli act concurrently and any concomitant conscious experience must be correspondingly complex. At this stage there is rather a contest of nerve impulses than any true synthesis, but Sherrington's experiments prove conclusively that the result is no mere algebraical summation but a co-ordinated reinforcement of a prepotent impulse combined with inhibition of opponent impulses— or at any rate of their normal effects when isolated There is integration without complete synthesis. We are justified in concluding that there is a similar integration of concomitant conscious experience, both in its cognitive and in its affective aspects. But doubtless, so far as the organism is regarded from the subjective side as experiencing, the synthesis is already more complete. Bergsonian interpenetration and merging are already in full swing.

So far we are dealing with the reflex stage and the admittedly theoretical "pure instinct" stage. But already, directly the reflex or the instinctive act is completed, the organism has become an experiencer and further contributions have been made to consciousness These consist in afferent impulses derived from the motor parts of the organism (the proprio-ceptive system)—muscles, tendons, joints and so on, as well as new sensory impulses (tactile, visual, etc.) resulting from change of position. They are added and incorporated in the conscious state, which they necessarily modify. They, too, consist in consciousness of a germinal cognitive part and a germinal affective part Of these the cognitive part is the more distinguishable, and the emotional becomes the more completely fused into the pre-existing emotional state. This we deduce from the accepted fact that in ourselves the cognitive elements are susceptible to introspective analysis, whereas emotional states are much more resistant of such analysis[1]. In most instinctive acts the cognitive element derived

[1] Cf. A. F. Shand in Stout's *Groundwork of Psychology*, Chap. XVI.

from the primary impulses is prepotent, whereas the emotional state is much more influenced by the "backstroke" effect of the completed act. Hence the emotional state is apt to be confused with the satisfaction of a successful conation or the reverse. In my conception of a pure instinct only the primary impulses should be taken into consideration. They give rise to (1) a cognitive element, which is the perception of the specific situation, and (2) an affective element, which is the synthesis of the affective elements of the afferent impulses and manifests itself as emotional tone So far as these are modified by the effect of the resultant action, they are acquired experience, and therefore food for intelligence as opposed to instinct.

4. Emotion

It is the cardinal difficulty of the study of mental evolution that at every step we have to argue back from our own consciousness. At no step is the difficulty greater than in that dealing with emotion, for, as has already been mentioned, no phase of consciousness is less susceptible to introspective analysis. And, though introspection in the restricted sense is by no means the only method of psychological research, its fundamental importance must not now be underestimated merely because it once filled the picture.

Probably either anger or fear is to be regarded as the most primitive of the emotional states to which we are justified in giving a definite name. Doubtless fear had its precursors in a vague uneasiness or, perhaps more likely, a scarcely conscious recoil which we can only with difficulty imagine. Let us, however, try to analyse the physiological bases underlying the emotion of fear in the relatively simple case of the moor-hen scared by the dog.

Here we have a specific group of presentations charged with meaning. From the physiological point of view a constellation of visual, auditory and other sensory stimuli sets up a complex group of afferent nervous impulses These arouse in consciousness (1) a cognitive state of knowledge of the whole situation, limited to a perceptual synthesis, but carrying a definite meaning, and (2) an emotional state which is the affective counterpart of the perception and which is co-extensive with its meaning. There result as motor responses (1) the specific bodily or somatic activity which we recognize as the essential objective signs of an instinctive reaction, and (2) certain efferent visceral reactions—changes of heart beat and of

respiratory rhythm, dilatation or contraction of the smaller blood vessels in more or less restricted areas (vaso-motor reactions), modifications of glandular and other activities, etc.

In dealing with emotion we have to segregate the affective elements of these several afferent and efferent processes, and to endeavour to allot to each its respective rôle. And first, before the instinctive act occurs, there is an ill-defined, unfocussed affective state already present, which is known as cœnæsthesis, and which acts as a panoramic background upon which the emotional state becomes delineated. Cœnæsthesis is the result of all those sensations which are derived from all the receptors of the body—extero-, intero-, and not least proprio-ceptors—which are at the moment undergoing normal stimulation. No one, nor any group, is sufficiently excited to "attract attention": the sensations are in the main subconscious or only dimly apprehended Upon this grey surface the emotion impinges like a splash of vivid colour

Of the impulses which give rise to the perceptual consciousness originating the instinctive activity, those initiated in some receptors possess more affective tone than those initiated in others. Sherrington points out that to consummatory reactions affective tone seems adjunct much more than to the anticipatory, especially the remotely anticipatory, of the projicient sense organs. Pain stimuli exciting nociceptors originate reactions which are to be regarded as consummatory. Taste is associated with strong affective tone. Physical pleasure or pain can scarcely be said to accompany the reactions from distance-receptors. Thus, the greatest physical pleasure (at the instinctive level) is experienced in the satisfaction of the sexual impulses in the act of coitus. It is essentially due to the stimulation of consummatory contact receptors together with cœnæsthesis at a high potential level. Somewhat similar pleasure is experienced in a warm bath or in the drowsy stage of awakening from sleep. In both, contact receptors and organic sensations form the source of the affective tone. On the other hand, even the strongest light on the retina fails directly to elicit physical pain. Yet such reactions are by no means ordinarily devoid of affective tone.

"The relative haste with which an animal when hungry approaches food offered to the visual field suggests that conation attaches to the visual reaction by association through memory with affective tone. By associative memory a tinge of the affective tone of the consummatory reaction may suffuse the anticipatory. The latter becomes directly a pleasure-pain reaction.... When 'after a few days the new-born chick leaves ladybirds unmolested while he seizes wasp-larvae with increased energy'

(Lloyd Morgan) he affords evidence that reactions of his projicient receptors have acquired a new value, and that value is made up *mediately* of affective tone."[1]

The meaning which the projicient sensation thus obtains greatly reinforces the conative intensity of the reaction to the stimulus.

"It has given the stimulus increased force as a spring of precurrent actions aimed at a final consummatory one. It has given this not by altering the external stimulus, nor the receptor organ, but by, among other alterations, altering internal connections of the receptor arc. Thus it is that, be it by associative memory or other processes, the reactions of the 'distance-receptors' come in higher animals to reveal a conative driving force which is perhaps the end for which these psychoses exist"[2]

Conversely, the series of reactions, short though they be, initiated by non-projicient receptors, are not wholly devoid of *conative* appearance.

It will be seen that the varieties of affective tone thus mediately acquired by anticipatory reactions are the results of experience, and must be attributed to intelligence rather than to instinct. If they possess any immediate affective tone, inherently bound up in them, it has become suppressed or replaced in man. It seems easier to adopt the view that some germ of memory and some germ of anticipation may be inherited. If so,

"we may suppose that, in the time run through by a course of action focussed upon a final consummatory event, opportunity is given for instinct, with its germ of memory, however rudimentary, and its germ of anticipation, however slight, to evolve under selection that mental extension of the present backward into the past and forward into the future which in the highest animals forms the prerogative of more developed mind."[3]

It is to be noted, however, that even in man, the stage of highest development, the anticipatory reaction is not necessarily focussed upon the final end. The attractions of the female, for example, arouse emotion and set appropriate reactions in train, without the final biological end being realized or having any conative value.

So far as the *first* occurrence of an instinctive activity is concerned the visceral reactions are part of the motor response and cannot have any effect in arousing the purely instinctive or proto-emotional state. This proto-affective state, however induced, is immediately modified by the backstroke sensory effects, not only of the visceral but also of the somatic reactions. We must conclude that the proto-emotion, which is only once experienced, if indeed it is ever experienced in its purity, is the resultant of the affective tones of the somatic stimuli.

[1] Sherrington, *op. cit.* p. 331.
[2] *Ibid.* pp. 331–2.
[3] *Ibid.* p. 332.

Just as the constellation of stimuli arouse meaning in cognition as the result of a perceptual synthesis, so they arouse emotion in affective consciousness by a parallel psychological synthesis. In these two syntheses, the potency of the individual stimuli of the constellation differs widely. As Sherrington has shown, it is the stimuli to the non-projicient receptors which play the dominant part in the affective state. They arouse sensations which are referred to some part of the body itself, and are therefore charged with pleasure-pain feeling. The stimuli to the projicient receptors prevail in initiating the cognitive state, and their messages are interpreted as qualities of objects in the external world. These only acquire affective tone by some of the many modes of association.

This wellnigh abstract proto-emotional state is a feeble thing compared with the emotion aroused by similar constellations of stimuli on subsequent occasions. Here the content of the affective state has been elaborated and enriched by backstroke and by associated memory. It is thus a fully developed emotional state, with its preponderant suffusion of bodily feelings, which has been the subject of so much discussion. So preponderant, indeed, is the bodily element that its influence permeates common parlance—"anger swells within the breast," "he is a good-hearted fellow," "his bowels yearned," and so on. It has penetrated psychology and is the basis of the theories of William James and Lange. Lange attributes all emotional tone to vaso-motor reactions in the viscera, skin, and brain. James attributes it to a wider field—all the visceral and organic disturbances, including sensations from the somatic muscles, tendons, joints, etc. (the proprio-ceptive field). Sherrington's experiments on dogs, in which not only the spinal cord was divided high up in the cervical region but also the vago-sympathetic nerves cut, appear to me to disprove these theories in their crude form as the all-embracing explanation of emotional tone. These animals' brains received no afferent impulses from any part of the body, including the viscera, behind the shoulder—yet they showed many manifestations of various emotions, notably disgust for dog's flesh The fact that one puppy was operated on when nine weeks old seems to negative Lloyd Morgan's objection that "re-presentative after-effects in the situation were not excluded "

But though the purely instinctive or proto-emotion owes nothing to intero- or proprio-ceptive stimulation, unless by inheritance, there is no doubt whatever that the emotion of the experienced animal owes much to it. When the blundering puppy first "frightened" the

moor-hen the instinctive dive was perhaps little more than the inherited reaction of an organic machine and the accompanying emotional tone primitive and immature. Yet no sooner was the dive started than the activity of the skeletal muscles poured "muscle sensations" into the consciousness of the bird, and to these were added others due to quickened respiration and heart beat and innumerable vaso-motor reactions Nor is this all, for it has been shown that fright leads to a sudden outpouring of secretion from various glands, notably from the suprarenal bodies The active secretion of these bodies, adrenalin, poured into the blood stream, has an enormous effect in raising the blood pressure by constricting the smaller arteries, as well as other effects. The influence of these internal secretions or hormones is only now becoming known That the most powerful yet discovered should play so important a part in relation to a primitive emotion such as fear is a discovery of far-reaching importance Others are known to affect the most important functions of life and reproduction, so that their biological significance is very great Thus, the pituitary secretion influences growth and structural development, secretions from the sexual organs influence the emotions and activities associated with sexual relations, the secretion of milk, etc., and intestinal internal secretions stimulate digestive glands, and so on We may conclude that the chemical actions of these hormones, themselves, as we have seen, sometimes set free by emotional states, originate vascular and other changes which are accompanied by alterations in the affective state. The increased blood pressure of the adrenalin reaction is accompanied by heightened tonus of muscles, quickened cerebration and a condition of alertness of the whole organism Where, as in higher vertebrates, an instinctive reaction implies coping with a prolonged and changing situation these changes occurring in the early stages prepare the way physiologically and psychologically. It may be that the immediate response is the almost undiluted reaction of an organic machine If so, it starts a train of physiological activities which tune up the psychological state It is to be noted that the accompanying affective response is organically precedent of the cognitive response and facilitates the latter. Thus it comes about that the emotional response is the most characteristic feature of the pre-eminently *instinctive* reactions.

Further, we see that the fully developed emotion of the experienced animal is the proto-emotion, as already defined, elaborated and enriched by backstroke from previous emotional *responses* to similar but only approximately identical, previous situations—and of these

two elements the emotional response attains ever increasing importance as a driving force. Cognition, even on the perceptual plane, carries meaning and is accompanied by an affective state. It is the affective state which initiates conation, and cognition which guides it intelligently by the appropriate modification of instinctive reactions. The proto-affective state is enriched and reinforced by backstroke. the cognition, associative memory, is enriched by backstroke and becomes intelligent.

CHAPTER IV

PERCEPTUAL PATTERNS

1. Presentation—Consciousness

The observations and analysis of instinctive behaviour in lower animals, briefly discussed in the previous three chapters, enable us to form some dim idea of perception divorced from most of the contaminating effects upon it of those higher mental activities which belong *par excellence* to man, and which are mediated by the neopallium.

We find that the behaviour of an animal is determined by (1) inherited factors, and (2) experiential factors.

Experiential factors are derived from the impressions received by all the sensory organs from all the adequate stimuli which they receive

Experience of a given presentation is the resultant effect on consciousness of (1) extero-ceptive impulses, (2) proprio-ceptive impulses, (3) intero-ceptive impulses, (4) affective responses, (5) cognitive responses, (6) past experience (α) the state induced by immediately preceding experience, (β) past experience of a similar nature, re-presentation, memory, (7) the future state—conation, pre-perception, (8) the effect of all the above on inherited dispositions.

All these form a single complex experiential pattern which, cognitively regarded, possesses meaning. It is linked to the immediate past, growing out of it by the change which the experiential pattern undergoes as new factors appropriate the focus of attention in the relatively indifferent field. It is linked to the future by the succeeding pattern, which is determined by the resultant behaviour. That behaviour is determined by innate instinct and acquired intelligence, being directed to the preservation of the individual and of the species, terms which in higher species include the manifold sublimations of these crude fundamental biological aims. This behaviour itself reacts upon the pattern, changing it independently of such new presentations as fortuitously arise.

This continuously changing pattern is the stream of consciousness. Though complex it is unitary, and *is* the individual's "self." Viewed from the vantage point of man's consciousness, it is continuous even though it is always in part potential, and sometimes appears to be

wholly potential. This potential consciousness is the so-called "unconscious."

There are those who deny the psychical existence of "unconscious presentations," but this is really due to the inadequacy of the terminology. As a matter of fact, most of our mental contents are unconscious, parts only rising above the threshold on appropriate stimulation. As James Ward says[1], "the threshold is not comparable to a mathematical line, on opposite sides of which there is an intensive discontinuity." There is an unconsciousness in time, *e.g.* during sleep, inattention, and in oblivescence; and in space, as in the periphery of the field of consciousness. The unconscious embraces "unwitting"[2] behaviour, such as is associated with much of instinctive activity and acquired habit, as well as "suppressed" ideas, which include memory images, implicit ideas[3] (which correspond to ideas which have undergone involution so as to form "presentational dispositions"[4] by a process comparable to the integration of reflexes by inhibition), and ideas suppressed by conflict (Freud). Suppression, or the replacement of kinetic consciousness by potential consciousness, is an adaptation which facilitates behaviour of the kind best designed for biological ends. It is, indeed, pragmatically as important a factor to consciousness as oblivescence is to memory.

It is universally admitted that the crude elements of consciousness, such as experience of pain, tactile, optical, and other impressions, are subserved by the nervous system. It has, however, been generally accepted that higher forms of consciousness are subserved only by the cortex cerebri I think this is wrong, both on physiological and on psychological grounds We have seen (Chapter III, 2) that a decerebrate (not a "mid-brain") animal is by no means unconscious, even so far as what I have called kinetic consciousness is concerned. Psychologically, consciousness is unitary, and is a complex made up of all the impressions derived both from the outer world and from the inner world of the body—including the memory traces of the past and the conative anticipations of the future. We cannot say when consciousness begins in the animal scale, but the simplest hypothesis is to attribute some form of consciousness to all living organisms. That it should be crude and undifferentiated in crude and undifferentiated lowly organisms is but in accordance with

[1] *Psychol. Principles*, p 91, Cambridge University Press, 1918.
[2] Rivers, *Instinct and the Unconscious*, p. 16, Cambridge University Press, 1920.
[3] See Stout, *Manual of Psychology*, p. 191.
[4] Ward, *op. cit.* p. 97.

biological principles. Here we regard it as a mere sentiency, embodying the germs of those differentiations which would be inconceivable but for the knowledge which our own highly differentiated consciousness enables us to acquire

Similarly, there is no good reason why we should refuse conscious concomitants to thalamic[1] or even spinal activities, even though they be suppressed in man. This may be regarded as a verbal quibble, but in the light of the admitted potentialities of the "unconscious" it does not appear to me to be so.

Enough has been said to show that the simplest experience is a highly complex event. Seeing that we must accept the participation in it of so many afferent impressions—extero-ceptive, intero-ceptive, proprio-ceptive, and so on—it is clearly a synthesis of these impressions. But it is a synthesis *sui generis*, quite unlike the physical, chemical, and other syntheses with which we are familiar. Yet, like any other complex, we may hope to gather some deeper knowledge of its nature by studying it from two points of view. We may endeavour to analyse it into its various constituents, or we may try to discover the laws which govern the synthesis of its components. Both methods are fraught with difficulty, and are liable to lead to erroneous or very doubtful results Yet each may be used as a control to the other, and some inkling of the truth may thus be attained.

It is, perhaps, natural that the synthetic method has found most favour in the past, for it seems to follow the essentially scientific method, which consists in the reduction of variables to a minimum. It is the method derived from the physical sciences, where it has been found eminently useful, for, in them, some near approximation to mathematical accuracy is possible Yet even there the synthetic method leads to surprising results. Hydrogen and oxygen can be made to combine in definite proportions, but the resultant is a new creation, water. However much we know about hydrogen and oxygen themselves, we could not have foretold this result, so that it is in a sense a creative synthesis, or, as Lloyd Morgan would call it, an example of emergent evolution on the physical plane. The endeavour to carry over this method to psychological problems has led to many errors, though with the countervailing advantage of eliciting many valuable discoveries. It has led to a particulate view of psychological processes which is at variance with the fundamental unity of consciousness. The syntheses which emerge on the biological

[1] *Vide infra*, p. 71.

plane seem to be of a different nature. Everything there seems to be more plastic—πάντα ῥεῖ

In dealing with events in consciousness we are dealing with plastic and ever-varying elements of sensation and so on; and these entities, belonging to apparently quite incongruous types, differing utterly from each other in their qualities, are synthesized or integrated into new units of consciousness in a manner which physical and chemical laws fail entirely to explain[1]. No known physics or chemistry affords help or even analogy in the integration of a complex of such incompatibles as extero-ceptive impulses (visual, tactile, auditory, etc.), intero-ceptive, proprio-ceptive, and so on, into the unit presentation of any given experience. Hence many have held that conscious processes are on so different a plane that they are independent of such material basis as the nervous system But, while it is quite scientific to deal with the body of psychological facts as a special domain, dominated by purely psychological laws, it is unscientific to refuse the possibility of some future ætiological correlation between nervous processes and all psychological processes, even the highest concepts. As C. S Myers has said

"When we come to consider the difference between mind and *living* matter the distinction is reduced almost to vanishing point. For it is essentially the same purposive, directive, plastic and constructive characteristics, distinguishing living from dead matter, which, raised to a still higher power, distinguish both nervous and mental activity from the activity of other living tissues The problems of life that confront the physiologist are precisely those of mind that confront the psychologist Life and mind must ultimately be solved in similar terms From each we can abstract the mechanical, comparable to what we know of the activities of lifeless matter. But it may be that the apparently blind mechanism of which physics treats is only an abstraction from a purposeful direction that plays its part in the larger universe regarded as an organism, just as we are bound to conceive of such direction even in the lowest living individuals, even in the lowest physiological levels of the higher living organisms"[2]

I would go further and point out that, in the limit, physicists are to-day practically admitting the identity of matter and energy, and the hypothesis of the creation of conscious processes out of nervous processes is, in form, as little unscientific as the creation of physiological impulses by the suitable application of physical energy. Thus Professor Eddington, a mathematician, astronomer and physicist, says[3]:

"There is nothing to prevent the assemblage of atoms forming the brain from being

[1] *Vide infra.*

[2] *Lancet*, Nov 29th, 1924, p. 1111.

[3] *Science, Religion and Reality*, edited by Joseph Needham, London, 1925.

itself a thinking machine. . . Our precise knowledge of certain aspects of the behaviour of atoms leaves their intrinsic nature just as transcendental and inscrutable as the nature of mind, so the difficulty of interaction of matter and mind is lessened."

Reasoning on these lines, we may ask why has consciousness "emerged"? I think that the answer is that the fundamental utility of consciousness for the animal species is for the very purpose of synthesizing and integrating the apparently incongruous elements of which consciousness is made up—extero- and intero-ceptive impulses and so on. Indeed, applying Sherrington's terminology, consciousness may be regarded as the aggregation of final common paths.

"A great principle in the plan of the nervous system is that an effector shall be at the behest of many receptors, and that one receptor shall be able to employ many effectors In respect to this there are two conditions which the nervous system satisfies. One is that the effector is at the behest of various receptors which can use it simultaneously and use it harmoniously all in more or less the same way. Thus an advantage accrues in that their reactions sum, *even though the receptors may be of different modality*[1]; and by summation the threshold is lowered and the organism more sensitized to the environment."[2]

This, as applied to consciousness, is the rationale of perception Scarcely less important is another condition which the nervous system satisfies, namely, *interference.*

"In animals of complex organization the activity of one effector organ may interfere with the function of another, *e.g* in the case of muscles which when contracting pull in opposite directions at the same lever This wasteful confusion is avoided by one receptor having power not only to throw a particular effector into action, but also to throw the opposed effector out of action. This action it exercises not peripherally but within the nervous system, at the entrance to a common path."[3]

There are thus two great co-ordinative processes—*plurireceptive summation and interference.* "Without these the nervous system is shorn of its chief powers to integrate a set of organs or an organism."[4]

The actual integration of diverse physiological impulses is an active—kinetic—process, and it manifests itself in kinetic consciousness. But there are hierarchies of integration, and when a lower level integration has proved sufficiently serviceable to any given species it becomes part and parcel of the make-up of the individuals of the species. It then generally assumes the characters of potential consciousness, or in common terms is relegated to the "unconscious"

Further, there are many such integrations at every level—and there are many levels, only great groups of levels being collected within the confines of such terms as reflexes, instincts, and so on.

[1] The italics are mine.
[2] Sherrington, *op. cit.* p. 310.
[3] *Ibid.* p. 311.
[4] *Ibid.*

Physiologically the lower levels are, in vertebrates, associated with the activities of the spinal cord and medulla; higher levels with the mid-brain and thalamus, higher still with the palæopallium and neopallium.

There are comparatively simple integrations and there are integrations of simpler integrations, forming different "patterns" *in* each level and *at* each level. And the most important point is that *all these patterns are of biological significance*—they are adaptations in the service of the individual or the species. Hence the most significant features of any pattern are themselves extremely complex.

Just before Lloyd Morgan's moor-hen made its first dive we may conjecture that its stream of consciousness was composed of a relatively placid undercurrent of cœnæsthesis upon which were superposed the iridescent ripples of perpetually changing perceptual patterns. The cognitive and affective responses to these patterns were relatively slight, and carried merely such traces of meaning as to stimulate mildly only such peaceful instinctive dispositions as curiosity, play, and so on. When the puppy arrived upon the scene the errant awareness of the moor-hen was suddenly activated by a peculiarly insistent presentational pattern. Stimulation of the visual, auditory, and perhaps olfactory and other organs gave rise to a perceptual pattern of quite exceptional potency in arousing awareness to a situation of profound biological meaning. It is to that *situation as a whole* that the bird reacted. In some manner, which we must later attempt to explain as best we can, the constellation of objective sensations are welded subjectively into a unit pattern from which there emerges a meaning which is different from and more than the sum of all the meanings which can be attributed to the individual factors which make up the pattern. Thus, the pattern as a whole may be regarded as the unique stimulus to certain innate dispositions, arousing in them the emotion of fear, thus giving rise to the appropriate instinctive response—a dive.

Another example may be taken from ontogenesis. In very early days of life a child's attention is attracted by a bright light, and the eyes are moved so that the image of the light is formed on the macula of each eye. A child is soon much more attracted towards its mother, and its behaviour towards her differs according to the tone of the mother's voice, her facial expression, and so on Now, facial expression is a very complex visual impression, and it is scarcely conceivable that in this very early age the child has succeeded in accurately correlating the innumerable visual impulses into which a

facial expression can be analysed. We must rather regard the child's impression as a psychological pattern made up of the integration of a number of relatively undifferentiated auditory, visual, and other complexes, of which the still relatively undifferentiated visual complex forms the focus. It responds to this complex by appropriate behaviour simply because through countless preceding generations its ancestors have responded to similar and even less differentiated complexes[1].

The lower down the animal scale, the less differentiated are the complexes to which the individual responds—and his responses are biologically determined, *i e.* they are strictly utilitarian. Hence we conclude that the behaviour response is dominated by the psychological pattern, and that higher patterns dominate lower patterns. But, since the lower patterns are more primitive they are the least vulnerable—teleologically because they are concerned with vital processes upon which the survival of individual and species depends. The higher patterns are more highly differentiated and, therefore, more vulnerable. So that even these complex psychological patterns can be divided into great groups—one, protopathic, dyscritic and of vital import, and another epicritic and of cognitive import.

2. Sensation—Perception—Meaning

Before passing on to investigate more closely the perceptual pattern it will be well to define more precisely the distinction between sensation and perception, a distinction which is often ignored or misunderstood, especially by physiologists.

In the last chapter I have spoken of "objective sensations" being welded into a subjective perceptual pattern. Psychologically, sensations are the objects presented to the subject—"objective changes as they first break in upon the experience"[2] of the subject, and a sensation may be defined as "the simplest element in our analysis of the objective factor in experience."[3] This strictly accurate psychological definition is recognized and emphasized by Sherrington in his use of the term "receptor," and "reception" and "recept" would remove ambiguity if employed for the act of sensing and the object sensed.

Perception, or the act of perceiving, consists in the integrating of recepts, which may themselves have undergone differentiation and

[1] See Koffka, *The Growth of the Mind*, London, 1924.
[2] James Ward, *op. cit.* p. 105. [3] *Ibid.* p. 114.

segregation of the differentiated products, resulting in the emergence of a percept. This process of differentiation, segregation, and integration, to which I have applied the term apocritic principle[1], occurs frequently in the evolution of higher modes of consciousness. The psychological unit is the percept which can be analysed into constituent "sensations" only by a process of abstraction. An isolated sensation is never experienced.

The percept, the product of this apocritic process, is not a mere collocation or summation of sensations These have been integrated into patterns, in which the whole is greater than the sum of its parts; something new has emerged in consciousness[2].

The lower we go down the scale, phylogenetically and also ontogenetically, the less differentiated is the recept derived from the sensory presentation, and its response in consciousness must be regarded as a "blooming buzzing confusion," to use William James's picturesque phrase None the less, it probably possesses affective tone and may give rise to motor acts of the nature of reflexes. Integration of recepts gives rise to percepts, whose response in consciousness is an integration of affective tones and their cognitive accompaniments, emerging as an emotion charged with meaning, resulting in an integration of motor activities of the nature of an instinct

Differentiation of receptors leads to differentiation of sensations, which thus become more amenable to analysis, especially when that stage is reached at which stimulation—adequate or inadequate—of the neural mechanism gives a specific response—the so-called "specific energy of nerves" of Johannes Muller Only then can we begin to talk of sensations and to submit them to analysis Such analysis shows that, in addition to determinate qualities, each possesses quantitative variations in respect of intensity, extensity, and protensity (duration). All these factors are primarily dependent upon and vary—in some cases according to a well-established law (Weber-Fechner Law)—with the nature, intensity, distribution, and time relations of the physical stimuli applied to the specific receptors. But in man, at any rate, these variations may be modified by the state of consciousness of the subject Thus, the inherent intensity[3] due to the objective stimulus is altered by the distribution of attention, so that its effective intensity may be greater or less, and is maximum when the recept occupies the focus of attention, in which case it

[1] *Brit Jl. of Ophth.* I, 1917.
[2] *Vide infra*, Chapter IV, 3.
[3] James Ward, *op cit.* pp 69, 119.

usually follows Weber's law. The inherent intensity is diminished when attention is diverted, and also if the integration of the presentations results in a perceptual pattern which arouses interest in the situation as a whole—in other words, by complication. This is another instance of backstroke, of which more will be said later.

At the risk of some repetition we may say that in the primitive or *dyscritic stage*, there is, as the term implies, little differentiation and little discrimination. The constellation of recepts from the presentation gives rise to changes in the primitive stream of consciousness or psychoplasm of such a kind that the cœnæsthesis is raised in potential, thus arousing an awareness charged with affective tone, which is either pleasant or unpleasant. The effector mechanism is thereby stimulated to bring about a mass reaction which is positive or negative according to the positive (pleasant) or negative (unpleasant) affective tone, the conscious response, and, therefore, also the motor response, being dominated by biological requirements, and accordingly in so far teleologically determined.

In the *epicritic stage*, differentiation of the receptor mechanism permits of differentiation of the recepts. The constellation of recepts gives rise to a perceptual pattern in which the cognitive elements are so differentiated that the diverse sensations are discriminated. Awareness is focussed upon those features of the pattern which are of greatest biological significance, and becomes attention. The perceptual pattern fills the field of attention, but attention leads to the selection and segregation of the most important features in this pattern, so that part of it occupies the focus of attention and becomes a more highly discriminative pattern in which qualitative and quantitative details of the constituent sensations spring into consciousness. At higher levels within the epicritic stage—but most of all within the syncritic stage, when biological significance has undergone sublimation—attention becomes interest. In both—attention and interest—there is a growth of the forward-looking tendency which is germinal in awareness, and which now becomes a definite conative tendency.

The psychical content of the experience, *e.g.* one which eventuates in an instinctive response, differs on the first occasion as compared with subsequent similar occasions. On the first occasion the sensory factors selected for integration are selected partly by natural selection—an inherited capacity which consists essentially in the *rejection* of biologically indifferent recepts—and partly by subjective selection, which consists in the selection of factors peculiarly germane

to the particular experience of the individual. In the stereotyped instinctive reactions of insects the latter mode is practically negligible. On the second and subsequent occasions subjective selection plays an increasingly important rôle, and is largely responsible for intelligent modification of instinctive reactions through "learning by experience."

The integration of the selected factors leads to the emergence of the meaning of the perceptual pattern which occupies the focus of attention. But not only have the cognitive elements undergone selection and integration. Differentiation and integration of the affective elements also occurs, but leads to much less discrimination. Whenever epicritic differentiation occurs the predominant dyscritic elements persist[1], but this is especially so with affective tone. It still retains the dyscritic character of pleasant or unpleasant, but becomes elaborated into an emotional state, which, though vague and difficult to analyse, possesses specific qualities in different situations. These changes are associated with widespread organic reactions—vaso-motor changes, outpouring of hormones, etc.—and while it cannot be admitted that they are caused by them, as the James-Lange theory suggests, they are certainly modified by them by backstroke. The organic conditions are a prepotent factor in the cœnæsthesis, and hence emotional states have a diffuse character which seems to pervade the organism as a whole. In experiences giving rise to more typically instinctive responses the affective tone looms large in consciousness, with relative inhibition or suppression of cognition. In higher syncritic stages, interest is essentially cognitive and affective tone is relatively inhibited or suppressed.

On the effector side the epicritic stage is characterized by a differentiation of the primitive dyscritic mass reaction. The laws which govern the integration of the selected differentiated responses, their modes of selection and of integration, are a fundamentally physiological problem, to the solution of which we owe most to Sherrington[2]

3. In Man

So great are the differences in the processes which occur in the inorganic world and in the world of living organisms that a sharp line of demarcation has been drawn between them. Many of the simpler processes occurring in living organisms are explicable by the physical and chemical laws which obtain in the inorganic world.

[1] *Vide infra.*

[2] *The Integrative Action of the Nervous System.*

Others are brought into this category only with great difficulty, and many seem to elude this explanation altogether. Rather than revert to the methods of the Dark Ages and appeal to a *deus ex machinâ* in the form of some hypothetical vital force, we should assume an attitude of agnosticism and attribute our failure to explain the facts to ignorance, always striving to build up our knowledge upon the foundation of the known before invoking the hypothetical unknown "Si nous pouvons définir la vie à l'aide d'une conception metaphysique spéciale, il n'en reste pas moins vrai que les forces mécaniques, physiques et chimiques, sont seules les agents effectifs de l'organisme vivant, et que le physiologiste ne peut avoir à tenir compte que de leur action "[1] "The more accurate the methods of investigation, the better is it found that chemical and physical laws are capable of explaining physiological phenomena "[2]

Yet the fact remains that most of the processes which occur in inorganic matter are explicable on strictly mathematical laws of summation. In the organic world, on the other hand, we are accustomed to phenomena which cannot at present be explained as a mere algebraic summation of the constituent parts.

"When a cat perceives a mouse he receives a vast number of sensory impressions Visual impressions convey to him the shape and colour of the mouse, and, in addition, those successive variations in shape and colour and relationship to surrounding objects which constitute the visual impressions of movement Olfactory, auditory, tactile, and other sensations derived from the mouse have their specific characteristics in relationship to the cat None of these impressions taken alone or in groups, or even altogether, suffices to constitute the perception of the mouse by the cat The mouse is perceived as a mouse, and indeed as a particular and unique mouse, only when many or all of the sensory impressions are sifted out of their context, and selected and organized into a new complex unit That unit is a new creation While it retains many of the essential characteristics of its constituent sensory "molecules," it endows them with entirely new properties The sensations have been synthesized into a perception, the outstanding feature of which, as emphasized by Professor Stout, is the "meaning" which it carries with it, and which is truly and scientifically described as being created by the synthesis "[3]

Similarly the child's perception of the mother's face "contains" more than the sum of the constituent visual impressions, the musical melody more than the sum of the impressions derived from the constituent notes, the spoken phrase more than the sum of the meanings of the constituent words.

These "patterns," in which the unit whole is greater than the sum

[1] Claude Bernard, *La Science expérimentale*, Paris, 1878.

[2] Bayliss, *Principles of General Physiology*, 2nd ed. p 630, London, 1918.

[3] Parsons, *Brit. Jl. of Ophth.* I, 1917.

of its parts, in which something new has emerged as the result of integration, have long been recognized by psychologists. In the voluminous literature which has been devoted to them, especially recently, little or no attention has been paid to their phylogenetic evolution, with the exception of Köhler's work on chimpanzees[1] Careful analysis of this aspect of the subject would, I think, have prevented some of the errors which have arisen. At the same time, of course, the analysis of the perceptual patterns of lower animals, as of other items of animal psychology, must perforce deal with inferences derived from our knowledge of perceptual patterns in man.

The first precise statement of the problem was made by von Ehrenfels in 1890[2]. He originated the term *Gestalt*, which has been translated "shape" by Spearman[3]; "pattern" seems to me to be a better term. von Ehrenfels defined patterns as "those psychical conditions and processes whose characteristic peculiarities and activities are not explicable by the mere summation of similar peculiarities and activities of their so-called parts"[4] He came to the conclusion that the essential quality which determines a pattern is its underlying *meaning*, *e g* that of a word or melody.

The subject was treated incidentally by Wundt, in his principle of "creative synthesis" (which is equivalent to Lloyd Morgan's "emergent evolution"), and his pupils[5], by Meinong[6], in his theory of complexes and relations, and his pupils[7], and Witasek[8]. Schumann[9] attributed the formation and saliency of a pattern to the distribution of *attention*, and one of his pupils[10] gave a great impulse to the theory of patterns by a paper on the Visual Perception of Movements (see Chapter IX) Wertheimer gave a physiological explanation which is very reminiscent of Sherrington's plurireceptive

[1] *The Mentality of Apes*, London, 1925

[2] "Ueber Gestaltqualitäten," *Vierteljahresschrift f wiss Philos.* 1890.

[3] *Brit Jl of Psychol* XV, 223, 1925 (Bibliography)

[4] "Diejenigen psychischen Zustande und Vorgange, deren charakteristischen Eigenschaften und Wirkungen aus artgleichen Eigenschaften und Wirkungen ihrer sogenannten Teilen nicht zusammensetzbar sind."

[5] *E g.* Kruger, *Philos Studien*, II, 221, 1907.

[6] *Untersuchungen*, p 303, Leipzig, 1904; *Arch f. d. ges. Psychol.* XXXII, 396, 1914.

[7] *E g.* Benussi, *Zeitschr f Psychol* XXIX, 264, 385, 1902; XLII, 22, 1906; XLV, 188, 1907, LI, 73, 1909; LXIX, 256, 1914.

[8] *Psychologie der Raumwahrnehmung des Auges*, Heidelberg, 1910.

[9] *Zeitschr. f. Psychol.* XXIII, 1, 1900; XXIV, 1, 1900; XXX, 241, 321, 1902; XXXVI, 161, 1903; reprinted, 1904.

[10] Wertheimer, *Zeitschr. f. Psychol.* LXI, 251, 1912.

summation and interference. It is expressed in obscure phraseology[1], but amounts to this—that the explanation is not to be found in the excitation of the stimulated cells, however produced, or in the sum of these excitations, but in a unified constellation of cross interactions which arise out of the primary excitation.

In 1918 Köhler[2] published a learned treatise to show that similar patterns, in which the whole is greater than the sum of the individual parts, also occur in physical states, *e g.* in the electrostatic condition of an isolated conductor. He concludes that similar stationary or oscillating ("periodic stationary") electrical currents, associated with corresponding movements of chemical ions, occur in the somatic visual field, and thus give rise to visual perceptual patterns.

Koffka[3] has explained and elaborated Wertheimer's theory and pointed out some practical applications in ontogenesis.

The veteran G. E. Muller has for many years been elaborating a theory of complexes of which the *Gestalttheorie* is really a part He has recently summed up his views in a brochure[4] in which he also criticizes Wertheimer, Köhler, and Koffka He holds that a complex is "a unified whole subserving the development or experiencing of psychical activities," and of this whole the pattern (*Gestalt*) is a characteristic (*Eigenschaft*). The distinction does not appear to me to be so fundamental as Muller thinks.

The theory of patterns has derived many of its facts and much of its importance from observations on the difficult problem of the perception of movement[5]. I propose to deal here chiefly with its application to other problems of perception.

If we look at a group of dots arranged thus .⁝ they may be regarded either as a square with a central spot ⊡, a cross with four dots ⁜, as parallel lines ☰ ⫼, etc. The apparent

[1] "*Nicht die Erregungsvorgange in den erregten Zellen selbst* (peripherwarts oder durch 'Assoziationsleitung' empfangen) *oder die Summe dieser Einzelerregungen* das einzig wesentliche sind: sondern eine wichtige und fur manche, psychologische herauszufassende, Factoren direct wesentliche Rolle charakteristischen *Quer- und Gesamtvorgangen zukomme, die aus der Erregung der Einzelstellen* (ev. als *Einfallstellen*) *als specifisches Ganzes* (grosseren Bereichs) resultieren" (*Zeitschr f Psychol* LXI, 251, 1912).

[2] *Die physischen Gestalten in Ruhe und im stationaren Zustand*, Braunschweig, 1918; Erlangen, 1924 Cf. Becher, *Zeitschr f. Psychol.* LXXXVII, 1, 1921.

[3] *Zeitschr. f Psychol.* LXVII, 353, 1913; LXXIII, 11, 1915; LXXXII, 257, 1919; *Psychol. Forschung*, II, 148, 1922; III, 397, 1923; *Brit. Jl. of Psychol* XIV. 289, 1924; *The Growth of the Mind*, London, 1924.

[4] *Komplextheorie und Gestalttheorie*, Gottingen, 1923.

[5] *Vide infra*, Chapter IX.

length of the line ←·—·→ differs according to whether the spots are ignored or whether they are linked up in various ways, *e.g.* joined to cut the line by two vertical parallel lines, or joined to the ends to form a Müller-Lyer figure. Both examples afford evidence of the ambiguity (*Mehrdeutigkeit*) of the complexes, and the latter gives evidence of the "inadequacy" of the presentation[1]. The latter again shows that perceptual patterns are an important factor in most of the well-known geometrical-optical illusions[2] That the configuration (*Auffassung*), and with it the judgment of localization, direction, size, and movement, depends largely upon attention, as specially insisted upon by Schumann[3], is undoubted, and is emphasized by the fact pointed out by Rivers[4] that illusions of size are most marked when attention is directed to the figure as a whole, and are diminished by isolation of the details In fact, the more familiar one is with the figures the less insistent are the illusions. Moreover, there are those who do not see the illusions, and Benussi thinks that people can be divided into isolating and synthesizing types. Children are said to see the illusions better than adults[5], though their visual discrimination of size is as well developed as in adults, but there are probably here also individual variations[6].

Attention alone will not account for the emergence of a pattern. As von Ehrenfels rightly pointed out, the essential factor is the meaning, and that is apparently the sense in which the term *Vorstellungsproduktion* is used by Meinong, Witasek, and Benussi[7]. In the examples already given there is little to determine the meaning which shall be chosen and which determines the pattern: it appears to be fortuitous It is different, however, in cases of geometrical per-

[1] Benussi, *Zeitschr. f Psychol* XLII, 22, 1906, XLV, 188, 1907

[2] Cf F. B Hofmann, *Die Lehre vom Raumsinnes des Auges*, pp 106 *sqq.*, Berlin, 1920.

[3] Cf Buhler, *Die Gestaltwahrnehmungen*, Stuttgart, 1913.

[4] See *Mind*, N S v, 71, 1896, *Reports of the Cambridge Anthropological Expedition to the Torres Straits*, II, Cambridge, 1901; *Ann d'Oculistique*, CXXXII, 455, 1904; *Brit. Jl. of Psychol* I, 321, 1905

[5] Binet, *Rev. philos.* XL, 11, 1895; van Biervliet, *ibid* XLI, 169, 1896; Hasserodt, *Arch. f. Psychol* XXVIII, 336, 1913

[6] Benussi, in Meinong's *Untersuchungen*, p. 429, Leipzig, 1904; Giering, *Zeitschr. f. Psychol.* XXXIX, 42, 1905.

[7] The term "presentation," which is derived from *Vorstellung*, should be reserved for sensory presentations of objects, *i.e.* on the perceptual plane In such a sense *Vorstellungsproduktion* is practically equivalent to *Gestaltproduktion*. German writers, however, do not adhere to this strict definition, and it is clear that Meinong and his pupils use it in a wider sense involving ideation. Thus, Witasek uses the word *Gestaltswahrnehmungsvorstellung*!

spective. Fig 2, for example, may be regarded either as a spherical square, or as the outline of a child's kite[1]. In the former case the sides and angles appear equal, in the latter the left upper angle appears more obtuse, the right lower more acute. Similarly with representations of a cube (fig 3). *A* gives no pattern of a cube. In *B* the perception of depth is aroused, either consciously or unconsciously, and the acute angles are over-estimated, the obtuse under-estimated[2].

Enough has been said to show that patterns must play a very important part in the discrimination of position, size, form, and distance.

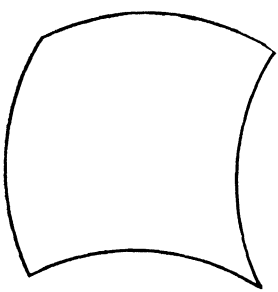
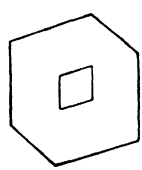


Fig. 2



A

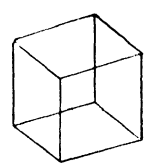


Fig. 3 *B*

The emergence of patterns is an adaptation which has proved useful to the organisms, otherwise neither it nor they would have survived Since it results from an integration of elementary sensations and perceptions, such as relative and absolute localization, direction, size, and so on, all of which can be proved to be based upon inherited dispositions subserved by innately adapted nervous mechanisms, it too must be based upon innate foundations. But, like them, it is elaborated by experience. A word is first read by the forms of its letters; later it is recognized as a unit pattern; and still later groups of words form a unit pattern. When a pattern has become familiar, it is aroused even if many of its parts are lacking or are unnoticed. Hence the expert reader makes an inefficient proof-reader. One of the most important functions of the pattern is, therefore, the arousing of meaning from incomplete data (*erganzende Gestaltproduktion*). The "incompleteness" of the data may be of various kinds. Factors may be lacking from the retinal presentation, or they may occupy only the periphery of the field of attention, or they may be entirely subconscious.

[1] F. B. Hofmann, *op cit.* p. 133. [2] Filehne, *Zeitschr. f. Psychol.* XVII, 15, 1898.

Allied to "incompleteness" is the very striking feature of the pattern that it is aroused by like presentations in spite of spatial and temporal differences. Thus a presentation which arouses a given pattern by direct visual fixation can arouse the same pattern when it falls upon the peripheral retina. A melody is recognized in spite of a change of key, and to the accomplished musician becomes salient even if hidden amidst variations of time, pitch, etc.—a good example of the effects of experience.

Another important feature of the pattern is rectifying capacity (*Umformung*), specially noticeable in the visual perception of depth. A circle, tilted so that its plane is not parallel to the frontal plane of the observer, forms an elliptical image upon the retina, but is recognized as a circle. An after-image varies in size according to the distance of the surface upon which it is projected, and the after-image of a bright rectangular cross ceases to appear rectangular when projected upon an oblique surface There are "memory forms" as well as "memory colours "[1]

The distortions produced by spectacles, especially such as contain correcting cylinders or prisms, are similarly rectified. F. B Hofmann[2] points out that the distortions are most disturbing for simple and familiar forms, such as lines. Linke[3] attributes many of the facts adduced by Witasek and Benussi in favour of *Vorstellungsproduktion* to *Gestaltumformung*.

Nearly allied to, if not identical with, this rectification is the "pregnancy" of the pattern on which Köhler[4] specially insists. Presentations tend to arouse "good" patterns, *i.e.* relatively simple and familiar patterns. Irregular polygons or ellipses appear circular on momentary illumination (Goldschmidt) or under a small visual angle[5]. Eidotropic movement[6] is another example[7]

G. E. Muller[8] attributes the development of the collective configuration (*collective Auffassung*) of complexes, which are characterized by patterns, to coherence factors, such as spatial proximity, equality, similarity, saliency (*Eindringlichkeit*), symmetry and contour According to him, the focussing of attention on a given part of the visual field raises the excitability of the corresponding part of

[1] Hering. See Parsons, *Introduction to the Study of Colour Vision*, 2nd ed p. 26, Cambridge University Press, 1924.
[2] *Op. cit.* p 111.
[3] *Philos Studien*, III, 393, 1908.
[4] *Op cit.* p 259.
[5] F B. Hofmann, *op. cit*
[6] G. E. Muller, *op. cit.* p. 54.
[7] *Vide infra*, p 171.
[8] *Op. cit.* p. 24.

the somatic optical field, which he calls the *formative zone*. Repetition of a given constellation of stimuli establishes a collective disposition to arouse the same pattern-response more promptly on appropriate stimulation. Such a collective disposition can be awakened by an incomplete constellation of stimuli, if the collective disposition is strong and easily aroused, and if the meaning of the presentation is sufficiently salient[1].

G E. Muller quotes some striking examples of completion of the pattern from pathological cases reported by Fuchs[2], *e g.* if the centre of a circle is fixated, so that one semicircle forms its image on the hemianopic half of the patient's field, the patient says he sees a circle, and so on. Cases of dissociation of collective dispositions are quoted from Poppelreuter[3] and Goldstein and Gelb[4]. Cases of a similar nature have been recorded and discussed by Gordon Holmes[5] A specially noteworthy case has been recorded by Winkler[6]. The patient had a visual acuity of $\frac{5}{6}$ with each eye. The fields of vision were slightly constricted. If circles, triangles, etc., were brought into the field from the left they were readily recognized If brought in from the right they were not recognized until they reached the fixation point. There was thus loss of form vision in the right halves of both visual fields. The post mortem examination revealed a tumour of the pulvinar of the optic thalamus with some degeneration in the region of the calcarine fissure of the occipital lobe.

4. The Physiological Basis

The analysis of the perceptual pattern is a psychological problem its synthesis is primarily a physiological problem.

Confining ourselves to essentially visual perceptual patterns, the neural basis, or what the Germans call the somatic optical sector, consists of the peripheral retinal receptors and their conducting paths through the layers of the retina, the optic nerves, chiasma, and optic

[1] "Es muss quasiemdeutige Beziehung zwischen empfundenem Felde und ubergreifender Simultanaufmerksamkeit bestehen" (*op. cit.* p. 34). (This sentence appears to me to be a masterpiece of confusion!)

[2] *Zeitschr f. Psychol.* LXXXIV, 1920; LXXXVI, 1920; *Psychol Forsch.* I, 1921.

[3] *Die psychische Schadigungen durch Kopfschuss im Kriege* 1914–16, Leipzig, 1917, *Zeitsch. f. d. ges. Neurol u. Psychiatrie,* LXXXIII, 26, 1923

[4] *Zeitschr f. d. ges. Neurol. u Psychiatrie,* XLI, 1918 Cf. Gelb, *Psychol. Forsch.* IV, 42, 1923.

[5] *Brit. Jl. of Ophth* II, 449, 506, 1918, Holmes and Horrex, *Arch. of Neurol. and Psychiatry,* I, 385, 1919.

[6] *Akad. van Wetenschappen te Amsterdam, Vergaderingen der wis- en natuurkundige Afdeeling,* deel XIX, 1911, S. 914 sqq ; quoted by G. E. Muller, *op. cit.* p. 46.

tracts to the so-called primary optic centres, which in man are the lateral geniculate body, the pulvinar of the optic thalamus, and the anterior colliculus or superior corpus quadrigeminum; the optic radiations from these centres through the posterior part of the internal capsule to the calcarine region of the occipital lobes; their association tracts *inter se*, and with neighbouring and distant parts of the cortex of the same hemisphere, and through the splenium of the corpus callosum with the opposite occipital lobe, etc., the centrifugal fibres from these cortical centres to the primary optic and other basal ganglia, and centrifugal fibres from the primary optic centres (lateral geniculate body and anterior colliculus) to the retinæ.

We have, therefore, to do with a peripheral mechanism, a complex lower level mechanism and a still more complex higher level mechanism, linked by long chains of centripetal and centrifugal neurones. The stimuli which fall upon the retinæ give rise to physiological impulses which traverse these complicated paths. The paths are composed of insulated fibres which carry mutually independent impulses. Whether anything of the nature of electrical induction takes place between neighbouring impulses or not is unknown, but it has been proved by the researches of Sherrington and many others that resistances are met with at the synapses. Sherrington's researches on reflexes have shown conclusively that there is a complex *physiological* interrelationship between afferent impulses of such a nature that the synaptic resistances vary in such a manner that the progress of certain groups of impulses are facilitated, whilst antagonistic impulses are impeded or inhibited. He has shown further that repetition of similar stimuli facilitates the normal responses[1] In other words, however it may be explained, physiological facilitation resulting from repetition of similar impulses occurs, and so far the theory of *Bahnung*[2] is substantiated.

The question arises whether this theory of facilitation will account for the facts of pattern perception. The chief objections to the theory have been stated by von Kries[3] and Becher[4]. It is quite certain that a mere summation of impulses, however facilitated, will not explain the facts. Moreover, as Becher points out, it is clear that since a

[1] Cf. Graham Brown, *Quart. Jl. of Exp Physiol* IX, 81, 117, 131, 1915, X, 97, 103, 1916.

[2] Exner, *Entwurf zu einer physiologischen Erklarung der psychischen Erscheinungen*, I, Wien, 1894; *Zeitschr. f. Psychol.* XXXVI, 194, 1904

[3] "Ueber die materiellen Grundlagen der Bewusstseinserscheinungen," *Programm der Universitat Freiburg i B*, 1898.

[4] *Gehirn und Seele*, Heidelberg, 1911; *Arch. f. Psychol.* XXXV, 125, 1916.

pattern produced by stimulation of the retina on central fixation is immediately reinstated when the periphery of the retina is similarly stimulated, no facilitation of the peripheral portion of the somatic optical sector can account for the phenomenon, though facilitation of higher levels still doubtless obtains von Kries concludes that the essential factor is to be found, not in intercellular associations alone, but within the cells themselves If a single cell, the fertilized ovum, is capable of containing within it, in some form or other, representatives of the characteristics of the species and of individual characteristics of the immediate ancestors, it is not improbable that nerve cells should be able to store up complex impressions and revive them on suitable excitation This theory supports the view of Hering[1] that a stimulus excites only those cells which are physiologically adapted to respond to it.

There would, therefore, appear to be two fundamental factors involved,—a constellation of impulses which spread along association paths, giving rise to a sort of physiological irradiation, and a cellular adaptation, the product of inheritance and experience, which determines the nature of the response. These factors constitute a more concrete conception of Wertheimer's rather nebulous *Quer- und Gesamtvorgange*

Perceptual patterns in man clearly involve the whole optical sector, including the higher cortical level. We must endeavour to analyse the functions of the respective parts The theory of levels, so brilliantly enunciated by Hughlings Jackson, has received such ample confirmation— anatomical, physiological, and psychological— that it may be expected to apply to the present problem. Anatomically there are two well-defined outstanding levels—the primary optic centres, and the cortical centres, though both are doubtless hierarchies of constituent sub-levels Sherrington's beautiful experiments on binocular flicker, which deal with a problem nearly allied to that now under discussion, led him to the conclusion that

"during binocular regard of an objective image each uniocular mechanism develops independently a sensual image of considerable completeness. The singleness of the binocular perception results from union of these elaborated uniocular sensations The singleness is therefore the product of a synthesis that works with already elaborated sensations contemporaneously proceeding "[2]

There seems, therefore, in binocular perception, to be a "formative zone" allied to that predicated by G. E. Muller for perceptual complexes.

[1] *Zur Theorie der Nerventatigkeit*, Leipzig, 1899.

[2] *Op. cit.* pp. 382–3.

G. E. Muller's levels[1] are three in number: (1) Peripheral, extending from the retina to the calcarine region of the occipital lobe; (2) Middle, including the formative zone; (3) Highest. It will be noticed that the second and third levels are above the calcarine level It is easy to see that this distribution of levels is dominated by current psychological doctrine, which limits consciousness to cortical processes It is quite at variance with Hughlings Jackson's levels, and it seems to me much more probable that the formative zone should be located in the primary optic centres.

Everyone agrees as to the great importance of attention in pattern perception in man, and so far as attention affects the formative zone it must be by backstroke from the cortex. May we not regard attention as in some manner a sensitizer of the formative zone, whereby the processes going on in the cells of this region are so modified and adapted that they modify and correlate the congeries of impulses impinging upon them, moulding them into a physiological pattern which is the substratum of the psychological pattern? We may imagine that on the first occasion the constellation of impulses reaches the cortex and arouses attention to what is a relatively formless or patternless percept—a percept of the lower order Attention sensitizes the formative zone with the result that the impulses are correlated into a pattern which arouses a definite perceptual pattern—a percept of a higher order. On subsequent occasions the impact of the excitation arouses a more and more highly developed pattern as a primary response, and in instinctive reactions this occurs upon the first occasion, owing to the innate configuration of the formative zone

The formative zone in the lower level centres is, therefore, to be regarded as the seat of what may be called patterns of the first or lower order These correspond very nearly to Semon's "engrams"[2] and to Head's "schemata."[3] The sensitizing of patterns is similar to, though not identical with, Semon's "ecphorizing" of engrams[4].

We shall see later[5] that important evidence has recently been brought forward to show that every stimulus to a given area of the retina results in inductive changes of excitability, not only, as was

[1] *Op. cit.* pp. 68–9.

[2] *Die Mneme*, Leipzig, 1904; *Die mnemischen Empfindungen in ihrer Beziehungen zu den Originalempfindungen*, Leipzig, 1909, *Bewusstseinsvorgang und Gehirnprocess*, Leipzig, 1920.

[3] Head and Gordon Holmes, *Brain*, xxxiv, 183, 1911.

[4] Cf G. G. Campion, *Brit. Jl. of Medical Psychology*, v, 65, 1925.

[5] Chap. xii.

formerly thought, in immediately neighbouring areas of the retina, but also in the retina of the other eye. There can be no doubt now that the character and distribution of inductive changes is much more complex than has hitherto been appreciated, and that these changes show a plasticity which can only be accounted for by an elaborate *physiological* adaptability of the neurones involved. These processes go on "automatically" and quite unconsciously. They increase the evidence already available of the functional plasticity of neurones and systems of neurones. They are particularly important as affording evidence of such plasticity in lower neurones. Hitherto the best evidence of plasticity has been derived from the highest—syncritic—zone. Perhaps the most striking example is that of Sherrington's experiments in stimulation of the cortex of monkeys before and after the administration of small doses of tetanus toxin or strychnine, in which excitations are transformed into inhibitions, flexions of limbs into extensions, and so on[1]. Though inhibition of cortical cells by other cortical cells probably occurs, Exner and Sherrington[2] consider that inhibitions from the motor cortex act at a sub-cortical level.

We may look upon the lower level centres as intricate neuronic networks of very considerable plasticity, though the plasticity is less than and of a somewhat different kind from the kinetic plasticity of the higher syncritic levels. Its chief characteristic is that it is more self-governing, just as lower level, essentially reflex, motor activities are largely self-governing Yet both are subject to backstroke excitation (modifying the local activities) and inhibition—both of which are *active* processes. And there is ample evidence to show that these modifications are at least as complex as the local self-regulating activities Thus, whilst *Bahnung* or facilitation undoubtedly occurs, the synthesis and integration of impulses into a patterned unit is a process of a more complex type, of the rationale of which we know little except that in man the dominance of higher levels plays an important part.

Physiological experiments which throw some light on the sensitization of the lower centres from the cortex have been made by Dusser de Barenne[3]. Hyperexcitability of sensory areas in the postcentral gyrus of monkeys was produced by local application of strychnine. The hyperexcitability is not limited to the cortex "because the

[1] Sherrington, *op. cit.* pp 292 *sqq*
[2] *Op. cit.* p 285.
[3] *Proc. Royal Soc.* B, XCVI, 272, 1924.

disturbances are still present in *both* fore limbs on strychnization of any part of the arm area of one hemisphere after extirpation of the whole sensory arm area of the opposite hemisphere and of the greater part of the arm area of the hemisphere homolateral to the poisoning."[1] "It is plausible to think in this connection in the first place of the optic thalamus, which in its ventral and ventro-lateral nuclei represents, as is already long known, one of the most important and functionally highest developed sub-cortical sensory centres."[2]

5 Onto- and Phylo-genetic Evidence

Little evidence is as yet available as to perceptual patterns in children. There is evidence that visual projection and relative localization in space is innate, and that perception of differences of localization are specially strong in children and also in uncivilized races[3]. It has already been mentioned that visual appreciation of relative sizes is also innate[4], and that, owing to their incapacity to analyse patterns, children see geometrical-optical illusions more readily than adults[5].

Better evidence is obtained from those who, born blind from congenital cataract, have been successfully operated upon in adult life. It is to be remembered that these people have a well-developed and educated perception of spatial relations and orientation in space, as well as perception of form (stereognosis) derived from tactile (kinæsthetic) data. On the other hand, it is possible that they do not afford flawless evidence of normal innate capacities owing to defective development of the visual neural apparatus from disuse[6]. These persons are undoubtedly able to localize visual impressions and their relations to each other, and they do not see objects inverted. They have not only relative, but also absolute localization—right, left, up, down—as innate capacities, independent of experience. Uhthoff[7]

[1] *Op. cit.* pp 285–6

[2] *Op. cit.* p 287. Cf. also Graham Brown, "Reflex orientation of the optical axes and the influence upon it of the cerebral cortex," *Arch. néerl. de Physiol.* VII, 571, 1922; Magnus, *Arch. f. d. ges. Physiol.* CXCIII, 396, 1922; *Korperstellung*, pp 611–2, Berlin, 1924

[3] Rivers, *Brit. Jl. of Psychology*, I, 321, 1905.

[4] Binet, *Rev. Philos.* XXX, 68, 1890, Binet and Henri, *ibid.* XXXVII, 348, 1894; Giering, *Zeitschr. f. Psychol.* XXXIX, 42, 1905; Wolfe, *Amer. Jl. of Psychol.* IX, 137, 1898.

[5] Binet, *Rev. Philos.* XL, 11, 1895; van Biervliet, *ibid.* XLI, 169, 1896; Hasselrodt, *Arch. f. Psychol.* XXVIII, 336, 1913.

[6] Mach, *Die Analyse der Empfindungen*, p. 111, Jena, 1918.

[7] *Festschrift f. Helmholtz*, p. 113, Leipzig, 1891; *Zeitschr. f. Psychol.* XIV, 197, 1897.

found, however, that perception of size was very defective, but improved by use. Dufour[1] also found that the perception of form was defective. These individuals appreciate differences of size and form, but do not understand what long and short, round and angular, etc., mean[2]. If they are allowed to touch the objects, and, less efficiently and permanently, if they are told the shapes, etc., they will on subsequent occasions recognize similar objects. There can be little doubt that they see objects as a mosaic of independent parts, that they appreciate quite well the differences in the different mosaics, but that they are unable to unify them into independent perceptual patterns because they are ignorant of their meaning. Meanings are bound up for them with their tactile impressions. It is only when they are correlated by experience with their newly experienced visual impressions that the latter can be integrated into a unit perceptual pattern.

It is to be noted that these observations refer to the highly complex objects of civilized life which have no profound saliency from the phylogenetic point of view: they are not of imperative survival value. It would be unsafe to conclude that there is *no* innate capacity to form and appreciate visual perceptual patterns.

We are now in a position to draw some inferences as to the perceptual patterns of lower animals[3]. We conclude in the first place that owing to the lack of differentiation of receptors they are extremely vague and ill-defined. That as differentiation occurs they and their constituents become more defined and variegated. That, according to their biological adaptation, the various factors assume hierarchies in which the prepotent factor differs in a broad sense according to the species, etc., *e.g.* in the dog smell is a dominant factor, in the cat vision. In a hypothetical purely dyscritic stage the pattern is a "buzzing, blooming confusion," but psychologically it spells awareness. The physiological substratum of this condition can be little more than a primitive formative zone, but phylogenetically it has been built up in such a way as to respond by massive responses which are beneficial—or as beneficial as the primitive conditions permit—to the individual or/and the species.

There is evidence to show that in the lowest vertebrates, *e.g.* fishes, there is not the same fusion of different sensations into a

[1] *Guérison d'un aveugle-né*, Lausanne, 1876.

[2] Cf. however Franz, *Phil. Trans.* I, 59, 1841.

[3] For experimental evidence see Révész, *VIIth Internat. Congr. of Psychol.* p. 29, Cambridge, 1924, and the papers referred to there.

complex perceptual pattern such as occurs in higher vertebrates If my hypothesis[1] of the function of consciousness be true, this is what might be expected of the less-developed consciousness of these animals. A dog-fish, for example, seeks its food by smell, and if its olfactory bulbs are severed or the forebrain destroyed, it ceases to feed spontaneously[2].

"There can be no doubt that soles also perceive objects approaching them.. yet they have no recognition of a worm hanging by a thread immediately over their heads, and will not take it even if it touch them, but will continue to feel for it aimlessly on the bottom of the tank, being aware of its presence by the sense of smell." [3]

We may take as an example of a higher level the cat's perceptual patterns of the mouse. This is largely epicritic; for though the cat possesses a cerebral cortex capable of syncritic activities these play probably only a subsidiary part in so instinctive a series of reactions as catching a mouse, though probably they take a larger share in playing with a mouse. The patterns must still be relatively ill-defined, for, confining attention to the visual pattern, which is probably predominant, the receptors have not attained the minute differentiation which obtains in the primates. There is little or no foveal vision and relatively poor binocular vision. Visual acuity must be poor, but the perception of movement very acute Awareness is probably aroused first by predominantly auditory and olfactory patterns. The first visual pattern is that merely of a moving object Awareness becomes attention fixed upon the moving object, and this leads to sensitization of the formative zone and increased saliency of the visually appreciated movement.

That the cortex plays a part in this backstroke of attention is fairly certain in cats[4] But in the more purely instinctive reactions of still lower vertebrates dyscritic differentiation alone probably suffices to permit of such saliency of the biologically important pattern as is needful to educe the appropriate response At the same time, it can scarcely be doubted that awareness, independent of the existence of a neo-pallium, increases in sensitivity and discrimination *pari passu* with epicritic differentiation

Such is the sort of vague conjecture which we can have at this stage of the phylogenetic development of perceptual patterns It

[1] *Vide* p. 40.

[2] Steiner, *Die Functionen des Centralnervensystems*, Abt 2, 1888, quoted by James Ward, *op. cit.* p 188.

[3] Bateson, *Jl. Marine Biol. Assoc* p. 239, 1890.

[4] Cf Chapter III, 2.

suffices to emphasize the very important point—which might with advantage be illustrated by many more examples derived from concrete instinctive reactions in various species—that perceptual patterns must be vaguest at the lowest levels, and yet that they are still efficient as the originators of responses which are biologically appropriate, and that their higher development is a double process of (1) apocritic differentiation and re-integration, and (2) sensitization from higher levels which have contemporaneously evolved.

It is the object of the following chapters to bring forward some of the evidence which may enable us to attain a more precise conception of details of the psychological processes involved and their physiological substrata, first cursorily for tactile and other sensations, and secondly and more comprehensively for vision.

CHAPTER V

CUTANEOUS SENSATIONS

CUTANEOUS sensations in man comprise touch, temperature, and pain. Nearly allied to touch are the deep pressure sensations which are experienced when firm pressure is applied to the surface, but which originate in receptors situated in the deeper tissues.

The experiments of Goldscheider, von Frey, and others have shown that the distribution of the cutaneous receptors is punctate, so that isolated and independent touch-, heat,- cold-, and pain-spots can be mapped out in any area of the skin, the numbers of each varying with the anatomical position of the area[1]. Stimulation of these spots gives rise to a specific response—tactile, hot, cold, or painful—which is referred more or less accurately to the spot stimulated, *i e.* they possess "local signs" in Lotze's terminology. Local signature permits not only of localization but also of discrimination of tactile acuity, comparable with visual acuity; its determination depends upon the minimum distance between two compass points touching the skin which can be distinguished as separate. It differs widely for different areas of the skin.

Division of the nerve fibres supplying an area of skin abolishes sensibility to light touch, temperature, and pain; but heavier touch arouses deep-seated sensibility and pain. These deep sensations can also be localized, but discrimination is possible only to successive, not simultaneous, stimuli. The experiments of Head and his fellow-workers[2] on the sensations experienced after section and during regeneration of the nerves supplying an area of skin in the arm and hand have thrown much light on cutaneous sensations. From them it appears that purely cutaneous sensations are of double origin[3]

"For, in addition to the apparatus for 'heat' and for 'cold,' demonstrated by punctate exploration of the skin, there is another system also in the skin, but non-punctate, which is concerned in the development of sensations of 'warmth' and 'coolness' It appears that while the response to superficially painful and to hot and cold stimuli is the functional expression of one system of cutaneous sensibility,

[1] See Sherrington, in Schafer's *Text Book of Physiology*, II, 920, 1900.

[2] See Head, *Studies in Neurology*, London, 1920 (with references to individual papers).

[3] The following brief *résumé* of Head's experiments is quoted from C. S. Myers, *A Text-Book of Experimental Psychology*, pp. 11–14, Cambridge, 1911.

the appreciation of light touch over hairless regions, warmth and coolness, and the power of precise cutaneous localization are the expression of another system of cutaneous sensibility For, during recovery after injury to peripheral nerve fibres, stages occur at which one of these two systems is absent, while the other remains

Thus during recovery from the effects of section of a cutaneous sensory nerve, a stage has been observed in which heat, cold and pain (corresponding to the heat, cold, and pain spots) and the light touches of hairy parts are felt, while sensations of warmth and coolness, and of light touch over hairless or shaven regions and the ability to distinguish two neighbouring touches from one another and to recognize the relative sizes of objects are wanting. Whereas, over the normal skin, the heat spots and the cold spots are set in an area sensitive to cool and warm stimuli, the result of nerve section is to produce a state in which only the heat and cold spots are present; that is to say, a state in which stimuli, having a temperature between about 26° and 37° C, produce no thermal effect Above or below these limits, the heat or the cold spots react explosively, yielding characteristically diffuse, tingling, remotely localized sensations, the intensity of which is apparently independent of the degree of heat or cold, so long as the stimulus employed is at all adequate Diffuseness at this stage is also characteristic of the pain sensations A prick applied to the forearm, for example, is not felt as a prick at all, it sets up a widely radiating pain over the thumb. It is an abnormally unpleasant sensation and requires a stronger stimulus than usual to elicit it at all The same diffuseness and remote reference characterizes the tingling sensations produced by the light touch of the hairs of hairy regions.

So far, then, we are led to recognize (1) a system of deep sensibility in which only deep pressures and pains can be experienced, localized and successively distinguished, and (2) a system of 'protopathic' sensibility in which accurate localization is lost and spatial discrimination is even worse than in (1) but which allows of response to extremes of temperature, to pain and to light touches of hairs

But this is not all While, at a certain stage after nerve section, the greater part of the affected cutaneous area shows the above protopathic state of sensibility, small outlying cutaneous areas may at the same time be found in which sensations of heat, cold, and pain are absent, while the sensibility to light touch, to warmth, and to coolness remains almost unchanged. The prick of a pin, under these conditions, is felt merely as a sensation of pointedness, the sense of pain is gone, but aemæsthesia (acuæsthesia) remains

Under other abnormal conditions, this latter, 'epicritic,' system of sensibility may prove to be the only one present over more extensive cutaneous areas, while in certain situations, *e g.* in the viscera, of the normal body there is evidence that it is altogether wanting, the protopathic system being alone present The protopathic appears to be more primitive than the epicritic It is characterized by imperfect power of localization It is less liable to disappear and is readier to reappear than the epicritic system

At present we have no evidence that to these two systems of cutaneous sensibility correspond two separate systems of peripheral nerve fibres A single physiological system may conceivably dissociate into separate psychological systems. Whether this is the case or not, it is important to remember that, when once they have reached the spinal cord, the impulses are found arranged in quite another manner. All thermal impulses are here grouped together, irrespectively of the systems in which those impulses may have arisen, and a similar homogeneous grouping occurs in regard to the impulses of touch and pain. Further, as the paths ascend in the cord, they cross, close by the central canal, to the opposite side, but the rapidity and completeness with which they cross vary with the kind of impulse conducted. In

the case of tactual impulses, the crossing is much less complete than in the case of painful and thermal impulses From this brief account it is sufficiently obvious that the effects which localized injuries to different areas of the cord produce upon sensibility to temperature, pressure, and pain, must differ profoundly from the (immediate or remote) effects of the section of peripheral sensory nerve fibres."

The cognitive element of the crude protopathic, or as I prefer to call it, dyscritic, response is diffuse, vague, and ill-defined. There is reason to think that the adequate stimulus produces the maximum response at the threshold—the reaction is of the all-or-none variety. The higher differentiation of the cognitive element introduces differentiation of another nature. The response, while retaining many of the characteristics of the protopathic response, especially as regards its quality, is better defined, susceptible of finer gradation, endowed with more accurate local signature and discrimination, less charged with affective tone, and of greater cognitive significance. This higher differentiation of sensory responses is termed epicritic, in contradistinction to protopathic or dyscritic It should be noted that it is to be regarded as differentiated and evolved from the protopathic, and, just as a highly differentiated cell in the multicellular organism still retains the fundamental characteristics of a living cell in spite of its special differentiation, so each epicritic sense retains the fundamental quality of the protopathic.

Head's conclusions have not been accepted without criticism[1]. His fundamental experiment of the division of cutaneous nerves and observations upon sensations during regeneration has been repeated by Trotter and Morriston Davies[2], and Boring[3]. There is remarkable agreement in the results of the experiments, but differences arise as to their interpretation.

Much of the ambiguity arises out of the temperature sensations. It is difficult to accept the view that the phylogenetically more primitive system should be excited by intense hot or cold stimuli only In this connection it is to be remembered that cutaneous temperature (and touch) sensations show very definite signs of adaptation and induction[4] As Trotter and Davies point out.

"If the skin be tested with decreasing temperatures from 50° C downwards, the

[1] Cf von Frey, *Zeitschr f Biol* LXIII, 335, 1914, Hacker, *ibid* LXV, 67, 1915; Harvey Carr, *Psychol Rev.* XXIII, 262, 1916.

[2] *Jl of Physiol* XXXVIII, 134, 1909, *Jl f. Psychol und Neurol.* XX, Erganzungsheft 102, 1913, see also Trotter, *Lancet*, p. 1252, 1924

[3] *Quart Jl. of Exp. Physiol* X, 1, 1916; *VIIth Internat. Congress of Psychol* p. 57, Cambridge, 1924

[4] *Vide infra*, Chap. XII, 2.

series of sensations produced is not a continuous one but is interrupted as soon as the temperature of the testing cylinder gets to within 5 or 6 degrees of the temperature of the skin, and is not resumed until the similar distance below the skin temperature is reached. Temperatures of this intermediate region are felt as indifferent, and moreover the sensations elicited by temperatures bordering on this region are of very slight intensity and shade gradually into the indifferent without there being abruptly marked off minimal sensations It is of great importance to the understanding of the state of affairs when thermo-hypoæsthesia exists, to realize that the skin is normally insensitive to temperatures of a certain intermediate range, that in the series of sensations from hot to cold there is a gap of anæsthesia ...The adjustment of the capacities of the temperature sense to the needs of the organism goes further, for, as is well known, the relation of the intermediate group of indifferent temperatures to the thermometric scale is not an absolute one but varies according to the temperature of the skin at the moment. By warming or cooling the skin the normal intermediate thermo-anæsthesia can be shifted upwards or downwards respectively in relation to the thermo-metric scale."[1]

Moreover, it is by no means certain, and indeed is improbable, as we shall see later, that dyscritic sensation, as revealed by experiments and observations on man, represents the unaltered primitive sensation.

Further, as Trotter and Davies rightly insist, the section of a cutaneous nerve is an injury which cannot fail to be accompanied by pathological processes. Of these there is ample evidence in the histological conditions found in regenerating nerves, and it may well be that the very active processes going on in the regenerating nerve fibres and the equally marked reactions of the non-nervous tissues cause a condition of raised threshold associated with explosive response which is characteristic of the "protopathic" stage. The analogy of the painful neurofibromata formed in amputation stumps, and the causalgia met with in wounds of peripheral nerves[2] are very pertinent to this view. It is also supported by the fact that the so-called hyperalgesia does not occur in the anæsthesias produced by sections of posterior roots, in which the peripheral nerve fibres do not degenerate owing to the retention of their continuity with the cells of origin of the axons in the posterior root ganglia. Head's explanation of this fact, *viz.* that the protopathic loss is equal to or greater than the epicritic loss in these cases, seems to beg the question.

Trotter[3] lays a great stress upon the normal insulation of nervous tissues, so that they are everywhere, except in the free nerve endings of noci-ceptors, specially protected from direct contact with meso-

[1] *Jl. of Physiol* XXXVIII, 146–7, 1909.

[2] Cf. Ranson, *Brain*, XXXVIII, 381, 1915; Ranson and Billingsley, *Amer. Jl. of Physiol.* XL, 571, 1916; Tinel, *Rev. Neurol.* XXIV, 243, 1917.

[3] *Lancet*, p. 1252, 1924; p. 107, 1926.

dermal tissues. Thus, sensory nerve endings are protected by various forms of laminated capsules, and the blood vessels of the central nervous system are carefully protected from direct contact with the nerve substance by perivascular sheaths. Trotter, indeed, says:

"We need not suppose that any form of cutaneous sensation experienced by us is unrepresented in the invertebrate, but there seems to be some ground for suspecting that in the latter all forms of sensation normally have some of the urgency that survives in us only in the case of pain. According to this view, it is the damping down of a large proportion of sensory fibres by complete insulation that has given us the finer kinds of cutaneous sensibility, and enabled us to make deliberate rather than impulsive reactions to the majority of our contacts with the outer world."

This ingenious theory appears to me to be at least as difficult to maintain as Head's.

A striking feature of human extero-ceptors is the fact that in two areas, the cornea and the glans penis, the normal reactions to stimuli are very characteristic of dyscritic responses. This fact, taken in conjunction with the many facts derived from comparative anatomy and physiology and human anatomy and physiology[1] which point to a dual mechanism at work in almost every domain of sensation with the exception of pain, leads one to the conclusion that Head's distinction of protopathic and epicritic systems is fundamentally correct in spite of grave difficulties and inconsistencies in detail.

Piéron[2] has tabulated the deductions of Head and his fellow-workers in the scheme shown on p. 66.

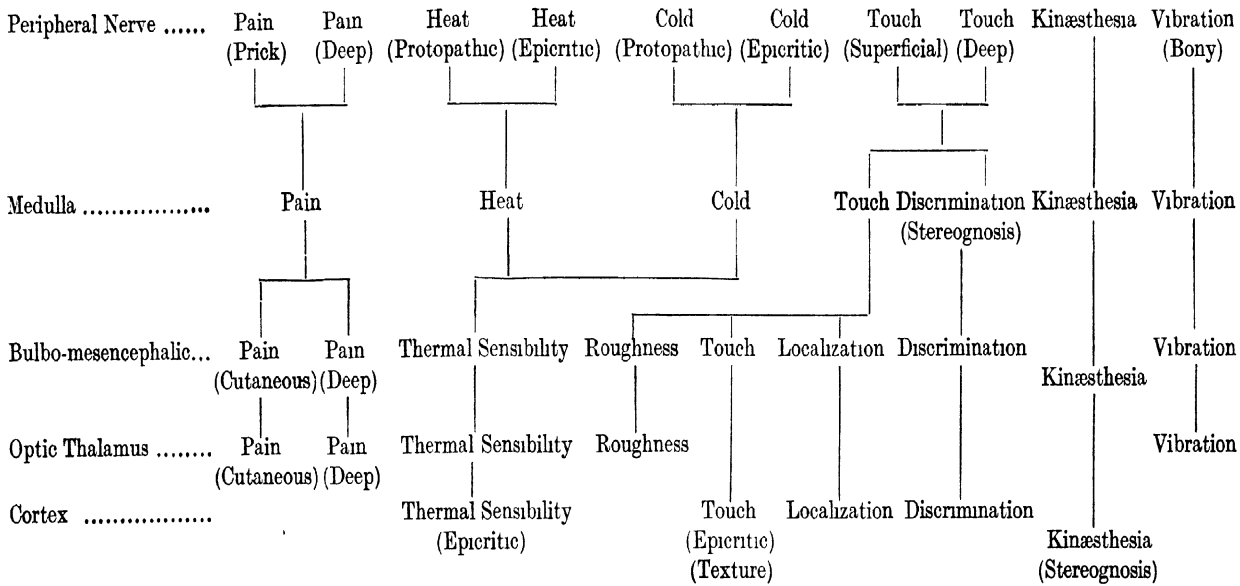
The crude dyscritic sensibility is to be regarded in its primitive form as essentially utilitarian in the most fundamental sense; upon it depended the survival of the individual and the species. So important is it that it cannot be wholly replaced by the more delicate epicritic mechanism. Hence it is found to persist alongside the epicritic in most of the senses even in the highest animals, though generally modified from its primitive character.

Moreover, the crude primitive dyscritic sensibility had to possess that *potential plasticity* which permits of differentiation along many lines. The more highly differentiated epicritic sensibility lost perforce this type of plasticity. Endowed, however, with richer and more sharply defined cognition, it was eminently suited to provide a more active, *dynamic plasticity* within a narrower field.

The dyscritic phase is seen in its most characteristic form in the lowest vertebrates; the epicritic in the highest. Between the

[1] *Vide infra.*

[2] *Le Cerveau et la Pensée*, p. 124, Paris, 1923.


Peripheral Nerve .....
Pain (Prick)
Pain (Deep)
Heat (Protopathic)
Heat (Epicritic)
Cold (Protopathic)
Cold (Epicritic)
Touch (Superficial)
Touch (Deep)
Kinæsthesia
Vibration (Bony)
Medulla .....
Pain
Heat
Cold
Touch Discrimination (Stereognosis)
Kinæsthesia
Vibration
Bulbo-mesencephalic...
Pain (Cutaneous)
Pain (Deep)
Thermal Sensibility
Roughness
Touch
Localization
Discrimination
Kinæsthesia
Vibration
Optic Thalamus .....
Pain (Cutaneous)
Pain (Deep)
Thermal Sensibility
Roughness
Vibration
Cortex .....
Thermal Sensibility (Epicritic)
Touch (Epicritic) (Texture)
Localization
Discrimination
Kinæsthesia (Stereognosis)

two are many gradations of each which are difficult to unravel; but both anatomical observations and physiological experiments support the view that there is a dual mechanism at work.

In the cyclostomes the histological structure of the central nervous system is extremely primitive and generalized. The grey matter borders the ventricles and central canal, and the axons of the cells radiate outwards.

"The nervous organization is such as to make possible a relatively small number of reactions for all sorts of sensory stimulations, and these reactions are for the most part simple total movements of the whole body (cf. Head and Riddoch, "Mass reflex," *Brain*, XL, 188, 1918) rather than complex adjustments involving precise co-ordination of many separate organs."[1]

The structure "may be regarded as typical of the primordial vertebrate ancestor. It is unspecialized, plastic, and capable of differentiation in any direction."[2] It may be described as *potential (or static) plasticity*.

Herrick contrasts this condition with that found in the true fishes, especially teleostean fishes, "where the various functional systems of neurones are segregated into as well-defined nuclei and fibre tracts as are those of the brain stem of mammals."[3] This condition is the anatomical basis of highly efficient functions on the reflex plane

"Both elasmobranchs and teleosts are very efficient types of fishes Biologically they dominate their respective environments This dominant position, however, has been brought about by very precise adaptation of each individual species to a particular habitat and mode of life on the reflex plane, rather than by an increase in capacity for individual adjustment to diverse and variable conditions And neither group has given rise to anything higher. They form terminal branches of the phylogenetic tree These types of fore-brain appear to be incapable of expansion in directions affording greater flexibility and modifiability of behaviour of the individual "[4]

The ancestors of the Amphibia were primitive ganoids like *Polypterus*, and the lung fishes (Dipnoi) sprung from a closely related stock. During the late Silurian and early Devonian periods the lakes and streams were drying up. The statically plastic nervous systems of the Dipnoi and their ancestors permitted them to adapt themselves to the diminished oxygen supply in the stagnant streams. Their brains show a more complete evagination of the primitive end-brain into the cerebral hemispheres which is characteristic of their descendants, the Amphibia. The evagination does not begin at the site of the future olfactory bulb, but at the caudal end of the end-brain,

[1] C J. Herrick, *Jl. of Comparative Neurology*, XXXII, 4, 429, 1921.
[2] *Ibid.* [3] *Ibid.* [4] *Ibid*

possibly owing to the caudal position of the nasal area in the precursors of the Amphibia. For "the initial functional impulse for the differentiation of the end-brain was undoubtedly the excitations arising in the nasal epithelium "[1]

"In Cyclostomes the entire end-brain and a large part of the between-brain are dominated by the olfactory system, the non-olfactory components entering this territory from the mid-brain being relatively small and incompletely known. As we ascend the vertebrate scale the non-olfactory systems assume progressively greater importance. In urodeles a considerable part of the thalamus is devoted exclusively to non-olfactory correlations, but no part of the cerebral hemispheres is wholly free from olfactory connections In reptiles the ascending systems are greatly enlarged and a portion of the corpus striatum complex appears to be devoted exclusively to them Here there is well-defined cerebral cortex, most of which is clearly dominated by its olfactory connections (hippocampus and pyriform lobe), though in another part (the general cortex) somatic systems predominate (Elliot Smith, *Lancet*, Jan 1910; *Jl of Anat* LIII, 271, 1919). In mammals somatic systems with no admixture of olfactory elements come to dominate the architecture and functions of the cerebral hemispheres, until in man, whose olfactory organs are greatly reduced, the olfactory centres are crowded down into relatively obscure crannies of the hemisphere by the overgrown somatic systems "[2]

"In higher vertebrates with fully evaginated cerebral hemispheres local thickenings of a different sort appear in the lateral walls of the hemispheres themselves in reptiles, and especially in birds Here again this structural form is correlated with the predominance of stable, heritable, reflex and instinctive behaviour patterns In mammals, on the other hand, where individual modifiable behaviour of the intelligent type is the most characteristic feature, so extensive solid thickenings of the hemispheres do not appear, but instead the highest correlation tissue of the brain is spread out in thin sheets as cerebral cortex (Kappers, 1913, 1914) "[3]

This is the condition we are familiar with in the human cortex, composed of a vastly intricate network of association tracts. It is the anatomical basis, not only of the highest type of epicritic sensibility, but also of those higher syncritic integrations of epicritic sensibility which become manifest in consciousness as conceptual thought. Whilst founded on a stable basis of heritable reflex and instinctive patterns, it is endowed with a *kinetic or dynamic plasticity* which is revealed in intelligent behaviour.

If we study the tactile sense and the anatomical structures which subserve it throughout the vertebrate series, we shall find that the primitive apparatus can be recognized from *Amphioxus* to man. In most vertebrates it is clearly recognized as the fibre system first described by Edinger. The afferent fibres from the skin pass into the spinal cord by the posterior roots, having their cell stations in the dorsal root ganglia. The axons join the median bundle of the

[1] C. J. Herrick, *Jl. of Comparative Neurology*, XXXII, 4, 429, 1921.
[2] *Ibid.* [3] *Ibid.*

posterior root fibres and arborize about cells in the grey matter of the cord. The axons of these intercalary cells pass ventrally through the grey matter to cross in the anterior commissure, whence they run in the antero-lateral tract (*a*) as spino-bulbar and spino-mesencephalic fibres close to the direct cerebellar tract, and (*b*) as spino-mesencephalic fibres close to the crossed cerebellar tract. They end in the ventral part of the optic thalamus. These fibres, according to Head and Thompson[1], in man conduct pain and temperature sensations. According to these authors, they do not conduct tactile sensations, which may indeed be the case in man. It is probable that in lower animals they conduct also tactile sensations, which are there purely dyscritic.

In man most of the tactile sensations are undoubtedly subserved by fibres which run in the posterior columns. Some, in both lateral and median bundles of the posterior root fibres, subserve local spinal reflexes. Others, in the median bundle, dichtomize, the descending fibres forming the comma tract and oval field, the ascending fibres forming the fasciculi cuneatus and gracilis, which end in the nuclei of Burdach and Goll, whence new fibres pass upwards and cross in the median fillet to reach the thalamus These are essentially the fibres mediating epicritic tactile sensibility, though, according to Head, they also contain the fibres subserving protopathic touch. Now, the nuclei of the posterior columns cannot be demonstrated with certainty below the level of the reptiles, though there is some evidence of their presence in Amphibia It is probable, therefore, that epicritic sensibility proper does not appear below the phylogenetic level of the Amphibia. Edinger's fibres, however, subserving protopathic sensibility, undoubtedly occur throughout the vertebrate series as low as *Petromyzon*. In *Amphioxus* there are no posterior root ganglia. The sensory cells (Rohde's cells) are intramedullary; they give off ventral arched fibres which probably correspond to Edinger's fibres in higher vertebrates This view is supported by the fact that the sensory cells are intramedullary in plagiostome and some amphibian embryos, but are all extramedullary in the adult forms of these animals. In many teleostean fishes intramedullary (Rohon-Beard) cells persist throughout life, though they have been superseded by extramedullary root ganglia,—a piece of evidence that teleostean are more primitive than selachian fishes The mesencephalic root of the Vth nerve in higher vertebrates, including man, is probably a vestige of primitive intramedullary primary sensory neurones, and

[1] *Brain*, XXIX, 537, 1907

possibly the same will be found to apply to the proprio-ceptive system to a greater extent than has hitherto been thought probable.

We have seen that, according to Head and Thompson, a regrouping of cutaneous sensory impulses occurs within the spinal cord. Painful impulses, superficial and deep, come together in a common tract, to be sorted out again only in the bulbar and thalamic levels. The impulses subserving temperature, both protopathic and epicritic, similarly gather together in a common tract. According to these authors, a new and remarkable dissociation of tactile impulses occurs in the cord. Those which subserve discrimination, such as the separateness of compass points applied to the skin, become segregated from the other epicritic fibres subserving localization.

At the mesencephalic level protopathic and epicritic impulses again become dissociated, and new distinctions appear in epicritic sensibility, the sensation of roughness being transmitted by a different tract from that of localization. Protopathic temperature sensations, both for heat and cold, superficial and deep pain, roughness, and bony vibration, all stop short in the optic thalamus. Epicritic touch (localization), discrimination and stereognosis, epicritic temperature (without distinction of heat and cold), and kinæsthetic sensibility are transmitted upwards to cortical representations.

This catalogue includes such primitive and elementary perceptions as those of crude touch and its localization, and such complex and highly apocritized perceptions as discrimination, stereognosis, and roughness and texture. Now discrimination is a judgment, and it appears to me impossible to conceive how nerve fibres can carry a judgment[1] Such judgments are the result of higher syntheses than the spinal cord is capable of. Even if we admit a wider view of the association of consciousness with neural processes than is usually accepted[2], we also predicate a suppression of lower level processes, and *a fortiori* of those of the lowest spinal cord level. Without kinetic spinal-consciousness it is impossible to imagine the integration of so complex a perception as discrimination at the spinal level. Discrimination, indeed, offers many of the difficulties which we shall find almost overwhelming in the case of movement[3]. It must, I think, be admitted that a crude form of discrimination and of movement

[1] Cf. Stout, *Manual of Psychology*, p. 245, 1913· "These hypothetical nerves of judgment seem a physiological and psychological monstrosity, not to be accepted save as a last desperate measure."

[2] *Vide supra*, p. 37.

[3] *Vide infra*, Chap. IX.

occurs phylogenetically far below the level at which a neopallium has been evolved. Even here, however, they must be subserved by the highest neural mechanism which has been evolved—that mechanism which permits of the highest forms of integration which is possible at the level[1]. And, in these lower forms, it is predicated that the neural processes subserve kinetic consciousness.

The observations on sensory losses and dissociations following injury and disease of the cerebral hemispheres[2] though differing in detail, prove conclusively that it is the higher syntheses—tactile, discrimination, position of limbs, and stereognosis—which are most affected, thermal sensations being less frequently impaired, and painful sensations not involved.

The absence of cortical projection of painful impulses[3] is fully in accord with Head and Holmes's[4] view of the importance of the optic thalamus as the seat of painful sensations and the chief centre for affective tone[5]. It seems to me probable that the pain of headache should be referred to this centre. Of all the sensory impulses the noci-ceptive are most vital to the animal from the point of view of survival. They are typically dyscritic, and appear to remain so with little differentiation throughout the vertebrates. The sensory response is characteristically protopathic. It is relatively diffuse and ill-defined; it appears to be of the all-or-none variety and of maximal, or very insistent, intensity. Above all, it is charged with affective tone.

Dusser de Barenne found that thalamic cats (*i.e.* decerebrate above the level of the optic thalami) withdraw their paws from hot or cold water, but only if it is very hot or cold, and after a prolonged latent period; they react to stimulation of the hair and whiskers, thus avoiding obstacles; they have no ataxia, and defend themselves against injury, although they localize badly and the reactions are crude. Minkowski found that in monkeys in which the central convolutions were ablated there is both qualitative and quantitative diminution of touch, and temperature sensibility; localization and

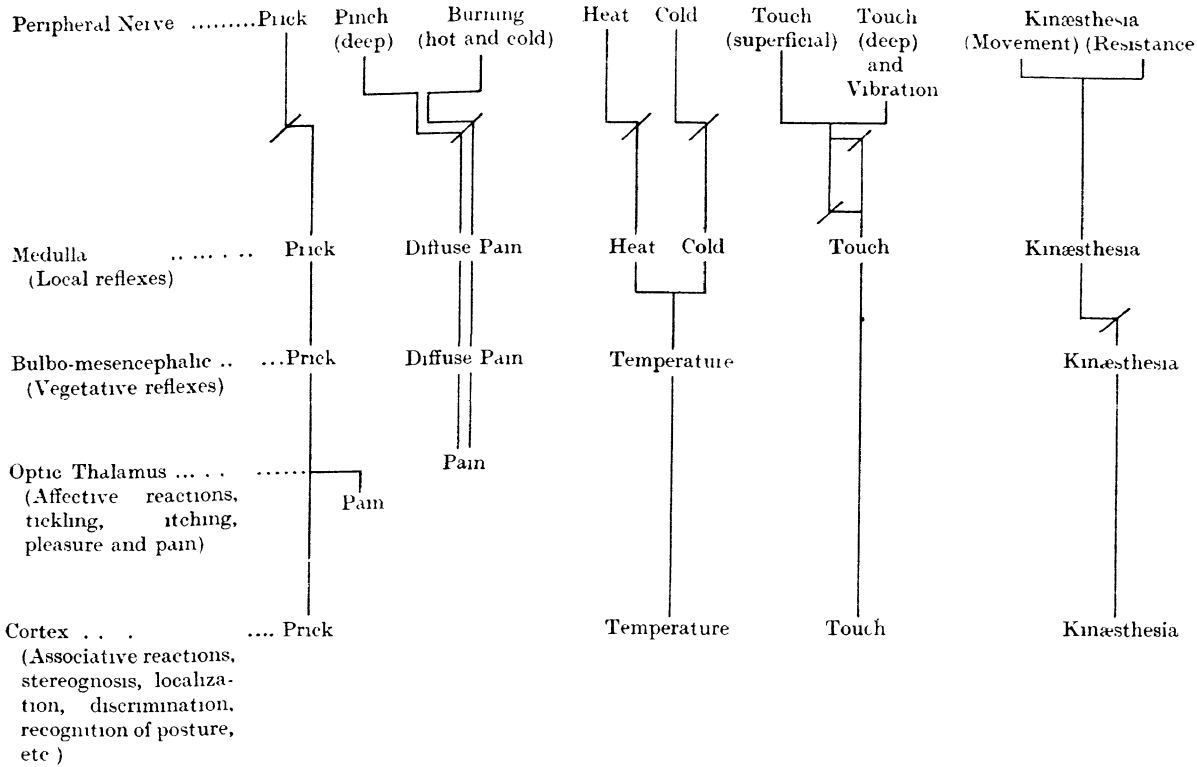
[1] Cf C. J. Herrick, *Jl. of Animal Behaviour*, III, 222, 1913; *Jl of Comp Neurol.* XXXII, 429, 1921.

[2] See Piéron, *op. cit.* pp 94 sqq.; Verger, *Arch. gén. de Méd.* pp 513, 662, 1900, Dejerine, *Séméiologie des affections du système nerveux*, 1914; Dejerine and Mouzon, *Rev. neurol.* XXII, 1265, 1915; Graham Brown and R. M. Stewart, *Brain*, XXXIX, 345, 1916; Piéron, *Rev. de Méd.* p. 129, 1919.

[3] Cf Sherrington, *op. cit.* p. 255.

[4] *Brain*, XXXIV, 102, 1911.

[5] Cf. Pagano, *Arch ital. de Biol.* 1906; Mott in Allbutt's *System of Med.* VII, 257, 1911.


Peripheral Nerve .....
Prick
Pinch (deep)
Burning (hot and cold)
Heat
Cold
Touch (superficial)
Touch (deep) and Vibration
Kinæsthesia (Movement)
(Resistance)
Medulla .. .. (Local reflexes)
Prick
Diffuse Pain
Heat
Cold
Touch
Kinæsthesia
Bulbo-mesencephalic .. (Vegetative reflexes)
...Prick
Diffuse Pain
Temperature
Kinæsthesia
Optic Thalamus ... . . (Affective reactions, tickling, itching, pleasure and pain)
.....
Pain
Pain
Cortex . . . (Associative reactions, stereognosis, localization, discrimination, recognition of posture, etc)
.... Prick
Temperature
Touch
Kinæsthesia

kinæsthesia are impaired, but painful sensations are unaltered and are accurately localized.

Such considerations have led Piéron[1] to revise Head's scheme and suggest that shown on p. 72, in which the sites of decussation are indicated by oblique lines.

The thalamic region in normal man may be regarded as the "formative zone" for all cutaneous sensations. The perceptual patterns elaborated there are all profoundly modified and in many cases resynthesized by backstroke from the cortex. And not only from that part of the cortex upon which the afferent impulses immediately impinge; for these are in intricate associative relation with all other parts of the cortex, not only of the same but also of the opposite cerebral hemisphere. In endeavouring to obtain an idea of the origin and development of lower and simpler perceptual patterns, such as probably constitute the highest of which lower vertebrates are capable, and form the nucleus out of which the higher perceptual patterns of man are apocritized and syncritized, it is necessary to analyse our human perceptions and correlate them with our knowledge of the anatomy and behaviour of lower types.

[1] *Op. cit.* p. 128.

CHAPTER VI

THE EVIDENCE FROM COMPARATIVE ANATOMY

1. The Spinal Cord

Some of the best evidence of dyscritic, epicritic, and syncritic factors in the hierarchy of apocritic differentiations, segregations, and integrations which occur in human perception is derived from comparative anatomy. Though the distinction of protopathic (or dyscritic) and epicritic is due to Head and Rivers, the distinction rests upon surer ground than they put forward. Even if their view of protopathic and epicritic systems in the peripheral nervous system of man should fall to the ground, the fact remains that two distinct levels in the hierarchy of differentiations which all admit must be distinguished—a lower level manifesting itself psychologically by some form of relatively undifferentiated "perception brute," subserved by lower level neural centres, and a higher level manifesting itself psychologically by more highly differentiated discriminative perception, subserved by higher level neural centres The syncritic factor, which manifests itself by differentiation and syntheses of already highly developed perceptual patterns, and which is subserved by still higher cortical centres, it is not my intention to discuss here.

The cutaneous receptors of all vertebrates below the level of the Amphibia consist entirely of free nerve endings between the epithelial cells, and even in the Amphibia only a few sparsely distributed Pacinian corpuscles are found In the lowest grades these free nerve endings subserve a relatively undifferentiated—dyscritic—tactile-temperature sensation, which with higher intensities of stimulation is painful. In more moderate degrees there are two responses, either positive or negative, and we may presume that they are accompanied respectively by pleasant or unpleasant affective tone, so that the receptors may be classified as *grato-ceptive* or *noci-ceptive*. This is a convenient terminology, but should be used without prejudice as to the accuracy of the principle of the specific energy of nerves of Johannes Muller[1], for the interpretation of the impulses may be essentially a function of the central organs rather than of the receptors themselves. We may again emphasize the fact that the noci-ceptors retain this primitive free nerve ending receptor throughout the

[1] Parsons, *Colour Vision*, p 21.

vertebrates, including man; and, so far as the structure of receptors is any criterion, they are *par excellence* dyscritic.

It is not until the reptiles are reached that more complicated end organs become common in the form of Pacinian corpuscles; but even here free nerve endings are the rule.

Proprio-ceptive endings occur in the muscles, the intermuscular septa, the tendons and the joints. In *Amphioxus* no fibres from the posterior roots have been traced into the muscles, but it is likely that there are sensory fibres in the motor nerves comparable to those found by Sherrington and Tozer in the eye muscles of higher vertebrates. If so, this type must be very primitive. Free intermuscular nerve endings are found as low down as *Petromyzon*[1]. Basket-like endings are found in the muscles of *Myxine*, fishes and Amphibia; and even muscle-spindles in cyclostomes. Tendon organs occur sparsely in selachian and teleostean fishes, and Rollet and Sachs corpuscles in Amphibia and reptiles.

The strongest evidence of a dyscritic or protopathic system is found in the universality in vertebrates of the sensory neurones of the second order which comprise Edinger's fibre system. This system has already been briefly described[2], but its phylogenetic development is of the greatest interest and importance We owe much of our knowledge of it to Brouwer[3].

It is probably represented in *Amphioxus* by the colossal Rohde cells and their axons (Fig. 4) These cells lie dorsomedian to the central canal, corresponding in position to the entry of the afferent spinal roots, which in this animal alternate with the motor roots. The axons pass below the central canal to the opposite side, the caudal ones passing alternately right and left frontalwards, the anterior ones similarly backwards

In *Amphioxus* the cells of the afferent spinal roots are intramedullary. In the *cyclostomes* the motor sensory roots alternate, as in *Amphioxus*, but the posterior roots have ganglia comprised of bipolar cells, but there are also large dorsal sensory cells (Rohon-Beard cells) within the cord. The neurones of the second order, homologous to the Rohde cells of *Amphioxus*, give rise to a well-marked system of ventral commissural fibres, of which many end in the cord, but many almost certainly pass forward in the antero-

[1] Johnston, *Jl of Compar. Neurol.* XVIII, 1908.

[2] *Vide supra*, p. 68.

[3] See Ariens Kappers, *Die vergleichende Anatomie des Nervensystems der Wirbeltiere und des Menschen*, Haarlem, 1920 (Bibliography).

lateral columns to the medulla oblongata. Both there and throughout the cord the sensory fibres are brought into intimate relation with the huge Muller's fibres, which arise from cells in the mid-brain and medulla and pass ventrally throughout the cord, without branching, to the tail. In this manner co-ordination between the crude dyscritic sensation and the supremely important reflex movements of the tail, which are controlled by the brain, is brought about The primitive muscle sense in cyclostomes is almost certainly effected by branches of the Rohon-Beard cells[1] Besides the cutaneous and the muscle senses, *Petromyzon* also responds to chemical stimuli, best from the

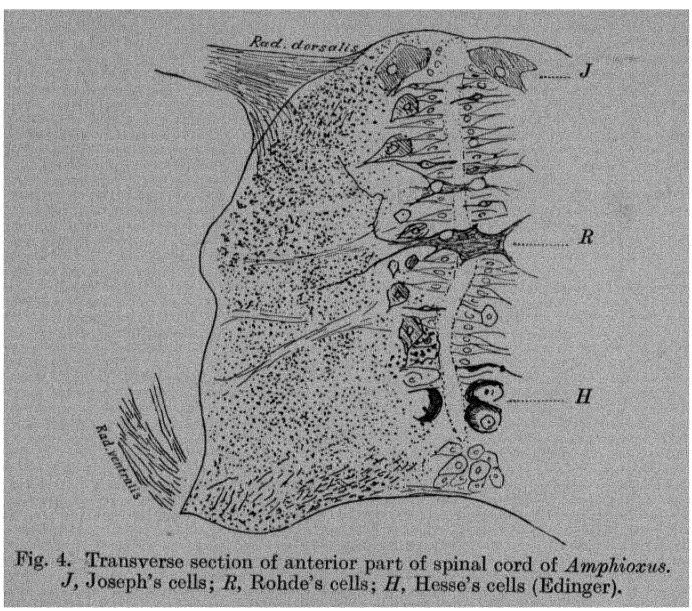


Fig. 4. Transverse section of anterior part of spinal cord of *Amphioxus*. *J*, Joseph's cells; *R*, Rohde's cells; *H*, Hesse's cells (Edinger).

head region, and also to light. G H Parker[2] has shown that the tail of *Petromyzon fluviatilis* is more sensitive to light than the head or body. The impulses must be carried by spinal nerves, but no specific receptor organs have yet been discovered

In *plagiostomes* the nerves are for the first time provided with medullary sheaths In the lowest stages there are intramedullary sensory cells, which give branches not only to the skin, but also to the muscles, they are replaced later by dorsal root ganglia. The

[1] Cf Figs 5 and 6

[2] *Jl of the Acad of Nat Sc Philadelphia*, xv, 1912.

afferent dorsal root fibres arborize around commissural cells in the grey matter of the cord. The axons of these cells cross in the ventral commissure, pass upwards for a short distance in the contralateral anterior column and then to the antero-lateral column, in which they run as spino-bulbar and spino-mesencephalic fibres to the medulla and mid-brain. There is no doubt that we have here a well-defined system of fibres entirely analogous to Edinger's fibre system in higher vertebrates. Elasmobranchs also have a cerebellar tract. There are as yet practically no posterior columns. The static innervation which is represented in cyclostomes by Muller's fibres is greatly increased in plagiostomes by descending neurones from the cerebellum, the lobus liniæ lateralis, and the VIIIth (vestibular) nerve nucleus. Fibres subserving photostasis descend from the tectum opticum to the medulla, where they form synapses with reticular cells, which bring them into relation with the cord; and similar fibres descend from the lobi inferiores hypothalami. In this manner co-ordination of dyscritic cutaneous and proprio-ceptive impulses with static, photostatic, and olfactory impulses is secured.

In *ganoids and teleostean fishes* intramedullary sensory (Rohon-Beard) cells have been often found in the larval stages[1], but it is remarkable that they persist throughout life in many bony fishes—evidence that the teleostean are more primitive than the selachian fishes. Several of these fishes (*Lophius*, *Trigla*) have relatively enormous sensory lobes in the dorsal part of the cord, immediately behind the medulla. These are not evidence of true posterior columns, but are due to the enormous development of cutaneous sensibility in the large heads of these animals. The secondary sensory neurones of ganoids and teleosteans form a system of crossed spino-bulbar and spino-mesencephalic tracts, exactly as in the plagiostomes and like the Edinger fibre system. In addition to the descending fibres mentioned in reference to plagiostomes, the bony fishes have descending taste fibres, all of which are derived from cranial nerve nuclei. Many of these fishes, *e.g.* cod, have the skin and pectoral fins richly supplied with taste-receptors, and the impulses from them are thus brought into relation with cutaneous, static, and photostatic impulses.

Rohon-Beard cells are found only in the larval stages of *Amphibia*, but the researches of Coghill[2] throw so much light on the primitive origin of the fibres subserving muscle-sense and the Edinger fibre system that a short description is desirable. Figs. 5 and 6 show that

[1] *Vide* Kappers, *op. cit* p. 138.
[2] *Ibid.* p. 146.

the dendrites of the Rohon-Beard cells supply both the skin and the myomeres: that their axons pass to commissural cells, whose axons cross in the ventral commissure and form synapses with motor cells

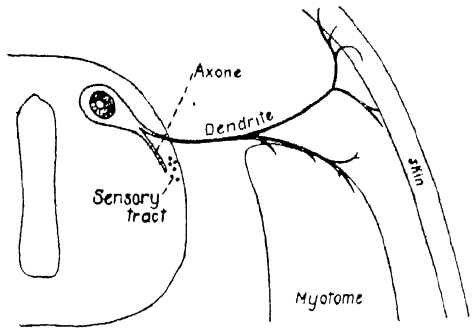


Fig. 5. Transverse section through body of early swimming stage of larval *Amblystoma*, showing connections of the transitory giant cells of Rohon-Beard (Coghill).

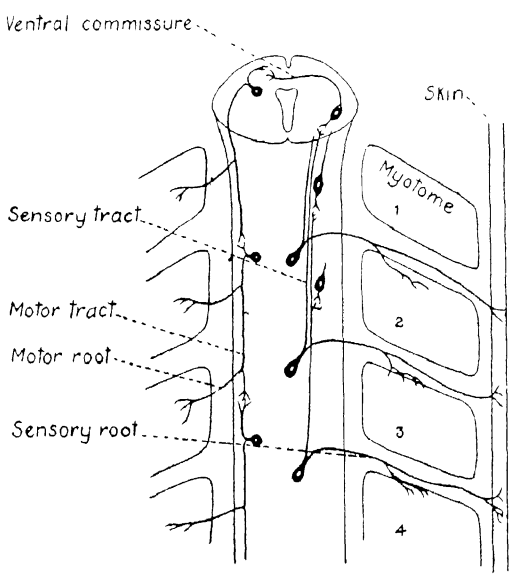


Fig. 6. Spinal cord of larval *Amblystoma*, showing relations of giant cells, commissural cells and motor cells.

on the opposite side of the cord. The motor cells have processes which pass upwards and downwards in the cord, the actual motor nerves

being collaterals. In the course of further development the Rohon-Beard cells disappear and are replaced by dorsal root ganglion cells, the cutaneous and proprio-ceptive elements becoming differentiated as separate neurones. The commissural fibres persist as dyscritic sensory neurones. The collateral of the motor axon becomes the motor nerve and contributes to the formation of a ventral spinal root. The Amphibia show another transition stage, in that, below their level, the afferent axons are brought into relation with the motor cells of the anterior horns by means of long dendrites of the latter which extend backwards far into the posterior horns, whereas in them and higher vertebrates the synapse is formed by long sensory collaterals which extend forwards into the anterior horns. The secondary sensory neurones are of the usual Edinger fibre system type. It is true that in Amphibia there are posterior columns, but these are composed almost entirely of descending fibres, and there are no posterior column nuclei (Goll and Burdach's nuclei). Moreover, the peripheral *sensory* receptors are almost entirely of the free nerve ending type. There is as yet no evidence of an epicritic system.

The *reptiles* are specially noteworthy, since in them, in addition to a typical Edinger fibre system, we find (1) complex peripheral sensory receptors—Pacinian corpuscles; Rollet and Sachs corpuscles in the muscles; (2) a definite frontal accumulation of ascending sensory neurones forming well-marked posterior columns; (3) posterior column nuclei of the Goll-Burdach type, (4) a median fillet; (5) neo-thalamic nuclei. In other words, for the first time in the phylogenetic series all the constituents of an epicritic system, though relatively sparse, appear; and this is contemporaneous with the adoption of life on the land.

It is a striking fact that in *birds* the posterior columns, both in proportion to the total white substance and to the grey matter, are relatively less than in reptiles. This is attributable in the first place to the lower cutaneous sensitivity of birds, whose life in the air minimizes the need of contact-receptors. In the second place, most of the afferent posterior root fibres end at once in the cord, as might be expected in such predominantly reflex animals[1], and as is shown *inter alia* by the well-known co-ordinated activities of a decapitated fowl. The median so-called tail nucleus (Bischoff's nucleus) in the posterior columns, which is found also in *Varanus* and the crocodile, is very constant in birds[2]; the median fillet is very small. On the other

[1] Streeter, *Amer. Jl. of Anat.* III, 1903; Kappers, *op. cit.* p. 176.
[2] Zeehandelaar, in Kappers, *op. cit.* pp. 165, 176.

hand, the dyscritic Edinger fibre system (Fig. 7) is well developed, and its ontogeny is very well depicted in Ramon y Cajal's figures. It is worthy of note that in the chick embryo the caudal commissural cells send their axons forwards, the frontal cells backwards, thus resembling Rohde's cells in *Amphioxus* (Bok). Birds are richly supplied with descending tracts from the vestibular nerve and cerebellum, and from the tectum, whereby the vitally important dyscritic cutaneous and proprio-ceptive (including mesencephalic Vth) impulses are correlated with those of gravistasis and photostasis, which "is not surprising in such exquisitely poised animals (Kappers) "

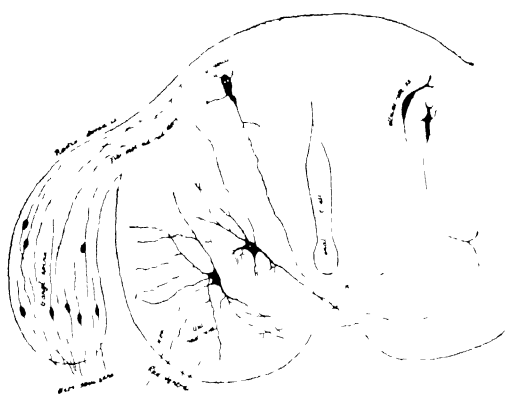


Fig 7 Transverse section of spinal cord of chick embryo, showing secondary sensory neurones (Edinger fibres). (Edinger, after Retzius)

Both the dyscritic and the epicritic systems are well developed in *mammals*, as has already been stated for man, but a study of the comparative anatomy brings out several points worthy of special mention. The Edinger system is reinforced by a crossed tract of completely homologous and analogous nature from the spinal trigeminal (Vth) nucleus. Edinger fibres, after passing through the anterior commissure, anterior columns, and antero-lateral column, pass to the corpus posticum in the mid-brain, the metathalamus (median geniculate ganglion)[1], and the tectum opticum (anterior colliculus or superior corpus quadrigeminum) (Fig 8). In this manner, co-ordination of vital dyscritic impulses occurs in the mid-brain—dyscritic cutaneous and probably proprio-ceptive, gravistatic (through the vestibular (VIIIth nerve system) and median geniculate body),

[1] Mott, *Brain*, xv, 1892.

and photostatic (through the tectum). There is evidence that the dyscritic system, far from being reduced in mammals, undergoes further development. The substantia gelatinosa of Rolando, which forms a cap to the posterior horns, is found in birds and reptiles only in upper cervical region and belongs to the spinal Vth nucleus. This nucleus emits only Edinger fibres. Thus, the corneal reflex, the afferent path of which is typically protopathic, is subserved by the spinal

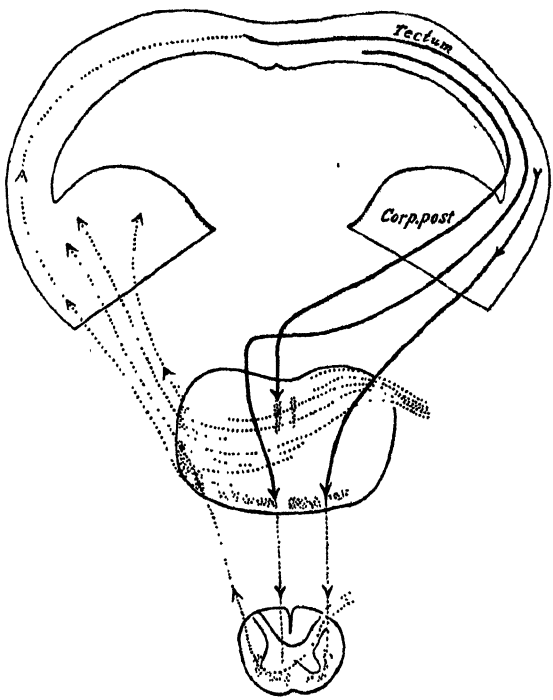


Fig. 8. Distribution of Edinger fibres (·····) to posterior colliculus and tectum and efferent tecto-bulbar and tecto-spinal fibres (——) (Edinger).

Vth nucleus[1]. It is true that in mammals there is a trigeminal fillet, entirely homologous and analogous with the median fillet; but this arises in the sensory Vth nucleus in the medulla. Hence the substantia gelatinosa is associated with dyscritic fibres only. Now, in mammals it is much more widely distributed throughout the cord, and its distribution has a well-marked relation to the cutaneous

[1] Wallenberg, *Neurol. Centralblatt*, 1896.

sensitivity of the animals. Thus, it is almost absent in Cetacea, whereas it is enormously increased in Ungulata, the dog, *Simia satyrus*, etc (Kappers). The epicritic system is subserved by the posterior columns and their nuclei (cuneatus (Burdach) and gracilis (Goll)), the median fillet, the ventral and median nuclei of the optic thalamus, and their cortical projections. It is concerned chiefly with stereognosis, and increases proportionately to the greater tactile discrimination, etc , of higher mammals. This greater development is manifested peripherally by highly organized peripheral receptors, especially Meissner's corpuscles, and by a more highly differentiated and organized deep sensibility in the muscles and joints. Hence we find that the proportion which the posterior columns bear to the total white substance in the cord varies, *e.g.* in the cervical region of the cat 22 per cent , monkey 26 per cent., and man 39 per cent. This increase, which is correlated with a similar increase in the cortical projection, is also associated with increase in the cortical efferent (pyramidal) tracts, which form in the dog 10 per cent., monkey 20 per cent., and man 30 per cent. of the white substance. The posterior root nuclei show similar variations[1].

2. The Medulla Oblongata

The medulla oblongata is characterized by a relatively enormous development of the sensory, as compared with the motor, system. The sensory system includes (1) a somatic part, and (2) a visceral part The somatic part includes the extero- and proprio-ceptor neurones of the head and face; it loses its segmental character, nearly all the neurones being aggregated into the trigeminal (Vth) nerve system; the only other representatives in man being the auricular nerve of the vagus (X), and a few branches of the glosso-pharyngeal (IX). The somatic part, however, also includes a highly specialized system, that of the lateral line organs of aquatic animals and the labyrinth of all vertebrates, subserved by the vestibular nerve (VIII), and in higher vertebrates, from the Amphibia upwards, that of the cochlea and auditory nerve (VIII). The visceral part includes the afferent fibres of the branchial nerves, the facial (VII), glossopharyngeal (IX) and vagus (X), derived chiefly from intero-ceptors, among which the gustatory fibres are included, having a specially wide distribution in fishes, where the taste receptors invade large cutaneous areas.

There are thus three systems which specially concern us, and which

[1] *Vide* Kappers, *op. cit.* pp. 213–216.

throw light upon the development of dyscritic and epicritic sensory systems, *viz.* the trigeminal, the gustatory, and the VIIIth nerve.

The Trigeminal System. The Vth nerve supplies the cutaneous

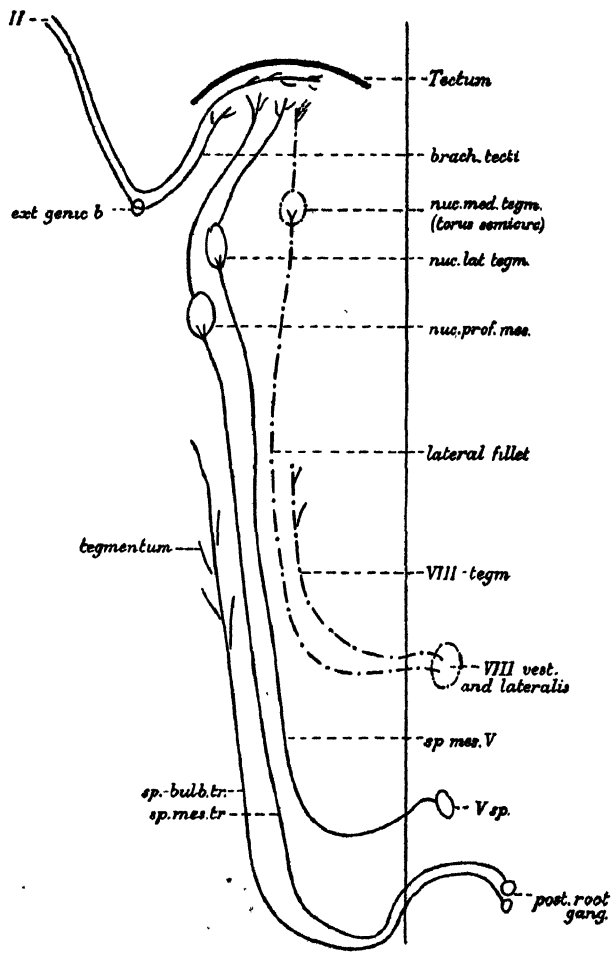


Fig. 9. Plagiostomes.

receptors of the head and shows the greatest resemblance to the posterior roots of the spinal cord. Like them, it has well-differentiated dyscritic and epicritic parts. The dyscritic fibres join the spinal Vth

nucleus ("descending root"), whence they cross in the anterior commissure to the anterior and antero-lateral tracts to form spino-bulbar and spino-mesencephalic tracts which end in the nuclei of the tegmentum, in the ganglion isthmi, which is the precursor of the median geniculate body, and in the tectum. They carry essentially vital impulses which in the mid-brain enter into relation with optic (II) and static (VIII) impulses, thus correlating cutaneous with photostatic and gravistatic impulses. This primitive system alone obtains in cyclostomes, plagiostomes, and teleostean fishes, and probably also in Amphibia. In the two latter there are well-marked correlations with the sensori-motor apparatus of the cord, in teleosteans especially with the pectoral fins, in Amphibia with the lumbar region, thus placing the chief motor extremities of these animals under the domination of the extero-ceptors of the head. In reptiles there is a well-marked bulbar sensory Vth nucleus, and it is probable that fibres from it which pass ventral run up to end in the thalamus and form the earliest phylogenetic evidence of a Vth nerve fillet, and therefore of an epicritic system. For here, too, we first find a medial thalamic nucleus which is homologous with the thalamic Vth nerve nucleus of mammals, and in reptiles, too, complicated receptor organs, such as Pacinian corpuscles, are common. In mammals the Vth nerve fillet forms a well-marked tract, originating in a bulbar sensory nucleus which is homologous with the Goll-Burdach posterior column nuclei. In birds, in which epicritic sensibility is so poorly developed[1], there is no definite fillet, but there is a quinto-frontal tract from this nucleus, passing up to the basal part of the fore-brain, thus effecting a correlation between the cutaneous receptors of the head and smell ("the oral sense"). van Valkenburg[2] has demonstrated the intimate relation in mammals between the trigeminal and the neck muscles on the one hand and the snout on the other. The latter correlation subserves the snout as the exploratory organ *par excellence* in many mammals, *e g.* cat, with its whiskers. Hence the size of the sensory root of the trigeminus bears a relation to the size of the area subserved, as in the large snouts of monotremes, and also to the high development of the innervation, as in the field-mouse (*Sorex*). The former correlation shows the anatomical basis of neck reflexes, which are so important in posture[3], and in which photostatic impulses also play a prominent part.

[1] *Vide supra*, p. 79
[2] *Monatschr f. Psychiatrie und Neurol.* XXIX, 1911
[3] *Vide infra*, Chap. VII, 2.

The mesencephalic nucleus of the Vth nerve is remarkable in that it represents the persistence throughout the vertebrates, including

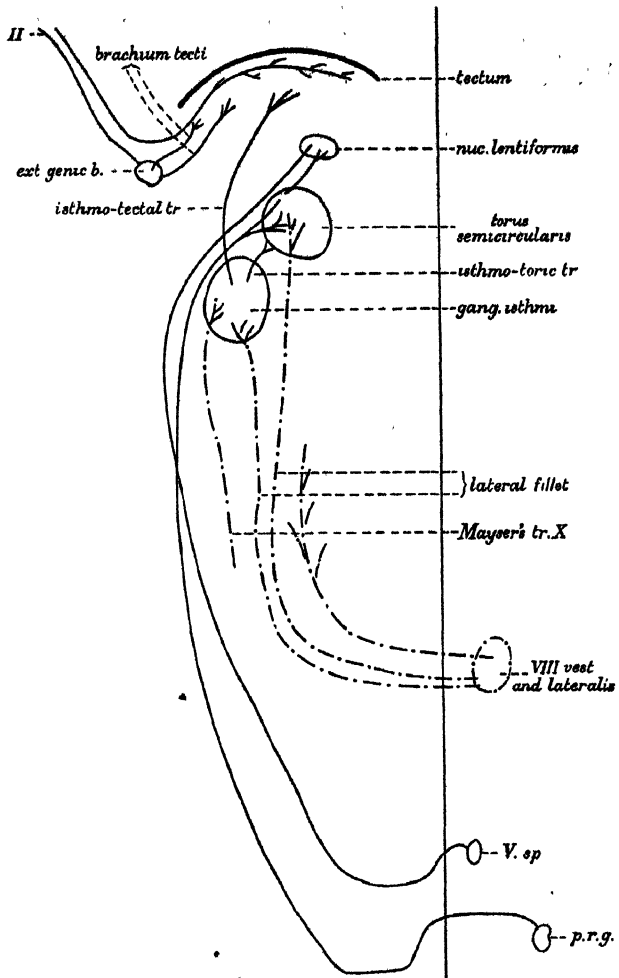


Fig. 10. Ganoidei and Teleostei.

man, of intramedullary sensory cells homologous with Rohon-Beard cells[1]. This nucleus has given rise to much discussion, but the evidence

[1] Johnston, *Jl. of Comp. Neurol.* XIX, 593, 1909; L. Kidd, *Rev. of Neurol. and Psychiatry*, VIII, 594, 673, 749; *Brit. Jl. of Ophth.* VI. 49, 1922.

is strongly in favour of the view that the dendrites are the proprioceptive fibres of the mandibular muscles. The nucleus is best developed in snakes, which have very powerful jaw muscles. The axons pass to the motor Vth and motor VIIth nuclei. Other proprio-ceptive fibres run in the trigeminal nerve[1].

The Chemical Sense and Taste. Complicated end-organs of taste occur in all the Chordata, except *Amphioxus*. In the larvæ of *Petromyzon* they are found in the pharynx and branchial clefts, in the adult in the skin In plagiostomes they are limited to the pharynx and mouth. In ganoids and teleosteans they extend over the head, especially on the barbels, and in many of the latter also over the body, and reach enormous numbers in deep sea fishes (Siluridæ). They do not occur in the skin above the fishes. In Amphibia they are numerous in the mouth and pharynx. Among reptiles they are few in snakes and alligators, more numerous in tortoises. They are fewest in birds (most in parrots). In mammals they are almost limited to the tongue. They have been estimated at 800 in the bat, 4000–6000 in the squirrel, 9000 in the hare and man, 10,000 in the sheep and marsupials, 15,000 in the pig and goat, 17,000 in the rabbit, 35,000 in the ox, and absent in Cetacea.

The dermal taste organs are always supplied by a branch of the facial (VIIth) nerve Others are supplied by the glossopharyngeal (IXth) and vagus (Xth). None are supplied by the trigeminal (Vth).

Taste is a higher differentiation of the chemical sense, which is subserved by somatic nerves, and is lost over those parts of the epidermis which become horny The receptors are free nerve endings, and, therefore, belong to the most primitive type Animals without taste buds in the skin (*e g.* larva of *Petromyzon*, elasmobranch fish, frog), respond to salts, alkalies, acids, and bitters, but not to sugar. The chemical sense persists[2] in animals with taste buds on the skin (*e.g.* silurian fishes) when the nerves supplying these are cut. The tactile sense is abolished before the chemical by cocaine[3]. The stimuli to both chemical sense and taste are the negative ions.

The chemical receptors are all noci-ceptors, the reaction being invariably a negative tropism. Fishes with cutaneous taste buds (Siluridæ, Cyprinidæ, Gadidæ) respond positively to sapid nutritive substances; those without taste buds (*Prionotus, Opsanus*) negatively or not at all[4]. If the gustatory nerves are cut fishes respond to salts,

[1] Edgeworth, *Quart. Jl of Micr Sc.* LVIII, 1913. [2] *Vide supra*, p. 8.
[3] Sheldon, *Jl. of Comp. Neurol.* XIX, 273, 1909; Cole, *Ibid.* XX, 601, 1910; Crozier, *Ibid.* XXVI, 1, 1916 [4] C. J. Herrick, in Kappers, *op. cit* p 278.

alkalies, acids, and bitters, but not to nutritive substances[1]. There is, therefore, a very intimate and primitive correlation between taste and touch.

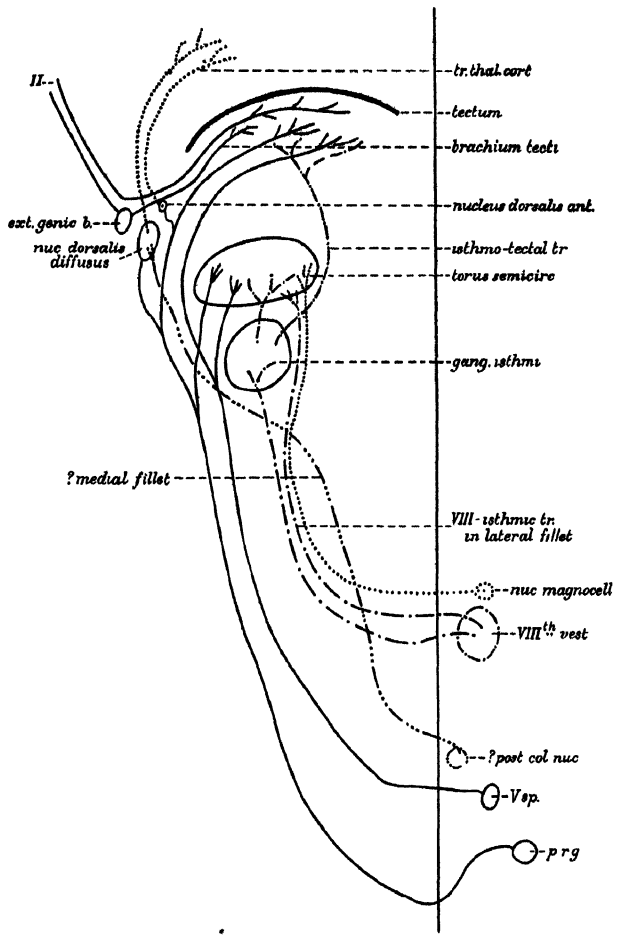


Fig. 11. Amphibia.

Investigation of the central connections of the gustatory tracts demonstrates the intimate correlation with tactile sensibility. This is well seen in siluroid and cyprinoid fishes. It is from this correlation centre that descending efferent tracts start, the latter thus forming

[1] G. H. Parker, *Jl. Acad. Nat. Sc.* Philadelphia, xv, 221, 1912.

a "final common path." There is a further intimate relation with the fasciculus solitarius in lung-breathing animals. In those animals in which the tongue is the chief organ of taste the nucleus of Staderini in the medial region of the medulla is specially large, and appears to be the principal gustatory nucleus. The secondary neurones from the bulbar centres are little known, but there is a definite projection to the ventral nucleus of the neothalamus. It is probable that they are here projected by tertiary neurones to the hypothalamus, the chief centre of visceral reactions.

Analogy would lead to the conclusion that the chemical sense is the more primitive and dyscritic. The elaborate taste-receptors suggest an epicritic differentiation. If so, it is remarkably early phylogenetically as compared with cutaneous sensibility. This is perhaps not surprising in animals so dependent upon taste, smell, and oral sense. It seems to me, however, more probable that such differentiation as has occurred is rather within the limits of the dyscritic system. It is to be remembered that these fundamentally vital senses of lower vertebrates—taste and smell—become side-tracked and even undergo degeneration in higher vertebrates, in which the progressive development of the visual sense becomes the prepotent factor in evolution. On this view the gustatory sense is an example of arrested development, the epicritic stage never having been actually reached.

In this connection the study of what may be called the *vibratory sense*, subserved by the lateralis, labyrinthine, and auditory system is illuminating.

The Lateralis and Auditory Nerve (VIIIth) System. Sensory organs whose function is probably that of receptors for variations in pressure, and whose adequate stimuli are mechanical, occur in the form of statocysts in invertebrates. They are essentially proprio-ceptive in function and their responses are concerned with muscle tone as subserving posture and equilibrium. While differing in detail, their most characteristic feature is a calcareous concretion or statolith which exerts varying degrees of pressure upon a sensory cell, which is provided with hair-like processes like other sensory cells. It is remarkable that this primitive mechanism, so common among invertebrates[1], persists up to man, where it is represented by the maculæ acusticæ and otoliths of the inner ear.

Aquatic vertebrates are provided with an elaborate system of

[1] See Butschli, *Vorlesungen uber vergleichende Anatomie*, Abt. 3, pp. 740 sqq. Berlin, 1921.

lateral organs to subserve the vibratory sense; they are present in all fishes, urodele amphibians, and the larval stages of anurans. Their function[1] is to respond to alterations in the pressure of the water produced by movements of the tail, and also to reflected waves from stationary objects, thus enabling the animals to find their way

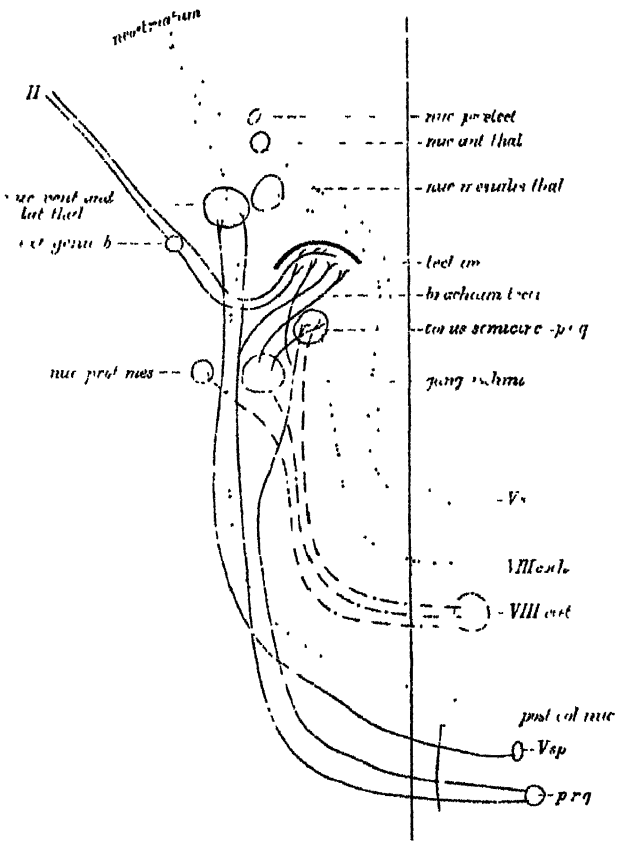


Fig. 12. Reptiles.

in the dark and in muddy water. It is probable that the accuracy of the flight of bats is due to a similar mechanism[2].

The sensory organs in the lateral lines show various degrees of

[1] C. H. Parker, *Bull. of the Bureau of Fisheries*, Washington, XXIV, 1905; XXX, 1912; Hofer, *Berichte der Bayr. Biol. Versuchsstation*, Munchen, I, 1907.

[2] Cf. Hartridge, *Jl. of Physiol.* LIV, 54, 1920.

complication. The simplest are sensory cells with hair processes, separated by supporting epithelial cells, in the skin surface (*e.g.* the "pit organs" or neuromasts of *Petromyzon*). Others nearly resemble taste buds. In selachian and other fishes the lateral lines are canals sunk in the skin, with pores opening on the surface or covered by a very thin membrane. Still more highly differentiated are the ampullæ of Lorenzini (*e g* Selachii) and the Savi-cysts (*Torpedo*). The largest organs are found in Teleostei, and are specially large in deep sea fishes (Macruridæ) and *Mormyrus*.

The labyrinth belongs to the same system of vibratory sense organs. In myxinoids there is only one canal, other cyclostomes have two (anterior and posterior), all other vertebrates have three (anterior, posterior, and external). The free opening of the ductus endolymphaticus on the surface of the head in Chondropterygii (*e.g.* dog-fish (*Acanthias vulgaris*) and skate (*Raia clavata*)) shows analogy to lateral line organs.

The cochlea, which also belongs to the same system of vibratory sense organs and is the essential receptor for hearing, appears first in the Amphibia, though there is reason to think that the sacculus and papilla lagænæ are sensitive to auditory impressions in fishes[1]. The frequency of the sinusoidal vibrations to which the lateral organs are sensitive is very small (6 per sec.), whereas the frequency of auditory vibrations is from 10 to 20,000 per sec

The area statica of the medulla oblongata, in which the lateralis and vestibular nerves end, is a somatic area continuous with the spinal posterior root areas Already in *Petromyzon* it is in near relation to the crista cerebellaris, and the cerebellum is an extension and differentiation of the static area. In higher vertebrates this area is specially represented in the auricles of the cerebellum, which becomes the flocculus in higher mammals. The flocculus is enormous in Cetacea and pinnepeds The corpus cerebelli is more concerned with proprio-ceptive impulses from the muscles and joints, and consequently the corpus increases and the auricles diminish in land-living animals, in which these impulses become of greater importance for orientation and equilibrium.

The secondary neurones from the static area form two groups, descending and ascending. The former are the final common paths to the tail (Mauthner cells and Muller fibres) and limb muscles. The latter are partly local reflex fibres, and partly arcuate fibres, which

[1] Cf Piper, *Zentralbl f Physiol.* xx, 1906, G. H. Parker, *Bull. of Bureau of Fisheries*, Washington, xxii, 1903; xxx, 1912.

join the lateral fillet and end chiefly in the tegmentum, and to a less degree in the tectum. The lateralis nerves take a large part in the formation of the lateral fillet in fishes, since it and its accessory (valvula cerebelli) and end nuclei show proportionate hypertrophy

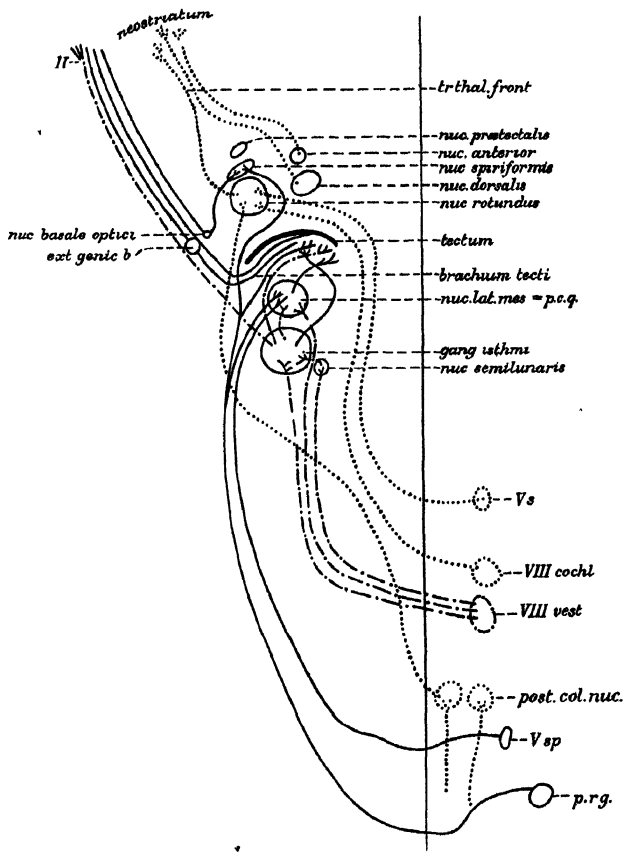


Fig. 13. Birds.

when the lateral lines are large (*e.g. Mormyrus*). In the mid-brain these fibres enter into relation with optic fibres, so that this region is a most important area for the correlation of static and visual impulses.

The secondary neurones of the VIIIth nerve in Amphibia form a

well-marked tract homologous to Edinger fibres, first decussating, and then travelling up to the posterior corpus quadrigeminum as a tract variously named bulbo-mesencephalic, fasciculus longitudinalis lateralis, lateral lemniscus or lateral fillet. This is chiefly composed of vestibular fibres, subserving gravistasis; but other fibres are derived from the nucleus magnocellularis, which is undoubtedly an auditory nucleus. This definite development of a true auditory mechanism is associated with the appearance of an inferior olive, which in higher mammals is known to have a function associated with hearing. The posterior corpus quadrigeminum, still hidden under the tectum in Amphibia, is a further development of the torus semicircularis of teleostean fishes.

Deiter's nucleus, very rudimentary in plagiostomes, becomes an important nucleus in immediate relation with the vestibular system in *reptiles*. It is the chief effector centre for reflex movements of the neck, head, and eyes, which accounts for its development as an offshoot of the predominantly gravistatic apparatus. Reptiles show marked increase in the posterior corpus quadrigeminum, which for the first time merits this designation, since in snakes and lizards it is so large as to escape from below the tectum and become visible upon the surface. In reptiles all the characteristics of the mammalian auditory apparatus are present, especially in crocodiles and lizards (Kappers).

The group of nuclei belonging to the VIIIth nerve in the medulla of *birds* show a great increase in size and higher differentiation, as might be expected from the habits of these animals. Their secondary connections are chiefly of the reflex type, both as regards their ascending and descending fibres.

The ascending secondary neurones of the vestibular system in *mammals* go chiefly to the lateral fillet, which is distributed to two distinct areas, the posterior corpus quadrigeminum and the internal geniculate body Of these the latter is derived from the ganglion isthmi The former is represented in fishes by the torus semicircularis, in reptiles by the corpus posticum, and in birds by the nucleus lateralis mesencephali. As it is also the end-station of most of the spino- and bulbo-mesencephalic tracts subserving cutaneous sensations, it forms a correlation centre for these and gravistatic impulses. The median geniculate body belongs to the oldest part of the optic thalamus—the metathalamus; it is largest in Edentata and Cetacea. It atrophies if the cerebrum is removed, though its precursor, the ganglion isthmi, has no cortical projection. It receives both vestibular

and auditory (cochlear) fibres, and the auditory fibres are projected to both sides of the mid-brain and cerebrum; it also receives protopathic sensory fibres. It must, therefore, be regarded as having both dyscritic and epicritic functions Specially noteworthy is the near association of the ascending vestibular fibres with the VIth nucleus.

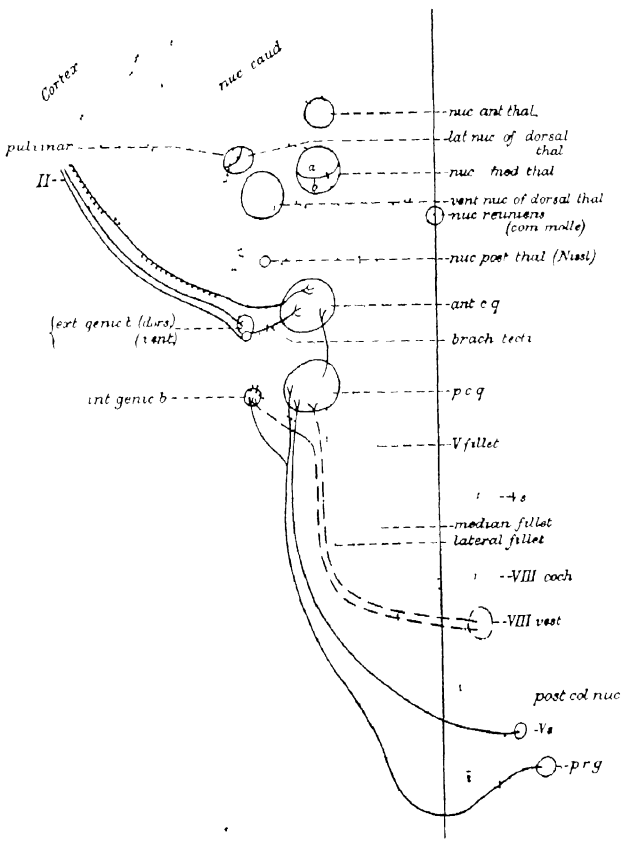


Fig. 14. Mammals.

It is also noteworthy that the nucleus principalis or triangularis vestibuli is found only in mammals and is probably concerned in the finer eye movements. Further, descending vestibular secondary neurones can be traced to von Monakow's nucleus (nucleus cuneatus

externus), situated lateral to the nucleus of Burdach. The importance of this connection is that it correlates the static impulses of the vestibular apparatus with the efferent motor impulses of the pyramidal tracts from the kinæsthetic areas of the cortex, and hence subserves stereognosis.

This inadequate sketch of the lateralis, vestibular, and auditory system suggests that the lateralis system, like the gustatory, has undergone considerable differentiation low down in the phylogenetic series. It confirms the view that this differentiation should be regarded as still confined to the dyscritic system, and that evidence of true epicritic differentiation is lacking. The vestibular and auditory parts of the VIIIth nerve system show a marked contrast. The former is at any rate predominantly dyscritic, and the latter is undoubtedly epicritic.

3. The Mid-Brain and Optic Thalamus

The mid-brain and optic thalamus form together the chief correlation centre for cutaneous sensory, gravistatic and photostatic impulses; and the optic thalamus is the supreme centre for dyscritic and instinctive reactions. Their importance as the chief central organs of the nervous system subserving perception is, therefore, so great that further attention must be devoted to them, even at the risk of some repetition.

It has been suggested that the tectum opticum is represented in *Amphioxus* by Joseph's cells—large intramedullary cells with palisade-like hair processes, situated in the dorsal part of the anterior end of the central nervous system; and that the pigment spot at the extreme anterior end of the nervous system is the rudiment of the retinal pigment epithelium of higher vertebrates. There is little evidence in favour of these conjectures.

Cyclostomes possess a well-differentiated mid-brain, extending between the level of the IVth nerve and isthmus behind and the pineal body in front, and comprising a tectum dorsally and tegmentum, with IIIrd nerve, ventrally. In front is a primitive but well-developed thalamus, consisting essentially of an epithalamus (ganglion habenulæ) dorsally, having chiefly olfactory connections, a hypothalamus ventrally, having olfactory and visceral connections; and an intermediate thalamus proper consisting of a dorsal part, with optic connections, and a ventral part with olfactory connections. In *Petromyzon* the cells of the tectum are very primitive and are situated chiefly near the ependyma of the ventricle. They

have all the characteristics of static or potential plasticity[1]. It is probable, though not definitely proved, that the tegmentum and tectum receive secondary sensory neurones of Edinger fibre type from the spinal cord and spinal Vth nucleus and from the static

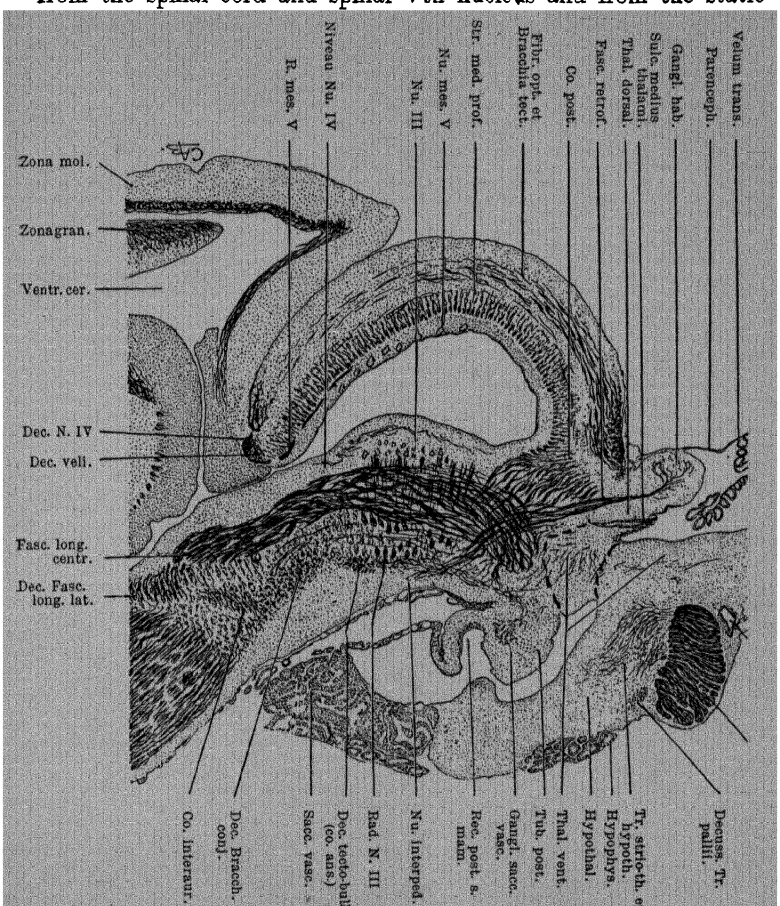


Fig 15. Paramedial sagittal section of mid-brain of dog-fish (*Scyllium canicula*) (Kappers)

(VIIIth) area in the medulla Most of the fibres to the tectum are derived from the optic (IInd) nerve, and these pass to the most superficial layer. By efferent, descending crossed and uncrossed

[1] *Vide*, pp 65, 67.

tecto-bulbar tracts the tectum is brought into relation with the medulla, and especially the motor nuclei of the eye muscles, and by the intervention of reticular cells with the cord. The movements of the animal are thus brought under the control of dyscritic optic,

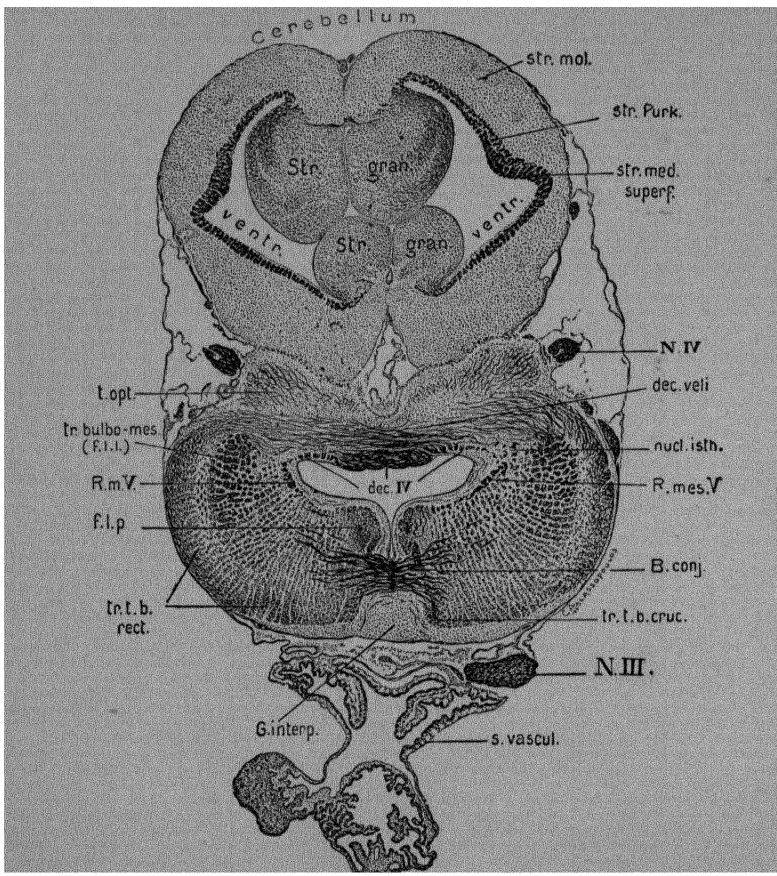


Fig. 16. Transverse section through posterior end of mid-brain of shark (*Acanthias vulgaris*) (Kappers) *f l p* posterior longitudinal bundle; *tr t b. rect.* direct tecto-bulbar tract; *tr.t.b cruc* crossed tecto-bulbar tract

common sensory, and gravistatic impulses. There is no frontal projection from the tectum. The dorsal nucleus of the thalamus is also primitive and very small. It has few afferent fibres from below, and there is little evidence of any connection with the fore-brain.

It is noteworthy, however, that even at this lowly level a few cells are separated off from the central mass and are situated more peripherally and somewhat dorsally. These are important as being

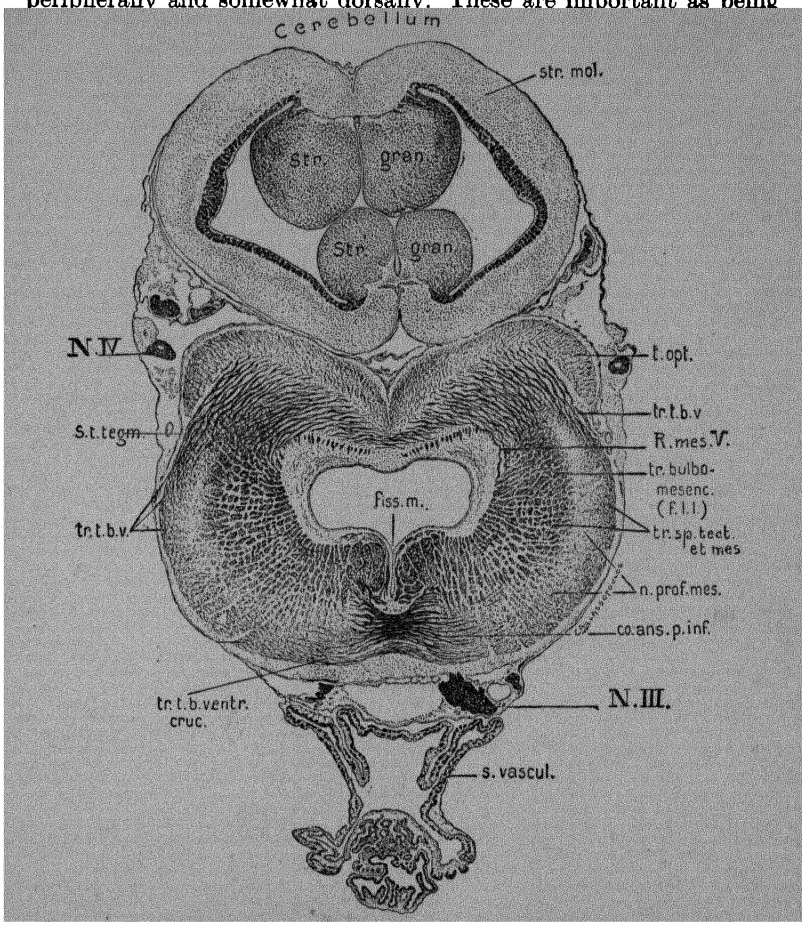


Fig 17 Transverse section through mid-brain of *Acanthias vulgaris*, frontal to Fig 16 (Kappers) *tr t b v* ventral tecto-bulbar tract, *f l l* lateral lemniscus or fillet, *tr sp tect et mes* spino-tectal and spino-mesencephalic tracts

the rudiment of what in higher vertebrates becomes the lateral geniculate body. These cells are in near relation with scanty optic nerve fibres. The whole sensory system appears to be on the dyscritic level.

In *plagiostomes* (Figs 15–19) the tectum is much more highly differentiated The remarkably well-developed mesencephalic nucleus

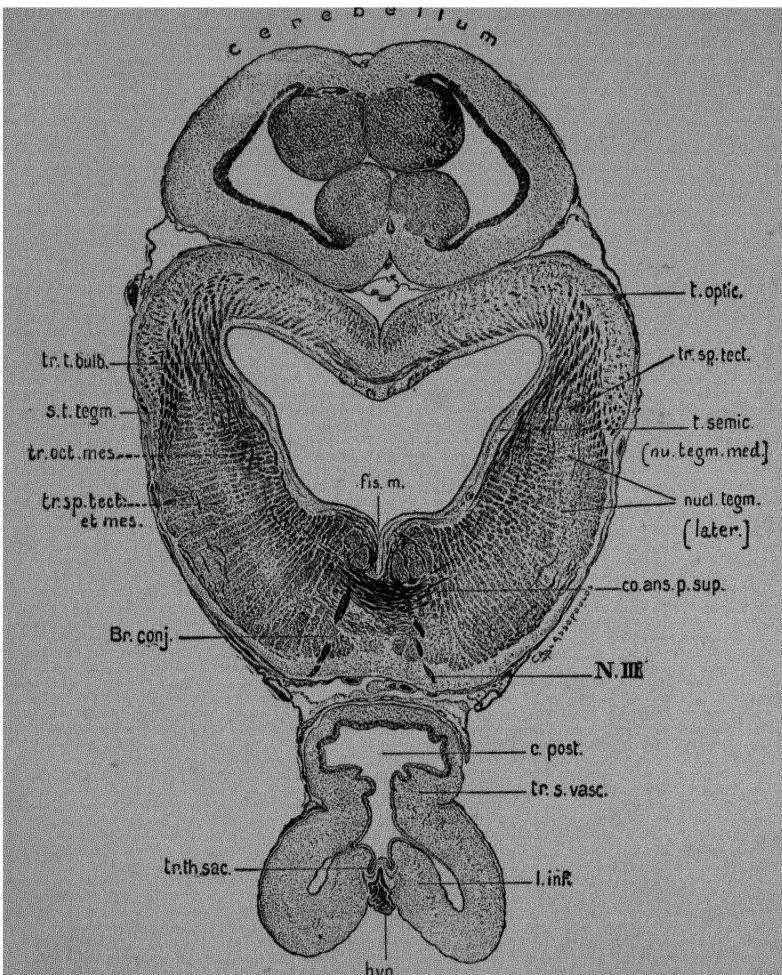


Fig. 18 Transverse section through mid-brain of *Acanthias vulgaris*, frontal to Fig. 17 (Kappers) *t semic* torus semicircularis; *co ans p. sup.* commissura ansulata pars superior = dorsal tecto-bulbar decussation.

of the Vth nerve lies in it just outside the ventricular wall. Several important nuclei make their first appearance. The nucleus isthmi is

found near the aqueduct at the level of the IVth and mesencephalic Vth nerves. It receives bulbo-mesencephalic fibres from the lateral longitudinal bundle or lateral fillet. These come from the area statica (VIIIth), and carry vestibular, *i.e.* gravistatic impulses. It is connected with the cerebellum through the decussatio veli, and also with the tectum. It is very constant in the vertebrates up to the mammals,

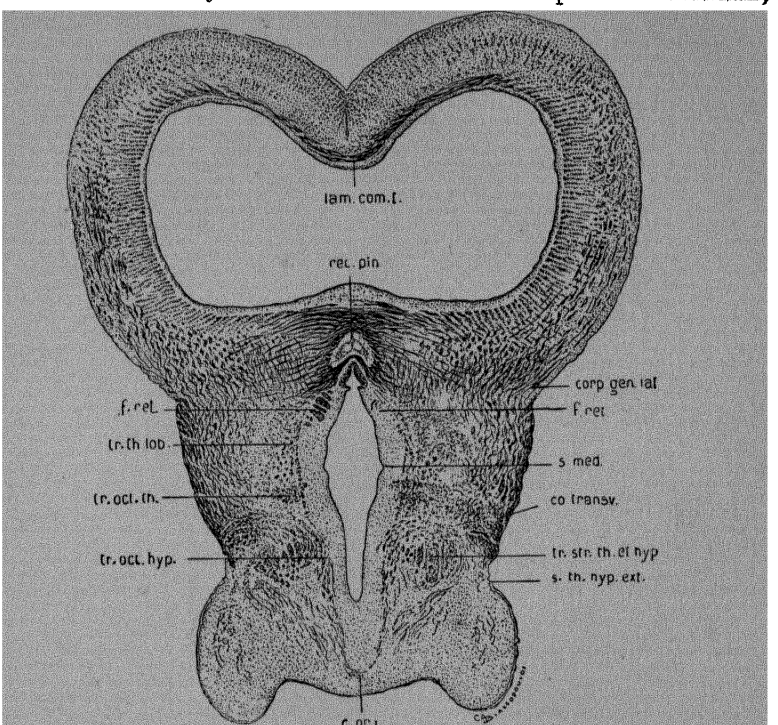


Fig. 19. Transverse section of mid-brain of *Acanthias vulgaris*, frontal to Fig. 18 (Kappers). *corp. gen. lat.* lateral geniculate body; *f. ret.* fasciculus retroflexus.

where it disappears, but is almost certainly replaced by the medial geniculate body The first rudiments of the torus semicircularis are also found in plagiostomes, just bordering on the ventricle where the tegmentum passes into the tectum (nucleus medialis tegmenti). In higher vertebrates it becomes the posterior corpus quadrigeminum. Two other tegmental nuclei, deep and lateral, are distinguished. The nucleus profundus receives the spino- and bulbo-mesencephalic

tracts, which carry dyscritic common sensory impulses. The nucleus medialis is the end of the lateral fillet, and therefore carries gravistatic impulses. The nucleus lateralis receives the sensory fibres from the spinal Vth nucleus, and transmits bulbar and spinal tracts to the tectum.

The optic nerve fibres give off collaterals to the still very primitive external geniculate body, and then pass on to be distributed on the surface of the tectum. The external geniculate body emits a bundle of fibres, the brachium tecti, to the tectum It has no frontal projection; and must, therefore, be considered still to carry only dyscritic visual impulses. The tectal optic fibres form synapses with cells whose axons pass into the deep layer of nerve fibres. These are efferent fibres which form very large descending tecto-bulbar tracts, thus bringing the movements of the body under the control of photostatic impulses.

The epithalamus and hypothalamus are chiefly concerned in olfactory, and to a less extent, visceral impulses. These, indeed, form the chief function of the thalamus in these fishes The dorsal nucleus is a minute nucleus, with no fore-brain fibres and few optic and spino-thalamic. The whole afferent system still seems to be essentially dyscritic.

In *ganoids and teleosteans* (Figs 20–23) the torus semicircularis varies in size with the development of the lateralis system, and hence attains its largest size in *Mormyrus* The tori are generally pushed apart by the valvula cerebelli (*e g.* perch, cyprinoids), hence the torus is often known as the nucleus lateralis mesencephali, although it is homologous with the nucleus medialis of plagiostomes (and birds) It receives most of the fibres of the lateral fillet (VIIIth-gravistatic), none of which pass to the tectum, thus differing from what obtains in plagiostomes. Why the two species should thus differ in their correlation of gravistatic and photostatic impulses is unknown. The torus also receives spino- and bulbo-mesencephalic fibres, many of which pass farther forwards to the sub-tectal nucleus lentiformis, the most frontal belonging to the spinal Vth (tractus spino-tectalis). All these fibres carry dyscritic impulses, the secondary Vth neurones including noci-ceptive impulses from the cornea.

The ganglion isthmi varies in size in different fish, being large in the perch, and very small in the cod It receives fibres from the lateral fillet and from the medulla (Mayser's tractus X). It communicates with the tectum and torus by isthmo-tectal and isthmo-tegmental tracts, and thus forms a correlation centre between

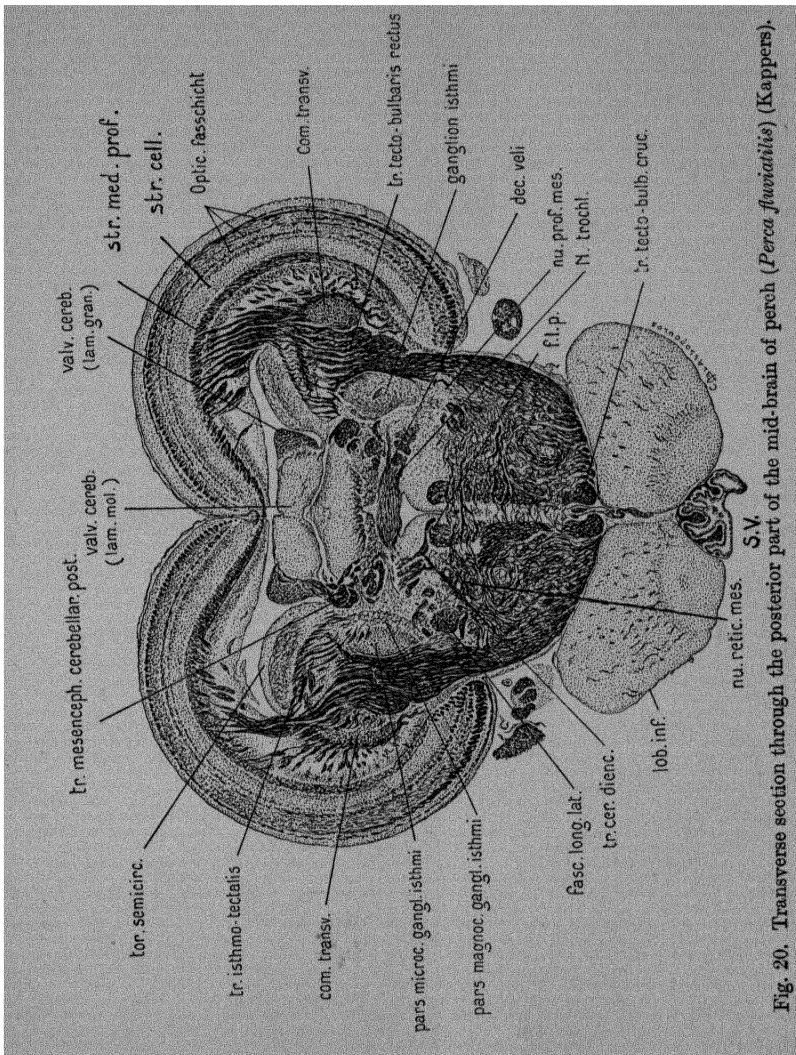


Fig. 20. Transverse section through the posterior part of the mid-brain of perch (*Perca fluviatilis*) (Kappers).

photostatic and vestibular (VIIIth) gravistatic impulses. These impulses are also correlated with the cerebellum The posterior mesencephalo-cerebellar tract varies with the lateralis system, and is, therefore, large in *Mormyrus* and the cat-fish (*Arius*). The tecto-cerebellar tract is largest in animals with large optic apparatus. It is noteworthy that lesions of the mid-brain cause much greater disturbances of equilibrium in fishes than lesions of the cerebellum[1].

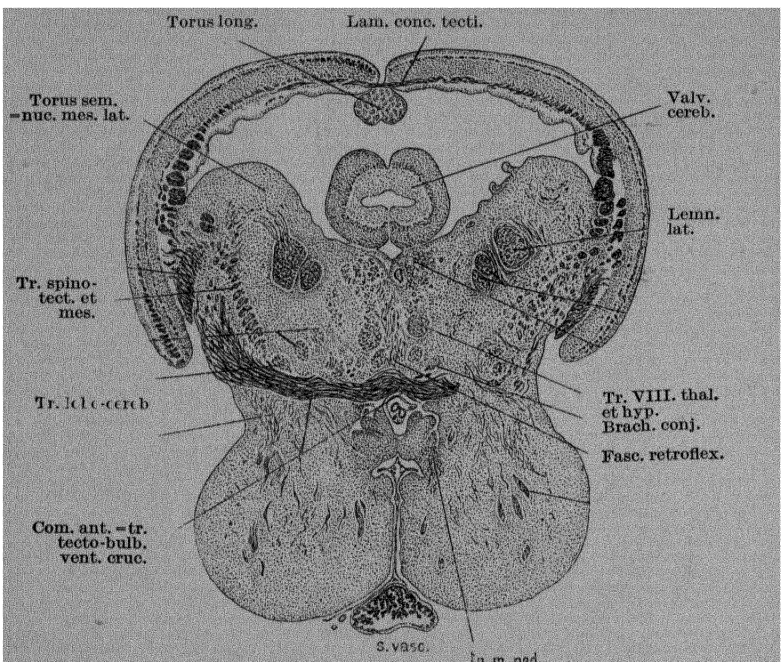


Fig. 21. Transverse section through the tori semicirculares of cod (*Gadus morrhua*) (Kappers).

The tectum is more highly differentiated than in plagiostomes, and most so in voracious fish (pike, perch, *Barbus*) and flat-fishes (*Pleuronectidæ*). In addition to the usual superficial optic fibres, it receives spino-tectal fibres conveying dyscritic sensory impulses from the body, head and neck. The efferent fibres in the deep layers form, therefore, a final common path for optic and sensory impulses These tecto-bulbar tracts are divided into dorsal and ventral sets, both of

[1] Reisinger, *Biol Zentralbl.* 1914.

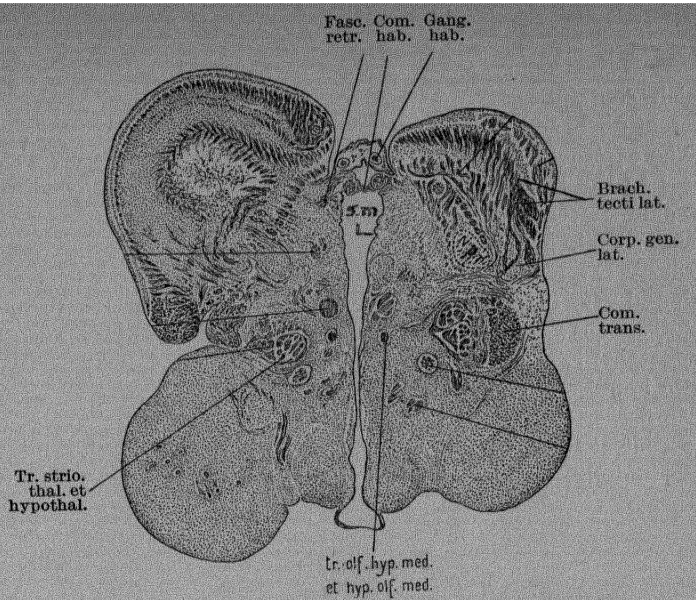


Fig. 22. Transverse section through the mid-brain of *Gadus morrhua*. The left eye was atrophied (Kappers).

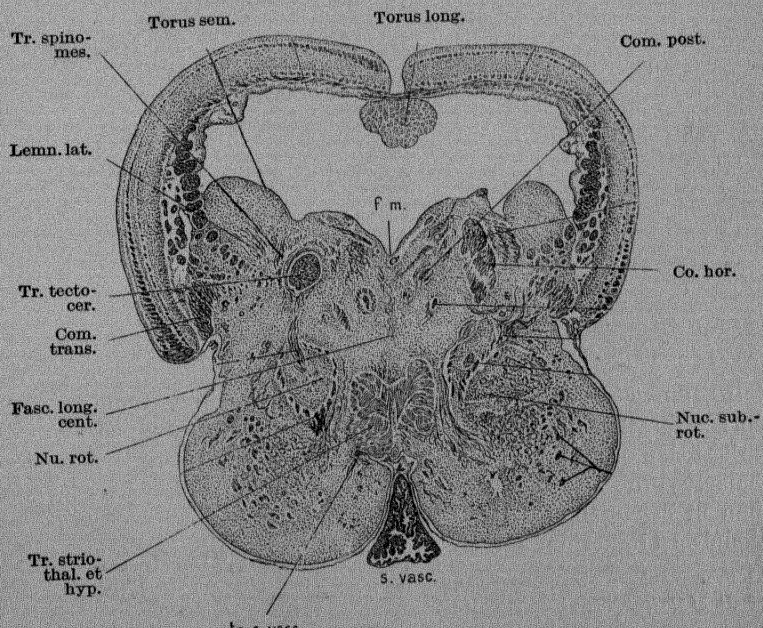


Fig. 23. Transverse section through the mid-brain of *Gadus morrhua*, frontal to Fig. 22.

which contain crossed and uncrossed fibres. The tectum sends efferent fibres to the optic nerve (fibræ tectalis nervi optici).

The external geniculate body receives few optic fibres. It sends fibres to the tectum in two well-marked lateral and medial tracts (brachium tecti). In fishes it belongs to the *anterior* part of the dorsal thalamus (cf. mammals). It varies much in size[1]. It is large in gurnards (*Trigla*) and flat-fishes (*Pleuronectidæ*). It is small in the cod, and very indefinite in deep-sea fishes (*Amiurus*, *Lophius*). The metathalamus (external geniculate body, nucleus lentiformis and nucleus prætectalis) is a correlation centre for optic, common sensory, and static impulses. The dorsal thalamus has no cortical projection in these fishes, and hence their sensory system is entirely dyscritic. The ventral thalamus is large and is a correlation centre for smell, taste, and visceral (sacculus vasculosus, sympathetic, etc.) impulses.

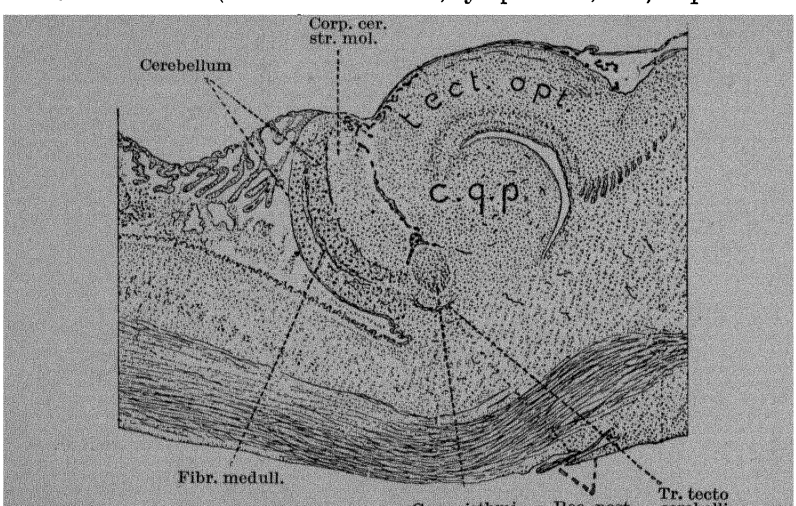


Fig. 24. Sagittal section through the mid-brain of frog (*Rana esculenta*) (Kappers).

In *Amphibia* (Figs. 24–28) the tori semicirculares fuse caudally, thus separating off a ventral canal from the optic ventricle, the earliest sign of an aqueductus Sylvii The metathalamus and dorsal thalamus proper are much larger, and the hypothalamus much smaller than in fishes, showing relative increased importance of visual and diminished importance of olfactory sensations. Herrick[2] has pointed

[1] Franz, *Folia Neurobiologica*, VI, 1912; see Kappers, *op cit* p 822, Fig 438.
[2] *Jl. of Comp. Neurol.* XXVIII, 1917.

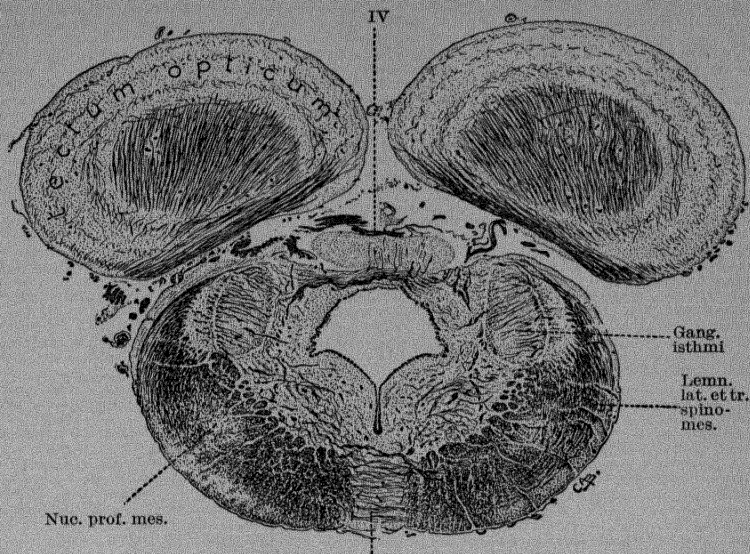


Fig. 25. Transverse section through the ganglion isthmi of *Rana mugiens* (Kappers).

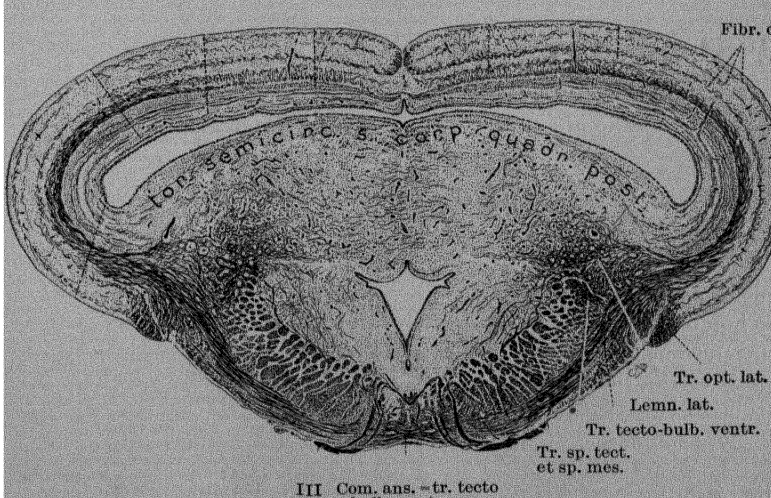


Fig. 26. Transverse section through the mid-brain of *Rana mugiens* (Kappers).

out the correspondence between parts of the thalamus and forebrain, thus. dorso-medial—epithalamus, primordium hippocampi; dorso-lateral—dorsal thalamus, pallium; ventro-lateral—ventral thalamus, corpus striatum, ventro-medial—hypothalamus, septum telencephali

The ganglion isthmi is very large in the ox-frog (*Rana mugiens* (*Catesbyana*)). It receives fibres from the lateral fillet and is intimately connected with the torus semicircularis and cerebellum. It is, therefore, a correlation centre for vital static and optic impulses, and probably plays an important part in eye movements.

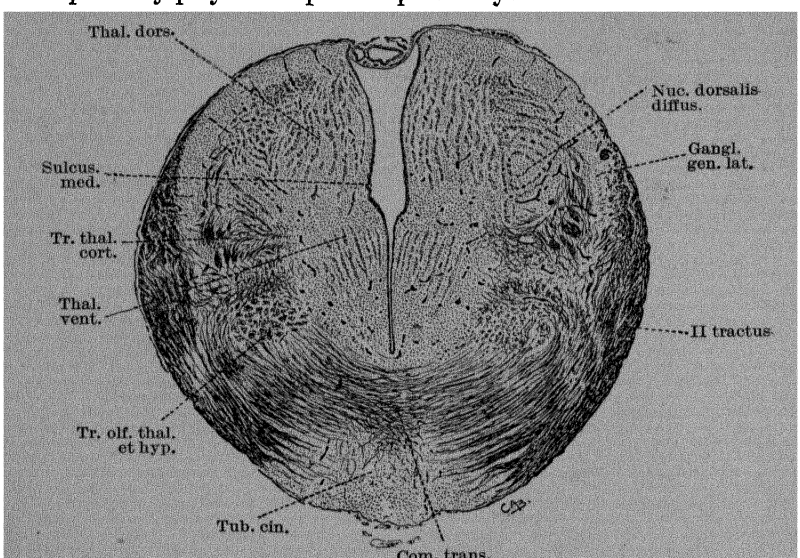


Fig. 27. Transverse section through the optic thalamus of *Rana mugiens* (Kappers).

The torus semicircularis appears to grow at the expense of the nucleus profundus mesencephali, which is small as compared with its homologues in fishes, the nucleus medialis tegmenti (plagiostomes) and nucleus lateralis mesencephali (Teleostei). The torus is of composite origin, the static (VIIIth) element derived from the tegmentum being in excess of the optic element derived from the tectum It receives spino- and bulbo (Vth)-mesencephalic common sensory fibres in its ventro-lateral parts, other fibres from this source passing to the tectum.

The tectum in Amphibia shows a reversion to the primitive static

plastic structure of the cyclostomes, the neurones being situated deep down near the ventricular wall, thus showing a noteworthy difference from the static fixity of structure found in selachian and teleostean fishes. As already mentioned, it receives spino- and bulbo-tectal, and isthmo-tectal fibres; and emits tecto-isthmic, tecto-bulbar, and tecto-cerebellar fibres. The tecto-bulbar fibres are crossed (commissura ansulata) and uncrossed, the latter going largely to eye-muscle nuclei The tecto-cerebellar fibres are fewer

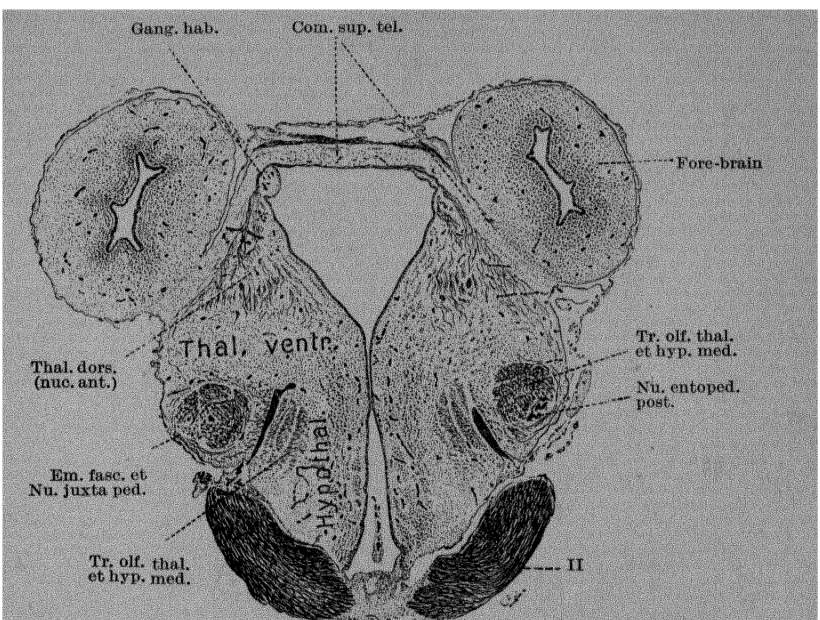


Fig. 28. Transverse section through the optic thalamus of *Rana mugiens*, frontal to Fig. 27 (Kappers).

than in fishes, in accordance with the less active movements of Amphibia, for the same reason the cerebellum is smaller than in fishes There is no posterior mesencephalic cerebellar tract as in fishes, owing to the absence of a lateralis system in the metamorphosed amphibian There is no cortical projection from the tectum

The dorsal thalamus receives spino- and bulbo (Vth)-thalamic fibres. It contains a frontally and dorsally situated nucleus anterior under the ganglion habenulæ, a dorso-laterally situated external geniculate body receiving optic fibres, and a nearly associated more

medially situated nucleus dorsalis diffusus receiving protopathic sensory fibres It receives no fibres *from* the fore-brain, but there is a tractus thalamo-corticalis *to* the fore-brain[1]. This is the phylogenetically earliest evidence of a cortical projection of neo-thalamic impulses, and is the first anatomical evidence of an epicritic system. These fibres pass to the dorso-lateral part of the palæocortex (the secondary olfactory cortex), which is thus "the cradle of the neopallium."[2] Phylogenetically older olfactory fore-brain tracts pass to the epithalamus (ganglion habenulæ), ventral thalamus, and hypothalamus.

In *reptiles* (Figs 29–32), the tori semicirculares resemble those of the frog in turtles and crocodiles. In most reptiles they are still covered and hidden by the tectum, but in snakes (boa, anaconda, python), owing to the diminution of the tectum, they appear upon the surface,



Fig. 29. Dorsal view of brain of snake (left) and crocodile (right) (Kappers).

and for the first time merit the designation posterior quadrigeminal bodies. The ganglion isthmi also forms a visible swelling on the surface in many reptiles it is largest in the chameleon, larger in crocodiles than in turtles, small in most lizards and snakes The dorsal thalamus shows further increase in size and differentiation, the two sides being fused in turtles and crocodiles. The ventral thalamus shows little development, and the hypothalamus is smaller. The mid-brain is characterized by the definite development of a nucleus ruber, well marked in lizards, crocodiles, and turtles, and receiving the anterior brachium of the cerebellum; and there is a rudimentary rubro-spinal tract. Ventro-medial, in front of the IIIrd

[1] Rubaschkin, *Arch f mikr' Anat* LXII, 1903, Herrick, *Jl. of Comp. Neurol.* XXVIII, 1917

[2] Kappers, *op cit* p 844

nerve nucleus, there is a large-celled nucleus which sends its axons into the posterior longitudinal bundle this is the earliest manifestation of Darkschewitch's nucleus. Lying just outside it is the nucleus interstitialis of Cajal, and dorso-medially is the nucleus of the posterior commissure

The lateral fillet ends in the nucleus profundus mesencephali, the ganglion isthmi, and the torus semicircularis The ganglion isthmi emits isthmo-tectal and isthmo-toric fibres. In addition to static

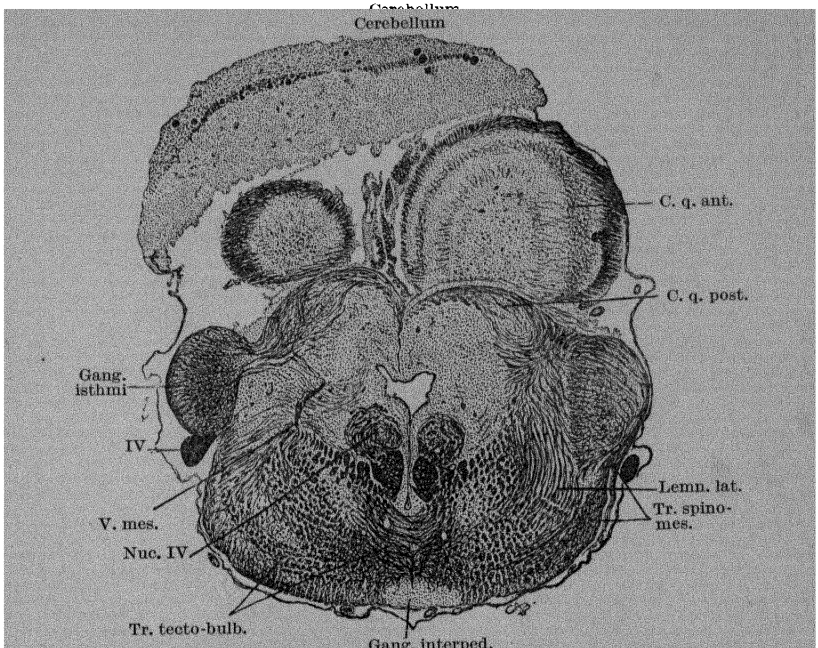


Fig. 30. Transverse section through the ganglion isthmi of chameleon (Kappers).

vestibular (VIIIth) fibres, the torus receives cochlear (VIIIth) fibres, an important development, indicating a development of epicritic auditory representation and that the lateral fillet in higher vertebrates is not concerned solely with gravistatic dyscritic impulses The torus also, as usual, receives dyscritic spino- and bulbo-mesencephalic impulses

The tectum receives optic fibres on the surface and spino- and bulbo-tectal fibres in the deep layers It emits crossed and uncrossed dorsal and ventral tecto-bulbar tracts Just under the anterior border

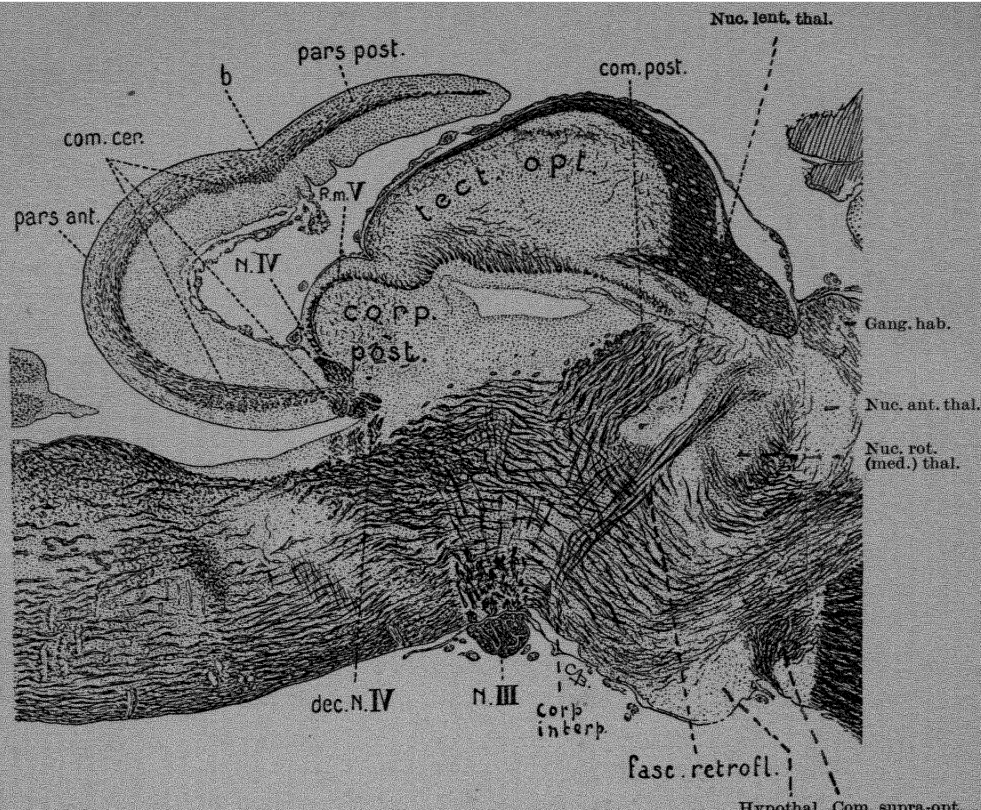


Fig. 31. Sagittal section of brain of lizard (*Varanus salvator*) (Kappers).

of the tectum are the nuclei prætectalis and lentiformis. The former sends axons to the posterior longitudinal bundle; and, therefore, probably subserves eye movements. The latter receives VIIIth and Vth nerve fibres and is homologous with the nucleus lentiformis of fish and the nucleus spiriformis of birds.

The dorsal thalamus of reptiles is large and highly differentiated. The anterior nucleus sends fibres (tractus thalamo-striatalis) to the corpus striatum (neostriatum); and, therefore, belongs to the neothalamus: it is also related to a hypothalamic tract probably homologous

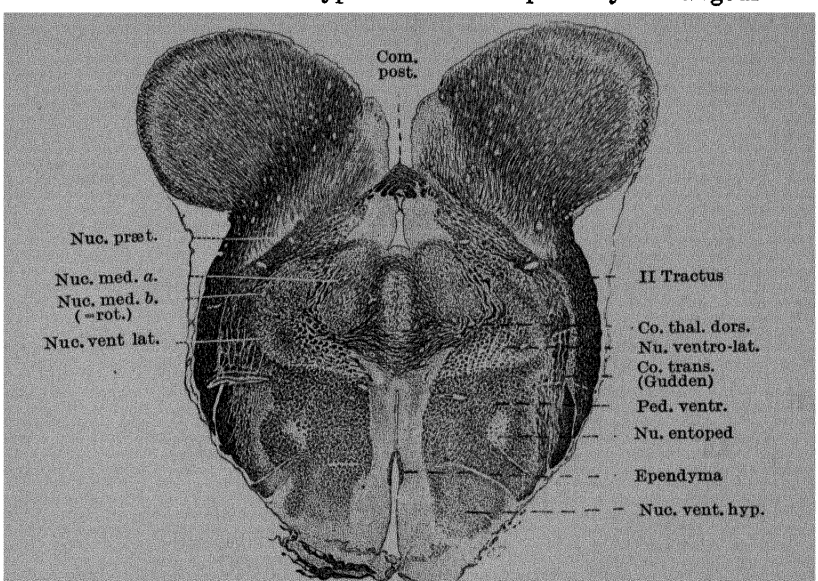


Fig. 32. Transverse section through the optic thalamus of *Crocodilus porosus* (Kappers).

with Vicq d'Azyr's tract, and, therefore, olfactory in function. The largest medial nucleus is homologous with the medial nucleus of mammals It also sends a thalamo-striate tract to the neostriatum. The ventral nucleus of the dorsal thalamus is continuous with its lateral nucleus, which in turn is not sharply delimited from the lateral geniculate body. It is uncertain whether the ventral nucleus receives a true medial fillet (epicritic) as in mammals, but it is probable since reptiles are the earliest species to have posterior column nuclei[1]. The lateral geniculate body, as usual, receives optic

[1] *Vide*, p. 79.

fibres and emits geniculo-tectal fibres (brachium tecti). In many reptiles, especially crocodiles, the dorsal thalami fuse in the middle line, where there is a nucleus reuniens thalami (Edinger) corresponding to the grey or soft "commissure" of mammals and man.

The chief nucleus of the ventral thalamus is the nucleus entopeduncularis, an archaic nucleus associated with olfactory tracts.

In *birds* (Figs. 33–36) the tecta are pushed aside by the enormous cerebellum, and the posterior corpora quadrigemina and ganglia isthmi again become buried. Birds are microsmatic, and consequently the hypothalamus is very small. All parts, indeed, concerned with

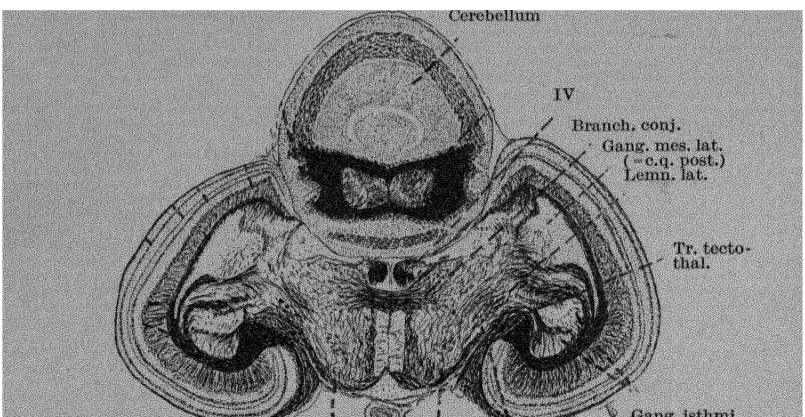


Fig. 33. Transverse section through the ganglion isthmi of *Pratincola rubicola* (Kappers).

smell are minimal, whereas all parts concerned with visual and static impulses are greatly enlarged. There is a large red nucleus, composed entirely of large cells, and, therefore, essentially reflex in function (cf. mammals). It receives the fibres of the anterior brachium of the cerebellum, and emits a rudimentary descending rubro-spinal tract, which, however, has not been traced into the cord.

The lateral fillet ends in the nucleus semilunaris, ganglion isthmi, and nucleus lateralis mesencephali. The semilunar nucleus lies mesial to the ganglion isthmi, to which it sends fibres as well as to the nucleus spiriformis. It also sends fibres laterally to Gudden's (supra-optic) commissure. The ganglion isthmi, in addition to lateral fillet fibres, receives cerebellar and tectal fibres: it emits fibres to

the nucleus lateralis mesencephali, to the tectum, and to the optic nerve (tractus isthmo-opticus)[1] The large nucleus lateralis mesencephali, covered by the tectum, and separated from it only by a potential slit representing the optic ventricle, is the homologue of the torus semicircularis and the corpus quadrigeminum posterius. It receives the VIIIth fillet dorsally and the Vth fillet ventrally, the latter part, and perhaps the former, emits a bulbo-tectal tract. It also receives the tractus occipito-mesencephalicus from the neostriatum The importance of the dorsal mid-brain area as a corre-

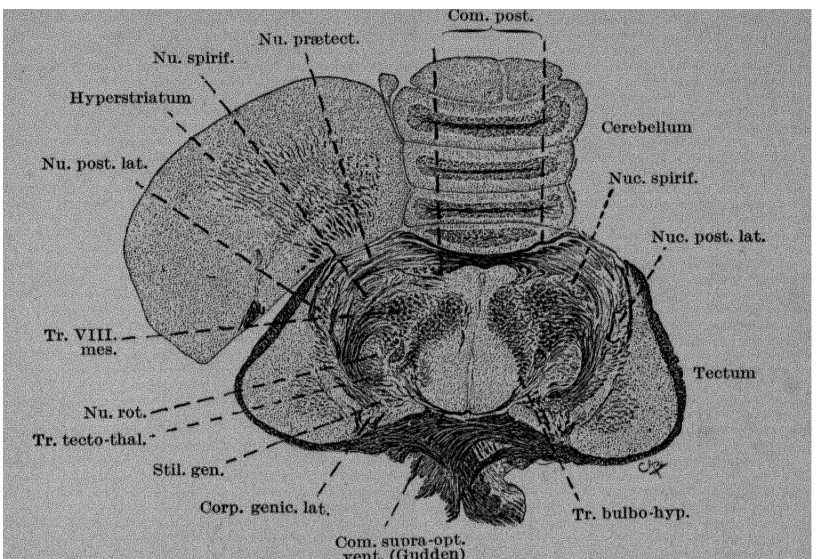


Fig. 34. Transverse section through the nucleus spiriformis of *Pratincola rubicola* (Kappers).

lation centre for dyscritic sensory, gravistatic, and photostatic impulses cannot be over-estimated It resembles the condition found in fishes rather than that in Amphibia, a striking support of the view that both birds and fishes are essentially reflex and instinctive animals, with fixed constitutions little amenable to adaptation and further evolution At the same time, birds possess small posterior column nuclei and a median fillet, and bulbo-thalamic fibres pass from these nuclei and from the VIIIth nucleus, and possibly from the spinal Vth nucleus to the nucleus intercalatus in the ventral part

[1] Wallenberg, *Neurol Zentralbl.* 1898, cf Perlia, *Arch f Ophth* xxxv, 1889.

of the thalamus. The fronto-ventral thalamic region in birds is much more developed than in fishes, and is an important orientation centre[1].

The tectum receives superficial optic fibres and deep spino- and bulbo-tectal, and isthmo-tectal fibres. It emits large dorsal and ventral descending tecto-bulbar tracts, both of which contain crossed and uncrossed bundles. The crossed dorsal fibres make important connections with the eye-muscle nuclei, and pass on to the anterior columns of the cord. It is noteworthy that in birds the dorsal crossed fibres are in excess, whereas in Teleostei it is the ventral uncrossed

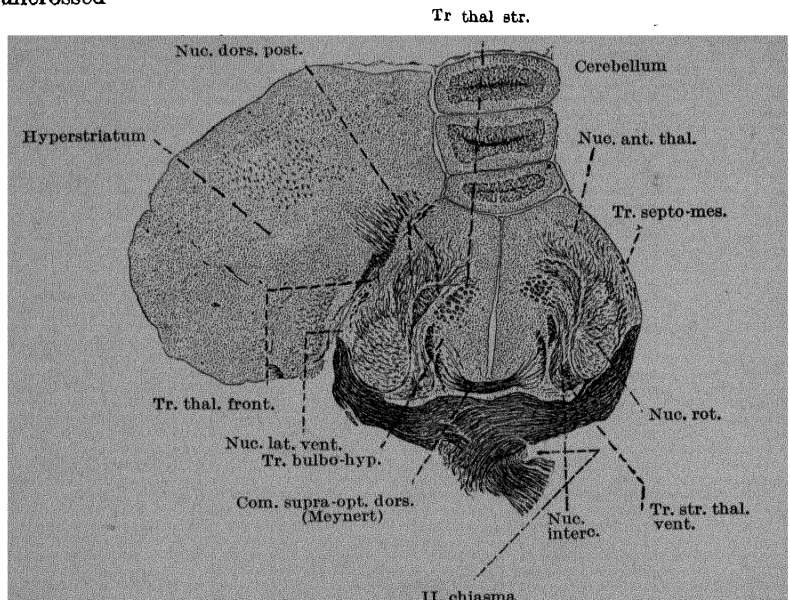


Fig. 35. Transverse section through the nucleus rotundus of *Pratincola rubicola* (Kappers).

Near the anterior border of the tectum, as in fishes and reptiles, there are intercalary nuclei correlating the ascending sensory neurones from the medulla and the optic neurones; namely, nucleus prætectalis and nucleus spiriformis. The latter is the homologue of the nucleus dorsalis thalami of selachians, and the nucleus lentiformis of Teleostei and reptiles. In addition to spino- and bulbo-mesencephalic fibres

[1] Kappers, *op. cit.* p. 872.

this nucleus receives fibres from the ganglion opticum basale[1], an optic connection additional to the tectal connection. It also receives fibres from the fore-brain (occipital) and from the occipital and lateral parts of the neostriatum (tractus strio-mesencephalicus). On the other hand, it has no ascending cortical projection.

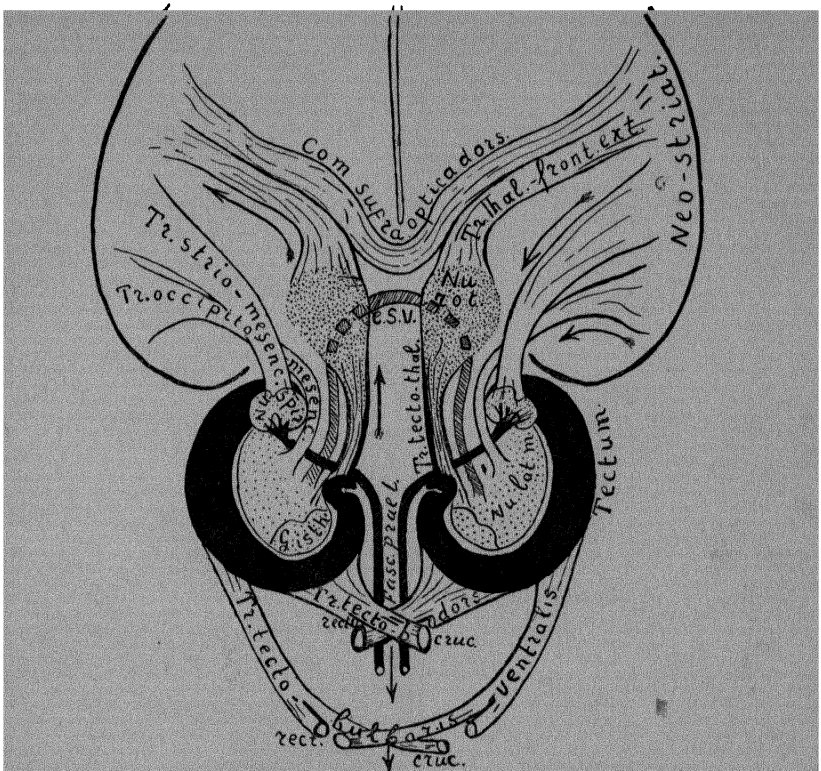


Fig. 36. Diagram of supra-optic commissures (dorsal = Meynert's, ventral (*e.s.v.*) = Gudden's) and mid-brain and thalamic tracts of *Pratincola rubicola* (Kappers).

The epithalamus in birds is small. Very striking compared with its dorsal position in fishes is the *ventral* position of the external geniculate body. The terms dorsal and ventral applied to the parts of the thalamus proper are indeed misleading in birds, for, in addition to the altered position of the lateral geniculate body, the large nucleus rotundus, which is homologous with part of the (dorsal)

[1] *Vide infra*, p. 123.

nucleus medialis of reptiles, is ventral in birds and situated just outside the external geniculate body. Dorso-mesial to it is the nucleus dorsalis, and dorso-lateral to this is the anterior nucleus. Dorso-lateral to the round nucleus and lateral to the anterior nucleus is the nucleus lateralis anterior. Of these, the nucleus rotundus receives the tractus octavo-thalamicus, and gives off the tractus thalamo-frontalis externa to the hyperstriatum (= neostriatum). The nucleus anterior sends axons to the neostriatum. The nucleus dorsalis also sends tracts to the neostriatum (tractus thalamo-frontalis, partes frontalis et occipitalis). This rich formation of ascending fibres forms the dorsal forebrain peduncle. It is absent in fishes and is, therefore, an important new—neocerebral—formation A ventral fore-brain peduncle is made up of descending fibres (strio-thalamic, strio-hypothalamic tracts). Some of these pass down in the medulla, making connection with the IIIrd, IVth, VIth, and motor Vth nuclei. In addition to these, there are strio-mesencephalic tracts to the nucleus spiriformis and nucleus lateralis mesencephali.

These relations show the enormous development of ascending fore-brain projection of mid-brain and bulbar impulses, correlating photostatic and gravistatic orientation, and descending effector fore-brain tracts. Hence the neostriatum (hyperstriatum of birds) plays an important part in the regulation of movements of these animals The activities of the two sides of the brain are correlated by means of two commissures, the commissura supra-optica dorsalis of Meynert between the corpora striata (putamen), and the commissura supra-optica ventralis or transversa of Gudden between the nuclei semi-lunares (*i.e.* the posterior corpora quadrigemina).

In *mammals* (Figs. 37, 38) the corpora quadrigemina are plainly exposed upon the surface of the mid-brain. The size of the anterior colliculi (tecta) is somewhat reduced owing to the diversion of the main mass of optic nerve fibres to the external geniculate body They are smaller than the posterior colliculi in the blind mole, and also in Carnivora, especially the bat[1] and Cetacea, owing to the large size of the lateral fillets. The optic thalamus is much larger than in lower vertebrates, especially the dorsal thalamus. The parencephalon, which is ependymal in many fishes, has gradually developed an increasingly differentiated nervous structure, and is distinguished in mammals by a new neothalamic formation, the pulvinar, which itself becomes progressively greater in higher mammals. In this species the neothalamus becomes fused anato-

[1] *Vide infra*, p. 89

mically with the neostriatum The red nucleus, small in marsupials, acquires an accretion of small cells, which is correlated with a new or increased cortical co-ordination The small cells are few in monotremes, marsupials, rodents, and ungulates, numerous in carnivores and primates The cortical connections of the red nucleus are with the frontal lobes specially, and the operculum and the temporal lobes Besides its main origin in connection with the anterior peduncle of the cerebellum, it has connections with the medial nucleus of the thalamus and the corpus striatum, and gives off the descending

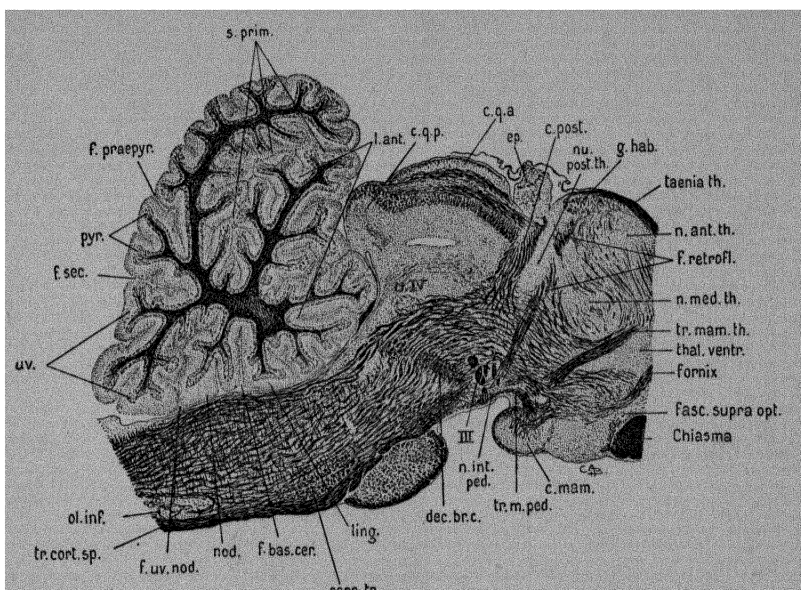


Fig. 37. Sagittal section through the brain of a marsupial (*Onychogale frenata*) (Kappers).

rubro-spinal tract The relative unimportance of the cerebellum and importance of the red nucleus in many postural conditions is strikingly shown by the experiments of Magnus and his fellow-workers[1].

The posterior corpora quadrigemina are the main end station of the lateral (VIII) fillet and of the dyscritic spino- and bulbo-mesencephalic fibres Each spreads forwards parasagittally under the corresponding anterior colliculus, and has intimate connections with

[1] Magnus, *Körperstellung*, Berlin, 1924

it. The central nucleus is homologous with the torus semicircularis of lower vertebrates (nucleus medialis tegmenti (Plagiostomi), nucleus lateralis mesencephali (Teleostei, Aves)). In mammals a greater number of the ascending spinal and bulbar afferent fibres are diverted to the medial geniculate body, which is a mid-brain differentiation, homologous with the ganglion isthmi of Sauropsida, which is absent in mammals. It thus differs from the external geniculate body, which is a differentiation of the thalamencephalon, and not of the tectum. It is important to lay stress upon the facts that the ganglion isthmi has no cortical projection, whereas the internal geniculate body atrophies if the cerebrum is removed (as also the external geniculate body) and has both ascending and descending connections with the cortex. Further, the lateral fillet, though found in animals without a cochlea, contains secondary neurones from the cochlear nuclei of the VIIIth nerve Hence it may be presumed that the internal geniculate body has predominant vestibular (static) functions, but that it also has auditory functions. Moreover, it receives fibres from the Edinger sensory fibre system[1]. We may, therefore, conclude that it has both dyscritic (sensory and static) and epicritic (auditory) functions The supreme importance of this region as the chief centre for postural reflexes has been amply demonstrated by the epoch-making researches of Sherrington on decerebrate rigidity and their more detailed exposition in the researches of Magnus and his fellow-workers[2].

Most of the optic nerve fibres are diverted from the tectum to the external geniculate body, which will be dealt with in the next chapter. Those which remain subserve chiefly, if not entirely, optic reflexes. These seem to have become stabilized, as compared with the condition in the sub-mammalia, for there are fewer intercalated cells, and the transmission of impulses from the optic fibres to the effector paths is thus simplified. The effector paths, as in lower vertebrates, consist of dorsal and ventral tecto-bulbar tracts, both of which contain crossed and uncrossed fibres. The tectum has no cortical projection; but it receives fibres from the cortex[3]

The epithalamus is small, though larger in macrosmatic mammals than in birds. The metathalamus, besides the lateral geniculate body, includes the nucleus posterior thalami of Nissl. It lies below the anterior margin of the anterior colliculus, just in front of the posterior commissure, and behind the fasciculus retroflexus. It is homologous

[1] Mott [2] *Op cit.*
[3] Bouman, quoted by Kappers, *op cit* p 906

with the nuclei prætectalis and lentiformis of reptiles and birds. It has no cortical projection.

The very large and important dorsal thalamus was divided by Burdach into an inner and an outer segment The inner segment includes large anterior and medial nuclei, homologous with the homonymous well-developed nuclei of reptiles The anterior nucleus lies immediately beneath the ganglion habenulæ (epithalamus), and

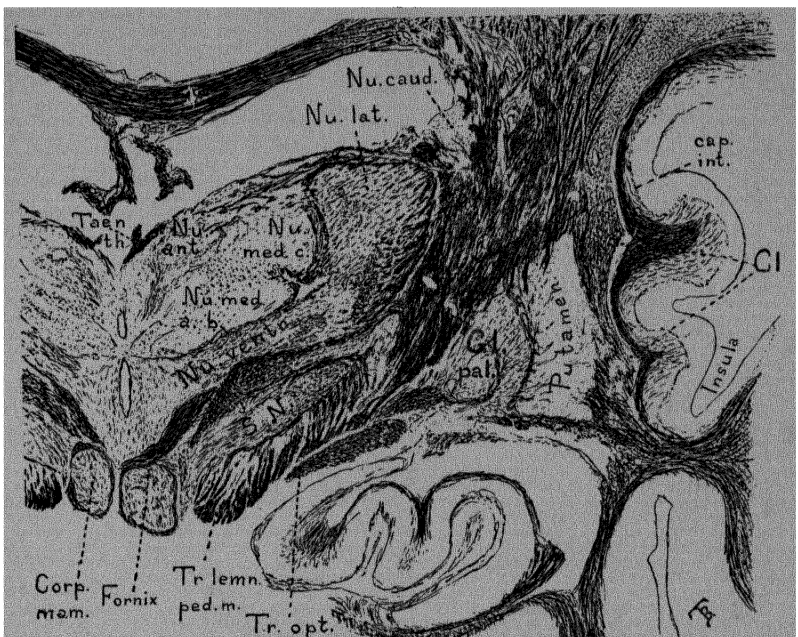


Fig. 38. Transverse section through the thalamo-striatal part of the internal capsule in man (Kappers).

sends fibres to the nucleus caudatus of the neostriatum[1]· it probably has a cortical projection The nucleus medialis is divided by von Monakow into three parts, *a*, *b*, and *c* The chief nucleus is *a*, nucleus medialis magnocellularis, it sends fibres to the cortex · *b* is the centre median of Luys; it probably receives most of the fibres of the Vth fillet, and has *no* cortical projection *c* is a small celled nucleus, not always present. The anterior nucleus is largest in macrosmatic

[1] Sachs, *Brain*, xxxii, 95, 1909

mammals, and has olfactory connections. The medial nucleus is largest in animals in which the trigeminal nerve is specially large. It probably receives sensory fibres from the muscles of the face, since its degeneration is associated with Nothnagel's symptom of mimetic paralysis. The inner segment of the dorsal thalamus is, therefore, specially concerned with smell and head sensibility, and subserves the "oral sense." The ventral parts probably have visceral and sympathetic functions.

The outer segment of the dorsal thalamus consists of two nuclei, ventral and lateral. The ventral nucleus is the end station of the medial fillet, and receives fibres from the Vth fillet and the nucleus parasolitarius It sends copious fibres to the cortex, not only to the postcentral, but also to the precentral (kinæsthetic) gyri: the projection to the precentral gyrus is, indeed, phylogenetically older than that to the postcentral *This nucleus is, therefore, the chief thalamic nucleus of epicritic common sensibility.* The dorso-lateral part of the lateral nucleus is the pulvinar thalami, and is specially large in primates and especially in man. It receives optic fibres from the optic nerve, fibres from the anterior cerebellar peduncle (Horsley and Clarke), and perhaps from the red nucleus (Sachs). It is in close relation with the thalamo-cortical fibres to limb centres in the cortex, and it sends out a copious flow of fibres through the posterior limb of the internal capsule to the angular gyrus. The prominence of this area in primates is, therefore, probably associated with minute (epicritic) correlation of eyes and limbs, especially arms and fingers, and subserves stereognosis.

Marsupials, rodents, and ungulates show a nucleus reuniens (Edinger) in the median raphe, like that in reptiles. It occurs as a commissura grisea or mollis in 30 per cent. of human brains. It receives fibres from the Vth fillet, and it may be conjectured that its function subserves sensibility in the mid-line of the scalp, etc.

The chief nucleus of the ventral thalamus is the corpus subthalamicum of Luys, which is probably homologous with the nucleus rotundus of birds. It has no cortical projection, but sends fibres through the ansa lenticularis to the putamen of the neostriatum. Karplus and Kreidl[1] have described a dilatator pupillæ centre in the subthalamic region, and there are other evidences of sympathetic connections in this region. The end of the sulcus limitans is, indeed, continuous with the intermedio-lateral region of the spinal cord. The hypothalamus has metabolic functions, and the tuber cinereum

[1] *Arch f d ges Physiol* CXLIII, 112, 1912

probably sympathetic, metabolic, and heat regulating functions. This region of the brain, so little known, is probably a highly important centre subserving the emotional accompaniments of instinctive activities.

4. The Visual Paths

The visual organs of *Amphioxus* will be discussed in the next chapter.

With regard to the optic nerve and retina of vertebrates, it is to be remembered that these are formed by an outgrowth, the primary optic vesicle, from the anterior vesicle of the brain. They differ, therefore, from an ordinary sensory nerve and its receptor organs in being parts of the central nervous system. Analogy of their consecutive neurones to those of common sensation rests upon a rather insecure foundation; but the central connections of the optic neurones in the so-called "primary optic centres"—external geniculate body, superior corpus quadrigeminum, and pulvinar of the optic thalamus—are so similar in plan to those of the secondary neurones of the paths of common sensation that there are good grounds for regarding them as secondary neurones. Since the cells of origin of these axons are the ganglion cells of the retina, the primary optic neurones must be sought in the retina itself. On this scheme, they must necessarily be the rod and cone bipolar cells, which are situated in the inner nuclear layer of the retina The outer nuclear layer is composed of the nuclei of the neuro-epithelium itself.

In all vertebrates below the mammals the optic nerves undergo complete decussation, though the mode of decussation varies in different animals[1]. The position of the chiasma varies, being usually near the junction of the fore- and mid-brain. In cyclostomes and Dipnoi it is situated within the brain, whereas in some teleostean fishes it is ventral, or even rostral, to the fore-brain, *e.g.* cod (*Gadus morrhua*), sun fish (*Orthagoriscus*).

Among *cyclostomes* the visual apparatus is degenerate in myxinoides. In petromyzontes the optic nerve fibres are distributed over the surface of the tectum, in which structure they are brought into relation with bulbo- and spino-tectal tracts. The evidence points to entirely dyscritic, vital, photostatic functions. In addition to the

[1] See Franz, in Oppel's *Lehrbuch der vergleichenden mikr. Anat* Theil 7, pp 325 sqq. Jena, 1913

ordinary visual organs the pineal bodies of petromyzontes show histological traces of retinal structure. There is, indeed, evidence that the pineal organ consisted of paired parietal eyes[1].

The optic nerve of *plagiostomes* is much better developed than in cyclostomes. After decussating in several bundles, it traverses the side of the thalamencephalon, giving off collaterals to the very rudimentary external geniculate body, and dividing into a larger lateral and smaller medial bundle, to be distributed over the surface of the tectum. The fibres communicate by intercalary cells with deeper motor cells, whose axons form the tecto-bulbar tracts. The tectum also receives afferent fibres from the brain stem, but these are far fewer than the optic fibres. Its influence, therefore, on the motor system is essentially photostatic. The epiphysis is glandular and shows no sign of a pineal eye.

In *ganoids and teleosteans* the eyes vary much in size. They are gigantic in some Acanthopterygii (*Cyclopterus*, *Leuciscus*); small in *Silurus glanis*. In some the eyes are degenerate and the optic nerves absent (*e.g.* the cave-fish *Amblyopsis spelœa*, the goby *Trypauchen*, some deep-sea fishes, *e.g. Typhlonus*). In most Teleostei the optic nerve crosses over the other, usually the left over the right; in the herring one passes through a hole in the other In the cod the optic tract gives off a deep fasciculus which runs near the wall of the ventricle to the tectum (fasciculus medialis nervi optici), but most of the tract is in two large bundles, lateral and medial, on the lateral surface These give off collaterals and possibly end fibres to the lateral geniculate body, but the main mass is distributed over the surface of the tectum, which, as already mentioned, varies very much in different fishes. The optic bundles are accompanied by corresponding lateral and mesial bundles of the brachium tecti from the medial geniculate body, similarly distributed to the surface of the tectum, so that photostatic and gravistatic impulses are brought into very close relation—possibly an example of neurobiotaxis. The efferent fibræ tectales nervi optici were first discovered in fishes by P. Ramon y Cajal and Krause

The conditions are very similar in *Amphibia*, except that the structure of the tectum shows greater static plasticity[2].

Among *reptiles* the pineal body manifests itself as a vestigial parietal eye more definitely in lizards, especially hatteria or tuatera

[1] Dendy, *Quart Jl. of Micr Sc.* LI, 1907

[2] *Vide supra*, pp 65, 67.

(*Sphenodon punctatum*), than in any other living species[1]. This eye is absent in turtles, crocodiles, and snakes, and the epiphysis is absent in crocodiles.

The arrangement of the bundles of nerve fibres in the chiasma of reptiles shows a greater variety than in any other species[2]. The fibres are distributed to the tectum much as in Amphibia. The structure of the tectum is more highly differentiated; it is more cellular, and the many cells are in closer relation with the optic fibres—probably an example of neurobiotaxis. The differentiation is probably limited to the dyscritic system, since no cortical projection has been described, in spite of the presence of rudimentary posterior column nuclei on the corresponding common sensory paths.

In *birds* the number of separate bundles of nerve fibres in the chiasma is said to bear a relation to the visual acuity. The decussation of fibres is complete even in birds with binocular vision, such as the owl A considerable bundle of optic nerve fibres ends in a ventrally situated ganglion opticum basale (Gang. ectomammillare, Edinger)[3], which is homologous with the nucleus of the tractus peduncularis transversi of some mammals. This ganglion sends many fibres to the nucleus spiriformis; and the function of the optic fibres is, therefore, photostatic.

As in fishes and Amphibia, there is an isthmo-optic tract in birds[4], and it is interesting to note that the fibres are distributed chiefly to the region of the external fovea, which is confined to birds.

In *mammals* the decussation of the optic nerve fibres is complete in the lower, but incomplete in the higher, the number of direct fibres appearing to have a relation to the degree of stereoscopic vision. Thus, they are few in the horse and rabbit, greater in the cat than the dog, and reach the highest number in man, where they form about one-fourth of the total number (so that the term semi-decussation is inaccurate). Ariens Kappers[5] explains the partial decussation on neurobiotactic grounds.

"Since with frontally directed, non-converging position of the eyes, the axes being nearly parallel—the *passive* binocular vision which precedes active binocular con-

[1] De Graaf, *Zool. Anzeiger*, IX, 1886; Baldwin Spencer, *Quart Jl of Micr Sc* XXVIII. 1886; *Proc. Royal Soc.* 1886, Dendy, *Quart Jl of Micr Sc* XLII, 1899; *Trans Royal Soc* 1910, Tilney and Warren, *Amer Anat Memoirs*, IX, 1919

[2] Franz, *op, cit* p 328

[3] Singer and Munzer, *Denkschr. d Kngl. Akad. der Wiss. zu Wien. Math.-naturwiss. Klasse*, LVII, 1890

[4] Wallenberg, *Neurol Zentralbl* 1898

[5] *Op cit.* pp. 898-900

vergence in many mammals—the nasal fibres of one retina and the temporal fibres of the other are always stimulated at the same time by laterally incident light, these fibres run in contiguity in the central nervous tract."

On the other hand, "an object situated in front in the median line of the head forms its image on the temporal sides of the retinæ of both eyes." Thus, the temporal region of one retina works partly with the opposite nasal region (with lateral objects), and partly with the opposite temporal region (with medio-frontal objects); whereas the nasal regions never work together. Hence, temporal fibres from both sides must also run in contiguity; *i e.* there are both direct and crossed temporal fibres in each tract, and, consequently, decussation is not a semi-decussation, but only a demi-semi-decussation. This theory supports the view that, the macula being situated in the temporal region, both crossed and uncrossed fibres are emitted from it.

In mammals most of the optic fibres pass to the external geniculate body (70 per cent. Bernheimer, 80 per cent. von Monakow) The remainder are distributed, not only to the tectum (anterior corpus quadrigeminum) as in lower vertebrates, but also to the pulvinar of the optic thalamus. All three "primary optic centres" receive both crossed and uncrossed fibres. A few fibres also pass to the nucleus of the tractus peduncularis transversi (ungulates, rodents, monkeys)[1], which is homologous with the ganglion basale optici of birds.

The tectum of mammals has a grey superficial layer, the optic fibres being distributed below it, they are thus brought into closer contact with the deep efferent neurones, and there are fewer intercalated cells Optic reflexes are at least as numerous and complex in primates as in lower vertebrates. The anatomical structure indicates that they are subserved by a less plastic mechanism, which is in accordance with the purely reflex activities of the tectum in primates. Moreover, the tectum has no cortical projection, though it receives fibres from the cortex.

The external geniculate body consists of two nuclei, dorsal and ventral, sharply delimited in rabbits. The ventral nucleus is undoubtedly the more primitive, for it gives off the brachium tecti, and has no cortical projection. Moreover, it receives only crossed optic fibres (goat, cat), and is connected with the reticular layers of the thalamus. The large dorsal nucleus receives the main mass of optic fibres, and provides the chief cortical projection of visual impulses, the emissary fibres passing through Wernicke's field and the optic

[1] See Kosaka and Hirawa, *Folia neurobiologica*, IX, 1915.

radiations to the area striata of the occipital lobe. This nucleus shows a laminated structure in and above the Carnivora (cat), and the lamellæ receive alternately crossed and uncrossed fibres from without inwards[1]. The macular fibres occupy a strikingly large area of the inner segment of the nucleus[2]

As already mentioned, both crossed and uncrossed fibres pass in primates to the pulvinar of the optic thalamus, and these are projected through the internal capsule principally to the angular gyrus[3].

Comparison with the paths of common sensation leads to the conclusion that the external geniculate body is the chief centre in mammals of epicritic visual sensations, but that the epicritic system is reinforced in primates by the pulvinar of the optic thalamus. There can be no doubt that the anterior corpus quadrigeminum, nucleus tractus peduncularis transversi, and ventral nucleus of the external geniculate body belong to the dyscritic system.

[1] Minkowski, *Schweizer Arch f Neurol u Psychiatrie*, VI, 201, 1920, *L'encéphale*, XVII, 65, 1922

[2] Ronne, *Zeitsch f. d ges Neurol u Psychiatrie*, XXII, 460, 1914

[3] *Vide*, pp 120, 233.

CHAPTER VII

THE DYSCRITIC MOTOR RESPONSE

1. Summary of Anatomical Evidence

We may now gather together the loose threads contained in the earlier chapters and briefly review them in the light of the evidence afforded by comparative anatomy.

We have seen that the most primitive sensory receptor mechanism is, so far as we can determine, bound up with the effector mechanism in the protoplasm of the protozoal cell, which exhibits "irritability" from which we conjecture a sentiency which is a merely dually differentiated awareness of a pleasant or unpleasant type. Whether of the positive or negative kind, it is a "blooming, buzzing confusion," devoid of any specific characteristics.

At a slightly higher stage the receptor-effector mechanism is structurally differentiated from the rest of the protoplasm. Above this cœlenterate stage receptors and effectors become dissociated by further differentiation. There follows upon this stage a differentiation of the receptors themselves, and this process varies in different species according to their economic demands. These partially differentiated receptors can, however, be classified into three main groups —mechano-, chemo-, and radio-receptors. The structural differentiation necessarily leads to the assumption that a corresponding functional differentiation occurs, with the emergence of different "modalities" (Helmholtz) corresponding to the three types of receptors. These modalities are still confused and relatively undifferentiated, and the perceptual patterns which they form under the stimulus of various experiential conditions are also confused and smudgy.

Still further differentiations, however, occur in the receptors and their central connections, so that not only is the number of modalities —touch, temperature, smell, sight, etc.—increased, but eventually in higher species receptors of the same modality undergo differentiation, allowing of the emergence of qualities within a modality, such as colour within the modality of sight.

From what has been said in Chapter III. 3, we learn that behaviour is largely made up of a chain of reactions, initiated by responses to the stimulation of distance receptors, and carried on by consummatory responses to the sequent stimulation of contact receptors. We learn

from Sherrington's researches that the impulses resulting from stimulation of receptors of different modality are integrated by means of the two great co-ordinative processes—plurireceptive summation and interference.

From the study of the perceptual patterns which are aroused as the result of these co-ordinative processes, we learn that the motor or conative response is determined by the biological requirements of the animal. In lower species, in which the perceptual pattern is least differentiated, the animal responds to the situation as a whole—appropriately, because of the inherited disposition of the nervous system thus to respond. Such relatively undifferentiated and confused perceptual patterns, laden with affective tone and possessing relatively little cognitive precision, but none the less possessing profoundly important "meaning," might be termed "massive perceptual patterns," and the responses to which they give rise are equally massive responses of the animal as a whole. It must be remembered, however, that they differ from the "mass reflex" of Head and Riddoch, which is a pathological and distorted response of analogous nature, in that they are accurately and appropriately co-ordinated to subserve the animal's interests in the given situation.

In higher stages the perceptual pattern, whilst retaining its confluent character, comes more under the control of higher nervous centres by backstroke from the cortex. One or other modality—smell, sight, hearing—becomes prepotent in the given pattern, and occupies the focus of attention. The cognitive element is enhanced, and this modality—usually the projicient modality of a distance receptor—takes the lead in initiating and controlling the response.

We may now briefly review the bearing of the evidence of comparative anatomy on these deductions, paying special attention to vision as the prepotent modality of which our knowledge is at the present time most precise.

Visual organs of an extremely primitive type occur very low down in the animal scale At first they consist of a single receptor cell, which, like nearly all receptor cells, is generally provided with hair-like processes. Like other receptor sensory cells, they are provided with diplosomes, and often fibrils can be shown passing from the diplosomes into a nerve fibre attached to the proximal end of the cell. Even at this lowly stage the visual cells are almost always situated in direct relationship with one or more pigmented cells, though this is not absolutely essential to the functioning of such cells as visual cells.

It may be considered definitely proved that these cells respond to luminous radiation, and give rise to appropriate motor responses in the organisms in which they occur. Thus the one primitive and indubitable response to the visual impulse is *motor*. What, if any, are the other responses is a matter of conjecture.

The motor response in the lowest forms is a tropism—a movement either towards or away from the light. The organisms certainly respond to wave-lengths which to us are luminous, but we are not justified in concluding that the range of spectrum which is adequate to their visual organs is the same as that adequate to ours. It may be less or more; and further research is needed on this point. Thus, it may well prove that the organs respond not only to wave-lengths which are luminous to us, but also to infra-red and ultra-violet radiations. It is only what might be expected if the crude dyscritic sensation of these organisms should prove to be an undifferentiated temperature—luminous response.

The essential feature of these tropisms, whether positive or negative, is that they are directional responses, and as such are the germ of that projicience which reaches its highest development in the visual sense of man.

The visual organs of the most primitive vertebrate, *Amphioxus*, are cells situated within the central nervous system. In this respect they resemble the intramedullary sensory cells of this animal, which correspond to the extramedullary dorsal ganglion cells of higher vertebrates[1]. It is, however, rare for receptor cells to be situated within the central nervous system, but there are other examples[2]. Three types of cells have been accorded visual functions in *Amphioxus*: (1) the anterior pigment spot; (2) Joseph's cells, which have no pigment mantle; and (3) Hesse's cells. There is no satisfactory evidence that (1) and (2) have any visual functions, but there is considerable evidence in favour of (3). Hesse's cells have large cell bodies with one edge radially striated; this edge is turned towards a crescent-shaped pigmented cell. A nerve fibre leaves the cell at the opposite side. The cells have, therefore, all the characteristics of receptor cells. They are situated ventral to, and on each side of, the medullary canal. On the left side the pigment cell is below, in the ventral regions and on the right side it is above the receptor cell. Such an arrangement of receptor cell and pigment cells is common

[1] *Vide*, p. 69.

[2] *Vide* Franz, in Oppel's *Lehrbuch der vergleichenden mikroscopischen Anatomie der Wirbeltiere*, Teil VII, Sehorgan, p. 7. Jena, 1913.

in the ocelli of invertebrates. It has the effect of adding to the appreciation of differences of luminosity a very primitive capacity to appreciate the direction from which the stimulus comes. Hence the left "eyes" look upwards, the ventral and right "eyes" look downwards, but as the animal is asymmetrical and generally lies on its side, the eyes practically look sideways, and most of them to the side on which the fimbrial apparatus of the mouth lies. Hesse's cells are most numerous in the anterior segments of the animal, least in the tail end. G. H. Parker[1] has shown that *Amphioxus* responds to stimulation by light, and that if the threshold stimulus when the light is directed to the head of the animal is represented by unity, the threshold to stimulation of the tail is 1·5, whereas that of the middle of the body is 25 Hence the response to light is much greater on stimulating the anterior end, though there is a good response on stimulating the tail.

As already mentioned, one of the greatest steps in the evolution of animals was the arrangement of the metameres serially along a longitudinal axis. "With the fore and aft arrangement of its segments the animal body has its first opportunity for really high differentiation."[2] Sherrington has pointed out[3] how important in this arrangement the head segments become In it the most important receptors become aggregated, and most important of these are the distance-receptors—the receptors of the projicient senses. This fact is well borne out in the responses of *Amphioxus* to light, but in this lowly type the supreme dominance of the head segments is not yet fully acquired.

"It is clear that in the visual functions of this animal we have to do only with very *primitive*, essentially *vital visual* functions. The organs do not apprehend objects, but serve merely to regulate the posture of the body in relation to the light (*Photostasis*)."[4] In other words, the sensation is purely dyscritic, and the fundamental dyscritic response to light is motor, *i.e.* postural

It is noteworthy here that in certain invertebrates, *e.g.* Hydromedusæ, some possess simple pigmented ocelli, whilst others have static organs with statoliths, similar to the otoliths in the ear. The function of the static organs in the orientation of the animal is

[1] *Proc. Amer Acad. of Arts and Sc.* XLIII, 1908.
[2] Sherrington, *op. cit.* p 315.
[3] *Ibid.* pp. 323 sqq.
[4] Kappers, *Die vergleichende Anatomie des Nervensystems der Wirbeltiere und des Menschen*, I. 111 Haarlem, 1920.

undoubted[1], and it would appear that at this lowly stage ocelli are capable of fulfilling the same purpose[2].

The immense importance of vision for equilibration and orientation is liable to be lost sight of, or at least under-estimated, when dealing with the visual functions of man. for there the static functions are overshadowed by the more patent dynamic functions, and both are overwhelmed by the highly developed sensory and cognitive functions. Our study of the anatomy of the central nervous systems and of the behaviour of vertebrates, however, demonstrates the supreme importance of photostasis in the life histories of these animals from the lowest to the highest. Throughout, in the mid-brain, we find an elaborate co-ordination centre for gravistatic and photostatic reflexes, of which the afferent impulses are predominantly dyscritic. This region is the great meeting place of primitive dyscritic sensory impulses—optic, static, tactile, olfactory, and gustatory—the median longitudinal bundle playing an important rôle as a collecting tract. In fishes the gravistatic system is enormously reinforced by impulses from the lateral lines, impulses which convey impressions of pressure and mechanical vibrations, controlling the movements of the animal with regard to depth below the surface of the water, and propinquity to solid obstructions. These impulses are mediated by the VIIIth nerve, which at this phylogenetic level is essentially vestibular.

It is probable that the mid-brain is also the chief intermediate neural level for the collection of proprio-ceptive impulses, which originate in the muscles, tendons, and joints It has been shown by Coghill that in amphibian larvæ intramedullary (Rohon-Beard) cells give off an axon which bifurcates, one branch going to the skin, the other to the myotome These cells are, therefore, the primary receptors of both extero-ceptive and proprio-ceptive impulses They are found, and persist, in cyclostomes and teleostean fishes, but disappear after the larval stage in plagiostomes and Amphibia As already pointed out, the mesencephalic nucleus of the Vth nerve in higher vertebrates, including man, is probably a vestige of these cells, and it may well be that the extremely primitive proprio-ceptive system persists in this form. "Not only the superficial tactile sense (including pain and temperature) belongs to the most primitive vital sensations, but a muscle sense is also represented in this system. This primitive vital muscle sense is transmitted by the same crossed

[1] *Vide* Chapter VII 2.

[2] Hesse, *Das Sehen der niederen Tiere*, Jena, 1908.

secondary paths as the other primitive vital sensations,"[1] *i.e.* by the Edinger fibre system.

In fishes the final common path subserving these optic, tactile, lateralis, and especially vestibular reflexes is the enormous Mauthner's fibre, which lies in near relationship to the median longitudinal bundle and runs the whole length of the cord to the region of the tail. In animals which possess no neck, like fish, it is of the greatest importance that the tail should be brought under immediate control of visual and vestibular reflexes.

In spite of the development of a rudimentary epicritic sensory apparatus—posterior columns, Goll and Burdach nuclei, and median fillet—in reptiles, we find a reversion to the more primitive dyscritic apparatus in birds. These animals are reflex animals *par excellence* Owing to their life in the air, their covering of feathers, and their small legs, their tactile apparatus is relatively small. Their posterior roots, posterior columns, Goll and Burdach nuclei, and median fillets are all very diminutive. Moreover, since they either fly *or* walk there is little need for co-ordination between the fore- and hind-limbs On the other hand, their dyscritic system is very well developed. The spino-bulbar and spino-mesencephalic tracts, which bring common extero-ceptive impulses into correlation with static and optic impulses in the tegmentum and tectum, are very prominent. So, too, are the spino-cerebellar tracts which, unlike the case in fishes, extend throughout the cord Similarly, on the efferent side, the vestibulo-spinal and tecto-spinal tracts contribute largely to the antero-lateral columns For the first time in phylogeny a nucleus ruber is present, though a definite rubro-spinal tract has not been demonstrated. There is no pyramidal tract.

"The spinal cord of these animals possesses, in addition to a well-developed, minutely localized, spinal reflex apparatus, extensive ascending connections with the cerebellum, vestibular apparatus, and visual system, as might well be expected in such exquisitely poised animals The tracts which influence the spinal cord are essentially vital in nature, *i e* they originate in centres for equilibration (vestibularis), stasis (cerebellum and adnexa), and photostasis (tectum), just those centres which enter into correlation with the primary ascending secondary neurones of the primitive spinal sensibility, including the primitive muscle sensibility (mesencephalic Vth nucleus)."[2]

Our knowledge of the extero-ceptive impulses in mammals is much greater than in other classes of animals, owing chiefly to the researches of Head and Rivers and their fellow-workers. The fundamental

[1] Kappers, *op. cit.* p. 146.
[2] *Ibid.* p. 182.

duality of the sensory impulses, discovered by Head and Rivers, and named protopathic and epicritic by them, is borne out not only by their physiological researches, but also by the anatomical facts already discussed.

There is evidence that protopathic and epicritic impulses are conducted by different fibres in the peripheral nerves. Probably the protopathic impulses are carried by finer and even unmedullated fibres[1]. In the higher mammals there is a marked tendency for the sensory nuclei to become covered with cortex-like layers of small cells, a condition well seen in the substantia gelatinosa Rolandi. Besides a few medullated fibres and many dendrites this substance contains afferent fibres for vaso- and pilo-motor reflexes associated with pain[2]. Now, the spinal Vth root, around which the substantia gelatinosa is most prominent, sends its fibres into the lateral fine-fibred root-bundle, whereas the larger fibred median bundle passes to the posterior column nuclei, and thence to the median fillet, belonging, therefore, to the epicritic system. Moreover, the Vth fillet, which is analogous to the median fillet, springs from the frontal sensory Vth nucleus, whilst the spinal Vth nucleus emits only Edinger's fibres[3]. We may, therefore, conclude that the substantia gelatinosa indicates a definite increase in mammals of protopathic factors.

Clinical observations, and especially Brown-Séquard lesions, show that all the protopathic fibres—mediating pain, temperature, and undifferentiated touch—have a cell-station immediately after entering the cord, and are then relayed into Edinger fibres, which decussate in the anterior commissure and pass up in the lateral columns of the opposite side to the medulla, mid-brain and thalamus. The epicritic fibres—mediating finer tactile discrimination, muscle- and joint-sensibility, and deep sensation—pass up the cord in the posterior columns to the nuclei cuneatus and gracilis, and are thence relayed to the median fillet, decussating only when they reach the medulla. (Petrèn, Fabritius, Brouwer) The epicritic system in the cord is, therefore, a collection of fibres carrying impulses specially concerned in *stereognostic* perception.

[1] Ranson, *Brain*, XXXVIII, 1915; Ranson and Billingsley, *Amer. Jl. of Physiol.* XL, 571, 1916; Tinel, *Rev. Neurol.* XXIV, 243, 1917.

[2] Sano, *Obersteiners Arbeiten*, XVII, 1909

[3] Brouwer has shown that lesions of the caudal Vth nucleus destroy pain and temperature sensations, leaving tactile sense little disturbed; and Wallenberg has shown that localized lesions in the descending root of the Vth nerve paralyse the corneal reflex, a unique noci-ceptive, protopathic reflex (Kappers, *op. cit.* p. 341).

Epicritic tactile sensibility mediates finer discrimination by finer differentiation of the crude protopathic sensation, and the psychological manifestations of this differentiation are more minutely accurate local signature and qualitative differences of greater cognitive (as opposed to affective) import. Thus, the protopathic or dyscritic sensations are of more immediately vital, the epicritic of cognitive import.

In support of these views may be noted the fact that the frontal accumulation of posterior column fibres and gradual increase in their nuclei is associated with life on the land[1]. Moreover, the relative size of the lateral nucleus cuneatus (Burdach), which receives the afferent fibres from the cervical and upper dorsal cord, and the medial nucleus gracilis (Goll), which receives the fibres from the rest of the cord, shows a definite relationship to the size and use of the upper and lower limbs respectively—*e g.* almost complete absence of Goll's nucleus in Cetacea; its great development in platyrrhine apes which make large use of their tails in arboreal life, and its smaller development in man; the great development of Burdach's nucleus in animals which specially use their fore-limbs (*e g Talpa, Myrmecophaga*) the fusion of Goll's nuclei in reptiles and birds and the analogous Bischoff's nucleus in the rat, kangaroo, and some apes is associated with the sensibility of the tail.

The epicritic fibres end in the ventral nuclei and partly in the medial nucleus (chiefly trigeminal fibres) of the dorsal thalamus, and have thence a cortical projection. The protopathic fibres end in the corpus posticum, medial geniculate body, and tectum opticum. Here they come into relation with optic nerve fibres and with vestibular fibres, thus co-ordinating extero-ceptive impulses with visual and static impulses, and providing the mechanism for photostasis and gravistasis.

It is probable, though it is not proved, that proprio-ceptive impulses are conveyed by the spino-mesencephalic, spino-tectal, and spino-thalamic tracts which convey the main protopathic extero-ceptive impulses to the medial geniculate body, tectum and medial nucleus of the dorsal thalamus. If so, these represent a primitive dyscritic proprio-ceptive system, which has no cortical projection and which is specially concerned with posture. It is further probable that proprio-ceptive impulses are also conveyed by the epicritic extero-ceptive tracts, and reach the ventral nucleus of the thalamus by the median fillet, where they are relayed into a massive cortical

[1] Cf. van Valkenburg, *Arch néerland. de Physiol.* 1917.

projection. If so, these represent an epicritic proprio-ceptive system, which is specially concerned in stereognosis. This view is supported by the fact that there is a definite correlation between the size of the posterior columns in the cord and the stereognostic sense in animals, and it can scarcely be doubted that proprio-ceptive impulses play a predominant part in this function. I leave aside here all the important proprio-ceptive afferent tracts to the cerebellum; for if, as is probably the case, the cerebellum in higher species is a proprio-ceptive ganglion, *subservient to the cerebrum*[1], this system forms a higher— syncritic— differentiation, concerned with higher functions than those discussed in this thesis.

Most important, however, among the extero- and proprio-ceptive fibres for gravistasis is the Vth nerve, which supplies the head, for the head dominates the tail This is a microcosm of the afferent system, for the epicritic fibres are derived from the Vth frontal sensory nucleus and run in the Vth fillet to the tectum and thalamus (medial nucleus), the protopathic fibres start in the Vth caudal nucleus and run like Edinger fibres to the tegmentum, tectum, and medial geniculate body, the proprio-ceptive fibres are represented by the mesencephalic root of the Vth, as well as by the fibres for the Vth and VIIth musculature in the descending root of the Vth nerve. The position of the Vth mesencephalic nucleus in the mid-brain, although it innervates muscles belonging to the mandibular branch of the trigeminal, is particularly striking, and is to be regarded as an example of neurobiotaxis, the cells being shifted to the great co-ordination centre of gravistatic and photostatic impulses[2].

In all species the dyscritic Edinger fibre system is well represented, but the first definite evidence of a Vth sensory frontal nucleus and fillet is found in reptiles, though it may be present in rudimentary form in Amphibia. The importance of the ophthalmic division of the Vth nerve as a receptor organ for motor reflexes is shown, *inter alia*, in its relationship to the motor tracts to the pectoral fins in fish, to the lumbar region for the hind legs in frogs, and to the neck muscles in mammals. The trigeminus supplies those important exploration organs, the snout (*e g* monotremes) and the whiskers (*e g.* the cat).

The proprio-ceptive centres are not limited to those already mentioned in the mid-brain To these must be added an important series of nuclei—the reticular nuclei—in the brain stem linked

[1] Walshe, *Brain*, XLIV, 539, 1921

[2] See Kappers, *op cit* pp 322–3 (plagiostomes), 327 (Amphibia), 330 (reptiles), 333 (birds), 341–4 (mammals).

together by the posterior longitudinal bundle. The prime exteroceptive impulses to these proprio-ceptive centres are carried by the vestibular nerve and the optic nerve, the whole system forming the anatomical basis of gravistasis and photostasis. Noteworthy in this respect is the very near anatomical relationship of the nuclei for the extrinsic ocular muscles to the posterior longitudinal bundle, and the peculiarly close relationship between the VIth nucleus and the vestibular system. The VIth nerve is, indeed, the functional anterior root of the VIIIth, although it belongs in origin to the trigeminal neuromere, an example of neurobiotaxis, which is further shown in all the eye-muscle nuclei. "Their secondary changes in position (in the phylogenetic series) runs entirely parallel to the changes in the paths of the optic, vestibular and co-ordinative reflexes."[1] It should be further noted that it is the cerebellar hemispheres which are particularly associated with the higher cerebro-cerebellar proprioceptive functions, the cerebellum of *Petromyzon* and the cerebellar auricles of higher species being an extension of the lateralis and vestibular static area.

Of the complicated VIIIth nerve system, the lateralis in fishes is undoubtedly dyscritic The cochlear nerve has a cortical projection and is equally undoubtedly epicritic. The vestibular nerve is essentially dyscritic, but also has a higher—epicritic—differentiation as is shown in the participation of the labyrinth in hearing and in stereognosis.

The vestibular impulses from the labyrinth, which are those chiefly concerned in orientation, pass up in the lateral fillet to the posterior colliculus, which is represented in fishes by the torus semicircularis, in reptiles by the corpus posticum, and in birds by the nucleus lateralis mesencephali. Other fibres from the lateral fillet pass to the tectum in plagiostomes, though apparently not in ganoid and teleostean fishes. In and above the reptiles there are fibres from the inferior to the superior colliculus, and all the mammalian characteristics of the acoustic apparatus are already represented in lizards and crocodiles Another important end station of vestibular tracts is the medial geniculate body, which is thus concerned in both auditory and vestibular functions, for the lateral fillet occurs in animals which do not possess a cochlea Unlike the lateral geniculate body, which is a higher differentiation from the superior colliculus, the medial geniculate body arises from the ganglion isthmi, which is found as low down as the plagiostomes, where it has connections

[1] Kappers, *op. cit* p. 559.

with the tegmentum, torus semicircularis and cerebellum (gravistasis) and with the tectum (photostasis).

Of the various contributing factors to the co-ordination of reflexes which subserve equilibration and orientation—proprio-ceptive, common extero-ceptive, VIIIth nerve system, and optic—instructive variations in proportional representation occur in fishes, according to their habits and modes of life In many the lateralis plays a predominant part; in some, special development of cutaneous sensory areas, especially the trigeminal area, leads to increase in the dyscritic tactile factor (*e.g. Lophius*), with which, in others, there is well-marked evidence of co-ordination with gustatory tracts (oral sense). In Amphibia the importance of the ganglion isthmi as a co-ordination centre for optic and vestibular (and cerebellar) impulses is specially definite. it is noteworthy that the structure of the tectum in these animals indicates a form of primitive static plasticity[1] which is in striking contrast with the fixity shown in teleostean and selachian fishes, giving evidence of the side-tracking of the latter in phylogenesis. In birds, the extero-ceptive representation is minimal, whereas all parts connected with the optic and vestibular (including cerebellar) systems are extraordinarily developed. Nearly all the mid-brain is concerned in correlation of head and body impressions in the interests of gravistasis and photostasis, and the same may be said of the thalamus, the nucleus rotundus of which is specially concerned with the correlation of eye and body movements.

In land-living animals, and particularly mammals, the proprioceptive impulses from the limbs attain exceptional importance. The two geniculate bodies, comprising the metathalamus, have attained their maximum development The outer receives the bulk of the optic nerve fibres, the tectum (superior corpus quadrigeminum) becoming correspondingly reduced in size The inner, with the posterior colliculus, receives practically the whole of the vestibular fibres. The transition of the ganglion isthmi to the medial geniculate body, which is most clearly seen in Edentata (the ant-eaters, *Tamandua* and *Myrmecophaga*), is very instructive This nucleus contains two main groups of cells, upper and lower or inner, most of the lateral fillet fibres, both crossed and uncrossed[2], pass into the inner group[3], and each ear is projected on to both sides of the mid-brain (and cortex). Both groups in the medial geniculate body show

[1] *Vide* pp. 65, 67

[2] Kreidl, *Monatschr. f. Ohrenheilkunde u. Laryngo-Rhinologie*, XLVIII, 1914; Fuse, *Arb. aus dem hirnanatom. Inst in Zurich*, 1916. [3] Cajal.

marked atrophy after removal of the cerebrum, and hence send projection fibres to the cortex. There is a very close connection, both ascending and descending, between the medial geniculate body and the tectum, corresponding to the isthmo-tectal and tecto-isthmic tracts of lower vertebrates. The position of the medial geniculate body near the tectum, as compared with that of the ganglion isthmi of lower animals between the cerebellum and tectum, is accounted for by this near relationship to the tectal optic centre, and is an example of neurobiotaxis. This relationship further accounts for the fact that the development of the medial geniculate body is by no means entirely parallel to the development of the cortical projection[1], and, therefore, supports the view that this body mediates both dyscritic and epicritic impulses.

2. Posture and Attitude

The importance of the knowledge of the anatomy of the mid-brain and thalamus, reviewed in the previous chapters, for the problem of perception lies in how the apparatus works Recent work by Sherrington[2] and Magnus[3] and their pupils has thrown a flood of light upon this subject. They have proved, what the anatomical conditions so clearly indicate, that the brain-stem, and especially the mid-brain, contains the supremely important group of centres concerned in the acquirement and maintenance of equilibrium and posture. The orientation of the animal in space and its outlook on the world depend upon its posture. Its mental equilibrium depends upon its physical equilibrium, and changes in physical equilibrium under changing circumstances must be so co-ordinated that the recurring play of perceptual patterns must themselves be so co-related that they reflect changes within a stable cosmic frame

Posture, therefore, is the solid foundation upon which perception is built, and it is of such pre-eminently vital importance to the animal that it is subserved almost entirely, even in man, by a dyscritic mechanism. Posture is a relatively static condition, maintained indefinitely so long as circumstances remain relatively unaltered. so far it demands a plastic pose, subserved by tonic impulses and muscular contractions. Posture on the verge of change assumes a dynamic aspect and becomes an attitude, in which the distribution

[1] Kappers, *op. cit.* p. 896.

[2] *The Integrative Action of the Nervous System*, Yale University Press, 1920, and many papers in recent numbers of the *Proc. Roy. Soc*

[3] *Korperstellung*, Berlin, 1924; Croonian Lecture, *Proc. Roy Soc* B, xcviii, 339, 1925.

of tone in various muscles is in a sense pre-current—prepared for active movement. Yet even so, it is still subserved, even in the primates, essentially and almost entirely by a dyscritic mechanism. Plastic muscle tone is, indeed, dyscritic; muscle tetanus is epicritic. Thus the whole nervous system, receptor and effector, is built upon a dual—dyscritic and epicritic—basis.

As Sherrington[1] has pointed out, "plant life orientates itself in regard to the line of gravity, geotropism; and so in the rabbit, cat, and monkey, standing, walking, running...are refined geotropic reflexes." The *point d'appui* of mental life is, through posture, gravitation.

The key to the solution of the problem of posture was the discovery of decerebrate rigidity by Sherrington. If the brain-stem of an animal—cat, dog, monkey, etc.—is transsected at the level of the posterior corpora quadrigemina the limbs assume a state of tonic extensor spasm. Such an animal, unlike a "spinal" animal, whose central nervous system has been transsected below the level of the medulla oblongata, can be placed upon its feet and will continue to stand up indefinitely. But it stands in an abnormal posture, with exaggerated extension of limbs, neck and tail, and if it is pushed to one side it immediately falls over, and has no power of regaining the standing posture or even the normal posture of repose It is a "caricature of standing."[2]

It has been proved by Sherrington that the receptors of the reflex in decerebrate rigidity are proprio-ceptive, situated in the muscles and tendons themselves. The adequate stimulus is the actual tension or stretch of the muscles and tendons[3], and if the corresponding posterior roots are divided the tone is abolished Other afferent impulses influencing posture are (1) the labyrinths of the inner ears, the otoliths reacting to changes of position, the ampullæ of the semicircular canals to accelerations, (2) extero-ceptors of the body-surface, chiefly from the pressure sense-organs, which are stimulated if the body touches the ground; (3) teleceptors, reacting to distance stimuli, such as those of vision, hearing, smell

Postural reflexes may be divided into two great groups—static and stato-kinetic. The former deal with changes in posture of the otherwise stationary animal, the latter with movements of the animal

Static reflexes are further divided into two groups—postural

[1] *Proc. Roy. Soc* B. XCVII, 262, 1925.
[2] Magnus, *op. cit.* p. 4.
[3] Sherrington and Liddell, *Proc. Roy Soc.* B. XCVI, 212, 1924.

reflexes proper (*Haltung*) or standing reflexes (*Stehreflexe*), and righting reflexes (*Stellreflexe*). The standing reflexes are found in unadulterated form in the decerebrate preparation Righting reflexes occur only in animals in which the transverse section of the brain stem passes more anteriorly—at least so far forward as to preserve both quadrigeminal bodies in continuity with the medulla and spinal cord. Such a preparation is called a "mid-brain animal" The "thalamus animal," in which the section is still farther forwards, retaining the optic thalamus, but severing the connection with the cerebrum, including the corpus striatum, behaves almost the same as a "mid-brain animal," and is more easily investigated owing to the preservation of the centres for the control of the body temperature In it the tone of the extensors is not exaggerated, as in the decerebrate preparation, but normal, as in the intact animal, and the flexors also have as much tone as in the normal animal The "thalamus animal" will stand in a normal posture and right itself if overturned. Rademaker has shown that the preservation of the red nucleus is essential for maintaining the normal distribution of tone, which is carried out chiefly by the rubro-spinal tract.

Experiments on the decerebrate preparation show that there are tonic neck reflexes and tonic labyrinthine reflexes, and that when both are active the resulting effect is the algebraic sum. The tonic neck reflexes can be studied free from complication after bilateral extirpation of the labyrinths. Rotation of the head on the long axis (snout—foramen magnum), lateral flexion (*negation*), and dorsal and ventral flexion (*affirmation*) all produce characteristic responses. Thus, rotation to the right (right eye down, left eye up) causes increased extensor tone of the left limbs, diminished extensor tone of the right limbs. Lateral flexion to the right causes the reverse effects, but the former are more potent. Dorsal flexion reinforces extensor tone in all limbs in the rabbit, affects the fore and hind limbs reciprocally in the cat, increasing extensor tone in the former and inhibiting it in the latter. Ventral flexion has the reverse effects to dorsal flexion. The "affirmation" effects can be easily demonstrated in the intact cat. All these effects are abolished by section of the posterior roots of the first, second and third cervical nerves.

The tonic labyrinthine reflexes act both on the limbs and on the body musculature, but most strongly on the former. Generally speaking, the labyrinthine reflexes act similarly on all four limbs, and are maximal when the animal is in the supine position and the line of the mouth (*e.g.* the cat) makes an angle of 45° above the horizontal,

and are minimal when the animal is standing, with the line of the mouth at an angle of 45° below the horizontal.

These standing reflexes are accompanied by *compensatory eye movements*. The tonic labyrinthine ocular reflexes are exhibited when the position of the head in space is altered, and consist of vertical and rotatory deviations. If the head is rotated to the right (right eye down, left eye up), the right eye moves upwards and the left eye downwards. If the head is rotated upwards around the bitemporal axis, the eye undergoes torsion, such that the top of the vertical meridian of the cornea moves forwards towards the nose. It will be seen that the labyrinthine reflexes are of such a character as to retain the visual field so far as possible in its normal orientation but in no case is this effect fully accomplished. The effectors of the labyrinthine ocular reflexes are the superior and inferior recti and the obliques The lateral recti play no part

The tonic ocular reflexes initiated in the neck muscles are demonstrated in lateral flexion (*negation*) of the head. When the head is turned to the right, the right eye turns forwards (towards the nose), the left eye backwards. Here, too, the eye movements are compensatory, and the lateral recti are involved

The combined effects of the neck and labyrinthine reflexes are almost completely compensatory, so that the orientation of the field of vision is maintained in spite of the (passive) movements of the animal. When active movements of the animal occur stato-kinetic labyrinthine reflexes are set in action by changes in velocity, owing to stimulation of the semicircular canals These also lead to vertical, horizontal, and rotatory deviations.

"These reactions are such that with a given movement of the head of an animal which is in the normal posture the eyes are moved into the position in which they will later be maintained by the static reflexes, so that they are deviated into the necessary direction at the very beginning of movement.

There is, therefore, an extraordinarily well-developed correlation of ocular labyrinthine and neck reflexes, by means of which, both in movement and at rest, and in the various physiologically possible positions of the head with respect to the body and in space the correct visual attitude and the suitable correlation of the two eyes are ensured "[1]

The mid-brain animal behaves very differently from the decerebrate animal Walshe sums up its chief characteristics as follows·

"After the operation is complete the anæsthetized animal is laid on its side As it emerges from anæsthesia, it raises its head, the fore part of the trunk follows, then the hind part, and finally the animal assumes a squatting position. The distribution

[1] *Brain*, XLVII, 383, 1924

and intensity of muscle tone is normal throughout, and there is no rigidity. Such an animal is an automaton deprived of all volition, and whatever activity it shows is purely reflex. All the normal nutritional reflexes and many pseudo-affective reflexes are present. It jumps when a loud noise is made in its neighbourhood. If such an animal be laid upon its side or back, it rights itself at once Under appropriate stimulation it can step, run and jump with perfect co-ordination, and when its movements cease it resumes the sitting posture In whatever position the animal be placed, the head at once rights itself, and the animal clearly is in possession of reflex actions which keep the head always right side up in the world, and since the position of the head governs that of the trunk and limbs it has reflex control over all postures The following groups of "righting reflexes" (for so Magnus favours the anglicizing of *Stellreflexe*) have been analysed: (1) Labyrinthine reflexes acting upon the head, (2) reflexes arising in the body wall and acting upon the head; (3) reflexes arising in the neck secondary to (1); (4) reflexes arising in and acting upon trunk and limb musculature; and (5) in the intact animal a fifth group of righting reflexes arising in the retinæ When the labyrinths are both destroyed and the animal is blindfolded it loses the capacity of righting the head in space. When vision is free it is able to do so, even after bilateral labyrinth extirpation Optic righting reflexes are present in cat, dog, and monkey, but not in guinea-pig or rabbit"

The fifth group of righting reflexes occurs only in those animals which have some degree of binocular vision, and then only in the intact animal They differ, therefore, fundamentally from all the other reflexes, in that they are subserved by the cerebral cortex (probably the visual cortex) After bilateral extirpation of the cerebral hemispheres dogs, cats, and monkeys behave exactly like rabbits and guinea-pigs.

"If both labyrinths are extirpated in these (intact) animals, and they are held up free in the air (to avoid reflexes arising in the body wall) a short time after the operation, the head is disoriented and can be kept in any desired position in space After a few days, however, the animals learn to use their eyes for orientation, and one can then see clearly that if any object—food, the observer, or objects in the room—is fixated, the head turns into the normal posture. After a few days, the animals have usually developed this capacity well, so that if one now, *i e* with intact cerebrum and open eyes, examines them free in the air, the head assumes the normal posture as soon as any object is fixated.

That the effect is really due to optical righting reflexes is shown by the fact that the capacity immediately disappears if the eyes are blindfolded; the animals' heads are now just as disoriented as is the case with labyrinthless rabbits and guinea-pigs."

Stato-kinetic reactions are evoked by initiation, variation, or cessation of movements. If a sitting animal be rotated to the right, its head being at the periphery and tail towards the centre of the circle, the head and eyes turn to the left; on stopping, the head and eyes turn to the right This is accompanied by head nystagmus, the rapid component of the nystagmus being in the direction opposed to that of rotation, the after-reaction being a reversal. These reactions are comparable to Bárány's clinical observations.

If an animal is sitting on a horizontal board and is moved rapidly upwards it sinks on flexed limbs; on stopping the limbs extend. If a guinea-pig is held vertically with head downwards and is suddenly lowered the fore-limbs extend Combined static and stato-kinetic reflexes explain the cat falling on its feet.

The reactions to movement are reflexes from the semicircular canals, whereas the static reactions are due to pressure of otoliths on the maculæ of the saccule and utricle, maximal extensor tone being developed when the otoliths depend from, minimal when they rest upon the maculæ

The rôle of postural reflexes in bringing about attitudes is shown in the following examples.

'If a cat is sitting in a cage and a piece of meat is held low down near the ground, the animal fixes the food with its eyes, bends the head in the ventral direction, evokes labyrinthine and neck reflexes, which tend to flex the fore limbs, and the whole body of the animal is in this way directed towards the food. By moving the meat upwards, one makes the animal follow the food with its eyes, flex the neck dorsally and give rise to labyrinthine and neck reflexes, by which the fore limbs are strongly extended, the fore part of the body raised, whereas in the hind limbs neck and labyrinthine reflexes just compensate each other, so that no change in their posture occurs The result is a somewhat "monumental" attitude, by which the body of the animal is again directed towards the meat, and, at the same time, brought into a posture which enables it to jump and to catch its prey.

Suppose a cat is standing in the middle of the room, and on its right side a mouse is running along the wall. The optic and acoustic stimuli act on the tele-receptors of the cat's head, and make it turn the heavy head to the right. By this the centre of gravity of the fore part of the body is displaced to the right At the same time, tonic neck reflexes are evoked, by which the vertebral column is curved and the right fore limb strongly extended, so that it carries the weight of the body alone and prevents it from falling The left fore limb has nothing to carry, and in harmony therewith this limb relaxes under the influence of the tonic neck reflex At the same time, the distribution of excitability in the motor centres of the spinal cord is rearranged by the turning of the neck, so that, if, for some reason, running movements begin, the limb which has no static function will always make the first step In this way the moving mouse impresses on the cat through the mediation of tonic neck reflexes an attitude, by which the cat is focussed towards the mouse and made ready for movement. The only thing the cat has to do is to decide: to jump or not to jump, all other things have been prepared beforehand reflexly under the influence of the mouse, which will be the object of the resulting jump."[1]

All static and stato-kinetic reflexes occur, apparently unaltered, in animals deprived of the cerebellum. The centres subserving them form three groups: (1) the centres of the attitudinal reflexes behind the plane of entrance of the VIIIth nerves; (2) the centres of the eye reactions between the entrance of the sensory nerves concerned

[1] Magnus, *Proc. Roy. Soc.* B, XCVIII, 344, 1925.

and the nuclei of the ocular muscles, (3) the centres of the righting reflexes (with the sole exception of the optical righting centres in the cortex in primates) in the mid-brain. Of the latter, the neck righting centres extend as far down as to the pons and upper part of the medulla, whereas the other righting centres lie at the level of the red nucleus. Rademaker has shown that the nucleus ruber is the centre of the labyrinth righting reflexes and of the body righting reflexes acting on the body, but not of the body righting reflexes acting on the head.

Magnus and de Kleijn's experiments, remarkable as they are, have done little more than bring positive confirmation and greater precision to the deductions drawn long ago by Sherrington from his own researches. His masterly description of the parts played by extero- and proprio-ceptive impulses, and particularly by the "distance receptors" of the former and the labyrinth of the latter, in determining posture, equilibration and orientation foretells all that has been revealed by Magnus and de Kleijn, and more which yet awaits experimental confirmation[1]. The projicient senses—vision (with its "glorified warm-spots"), hearing (with its "glorified touch-spots"), and smell ("taste at a distance")—in the head segments provide those sensations which occupy the focus of the perceptual pattern, the field of attention, and dominate and co-ordinate all those motor responses which, when thus integrated, determine the postural attitude of the animal and its reaction to the experiential presentation They induce anticipatory reactions which are precurrent to the final consummatory reactions.

Similarly, the labyrinth dominates the proprio-ceptive system "It keeps the world right side up for the organism by keeping the organism right side up to its external world "[2]

"The labyrinthine proprio-ceptors are largely the equilibrators of the head, and since the retinal patches are movably attached (in mobile eyeballs) to the head, and since each retina has its normals of direction conforming with those of the head, these equilibrators of the head are closely connected by nervous arcs with the musculature maintaining the postures of the eyeballs." From secondary association with the distance-receptors "the reactions of the labyrinth come in their turn to have anticipatory character They retain, however, their own special features of equilibration and tonus. The locomotion of an animal impelled by its eye towards its prey involves co-operation of the labyrinth with the retina. And the tonic labyrinthine reflex which maintains an attitude may be just as truly an anticipatory action as any movement is. The steady flexed posture of the frog directed toward a fly

[1] Sherrington, *op cit* esp. Lecture IX.
[2] *Ibid.* p. 342

seen on the aquarium wall is a co-ordinate innervation securing preparedness for the seizure of the food. Its character is as truly anticipatory as is that of any movement. We might speak of the animal as 'at rest,' but it is the tense quietude of the hunter watching quarry rather than rest, such as supervenes in sleep and other conditions where active innervation is actually relaxed or reflex action is truly in abeyance "[1]

Thus, the co-ordination of distance- and proprio-ceptors is the physiological basis of awareness and attention.

In active movements these co-ordinations between eyes and labyrinths are equally important, as are also the compensatory effects of each upon the other. In the primates and in man, with the development of binocular vision, vision comes more and more to dominate the labyrinth, acting vicariously for the labyrinth in case of need. The distance-receptor, smell, was the foundation upon which the neopallium was begun, and upon the distance-receptor, vision, it attained its highest perfection in man "In the higher types there is based upon the 'distance-receptors' a relatively enormous superstructure possessing million-sided connections with multitudinous other nervous arcs and representing untold potentialities for redistribution of so-to-say stored stimuli by associative recall"[2] (dynamic plasticity)[3]. Upon the labyrinth was built the "ganglion of the proprio-ceptive system," the cerebellum. Just as the cerebrum is the highest—syncritic—differentiation and integration of extero-ceptive impulses, so the cerebellum is the highest—syncritic—differentiation and integration of proprio-ceptive impulses, itself under the domination of the cerebrum.

[1] Sherrington, *op. cit.* p. 344.
[2] *Ibid* p. 352.
[3] *Vide* p. 65.

CHAPTER VIII

THE PERCEPTION OF SPACE

1. In Lower Animals

The development of stereoscopic vision in man undoubtedly raises his space perception to a state more nearly approximating the conception of ideal geometrical space than has been attained by any other animal. Deductions drawn from the bodily structure, sensory organs, nervous mechanism, and behaviour of lower animals as to their space perception reveals so indefinitely great a diversity that one is astonished that so many diverse physiological space-worlds can be not only fitted into the common geometrical space-world without producing chaos, but that each is biologically determined as most serviceable to its species in the struggle for existence with other species. Not only so, but on evolutionary principles we must conclude that higher and highest must have been reached by the application of the apocritic principle of successive differentiations, segregations, and integrations, resulting, not only in the final product as met with in man, but also in innumerable products which have become side-tracked because they were the best possible for the given species in their given environments. The latter have been sidetracked because the species were incapable of further advance; so that when we attempt to adjudicate as to their value as evidence of stages in the highway of progress we have to take into account the absence of dynamic plasticity in the species which doomed them to a fixity of tenure only escaping annihilation by the persistence of the same environmental conditions.

Space perception in man has been the great battle-ground of "empiricism" and "nativism" in the past[1] As will be seen in the next chapter, the tendency to-day is to attribute many of the essential factors of space perception to inherited characteristics. The attempt to explain them as the result of learning by experience, founded on proprio-ceptive and other impulses consciously or unconsciously felt and co-ordinated, such as appreciation of impulses derived from the extrinsic ocular muscles as a guide to the position of the eyes, appreciation of degree of accommodation as a guide to estimation of

[1] See Helmholtz, *Physiol. Optik*, 3rd ed. vol. III, and especially the critical addendum by von Kries, pp. 497–534.

distance, and so on, is generally held to have failed Physiologists have been forced to bend the knee to psychologists, who have invoked "attention" as the *deus ex machinâ*. None the less, the theory of evolution provides the physiologists with potent weapons for the defence of the last ditch, and space perception is now becoming the battle-ground for the pros and cons of inherited neural dispositions. No stretching of a crude conduction theory by facilitation (*Bahnung*) or otherwise, however ingenious, will alone account for the facts of space perception in man. But given the inheritance of neural pathways co-ordinated and integrated by *Bahnung* or otherwise in lower species, the problem, though still unsolved, is simplified.

Even such a theory is wellnigh inexplicable except on the hypothesis of the inheritance of biologically useful acquired characteristics, and the perturbed physiologist finds himself navigating the troubled waters between the Scylla of Lamarck and the Charybdis of Weisn ann. It would be contrary to the fundamental principles of evolution to expect that biologically useless acquired characteristics would be transmitted, and the failure of transmission of taillessness by the serial section of the tails of successive generations of rats proves nothing if a tailless rat in captivity has no biological superiority over his tailed brother. Indeed, it is interesting to note that writers on the evolution of the human brain from ape ancestors living an arboreal life tacitly assume the inheritance of biologically useful acquired characters, and do not even apologize for their heresy, if indeed they are conscious of it[1]. The proved effect of hormones derived from the internal secretions of endocrine glands, not only upon bodily growth, but also upon secondary sexual characteristics, has done much to undermine the strict theory of the germ plasm of Weismann Instead of wasting time and energy on devising contorted arguments to escape from the admission of the inheritance of acquired characters it seems likely to conduce most to scientific advance to accept the principle so far as it concerns *biologically useful characters*, until it is disproved by some crucial observation.

That being so, we are free to search for the germs of the guiding factors in human space perception where they are most likely to be found, *viz.* in the vertebrate and other ancestors of man, and in modified form in the sidetracked cousins of human ancestors, and

[1] Cf Elliot Smith, *The Evolution of Man*, e g p 39, London, 1924; Wood Jones, *Arboreal Man*, London, 1916; Treacher Collins, Bowman Lecture, *Trans Ophth Soc.* XLI, 10–90, 1921

in man's own "formative zone." Of these, the last is likely, with our present ignorance, to be the least fruitful field. Moreover, we may expect to find that in these ancestral types proprio-ceptive and other impulses, which in man have no proved concomitant in consciousness, provide conscious guidance which contributes materially to space perception.

Every sense in some degree contributes to space perception, for it contributes to the presentation of objects in the outer world It is true that the simple contact receptor gives knowledge only of an object touching a particular part of the animal's body, and this hardly comes into the category of true space percepts, yet it is the germ of space perception, which even in man is egocentric and derived from a knowledge of the body and its parts in space. James Ward[1] denies to the phototropic reactions of invertebrates any trace of spatial perception.

"We can hardly call translatory movements of the body as a whole positional signs, for, though they have altered the body's place in space, yet since the body itself is the *point de repère*, which all spatial perception implies, things are so far just where they were ..Such sensations have extensity; but, at this early stage, they have no local signs and therefore nothing for positional signs to relate The first requisite for spatial perception then is still wanting "

But it is not quite true that phototropic movements are merely random—into and out of the light At any rate, at a very early stage they acquire directional value Even a flagellate, *e g. Euglena*, only a small part of whose body is responsive to light, reacts positively and progresses along the gradient of greater light intensity

In higher organisms, like the Metazoa, with multiple sense receptors, the intensity of the stimulus varies with the position of the receptors when the stimulus is derived from a source of radiant energy or from diffusing substances (*e.g* olfactive and sapid substances) There is thus introduced a primitive perception of the spatial distribution of stimulus intensity which is absent from the merely directional intensity of the flagellate

Vibratory stimuli, such as impinge upon the lateral line organs of fishes and the sound stimuli of auditory receptors, are notoriously deceptive indicators of direction, since, owing to their transmission by water and air, they readily turn corners and throw inappreciable shadows. The same applies to chemical stimuli—taste in fishes, and smell—hence, the great superiority of visual over all other senses for space perception. And this is largely due to the low reflection

[1] *Psychological Principles*, Cambridge University Press, p 156, 1918.

coefficient of natural objects, for if they were all effective mirrors orientation would be as difficult as in a room with a thousand mirrors.

Whereas tactile sense, as mentioned above, when purely passive, scarcely merits the designation of a spatial sense at all, it becomes of great importance in this respect when the tactile organs are moved over objects in active touch. Its importance is greatest in the absence of radiant and other distance stimuli, as in darkness and in the blind. Perhaps, after all, its supreme importance is phylogenetic, as the primordium from which all the other, and especially the distance senses, were derived. And ontogenetically, the tactile sense, in developing consciousness of the parts of the individual's body builds up the egocentric "self" which is the point of reference of all other spatial percepts and concepts[1].

Interesting as may be the theoretical conception of various animals' spatial perception, it must be carefully borne in mind that its essential biological function is the control of movement—for the avoidance of obstacles, the pursuit of prey, the escape from enemies, and so on. Hence, visual organs, the organs *par excellence* of spatial perception, are almost entirely confined to actively moving animals[2].

The rôle of the visual organs in different species of vertebrates might in itself form the subject of a bulky treatise. The various size, structure, position, and mobility of the eyes of animals necessarily entail differences of space perception which are of great significance, not only practically to the animals but also theoretically in connection with man. And if we accept the view that proprio-ceptive and other impulses in these lower animals are attended with concomitant correlates in consciousness, the conditions of mobility, accommodation, etc. have yet another bearing on the subject in affording evidence of the evolution of the formative zone and the suppression into the unconscious of processes of vital significance.

Only the briefest reference can be made to details here. Fundamental likeness of plan with almost infinite variety is exemplified in the receptor cells, the dioptric mechanism and especially the almost universal presence of some form of optical lens (a mere transparent cuticular thickening or a fully developed crystalline lens of epidermal origin), a muscular accommodative apparatus, retinal and neural mechanism, etc.

[1] Cf. J. Mark Baldwin, *Mental Development in the Child and the Race*, New York, 1895.

[2] *Vide infra*, p. 150.

It is noteworthy that the accommodative muscle always consists of unstriated muscle fibres, except in reptiles and birds: perhaps this is associated with conscious voluntary efforts of accommodation. All animals except fish are hypermetropic or emmetropic, and accommodation is very slight in rabbit, horse, cat, and dog. In the Sauropsida the ciliary muscles are specially developed (Crampton's, Muller's and Brucke's), and snakes and birds have a wide accommodative range. Teleostean fishes are myopic in water, and diminution of the myopia is effected chiefly by retraction of the lens, which also causes movement of the retinal image. Selachian fishes appear to have very little accommodation. Frogs and some urodeles have no accommodation; there is no satisfactory information as to the change in the visual conditions entailed by life in the air and in the water. The mode of alteration of accommodation varies greatly in different species[1].

The steps in the development of binocular vision reveal many devices for the increase in the binocular field. We are apt to regard the diminished divergence of the orbital and visual axes as the chief, but long before this became prepotent the prominent hemispherical cornea associated with a spherical lens and a visual axis passing many degrees nasally to the optic axis through the centre of the cornea (50°–60° in Herbivora as compared with 5° in man) contributed materially to forward, at the expense of lateral, vision. The lion is said to have a binocular field of 120°, the elephant a monocular field of 190° (as compared with 160° in man) and a binocular field of 67°, whilst the rabbit has an anterior binocular field of 20°, and the fields touch or even slightly overlap posteriorly[2].

The development of a specially sensitive area in the retina is not the sole prerogative of anthropoid apes and man. An area centralis[3] occurs very frequently throughout the vertebrates. It occurs regularly in birds and reptiles, but is absent in some mammals and Amphibia (rat, salamander, triton). It is present in the frog, chameleon, crocodile, horse, pig, ox, sheep, cat, dog, rabbit. In some birds, including the owl, it is situated at the periphery of the retina; above the optic disc in the tortoise and horse (where it is band-

[1] See Rivers, in Schafer's *Physiology*, II, 1040, Edin and London, 1900; Putter, in Graefe-Saemisch, *Handb. der ges. Augenheilk.* (Organologie des Auges), II, 1, chap x, pp 276 sqq Leipzig, 1908, and especially Beer, *Arch f. d. ges Physiol.* LIII, 175, 1893 (Birds), LVIII, 523, 1894 (Fishes), LXVII, 541 (Cephalopods), LXIX, 507, 1898 (Reptiles); LXXIII, 501, 1898 (Amphibia).

[2] Grossmann and Meyerhauser, *Arch f Ophth.* XXIII, 217, 1877

[3] Chievitz, *Arch f Anat u. Physiol* Anat Abt pp. 139, 332, 1889; p 311, 1891.

shaped), below in the fox and hare (also band-shaped). Many such areas possess one and even two foveæ. Birds have two, one peripheral and the other central The cat is the only domestic mammal provided with a true fovea, but it is an external fovea, *i e* the pit is on the *outer* (*i.e.* choroidal) side of the retina[1]. It would seem that the development of an area centralis is an early differentiation of panoramic vision[2] which originally has nothing to do with binocular vision, but subserves the special requirements of individuals of different species, thus cutting across the usual phylogenetic series. Thus, its precocious development in birds, with the formation of two foveæ is easily correlated with their habits, the external foveæ acting like a range finder in distant binocular vision This type of area centralis is relatively static, and is not even transmitted to those members of a species whose habits do not require it. On the other hand, with increased differentiation affecting chiefly the central nervous connections, it is made available for the development of true stereoscopic, as opposed to merely binocular vision in the primates. The two factors which form the anatomical basis of stereoscopic vision are (*a*) two central foveæ which have attained the dignity of corresponding points, combined with (*b*) a partial decussation of the optic nerve fibres The latter alone may account for the rudiments of stereoscopic vision, as in the rabbit and the cat, but the higher grades demand great central visual acuity and a demi-semi-decussation.

The chief functions of vision, however, biologically considered, are the control of the individual's movements and the perception of movements in objects in the outer world As already mentioned, visual organs are found almost solely in actively moving animals, and in such as assume a sedentary phase (*e g.* ascidians, cirripedes) they degenerate and disappear There are, however, freely moving animals which possess no eyes or functionless eyes (*e g.* the degenerate *Myxine*), and others which live in total darkness yet possess eyes, which are sometimes enormous (*e.g. Lophius*) In the latter the eyes are often degenerate (*e g.* mole, cave fishes), and in some cases where they are well developed the animals possess light-producing organs (*e g.* some deep-sea fishes)

The very great importance of vision, and especially its reaction time, in the control of movements, can be shown by a few examples A man, moving at a walking pace of about $1\frac{1}{2}$ m per sec., can see every object clearly, even such as are close to him. In an aeroplane

[1] Zurn, *Arch f Anat u Physiol* Anat Abt, Supplementband, p. 99, 1902.

[2] *Vide infra*, p 151

travelling at 30–40 m. per sec. only distant objects are clearly defined, and such movement would be impossible if many obstacles had to be avoided. Yet some birds are said to fly at 90 m. per sec., and that in rapidly wheeling compact flocks (*e.g.* starlings), where each bird is calculated to have only about one cubic foot of space. Possibly these birds, like bats[1], have other than visual perception to aid their orientation. A mammal with a reaction time of 0·15 sec. and a velocity of 2 m. per sec. moves 20 cm. during the reaction time; an insect, with a reaction time of 0·003 sec and a velocity of 2 cm. per sec. covers only 0·7 mm. during the reaction time. These factors are of still greater importance when an obstacle is also moving towards the animal Attempts have been made to correlate the visual acuity, based on visual angle, number of retinal receptors in a given area, with size of eye, reaction time, etc , in order to obtain some estimate of visual capacity[2]. But, as Putter says, "we cannot estimate the capacities (of visual organs) by any ideal standard, but must seek them in relation to the specific kinds of movement and velocities, and above all in relation to the peculiarities of the nervous systems of the given animals, the most important factor being the reaction time "

The panoramic vision of lower vertebrates is adapted primarily to the perception of movement of objects in the outer world[3] Alone it provides a very poor visual acuity or capacity for the perception of shapes and forms; yet it is eminently serviceable biologically for fundamentally vital purposes, and therefore this function occurs far down in the animal scale, even in invertebrates, and is subserved by a dyscritic nervous apparatus. We shall see that it is largely dyscritic even in man. The histological criteria of a true area centralis are somewhat indefinite, and the statements made by Chievitz, Zurn, and others as to its distribution in different animals require confirmation. They are not easily correlated with the habits of different animals; for example, it is notorious that cats see very much better than dogs, yet both have central areas We should expect them to be absent in Herbivora, in which the appreciation of movement of objects is of chief importance, and well developed in Carnivora, which would seem to require much more accurate vision[4].

[1] *Vide* p 89

[2] See Putter, *op cit* pp 370–377

[3] *Vide* Chapter IX

[4] See von Tschermak, *Arch f d ges Physiol* XCI, 1, 1902; *Tierarztliches Zentralbl.* 1910, W Harris, *Brain*, XXVII, 107, 1904.

2. In Man

Every animal, if it has any perception at all, must have some form of space perception, however vague. In the animal with only undifferentiated contact receptors its space world must be limited to its own body. With the development of distance-receptors the space world is extended, and the animal guided prepotently by smell, sight, or hearing must have a practically serviceable perception of "over there"

We are accustomed to regard ourselves and the outer world as existing in a tri-dimensional Euklidean space, but this is a deduction from our own varied and complex experiences; and modern mathematical speculations have shown that some, at any rate, of our experiences can be better explained by perfectly consistent non-Euklidean spaces deduced from different, but equally rational, postulates. Even for ourselves one thing is certain, that physiological and geometrical space (of whatever kind) are not identical.

Our own physiological space perception, like every other mental process, has been evolved from the space perceptions of our animal ancestors, but the inferences which we can draw from experience as to the space perception of lower animals are even more uncertain than the corresponding inferences with regard to other sensations and perceptions. Human space perception, whilst, like all perceptions, a psychological complication and correlation of many sensations of different modality and quality, has so come under the domination of vision, and indeed of binocular vision, that the subtraction of those factors which are manifestly absent in lower types is fraught with difficulty and danger of grave error. For we have already had ample evidence to prove that, at any rate in the mental stage of emergent evolution, the newly acquired higher emergent has a profoundly important backstroke influence upon the lower. We are conscious only of the final products of the nervous impulses which traverse long and complicated paths, with many junctions and collateral deviations and it is only by the most searching observation, experimentation, and analysis that we gain the merest inkling of what goes on in the formative zone which underlies the final finishing shop, and which holds the secrets of earlier evolutionary stages.

None the less, we even now have sufficient knowledge to make *some* reasonable conjectures as to the space perception of lower vertebrates, and, though it savours of reasoning in a circle, the

deductions thus made repay the debt by throwing light on some of the most difficult problems of space perception in man.

Sherrington and Magnus's work has consolidated the foundation upon which space perception rests. They have proved conclusively that it has a gravitational basis, and they have shown the physiological mechanism which underlies the animal's state of right side up to the world.

When a man in the erect posture looks straight forward his binocular field of vision embraces almost half a sphere. In the horizontal plane, passing through the centres of rotation of the eyes, the section of the visual field is a complete semicircle. An imaginary medial sagittal plane divides the field into lateral halves It is bounded posteriorly by a frontal plane passing through the centres of rotation of the eyes Objects in this visual field form images upon the retinæ in such a manner that their relative position to each other is subjectively determined; but it does not follow that their objective position coincides accurately with the subjective position. The relative positions of objects enables estimates to be made of distances and sizes; but, again, subjective distance and size do not necessarily coincide with objective distance and size.

So-called absolute, better egocentric[1], localization depends upon reference to the body. Things above the eyes in the visual field, with the eyes in the primary position, are above, things below, under, things to the right and left of the median plane, right and left. Thus the axes of reference are fixed, and there is no visual field behind. Hence physiological space differs from Euklidean geometrical space, which is a universalized abstraction from it. In the former case the axes of co-ordinates are fixed, and determined by gravity. in the latter they are generalized and independent of everything except their rectangular relationship to each other. Visual space is finite and of unequal extent in different directions. geometrical space is uniform in all directions, unlimited, and infinite (in Riemann's sense). The alteration in size of visual objects according to distance makes visual space resemble the space of metageometricians rather than Euklidean space. The latter is arrived at only by deductions from the changes in physiological space resulting from alterations in orientation and movement; and even so, geometrical space does not wholly free itself from the implications of physiological space in that it retains physiological conceptions of direction[2].

[1] G E. Muller, *Zeitschr f Psychol* Ergänzungsband IX, 1917

[2] See Mach, *Die Analyse der Empfindungen*, pp 148–9, 9th ed Jena, 1922

It does not fall within the limits of this thesis to discuss in detail the difficult problem of space perception in man. The older work on this subject has been fully discussed by Helmholtz[1] and Hering[2], and abstracted by Rivers[3]. Both the older and more recent work has been admirably discussed by F. B. Hofmann[4]. The questions of chief importance from the present point of view are the relations of visual space perception to tactile, and in less degree auditory, olfactory, and gustatory space perception, and whether localization is inherited or acquired.

The evidence is wholly in favour of the view that localization and fixation of an object by the eye is innate, being effected by an inherited neural disposition Thus chicks peck with extraordinary accuracy almost immediately after escaping from the shell, as is proved by Lloyd Morgan's experiments[5]. The short delay in the acquiring of fixation in babies is due to the immaturity of the new-born human offspring Objects are commonly said to be projected outwards along the line of vision passing from the fovea through the nodal point of the eye. It would be more accurate to say that they are seen *as if* projected to a point on this line Even this statement is not strictly accurate in normal human binocular vision Hering first showed that projection is along a line which passes mid-way between the two eyes. It is as if each eye were superposed in the sagittal plane, so that the foveæ and nodal points coincided respectively, thus forming a sort of "cyclopean" eye This is due to the fact that in binocular vision each retina can be mapped out into corresponding points (Fechner), a point in one retina having a corresponding point in the other such that each has a common and identical visual projection. Such corresponding points are also innate, and subserved by an inherited neural disposition, but, perhaps owing to the phylogenetically late development of binocular vision, corresponding points can also act as disparate points, just as the relationship between accommodation and convergence is not absolutely fixed

Moreover, it has been shown that the centre of directions is not generally accurately in the sagittal plane on the level of the nodal

[1] *Physiol Optik*, 3rd ed 1909–1911; translated by the Optical Society of America, 1924–1925

[2] In Hermann's *Handb d Physiologie*, 1880, *Beitrage zur Physiol* Leipzig, 1861-4; *Arch f Ophthal* XXXVII, 1, 1891, XXXIX, 274, 1893

[3] In Schafer's *Text-book of Physiology*, II, 1900

[4] *Die Lehre vom Raumsinn des Auges*, Berlin, 1920–1925

[5] Cf Hamburger, *Klin Monatsbl f Augenhlk* Beilageheft, 106, 1905, Engelmann's *Arch f Physiol* p. 400, 1905

points, but farther back and somewhat eccentric[1]. Hering himself[2] observed that in one-eyed people, or people who often use only one eye (*e g.* microscopists) the centre is towards that side. Moreover, it is well known that most people have a "master eye," as is generally discovered by sportsmen. In pathological cases of squint[3] and hemianopia[4] a "pseudo-fovea" is often established and dominates visual direction.

Though the normal apparent median and other directions are dominated by the cyclopean eye, the relation is not absolutely fixed. But just as localization and fixation depend upon an inherited mechanism, so the impression that a point of light lies in the median plane appears to be immediately given in consciousness[5]. Experiments by Bourdon[6], Sachs and Wlassak[7], Dietzer[8] and others, have shown that the accuracy of estimation of the apparent median in daylight is very great, and the same applies to the apparent horizontal[9]. Similar estimates in the dark show greater variations, and throw light upon the influence of contingent factors—consciousness of the position of the head and body, etc. Most striking are the considerable deviations from accuracy when the estimates are made with the head laterally inclined, whether it alone be inclined or both head and body[10] The disorientation produced by the displacement from the normal influence of gravity has a marked effect upon these judgments.

When the eyes move from one fixation point to another, objects appear to remain in the same place, in spite of the fact that their images pass across the retinæ. It has been suggested that this movement is compensated by some sense of position of the eyes

[1] Kollner, *Arch f d. ges Physiol* CLXXXIV, 134, 1920, *Arch f Augenhlk* LXXXVIII, 117, LXXXIX, 67, 121, 1921; Weinberg, *Arch f d ges. Physiol* CXCVIII, 421, 1923, F B Hofmann, *Skand Arch f Physiol* XLIII, 17, 1923

[2] *Beitraye zur Physiol* Leipzig, 1861–4

[3] Schlodtmann, *Arch f Ophth* LI, 256, 1901, Tschermak, *ibid* LV, 1, 1902

[4] Best, *Arch f Ophth.* XCIII, 49, 1917, C, 1, 1919, *Neurol Zentralbl* XXXVIII, 427, 1919, Poppelreuter, *Die psychische Schadigungen durch Kopfschuss*, Leipzig, 1917, Fuchs, *Zeitschr f Psychol* LXXXIV, 129, 1920, *Psychol Forsch* I, 157, 1921

[5] F. B Hofmann, *Die Lehre vom Raumsinn des Auges*, p 395, Berlin, 1925

[6] *La Perception visuelle de l'Espace*, pp 149 sqq Paris, 1902

[7] *Zeitschr f Psychol* XXII, 23, 1899

[8] *Zeitschr f Biol* LXXX, 289, 1924

[9] Bourdon, *op cit* pp 153 sqq ; R. MacDougall, *Psychol Rev* Monograph Suppl IV, 145, 1903, Hoppeler, *Zeitschr f. Psychol.* LXVI, 249, 1913, Fischer, *Arch f d. ges Physiol* CLXXXVIII, 161, 1921.

[10] Bourdon, *op cit* pp 166 sqq.

Exhaustive investigation shows that consciousness of position of the eyes in the absence of visual control is extremely inaccurate, and such as it is, is not due to sensations derived from the conjunctiva, as shown by Sherrington[1], Bourdon[2], and Marx[3]; or from the lids, as advocated by Bourdon; or from the muscles, as advocated by Tschermak and his pupils[4]; or to the stimulation of sub-cortical centres, as advocated by Köllner[5]. Observations on cases of paralysis of eye muscles shows that localization is not determined by sensory impulses from the muscles[6], for the sensory nerves of the muscles run in the motor nerves[7].

The explanation appears to lie in the direction of attention, as long ago suggested by Hering[8]. Change of attention determines the change of fixation. Even before the movement begins the point aimed at occupies the attention, and the position of this point in the visual field determines the direction and amount of movement. In the same degree as attention changes its fixation point in space, so the spatial values of the retina change and thereby compensate for the movements of the retinal images.

It will be seen that this explanation agrees with that of many of the phenomena which we met with in other perceptual patterns. We have seen already[9] that attention modifies and controls the activities of the formative zone. It may well be that Köllner's conjecture is not altogether wrong. Attention in higher animals appears, in some manner which we cannot at present fathom, to short-circuit and replace the functions performed by factors which have been phylogenetically suppressed.

"In the concrete, the body is the origin or datum to which all positions are referred, and thus "here" for the individual percipient is an absolute position, one that has no counterpart in the thoroughgoing relativity of pure space Also "the body sense" in contrast with what may be called "the projecting senses" yields the further absolute distinction of internal and external, marking off the bodily self from its environment "[10]

[1] *Proc Roy Soc* LXIV, 120, 1898

[2] *La Perception visuelle de l'Espace*, p 66, Paris, 1902.

[3] *Zeitschr f Sinnesphysiol* XLVII, 79, 1913

[4] Tschermak, *Ergebnisse d Physiol* CLXXXVIII, 222, 1921. Cf. Sherrington, *Brain*, XLI, 332, 1918.

[5] *Klin Wochenschr* pp 482, 1293, 1923; *Arch. f Augenheilk* XCIII, 130, 1923

[6] See C S Myers, *Text-book of Exp Psychol.* pp 214–217, Cambridge, 1911.

[7] Sherrington, *Proc Roy. Soc* LXIV, 120, 1898, Tozer and Sherrington, *ibid* LXXXII, 450, 1910

[8] In Hermann's *Handb d Physiologie*, p 534, 1880. [9] *Vide supra*, Chap. IV, 3.

[10] James Ward, *Psych Principles*, p 145, Cambridge, 1918.

Touch, as already mentioned, possesses the characteristic of extensity, and the extensive continuum, at first relatively undifferentiated in the primitive dyscritic stage of evolution, becomes differentiated in the epicritic stage, with the development of "local signs" (Lotze). To every distinguishable part of the body there corresponds a local sign, and these local signs have an invariable relation to each other. The qualitative difference of local signature is experienced by passive touch, independently of movement, but the presentation of occupied space is only attained "after its several local signs have been complicated in an orderly way with active touches,"[1] *i. e.* by active movements. It is only by active touch that the distinction, *quâ* the tactile sense, is made between one's own body and foreign bodies; and thus "active touches" come at length to be "projected," passive touches alone being "localized" in the stricter sense[2].

As was first pointed out by Berkeley[3], visual space perception, so far as magnitude is concerned, presupposes tactile or haptic space perception, for measurement depends upon active touch, which is due, not only to the superficial and deep local signs, but also to the proprio-ceptive impulses from muscles and joints, all together constituting kinæsthetic impressions. Such active touch gives knowledge of position relative to the body, form, size, and distance. Vision may be said to have inherited function in space perception from the tactile sense of which it is a higher differentiation, and the analogy of macular or active vision with active touch is very complete. The macula corresponds to the tip of the finger[4]; and it is of considerable interest to notice that we are quite well able to distinguish whether the finger moves over an object or the object over the finger, just as it makes all the difference in vision whether the image moves over the retina when it is still or when it takes up fixation.

Cases of almost complete blindness from congenital cataract, which have been successfully operated upon in later life, afford the opportunity of judging tactile space perception almost entirely divorced from vision. Most of the cases on record have been collected and carefully discussed by Bourdon[5]; such cases now rarely escape

[1] James Ward, *op. cit.* p. 149.

[2] *Ibid.* p. 152.

[3] *Essay towards a New Theory of Vision*, §§ 55–61. Ed. A. C. Fraser, Oxford, 1901.

[4] Mach, *op. cit.* p. 152.

[5] *La Perception visuelle de l'Espace*, pp. 362–391, Paris, 1902. See also, Helmholtz, *Physiol. Optik.* I, 586; Stumpf, *Ueber den psychol. Ursprung der Raumvorstellung* Leipzig, 1873; von Hippel, *Arch. f. Ophth.* XXI, 101, 1875; Uhthoff, *Festschrift f. Helmholtz*, p. 113, Leipzig, 1891; *Zeitschr. f. Psychol.* XIV, 197, 1897; Francke,

operation in infancy. The difference between tactile and visual space perception was posed in the famous letter of Molyneux to Locke[1]. Could a blind man, who knew a cube from a sphere by touch, distinguish them by vision alone if he regained his sight? Molyneux and Locke said, No. It is, however, quite wrong with Berkeley and Diderot[2] to conclude that the space perception of the blind is of a totally different order from that of the seeing. As Mach[3] points out, if that were so, how could the blind Saunderson write a treatise on geometry which was perfectly consistent with the geometry of sighted mathematicians?

Most such blind people have perception of light and fair "projection of light." They can generally, if sufficiently intelligent, "project accurately the phosphene produced by pressure on different parts of the eyeball "[4] Their space perception, though thus almost entirely non-visual, enables them by means of kinæsthetic sensations, hearing, etc., to orient themselves fairly accurately and on a gravitational basis, to recognize shapes (stereognosis), near distances with greater and distances which involve bodily progression with less accuracy, and so on.

On recovering sight they recognize visually the position of objects not only right side up, but also egocentrically, *i.e.* above, below, right, left, the shape and difference of colour of objects, etc. Estimates of size are at first very vague, and they often complain of objects touching them. Visual acuity with correcting glasses is generally poor, as may be explained by other than neural causes, but is as good as can be expected. The correlation of movements under visual control is at first poor. The retinal perception of movement, which is probably innate, is badly co-ordinated with movements of the head and eyes in these cases, and probably differs materially from tactile perception of movements. As already mentioned, there is perception of form, but the correlation between visual and tactile form has to be learnt[5]. The perception of depth is very poor, since the patients are usually uniocular.

Deutschmann's Beitrage z. Augenheilk. II, 473, 1894, Seydel, *Klin Monatsbl f Augenheilk* XL, 197, 1902, Latta, *Brit Jl. of Psychol* I, 135, 1905, Miner, *Psychol Rev* Monograph Supp VI, 5, 1905, Le Prince, *Jl de Psychol norm et path* XII, 46, 1915

[1] In the *Essay on the Human Understanding*

[2] *Lettre sur les Aveugles*

[3] *Op cit.* p 112

[4] See Schlodtmann, *Arch. f Ophth* LIV, 256, 1902

[5] *Vide supra*, p 58

Space perception in the normal sighted is not determined solely by visual space perception but is certainly dominated by it. The influence of tactile and kinæsthetic factors is shown in the position of the centre of directions[1] when the pointing is done under direct visual observation, special means not being adopted for preventing it interfering with the purely optical estimation of direction It is then found[2] that the centre of directions is at or near the centre of lateral movements of the head, as was anticipated by Roelofs and de Fauvage-Bruyel[3], and much earlier by Helmholtz[4]—"it gives the impression that one looks out upon the world from a certain depth in the head."

The perception of depth and distance in man is rendered possible by the co-operation of many factors, of which binocular vision is the most important. Others include parallax, aerial perspective, the relative sizes of familiar objects, shadows, etc. Hering's view that retinal points possess "depth values" is now generally rejected. Hence we may conclude that those animals which do not possess binocular vision must possess very poor perception of depth.

In the phylogenetic stage, at which an animal has lateral eyes with no overlapping of the fields of vision, its visual space perception must, therefore, be derived from a flat field and limited to the relative positions of neighbouring visual images. Those images would be endowed with relative localization values, but no egocentric localization value—exactly as in the case of tactile space perception With the development of binocular vision space perception of a higher order is brought about It is tridimensional, and it possesses egocentric localization. Whereas the former can be correlated directly with known physiological principles, the latter belongs to the more complex type of perceptual patterns, embodying entirely new psychological features

It is noteworthy that von Kries[5] considers that these two forms of visual space perception, which he calls *primitive* and *definitive*, occur ontogenetically in man, and are subserved by different neural substrata. They are clearly analogous to the general characteristics of dyscritic and epicritic sensations respectively, but since spatial

[1] *Vide supra*, p 154

[2] Funaishi, in F. B. Hofmann, *Die Lehre vom Raumsinn des Auges*, p 393, Berlin, 1925

[3] *Arch f Augenheilk.* xcv, 111, 1924

[4] *Physiol. Optik*, 1st ed p 556

[5] *Allgemeine Sinnesphysiologie*, pp 220 sqq Leipzig, 1923.

(and temporal) percepts have fundamental characteristics, which distinguish them from all other sensory phenomena, they must not be regarded as "sensations"—as is so often done, verbally at any rate—and the analogy serves merely to emphasize the dual phylogenetic and ontogenetic principles underlying diverse psychological processes.

The primitive form of space perception is clearly the older and the less differentiated. The definitive form is the younger, more highly differentiated, more complex and more comprehensive. It cannot be explained on empirical grounds as a further development of the primitive as the result of experience; but in the course of individual experience, although founded on independent inherited neural dispositions, they interact much in the same manner as dyscritic and epicritic systems interact and become modified by syncritic processes. Thus, the perception of direction is immediately given as the direct result of the presentation stimuli, but the perception of above, below, right, and left depends not only upon retinal local signs but also upon conditions of innervation associated with the position of the eyes, etc. Similarly, things appear to us at definite relative and absolute (egocentric) distances; these are immediate deductions (judgments of the lowest, sub-cortical, order), dependent upon different circumstances—visual angle, shadows, aerial perspective, binocular retinal disparation, perspective, parallax—in different cases, yet in no case do these factors enter into consciousness. These phenomena are, therefore, fundamentally the same as occur with many other complex perceptual patterns, as is indeed pointed out by von Kries[1], who quotes examples already referred to from Schumann[2], von Frey[3], and Katz[4].

[1] *Op cit.* p 223.
[2] *Zeitschr f Psychol* LXXXV, 224, 1920
[3] *Zeitschr f. Biol* LXXIII, 263
[4] *Centralbl f Physiol* XX, 1906; *Zeitschr. f Psychol* Erganzungsband VII, 1911

CHAPTER IX

THE PERCEPTION OF MOVEMENT

WHEN the eye changes its fixation from one point to another the objects in the field of vision do not appear to move, in spite of the fact that their images travel across the retina. Change of attention appears to compensate for the movement of the retinal images by altering the spatial values of the retinal points[1]. If, however, the images pass across the retina of a stationary eye, or if an actually moving object is observed by the eye, even if the latter be moving so as to keep up fixation of the moving object, there is perception of movement. There are also several types of apparent movement, *i e.* perception of movement in the absence of real movement; such as (1) when, objects being stationary, the eyes or head are moved without a corresponding compensation of egocentric localization; (2) subjective movements of after-images, both eyes and objects being stationary; (3) stroboscopic, when images of an object fall rapidly in succession upon very closely neighbouring retinal spots, or when slightly different images fall rapidly in succession upon the same spot.

"*Real*" *Movement.* The explanation of the perception of movement, even in the simplest of these cases, is even more difficult than that of the perception of space It is, indeed, a nearly allied problem, and it is often tacitly assumed that the theory of local signs in itself accounts for the perception of movement in really moving bodies. It is clear, however, that this affords no satisfactory explanation. An image falling upon successive retinal spots of different local signature, need theoretically give rise to nothing more than a sort of mosaic vision differing from continuous motion, and this has been observed in some pathological states[2]. Witasek[3] holds that movement is not a perception, but a judgment derived from a comparison of estimates of different positions of objects at different times. Whilst we may agree that in many movements experienced by man such higher mental processes as judgments are involved, it cannot be accepted that the primitive appreciation of movement depends upon

[1] *Vide* Chapter VIII, 2, p. 156.

[2] *Vide* p. 52.

[3] *Psychol. d Raumwahrnehmung des Auges*, p. 325, Heidelberg, 1910

such highly differentiated mental processes. For appreciation of movement must be one of the most primitive acquirements of animal consciousness, of the utmost biological and vital importance, occurring in lowly stages, before even epicritic differentiation has become manifest, much less higher syncritic processes. Judgment alone, indeed, does not suffice to explain the experience of movement on the basis of local signs alone: some other factor, bridging the gap between two presentations of different local signs, being essential. We may therefore agree with Exner[1] and Hering[2] that the appreciation of movement is a new and peculiar type of perception.

We have already stated that pure sensations are never experienced alone, and so complex a phenomenon as movement is no simple sensation. But analysis of our perceptions shows that sensations are characterized by intensity, extensity, and protensity, these factors varying in different sensations. The element of protensity, *i. e.* the time element, is specially prominent in conjunction with extensity in the perception of movement, and in this respect it is comparable to melody in hearing. More nearly allied is the perception of movement by the tactile sense. Two spots, suitably far apart in the skin, can be discriminated when stimulated by compass points, and most readily if the stimuli are successive, yet no movement is perceived. Movement is perceived if a point is drawn across the skin, or the edge of a card is successively made to stimulate contiguous spots, as in Sherrington's experiment[3]: there can be little doubt that "immediate induction" is an important factor. The cutaneous spatial threshold varies greatly in different parts of the body, diminishing in the limbs towards their extremities, which are most used for exploration. Distances are judged smaller or greater according as spatial sensitivity is coarse or fine, and the apparent rate of a point moving over the skin waxes and wanes with the rise and fall of the spatial threshold[4].

Similarly, there is a certain parallelism between visual acuity or the discrimination of two points by retinal stimulation and perception of movement. It has been shown by Aubert[5] and Bourdon[6] that the minimum angular velocity of a moving object to permit of perception

[1] *Sitzungsberichte d. k. Akad. d. Wiss. in Wien, Math.-nat. Kl.* III, p. 156, 1875.
[2] In Hermann's *Handb. der Physiol.* III, p. 556, 1880.
[3] *Vide infra* p. 180.
[4] See C. S. Myers, *op. cit.* p. 221.
[5] *Arch. f. d. ges. Physiol.* XXXIX, 347, 1886.
[6] *La Perception visuelle de l'Espace*, p. 185, Paris, 1902.

of movement is 1–2 min. per sec. when there are also stationary objects in the field of vision: if there are no such stationary objects the angle is 10 (Aubert) to 20 (Bourdon) times as great. With fixed reference objects and central vision the minimum angular displacement for the perception of movement is 10–20 sec. (Volkmann)[1], 20 sec. (Basler)[2], 15 sec. (Stern)[3], 6·8–8·8 sec. (Stratton)[4]. Stratton showed that the threshold for movement and that for displacement agreed. Just

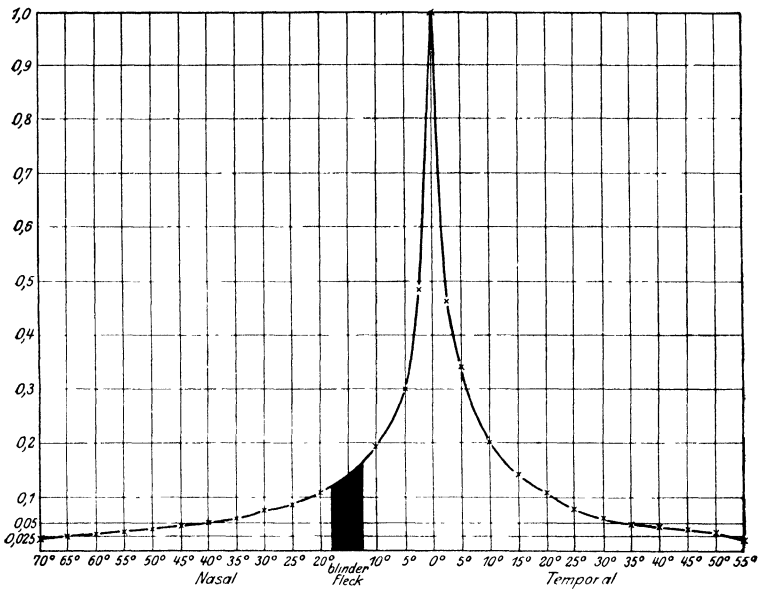


Fig. 39 Visual acuity curve Abscissæ, degrees eccentric to fixation point, ordinates, visual acuity (foveal = 1) (Wertheim).

as the visual acuity (for discrimination of two points) (Fig. 39)[5] diminishes rapidly in passing out towards the periphery, so, too, the acuity for movement (Fig 40)[6]. On the other hand, both the acuity for movement and the acuity for displacement[7] are much greater in

[1] *Physiol Untersuchungen im Gebiete der Optik*, Leipzig, 1863.
[2] *Arch. f d ges. Physiol.* CXV, 582, 1906
[3] *Zeitschr f Psychol.* VII, 321, 1894.
[4] *Psychol Rev* VII, 429, 1900
[5] Wertheim, *Zeitschr. f Psychol* VII, 177, 1894
[6] Basler, *Arch. f. d. ges. Physiol.* CXXIV, 313, 1908.
[7] Stratton, *loc cit* ; Lauens, *Zeitschr f Sinnesphysiol.* XLVIII, 233, 1914

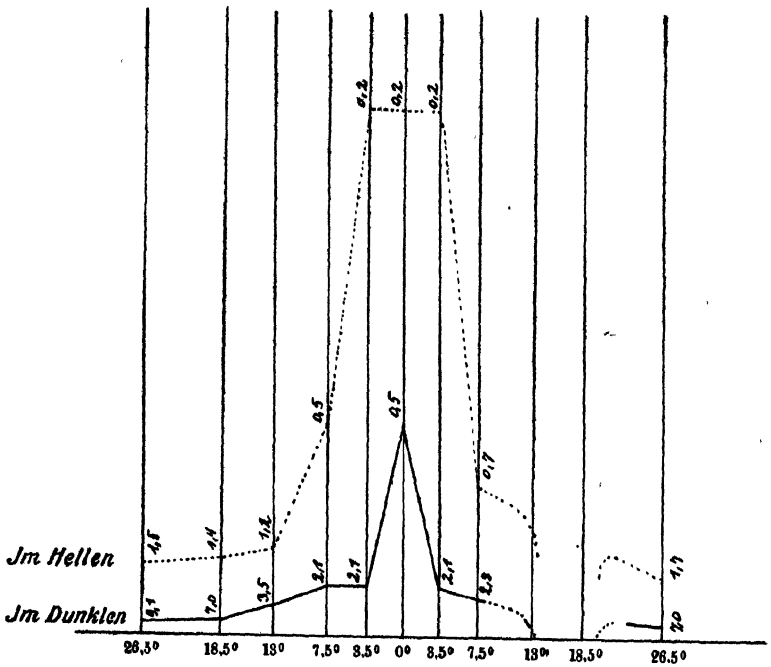


Fig. 40. Movement discrimination in light (...) and dark (—) adapted eye. Abscissæ, degrees eccentric to fixation point, temporal side of retina to left, nasal to right; ordinates, discriminable excursion in millimetres with an object 2 metres from the eye (Basler).

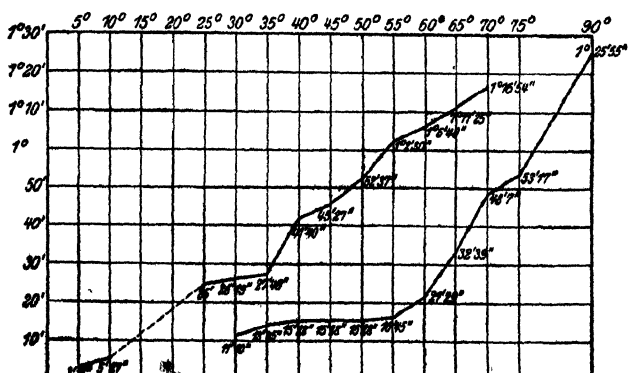


Fig. 41. Peripheral movement—(lower curve) and displacement—(upper curve) discrimination in temporal field. Abscissæ, degrees eccentric to fixation point; ordinates, discrimination angle (Ruppert).

the periphery than at the fovea, as is well shown in Fig. 41[1], where it is seen that the threshold for visual acuity is much higher than that for movement at the same spot on the retina out to the extreme periphery.

The discrimination of differences of rapidity of movement follows Weber's law for higher, but not for lower rates[2]. The apparent rate is almost twice as great if a near stationary spot is fixed as compared with following the moving object with the eye[3]. The apparent rate of movement is two or three times as great in indirect vision as in direct[4].

The periphery of the retina acts therefore as a specially differentiated organ for the perception of movement (Exner) In this region the threshold for discrimination of the distance between two luminous points is high, but the threshold for the discrimination of differences of position is low. In this region specially active local adaptation renders stationary objects soon invisible, but much increases the saliency of moving objects.

Some recent experiments by Lythgoe and Neustatter[5] show that, as might be expected, the perception of moving objects runs parallel with the perception of flicker. Movement is less easily perceived in the periphery under dark- than under light-adaptation, rapid movements being more affected than slow. The higher the illumination the farther out in the peripheral field will movement at any speed be appreciated. Movement is perceived farther out and more easily with the dark-adapted eye when a "glaring" light is shone into the eye or when the surroundings are uniformly illuminated than when they are dark.

"*Apparent*" *Movement.* There are many examples of apparent movement when the eyes move, but the objects really remain stationary. In these cases the movement of the retinal images is not compensated by a corresponding change in absolute localization Objects appear to move, for example, if the eye is slightly displaced by pressure with the finger or lid, a phenomenon specially studied by Carr[6], or by involuntary contraction of extrinsic ocular muscles

[1] Ruppert, *ibid* XLII, 409, 1908

[2] Bourdon, *op cit* p 191

[3] Von Fleischl, *Sitzungsber. d Wiener Akad.* LXXXVI, 8, 1882; Aubert, *Arch f. d. ges Physiol.* XL, 459, 1887.

[4] Exner, *ibid.* XXXVIII, 217, 1886 Cf Dressler, *Amer. Jl. of Psychol* VI, 312, 1894; Stevens, *Psychol. Rev* XV, 69, 1908, Fujita, *Zeitschr. f. Sinnesphysiol.* XLIV, 35, 1909.

[5] Not yet published.

[6] *Psychol. Rev* XIV, 160, 1907.

In the dark points of light, such as stars, waver about or even appear to move through 30° or more[1]. These apparent movements are produced by involuntary movements of the eyes, owing to defective fixation by the dark-adapted eye, and they may occur in a sleepy condition, when the eyes assume an "interestless" posture[2] and subcortical centres are less under the control of higher centres[3] "Point-wandering" may also arise from change of egocentric or absolute localization, largely due to change of attention[4].

The many forms of parallactic movement belong to apparent movements[5].

Movement after-images comprise another group of apparent movements, *e.g.* the movement in the opposite direction of stationary objects after watching a running stream or waterfall, Plateau's spiral[6], Thompson's circles[7], and stroboscopic experiments[8] Von Szili[9] has estimated the minimal and maximal velocities for the production of movement after-images, and finds that the lower threshold agrees with that for the perception of movement there is no after-image if the velocity is so great that contours are blurred. Wohlgemuth[10] obtained no after-image if the whole field of vision was in movement, but this is denied by Thalman[11], and von Szili[12] and Hunter[13] obtained a central after-image moving in the same direction as the inducing stimulus under these conditions. The velocity of the after-image has been studied by Borschke and

[1] See Exner, *Zeitschr. f Psychol* XII, 313, 1896, Charpentier, *Comptes rendus*, CII, 1155, 1462, 1886; Öhrwell, *Skand. Arch f Physiol* XXVII, 33, 50, 1912; Schilder, *Arch f d ges Psychol* XXV, 36, 1912; Carr, *Psychol Rev.* XVII, 42, 1910

[2] Hillebrand, *Jahrb f Psychiatrie u Neurol* XL, 252, 1920

[3] F B Hofmann, *op cit* p 547

[4] Dietzel, *Zeitschr f Biol* LXXX, 289, 1921; Goldstein and Riese, *Klin Wochenschr.* p. 2338, 1923, F. B Hofmann and Frubose, *Zeitschr f Biol* LXXX, 91, 1923, Carr, *Psychol Rev* XIV, 357, 1907; XV, 139, 1908; XVI, 219, 1909.

[5] See Sternbeck, *Der Sehraum auf Grund der Erfahrung*, Leipzig, 1907, Weinhold, *Arch f Ophth* LVIII, 202, 1904, LIX, 581, 1904; LXIII, 460, 1906, Best, *Klin Monatsbl f Augenheilk.* p 449, 1903; Heine, *ibid* p 369, 1902, *Arch f Ophth.* LIX, 189, 1904.

[6] See Dvořák, *Sitzungsber d Wiener Akad* LXI, 257, 1870; Kleiner, *Arch. f d. ges Physiol* XVIII, 542, 1879, Hoppe, *Die Scheinbewegungen*, Wurzburg, 1879; Exner, *Biol Zentralbl* VIII, 437, 1888, von Szili, *Zeitschr f Psychol* XXXVIII, 81, 1905, *Zeitschr f. Sinnesphysiol* XLII, 109, 1907; Kinoshita, *ibid.* XLIII, 420, 434, 1909.

[7] Thompson, *Brain*, III, 293, 1880; Cobbold, *ibid* IV, 75, 1881.

[8] Exner, *Zeitschr f Psychol* XXI, 388, 1899; von Szili, *loc. cit*; Wertheimer, *Zeitschr. f Psychol* LXI, 232, 1912.

[9] *Loc. cit*

[10] *Brit. Jl of Psychol* Monograph Suppl. I, 1911.

[11] *Amer Jl. of Psychol.* XXXII, 429, 1921.

[12] *Loc cit.*

[13] *Psychol Rev* XXII, 479, 1915

Hescheles[1], Cords and Brucke[2], Basler[3], and others. The velocity is not strictly proportional to that of the inducing stimulus. According to Wohlgemuth, the after-image is at first stronger in the periphery, but fades out quicker there, this is attributed to the different reactions of rods and cones The duration of the after-image varies with the duration of fixation and the light intensity of the inducing stimulus[4]. The intensity effect depends solely upon brightness[5], but Takei[6] found the duration longer for yellow than other colours. Many people do not see a movement after-image at all[7] If the right eye (for example) fixes the moving object, the left eye being closed, and then the left eye fixes a stationary object, the right eye being closed, a faint after-image is still seen[8], but only with parallel lines, not with Plateau's spiral, according to Hunter If opposite movements are observed with corresponding retinal points, no after-image is seen[9]. No one has confirmed Stern's[10] observation of a positive after-image, *i e* in the same direction as the inducing stimulus.

When an object moves between stationary objects, the latter often appear to move, the object appearing stationary, *e.g* movement of the moon behind clouds, of the bank of a stream, etc. This phenomenon has been attributed to simultaneous contrast by von Tschermak[11] There is, however, no true contrast, and it is better explained as a perceptual pattern phenomenon, dependent upon the focus of attention.

Movement after-images have commonly been attributed to the successive fading of ordinary after-images, the stationary object seen through the streams of after-images appearing to move in the opposite direction. There are many objections to this theory[12]. Hunter attributes them to the ordinary entoptic streaming movements, but how these act is not quite clear. The influences of sensations derived from the muscles was early invoked[13], but is as

[1] *Zeitschr f Psychol* XXVII, 387, 1901
[2] *Arch f. d ges Physiol* CXIX, 54, 1907.
[3] *Ibid* CXXVIII, 145, 1909.
[4] Kinoshita, *Zeitschr. f. Sinnesphysiol.* XLIII, 420, 434, 1909.
[5] Wohlgemuth, *loc. cit.*
[6] *Zeitschr. f Sinnesphysiol.* XLVII. 377, 1913.
[7] Plateau, *Poggendoff's Ann.* LXXX, 289, 1850, Basler, *loc. cit.*
[8] Dvořák, Exner, Kleiner, von Szili, Wohlgemuth.
[9] Exner; cf Wohlgemuth.
[10] *Zeitschr. f Psychol* VII, 321, 1894
[11] *Arch f. d. ges. Physiol* CXXII, 98, 1908
[12] See Wohlgemuth, Hunter, von Szili
[13] Classen, *Ueber das Schlussverfahren des Sehaktes*, Rostock, 1863.

unsatisfactory as an explanation of apparent movement as it is of localization or "real" movement.

These autokinetic movements are, indeed, similar to the apparent movement of the whole body after a sea voyage, etc. In both there is the feeling of movement, and yet the objects which appear to move never *do* move, and one is conscious of a directed instability rather than of a true movement. There can be no doubt that they are in some way due to interrelations of parts of the perceptual pattern taken as a whole.

Stroboscopic phenomena throw some light on this difficult problem[1]. In the ordinary stroboscopic or cinematographic observations apparently continuous movement is perceived as the result of successive exposures of pictures representing successive phases of a moving object. The gap between each exposure is bridged over. The movement is equally manifest if successive pictures are exposed alternately to the right and left eye[2]. *Per contra*, a really moving object may be seen stroboscopically stationary[3] or the movement reversed, as in watching the spokes of carriage wheels through railings[4]. Two similar cogwheels rotating in opposite directions on the same axis may look like a stationary wheel with double the number of teeth[5]. The explanation that the image of a new phase fuses with the after-image of its predecessor[6] is not satisfactory[7], for the interval may be too long for persistence of the after-image[8]. Moreover, there is a change in perceptual pattern which is not explained by a mere fusion of this nature. Indeed, many of the phases can be dropped out without the gap being noticed[9], though it is noticed if special attention is directed to it, and if care is taken not to follow the movement with the eyes but to keep up accurate fixation[10] The phenomenon, therefore, appears to be an example of *erganzende Gestaltproduktion*[11].

[1] See Helmholtz, *Physiol. Optik*, 1st ed p 350, 2nd ed p 494; Marbe, *Philos. Studien*, XIV, 376, 1898

[2] Exner, *Arch f d ges Physiol* XI, 403, 581, 1875

[3] See Burmester, *Sitzungsber. d. Bayr. Akad.* p 141, 1914.

[4] Roget, *Phil Trans* p 131, 1825, Plateau, *Poggendorff's Ann* XX, 304, 543, 1829.

[5] Faraday, *Jl of the Royal Institution*, 1831

[6] O Fischer, *Philos Studien*, III, 128, 1886

[7] Linke, *ibid* III, 393, 1908; *Zeitschr f Psychol.* XLVII, 203, 1908, *Arch f d. ges. Psychol.* XXXIII, 261, 1915; *Grundfragen der Wahrnehmungslehre* Munchen, 1918; Hillebrand, *Zeitschr f Psychol.* LXXXIX, 209; XC, 1, 1922.

[8] Bourdon, *op cit.* p 196; Linke, *Psychol Studien*, III, 472, 1908.

[9] Grutzner, *Arch f d. ges. Physiol.* LV, 508, 1904

[10] Durr, *Philos. Studien*, XV, 501, 1900.

[11] *Vide* p 50.

The crucial factor in stroboscopic apparent movement is that there shall be no obvious gap between two successive phases: this is known as the *stroboscopic elementary phenomenon*[1] or the *β-movement*[2]. It can be studied in its simplest form by determining the time and space relations between two instantaneous light stimuli which produce the impression of movement[3]. Wertheimer showed that movements of the eye are not necessary, and that the impression of movement is not due to rise and fall of the sensory responses from the stimulated retinal points. If two vertical narrow light streaks are exposed for 0·05 sec. at an interval of 0·03 sec. they are seen as though simultaneous (*Sim-Stadium*); at an interval of 0·2 sec. they appear successive but stationary. At intermediate intervals there is apparent movement, which may be a complete movement from the first to the second (*Opt-Stadium*), or, with longer intervals than the optimum, either dual partial movements of each light or single movement of the first light Wertheimer hypothecates a pure visual perception of movement without vision of a moving object ("the pure *φ*-phenomenon"), an hypothesis which most people will agree with Linke and Hillebrand is difficult to accept.

If the first stimulus is a white streak on a black background and the second a black streak on a white background, the white streak appears to rush into the black streak[4] This experiment suggests that the form and meaning of the perceptual pattern plays a large part in determining the type of sensory response. Similarly, if a picture of a small circle in contact with a large semicircle at one end of the diameter is succeeded by a picture of the small circle in contact with the other end of the diameter, the circle does not appear stroboscopically to move across the diameter, but to roll round the semicircle, and that whether it be in contact with the inner or the outer side of the semicircle[5]

If three points of light in a straight line are successively exposed instantaneously the distance between them appears less if the time interval is diminished[6] the same applies to tactile and auditory

[1] Hillebrand, *loc cit.*

[2] Kenkel, *Zeitschr. f Psychol.* LXVII. 358, 1913.

[3] Exner, *Arch f d ges Physiol* XI, 403, 581, 1875, Bourdon, *op. cit* p. 193; Linke, *Psychol Studien*, III, 393, 1908; Schumann, *Bericht u. d V Kongress f exp Psychol* p 179, 1912, Wertheimer, *Zeitschr f Psychol* LXI, 161, 1912.

[4] Linke, *loc. cit.*

[5] Linke, *loc. cit.*, Koffka, *Psychol Forsch.* II, 148, 1922; Wittmann, *ibid.* II, 154, 1922.

[6] Benussi, *Psychologie der Zeitauffassung*, p 285, Heidelberg, 1913; Gelb, *Bericht der VI Kongress f. exp. Psychol.* p. 36, 1914.

stimuli[1]. If two pairs of points of light are arranged to form angles of a square and the pairs are successively exposed instantaneously at an interval of more than one second, the distance between them looks the same as for continuous exposure. If the interval is diminished, the distance between them appears diminished up to an optimum which coincides with that of optimum stroboscopic movement[2]

The influence of intensity of stimulus, time relations, eye movements, etc , on stroboscopic movement have been investigated by Korte[3] and Hillebrand[4]

Anorthoscopic illusions, produced by the changes in a moving figure as seen through a stationary or moving slit, are nearly allied to stroboscopic movements[5] An object appears shortened in the direction of the movement, a circle looking like an ellipse, etc The phenomenon is due to the displacement of the image relative to the edge of the slit[6] If the figure moves behind a stationary slit, distortions and alterations in the saliency of different parts may occur In these much depends upon attention to the moving figure and not to the stationary slit[7].

There are other apparent movements of great theoretical importance The apparent movement of the principal lines of geometrical-optical illusions, *e g.* Zollner's and Muller-Lyer's, when the subsidiary lines are added, can be studied by Wundt's projection method[8] or by Buhler's[9] method, in which the chief lines are ruled on one side and the subsidiary lines on the other side of transparent paper. The movement is known as the S-movement[10] or α-movement[11] More complicated combinations have been studied by Benussi[12] There is an appreciable latent period—on the average 0·346 sec [13] Wingender

[1] Kohler, *Psychol Forsch.* III, 401, 1923, Scholz, *ibid.* V, 219, 1924.
[2] Kohler, Scholz
[3] *Zeitschr f. Psychol* LXXII, 193, 1915
[4] *Ibid* LXXXIX, 209, XC, 1, 1922
[5] Plateau, *Poggendorff's Ann* XXXVII, 464, 1836, Zollner, *ibid.* CXVII, 477, 1862; Gertz, *Skand Arch f Physiol* X, 53, 1899, Stewart, *Amer. Jl of Psychol* XI, 340, 1900, Rothschild, *Zeitschr f Psychol.* XC, 137, 1920, Hecht, *ibid* XCIV, 153, 1924
[6] Linke, *Psychol Studien*, III, 428, 1908
[7] F. B Hofmann, Hecht
[8] *Psychol Studien*, II, 493, 1907.
[9] *Die Gestaltwahrnehmungen*, Stuttgart, 1913
[10] Benussi, *Arch f d. ges Psychol* XXIV, 31, 1912
[11] Kenkel, *Zeitschr f Psychol.* LXVII, 358, 1913
[12] *Arch f. d ges Psychol* XXXVII, 233, 1918
[13] Wingender, *Zeitschr f. Psychol.* LXXXII, 21, 1919.

also estimated the threshold of alternation of the coming and going of the subsidiary lines consistent with absence of apparent movement of the chief lines, and found the average 0·263 sec. If this is compared with Marbe's critical period for the fusion of successive light stimuli, 0·02 to 0·1 sec, or Wertheimer's *Sim-Stadium* of 0·03 sec., the difference shows a delay, due probably to backstroke processes from the upper visual centres, a view which is supported by the fact that the delay increases with the complication of the figures[1]

Another peculiar apparent movement was described by Bethe[2]. When one looks at a large uniform surface by a momentary flash of light it seems to spread from the centre to the periphery and then shrink towards the centre again Attentive fixation diminishes the movement near the fixation point. The same phenomenon is observed if a figure is exposed for 0·111 to 0·22 sec according to the intensity of the light the figure appears to spread and then shrink[3]. Kenkel has called these movements the γ-movement

A somewhat similar apparent movement is the eidotropic movement of G. E Muller[4]. This seems to be fairly definitely due to the completion of a "pregnant" or "good" perceptual pattern[5] If a circle is indicated by twelve points, of which one is slightly out of place, the displaced portion appears to move into its proper place on momentary illumination

Another apparent movement is the δ-movement of Korte[6] If one exposes two lights successively, the first being more intense than the second, on fixing between the lights and paying attention to the stronger there is an apparent movement from the second to the first and back again.

Exner[7] observed that if the illumination of a surface was brightest in the centre, then, on indirect fixation, diminution of illumination causes an apparent movement towards the centre, increase towards the periphery. Stern[8] stated that mere momentary stimulation of the periphery of the retina by a spot of light causes the impression of movement

[1] Kenkel, *Zeitschr f Psychol* LXVII, 358, 1913, see also Bates, *Amer Jl of Psychol.* XXXIV, 46, 1923

[2] *Arch f d ges. Physiol* CXXI, 1, 1907.

[3] Lindemann, *Psychol Forsch.* II, 5, 1922

[4] *Komplextheorie und Gestalttheorie*, p 54, Gottingen, 1923.

[5] *Vide* p 51

[6] *Zeitschr. f. Psychol.* LXXII, 205, 1915

[7] *Arch. f. Ophth.* XXXII, 233, 1886.

[8] *Zeitschr. f Psychol.* VII, 358, 1894

Apparent rest of actually moving objects may occur. If a disc is divided into two sectors of different colour and is watched monotonously whilst rotating, attention becomes fixed on one, which thus becomes the more salient, and it appears to rotate over a stationary field of the colour of the other[1].

All experience is experience of change, which in itself is a form of movement. Movement being thus so fundamental a factor in experience, it is not surprising that it pervades mental life from the simplest to the highest processes. We may therefore expect to find it manifested in the least differentiated as in the most differentiated perceptual patterns presented to the animal In the primitive dyscritic perceptual pattern we must accept the emergence of the perception of movement by the bridging of the gaps between local signs, a bridging which we can, at present at any rate, merely accept as an axiom. We shall find it more fruitful to confine ourselves to eliciting the laws which govern the perception of movement than to attempt to discover the cause. But we may rest assured that it is a biological necessity of the most vital kind, and therefore subserved by the most primitive neural apparatus That apparatus persists as the hypothetical formative zone in the lower sensory centres, but as more and more differentiation occurs, that zone comes more and more under the dominance of higher centres We must not regard what are the simplest conditions for the perception of movement in man as holding the key to the problem. Such conditions would be of no biological significance to lower animals, and would probably be accompanied by little or no response of any kind. A momentary flash of light would probably not interest a cat, but a mouse stirring in the periphery of its field of vision would at once arrest its attention Yet the arousing of a percept of movement by a flash of light in the periphery of the field of vision of a man is the sublimated expression of the all-important appreciation of moving objects by lower animals It works through the primitive formative zone which man has inherited—vastly elaborated—from his animal ancestors This zone has so come under the dominance of the minutely discriminative epicritic and syncritic mechanisms which have been superadded to it that its primitive workings and functions have become buried in obscurity: hence the predominant part so plainly revealed in the examples which have been described of the exact focus of attention

[1] Wittmann, *Ueber das Sehen von Scheinbewegungen und Scheinkorpern*, p. 30, Leipzig, 1921; cf. Pikler, *Sinnesphysiologische Untersuchungen*, p. 377, Leipzig, 1917.

to details of the perceptual pattern and the varied meanings which can be read into those patterns by man.

The importance of these higher factors in such sublimated perceptions of movement as have been described is still more clearly revealed in other examples. Thus, as Bourdon has pointed out[1], the illusion of movement is seldom seen in objects which are ordinarily immobile, *e.g.* rocks, houses. Moreover, there is a well-marked tendency to rectify unusual appearances. Thus, if letters, words, etc., are seen upside down with the tachistoscope they can often be seen to right themselves[2]. Ambiguous drawings in perspective may suddenly change their appearance and meaning, *e.g.* the flight of steps or overhanging cornice figure. Carr and Hardy[3] have shown that if two lights are set one above the other in the dark room and one is set in rhythmic movement to right and left, illusions occur which depend upon the interpretation of the observer. If the upper moves and the system is regarded as a pendulum, the lower appears to move, if as a metronome, the upper appears stationary and the lower moving, and so on. Inversion of movement was long ago described by Sinsteden[4] in the wings of windmills, and is well seen in the cups of anemometers The more meanings that can be read into a perceptual pattern the more illusions of movement and such like phenomena are likely to be experienced.

[1] *Op cit* p 201
[2] Lewin, *Psychol Forsch* IV, 210, 1923
[3] *Psychol Rev* XXVII, 24, 1920
[4] *Poggendorff's Ann* CXI, 336, 1860

CHAPTER X

THE DUAL MECHANISM OF VISION

1. Dyscritic and Epicritic Vision

The universality of the dual mechanism in the extero-ceptive sensations would naturally lead one to seek for the evidence of the same duality in vision It must, however, be remembered that the superposition of an epicritic upon a dyscritic mechanism not only leads to the subordination of the latter, but also to alterations in its characters Before proceeding to consider vision it will be well to review the changes which occur in the protopathic or dyscritic tactile sense, the one which has been most exhaustively studied.

Protopathic touch is characterized by the intensity of the reaction, though accompanied by vagueness and crudity, absence of exact localization and discrimination, radiation to distant parts, and pronounced affective tone, usually unpleasant. The response is of the all-or-none variety, *i.e.* any stimulus which surpasses the threshold produces the maximum effect—there is no gradation Any reflex motor response is of the same ungraded nature, *i e* it is a mass-reflex[1]. When, after a division of a sensory nerve, epicritic sensibility returns, protopathic sensibility undergoes definite modifications.

"Some of its elements persist and combine with elements of the epicritic stage to form features of normal cutaneous sensibility Thus, the cold and heat of the protopathic stage blend with the modes of temperature sensibility proper to the epicritic stage, and form the graded series of temperature sensations which we are normally able to discriminate The crude touch of the protopathic system blends with the more delicate epicritic sensibility of this kind, while protopathic pain, with its peculiarly uncomfortable rather than acute quality, forms a much larger element in the normal sensibility to pain"[2]

Certain characters are suppressed or inhibited, especially radiation and distant reference. but these spatial features of protopathic sensibility do not disappear entirely, but persist in a latent form ready to come again into consciousness if the appropriate conditions are present. It is important to note that, though this suppression becomes manifest "through the changes in consciousness we call sensations, they are nevertheless the expression of purely physio-

[1] Head and Riddoch, *Brain*, xl, 188, 1915; Riddoch, *ibid.* xl, 264, 1918.
[2] Rivers, *Instinct and the Unconscious*, p 24, Cambridge, 1920.

logical processes in the peripheral nervous system."[1] Similarly, the mass reflex occurring in complete transverse lesions of the spinal cord is suppressed in the normal subject.

Head and Holmes[2] have adduced strong evidence, well supported by other clinical observers and by physiologists, that the relation between the cerebral cortex and the optic thalamus is very similar to that existing between epicritic and protopathic sensibility.

"When by injury, disease, or operative procedure, the cortex cerebri has been put out of action, stimulation of the skin produces sensations characterized by a peculiar quality such as would be produced by over-weight of the affective aspect of sensation, very similar to that shown by protopathic sensibility Moreover, there is an absence of objective character very similar to that of this form of sensibility When the cortex is in action the affective over-response of the thalamus is largely suppressed under ordinary conditions, but the process of suppression does not come out so strongly as in the case of the peripheral nervous system because some of the primitive features which most need suppression have already suffered this fate Thus, removal of cortical activity does not produce radiation and reference of localization because the suppression of these characters is still being maintained at the periphery"[3]

In this suppression of protopathic characters "we are not dealing with the suppression of individual experience, but with the suppression in the race of experience belonging to the earlier phases of its history"[4], and it is probable that the racial suppression is repeated in every individual as part of the recapitulation of the racial history. "*Such elements as are serviceable are utilized when the later and higher forms of sensibility came into existence . . It is only those features of early sensibility which are incompatible with later developments which are suppressed*"[5]

Similarly, there is reason to think that the all-or-none principle becomes modified, though as Keith Lucas and Adrian[6] have shown, it is probably a universal law of the actual transmission of the nervous impulse in nerve fibres. Whereas the typical protopathic response is of the all-or-none character, the epicritic is graded and within wide normal limits follows Fechner's law that the sensation is proportional to the logarithm of the stimulus Rivers has shown that instincts can be profitably classified into protopathic or epicritic according to this criterion, but it is probable that primitive instincts are all primarily protopathic and that the epicritic differentiation is

[1] *Ibid* p 27
[2] *Brain*, xxxiv, 102, 1911.
[3] Rivers, *op cit* pp 27–8
[4] *Ibid* p. 29
[5] *Ibid* pp 31–2.
[6] *The Conduction of the Nervous Impulse*, London, 1917.

rather of the nature of a response due to intelligence. Hence the difficulty experienced in drawing a sharp line between instinct and intelligence.

One of the best supported hypotheses relating to vision is the so-called duplicity theory[1]. According to it, scotopic vision, or vision under low intensities of illumination by the dark-adapted eye, is carried out by means of the rods, and photopic vision, or vision under higher intensities of illumination by the light-adapted eye, is mediated by the cones. It would seem at first sight that we have here, ready to hand, the duality which is demanded by the dyscritic and epicritic theory. And, indeed, there are many facts which strongly support this view[2]. Scotopic vision shows many of the characteristics of protopathic sensibility, especially in its vagueness and crudity, its undifferentiated character, and lack of exact localization and discrimination. Photopic vision shows many of the characteristics of epicritic sensibility, especially in its meticulous exactitude of localization and discrimination—the highest, indeed, which has been acquired by any form of sensibility[3]—and in its greater differentiation qualitatively in the perception of colours.

On the other hand, special features of protopathic sensation are its "all-or-none" reaction and its tendency to initiate a "mass reflex" The dyscritic light-sense, so far as it has been investigated at present, does not exhibit either of these characteristics. But if we regard it in its primitive manifestations it is more than probable that it then exhibited both. In higher animals it has become differentiated into the epicritic phases, but still persists in modified form underlying the epicritic manifestations The primitive dyscritic light-sense we must regard as vague, diffuse, and not accurately localized If it persisted in this form unmodified, when the light-sense became more definitely projicient it would interfere with exact discrimination. The suppression of these features, however, has become complete only in the macula, the area of distinct vision Further, the projicient senses are concerned with the initiation of anticipatory or precurrent reactions. It is the contact extero-ceptors which are specially concerned in consummatory reactions[4]. Anything in the nature of a mass reflex action to projicient sense stimulation would frustrate the object of this adaptive mechanism. hence the modification of such

[1] See Parsons, *Introduction to the Study of Colour Vision*, p. 215, 1924.
[2] See Parsons, *Trans Ophthal. Soc* XLI, 97, 1921.
[3] Cf. Parsons, *Nature*, CX, 824, 1922.
[4] Sherrington, *op cit.* p. 329.

a response from the dyscritic light-sense. Here projicience implies anticipation, and anticipation demands positive phototropism—a turning of the eyes towards the light. (We may suspect that in its most primitive form the protopathic light-sense elicited much more definite affective tone). As already stated, "such elements (of protopathic sensation) as are serviceable are utilized when the later and higher forms of sensibility come into existence ... It is only those features of early sensibility which are incompatible with later developments which are suppressed."[1] In psychological phraseology, just as in the interference of antagonistic reflexes which both use a common path, incopresentability leads to adaptive suppression.

But if dyscritic vision has lost some of the characteristics of primitive protopathic sensibility it appears to have gained some epicritic characters in its manifestations in normal man. Thus, it shows gradation, exemplified in the luminosity curve of scotopic vision. Moreover, it is not improbable that in certain conditions it can show some of the qualitative differentiations of epicritic vision under strong intensities of excitation There is practically no evidence as to what happens to the scotopic mechanism when the intensities of stimulation are such as to educe photopic vision. If the stimulus is increased above the chromatic threshold, what happens with regard to the scotopic mechanism? Is it inhibited, as the dyscritic optic thalamus is inhibited by the cortex, which is predominantly epicritic in function? Is it short-circuited—perhaps owing to the complete bleaching of the visual purple—or does it contribute to the brightness element of photopic vision, or does it acquire all the characteristics of photopic vision, contributing not only to the brightness, but also to the other qualitative—chromatic—effects? Now, one of the greatest difficulties, hitherto unsurmounted, of the duplicity theory is the behaviour of the periphery of the field of vision. There is overwhelming proof, derived from peripheral luminosity curves, minimal field and minimal time luminosity curves[2], that peripheral vision behaves in exactly the same manner as central vision, but with diminished sensitivity. Greater stimuli are required to produce equivalent responses, but if the stimuli are sufficiently great, the differences disappear, including even the qualitative differences, so that the fields of vision for colours extend to the extreme periphery[3]. Anatomically, the peripheral retinal neuro-epithelium consists almost

[1] Rivers, *loc. cit.* pp. 31–2
[2] See Parsons, *Colour Vision*, pp. 76–8.
[3] *Ibid* p. 73.

entirely of rods—the scotopic or dyscritic mechanism. It seems probable, therefore, that under high intensities of excitation in normal man, the dyscritic mechanism is capable of giving the same chromatic responses as the cones, or essentially epicritic mechanism.

In favour of this view is the fact that Piéron[1], who does not accept the Ferry-Porter law[2], $D = \frac{1}{k \log I}$, but supports Charpentier's law, $D = \frac{k}{\sqrt[n]{I}}$, where $n = 4$ for the cones and 7 for the rods, finds that with intermediate wave-lengths, outside the fovea, the times of persistence (D), which correspond to those of the rods (at low intensities of stimulation), "progressively approximate to those which characterize the cones"

Cases of total colour blindness are particularly interesting in this connection. It has long been a disputed point as to whether all such cases have a central scotoma or not, and good observers have held the view that there are at least two forms of monochromatic vision. In most of the cases the luminosity curve is that of the normal scotopic luminosity curve, with its maximum at about 530$\mu\mu$, at what to the normal observer is green, but unlike the normal it persists unchanged in form with higher intensities of excitation, showing no shift of the maximum towards the yellow as in the normal photopic luminosity curve. This fact, combined with the central scotoma and other features, has led to the conclusion that the condition is one of pure rod vision, and it may, therefore, be regarded as a reversion to the primitive—dyscritic—type of vision. If there are cases without central scotoma, and if, as has been asserted, some cases show the normal photopic luminosity curve, with its maximum in the yellow region of the spectrum, these may be regarded as cases of pathological epicritic sensibility in which qualitative differentiæ of colour are in abeyance. In them epicritic vision shows an abnormal approximation to dyscritic vision, but fails to reproduce all its typical primitive characteristics. In any case, most observers are agreed that the facts of monochromatic vision are inconsistent with the view that it is a simple reduction form of trichromatic vision.

One outstanding feature of vision in the lower vertebrates is the appreciation of movement. This is an adaptation of the highest biological significance, since upon a rapid apprehension of movement

[1] *Arch. néerland. de Physiol* VII, 199, 1922

[2] See Parsons, *Colour Vision*, p 112.

in enemy or prey may depend the preservation of life. It is, therefore, to be expected that this characteristic will be bound up with the most primitive type of visual sensibility. There is no doubt that great acuity in the perception of moving objects is a prominent characteristic of the panoramic vision of lower mammals, both Herbivora and Carnivora—probably more in the former than in the latter. There can also be little doubt that in these animals, although vision has already undergone some differentiation and has acquired some epicritic characters, it is essentially dyscritic, even if not of the most primitive type. If in man the rods are the organs of dyscritic vision, we should expect them to exhibit those physiological attributes which, when synthesized with other attributes, permit of the perception of movement. And it is, indeed, found that perception of movement is most acute when the image falls upon peripheral parts of the retina. This is very strikingly demonstrated by the persistence of flicker in the periphery when it has already ceased for the same rate of alternation of stimuli at the centre[1]. We might also expect that in recovery from lesions which abolish peripheral parts of the field of vision the appreciation of movements of objects would be restored before the appreciation of shape or colour. Wilfred Harris[2] in 1897 pointed out that this was so in cases of transient hemianopia following epileptic attacks, and Riddoch[3] has brought forward still more conclusive evidence derived from war injuries of the occipital lobes.

The conclusion which Riddoch draws, which is comparable with Head's tracts of tactile discrimination, *viz.* that a sensation of movement should be regarded as a primitive function of the peripheral retina, cannot be admitted. Like tactile discrimination, the appreciation of movement is a perception, dependent upon change of local sign, and, therefore, involves a synthesis of such a nature that the peripheral mechanism alone cannot effect. Striking evidence of the part played by the cortex in the perception of movement is afforded by a case of bilateral lesions of the occipital lobes reported by Pötzl[4]. If a strong source of light was moved slowly or rapidly before the eyes the patient did not seem to apperceive the movement of the object, but interpreted it as several separate lights.

[1] See Parsons, *Colour Vision*, p. 108.

[2] *Brain*, XX, 307, 1897.

[3] *Ibid.* XL, 15, 1917.

[4] *Wiener klin. Wochenschr.* XXIV, 518, 1911, cited by Wertheimer, *Zeitschr. f. Psychol.* LXI, 247, 1912.

The extreme sensitivity to movement is due to the low stimulus threshold of the scotopic mechanism and its capacity for summation whereby subliminal stimuli surpass the threshold if they are reinforced numerically, whether by increase in the area excited or by successive excitation of neighbouring points. In addition to these factors, it is necessary that the response should be of short duration, dying away rapidly under continued excitation. This is, indeed, a very well-marked feature of stimulation of the peripheral parts of the retina. It is usually attributed to rapid fatigue, but it is very doubtful in my mind whether fatigue, properly so-called, occurs in the retina at all. It is much more likely to be due to a form of induction, which produces a refractory period[1]. It is very similar to the inhibition of a visual image by a competing image in the same visual field, which occurs the more readily when the first image has acted for some time than when first perceived[2]. The response to a stimulus moving across the field of vision is very similar to facilitation of successive allied reflexes, such as the act of deglutition, an object moving along the skin, or a parasite travelling across the receptive field of the scratch reflex. This is a form of *Bahnung* which Sherrington has aptly termed "immediate induction" He[3] has shown that in such reflexes the threshold of each succeeding reflex in lowered by the excitation just preceding its own.

"A subliminal stimulus applied at a point *A* will render a subliminal stimulus applied at a point *B* near *A* supraliminal if the second stimulus follow within a short time, *e.g* 500σ But the phenomenon is characteristically and simply illustrated by the difference between the potency as a stimulus of the edge of a card say six inches long, pressed simultaneously its whole length against the receptive skin field, say for five seconds, and on the other hand lightly drawing one corner of the card along the same line in the skin field also for five seconds The former application simply evokes a reflex of a few beats, which then dies out The latter evokes a vigorous reflex that continues and outlasts the application of the stimulus"

The extreme importance of the visual perception of movement is only equalled by the importance of visual perception to the moving animal. It may be said that, with a few exceptions, for the most part easily explained, visual organs occur only in those animals which are capable of movement I have already dwelt on the fundamental relationship between vision and the motor mechanism for orientation and equilibrium. Its relation to active movements is equally important, but usually entails activities at higher neural levels. But

[1] On the perception of movement, see Wertheimer, *loc. cit.* p. 161.
[2] MacDougall, *Mind*, x, 1901.
[3] Sherrington, *op cit.* p. 184.

these activities must necessarily conform to the lower activities which subserve them, and among these are the reactions in the retina. Since most animals, both vertebrates and invertebrates, move and have visual organs, the visual sensibility must on our theory be primarily dyscritic. That dyscritic vision has undergone diverse and divergent modes of differentiation in relation to movements is only an example of what a more minute analysis proves conclusively for other manifestations. We have only to consider the variety of rate of movement in different animals to realize the importance of this aspect[1].

The all-or-none reaction of the most primitive form of dyscritic sensibility negatives not only gradation, except in so far as this can be accounted for by recruitment[2] but also adaptation in the sense in which this term is used in physiological optics. Yet, being the most primitive form of sensation, it must possess in high degree the potentialities of adaptation in the biological sense of the term, and hence its underlying mechanism must be characterized by that potential or static plasticity to which reference has already been made. Of the two factors in the dual mechanism of vision in man it is beyond doubt that the rod apparatus is the one which, *par excellence*, exhibits physiological adaptation: it is, indeed, this feature in particular which fits it to perform the functions of scotopic vision. The cone mechanism, on the other hand, gives less evidence of physiological adaptation[3].

Dyscritic vision in man has therefore become endowed, not only with some measure of gradability, but also with a very high degree of adaptation, whereby its sensitivity to feeble stimuli is greatly increased and the threshold stimulus value greatly lowered. The sensitivity of the dark-adapted eye is many thousand times greater than that of the light-adapted eye. It must, however, be borne in mind that our knowledge of the conscious response to primitive dyscritic stimulation is entirely a matter of conjecture and inference, apart from the experience derived from a pathological state in man, *viz.* the regeneration of a cutaneous nerve. And, seeing that the anatomical evidence so strongly supports the view that sensation is purely dyscritic in all vertebrates below the Amphibia (and probably in most of them), it may be regarded as certain that dyscritic sensation in these animals is, as in man, subject to some gradation

[1] *Vide* p. 157.
[2] *Vide infra*
[3] Parsons, *Colour Vision*, Sec. III.

and probably a high degree of physiological adaptation. When we consider the habits of these animals such a conclusion seems inevitable.

Dyscritic vision shows scarcely any trace of gradation in what is commonly described as "form vision." The most primitive light sense must necessarily introduce some distinction between the excited and the non-excited fields, and this is the germ of the distinction of contours. At the lowest level it is a distinction between stimulation of a receptive organ, *e.g.* an ocellus, as a whole, and the absence of all luminous response from surrounding parts; but at quite low levels we find visual organs adapted to discriminate the direction from which the light comes, giving rise to the germ of projicience. The latter stage involves the distinction between excited and non-excited areas of the photo-receptive field. So far as human consciousness is any guide, there is a vast difference psychologically between these two conditions, exemplified by the difference between the blind spot and an unstimulated area of retina. Only the second condition can be properly associated with contour discrimination.

Doubtless, in primitive stages contour discrimination was very vague, comparable probably to its vagueness in the extreme periphery of the field of vision in man. Yet vague as it was, it marked a great stride in advance, *viz.* the transition from sensory stimulation capable of originating only the crudest dyscritic responses to projicient sensations capable of directing motor responses. Only the latter seems worthy of being termed "vision." For the essence of vision is the discrimination of contours, whether they be contours of light and shade, or contours of differently coloured or toned areas. Goethe, in 1810, realized this fact when he wrote: "The eye sees no form, inasmuch as light, shade and colour together constitute that which to our vision distinguishes object from object, and the parts of an object from each other." And, if we accept Hering's broad use of the word colour to include both toned and untoned colours, we may agree with Clerk-Maxwell's statement (1871) that "all vision is colour vision, for it is only by observing differences of colour that we distinguish the forms of objects."

2. "Form" and Contour: Colour Vision

Visual acuity, in ordinary ophthalmological terminology, is the power of distinguishing the "forms" of objects, and is measured clinically by means of Snellen's test types. The discrimination of shapes, however, depends upon very complex physical and physio-

logical conditions. Fundamentally, it is held to depend upon the capacity to discriminate two points of light as disparate, but this obviously depends primarily upon the capacity to perceive a single point of light. The minimum visible point of light depends upon the intensity and quality of the light, the dioptric apparatus of the eye and its errors, the neuro-epithelium of the retina and its connections, the adaptation of the retina, spatial and temporal induction (*i.e.* simultaneous and successive contrast), and probably other factors[1].

For the macular rod-free area of the retina Riccò[2] found that the total quantity of light, *i.e* the product of the area stimulated into the light intensity must attain a certain value, and it makes no difference how the intensity and the area (up to a visual angle of 40–50 min.) are varied so long as the product is constant. Asher[3] found that for the range of light intensities used by him the apparent size of a visual angle of 2–3 min. depends entirely upon the quantity of light. By varying the area and the intensity of the light smaller areas may be made to appear larger than really larger areas The so-called "magnitudes" of the stars depends upon this fact Similarly, with regard to colours, Charpentier[4] showed that the chromatic threshold also depends upon the area stimulated As might be expected for the more highly differentiated colour sense, the law associating area stimulated with intensity is not so simple as for white light Further, as Abney[5] has pointed out, as the intensity of the light is diminished gradually to extinction of the sensation, a coloured square or disc becomes first an ill-defined fuzzy patch of grey and appears finally to depart almost as a point. It appears to me that these liminal responses reproduce the characteristics of primitive chaotic sensations, in which size, colour, and other qualities are but little differentiated, *i.e.* the dyscritic sensation.

Loeser[6] has confirmed Riccò's law for foveal vision, but Piper[7], Loeser[8], Henius[9], and Fujita[10] have shown that it does not hold for the peripheral parts of the retina[11].

[1] See Parsons, *Royal Lond Ophth Hosp Rep* XVIII, 239, 1912, XIX, 104, 1913, *Colour Vision*, pp 130 sqq Cambridge, 1924.

[2] *Ann di Ottalm.* VI, 1877.

[3] *Zeitschr. f Biol* XXV, 394, 1897.

[4] *La Lumière et les Couleurs*, pp. 213, 238, Paris, 1888

[5] *Researches in Colour Vision*, p 177, London, 1913

[6] *Hirschberg's Festschrift*, 1905, Feilchenfeld and Loeser, *Arch f Ophth* LX, 97, 1905

[7] *Zeitschr f Psychol u Physiol d Sinnesorg.* XXXII, 98, 1904

[8] *Loc cit.*

[9] *Zeitschr. f. Sinnesphysiol* XLIII, 99, 1908.

[10] *Ibid* XLIII, 243, 1908.

[11] See Parsons, *Colour Vision*, p 136

The "minimum separabile" for the visual discrimination of two luminous points has long exercised the minds of astronomers[1], and a vast literature has accumulated upon the subject[2]. For clinical purposes a minimum visual angle of 1 min. has been adopted for Snellen's and other test-types; but this value is considerably above that obtained for normal eyes.

Volkmann[3], in 1863, showed that the visual acuity for contours was much lower than one minute. Wulfing[4], by the vernier method, obtained values from 10 to 12 sec., and Hering[5] 10 sec., Stratton[6] 7–9 sec., Bryan and Baker[7] 8–12 sec., and Hartridge[8] 8·5 sec Best[9], using the separation line between a black and white surface, obtained a value of 13 sec. Bourdon[10] obtained 5 sec. binocularly. More recently, Andersen and Weymouth[11] have obtained as low a value as 2 sec. binocularly. They attribute an important function to movement in the binocular discrimination of depth. As already mentioned, they find the threshold extremely low, corresponding to retinal displacements far less than one cone diameter. They think that this can be explained by visual stimuli giving rise to a complex percept of position, which they call the retinal mean local sign At least three factors contribute to this: (1) the mutual effect of adjacent retinal elements in either retina, (2) the averaging of the successive stimulus patterns on each retinal mosaic caused by the constant slight eye movements, (3) the combining of the two simultaneous stimulus patterns presented to the two eyes They do not, I think, take sufficient account of induction, whereby the irregularities produced by the irregularly distributed cones are smoothed down by inhibition of the unstimulated or relatively unstimulated neighbouring cones, a function comparable to reciprocal innervation Moreover, as Sherrington has pointed out, this facilitation of visual acuity is an example of immediate induction[12] He has found that

[1] See Parsons, *Royal Lond Ophth Hosp Rep* XIX, 264, 274, 376, 1913

[2] See Helmholtz, *Physiol Optik*, Zoth in *Nagel's Handb d Physiol d Menschen*, III, Braunschweig, 1904, F B Hofmann, *Die Lehre von Raumsinn des Auges*, Berlin, 1920, Hartridge, *Jl of Physiol* LII, 176, 1918, *Phil Mag.* XLVI, 49, 1923

[3] *Physiol Untersuch im Gebiete der Optik*, Leipzig, 1863.

[4] *Zeitschr f Biol* XXIX, 189, 1892.

[5] *Ber d Sachs Ges d Wiss* LI, 16, 1899.

[6] *Psychol Rev* VII, 429, 1900, IX, 433, 1902

[7] *Proc Opt Convention*, p 252, 1912

[8] *Phil Mag.* XLVI, 57, 1923

[9] *Arch. f. Ophth* LI, 453, 1900.

[10] *Op. cit.* p. 145.

[11] *Amer. Jl. of Physiol* LXIV, 561, 1923

[12] *Vide* p. 180.

osmic-stained nerve fibres of 4μ diameter are visible to the naked eye. Similarly, just as a moving point in the peripheral field is more visible than a line of similar length, direction and duration, so a row of dots, individually below the minimum visible and too far apart for their retinal images to overlap by diffusion, becomes visible. Hartridge also says[1],

"Contours of all kinds are met with to a very great extent in ordinary visual observation, and it would appear that the important phenomenon of simultaneous contrast has been specially developed in order that the appreciation of contours should be facilitated. The narrowness of a contour, of which the eye can perceive the existence, is therefore a matter of far greater importance in vision than the fineness of a grating or the closeness of two double stars that can just be resolved."

It is noteworthy that physicists have discovered empirically this, the most highly differentiated discriminative capacity of any sensory organ, and have applied it by means of the vernier to physical measurements[2].

It is found that the discrimination of minimum displacement for the appreciation of movement is of the same order of magnitude as that for contour Thus, Volkmann obtained for the former 7–18 sec., Stern[3] 15 sec., Basler[4] 20 sec., and Stratton[5] 6·8–8·8 sec.

Visual acuity discrimination (for letters, etc.) diminishes rapidly in passing from the fovea to the periphery (Fig. 39); from 1 to about $\frac{1}{2}$ at 2·5°, to $\frac{1}{3}$ at 5°, to $\frac{1}{5}$ at 10°, to $\frac{1}{10}$ at 20°. Bourdon[6] found that contour discrimination also fell off rapidly from 1 (=7 sec.) at the fovea to $\frac{1}{3}$ at 1°, $\frac{1}{34}$ at 5°, $\frac{1}{79}$ at 10°, and $\frac{1}{120}$ at 20°; but F. B. Hofmann found much less diminution, from 2° it was proportional to the distance from the fovea[7].

The falling off of visual acuity towards the periphery can be explained on the duplicity theory if there be taken into consideration the anatomical fact that in this part of the retina several rods and cones transmit their impulses to a single bipolar cell, and that several bipolar cells transmit their impulses to a single ganglion cell. As regards contour discrimination, Laurens[8], in the dark-adapted eye, found the ratio of liminal contour discrimination (by the vernier

[1] *Jl. of Physiol.* LVII, 59, 1922.
[2] See Parsons, *Nature*, CX, 824, 1922.
[3] *Zeitschr. f. Psychol* VII, 321, 1894
[4] *Arch f. d. ges Physiol* CXV, 582, 1906.
[5] *Psychol. Rev.* VII, 429, 1900
[6] *Op. cit* p 146.
[7] *Op. cit* p. 58.
[8] *Zeitschr f Sinnesphysiol* XLVIII, 233, 1914.

method) to "visual acuity" 1 : 4; that of liminal movement discrimination to "visual acuity" 1 : 3. As already mentioned[1], Ruppert's[2] observations (Fig. 41) show that the "visual acuity" threshold at any spot on the retina out to the extreme periphery is always higher than that of movement discrimination. This fact accounts for the extreme sensitivity of the peripheral retina to movement, but is difficult to explain[3].

Such evidence as is available, therefore, tends to show that dyscritic vision has retained its primitive characteristics more completely in regard to "form sense" than to any other quality The anatomical basis for the difference between rods and cones in this respect may be the linkage of one bipolar with a single cone in the macular area as compared with one bipolar to several rods.

The photopic mechanism, mediated by the cones of the retina, shows all the characteristics of epicritic sensibility. It is minutely graded, following, like other sensations and most perceptions, the well-nigh universal Weber-Fechner law over all ranges of intensity except the high and the low. It is not only thus graded in intensity, but also in extensity, displaying minute discrimination as regards local sign This is the basis of visual discrimination, which, as already mentioned, in the case of contour displacements may reach the extraordinarily high value that is involved in the discrimination of so low a visual angle as 2 sec.[4]

Photopic vision also shows the richest qualitative differentiations of any sense, its only competitor being hearing. Whereas scotopic vision under normal conditions is capable only of an undifferentiated "vision brute," photopic vision manifests itself in all the colours of the rainbow and a few more.

But, while photopic vision is pre-eminently epicritic in these higher differentiæ, it also resembles epicritic sensibility in general in retaining the fundamental quality of dyscritic vision The mere untoned brightness or luminosity of scotopic vision pervades every photopic response as a brightness which everyone recognizes but which is so difficult to define. Thus, Helmholtz says "I have the impression that in heterochromatic luminosity equations it is not a question of the comparison of one magnitude, but the combination of two, brightness and colour glow, for which I do not know how to

[1] *Vide* p 165
[2] *Zeitschr. f. Sinnesphysiol.* XLII, 409, 1908
[3] See F. B Hofmann, *op. cit.* pp. 69–70
[4] Andersen and Weymouth, *Amer. Jl. of Physiol.* LXIV, 561, 1923.

form any simple sum and which I cannot further define in scientific terms." The perceptual pattern is still relatively undifferentiated, and at the lowest intensities it becomes indistinguishable from the dyscritic pattern.

If Head and his colleagues are correct in saying that the temperature sensations are common to both protopathic and epicritic systems, but differ in the two systems in range, etc., these are comparable to luminosity in dyscritic and epicritic vision.

So far as affective tone is concerned, it is undoubtedly enhanced in epicritic vision in man, owing to the appreciation of colours. It is, however, probable that the affective tone of dyscritic vision in lower animals is much greater than in man; and the affective tone in man is largely the result of higher—conceptual—syntheses, mediated by the complex association system of the cortex. Epicritic differentiation reaches its highest development in vision among all the senses, for upon it depends the appreciation of colours. The study of colour vision, however, shows that, complex as it is, it is by no means so elaborate as the vast range of hues which we can discriminate would lead us to suspect. The late Lord Rayleigh claimed to be able to discriminate between the hues of the two sodium lines, a difference of less than 1$\mu\mu$ wave-length, and under favourable conditions 150 or more hues can be detected in the spectrum[1]. Newton, however, proved that all these hues and others outside the range of the spectrum (the purples)—in fact, with very few exceptions[2] every perceptible hue—can be reproduced by the mixture of radiations of three wave-lengths suitably chosen. This is a fact of such profound theoretical importance that, in my opinion, no theory of colour vision is adequate in which it does not play a fundamental and preponderant rôle. Thomas Young first recognized that the totality of physiological activities comprises far fewer elements than the objective stimuli, and that a triplex physiological mechanism, each part of which responds appropriately to spectral radiations, would suffice to explain a vast number of the facts of colour vision, thus reducing the independent variables from an indefinitely large number to three.

It is not my intention here to discuss theories of colour vision. The data in favour of the trichromatic theory are well known, and the arguments against it have been even better advertised. It is clear that, if the trichromatic theory is true, the explanation of the evolution of epicritic vision from the primitive dyscritic form is

[1] Parsons, *op. cit* p 33

[2] *Ibid.* pp. 28, 39.

much simplified. The theory was founded upon the responses of the eye to mixtures of various light stimuli, and for many years rested upon these facts. Of recent years much confirmatory evidence has been derived from the study of the time relations of the responses. The antagonistic facts were derived chiefly from observations upon simultaneous and successive contrast, and Helmholtz did scant service in attributing these to psychological causes. Recent work has shown that many if not all of these facts are elucidated by a better knowledge of induction, and are as much "physiological" as the facts of colour mixture[1].

I have dealt elsewhere[2] in considerable detail with the facts and theories of Colour Vision I shall therefore confine myself to some details only briefly alluded to in that work, but of great theoretical importance.

[1] *Vide infra*, pp. 201, 209

[2] *Colour Vision*, 2nd ed Cambridge, 1924

CHAPTER XI

EPICRITIC VISION

The Sensory Response and its Duration

The response to a momentary flash of light is a wave of sensation[1]. The curve and its time relations have been studied by Broca and Sulzer[2], and Bills[3]. The rapidity of its ascent and its height varies

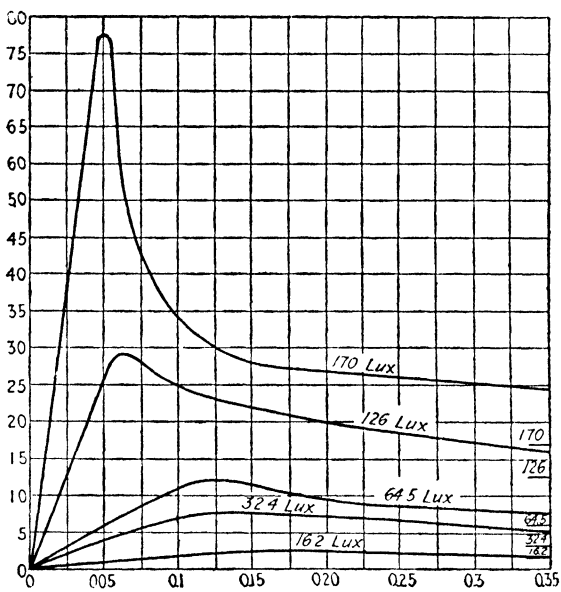


Fig 42 Curves of response to white light Abscissæ, seconds, ordinates, illumination in metre-candles (Broca and Sulzer)

with the intensity of the stimulus and with the wave-lengths of monochromatic lights. The rise is most rapid with red, intermediate

[1] See Parsons, *op. cit* pp. 94 sqq.

[2] *Jl. de Physiol. et Path. gén* IV, 632, 1902; *Comptes rendus*, 1903, pp. 944, 977, 1046.

[3] *Psychol. Monographs*, XXVIII, 1920

with green, and least with blue[1]: the maximum is greatest with blue, intermediate with red, and least with green. The rapidity of the fall of the curves varies with the rapidity of the rise. With strong excitations the curve overshoots the mark, *i.e.* the apparent brightness of the light rapidly surpasses the threshold, rises to a maximum (the so-called "hypermaximal phase"), rapidly falls to an intermediate supraliminal value, and then gradually falls below the threshold. In all cases with relatively low intensities the hypermaximal phase is flattened out. For durations of excitation between $1{\cdot}73\sigma$ and 58σ the intensity necessary to produce the minimum perceptible response varies inversely as the duration of the stimulus[2]. The hypermaximal phase accounts for the fact that with appropriate rapidity of alternation of light and dark the brightness of the flickering light is greater than that of the uninterrupted light[3].

One of the most striking facts of colour vision is the eliciting of chromatic responses by pure black and white stimuli. Fechner[4], in 1838, with an arrangement of black and white sectors on a revolving disc, noticed blue and yellow rings, altering with the rate of rotation. Subsequently Helmholtz[5], E. L. Nicholls[6], Charpentier[7] and others observed similar colour phenomena; but general attention was first called to the subject in 1894 by Benham's top (Fig. 43). The explanation of the colours seen on rotating this disc has given rise to much discussion[8]. There can be little doubt that the true explanation in its main outline has been shown by Piéron[9].

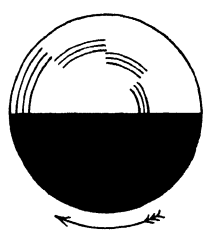


Fig. 43. Benham's Top.

Doniselli gives the following colours of the four groups of lines with Benham's top.

[1] Helmholtz, *Physiol Optik*, p 380, 1867; Exner, *Sitzungsber. d Wiener Akad.* LVIII, 601, 1868; Kunjel, *Arch f. d ges Physiol.* IX, 197, 1874.

[2] Bloch, *Comptes rendus de la Soc de Biol* II, 1885; Charpentier, *Arch d'Ophtal.* X, 110, 1890.

[3] Brucke, *Sitzungsber. d. Wiener Akad.* XLIX, 128, 1864.

[4] *Ann. d. Phys u. Chem.* XLV, 227, 1838.

[5] *Physiol Optik.* p. 215

[6] *Amer. Jl. of Sc.* XXVIII, 243, 1884.

[7] *Comptes rendus de la Soc. de Biol.* p. 533, 1892

[8] See *Nature*, LI, 113, 167, 1894; LII, 292, 1895, Bidwell, *Proc Roy Soc.* LX, 368, 1896; LXI, 268, 1897, Sherrington, *Jl. of Physiol.* XXI, 33, 1897, Doniselli, *Arch di Fisiol.* IV, 561, 1907; Percival, *Trans Ophth Soc* XXIX, 119, 1909; Baumann, *Arch. f. d. ges. Physiol.* CLXXI, 496, 1918; G. Young, *Brit. Jl. of Ophth.* II, 430, 1918.

[9] *L'Année psychol.* XXIII, 1923.

Full daylight

Rotations per sec.	I	II	III	IV
2	yellow green	bluish violet	greenish	black
3–4	greenish yellow	azure blue	olive green	greenish
5	yellow	greenish blue	greenish blue	olive green
7	metallic yellow	green	indigo blue	bluish green
9	orange	yellowish green	pale blue	violet blue
12	orange red	yellow	green	blue
15–17	reddish	orange	yellow	green

Moderate daylight

2	green	violet	black	black
3–4	green	green	violet	black
5	green	green	green	blue black

The colours are still seen, though modified, by pure monochromatic lights. This alone proves that the phenomena are not due to contrast, which is further shown by the fact that the time is too short to permit

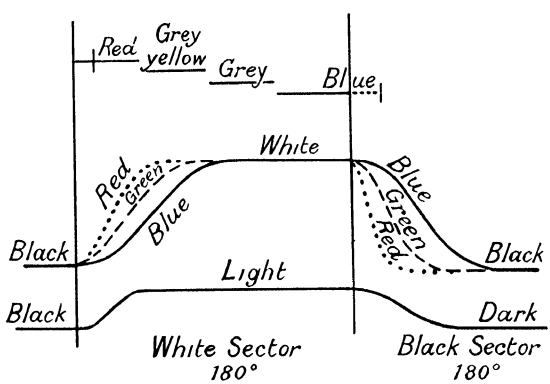


Fig. 44 Scheme of the development of the colours as due to unequal rapidity of rise of the response to red, green and blue (Piéron).

of the development of after-images. Piéron has shown conclusively that they are due to the time relations of the development of different colour sensations; and the fact that they occur with monochromatic lights shows that these lights stimulate all the fundamental colour components, whether these be three, according to the Young-Helmholtz theory, four, according to the Hering theory, or more. This is a point of great theoretical significance.

The hypermaximal phases of the sensation responses play a very important rôle in the development of the colours. If the intensity

is such that these are negligible, the colours will be as shown diagrammatically in Fig. 44, and will depend only on the unequal rapidity of development of the fundamental sensation curves. With stronger stimuli, accompanied by responses with hypermaximal phases, the colours will be as in Figs. 45–48, according to the intensity of the stimulus or the velocity of rotation.

Piéron found that for a given intensity of stimulus there is a characteristic delay in the development of each colour, and that this delay varies inversely as the fourth root of the intensity, which agrees with Charpentier's law for the cones[1].

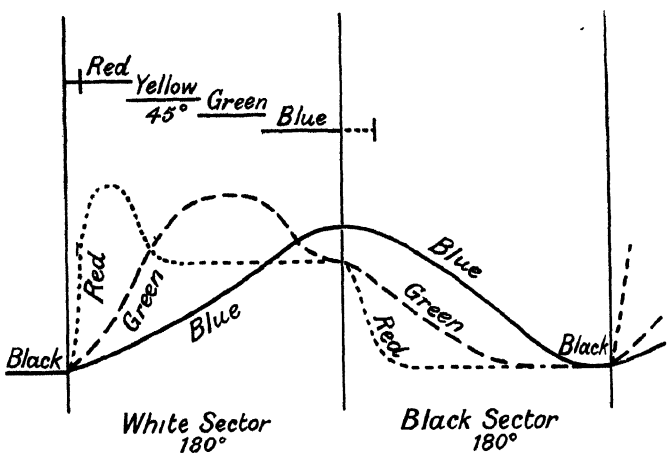


Fig. 45. Scheme of development with equal black and white sectors and 45° arcs of the rings (Benham's arrangement (Fig. 43)), with suitable rate of rotation and illumination (Piéron).

The colours are seen only on the fine lines or on the edges of broader lines, if such be used—never on the white surface. Piéron's explanation of this fact is obscure and unsatisfactory. He says, "Lorsqu'une petite surface rétinienne n'est pas, ou n'est que faiblement excitée au voisinage d'une région qui est le siège d'un processus lumineux et chromatique, l'excitation de cette surface par diffusion comporte une prédominance des processus chromatiques, qui se propagent avec une intensité plus grande que le processus lumineux." It is more probable that the true explanation depends upon reciprocal induction[2], but that theory also involves difficulties in time relations.

[1] *Vide* p. 178.
[2] *Vide infra.*

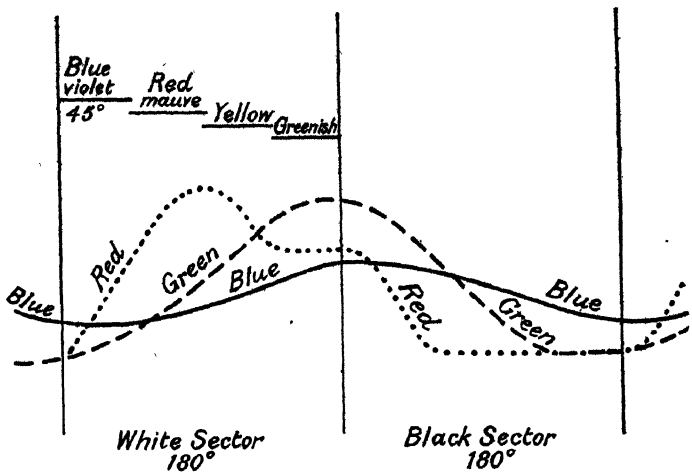


Fig. 46. Scheme of development when the rate of rotation is increased or the illumination diminished (Piéron).

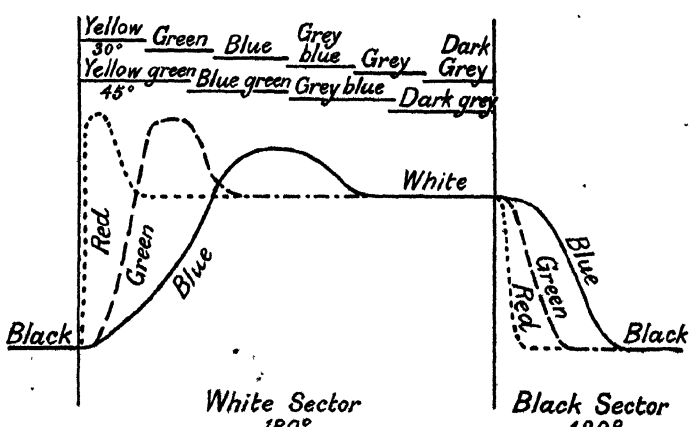


Fig. 47. Scheme of development when the rate of rotation is diminished or the illumination increased. Indication of the colours of the rings for 4 sectors of 45° or 6 of 30° (Piéron).

By means of a rotating sector or episcotister Charpentier and others have studied the duration of the visual response to a flash of light[1]. The criterion of duration is the critical frequency of light and dark, *i.e.* the point at which flicker disappears. Ferry (1892) and T. C. Porter (1898) made observations to find out the rate at which bright flashes must succeed each other in order that the sensation of light may be continuous. This may be done by rotating a circular disc (episcotister) in the path of the beam of light, one half of the disc being opaque and the other half left open by means of a movable sector. It was found that the relationship between the intensity of

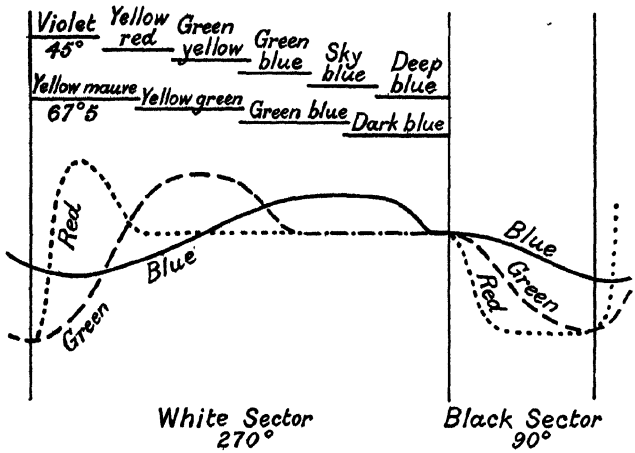


Fig. 48. Scheme of development with suitable rate of rotation and illumination when the white sector occupies three-quarters of the disc. Indication of the colours for 4 sectors of 67·5° or 6 of 45° (Piéron).

illumination (I) and the number of revolutions of the disc per minute (n) is represented by the equation

$$n = k \log I + k',$$

where k and k' are constants. That is, the relationship is exactly the same as obtains between stimulus and sensation in the Weber-Fechner law. If the intensity of the light is raised in geometrical proportion, the number of revolutions of the disc must be increased in arithmetical proportion. Now, when such a disc is rotated slowly, the alternation of light and dark gives rise to flicker, which gradually becomes less and less marked until the sensation is one of continuous illumination: this point is called the "critical frequency" of flicker.

[1] See Parsons, *op. cit.* pp. 101 sqq.

In the gross flicker at slow rates with coloured lights two possibilities must be taken into account, the physical intensity of the light, *i.e.* psychologically its brightness or luminosity, and the colour. Now, it is found that for ordinary intensities the effect of colour flicker is negligible Under these conditions Porter found that the duration of the undiminished sensation produced by different spectral hues depends solely on the luminosity of the colours and not on their wave-frequency. At the critical frequency the succession of waves of sensation is such that the fall of one wave is immediately counteracted by the rise of the next. This is what Porter means by the "undiminished sensation." It is clear that this condition is subject to further analysis. But, accepting this definition of "duration," it is obviously the reciprocal of the number of the revolutions of the disc, and the equation may be written

$$D = \frac{1}{k \log I}.$$

When these durations for individual wave-lengths of a spectrum are plotted as ordinates against the wave-lengths as abscissæ, a curve is obtained which is called a "persistency curve." Since the duration varies inversely with a function of the brightness—as proved for a very wide range of intensities by Porter, and confirmed by innumerable observers since[1]—the lowest part of the persistency curve corresponds to the brightest wave-lengths, *i.e* lower points mean greater brightness. Obviously, too, if the reciprocals of the durations are plotted against the wave-lengths, we obtain the luminosity curve of the spectrum. In fact, flicker photometry is now recognized as the most accurate method of heterochromatic photometry.

[1] Parsons, *op cit* p 102

CHAPTER XII

INDUCTION

1. Visual

By investigating the effect of so-called "fatigue" with spectral colours upon the persistency curve, Frank Allen[1], Professor of Physics at Winnipeg, has discovered a number of facts which are of great importance to the theory of vision.

When the eye is fatigued[2] with light of the wave-length 670$\mu\mu$ or 680$\mu\mu$ (Fig. 49), the other eye being kept in a condition of dark adaptation, the curve is unaltered except at the red end, where it is elevated. That is, the effect of stimulating the retina for a few minutes[3] with this wave-length is to lower the sensitivity of the visual mechanism so that the apparent brightness of a considerable portion of the red end of the spectrum is now found to be diminished, that of the rest of the spectrum being unchanged. With 589$\mu\mu$ there are two elevations, one in the red, the other in the green. With 660$\mu\mu$ the curve coincides exactly with the normal. Similarly, with 560$\mu\mu$ and 540$\mu\mu$ the curves have a single elevation in the green (Fig. 50), while with 577$\mu\mu$ (Fig. 51) both red and green elevations occur

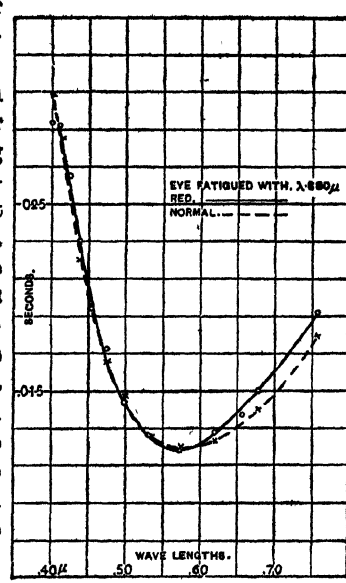


Fig. 49. Persistency curve of eye fatigued with red (680 $\mu\mu$). Abscissæ, wave-lengths (μ); ordinates, duration in seconds (Frank Allen).

[1] *Physical Rev.* XI, 257, 1900; XV, 1902; XXVIII, 45, 1908; *Trans. Royal Soc. of Canada*, II, 195, 1909; *Phil. Mag.* XXI, 604, 1911; XXXVIII, 55, 81, 1919; *Jl. of Optical Soc. of Amer.* VII, 583, 913, 1923; VIII, 275, 1924; IX, 375, 1924. See also M. S. Hollenberg, *ibid.* VIII, 713, 1924.

[2] I use this inaccurate term for the sake of brevity. Similarly, I sometimes use the term "eye" or "retina" when some more cumbersome term such as "retino-cerebral apparatus" would have the advantage of implying that I do not necessarily consider that the process under discussion is strictly limited to the retina itself.

[3] *Vide infra.*

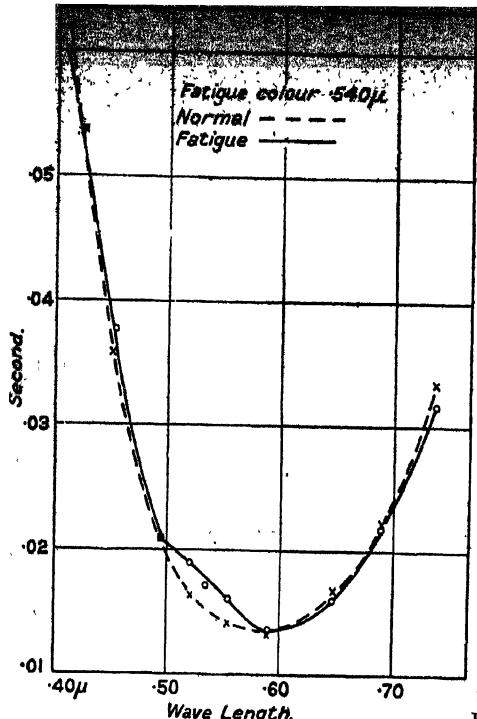


Fig. 50. Persistency curve of eye fatigued with green (540μμ) (Frank Allen).

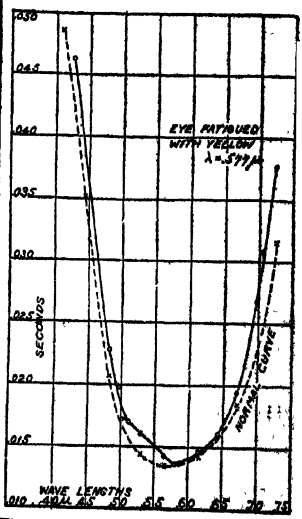


Fig. 51. Persistency curve of eye fatigued with yellow (577μμ) (Frank Allen).

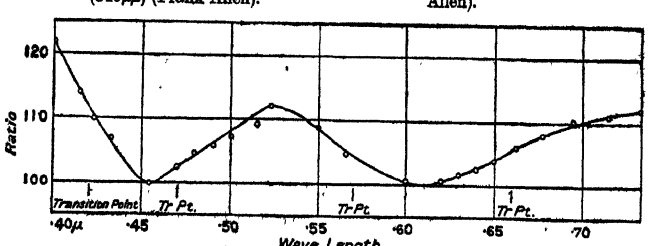


Fig. 52. Mean values of all the elevations of the persistency curves (Frank Allen).

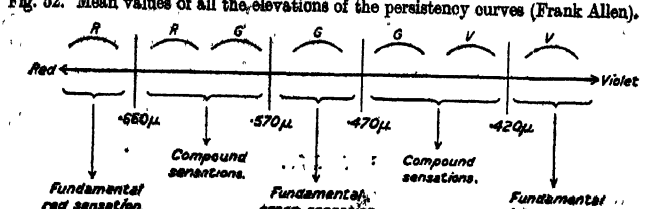
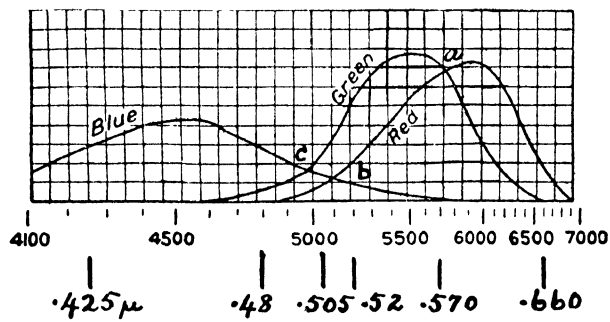
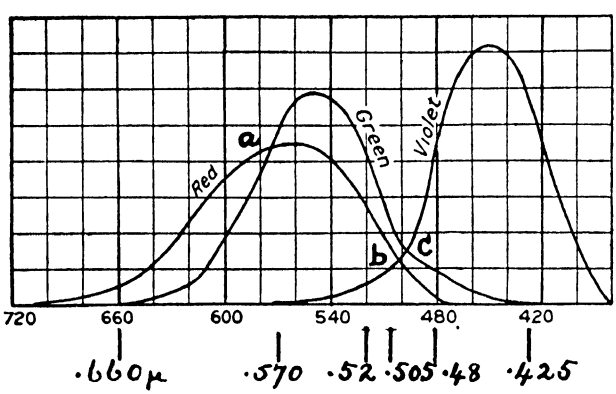


Fig. 53. Diagram of deductions from persistency curves (Frank Allen).

as with 589$\mu\mu$. At 570$\mu\mu$ the curve again coincides with the normal. 480$\mu\mu$ gives a single green elevation, whereas 440$\mu\mu$ gives both green and violet elevations. 470$\mu\mu$ again gives the normal curve. 400$\mu\mu$ gives a single violet elevation, whilst 420$\mu\mu$ gives the normal curve. Fatiguing with white light diminishes the brightness



Normal Sensation Curves (Abney and Watson.)



Normal Sensation Curves. (Konig and Dieterici.)

Fig 54. Intersection points of sensation curves and equilibrium points (Frank Allen)

of all parts of the spectrum. It looks at first sight as if the "equilibrium colours"—the wave-lengths which fail to alter the curve—do not "fatigue" the retina at all; but this is probably not the true explanation[1].

The first deduction to be drawn from these observations is that it

[1] *Vide infra.*

strongly confirms the trichromatic theory, and shows that red, green and violet are the fundamental "sensations." The compound character of yellow is abundantly confirmed, and the suspected compound character of blue is demonstrated. When the equilibrium points are studied in relation to the sensation curves of Abney and Watson, Konig and Dieterici (Fig. 54), and to the determinations of the intersection points of the sensation curves by Exner (Fig. 63)[1], it is found that three of them—570$\mu\mu$, 520$\mu\mu$ and 505$\mu\mu$—correspond to the intersection points *a* (red and green), *b* (red and violet), and *c* (green and violet). It is probable that 480$\mu\mu$ corresponds to the end of the red curve, or to *d*, the intersection of the red and green curves (Exner), and 425$\mu\mu$ and 660$\mu\mu$ to the ends of the green curve.

I have here been employing the physicists' term "fatigue" for the effects of previous stimulation of the retina. These effects, however, are quite different in character from those which are produced when a muscle becomes fatigued.

If an area of the retina is stimulated with light, the sensitiveness of surrounding areas is altered. This process may be termed spatial induction, and is the cause of simultaneous contrast. The area stimulated is also affected by the excitation, and the effect does not pass off immediately on removal of the stimulus, so that subsequent stimulation causes responses which differ from those produced by the same stimulation applied to the resting retina. This process may be termed temporal induction, and is the cause of successive contrast. Both forms of contrast show features of the same fundamental character, and are doubtless produced by similar inductive processes. What I have hitherto called "fatigue" is better described as "tuning" (*Umstimmung*)—previous stimulation (the tuning light, *das umstimmende Licht*) induces changes in the receptive organs which modify the responses to subsequent excitation (the reacting light, *das reagirende Licht*): except that these terms are unfamiliar.

The ordinary phenomena of spatial and temporal induction are well known and need not be recapitulated here. Their explanation has been a matter of great difficulty, and the Hering theory was based chiefly upon them, itself in turn failing to explain other facts of colour vision. As already mentioned, Helmholtz resorted to a psychological explanation of contrast, attributing it to an error of judgment. Rollet[2] and McDougall[3] pointed out that the white light

[1] See Parsons, *Colour Vision*, pp. 241–2.

[2] *Berichte d Wiener Akad* LV, 344, 424, 741, 1867.

[3] *Mind*, N.S X, 348, 1901.

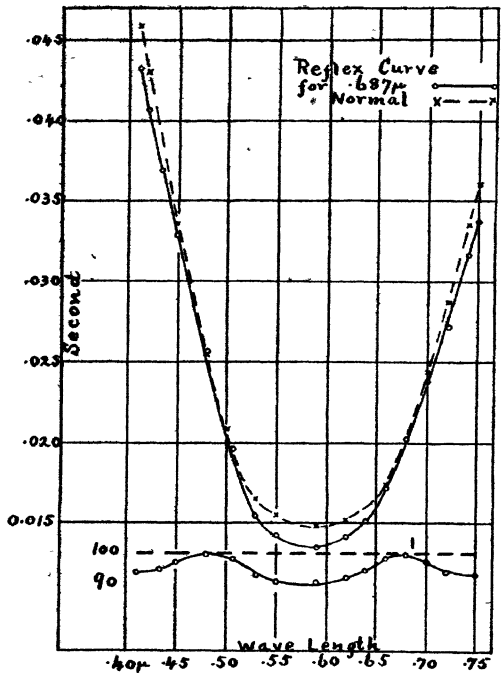


Fig. 55. Persistency curve showing contralateral enhancement. Left eye fatigued with red (687$\mu\mu$); right eye examined. Reduced curve below (*vide* Fig. 57) (Frank Allen).

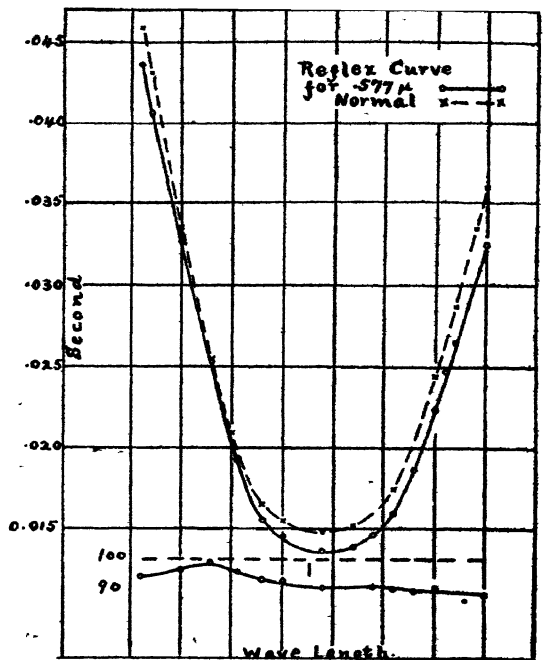


Fig. 56. Contralateral enhancement for green (577$\mu\mu$) (Frank Allen).

by which the contrast surface in simultaneous contrast is seen contains light of all wave-lengths, and therefore includes those wave-lengths which give rise to the induced colour. Hence the contrast colour is present objectively, and requires no purely psycho-

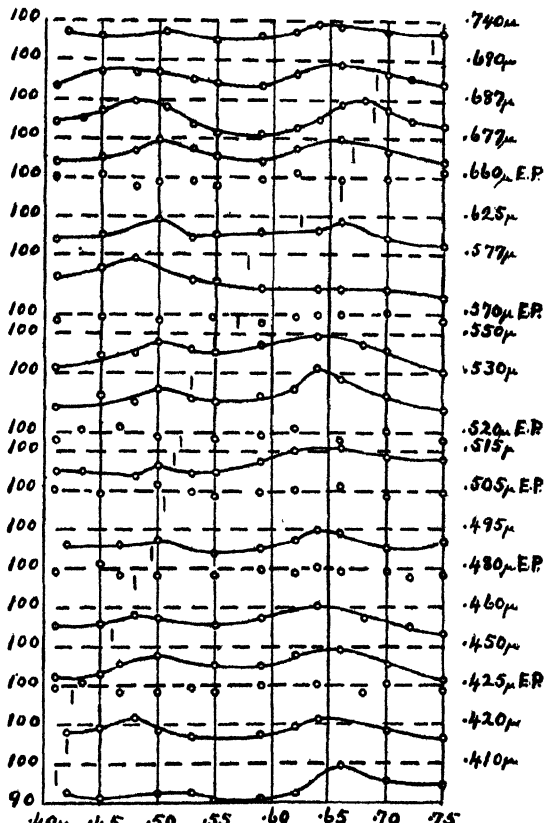


Fig. 57. Reduced curves of contralateral enhancement in which the normal curve is represented as a straight line (100). E.P., equilibrium colours (Frank Allen).

logical explanation[1]. This physiological explanation accounts for the broad facts of contrast: it does not, however, satisfactorily account for other facts, *e.g.* the fact that the induced colour is seldom the exact complementary of the inducing colour.

[1] *Vide infra*, p. 209.

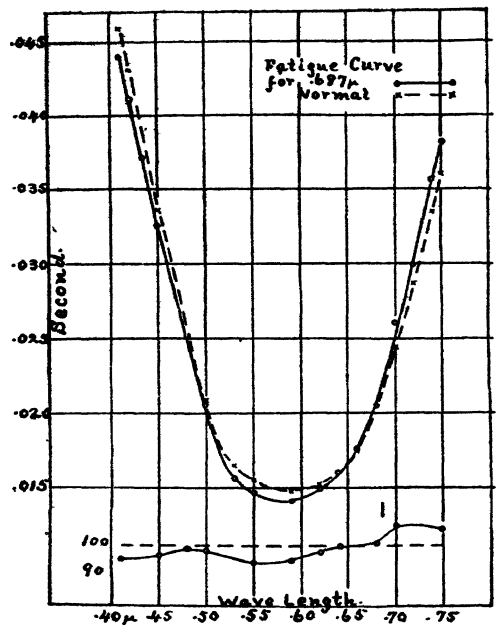


Fig. 58. Ipsilateral direct depression and induced enhancement. Left eye light-adapted; right eye fatigued with red (687$\mu\mu$) and examined (Frank Allen).

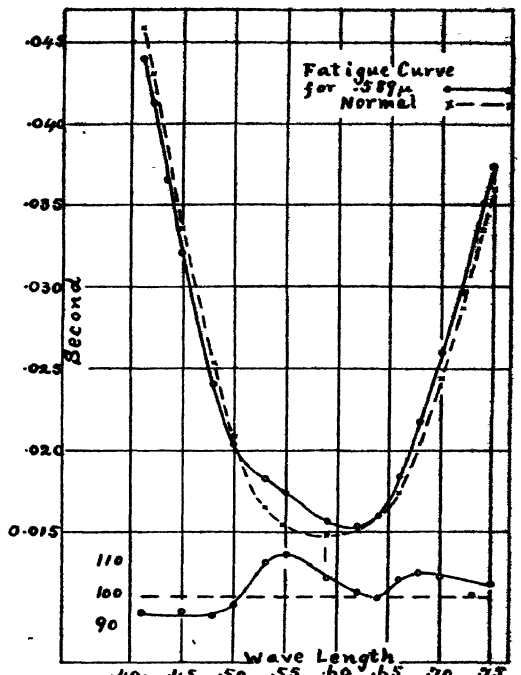


Fig. 59. Ipsilateral effects on right eye fatigued with yellow (589$\mu\mu$) (Frank Allen).

Frank Allen's researches have thrown a flood of light upon this subject, and tend strongly to show that induction is a reciprocal physiological activity completely analogous to Sherrington's reciprocal innervation.

In Allen's first investigations of the persistency curve for one eye the other eye was in a condition of dark adaptation, and it was thought that the condition of adaptation of one eye had no effect upon the other. In another series of experiments[1] the right eye was

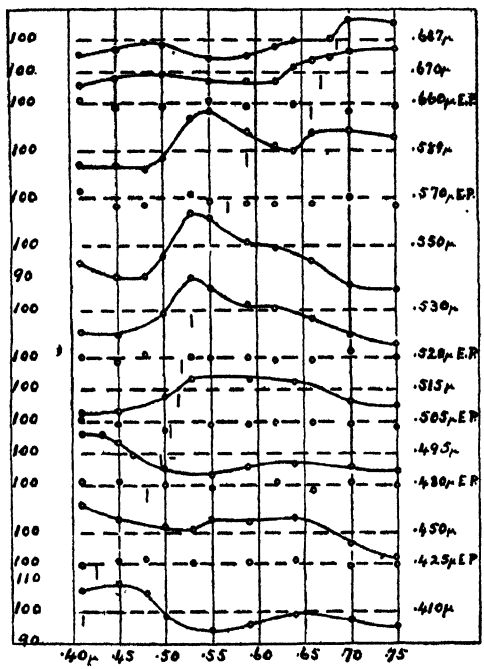


Fig. 60. Reduced curves of ipsilateral effects (Frank Allen).

in daylight adaptation, while the left was fatigued with spectral lights. All measurements of the critical frequency of flicker were made with the right or resting eye. It was found that the stimulus applied to the left eye was transferred to the right eye by some "reflex process" resulting in an enhancement of the brightness of three colours, which were always red, green and violet. In most, if not all, of the curves the greatest enhancement is complementary to

[1] *Jl. Optical Soc. of Amer.* VII, 583, 1923.

the fatiguing colour. Six colours—660$\mu\mu$, 570$\mu\mu$, 520$\mu\mu$, 505$\mu\mu$, 480$\mu\mu$, and 425$\mu\mu$—were found which produced no effect. The "reflex" and normal curves always coincided in two places which averaged about 653$\mu\mu$ and 500$\mu\mu$. The magnitude of the "reflex" effect is greatest for violet; it seems to vary to some extent with the brightness, but to a far greater extent as some inverse function of the wave-length. Fatiguing with white light causes contralateral induced enhancement of the brightness of all parts of the spectrum.

In a further series of experiments[1] the right eye was fatigued and the measurements of the critical frequency of flicker were made upon this eye, whilst the left eye was kept in a condition of light adaptation (daylight). It was found that fatigue produced both a direct and a "reflex" effect. The red, green, and violet colours showed one elevation of the fatigue curve above the normal in the part corresponding to the colour used, and two "reflex" depressions in parts corresponding to the remaining primary colours. The compound colours, yellow and blue, produced two elevations in the parts of the curves corresponding to the colour sensations of which they are compounded, and one "reflex" depression in the part corresponding to the remaining colour. The number of elevations or depressions in each curve was always three, corresponding to red, green, and violet. The equilibrium colours produced no effect.

If, therefore, whilst one eye is kept in a condition of daylight adaptation the other eye is fatigued with red (*e.g.* 687$\mu\mu$), the brightness of the red portion of the spectrum as seen by the fatigued eye will be found to be diminished, whilst that of the green and violet parts will be enhanced. The depression of the fatigued part has long been known and has been attributed solely to the effect of fatigue. The enhancement of brightness of the other parts of the spectrum has hitherto escaped observation. Allen attributes the depression to the algebraic sum or net result of fatigue and reflex enhancement, the balance being in favour of fatigue. But whilst fatigue with a primary colour causes "reflex" enhancement of all three parts of the spectrum corresponding to red, green, and violet in the other eye, it does not appear to me to be conclusively proved that this occurs in the actual area fatigued; so that the old view may still be correct so far as this point is concerned.

It is to be noted that Allen found no spectral colour which produced elevations simultaneously in the red and violet. There is, therefore, now abundant evidence that violet is a simple sensation, and the

[1] *Jl. Optical Soc. of Amer.* VII, 600, 1923.

ambiguity as to whether blue or violet should be chosen as the fundamental colour—felt by all the earlier workers including Abney[1],

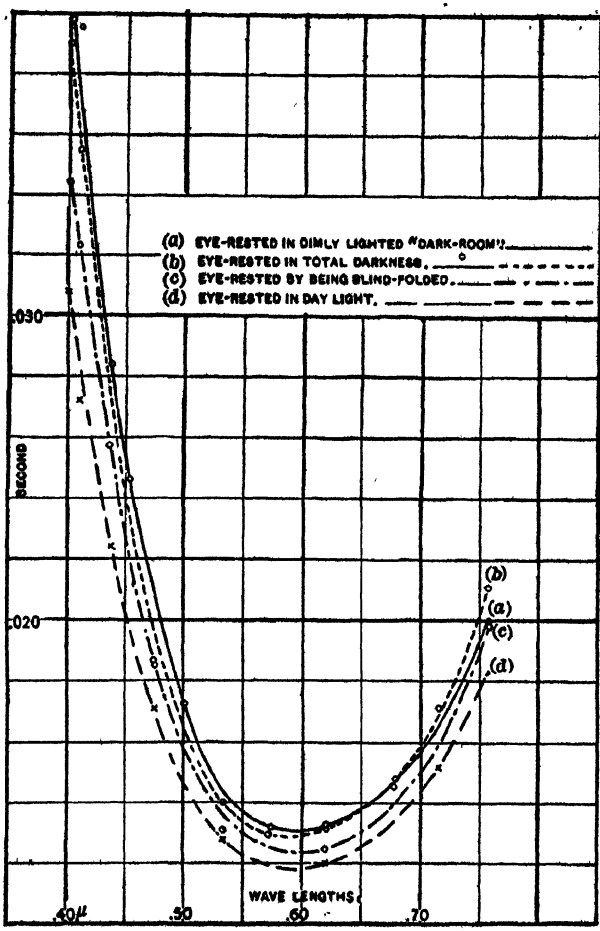


Fig. 61. Persistency curves showing various degrees of dark adaptation. Right eye examined: *a*, both eyes dimly lighted; *b*, both eyes dark adapted; *c*, right eye blindfolded, left eye light adapted; *d*, normal curve (Frank Allen).

as well as Burch[2], who saw reasons for adopting both as primary colours—is set at rest.

[1] *Researches in Colour Vision*, p. 230, London, 1913.
[2] *Phil. Trans.* B, CXCI, 1, 1898.

Charpentier[1] came to the conclusion that dark adaptation of one eye produced no effect upon the other, and this conclusion has been universally accepted. Allen has shown that it has a well-marked effect, so that many earlier researches are vitiated by this fact. Indeed, it may be specially remarked that it vitiates all the sensation

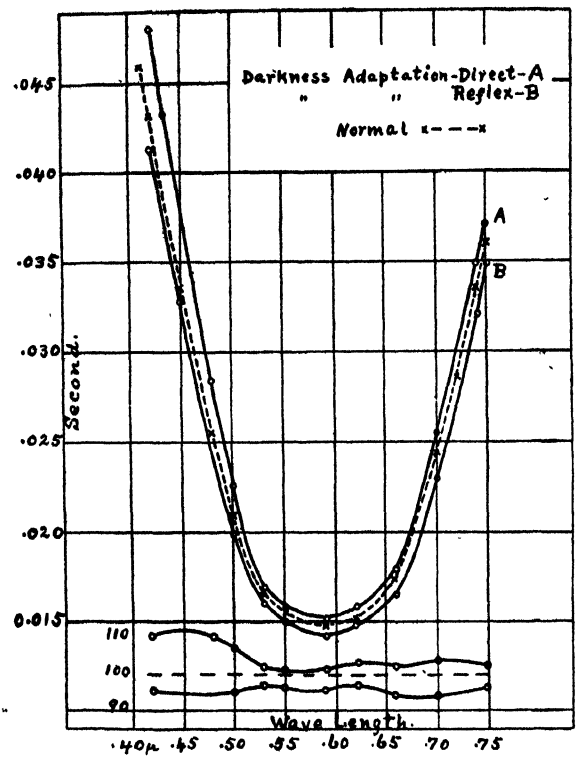


Fig. 62. Persistency curves under different conditions of dark adaptation. A, direct effect of dark adaptation; B, ipsilateral induced enhancement in contiguous area from dark adaptation (Frank Allen).

curves which have hitherto been worked out. It is much to be desired that the sensation curves be redetermined with a spectrum whose energy equivalents have been accurately measured, and with due regard to the condition of adaptation of the other eye, etc. Unfortunately this is an extremely laborious and difficult piece of work, and, considering all the possible sources of error, it is not to be

[1] *La Lumière et les Couleurs*, p. 175, Paris, 1888. See Parsons, *op. cit.* p. 54.

expected that any very serious modification of Abney's curves would be discovered.

The effect of dark adaptation of the unfatigued eye is peculiar, for the maximum "reflex" effect is not obtained with maximum dark adaptation, but with very dim light. It must be remembered, however, that the curves are for bright colours which involve the photopic mechanism, and the results may not be valid for the scotopic mechanism alone. Further, it is not necessary to assume that darkness acts as a stimulus. Under ordinary circumstances both eyes are exposed to approximately the same stimuli, and the resulting responses are the algebraic sum of the direct and "reflex" effects. Protecting an eye from light leaves the reciprocal effect of the light unbalanced.

Yet another series of researches[1] has shown that exactly the same direct and reciprocal effects are produced on different areas of the *same* eye. Under these conditions also white light on one area of the retina produces "reflex" enhancement throughout the spectrum on a neighbouring area. Darkness adaptation of one area causes "reflex" enhancement throughout the spectrum on a neighbouring area, and reversal of the areas shows that the direct effect is a diminution (Fig. 62).

These results may be summarized as follows.

(1) Stimulation of one area of a retina with light causes.

- (*a*) *Direct effects* upon that area,
- (*b*) *Induced effects* in all other areas, *i.e.* both in the same eye and in the other eye;

(2) *Direct Effects.* With both eyes in a condition of moderate photopia.

- (α) Stimulation with white light depresses the sensitivity throughout the spectrum;
- (β) Shading the eye also depresses the sensitivity throughout the spectrum;
- (γ) Stimulation with any given wave-length depresses the sensitivity to this region of the spectrum and enhances it for the complementary colour;
- (δ) With any given wave-length the depressions and enhancements show three curves affecting respectively the red, green and violet,
- (ϵ) Stimulation with the equilibrium colours—660$\mu\mu$, 570$\mu\mu$, 520$\mu\mu$, 505$\mu\mu$, 480$\mu\mu$, 425$\mu\mu$—has no apparent effect upon the sensitivity of the visual apparatus.

[1] *Jl. Optical Soc of Amer* VII, 913, 1923.

(3) *Induced Effects.* With both eyes in a condition of moderate photopia the effects on the unexcited areas of the same and the opposite retina are:

(α) Stimulation with white light enhances the sensitivity throughout the spectrum;

(β) Shading an area or an eye depresses the sensitivity throughout the spectrum;

(γ) Stimulation with any given wave-length enhances the sensitivity throughout the spectrum, the enhancement being most marked in every case in the red, green, and violet;

(δ) Stimulation with any given wave-length enhances the sensitivity most for the complementary colour;

(ϵ) Stimulation with the equilibrium colours has no apparent effect.

These experiments appear to show that stimulation of the retina with *any* wave-length excites all three fundamental sensations—red, green, and violet. This was the original theory of Young and Helmholtz. Abney[1], however, thought that the extreme red end of the spectrum affected only the red sensation, and the violet both the red and the violet. The discrepancy may be due to inaccuracy in Abney's sensation curves[2]. These were estimated by a luminosity method, which is least accurate in the violet end of the spectrum, the luminosity values of the red, green, and blue curves for the electric arc being 579 : 248 : 3·26. It is noteworthy in this connection that Allen and M. S. Hollenberg found that the maximum induced effect was in the violet, though the brightness of 410$\mu\mu$ was only about one seven-hundredth of that of the yellow, 589$\mu\mu$. Hence the magnitude of the induced effects is not a direct function of the luminosity of the stimulus. It is probable that further investigation and minute analysis of the quantitative effects will give valuable results.

Moreover, just as the response to a stimulus is in the form of a wave or waves, which have different time relations for different colours, so there can be little doubt that the rates of development of the induced effects vary. Their time relations are also likely to afford valuable information as to the exact mechanism at work both in the propagation of the direct and of the induced nerve impulses.

As the result of Allen's researches, we are able to envisage more

[1] *Researches in Colour Vision*, p. 231, London, 1913.

[2] Cf. Exner's (Fig. 63).

accurately the phenomena of induction. As he has pointed out, they serve to prove most conclusively the physiological—as opposed to psychological—foundations of contrast. They explain on purely physiological grounds many of the greatest difficulties associated with contrast, such as the divergence from the precise complementary in induced colours[1], changes in hue and saturation after prolonged fixation[2], coloured shadows[3], the "memory colours" of Hering[4], the Ragona Scina experiments[5], some of Abney's experiments[6], binocular contrast[7], Fechner's paradox[8], Bidwell's experiment[9], and some of Edridge-Green's observations[10].

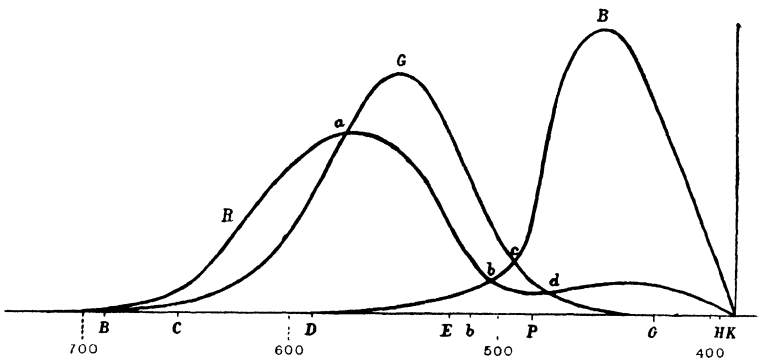


Fig. 63. Konig and Dieterici's sensation curves corrected to new determinations of the points of section *a*, *b*, *c*, *d* (Exner).

It is interesting to note that Allen's researches give direct experimental evidence of the truth of Rollet[11] and McDougall's[12] physiological explanation of induction. According to their theory, if a grey surface with a red patch upon it is fixated, the cortical area excited by the red differs only in activity from that excited by the grey in that the red apparatus is the more powerfully stimulated in the former. It is, therefore, hypothecated that the highly excited activity of the cortical "red area" depresses the activity of the red apparatus in the neighbouring cortical "grey area," so that the blue and green

[1] *Jl of Optical Soc of Amer.* VII, 932, 1923
[2] *Ibid* p 933.
[3] *Ibid* p 936
[4] *Ibid* p. 938.
[5] *Ibid.* IX, 375, 1924.
[6] *Ibid* p. 379
[7] *Ibid* p. 381.
[8] *Ibid.* VII, 609, 1923.
[9] *Ibid* p. 618
[10] *Ibid* p 620.
[11] *Berichte der Wiener Akad* LV, 344, 424, 741, 1867.
[12] *Mind*, N.S. X, 348, 1901.

in the latter area predominate over the red. According to McDougall, therefore, the red in the inducing or "tuned" area *inhibits* the red in the induced or reacting area. Allen's experiments show that the red enhances the sensitivity throughout the spectrum in the induced area, but the enhancement for the three fundamental colours, red, green, and violet, is such that the complementary colour is most enhanced.

Exceptions to a law are often most pregnant with new discoveries. Brown and olive green are exceptions to the general law that "every conceivable light or light mixture gives rise to a sensation which can be accurately matched by a suitable mixture of only three lights." Now, the sensation of brown cannot be obtained by reducing the intensity of orange, nor that of olive green similarly from green. In order that brown may be sensed, the stimulus effect of the orange must be "blackened" by simultaneous or successive contrast[1], or the pigment must be mixed with black. This is probably due to the fact that under conditions for observing diminution of intensity, as, for example, with Abney's colour patch apparatus, the neighbouring and peripheral parts of the retina are dark adapted. Surrounding the area with a white area leads to "blackening" of the colour patch and the sensation of brown. From Allen's experiments one would anticipate that there is an optimum brightness of the white area for different intensities of the orange. That other spectral colours do not give such specific results is probably due to the fact that orange and yellow green stimulate all three colour sensations, but that the induced effect on the violet end of the spectrum is most marked. The subject merits further investigation from this point of view.

Temporal induction, however, may be regarded as a form of adaptation; which is thus not confined to light and shade, but also occurs with colours. If coloured glasses are worn for some time the alteration in hue of objects ceases to be noticed, when the glasses are removed objects appear tinged with the complementary colour. The photopic eye normally is adapted for the yellowish-red of hæmoglobin, owing to light entering the eye through the sclerotic and light scattered within the eye[2]. This has been adduced as an explanation of erythropsia[3]. We may suppose that under low

[1] First pointed out by Sir John Herschel in a letter to Dalton (1833): "brown is black+red, or black+orange, or black+yellow as the case may be, it is essentially sombre and depends for its effect *as brown* entirely on the proximity and contrast of bright hues." Quoted in *Colour-Blindness*, by Julia Bell, p. 182, Eugenics Laboratory Memoirs, XXIII, Cambridge University Press, 1926.

[2] Brucke, *Ann. d Phys. u Chem.* LXXXIV, 418, 1851.

[3] Rivers, *Trans. Ophth. Soc* XXI, 296, 1901

illumination below the chromatic threshold the photo-chemical substance—almost certainly visual purple—responds uniformly to different wave-lengths but in different degree, thus giving the characteristic achromatic scotopic luminosity curve. Under photopic intensities the luminosity response is similar, though not identical, but the hypothetical photo-chemical substrata show a new type of adaptation, as exemplified by induction. An alternative view is that there is interaction between the dyscritic and epicritic systems, but this is less likely—and in any case these speculations with our present knowledge are rather barren.

Anderson[1] and A. Hollenberg[2] have studied the persistency curves for two cases—themselves—of anomalous colour vision. The only safe conclusion to be drawn from them is that in both cases the vision was definitely trichromatic. There is a vast field of research opened here, but it is imperative that each case of colour blindness should first be tested by the methods devised by Abney and Watson, and particularly that the luminosity curve, or characteristic parts of it, should be carefully worked out by the flicker method[3].

2. Auditory, Tactile and Gustatory

Frank Allen and his pupils have applied the flicker method to auditory[4], tactile[5], and gustatory[6] sensations with results which confirm his observations on vision.

The critical frequency of pulsation of *auditory* tones was studied with a Stern tonvariator inside a box in which a hole was cut The sound was interrupted by means of an aluminium disc, with a hole in it, rotating opposite the hole in the box. Various pressures of air were employed, and tones through the octave 142 to 284 vibrations studied. The critical frequency at which the flicker or pulsation ceases was measured. With light the brightest colours have the smallest values of the duration of the light at the critical point, with sound the greatest intensities (*i e.* pressures) have the largest values. These differences are due to the physical differences of the actual

[1] *Jl of Optical Soc of Amer.* VIII, 731, 1924.

[2] *Ibid.* IX, 389, 1924

[3] Parsons, *op. cit.* pp. 252 sqq.

[4] Frank Allen and M Weinberg, *Phil. Mag.* XLVII, 50, 126, 1924; Frank Allen, *ibid* 941, 1924; M Weinberg, *ibid.* 142, 1924.

[5] Frank Allen and A. Hollenberg, *Quart. Jl of Exp. Physiol.* XIV, 351, 1924; Frank Allen and M. Weinberg, *ibid.* XV, 377, 1925.

[6] Frank Allen and M. Weinberg, *ibid.* XV, 385, 1925.

nerve stimuli, light acting probably photo-chemically, sound mechanically.

As already mentioned, the relation between duration and brightness or intensity for light is

$$D = \frac{1}{k \log I} \quad \text{(Ferry)},$$

or

$$n = \frac{1}{D} = k \log I + c \quad \text{(Porter)},$$

where k and c are constants.

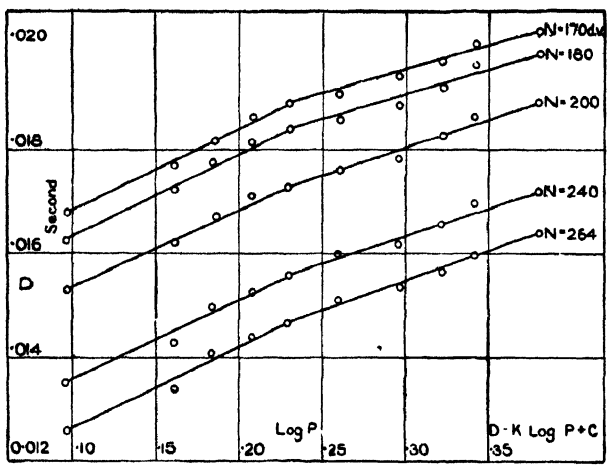


Fig. 64. Normal auditory persistency curves reduced to linear form (Frank Allen).

Weinberg and Allen found that

$$D = k \sqrt{\log P} + c$$

best satisfied the results obtained for sound, where P is the blowing pressure, to which the intensity of the sound is proportional. If the pressure is kept constant,

$$D = \frac{k'}{\sqrt{\log N}} + c',$$

where N is the frequency of the tone; and if the rate of pulsation (D) is kept constant,

$$\log N = k'' \log P + c''.$$

Allen subsequently[1] found, however, that if the experimental results were plotted according to the equation

$$D = k \log P + c,$$

each tone gave a curve of two straight lines meeting at an angle at

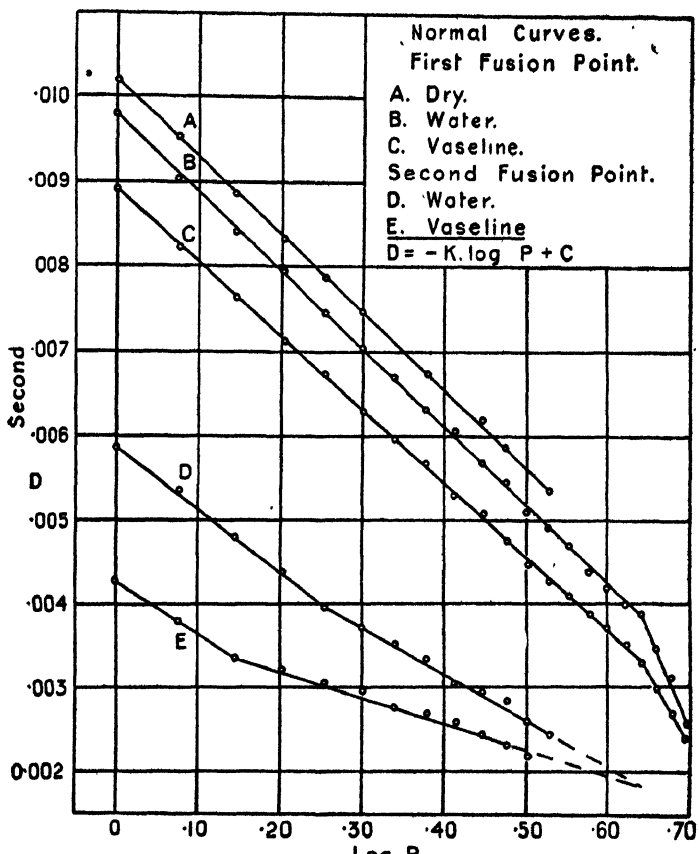


Fig. 65. Normal tactile persistency curves reduced to linear form (Frank Allen and Hollenberg)

an air pressure of 1·7 cm. of water, exactly comparable to the change in direction of the similar curves for light at 0·25 metre candle[2].

[1] *Phil. Mag.* XLVII, 941, 1924.

[2] Porter, Ives, and others; see Parsons, *Colour Vision*, p. 104.

The effects of fatigue were next studied[1]. The curves indicate that fatigue greatly increases the persistency of sound impressions. The increase is maximum when the vibration frequency of the fatiguing tone is the same as that upon which measurements are taken, and diminishes very rapidly as the vibration frequency is increased or

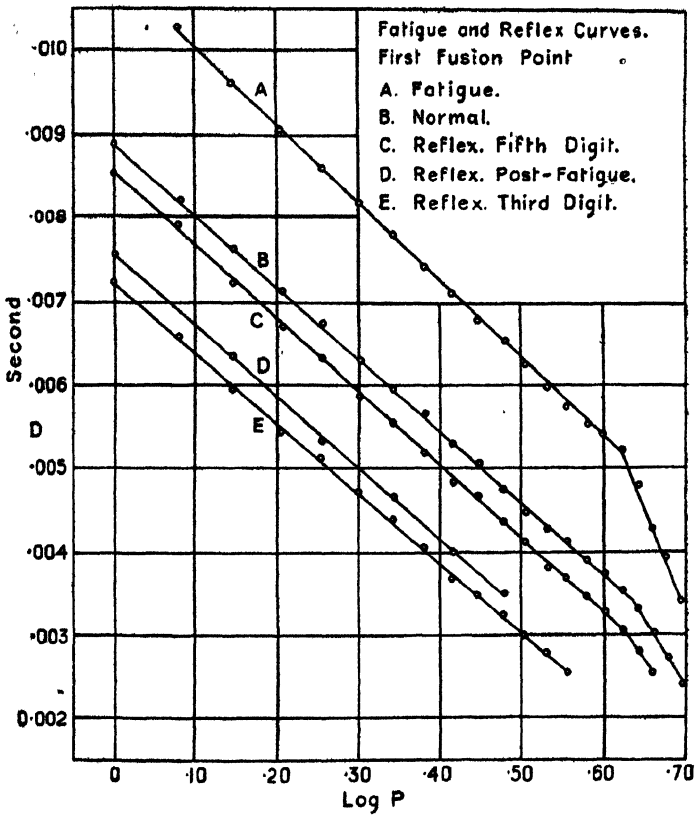


Fig. 66. Direct depression and induced enhancement of superficial tactile persistency curves (Frank Allen and Hollenberg).

diminished. The entire range affected is about 16 vibrations, and the steepness of the slope of the fatigue curve shows that only a few tones very near the maximum on both sides are affected to any great extent. The fatigue curve is least for the loudest tones, indicating

[1] *Phil. Mag.* XLVII, 126, 142, 1924.

past a loud tone in itself produces fatigue so rapidly that it occurs during the actual measurement of critical frequencies.

The critical frequency of *tactile* sensations was measured by the fusion of the sensations derived from pulsations of air impinging upon the skin. Air at different pressures was directed upon the skin by a

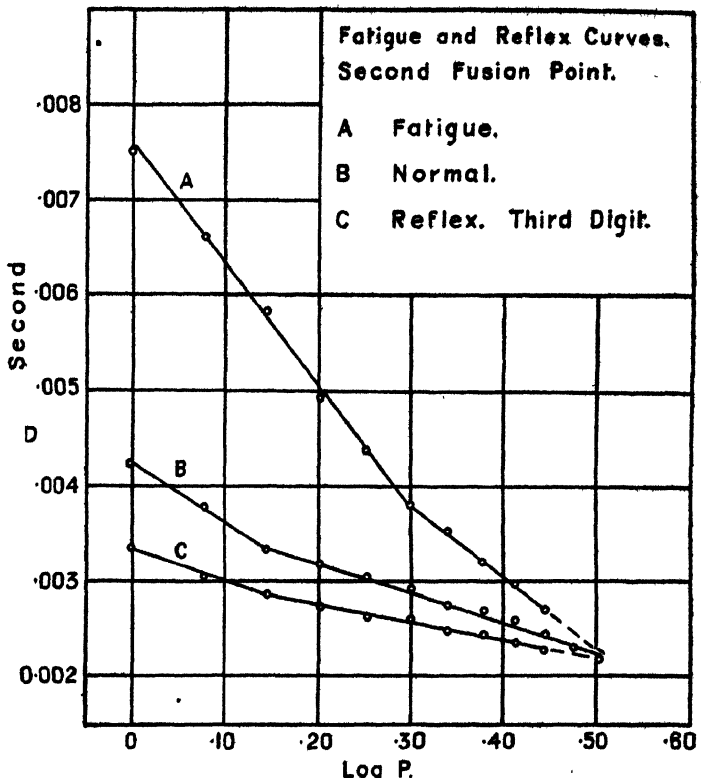


Fig. 67. Direct depression and induced enhancement of deep tactile persistency-curves (Frank Allen and Hollenberg).

nozzle, and interrupted by a rotating disc with holes in it. On the index finger of the right hand a normal curve is obtained for a range of air pressure from 1 to 5 cm. Hg. The measurements show that there are two critical frequencies, corresponding to light and deep touch. By plotting the time values of the critical frequency of

percussion against the logarithms of the air pressure, the curves become straight lines conforming to the equation

$$D = -k \log P + c.$$

Each curve consists of two straight lines of different slope, exactly comparable to the effects in light and sound perception. The effect of fatigue was measured and its curve was found to lie above the normal but exactly similar to it.

"Reflex" enhancement of sensibility in the index finger was obtained by "fatiguing" another finger by firmly bandaging it. The measurements showed that the enhancement curve lies below the normal, like the effect produced in one eye by fatiguing the other. Similar effects were obtained for both fusion points (superficial and deep touch). The curves for each fusion point converge and intersect at what is termed an "equilibrium pressure," where "reflex" and "fatigue" effects appear to vanish.

The critical frequency method shows that the tactile sensation is most responsive, then hearing, and finally sight; but if the dynamical equivalents of the liminal stimuli of the sensations be accepted as criteria of relative sensitiveness the order will be reversed. Roughly, the responsiveness to intermittent stimuli varies inversely as the sensitiveness. There is a definite enhancement of sensitivity if an interval of a few minutes is allowed to elapse between fatiguing and measuring the critical frequency. This is comparable to successive contrast in vision. Often when the sensations aroused by intermittent air pressure appeared to be continuous on the area of the finger studied, they were instantly perceived as intermittent on an adjacent area. This is comparable to simultaneous contrast in vision.

Itching and tickling may be due to these reciprocal effects. In itching, scratching affords relief by fatigue, whereby the sensitivity of the receptors of surrounding areas is enhanced, and a post-fatigue (after-image) enhancement also occurs in the scratched area.

Light touch acts like dim light, enhancing the sensitivity not only in the area stimulated, but also in surrounding areas. When the tickling point is moved it is constantly coming in contact with enhanced receptors, causing their further enhancement by the same process "It would appear to follow that if the tickling point move across the skin with a speed equal to the rate at which the enhancement spreads, which is the latent period of the reflex, no tickling would be produced. This would imply a critical velocity of tickling,

which experience shows exists, above which no tickling could be elicited."[1]

Allen and Weinberg[2] made use of the fact that electrical stimulation of the tongue gives rise to a sour taste in measuring the critical frequency for *taste*. The range from 0·16 to 0·7 volt was employed,

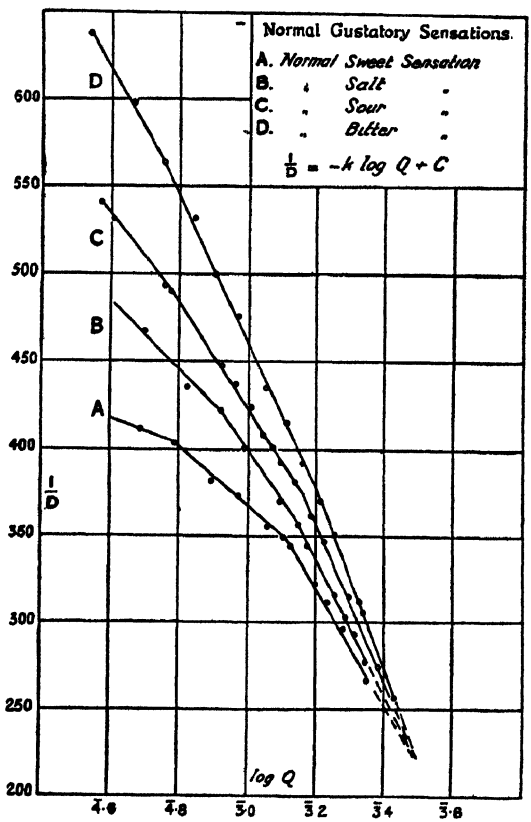


Fig. 68. Normal gustatory persistency curves (Frank Allen and Weinberg).

lower values giving no sensation and higher muscular twitches. The results appeared to be quite irregular, but when plotted with voltages against durations they fell into four well-defined curves, indicating four degrees of sensitivity to a single stimulus intensity. This confirms

[1] Allen and Hollenberg, *Quart. Jl. of Exp. Physiol.* XIV, 375, 1924.
[2] *Quart. Jl. of Exp. Physiol.* XI, 385, 1895.

the view that there are four primary taste sensations with corresponding receptors[1]. The duration of the sensation at the critical point increases with the potential. The actual excitation was a sour stimulus, and hence it appears that, as in vision, each gustatory stimulus acts upon all the receptors, so that no perfectly saturated taste is ever experienced.

Since the physical stimulus is electrolytic, its intensity varies with the quantity of electricity and not with the voltage. It was found that the equation

$$\frac{1}{D} = -k \log Q + c$$

applied to the results gave four curves, each consisting of three straight lines changing slightly in slope (Fig. 68).

The action of gymnemic acid in abolishing sweet, and, to a less extent, bitter tastes, was used for distinguishing the four curves. One curve, obviously the sweet, was absent, one was present only at high intensities, the bitter, and this was higher than the normal, showing that the sensation was depressed, the other two curves, salt and sour, were also higher, showing that gymnemic acid also depresses these sensations The curves agree with the order of sensitivity of the four tastes, the threshold values being sweet 0·5 per cent. sugar at tip of tongue, salt 9·25 per cent. NaCl at tip of tongue, acid 0·007 per cent. HCl on border of tongue and bitter 0·00005 per cent. quinine at root of tongue[2].

Measurements of the "direct" action of stimuli showed that quinine ($\frac{1}{8}$ per cent.) depresses all four gustatory responses to the same extent. Sour (1·5 per cent. acetic acid) depresses the salt, sour, and bitter receptors, and enhances the sweet. Salt (10 per cent. NaCl) depresses the bitter, sour, and especially the salt receptors, and enhances the sweet There is an extraordinary enhancement of the sweet sensitivity over one particular narrow range of intensities (Fig. 69). Sweet in 20 per cent. solution of sugar enhances the responses from all four receptors, but in 5 per cent. solution salt, sour, and especially sweet are depressed; there is no record for bitter. Hence enhancement or depression by "direct" action, *i e* "fatigue," appears to depend upon the high or low concentration of the stimulus respectively, and one may infer that at the changes in slope of the logarithmic graphs these effects cancel out

[1] *Vide* p 8

[2] Howell, *Text-Book of Physiol.* p. 295, 1922.

Measurements of the "reflex" action of stimuli, one side of the tongue being stimulated and records taken from the other side, show that sour (1·5 per cent. acetic acid) and salt (20 per cent. NaCl) cause "reflex" enhancement of all four receptors. These effects correspond exactly with the "reflex" effects for vision and touch. On the other hand, bitter ($\frac{1}{8}$ per cent. quinine) causes "reflex" depression of all four receptors, a phenomenon which Allen regards as comparable to the Fechner paradox in vision.

Summarizing the results of Frank Allen's observations, we find that a logarithmic relationship obtains for all sensations, *viz.*

$$\frac{1}{D} = k \log I + c \qquad \text{(vision)},$$

$$\frac{1}{D} = -k \log Q + c \quad \text{(taste)},$$

$$D = k \log P + c \qquad \text{(hearing)},$$

$$D = -k \log P + c \quad \text{(touch)}$$

Hence the Weber-Fechner law is found to apply to all sensations, even at high and low physiological intensities of stimulation if the constants of the equations be suitably changed.

The rather unstable mathematical foundations upon which the Fechner elaboration of Weber's law rests has been discussed by me elsewhere[1]. We have no mathematically defined unit of sensation, so that the basis of the law is insecure. None the less, it has been found to fit in with experimental observations on all sensations to a remarkable extent, but most observers agree that it fails for low and high intensities of excitation even if these be undoubtedly within physiological, as opposed to pathological, limits.

It has already been pointed out that Charpentier abandoned the law, finding that interpolations on a different exponential basis gave better results, and that Piéron supports his contentions[2]. More recently S. Hecht[3] has thrown serious doubts on the validity of the law, based upon a re-examination of the most accurate available experimental results, *viz.* those of König[4], König and Brodhun[5], and

[1] Parsons, *Colour Vision*, p. 24, 1924; see also C. S. Myers, *Text-Book of Exp. Psychol* I, chap XIX, 1911.

[2] *Vide* p. 178

[3] *Jl. of Gen. Physiol* VII, 235, 1924

[4] *Sitzungsber. d. Wiener Akad.* p 559, 1897, *Gesam Abhandlungen*, p. 378, Leipzig, 1903.

[5] *Sitzungsber. d Berliner Akad* p 917, 1888, 641, 1889; Konig, *Gesam. Abhandlungen*, p. 116, 135, 1903.

Blanchard[1]. By re-plotting the curves it is found that the range which conforms even approximately to the Fechner law is small. Some unpublished experiments by Hartridge on the effects of illumination on visual acuity were found to fit in with König's results, and so far confirm these strictures.

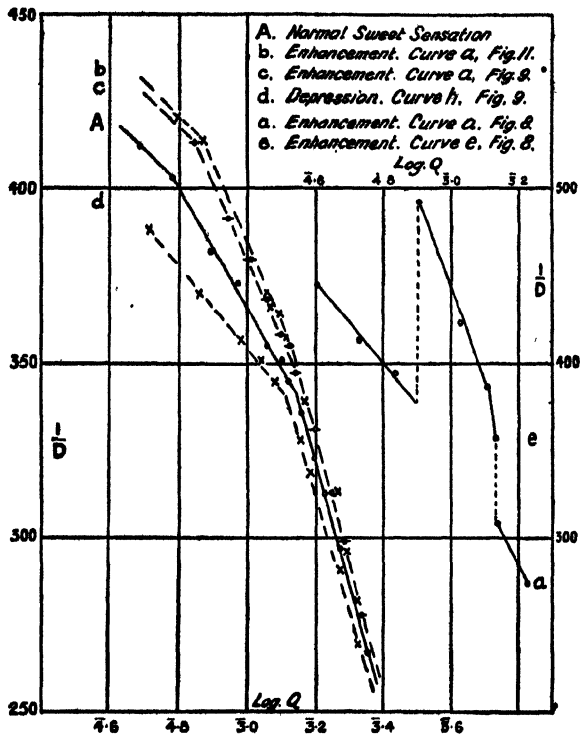


Fig. 69. Normal, enchancement and depression persistency curves for the sweet gustatory sensation; *b*, 20 % NaCl (induced); *c*, 20 % sugar (direct); *d*, 12 % sugar (direct); *a*, 12 % NaCl (direct); *e*, 10 % NaCl (direct). Curves *a* and *e* show the extraordinary anomalous enhancement over a special narrow range of intensities (Frank Allen and Weinberg).

The change in slope of the logarithmic curves for visual acuity under different intensities of illumination at 0·25 metre candle, confirmed by the same change on the critical frequency curves at the same point, points strongly to a change over from the scotopic

[1] *Physiol. Rev.* XI, 81, 1918; *Zeitschr. f. Beleucht.* p. 25, 1922.

to the photopic mechanism, *i.e.* from rods to cones. *Three* changes of slope, however, as found by Allen[1], are difficult to reconcile with different receptor organs, for which there is no anatomical evidence; and suggests the further complication that changes of sensitivity occur, possibly brought about in the synapses, for different ranges. Allen adopts this explanation, and attributes the changes of sensitivity to the reciprocal effects of "direct" and "reflex" activities. He writes[2]:

"While these experiments were in progress, an investigation, conducted by one of the writers (Allen) into the effects of colours of varying intensity upon the colour sensations, disclosed the fact that colours corresponding in intensity to the lowest branch of the curve for vision, in Fig. 70, depressed the three primary sensations, whether stimulation was in the same eye as was used for measurement, or in the other. When, however, the colours were of medium intensities corresponding to the second branch of the curve, the opposite effect, enhancement, was produced in all the sensations.

"These investigations, to be published shortly, lead to the conclusion that depressory effects upon the receptor end-organs are also transferred by reflex action in a thoroughly systematic manner. Since reflex action causes opposite effects, the complete theory must embrace both.

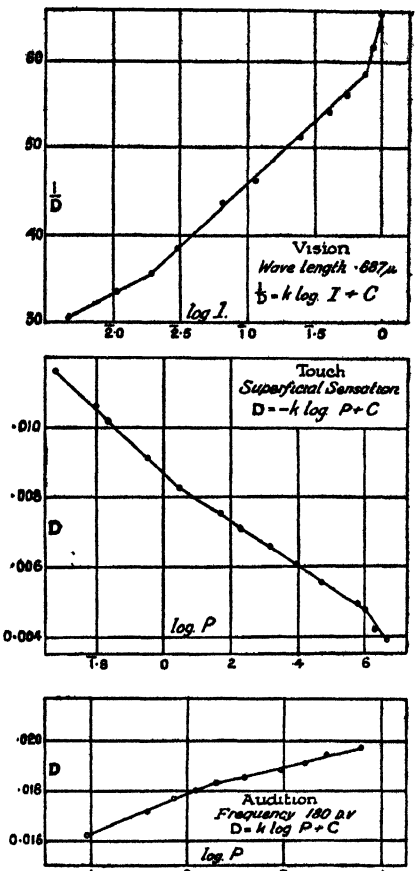


Fig. 70. Visual, tactile, and auditory persistency curves for different intensities of stimulation (Frank Allen and Weinberg).

The conclusion follows that stimulation of a sensory end-organ, in addition to the excitation of a sensation in the central organs, causes the simultaneous production or release of two sets of efferent nerve impulses, one causing depression and the other enhancement of the sensory receptors. When the stimulus is weak, depression exceeds enhancement; when strong, enhancement exceeds depression....

[1] *Quart. Jl. of Exp. Physiol.* xv, Figs. 4 and 13.

[2] Allen and Weinberg, *Quart. Jl. of Exp. Physiol.* xv, pp. 410–411, 1925.

"These phenomena indicate very clearly that the state and phenomena of reciprocal innervation that Sherrington has so elegantly demonstrated in muscular movements are also to be found underlying all sensory actions."[1]

The relative sensibility of the four sensory modalities, taste, touch, audition, and vision, as shown by the critical frequency method, shows decreasing sensitivity in the order mentioned. Thus, the persistency of the response for taste is 0·0015 to 0·004 sec , for touch 0·0024 to 0·0089 sec., for audition 0·0127 to 0·0215 sec., and for vision 0·013 to 0·045 sec.

3. Induction and Adaptation

It has already been pointed out that the epicritic visual mechanism, subserved by the cones, shows only slight traces of adaptation to different intensities of the stimuli It has now become clear, however, that while it shows a very delicate and highly differentiated responsiveness to different qualitative characteristics of the light stimuli, these are accompanied by equally delicate and differentiated reciprocal responses which are better described by the term induction than the term "reflex visual sensations" applied to them by Frank Allen. For, on the one hand, they are obviously a factor in those phenomena of contrast to which Hering applied the term induction, and on the other hand, they extend the meaning of the term reflex action beyond that which is desirable. Yet, when one comes to speculate upon the possible modes of conveyance of induced reactions from the site of stimulus to the field of induction, it may well be that the path is most allied to that of the "axon reflex"—a term which has already acquired an assured position in the physiological vocabulary. At present, however, it is clearly best to confine the term reflex action to the active—motor or secretory—responses to stimuli, using the term induction for the transference of passive—purely sensory—alterations in excitability.

The striking analogy which exists between reflexes and the phenomena of induction has already been recognized by Sherrington and indicates a fundamental similarity in the physiological processes which underlie them. Examples of "immediate induction," both in the spinal reflex and the visual spheres, have already been cited[2]. The analogy between the reciprocally antagonistic effects of visual induction and antagonistic spinal reflexes cannot fail to strike the reader of Sherrington's *Integrative Action of the Nervous System* (especially Lectures IV and X).

[1] *Ibid.* p. 412.

[2] *Vide* pp. 180, 184.

It can scarcely be doubted that Sherrington was led to adopt the term spinal induction from the analogy to visual induction. Besides immediate induction there is also successive induction.

"If the crossed-extension reflex of the limb of the spinal dog be elicited at regular intervals, say once a minute, by a carefully adjusted electrical stimulus of defined duration and intensity, the resulting reflex movements are repeated each time with much constancy of character, amplitude, and duration If in one of the intervals a strong prolonged (*e.g.* 30 sec.) flexion-reflex is induced from the limb yielding the extensor-reflex movement, the latter reflex is found intensified after the intercurrent flexion-reflex' The intercalated flexion-reflex lowers the threshold for the aftercoming extension-reflexes, and especially increases their after-discharge This effect may endure, progressively diminishing, through four or five minutes, as tested by the extensor-reflexes at successive intervals Now, as we have seen, *during* the flexion-reflex the extensor arcs were inhibited *after* the flexion-reflex these arcs are in this case evidently in a phase of exalted excitability. The phenomenon presents obvious analogy to visual contrast If visual brightness be regarded as analogous to the activity of spinal discharge, and visual darkness analogous to absence of spinal discharge, this reciprocal spinal action in the example mentioned has a close counterpart in the well-known experiment where a white disc used as a prolonged stimulus leaves as visual after-effect a gray image surrounded by a bright ring (Hering's 'Lichthof') The bright ring has for its spinal equivalent the discharge from the adjacent reciprocally correlated spinal centre. The exaltation after-effect may ensue with such intensity that simple discontinuance of the stimulus maintaining one reflex is immediately followed by 'spontaneous' appearance of the antagonistic reflex. Thus the 'flexion-reflex' if intense and prolonged may, directly its own exciting stimulus is discontinued, be succeeded by a 'spontaneous' reflex of extension, and this even when the animal is lying on its side and the limb horizontal, a pose that does not favour the tonus of the extensor muscles Such a 'spontaneous' reflex is the spinal counterpart of the visual 'Lichthof.'"[1]

Adaptation is most delicate and manifest in vision, but it occurs in other senses also. Visual adaptation throws some light on these cases. It seems to have been little studied for touch, but that it occurs is an everyday experience, *e.g.* the pressure of spectacles upon the nose rapidly ceases to be felt. Adaptation to temperature is more obvious and has attracted more attention, having been drawn into Hering's general metabolic theory. It also occurs in labyrinthine sensation, hearing, and motor phenomena. In vision adaptation is pre-eminently associated with the dyscritic system. It would appear from Head's researches on tactile and temperature sensations that it is associated rather with the epicritic than the protopathic system. It is, however, to be remembered that Head's experiments produce a pathological dissociation, the results of which must be accepted with reserve as denoting the true physiological condition. Moreover, adaptation must be considered a feature of primitive sensation, and

[1] Sherrington, *op. cit.* pp 207–208.

it is a feature which persists, though feebly, in the visual epicritic system. It may well be that in some senses differentiation leads to its elaboration on the epicritic rather than on the dyscritic side. It is *à priori* more probable that it should remain always more attached to the diffuse dyscritic sensation, thus underlying *all* the responses of the given sense, than to the epicritic sensation, which in the cases of touch, temperature, and vision is punctate in character. The relative diffuseness of rod vision has its anatomical basis in the relationship of several rods with the dendrites of a single retinal bipolar cell, whereas each macular cone has its own bipolar. It is probable that a similar anatomical arrangement occurs in the skin. At any rate, it is certain that the "indifferent" temperature of the skin—a range of only 2° or 3° C.—depends upon the temperature to which a considerable area of the skin has become adapted by previous stimulation. As Head and Rivers say, "in the normal skin the hot and cold spots are nothing more than minute areas peculiarly sensitive to either heat or cold, set in a territory over which temperature stimuli can also be appreciated."

There is less evidence of induction in the other senses, but it is by no means lacking, and Frank Allen's experiments have already given examples[1]. These experiments tend to show that it is a more important feature of tactile sensibility than has hitherto been thought. Since the discovery of touch, pain, heat, and cold spots—"a mosaic of tiny sensorial areas each sensitive to a specific stimulus"[2]—the existence of these spots has been amply verified, but great difficulty has been experienced in mapping them out for a given area of skin. As Boring[3] says, it is one thing to map an area for cold or warm spots, and quite another thing to find these spots a second time and not to find new ones. Waterston[4], who has specially investigated this subject lately, finds that in an area 5 cm. by 2·5 cm. one person may show 8–18 cold spots, another 60–70; the sum total of the spots elicited by a number of successive investigations on the same person is vastly in excess of that found at any one time, thus confirming Goldscheider[5], the spots are readily exhausted by a repetition of the stimulus, dulling of one spot being accompanied by awakening of thermal sensibility of an adjacent spot, the effect of artificially

[1] *Vide* p. 211.
[2] Sherrington.
[3] *Quart. Jl. of Exp. Physiol.* x, 1, 1916.
[4] *Brain*, xlvi, 200, 1923.
[5] *Gesammelte Abhandlungen*, Leipzig, 1898.

produced erythema is to disturb the punctate arrangement of warm spots, so that all parts of the surface may become sensitive for warmth.

Waterston regards these results as an example of the Law of Fluctuation, or of alternating periods of activity and rest in living tissues, a general law enunciated by Sir James Mackenzie[1]. But so far as tactile sensibility is concerned no new term—certainly not an indefinite one like fluctuation—is required. The facts are adequately explained by induction, especially in the light of Allen's researches, though, unfortunately, no means have yet been devised for applying the critical frequency method to temperature sensations.

The relative parts played by the protopathic and epicritic systems in normal tactile responses are difficult to unravel, but if it be true that re-arrangement occurs in the cord, as Head believes, spinal lesions might afford opportunities for investigation of the phenomena of induction and their relations to each system.

Adaptation of the visual apparatus to different intensities of stimulation by light has striking analogy to the tonus of muscle. Now, tonus is characterized by indefinitely prolonged, unchanging activity, with little evidence of fatigue. It has been suggested that the actual muscle fibres which subserve tonus are different from those which subserve voluntary movement, and that they are supplied by a very different set of nerve fibres, belonging to the sympathetic system[2]. The anatomical, experimental, and surgical grounds on which this theory has been founded are unconvincing[3].

We have seen that visual adaptation is essentially a function of the dyscritic system, whilst epicritic vision shows gradations of activity which have their analogy on the motor side in the delicate responses of voluntary movements. It may be that there is a similar duality on the motor side, tonus being the expression of a more primitive dyscritic, voluntary movement that of a more highly differentiated epicritic form of motor activity.

The ambiguous use of the terms fatigue, adaptation, and induction cannot fail to have been noticed. It was not unnatural that "fatigue," appropriate in the case of muscle, should have been used for the phenomena following the prolonged stimulation of sensory receptive

[1] See Herring, *Brain*, XLVI, 209, 1923.

[2] J. T. Wilson, *Brain*, XLIV, 234, 1921; J. I. Hunter, *Surgery, Gynæcology, and Obstetrics*, XXXIX, 721, 1924; *Brit. Med. Jl.* pp. 197, 251, 298, 350, 398, 1925; Kulchitsky, *Jl. of Anat.* LVIII, 152, 1924; LIX, 1, 1924.

[3] See Walshe, *Med. Science*, XII, 437, 1925; also "Discussion on the Sympathetic Innervation of Striated Muscle," *Brain*, XLIX, 135, 1926.

areas. These can be studied most accurately in the case of vision, and it is soon recognized that the term is unsuitable. The difference doubtless depends in large part upon the different physico-chemical effects of stimulation. In the case of muscle, chemical changes result from the activity of the muscle, and many, at any rate of the phenomena of fatigue, are due to the accumulated products of metabolism. There is good reason to think that the immediate results of the stimulation of the retina are chemical changes of a reversible character[1], and that within the limits of physiological intensities of excitation true fatigue does not occur, or if it occurs at all, it is so transient as to be masked. Human eyes are exposed to bright light for many hours and are capable for many hours of performing near work involving precise discrimination by the macular regions without any evidence of functional fatigue. "Eye strain" undoubtedly occurs, but there is no evidence to show that it is due to retinal fatigue. Under pathological intensities of excitation prolonged or permanent impairment of vision may occur (*e g.* "eclipse blindness"), but this is due to changes for which the term fatigue is quite inappropriate.

On the other hand, stimulation within physiological limits produces changes in excitability which are readily revealed by the responses to subsequent stimulation. If the changes are the result of prolonged stimulation, and still more if they are the result of prolonged rest, which, however, is never a condition of complete rest, they are usually spoken of as adaptation. If they are the result of transient stimulation they are now generally spoken of as phenomena of induction. The similarity of the results of simultaneous contrast to those of successive contrast or temporal induction leads to these also being included in the term induction (spatial induction). There is indeed no crucial difference between induction and adaptation. Yet it is still desirable, at any rate in the case of vision, to retain both terms. For adaptation is most commonly employed for the results of prolonged darkness, or prolonged exposure to light, and there is a mass of evidence to show that this form of adaptation is associated with the chemical changes in the visual purple, whereas the changes commonly included under the term induction are photo-chemical changes of a different nature, *viz.* those which give rise to the qualitative differentiæ of photopic vision.

[1] *Vide infra*, p. 227.

CHAPTER XIII

VISUAL EXCITATION AND CONDUCTION

THE facts at our disposal do not render an exhaustive discussion of the elementary physiological processes occurring in the receptors, conductors, and synapses very profitable. A vast group of theories as to the physical basis of the genesis of visual impulses from light stimuli does little but express the same facts in terms of various physical theories. It seems of little importance whether one explains them in terms of photo-chemical reactions, electrical reactions, or the quantum theory[1]. The one firmly established fact is that visual purple is the physico-chemical substratum of scotopic vision, and hence it is natural to have some predilection for thinking in photo-chemical terms. The most accurate recent work on this subject is that of S. Hecht[2]. He holds that the underlying retinal process is chemical both for the rods and the cones. When light falls on the retina a bimolecular reaction occurs, with a velocity varying directly with the intensity of the light. Hecht and Williams measured the relative energy in different parts of the spectrum necessary to produce the achromatic threshold. The reciprocal of this relative energy at any wave-length is proportional to the absorption coefficient of the sensitive substance. The achromatic scotopic and the chromatic photopic luminosity curves are identical in shape, but the latter is shifted $48\mu\mu$ towards the red end of the spectrum. Hecht holds that visual purple is the sensitive substance both for low (scotopic) and high (photopic) intensities. Kundt[3] proved that if one colourless solvent has a greater refracting or dispersing capacity than a second, then the absorption bands of a substance dissolved in the first will be nearer the red end of the spectrum than when dissolved in the second. The absorption maximum of visual purple in water solution is $503\mu\mu$, in the rods $511\mu\mu$, in the cones $554\mu\mu$ (or $540\mu\mu$ if macular absorption is taken into account). For the difference threshold at different intensities of illumination a constant amount of the sensitive

[1] See Parsons, *Colour Vision*, p 212.

[2] *Jl. of Gen. Physiol.* II, 337, 499, 1920; IV, 113, 1921; VII, 235, 1924; Hecht and Williams, *ibid.* V, 1, 1922.

[3] *Ann d. Physik u. Chem.* IV, 34, 1878; Kayser, *Handb. d. Spectroscopie*, III, Leipzig, 1905.

substance must be broken down in excess of that broken down at the level of adaptation under consideration. The rate of regeneration of the substance is quicker for the cones than for the rods, which accounts for the much quicker adaptation of the former (cones, 3 minutes; rods, 30 minutes). The change over from rod to cone mechanism occurs at a brightness of 0·0134 millilambert. Hecht calculates that there are 572 steps in luminosity discrimination, of which one-third are due to rod, two-thirds to cone vision. This theory accounts for the falling off of luminosity discrimination at both high and low intensities of illumination.

When one comes to conduction of the visual impulses, there is no good ground for imagining that it is different from the conduction of nervous impulses in other nerves. If that be so, the all-or-none character of the response discovered by Adrian and Keith Lucas holds good. The theory of recruitment for the explanation of the graded muscular response to different intensities of stimulation in motor nerves, whereby increased intensity increases the number of nerve fibres stimulated and of muscle fibres responding, meets with difficulties in the case of tactile and visual responses. As already mentioned, it may suffice to explain some of the effects in the scotopic mechanism, but it is not easy to apply it to the single cone bipolar mechanism of the epicritic system. Here it seems as if we must fall back upon Lapicque's chronaxie—but this theory is in too embryonic a condition to afford safe grounds for theory at present. It is possible, however, that recruitment occurs in higher neurons, for the optic radiations contain far more nerve fibres than the optic nerve. At the same time, it is not unlikely that the visual apparatus may be a valuable *corpus vile* for experimental research on these problems. The extraordinarily delicate electrical responses of this apparatus to light stimuli have not yet been exploited as much as they might be, probably owing to the extreme delicacy of the apparatus entailing peculiar technical difficulties. Yet this field of research is bound to produce valuable results.

Per contra, a wider and deeper knowledge of the events which occur at the synapses cannot fail to have its reverberation in the elucidation of the facts of colour vision. We have become familiarized with inhibition as a potential property of all highly differentiated nervous mechanisms. The up-to-date theories of inhibition are well discussed by Adrian[1] and Sherrington[2], but in their present stage they afford little help in elucidating visual problems.

[1] *Brain*, XLVII, 399, 1924.

[2] *Proc. Roy. Soc.* B, XCVII, 519, 1925.

On the other hand, many instances of inhibition occurring in visual phenomena can be readily brought forward, whatever may be its actual mechanism. Most striking among these are the phenomena of binocular and uniocular struggle, of which we owe many examples to McDougall. Indeed, the most plausible theory of the central processes which underlie visual sensations was enunciated as far back as 1901 by McDougall[1], and is founded largely upon the facts of induction and "mutual inhibitions." This author is a strong upholder of the Young trichromatic theory, which, combined with Rollet's theory of contrast, he considers explains all the phenomena which he has described. "With the exception of certain observations of a complex character, very difficult to interpret, such as Muller's experiments on galvanic stimulation of the eyes and some of Professor Sherrington's flicker experiments, I cannot discover any important fact connected with light and colour-vision with which it is incompatible or that it fails to illumine."[2] The undeserved neglect of McDougall's work on this subject is probably due to the obsession of physiologists and psychologists for Hering's theory and the great prestige of its author, and to the small circulation amongst physiologists of the journal in which the work appeared.

McDougall's scheme bears some resemblance to von Kries's[3] theory of zones and to G. E. Muller's[4] very complicated elaboration of Hering's theory. Both of these theories involve retinal processes giving rise to impulses which are redistributed and elaborated in higher cerebral centres. This fundamental idea has been familiarized to us in recent times by Head's views on the dissociation of cutaneous sensations and their redistribution in the central nervous system.

McDougall is not very precise in his statements as to what occurs in the periphery and what in the higher centres. His original papers should be studied, and it will suffice here to reproduce his diagram with his own description (Fig. 71). It will be seen that antagonism or inhibition plays a very prominent rôle, and that any other relation between the several parts is limited to a sympathetic relationship, which does not appear to imply reinforcement.

This scheme fits in better than any other which has been suggested with the facts of colour vision and would not be difficult to reconcile

[1] *Mind*, N.S. x, 52, 210, 347, 1901; see Parsons, *op. cit.* p 288.

[2] McDougall, *op cit* p 372.

[3] See Helmholtz, *Physiol. Optik*, 3rd ed. II, 359; Nagel's *Physiol. des Menschen*, III, 269, 1904.

[4] *Zeitsch. f Psychol. u. Physiol. d. Sinnesorg.* x, i, 321, 1896; XIV, i, 161, 1897.

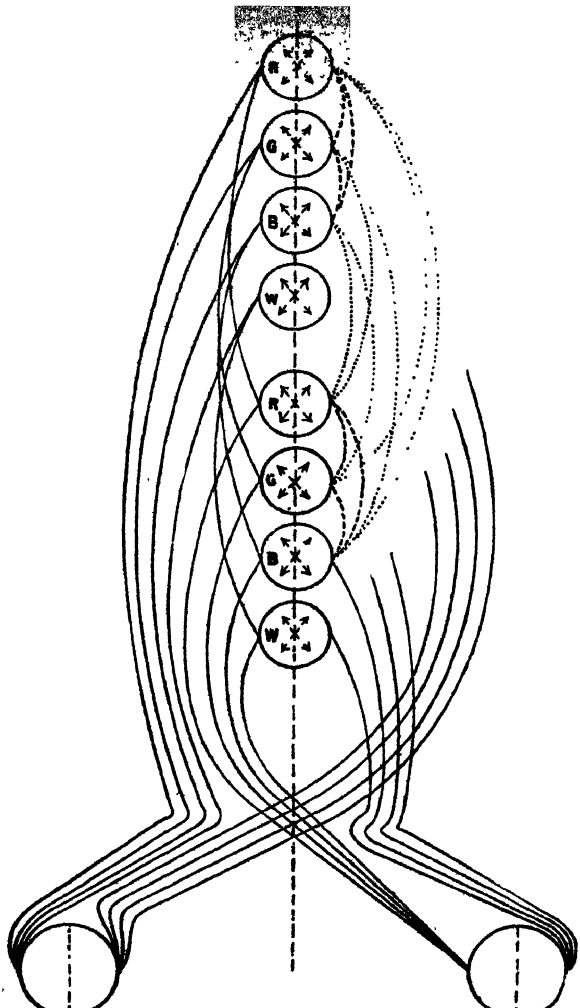


Fig. 71. Diagram representing the two retinae and the cortical centres connected with them. The upper four circles represent the cortical levels of the red, green, blue, and white systems connected with the left retina, the lower four those connected with the right retina. The broken line bisecting all the circles represents the purely anatomical separation of each centre into two halves lying in opposite cerebral hemispheres. The continuous lines on the left side represent the sympathetic relation between corresponding points of the two systems of similar function connected with the right and left retinae respectively. The dotted lines represent the antagonism between any point of any one colour-system of the one eye and the corresponding points of the other two colour-systems of the other eye. The broken lines represent the feebler antagonism between any point of any one colour-system of one eye and the corresponding points of the other two colour-systems of the same eye. The arrows radiating from the centre of each circle represent the antagonism between any point of the cortical level of any one of the systems and every other point of the same. (McDougall.)

with Frank Allen's observations. We should have to replace blue with violet, and W, which refers to scotopic white, might be eliminated until we know more about the interaction, if any, of the dyscritic and epicritic systems. Applying Allen's results would involve an elaborate system of reinforcements, which might to a large extent replace some of McDougall's inhibitions, but probably not all. I do not propose, however, to enter into this speculative problem in detail.

Turning now to the anatomical basis of the lower visual impulses, have we any knowledge or can we reasonably conjecture the structures which mediate the conduction and central connections of the dyscritic and epicritic systems? One of the most striking features of comparative neurology is the persistence from the lowest to the highest species of the Edinger fibre system, which subserves dyscritic cutaneous and other extero-ceptive sensations. The epicritic system is superposed upon this, and the chief anatomical criterion that any given afferent tract in the central nervous system belongs to this system is the amount, if any, of its cortical projection. The mere absence of cortical projection of noci-ceptive impulses, already mentioned[1], is sufficient to relegate these impulses to the dyscritic system. There can be little doubt that some grato-ceptive impulses also belong to this system and have no cortical projection, *e.g.* the pleasurable feeling derived from stimulation of the "protopathic area" of the hand by a suitable temperature[2] or stimulation of the corona of the glans penis by water at 45° C.[3]

According to Head and Thompson[4], from evidence derived from pathological cases—lesions of the spinal cord—there is a redistribution of protopathic and epicritic impulses in the central nervous system, so that impulses of the same quality are collected into the same tracts. It is true that anatomical evidence is of secondary importance to physiological in a question of this kind; but, so far as it goes, it is not favourable to Head's views.

The afferent visual tracts from the retina in the optic nerve and tract pass to three so-called primary visual centres—the lateral geniculate body, the pulvinar of the optic thalamus[5], and the superior colliculus. Of them, those passing to the colliculus are undoubtedly

[1] *Vide* p 71.

[2] Head, *Studies in Neurology*, p. 258, London, 1920.

[3] *Ibid* p 274 See also Head, Croonian Lecture, *Proc. Roy. Soc* B, XCII, 184, 1921.

[4] *Brain*, XXIX, 537, 1907; Head, *Studies in Neurology*, London, 1920.

[5] Henschen does not regard the pulvinar as a primary visual centre (see Brouwer and Zeeman, *Brain*, XLIX, 29, 1926): this does not negative the view that the pulvinar has visual, probably stereognostic functions (*vide infra*).

the most primitive phylogenetically, since they are a residuum representing the survivors of practically the whole of the afferent visual fibres in lower animals, which pass to the tectum. Here they form the superficial layer of fibres, and are brought into relation with the bulbo- and spino-tectal fibres. There is no doubt therefore that in these animals, going down as low as the cyclostomes, the function of these optic fibres is almost entirely photostatic, and that they are dyscritic. The tectum shows histological differences in mammals from the condition in lower vertebrates. The optic fibres are reduced in number and are situated below a layer of nerve cells and therefore less superficially. Moreover, the efferent cells are raised and somewhat approximated to the optic fibres. These efferent cells send axons to the retina (tect-optic fibres of Ramon y Cayal and von Monakow) and to the tecto-bulbar tracts. Kappers attributes this approximation to neurobiotaxis, and sees in it an expression of the predominantly reflex function of the optic fibres. "Optic reflexes in mammals are certainly not fewer, but in the primates are much finer than in lower animals "[1] The tectum receives no macular fibres, and has no cortical projection. We may conclude, therefore, that the optic fibres to the superior colliculus in man are dyscritic.

Even in the cyclostomes there seems to be present the primitive *Anlage* of a lateral geniculate body[2]. This is a differentiation of the dorsal thalamus (metathalamus), to which in plagiostomes the optic nerve gives off a number of collaterals on its way to the tectum It is already well-developed in teleostean fishes[3], but still receives only a small proportion of the optic nerve fibres. The first indications of a cortical projection are found in Amphibia, the tractus thalamo-corticalis[4]. In man 70 per cent.[5] to 80 per cent.[6] of the optic nerve fibres end in the lateral geniculate body Now, there is evidence that the external geniculate body consists of two parts. This is well-marked in marsupials and in the rabbit, where there are definite dorsal and ventral parts. Experiments have shown that the dorsal part is in direct relation with the cortex, the ventral not. The ventral part is phylogenetically older and corresponds to the lateral geniculate body of lower vertebrates, which also has no connection with the

[1] *Op. cit* p. 902.

[2] C. J. Herrick and Obenchain, *Jl of Comp. Neurol* XXIII, 1913.

[3] Kappers, *op cit* p 821

[4] Rubaschkin, *Arch. f. mikr. Anat.* LXII, 1903; C. J. Herrick, *Jl of Comp. Neurol* XXVIII, 1917.

[5] Bernheimer.

[6] Von Monakow.

fore-brain, gives off the brachium tecti and receives only crossed optic fibres[1], as is also the case even in the goat and cat. The ventral part in man persists after lesions of the optic radiations[2] and is the rudiment of the lateral geniculate body of lower vertebrates or of the grisæum prægeniculatum of Vogt, Friedmann and Minkowski, which also only receives crossed optic fibres[3]. In the course of phylogenesis the ventral part diminishes as the dorsal part increases and becomes the nucleus principalis geniculati[4]. Its structure becomes lamellated in the cat, and more definitely so in primates and man. Here the outermost layer receives only crossed fibres, the next only uncrossed, and so on alternately[5]. A remarkably large part of the inner segment of the nucleus receives macular fibres[6]. The chief nucleus gives off a large triangular mass of axons on the anterior and upper side (Wernicke's field), the commencement of the optic radiations to the area striata of the occipital cortex.

There is therefore good reason to think that the great majority of retino-geniculate fibres carry the impulses of the epicritic system, but that those which pass to the ventral nucleus are probably dyscritic.

In primates and especially in man some of the optic nerve fibres, both crossed and uncrossed, pass to the pulvinar of the optic thalamus. This increase in the dorso-lateral part of the thalamus is associated with the adoption of the erect posture. It is a correlation area, receiving besides the visual fibres also fibres from the anterior peduncle of the cerebellum[7] and the red nucleus[8]. It is in near relation with the thalamo-cortical fibres to the arm region of the precentral convolution, and its development is probably related to the increased importance of the hand and fingers as organs of exploration[9] It may therefore be regarded as a "centre" for the

[1] Minkowski, *Schweitzer Arch f. Neurol. u Psychiatrie*, VI, 201, 1920

[2] Von Monakow, Winkler, Minkowski, Brouwer See Brouwer, *Monatsch. f. Psychiatrie u. Neurol.* XLI, 129, 1917, *Schweitzer Arch. f. Neurol. u. Psychiatrie*, XIII, 118, 1923, Brouwer and Zeeman, *Jl. of Neurol. and Psychopath.* VI, 1, 1925; *Brain*, XLIX, 1, 1926.

[3] Kappers, *op cit* p 904.

[4] See Woollard, *Brain*, XLIX, 77, 1926, for microscopic examinations of the retinæ and lateral geniculate bodies of the tree-shrew (*Tupaia*), *Tarsius*, the lemuroid *Nycticebus*, and the marmoset (*Hapale*).

[5] Minkowski.

[6] Ronne, *Arch. f. Ophth.* LXXXV, 489, 1913; *Zeitschr f. d. ges. Neurol. u. Psychiatrie*, XXII, 460, 1914; Brouwer and Zeeman, *loc. cit.*

[7] Horsley and Clarke, *Brain*, XXVIII, 13, 1905

[8] Sachs, *Brain*, XXII, 95, 1909.

[9] Kappers.

correlation of eye and hand, and therefore of the utmost importance in stereognosis. This view is strongly supported by the fact that the pulvinar has an extremely rich cortical projection to the angular gyrus. There can be no doubt therefore that the retino-pulvinar fibres belong to the epicritic system.

It is easy to correlate these anatomical deductions with the vital import of the reflexes which are chiefly dependent upon dyscritic vision, and with the cognitive import of visual sensations which are chiefly dependent upon epicritic vision. It is more difficult, and perhaps in our present state of knowledge impossible, to correlate them with the relatively feeble, but still very appreciable, cognitive import of scotopic vision.

CHAPTER XIV

COMPARATIVE ANATOMY OF THE EYE

In agreement with the views expressed in Chapter IV, I have built up the argument of this thesis chiefly on the known facts of visual sensations in man, in whom alone we have immediate knowledge of them. The visual organs of lower animals might be expected to afford a vast amount of evidence for or against the theory. It must be freely admitted that the evidence from this source, in the present state of our knowledge, is very ambiguous. Nor should this, indeed, be unexpected. Light-responsive organs are found in nearly all moving animals, including many of the lowliest invertebrates. There is, it is true, a remarkable uniformity in the general plan of the structure of the receptor cells; but it is a uniformity which characterizes all sensory receptor cells. The mosaic eyes of insects show that it is possible to have a visual organ built on so different a plan from the mammalian eye that scarcely any analogy can be drawn between them.

Confining ourselves to vertebrates, we find great diversities within a common type. Speaking teleologically, this was inevitable. Adaptation to terrestrial life necessarily involved changes in the visual apparatus, life in the air yet other changes. But, apart from these gross adaptations, each species has become specially adapted to a particular environment and mode of life. In these adaptations vision, whilst nearly always retaining an important rôle, has not necessarily been the predominant sense. It cannot be too forcibly insisted that all the facts of perception are biologically determined. An exhaustive investigation of the correlation of the various senses in different animals could not fail to elicit facts of profound physiological and psychological importance. The most cursory observation of their habits and anatomical structures reveals striking differences, such as the lateral line system in fishes, the colossal lobus visceralis associated with taste in certain fishes, the great development of the trigeminal in cyclostomes, some birds (ducks and geese), the crocodile, etc., the high development of smell in monotremes, dogs, and so on. As is well known, the cortex cerebri was built up upon the basis of the sense of smell, to be replaced only later by a neopallium built up upon the basis of vision, to which man owes his supremacy. Hence

the position of the primates is peculiar, and analogies which might well be expected to obtain among them are scarcely to be looked for between them and species of a totally different mode of life.

Moreover, investigations of the vision of lower animals are extremely difficult and have led to very untrustworthy results. We have no certain knowledge of the range of spectral radiations to which lower animals respond, nor the modes of their reactions. The experiments of Hess and others[1], elaborate and interesting as they are, have led only to tentative conclusions.

The most promising field of investigation, from the present point of view, is the structure of the retina in vertebrates. The duplicity theory originated in the observations of Max Schultze and Parinaud on the neuro-epithelium of diurnal and nocturnal animals. Greeff[2] found that there are rods and cones in the retinæ of most mammals, Amphibia, and fishes, the number of the rods much exceeding that of the cones. In birds cones are much in excess of rods. In most reptiles (lizards, snakes, tortoises) only cones are found; diurnal saurians have no rods, nocturnal no cones. There are vertebrates possessing only rods, *e g.* among fishes, rays, and dogfish; among mammals, hedgehog, bat, mole, and night-ape (*Nyctipithecus felinus*). There are also animals of nocturnal habits possessing only rods. Owls, mice, and rell-mice have only a few rudimentary cones; rats also possess a few cones. Hess found rods in fowls and pigeons, though they are scanty in the posterior and superior parts of the retina, which are most used in pecking.

So far, then, the observations seem to confirm the thesis set forth above. But if one investigates the subject more closely doubts arise. It is by no means easy—indeed, it seems to be impossible—to find any definite criterion as to what is a rod, and what a cone. The foveal cones in man, for example, are in no sense conical, but resemble elongated rods—and these are the organs of "cone" vision *par excellence*! The extreme ambiguity is shown by Putter's[3] morphological classification:

I. Outer Limb cylindrical:
  (*a*) Inner Limb cylindrical·
    (1) Foot-piece knobbed: *e.g.* "rods" of rats and selachian fishes.

[1] See Parsons, *op. cit* p 144.

[2] *Ibid.* p. 14; see also Franz, in Oppel's *Lehrbuch der vergleichenden mikr. Anat. der Wirbeltiere*, Theil VII, Sehorgan, Jena, 1913.

[3] In Græfe-Sæmisch, *Handb. d. ges. Augenheilkunde*, II, i, chap. X.

(2) Foot-piece branched: *e.g.* "rods" of sparrow, "cones" of macula of man.

(*b*) Inner Limb swollen:

(3) Foot-piece knobbed: *e.g.* "rods" of man.

(4) Foot-piece branched: *e.g.* "cones" of pigeon.

(*c*) Inner Limb filamentous:

(5) Foot-piece knobbed: *e.g.* "rods" of perch, *Esox*, chondrostoma.

(6) Foot-piece branched: *e.g.* green "rods" of frog.

II. Outer Limb conical:

(*a*) Inner Limb cylindrical:

(7) Foot-piece branched: *e.g.* "cones" of fovea of sparrow, "rods" of *Siredon*.

(*b*) Inner Limb swollen:

(8) Foot-piece branched: *e.g.* peripheral "cones" of man and birds, "cones" of many fishes, etc

III. Outer Limb filamentous:

(*a*) Inner Limb cylindrical:

(9) Foot-piece branched (?): *e.g.* "cones" of *Esox*.

(*b*) Inner Limb swollen:

(10) Foot-piece swollen: *e.g.* "cones" of *Siredon*.

An examination of our present knowledge of the comparative histology of the retina is disappointing, and we must await further information before much help can be derived from this source.

CHAPTER XV

MAN AND HIS ANCESTORS

THE traditional equipment of human beings with five senses is the result of crude psychological analysis of experience, as is also their association with sense organs—smell with the nose, taste with the tongue, touch with the skin, hearing with the ears, vision with the eyes. With the exception of touch these associations are not the immediate result of experience. Crude analysis, too, finds expression in speech of a twofold reference of sensations—to the bodily individual and to the environment, subjective and objective. We feel hot or cold, and we localize touch, temperature, and painful sensations in a certain part of the body; we can even localize a sweet or a bitter taste in different parts of the tongue, but we have no somatic localization of smell. Still less have we somatic localization of hearing or vision. These are pre-eminently objectified—we hear a sound, we see something; similarly we smell something, and we even objectify touch and temperature sensations, as when we say that ice is cold.

This outward reference of our sensations is the basis of reification; it confers adventitious properties upon the sources of our sense stimuli, so that they become *things*. In this way things come to possess colour, etc.; and these properties become so closely knit with the things that they are only with difficulty separated from them. But some properties are more closely knit than others, and those which vary least under the ever-changing conditions of experience become most firmly inherent in the objects. They thus confer a relative stability upon *things*, which indeed is often so fixed that these stable properties persist psychologically in the apparent absence of adequate physiological stimuli.

All experience is experience of *change*, and sensory changes impinge upon a background of cœnæsthesis, a relatively indifferent background which is the resultant chiefly of organic sensations and the traces of immediately prior experience[1]. This background is liable to vague, but widespread and insistent change of tone due to the vital organic needs of the organism—hunger, thirst, etc.—and to emotional disturbance.

[1] *Vide* p. 31.

Nearly allied to these organic sensations, because vital and fundamental to survival, is the sense of position and of change of position, *i.e.* movement of the organism as a whole. These are referred primarily to a so-called static sense, of which we now know that the chief sense organ is the labyrinth. But changes of position or movement of the body or its parts are not referred to this organ or indeed to the outer world, but reveal themselves through the mediation of other senses, especially superficial and deep touch, and vision. This sense of position and movement of the body is to be carefully distinguished from that of the position and movement of things, *i.e.* relative position and relative movement. The former is purely somatic and is not objectified.

Investigations have shown that the sensations into which our perceptual experience can be analysed are subserved by analytically separable receptor-conductor-effector systems. Investigation and analysis have further shown that we cannot experience a pure, isolated sensation. We can reduce the variables to a minimum and then proceed to apply an adequate stimulus to a given receptor and study the results. Such experiments have afforded highly valuable results, but they have also conclusively shown that the results depend not only on the stimuli and state of the receptor organs, but also on the state of the central effector organs, the conducting paths being the most stable part of the system. They have further shown that the functional activity of the central organs is modified by a multitude of factors, especially the results of previous excitation and the backstroke influence of higher centres.

It is even found that not only the same stimulus may produce different sensory responses, but also that different stimuli may produce the same response. This is especially demonstrable in the case of vision, whereas it does not apply to hearing. Moreover, in ordinary experience isolated stimuli do not occur; the sensory response is a response to a congeries of stimuli affecting many sense organs and is the psychological (not mathematical) resultant of the activities of these sense organs acting as a unit whole. Hence it is extremely difficult to classify the senses—even those which have been analytically segregated. The ordinary classification is on a psychological basis, but this is not directly applicable to lower animals, since we can only infer with much trepidation the conscious accompaniments of sensory phenomena in them. Hence the senses of lower animals are usually classified according to the physical stimuli[1].

[1] *Vide* Chapter II.

The physical sources and various manifestations of energy capable of stimulating receptor organs are common to all animals. In lower animals there is little differentiation of receptor mechanisms, and we are forced to the conclusion that composite physical stimuli produce a vague and ill-defined sensory response of the type which I have called dyscritic. Ill-defined as it is it possesses biologically significant meaning, and on the principle that useful acquired characteristics are transmitted we may suppose that repeated exposure to biologically beneficent stimuli will improve the apparatus and its response[1]. Moreover, such improvement and adaptation as is possible will affect the whole system, including the central organs, and not merely the receptor mechanism[2]. Such a process facilitates the utilization of favourable variations, which, leading to differentiation, causes the evolution of specific responses. It further affords some explanation for the evolution of those specific differentiations which are most useful to the animal in its special environment.

It has already been pointed out that the distance-receptors are those upon which the objectifying or reification of the outer world chiefly depends; and these are of relatively late development. Hence we may conclude that primitive sensation is essentially somatic, and that the earliest great forward step in evolution was the development of a projicient sense, such as photo-receptive organs, however poorly equipped it may have been at the start.

If we hypothecate a plasticity of the nervous mechanism as *sine qua non* of phylogenetic advance, we must with even greater urgency hypothecate a plasticity available for everyday use. For no sensory presentation is ever exactly repeated. Even if the congeries of stimuli is practically identical, the responding organs have undergone change. The moor-hen's second dive, and the chick's second peck, are not identical with the first. The first has left memory traces which somehow or other persist, and the second response is a response to a presentation (generally not identical) *plus* a re-presentation.

Moreover, the presentation itself is a complex perceptual pattern, made up of the confluence of sensations of different modality and quality, which confluent complex acts as a unified stimulus. In this confluence or synchysis[3] plurireceptive summation[4] doubtless plays a part, but this alone does not afford an exhaustive explanation.

[1] Cf. Tigerstedt, *Lehrbuch d. Physiol.* 9th ed. II, p. 81.
[2] Cf. Hober, *Lehrbuch d. Physiol.* p. 407.
[3] von Kries, *Allgemeine Sinnesphysiologie*, p. 98, Leipzig, 1923.
[4] *Vide* p. 40.

In it allied—not merely similar—factors from every source, including memory traces, are integrated; and there is a further moulding and modification by backstroke from higher centres. And repetition, however nearly identical, further enriches the conscious content of the experience derived from the presentation by bringing to light elements in it previously unnoticed. When we look at a flower we get at first only a generalized impression of its shape, colour, etc. This generalized impression persists as a memory trace; and on each repeated inspection, if attention be directed to the presentation, as is assumed, fresh traits spring into view, added to the residua of previous presentations. Hence, as James Ward says[1], "such increase of differentiation through persistence of preceding differentiations holds of the presentation-continuum as a whole...;" and "in those circumstances in which we now have a specific sensation of, say, red, or sweet, there would be for some more primitive experience nothing but a vague, almost 'organic,' sensation, which, however, on every repetition of the circumstances, would become somewhat further differentiated."

It seems reasonable to suppose that this ontogenetic mode of differentiation and enrichment of the perceptual pattern reveals also the phylogenetic mode in its fundamental characteristics. In other words, mere repetition of approximately the same presentations to the plastic sensitive plate of the receptive nervous mechanism develops in it more and more highly differentiated perceptual patterns, and the primitive dyscritic response becomes differentiated. Thus, so far as these differentiations are biologically serviceable, neural dispositions are set up, and such neural dispositions, without changing in their fundamental character, become more complex by differentiation, thus subserving more complex conscious responses. And these, since they are biologically serviceable, are transmitted. The fact that the dyscritic and epicritic forms of response are subserved by different anatomical neural structures indicates that some other, as yet unknown, factor comes into play. It seems as if the dyscritic apparatus is capable of only a moderate amount of differentiation, and that at higher phylogenetic levels, alliance is made with structures of greater plasticity. That such is not unlikely is emphasized by the fact that a notably different mode of plasticity by association is superposed upon both dyscritic and epicritic modes at the highest, syncritic, level.

The perceptual pattern, however mobile and fluctuating some of

[1] *Psychol. Principles*, p. 82

its parts may be, is held together by a framework of more constant parts. And these more constant parts are primarily those which are the essential characteristics of *things*, such as form, colour, etc. The constancy of these parts is not a constancy of exact identity, but one of similarity of relations, and similar relations may obtain between parts not necessarily cognate, but of different modality and quality. This is a further elaboration of the principle of plurireceptive summation of different modalities and qualities. This similarity of relations which binds perceptual patterns together is not consciously appreciated in most cases in man, any more than the separate sensations which enter into the manifold of properties which comprise thing-hood are consciously appreciated. What is appreciated is the percept of the thing, which remains the same thing even if seen under very different conditions of illumination, etc.—conditions which arouse very different sensory responses, some of which may even be contradictory.

The source of this remarkable constancy of similar relations in the midst of everlasting change must be sought in its biological significance; for it is obviously of most vital importance. Without it animals would be mere shuttlecocks blown hither and thither by every wind of circumstance. It is the bond which links them to reality. Hence similarity of relations, everlastingly recurring, has moulded neural dispositions, which have been transmitted, so that like presentations cause like responses. Yet these, too, are under the domination in man of syncritic thought, and are reacted upon and re-moulded by backstroke from above.

The profound importance of relative stability of the perceptual pattern, even in the lower psychological levels, is exemplified by the instinctive behaviour of the young chick. It has already been pointed out that instinctive behaviour consists usually of a series of enchained reactions. It is essential that during these reactions the prepotent focus of awareness should be relatively stable.

"The pecking response, as a link in the chain, is elicited by retinal stimulation, when the rice-grain or other small thing is at the right distance On receipt of this, stooping and pecking follow But if the eye stimulus is different, when the grain is further off, the chick goes towards it Thus we have a chain of observable responses, namely, step or two forwards, stooping, pecking, and all that follows. But during the stepping forwards the visual pattern and the posture progressively change To bring the thing off there must be—I believe there observably is—a postural attitude of head and neck, and a *clinging of gaze*, that are maintained If this be so, the *first* observable link in the chain of responses is this postural clinging of gaze. *This is probably the initial and primary response in all effective vision* It is readily observable in the human infant (Cf Miss M Shinn, *Biography of a Baby*, p. 58.)

"Now when a chick has pecked once or twice at medicated rice-grains, the initial response on subsequent occasions is, I believe, *aversion of gaze* with change of postural attitude. . . . The *primary* response to any adequate visual stimulation appears to be clinging of gaze. It seems, then, that *only on subsequent occasions* is aversion in evidence. And it may well be connected with the gustatory stimulation giving rise to shaking of the head which entails change of postural attitude. One must remember that the normal procedure on these later occasions is a restless peering this way and that—"in search of food," as we say. In this process there seem to be (1) clinging of gaze to maggots and things good to eat; (2) not-clinging to things indifferent; (3) aversion of gaze from things nauseous. And when later on nauseous things are ignored, it is hard to be sure whether there is "not-clinging" only or still some aversion of gaze also."[1]

We thus see how ancient and deep-seated is the principle of "keeping your eye on the ball."

There is great resemblance between similarity and movement. Primarily each is a sensory experience, immediately given, and in its most primitive form subserved by a dyscritic mechanism and accompanied by an awareness of "sameness" or "shift." Now this, like every comparison, involves what is to us the concept of judgment, but it is judgment in embryo, as it were. As such it is a lowly form of perception and is very nearly allied to what Helmholtz, in speaking of space perception, calls *Wahrnehmung*. In higher forms both similarity and movement have become susceptible of more detailed analysis by more highly differentiated conscious processes: and thus the conscious appreciation of similarity or movement in man is the function of higher neural centres. Each is a perception in the more ordinary psychological use of the term, and of its German equivalent, *Wahrnehmung*. Hence we find that the perception of movement in man depends upon angular displacement, rate of displacement, and so on[2]. Yet none of these criteria is taken account of in actual experience. This teaches us that the primitive state is not necessarily immediately revealed by the results of experiments on man in which the variables have been reduced to a minimum. Such deductions are like the rationalization of an instinctive act *after* it has been performed, and are equally likely to lead to error. *Because* the primitive condition is a response to the whole situation, which alone has biologically important meaning, it is the "whole" which in some way builds up a nervous disposition which is inherited With greater differentiation parts of the whole can be analysed and observed, and in the highest stage the determining factors, such as minimum displacement in

[1] Lloyd Morgan, *Life, Mind and Spirit*, pp. 106–7, London, 1926.

[2] *Vide* p. 163.

movement, etc., can be elicited, though their neural foundations can only be surmised.

Another instructive example can be taken in the perception of shape or form. A square is a plane figure, bounded by four equal sides at right angles to each other. These are its characteristics, and many other such, *e.g.* the parallelism of the sides, etc., might be mentioned. Yet no heed is taken of these in the immediate concept or actual perception of a square. None the less, the recognition of the form depends upon the unconscious recognition of individual characteristics, and this depends upon physiological processes[1].

It has been proved that the recognition of forms cannot be explained by kinæsthetic impressions derived from movements of the eyes[2], and the same statement applies to movements. Yet it is not improbable that such factors were active in the phylogenetic development of these perceptions. They have become so deeply embedded in the innate neural dispositions that no psychological analysis reveals them. Similarly, it has been proved that the muscular act of accommodation affords no physiological evidence of appreciation of distance; yet a strong attempt to accommodate when the ciliary muscle is paralysed with atropin causes an apparent diminution in the size of objects ("micropsia beyond the fixation point"). Another phenomenon which seems to depend upon ineffective volitional muscular effort is the faulty projection when an extrinsic ocular muscle is paralysed.

The phenomena of simultaneous contrast show that parts of the perceptual pattern have reciprocal effects upon neighbouring parts, and that these are generally of an opposite nature, brightness of one area lowering the apparent brightness of surrounding areas, colour of one area arousing complementary coloration of neighbouring areas, and so on Moreover, continued fixation tends to diminish differences by reciprocal action. Many phenomena have been included in the category of contrast from a superficial resemblance or reciprocity, though quite different from those mentioned. Thus, many apparent movements, such as so-called movement after-images, have been attributed to contrast. Analysis of the typical forms of simultaneous contrast have shown that these depend fundamentally on quite definite physiological processes, for which Hering's term induction is most suitable. The exact rationale of these processes is so obscure that Helmholtz resorted to a psychological explanation of them. As

[1] See von Kries, *Allgemeine Sinnesphysiologie*, pp 120–121.

[2] See F. B Hofmann, *op cit.* p. 160.

already mentioned, they are in their essential features explicable on purely physiological grounds[1].

Nevertheless, many of the phenomena included under the comprehensive term contrast cannot at present be explained on purely physiological grounds. It has already been pointed out that the perceptual pattern is a psychological whole of a nature different from the whole which is the mathematical sum of its parts. It is a new formation which emerges, but, like many of the examples of emergent evolution already cited, it does not follow that it will not ultimately become explicable in terms of a lower order, in this case physiological terms, with the greater advance of knowledge. Incidentally, one may point out that our knowledge of the parts of the perceptual pattern is very incomplete. Certain parts can be analysed from it and are revealed as sensations of manifold modality and quality acting together to the common end. And since we have never experienced an isolated pure sensation, and know little of plurireceptive summation, etc., except that they are experimentally observed facts, it would be premature too dogmatically to infer that they transcend known physical and physiological laws. And further, Frank Allen's experiments have shown that there is more in physiological induction than had been dreamt of in our philosophy They have shown that the reciprocal activities are much more complex than had previously been discovered; and they have afforded a physiological explanation for many facts which were formerly obscure. It is by no means improbable that they lie at the root of many of the "backstroke" influences of higher centres, of which the modifying and transforming effects of attention are the most striking.

One of the most important effects of purely physiological spatial and temporal induction is that of minimizing differences in the appearance of *things* under varying conditions. Thus, one effect of spatial induction is approximately to equalize the responses to changes in illumination by arousing corresponding changes in the excitability of the receptive organs[2]. Particularly noteworthy, too, is its effect in emphasizing the contours of objects and thus stabilizing their forms. It therefore plays a preponderant part in establishing that constancy of visual objects which is a fundamental necessity amid the ever-changing conditions of experience.

Typical examples of "contrast" which cannot be explained by the

[1] *Vide* p. 209.

[2] Cf Mach, *Sitzungsber. d. Wiener Akad.* LIV, 123, 1866; LV, 11, 1868.

known facts of physiological induction are movement after-images[1] and direction-contrast, such as the lines in Zöllner's figure: and in discussing perceptual patterns many examples have been given which cannot at present be explained in physiological terms. So apparently simple a matter as the visual perception of direction is in reality extremely complex. Dependent primarily on retinal local sign, it is subject to all sorts of modifications, errors, and ambiguities according to the position of the head, the position of the eyes, movements of the eyes, head, or body, etc. The ultimate percept is the result not only of primary sensory stimuli, but also of the interaction of many accessory factors. Such modifications have been described as interpolations (*Umschaltungen*) by von Kries and transformations by Jaensch[2]; they belong to the same class of phenomena as those described as *Gestaltauffassung*, *Vorstellungsproduktion*, *collective Auffassung*, etc.[3] In them the percept, which is the immediate conscious response, is not equally an immediate reflection of the presentational stimuli. It is fired off by them, and in so far is explicable on purely physiological grounds; but it possesses characteristics which appear to be independent of ordinary physiological processes. These, in our present state of knowledge, must be approached and analysed from the psychological aspect; and it is then found that they are to a large extent dependent upon accessory factors of empirical origin, the result of individual experience. They have thus obtained meanings which spring into being, attract attention to parts of the perceptual pattern, modifying it and endowing it with a plasticity which is the superlative characteristic of those higher processes of thought which are subserved by the cerebral cortex.

The attempt to correlate these higher modes of perception with physiological processes in the brain must be left to the future. There is evidence that they are elaborations of the same types of processes as occur at lower levels. Of these, the knowledge which we gain from experimental and comparative physiology, controlled and judicially interpreted in the light of psychological analysis of our own conscious processes, has revealed much and is destined to reveal more.

[1] *Vide* p. 166.

[2] Jaensch and E A. Muller, *Zeitschr. f. Psychol* LXXXIII, 206, 1920; Kroh, *Zeitschr. f. Sinnesphysiol.* LII, 113, 1921.

[3] *Vide* Chapter IV, 3.

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