The plan of the central nervous system : a thesis for the degree of Doctor of Medicine in the University of Cambridge / by Alex. Hill.

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A THESIS

FOR THE
DEGREE OF DOCTOR OF MEDICINE
IN THE
UNIVERSITY OF CAMBRIDGE

BY

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THE PLAN OF THE CENTRAL NERVOUS SYSTEM.

THE anatomical elements of which the central nervous system is composed to which we can attribute specific functions are of two kinds only: nerve cells with their processes branching and anastomosing to make up the matrix felt-work, and nerve fibres. Nerve cells vary extremely in form and size throughout the system, and a proper anatomical classification of these elements would probably throw much light upon the functions of the parts in which they occur. The grey masses we know to be the centres of activity, the white but the roads along which the products of this commerce and traffic are conducted. The conspicuous elements in the grey masses are the cells, and to these we are in the habit of attributing functions indefinitely expressed by the terms Automatism and Reflex Action. Automatism in the absolute sense may or may not be a philosophical necessity. Of its existence as an attribute of any particular group of cells we have no physiological evidence; one after another its strongholds have been invaded and its imperial function replaced by the subordinate one of Reflexion. Nor even of reflexion as an active property of nerve cells have we any evidence. That it is an action which can only be carried out by a combination of which they constitute a part, is obvious, but it cannot be proved that they exercise, in virtue of their properties as cells, any selective influence upon this action. Large and attractive as some of the cells appear in the cord of a mammal, a very different opinion as to their importance would be formed if the cord of a fish were first examined; in the fish the filaments of the meshwork are coarse and conspicuous, the cells little more than nuclei situate at their meeting points. Indeed it would appear that the course taken by the disturbance of nerve force which constitutes an impulse, depends upon the resistance in the matrix felt-work, not upon that in the cells. An impulse travelling up a certain sensory fibre reaches the cell in the spinal cord with which that fibre is in connection; from this it travels, if the road be open, up the sensory tract, either by means of felt-work, or of long or short commissural fibres, because the resistance is less in this direction than it is across from sensory to motor cell. If however the æsthesodic route be blocked, transference across to a motor cell of its own metamer occurs, and a simple reflex action is the result. We can only describe the functions of the cell in this connection as *distributive.* It is the *shunt* at which meet many lines of conduction, and through which alone therefore can a redistribution of the impulse occur; while the course which the impulse now takes depends not upon the resistance within the cell but in that in the various lines of conduction which diverge from it. I should regard the distributive function of the cell in this instance as *re-directive.* A simpler arrangement appears however to obtain in the case of the ganglion cells of the retina. Here the fibres connecting the rods and cones with the ganglion cells are much more numerous than those connecting the ganglion cells with the primary optic centre, and the object of the interposition of the cells is to condense, in other words, the *distribution is associative.* Many instances occur to us of an arrangement the reverse of this; compare for instance the single process reaching each cell of Purkinje in the cerebellum (cells not wholly unlike the ganglion cells of the retina in external appearance) with the number of processes leaving it. In this case the *distribution is dissociative*, and probably the function of nerve cells throughout the system is to a very large extent that of increasing the number of fibres towards the periphery. *Nerve cells may be regarded as the nodal points of the nerve-network.*

The fibres, by which term when used without further qualification is to be understood the essential elements of the fibres, the axis-cylinders, were described by His as outgrowths of the cells. This description has been fully confirmed by Vignal's[1] recent researches. They may therefore be regarded as, permanently and throughout their whole length, cell processes. This explains their dependence for nutrition upon the cells.

Nerve fibres differ from one another in two respects. Firstly in the presence or absence of a medullary sheath, and secondly in regard to size.

Histogenetically the medullary sheath is a secondary structure, formed of mesoblastic cells applied around the exterior of the fibre. Composed almost entirely of a phosphatic fat it constitutes a barrier to the passage to the fibre of the fluids of surrounding tissues, and would also prevent, if the disturbance of nerve force resembles in this respect an electric current, the dissipation of its energy to surrounding conductors and the inductive action of neighbouring currents. The analogy in structure between a medullated nerve and an insulated electric conductor is so obvious as to tempt one to suppose that the *presence of a medullary sheath depends upon the need for insulation only.* Various anatomical facts occur to me in justification of this hypothesis. For example, the long unprotected course of fibres of Remak in the olfactory mucous membrane, seat of origin of the least localized of our senses. In the case of efferent nerves, it is impossible by stimulating the grey fibres of the sympathetic to bring about a localized contraction of plain muscle fibres; the result is always on the contrary a reluctant long-drawn spasm or peristalsis. As an instance intermediate between these two extremes of nerve fibres, those on the one hand conveying sudden impulses to each individual muscle-fibre and those on the other hand carrying gradual impulses, one might almost say contractive influences rather than impulses, to a muscular mass, through which they will further travel from fibre to fibre, we may take the case of the nerve fibres supplying the red muscles in the rabbit. I find

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[1] *Travaux du lab. d'Histologie du Collége de France*, 1885, p. 141.

those going to the soleus, for example, to measure only two-thirds as much in diameter as those going to the gastrocnemius; a proportion in harmony with the structure and mode of contracting of the two muscles. I cannot help thinking that the size of the whole structure depends principally upon the amount of the medullary sheath, and that this varies with the need for rapid, undiminished conduction and localized action. On this ground I should account for the great thickness of the medullary sheath in the long sensory nerves and also in the peripheral fibres of the posterior columns of the spinal cord, these latter being the fibres which, there are reasons for believing, run the longest course.

These are the only elements which as far as we are aware enter into the construction of the central nervous system ; and were it possible to unravel this system, we should probably find it to be composed of simple combinations of these elements, the combinations constituting as it were primary couples by the complex connections of which the whole intricate machine is made up. The direction which an impulse takes through this machine, whether it be immediately reflected through the mechanism of a primary couple or whether it be broken up and distributed through many couples, depends upon the resistance in the lines of conduction. No specialized structures are set apart for the reflexion of certain sets of impulses. The nerve centre is the chimera of anatomists, a fabulous mixture of incongruous elements, which is nowhere to be found. Our so-called centres are merely the meeting points of lines of conduction. Suppose an impulse to be generated in a sensory nerve of the foot. This is conducted up a well-insulated nerve to the æsthesodic region of the spinal cord. From this, through the mechanism of a primary couple, it may be immediately redirected to a motor nerve of the region in which it originated. If the route up the æsthesodic part of the cord be blocked by section, or what comes to the same thing by the functional depression of the receptive nerve mechanism in the brain, this immediate primary reflexion occurs. In the case of ordinary sensory conductors, however, the resistance interposed between the termination of the posterior root in the cord and the cortex of the brain, is less than that between the neighbouring sensory and motor parts of the cord, and as long as the way is open the impulse takes the longer route. Where however a so-called "centre" exists, the constant passage across of impulses has broken down the resistance; has widened as it were the conducting roads. For instance, an impulse from the lungs, travelling up the sensory fibres of the vagus nerve, reaches the æsthesodic part of the medulla. Between this and the motor fibres by which the respiratory muscles are innervated, the resistance is slight. The constant passage of impulses has beaten down a broad path, and without the awakening of our consciousness, the mechanism of inspiration is called into action. It is however possible for us, by exalting the activity of the cortical connections of the vagus nerve, by directing our attention to the impulses received through this nerve, to diminish the resistance in the longer circuit, so that either the whole or a part of the nerve current (we have no means of determining which) takes the longer route, and the movements of respiration are carried out through our consciousness and volition. Let, however, the stimuli from the lungs gather head and reach a certain degree of urgency, and no effort of the will can prevent their breaking through the shorter circuit. I propose now to show how the anatomy of the nervous system admits of the existence of these two kinds of mechanism only, the simple couple of corresponding sensory and motor elements, situated in the basal part of the system, and the higher cortical mechanism with which it is connected.

Anatomy.—The study of the structure of the brain presents very considerable difficulties, owing to its resistance to staining agents and the impracticability of all methods of dissociation. Hence its investigation with the aid of the microscope, from which so much was expected, has proved a signal failure. In justification of the use of such a strong expression I have only to appeal to the discordant results of various observers. A conspicuous mass of large cells, the nucleus ambiguus, I find allotted by different neurologists to each of the four nerves connected with the medulla. At the present moment a controversy is being waged as to whether the largest mass of grey matter in the brain, the nucleus lenticularis, is or is not connected with the overlying cortex from which it is separated (at the seat of origin of the supposed connecting fibres) by less than a quarter of an inch. The huge mass of fibres composing the corpus callosum is by some anatomists supposed to consist of transverse commissural fibres between the hemispheres only—by others to be restricted to the fibres of decussation derived from the crura cerebri. If after all the time and labour which have been devoted to microscopic investigation of the brain such discrepant opinions are possible, it is time that this method as well as naked-eye observation was treated with the utmost distrust, and recourse was had to fundamental morphological and physiological considerations to obtain a conception of the plan of structure of the system.

Originating as an involution of the epiblast, the tubular character of the primitive central nervous system is the key to the position. Although the tube is dilated in the anterior region (fig. 1), this character is recognisable throughout its whole extent. The first differentiation, which occurs in the tube, results in its separation into three concentric parts, of which the inner becomes the epithelium of the central canal, the middle, what I propose to call the CENTRAL GREY TUBE, and the outer, the conducting matter of the white columns.

Fig. 1.

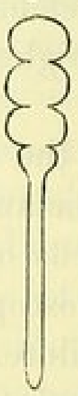


Fig. 2.

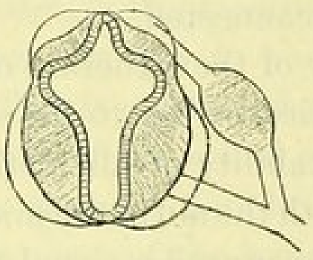
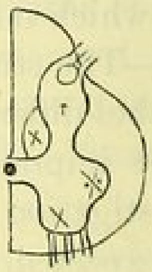


Fig. 3.



[*In figures* 3—11 *the cells of anterior horn are marked by the large cross, of lateral horn by the large cross with dots, of visceral horn* (*Clarke's column*) *by the small cross, of posterior horn by dagger.*]

The sequence of the changes by which this grey tube is converted into the several cell groups has not been satisfactorily determined. But it would appear that the lozenge shape of the central canal early divides it into four columns, which constitute eventually the two anterior and two posterior horns (fig. 2). Although the assumption of a permanent form by the nerve cells would appear, from Kölliker's description, to occur first in the posterior horns, the anterior are, at an early period, by far the larger, while the small size of the posterior is compensated for by the large ganglia of the posterior roots. Whatever may be the history of their formation, we eventually find, in any typical section of the cord, four groups of cells, consisting of three well defined classes (fig. 3). Of these, two groups are situate in the ventral part, the cells of the anterior and lateral horns respectively, which blend together in the cervical and lumbar enlargements, but in other regions are separate. The relative sizes of the cells of these two groups vary somewhat in different parts of the system, but their structure is sufficiently similar to justify us in considering them as belonging functionally to the same class. Their diameter varies from 67 to 135μ (Schwalbe); as seen in hardened preparations, they appear angular, but when examined fresh, in a drop of serum, they are globular or ovoid in form; the nucleus is extremely large (20μ in diameter) and contains a single round nucleolus; they are provided with numerous branching, and a single unbranched (axis-cylinder) process. In short, the characters of these cells are sufficiently well defined to enable us to recognise them in whatever part (of the central grey tube) they may occur. These cell groups constitute continuous columns extending throughout the whole central grey tube, presenting nevertheless, in certain animals, the eel for instance, well marked alternations in number coincident with the somatomes. This metameric arrangement Schiefferdecker poetically characterized as a "Rosenkranz."

Further, the number of cells in any region varies obviously as the number of motor fibres derived from that region. Birge[1] thinks that by the method of counting, he has proved, in the frog, an exact numerical equivalence, and although there may be some difficulty in accepting his conclusion as justified by

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[1] *Archiv für Anat. und Physiologie*, 1882, p. 435.

observation, owing to the impossibility of recognising with certainty different parts of the same cell, when occurring in several sections, we are, nevertheless, fully justified in believing that *every motor fibre* is immediately, before leaving the cord, *connected with a motor cell of its own metamer.*

Lying on the inner side of the cervix cornu posterioris, is a column of cells, known generally as the columna vesicularis of Lockhart Clarke, and long occupying an anomalous position. Evidently distinct from the posterior horn, the column contains cells agreeing in form, but not in size (diam. 40 to 90 μ), with the cells of the anterior and lateral horns. In their pathological changes, these cells stand apart from both anterior and posterior horns. In number, as Gaskell has shewn, they *vary with the leucenteric fibres of the visceral root,* of which indeed there can be no doubt they constitute the primary metameric centres. The posterior horns contain the Substantia gelatinosa of Rolando, a tissue still as enigmatical as ever, but in consideration of its early formation, its large amount in the foetus and in lower vertebrates not to be safely passed over as non-nervous; they also contain numerous spindle-shaped cells (diameter 18 μ). Direct connection between these and fibres of posterior roots has never been observed. The exact mode of termination of sensory fibres in the central grey tube I shall treat of in detail further on. The cells are not sufficiently well defined to admit of counting, nevertheless the obvious correspondence between the amount of grey matter in the posterior horn and the number of fibres in the posterior roots can leave us in very little doubt as to the *termination of every sensory fibre, either directly or indirectly in a cell of its own metamer.* We thus find, and this I think should be accepted as a physiological axiom, that throughout the cord, *the whole of the central grey tube is taken up in forming the primary metameric centres of the anterior, visceral and posterior branches of the spinal nerves.*

In the Medulla Oblongata, although for functional reasons the dorsal wall of the tube is in part undeveloped and the grey matter constitutes therefore a plate rather than a tube, it is easy to show that the disposition of the cell groups with regard to the three kinds of nerves is the same as in the cord. By the divergence of the posterior white columns, the posterior cornua with their substantia gelatinosa Rolandi are dislocated outwards (figs. 4, 5 and 6). The anterior cell columns are brought up into the mid-dorsal line. The column of Clarke occupies the same position with regard to the cervix cornu posterioris, and lies therefore in the floor of the 4th ventricle midway between the anterior and posterior horns (fig. 7). In the position of the lateral horn, a strange displacement has occurred. By the crossing of

Fig. 4.

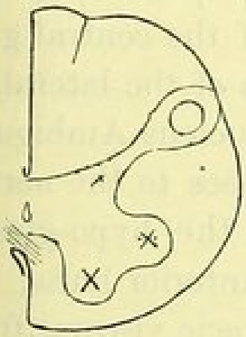

Fig. 5.

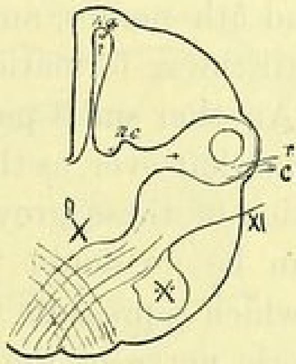

Fig. 6.

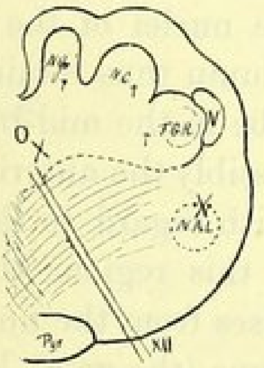

FIG. 4. Showing dislocation of posterior horn outwards and first crossing fibres of anterior pyramids.

FIG. 5. Showing isolation of lateral horn by crossing fibres.
C 1 ramus posterior of first cervical nerve.

FIG. 6. Origin of hypoglossal nerve.
NG nucleus funiculi gracilis; *NC* nucleus funiculi cuneati; *TGR* tuberculum Rolandi; *N.AL* nucleus antero-lateralis of Clarke.

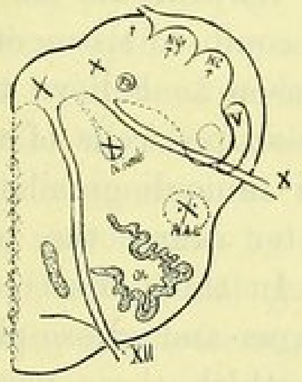

FIG. 7. *FS* fasciculus solitarius; *N.Amb* nucleus ambiguus; small cross enlargement of visceral horn into common nucleus of leucenteric fibres of vagus, glossopharyngeal and pars intermedia of seventh.

the fibres of the lateral white columns, it has become detached from the rest of the grey matter and lies in the middle of the lateral part of the medulla, as marked off by the fibres of the hypo-glossal and vagus nerves. In this part of the medulla it is known as the antero-lateral nucleus of Clarke, but there can be little doubt that this is serially if not directly continuous with the nuclei of the 7th and 5th nerves, and the position of the column thus retained until the re-formation of the central grey tube in the mid-brain. Another small portion of the lateral, or possibly the anterior horn, is left over, as the Nucleus Ambiguus. With regard to the relation of these grey masses to the nerves of this region; there can be no doubt that the hypo-glossal arises from the nucleus, which represents the anterior horn; the vagus (the great leucenteric nerve of the thoracic viscera) from the continuation of Clarke's column; but much time and laborious research have been devoted to the determination of the nuclei of the spinal accessory and glosso-pharyngeal nerves. And so various are the opinions of different observers upon this subject, that I think we are justified in setting aside the results of microscopic research, and allotting the grey matter of this region among the nerves of different function, according to the character of its cells and their relation in situation to the several columns of the cord. Now even in the cord the direct connection of posterior root fibres with cells of the posterior cornu has never been observed. Why should we expect to find such a connection in the more confused tissue of the medulla? In the cord we have every reason to believe that the sensory fibres join at last the spindle-shaped cells of the posterior horn. In the medulla the nuclei funiculi gracilis et cuneati as well as some of the grey matter nearer the median line, consist of similar fusiform cells. In them must terminate therefore the sensory fibres of the vagus and glosso-pharyngeal nerves, while the leucenteric fibres which these nerves contain go to the columna vesicularis. The antero-lateral column of Clarke corresponds in situation and cell formation with the lateral horn, and must give origin therefore one would suppose to fibres of the spinal accessory nerve, which has been arising from this lateral horn for some distance down the cervical cord. The large cells of the nucleus ambiguus give origin to motor fibres, either of the spinal accessory or the hypo-glossal nerve.

In an anterior section carried through the region of the Pons (fig. 8), we find the fibres of the 8th pair of Willis. Of these the auditory pass partly to the swollen posterior horn, partly cross the floor of the ventricle as the striae acusticae, partly up, in the middle peduncle, to a portion of the dorsal wall of the central grey tube, which has here, owing to the local retention of the primitive tubular form, been developed above the central canal as the "nucleus of the roof" of Stilling. Outside the substantia gelatinosa, and therefore quite beyond the posterior horn, another group of cells is to be found, lying on the auditory nerve (Meynert's anterior nucleus, Schwalbe's nucleus accessorius). But this nucleus consists, as remarked by Schwalbe, of small globular cells, surrounded by nucleated capsules and resembling the cells of the spinal ganglia. Indeed, this is nothing more, as shown by its position, as well as by the nature of the cells of which it is composed, than the ganglion on the posterior root of the nerve of this region (8th), included by the great late development of the commissural fibres of the two sides of the cerebellum, which surround the primitive nerve tube, and only apparently increase its bulk. It is worthy of note that a ganglionic enlargement is a conspicuous feature of

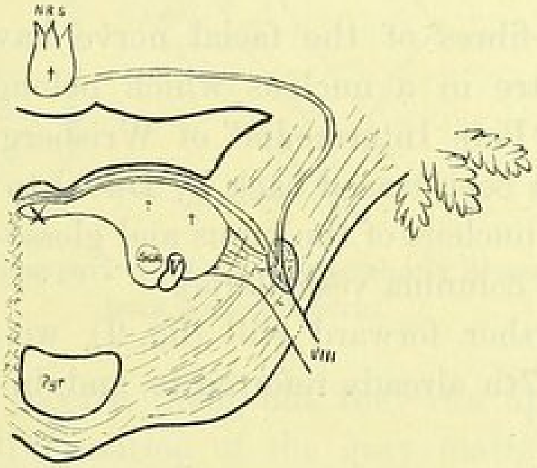

FIG. 8. Showing triple origin of eighth nerve and position of its posterior-root-ganglion.

SGR substantia gelatinosa Rolandi; *V*, as in other figures, ascending root of fifth nerve; *NRS* nucleus of roof of Stilling.

the developing auditory nerve as observed in chicks and in dog-fishes, and that a group of nerve cells is to be found upon the auditory nerve of the frog just after it has parted company with the facial (a point not hitherto noticed, as far as I am aware).

The motor fibres of the facial nerve have their primary metameric centre in a nucleus which belongs to the lateral column. The "Pars Intermedia" of Wrisberg, visceral branch of this pair, has been traced back by Duval to the anterior part of the common nucleus of the vagus and glosso-pharyngeal (continuation of the columna vesicularis).

A little farther forward still (fig. 9), we cut through the nucleus of the 7th already referred to, and, in the same section, appear the nucleus of the 6th, and, to a slight extent, even that of the 8th, showing, in their relative arrangement, perhaps even better than anywhere else, the position assumed by the several columns of the cord, in their continuation upward through the basi-cerebral part of the central grey tube. In the mid-dorsal line lies the anterior column, forming here the nucleus of the 6th. Clarke's column has disappeared. The posterior horn receives the fibres of the auditory nerve. Still isolated in the lateral region lies the lateral horn, giving origin here to the fibres of the facial.

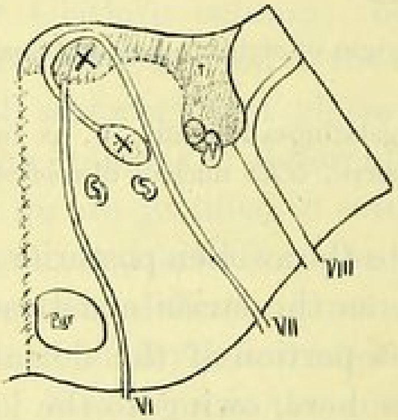

Fig. 9. Origins of sixth, seventh and eighth nerves from anterior lateral and posterior horns respectively.

In the next section (fig. 10) is seen the entrance of the sensory fibres of the 5th, which divide to embrace the substantia gelatinosa, just as do the fibres of a posterior root of the cord. No local swelling of the posterior horn occurs, however, in this region to receive them, but they run up and down the spindle-shaped cell formation of the grey matter of the whole mid- and hind-brain. An extensive intra-cerebral distribution, quite justified by the wide distribution of the Trigeminus upon the scalp and face.

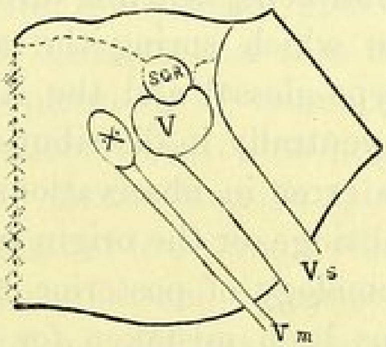

Fig. 10. **Origin of motor part of fifth from lateral and of sensory part of fifth from posterior horn.**

Arrived now at the mid-brain, the several cell columns reunite, and we find, around the aqueduct of Sylvius (fig. 11), the least altered portion of the central grey tube, which anywhere occurs in the central nervous system. In the ventral part of the tube, continuation upward of the anterior horn, lies the large-celled nucleus of the motor oculi nerve. Issuing from this nucleus, fibres, like those of an anterior root of the cord, pass ventrally through the white column. From the point of view

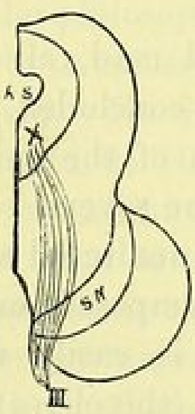

Fig. 11. **Origin of third nerve from ventral part of reunited central grey tube.** *AS* **aqueduct of Sylvius.**

of adult anatomy, no one could imagine that this nerve is homologically other than an anterior root. It originates in a group of typical motor cells, which is directly continuous with the cell column from which spring the anterior roots of the spinal nerves, the Hypo-glossal and the Abducens. In course, the nerve is directed ventrally, in distribution it is purely motor. Either there is some error in observations which connect this nerve with the neural ridge, or the origin from this ridge is no test of the serial homology of posterior roots. Is it possible that the 4th nerve has been mistaken for the 3rd? That the 4th, the Trochlearis, has a history, of the early periods of which no record is preserved in vertebrate archives, is shown in its anomalous origin from motor cells, in the dorso-lateral part of the central grey tube, in its decussation above the mid-brain, in its mixed motor and sensory distribution in Selachians and Amphibia. No one who has seen it in the Skate, for example, issuing from beneath the cerebellum close to the middle line, passing obliquely forwards and outwards to the roof of the cranial cavity, there to break up into several branches, can have failed to notice that it stands quite apart from all other cranial nerves.

Throughout the spinal cord, all the grey matter of the central tube is, we have concluded, devoted to forming the primary metameric centres of the spinal nerves. Throughout the hind- and mid-brain, the several columns of which this grey tube is composed remain unaltered as to the character of the cells of which they are composed, and although displaced in position, their continuity is easily recognisable. Excluding certain new cell formations (the olives), of the meaning of which we are entirely ignorant, the amount of grey matter, proportionately to the number of fibres of the several entering and issuing nerves, remains unaltered. It is only logical therefore to conclude that the *whole of the central grey tube of the hind- and mid-brain is devoted to forming the primary metameric centres of the nerves of these regions.*

Physiological.—In no part of the hind- or mid-brain have we found any compound structure corresponding to the anatomically mythical "nerve centre." Whether or not physiologists at the present day, when referring to these nerve centres, have in their minds the conception of a composite structure, like the fabulous chimera, with lion's head, goat's body and dragon's tail, I do not know. Certain it is that the physiologists who first described them, pictured, in these centres, collections of cell elements, by means of which what might be termed official work was carried out. In the Medulla Oblongata was situated the "nœud vital," a kind of little brain, which presided over the entire mechanism of respiration. Apparently coincident with the antero-lateral nucleus of Clarke, lies Owsjannikow's vaso-motor centre, which, from the careful measurements of size, one must suppose was regarded as a cellular structure; possibly the large multipolar ganglion cells in this region were considered as having the specific function of vaso-constriction, and to remain over after cells had been allotted to each afferent and efferent nerve. In the medulla again are situated the centres for deglutition, vomiting, inhibition of the heart, general convulsion and many other co-ordinated actions. Indeed any physiological theory is immediately rendered intelligible by throwing the onus of responsibility upon a "centre" in the medulla. The centre is the philosopher's stone of the physiologist, with which he expects to transmute his edifice of hay and stubble into substantial gold. No doubt the term centre is a convenient one, but it should be clearly understood that, like the term "cell," the word has acquired a purely technical significance, and that the structural arrangement would be better expressed by the terms *junction* or *shunt*.

The great visceral sensory nerve, the vagus, discharges a torrent of impulses into the æsthesodic region of the medulla. Some few of these travel through to the cells of the cerebral cortex, and knock there with sufficient force to awaken consciousness; but the great majority are diverted along the broad tracks, the resistance in which, by the passage of innumerable similar impulses, has been broken down, to the associated motor cells. Thus an impulse of a certain kind, proceeding from a certain visceral area, gives rise to a definite organic process with or without the provocation of consciousness and the acquiescence of the will. In some cases, it is possible for us, by directing our attention to the matter, to inform ourselves of what is taking place; in others, and these are the reflexions peculiar to vegetative life, the impulse has long since ceased to travel upwards to the seat of consciousness. The existence of so many "centres" in the medulla depends upon the fact that this is the lowest limit in the central grey tube at which it is possible for a visceral afferent impulse to be brought into connection with a motor mechanism, and the inhibitory influence of the cortex depends to a very large extent merely upon its sharing the impulses with the medulla. Conversely the increase in the amount of reflexion which takes place through the medulla in hypnotism and cerebral disease is due to the lowering of the receptivity of the cortical mechanism.

During hypnotism Heidenhain[1] notices beside spasm of the accommodating mechanism of the eye and active dilation of the pupil, increased rapidity of breathing, perspiration and (?) increased flow of saliva. He, however, as it appears to me regards these phenomena from the wrong standpoint when he speaks of them as due to "irritation," "stimulation of the respiratory centre in the medulla," and so forth. Rather do they indicate that as long as the cortex is normally receptive a considerable amount of the nerve current is diverted towards it; when its excitability is depressed all the nerve current passes immediately across from the aesthesodic to the kinesodic region of the medulla.

During functional depression of the cortex due to disease or to concussion, rapid shallow breathing, slow full pulse and vomiting are the usual symptoms, due, as I should suggest, to the transference across from sensory to motor tract of the impulses calling for respiration, for cardiac inhibition and for vomiting respectively, undiminished by the diversion of a part of their force to the higher regions of the brain. The increased reflexion in the medulla is due, not to a removal of the restraining influence of the cortex, but to the blocking of the channels along which a part of the force travelling through it would otherwise have been directed. Conversely the diminution

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[1] *Animal Magnetism*, trans. by Wooldridge, pp. 30 and 31.

of reflexion while the cortex is functional is not an active "inhibitory" phenomenon but a question of physical subdivision of force. The language which has grown up around the subject owes its origin to the commercial conception of "centres." No such centres in this sense exist.

In no case does the theory of centres and its terminology become so incomprehensible as when it allows of the formulation of a "convulsive centre." A brain within a brain. A unit of the central nervous system yet holding the reins of all, and capable of starting every motor cell which it contains into activity. Nor is it possible to dissociate in one's mind from the idea of such a centre the picture of it as consisting of a group of cells, although, as we have shown, no motor cells in the medulla would remain unallotted if a single one were given to each issuing motor fibre. It is possible to give an intelligible explanation of the onset of convulsions in asphyxia without the use of the term centre or the suggestion of ideas contrary to anatomical facts. The impulses reaching the aesthesodic tract of the medulla from the regions in which the need for arterialization of the blood is felt are directed in the first instance through certain motor cells to the fibres by which the muscles of inspiration are innervated. The movements so produced failing to improve the condition of the blood, impulses of ever increasing force pour in insisting upon this result. These more powerful impulses overflow the channels through which the respiratory reflex is ordinarily carried out and traverse routes in which the resistance is normally greater than it is in these well-beaten paths. Their passage is aided by the direct action of the venosity of the blood which like strychnia and certain other poisons increases the transverse conductivity of the cord, and so at last the impulses are distributed to all the motor cells of the system. It is quite possible no doubt to speak of centres of deglutition, vomiting, respiration and all the other reflex actions in which the vagus nerve plays a part without imagining the existence of separate cell-groups in the medulla to serve as offices from which they are directed, but the term "centre" is a misleading one and the real state of affairs would be better expressed in language borrowed from the science of electricity. In electricity the expressions *shunt* and *lines of conduction* have acquired a definite meaning and would well serve our purpose. The views here advocated are by no means new. G. H. Lewes, for instance, bitterly resented the tyranny of the nerve cell, and since the date at which he published, various groups of cells, which, by presiding over special reflex actions were supposed to diminish our difficulty in understanding the initiative of vital processes, have been shown to have no such function. My protest is based on different grounds to Lewes', and my wish is, not to introduce any new theory of nerve action, but merely to curtail those already in circulation. The *centre* theory exaggerates the phenomena of localization of reflexion. It compels one to picture a specialization of structure which does not exist—from sacral cord to optic thalamus the central nervous system consists of sets of elements in definite numerical relation to its entering and issuing fibres, no alteration in this proportion occurring in the medulla or elsewhere at the seats of the so-called centres. It is impossible to imagine these centres except as consisting of cells, whereas physiologically the cells are of secondary consequence, the fibres and meshwork of processes being first in importance. In lower Vertebrates these latter constitute a simple strongly marked system while the cells are inconspicuous. In certain instances, on the other hand, the retina for example, the cells although large and structurally indistinguishable from others supposed to be endowed with high functions, serve as we know the purposes of nutrition and distribution of impulses only.

It may be noted by the way that one of the most marked phenomena exhibited during reflexion through the medulla is the *blocking of neighbouring conductors while impulses are being reflected through a particular shunt.*

Meltzer[1] has noticed that during the act of swallowing the heart's beats are quickened, the blood pressure falls, respiration is postponed. The same depression of the tendency to reflexion through other "centres" appears to me to accompany any reflex act.

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[1] *Archiv f. Anat. u. Physiologie*, 1883, p. 209.

The most sensitive measure of the quantity of impulses passing across the medulla is the beating of the heart. There is every reason for believing that impulses are constantly reaching the medulla and being there reflected down the vagus nerve to the heart, upon which they exercise a slowing influence. Whenever the amount of reflexion is diminished the heart's action quickens, and such a diminution of reflexion is produced not only during the passage across of the impulses which lead to *swallowing* but during *inspiration,* during (?) *vomiting,* and as I find to be remarkably the case during *sneezing* and *yawning*, although in the latter instance it depends principally perhaps upon the deep inspiration. The quickening and slowing of the pulse during respiration is commonly explained by saying that the cardio-inhibitory centre is stimulated into sympathetic activity, despite the fact that it is during inspiration that its activity is diminished and the heart allowed to beat more quickly.

To return to the anatomical question; Does this distribution of the grey matter of the central tube cease at the anterior limit of the mid-brain? Are the so-called "basal ganglia" structurally and functionally superior to the metameric centres of the spinal cord? Or, approaching the question from the other side, do the optic and olfactory nerves differ from all others in being unconnected with the central grey tube? In the first place, we must make a broad distinction between the optic thalami and the corpora striata. The former are developed in the wall of the third ventricle, in the direct continuation, that is to say, of the nervous axis. The latter belong to the paired outgrowths of this vesicle, the cerebral hemispheres; there is therefore no reason for supposing that they ought to be placed together in a single category, or that what applies to one must necessarily be equally true of the other. Taking the optic thalamus first therefore, we note (1) that it is impossible, in the adult, to separate it from the grey matter surrounding the aqueduct of Sylvius; it is also absurd to attempt to make a distinction between the thalamus and the rest of the grey matter lying at the sides of and beneath the third ventricle. In other words the thalamus is an integral part of the grey tube, which extends throughout the whole length of the nervous axis. Further, (2) like the small-celled grey matter of the spinal cord, the thalami are connected together by a grey commissure. (3) Although the minute structure of the thalamus is not sufficiently well known for us to assign to it, with any degree of certainty, its functions by comparing its structure with that of the spinal cord; it is certainly very similar to the parts which we have elsewhere regarded as the primary metameric centres of the sensory nerves. More particularly does it resemble the small celled formation of the Medulla Oblongata. (4) In its development it follows the same sequence as the rest of the grey tube both in time and in cell differentiation. It lies immediately on the outer side of the epithelium, on the inner side of the white tube. Everywhere else the grey matter of the posterior horn is built up around the substantia gelatinosa of Rolando, a tissue of remarkable importance in the foetus. Löwe[1] has shown that this substance constitutes, in the thalamus, the "centre médian" of Luys. What reason is there therefore for supposing that the plan carried out in every other metamer of the body is suddenly abandoned when we reach the first? In other regions the sensory nerves terminate in a small-celled formation of their own metamer; the connection between the optic nerve and the thalamus (including in the thalamus the habenula and geniculate ganglia) is so well known as to need no illustration. *The optic thalamus is therefore the primary metameric centre of the optic nerve.* Is it exclusively devoted to this nerve? This question can only be satisfactorily answered by noting its development in blind animals. In the mole the thalamus is small but not absent. We have, moreover, another nerve developed in connection with the anterior cerebral vesicle, the olfactory. As Marshall[2] has shown, this is to be seen in third-day chicks, arising from the neural ridge of the anterior cerebral vesicle. It must therefore be primarily connected with the grey matter lining this part of the involuted epiblastic tube. There is good reason

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[1] *Beiträge zur Anatomie u. z. Entwick. des Nervensystems.* Bd. I. s. 102.

[2] *Proc. Royal Society*, No. 193, 1879; also Vol. XXVI. p. 50; also *Quart. Journ. Microscopical Science*, 1878, p. 17.

for believing that the primary nerves are not only early connected with the central grey tube, but are actual outgrowths of this structure, their axis cylinders being nothing more than the processes of the first nerve cells. As Marshall points out, the connection of the olfactory nerve with the cerebral hemispheres is secondary and adaptive only. If this be so, I should insist that their primary connection must remain, however much this connection is obscured by adherence to the margin of the cerebral mantle, and possibly even by interruption by cell elements. Nor is this connection with the anterior part of the grey matter so difficult to realize in the adult. In all animals with a well developed sense of smell, the external olfactory stria passes into the pyriform lobe, which is again connected with the anterior part of the thalamus by the strongly developed fornix. In the hardened brain of the ox, as shown in fig. 12, these parts can be most easily broken off, and constitute a single piece, with a spiral twist, the continuity of which it is impossible to doubt. The olfactory nerve, on its course to the thalamus, does not appear to become directly connected with the cerebral hemisphere, but merely involved in

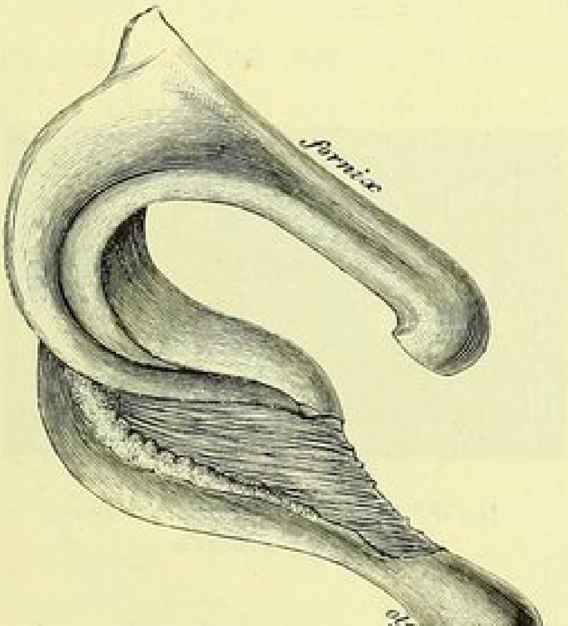
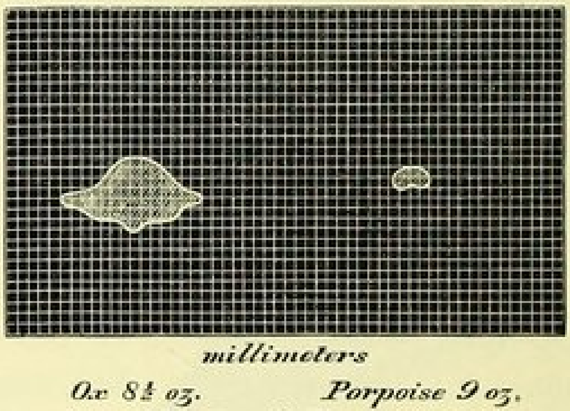


Fig. 12. Fornix, pyriform lobe and olfactory bulb, broken off from hardened brain of Ox.

the lower free border of its cortex. That a functional continuity exists, I have proved by examining the brain of a porpoise (Phocæna vulgaris, kindly placed at my disposal by Mr Clark). In this animal no olfactory nerve is developed, no pyriform lobe, no hippocampus major, and but a rudimentary fornix. Indeed the fornix proper cannot be said to exist, for the part developed contains merely the longitudinal commissural fibres which, in addition to its olfactory elements, belong to this structure. As far as I am able to trace them, the fibres contained in the body of the fornix are those denominated by Huxley "precommissural." The columna fornicis does not appear to be present. [These and other allied questions however I shall hope to be able to answer as soon as I can obtain a supply of fresh porpoise brains.] The brain of the porpoise is remarkable for the great quantity of commissural fibres which it contains as compared with the direct fibres from the crura; the Cingulum for instance is extremely developed.

Fig. 13.



Body of Fornix

In fig. 13 I have represented, for the sake of comparison, the actual size of the body of the fornix as found in the brains of an ox and of a porpoise. The former brain weighed 8½ ounces, the latter 9. When the posterior pillar is traced back to the hippocampus, the comparison is still more instructive. I have not, however, as yet succeeded in obtaining the brain of a porpoise in sufficiently good condition for close microscopic study, and will not therefore at present enter into particulars as to the structure of the hippocampus. It is, however, certain that the cortex mantle terminates in this region, as it does above the corpus callosum, in a blunt border, over which is folded the plicated velum interpositum, on which again rest but a few scattered bundles of fibres as sole representatives of the corpus fimbriatum.

Although, for reasons to be stated further on, I consider the fornix root to be the primary and important one, it is not necessarily in the adult the only course taken by fibres of the olfactory nerve in reaching the thalamus. In the higher mammals, the stria interna is almost as large as the stria externa. What becomes of its fibres, however, is extremely doubtful. It used to be supposed that they crossed to the opposite temporo-sphenoidal lobe in the anterior commissure. This commissure is certainly large in most animals with a keen sense of smell. On the other hand, it reaches its greatest development in the Monotremata, in which the stria interna is absent. Broca traces the stria interna to the "carrefour" at the anterior end of the gyrus fornicatus. This again, for comparative reasons, I should regard as absolutely out of the question. As this question of the cortical distribution of the olfactory nerve has an important bearing upon the theories enunciated in the latter part of this thesis, I have reproduced here Broca's scheme. Fig. 14 is copied from his paper, "Sur les centres olfactifs" (Rev. d'Anthropologie 2^e série, T. II. p. 386. See also "Le

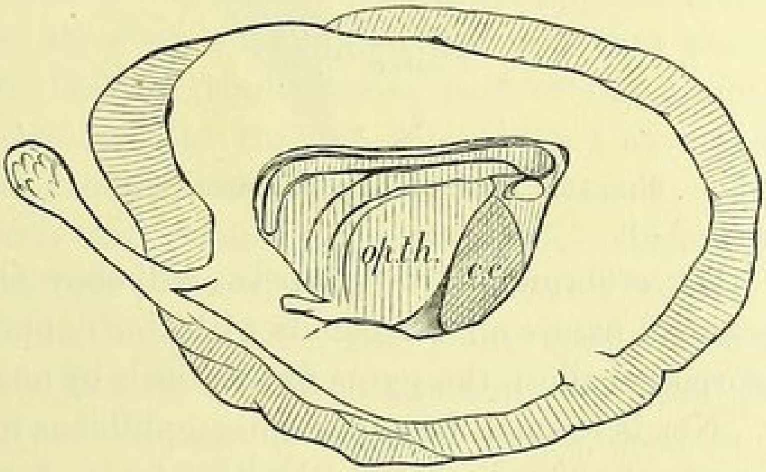


FIG. 14. Copied from Broca's paper. The olfactive region left unshaded.

grand-lobe limbique et la scissure limbique dans la série des mammifères," Rev. d'Anthropologie T. I. p. 385) and shows the area of the cerebrum which he regards as olfactive; all the parts of the figure left unshaded. "Le grand-lobe limbique peut donc être comparé à une raquette dont l'anneau entourant le seuil de l'hémisphère, est formé en haut par le lobe du corps calleux, en bas par le lobe de l'hippocampe, et dont la queue est formée par le lobe olfactif." In all the marine mammalia the sense of smell is either completely absent or very little developed; these animals will therefore best teach us, by their deficiencies, which regions of the brain are concerned with this sense. A glance at fig. 15, in which is represented the inner surface of the cerebrum of the porpoise, will show that, while the hippo-campal fissure almost blends with the dentary, at the splenium corporis callosi, the gyrus fornicatus is by no means ill-developed. Nor is it small in any of the amphibious mammalia, the only groups of animals among which, as far as I am aware, instances are found of the total suppression of the sense of smell. Broca is fully aware of this fact and yet rejects the evidence of these animals, they being as it appears to me the only important witnesses in the case, on the ground that "La psychologie des Cétacés est actuellement (et pour longtemps sans doute) trop inconnue pour que l'on puisse savoir ou présumer quelles sont

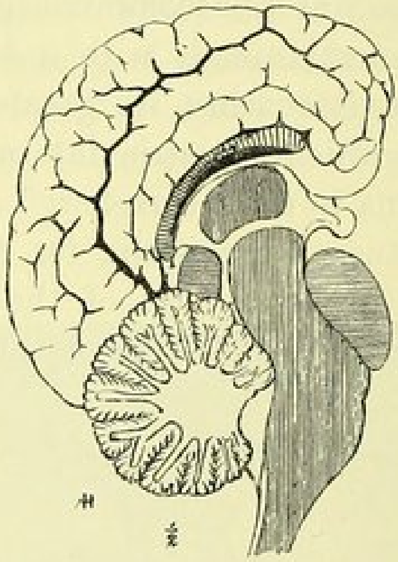


FIG. 15. Brain of Porpoise, inner view.

ces fonctions cérébrales qui se sont développées chez eux au delà du degré que l'anatomie permet d'admettre chez les autres animaux." An argument strangely out of place, as it appears to me, in an anatomical proof! In my opinion the olfactive area does not reach farther forward than the limits of the hippocampal lobule, the extension of which varies greatly in different animals. On the inner surface of the brain the area has rather the form of an upturned sickle than a racquet. To this question I shall be obliged to return when treating of the olfactory nerve.

It appears that in the higher mammalia at any rate a large number of fibres of Broca's middle root pass backwards, in scattered bundles, across the anterior perforated space to join, as Broca thinks, the motor tracts of the crura cerebri; a strange course, as it would seem to me, for the fibres of a sensory nerve, and not to be explained by supposing that the nerve cells of the olfactory bulb are both sensory and motor, and that this root forms a direct path for motor impulses, generated by reflex action in the cells of the olfactory lobe, in response to stimuli from the nasal mucous membrane, thus enabling the dog to "follow his nose" without the cumbrous intervention of a higher cerebral mechanism. To me it appears more probable that these fibres of the middle root pass into the substantia innominata beneath the anterior part of the optic thalamus. In transverse sections through this region I have thought that I could trace them along this course. Even if a direct communication is thus established between the olfactory nerve and the anterior part of the thalamus, this is, as I believe, the result merely of late adaptation. The point upon which I wish to insist is this, *that the olfactory nerve being developed, in the first instance, from the anterior cerebral vesicle, must be primarily connected with a metameric centre in the grey matter on the side of the third ventricle, that the anterior part of the thalamus constitutes this primary æsthesodic centre, and that the original connection is via the fornix.*

The Corpora Striata have always hitherto been classed anatomically with the optic thalami as "basal ganglia," the conjoint system being regarded as connected on the one side with the cord, on the other with the cortex. This classification was based rather upon physiological considerations than upon direct observation. Recently Wernicke has called in question the connection, by fibres, of the nucleus caudatus with the cortex. Microscopically he is unable to trace the exit of fibres of the corona radiata from the convex border of the nucleus. Morphologically, he points out that the connections of the nucleus caudatus, by its head with the anterior perforated spot, by its tail with the cortex of the temporo-sphenoidal lobe (fig. 16), indicates that it is an involuted part of the mantle. With this conception of Wernicke's I entirely agree and should urge the following additional considerations in favour of separating the nucleus caudatus from the optic thalamus.

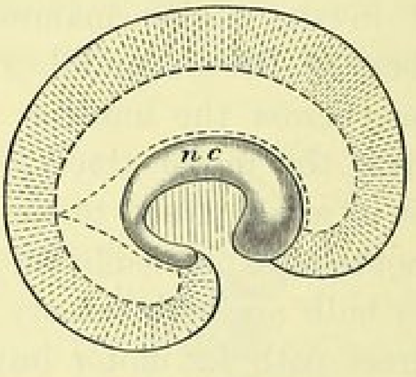


FIG. 16. Diagram showing the relation of the corpus striatum to the cerebral cortex, after Wernicke.

1. It developes from the prosencephalon and not from the anterior cerebral vesicle.

2. In minute structure, it differs notably from the optic thalamus. The structure of these grey masses however is not sufficiently well understood to justify a detailed comparison.

3. It resembles very closely another grey mass, the nucleus amygdaleus, the origin of which, from the cortex, is never doubted.

4. It is characteristic of the aesthesodic portion of the central grey tube that it is built up around the substantia gelatinosa Rolandi. There is no evidence of the prolongation of this formation into the prosencephalic region, and therefore, as far as this character is concerned, no evidence that the corpora striata belong to the central grey tube.

The nucleus lenticularis is inseparably connected with the nucleus caudatus, and must be regarded in the same light.

Our ideas, however, with regard to the anatomy of these structures are derived rather from functional than structural considerations. In the original physiological classification of reflex actions of Carpenter and Todd, intermediate centres were required to carry out such reflexes as they termed ideo-motor. In Meynert's scheme, this work was allotted to the "basal ganglia," which constitute thus his middle node or projection area. Any classification however of reflex actions into serially ascending grades, is unjustifiable. The differences in purposefulness and complexity of different reflex actions depend, as I have attempted to show in my lectures at the College of Surgeons (*Brit. Med. Journ.* Mar. 14 and 21, 1885), not upon the particular centre, by which they are carried out, but upon the number of elements in connection with the primary metameric centre, at which the sensory impulse is first received. The simple twitch, produced by an afferent impulse reaching a detached portion of the spinal cord, differs from the cry of affright, which follows the explosion of a pistol near the head of an animal deprived of its cerebral hemispheres, not because the former is produced in the cord, and the latter in the basal ganglia, but because, in the one case, only the elements belonging to a few metamers, and these devoid of any highly specialized sense organ, compose the reflecting machine, while, in the other, all the centres of the central grey tube retain their normal connections. Further than this, a physiological classification of reflex actions, according to kind, is impossible. Every conceivable grade is represented, from the imitative automatism of a hypnotized person down to the mechanical transference of an afferent into an efferent impulse by the fragmentary nervous system of a brainless frog.

Neither anatomically nor physiologically, far less morphologically, are we justified in placing together the optic thalami and corpora striata in a special group. I propose now to bring forward evidence which to my mind proves absolutely that the corpora striata are not middle men between the cortex and the cord. In studying a hydro-microcephalic brain, the detailed description of which will be published in the July number of the *Journal of Anatomy and Physiology*, I directed my attention particularly to the corpora striata with a view to determining what alteration, if any, in size was associated with extreme congenital deficiency of the cortex. The man was 19 years old at the time of death. The total weight of the brain after hardening in spirit, was only 10¼ ozs. As it was six days old when it reached me and was therefore somewhat decomposed at the time that it was put into spirit I concluded that it could not have weighed when fresh more than 15 or 16 ozs. Four-fifths of the cortex was undeveloped. The nucleus caudatus as shewn in fig. 17 projected freely into the cerebral cavity. There was no possibility of its connection by fibres with the cortex except at its anterior part; it appeared to be abundantly connected with the fibres of the crura. It is perhaps worthy of remark that the region of the cortex commonly regarded as motor (the transverse convolutions and paracentral lobule) was absent.

The whole base of the brain was small, the corpus callosum absent. The condition of the brain presented no obstacle to the determination of the sizes of the corpora striata and optic thalami. A well developed brain was hardened in spirit and cut with the same section cutter as a control experiment. Despite the deficiency in the cortex and the general smallness of the base of the brain, the nuclei caudatus and lenticularis proved to be of as nearly as possible normal size. The only possible escape from the conclusion that this observation effectually disposes of the theory of either anatomical or physiological mediation between the cord and the cortex by the corpora striata, is in the assumption that it is possible for these organs in the absence of the cortex, to appropriate its functions. Such a supposition of vicarious action is only justified by our ignorance of the real structure and functions of the different parts of the brain. Because our own ideas on the subject are indistinct, we conceive that there may be an actual want of definiteness in the structures themselves. That the pancreas should assume the functions of the liver, strikes one as obviously impossible and absurd; when we know thoroughly the differences in

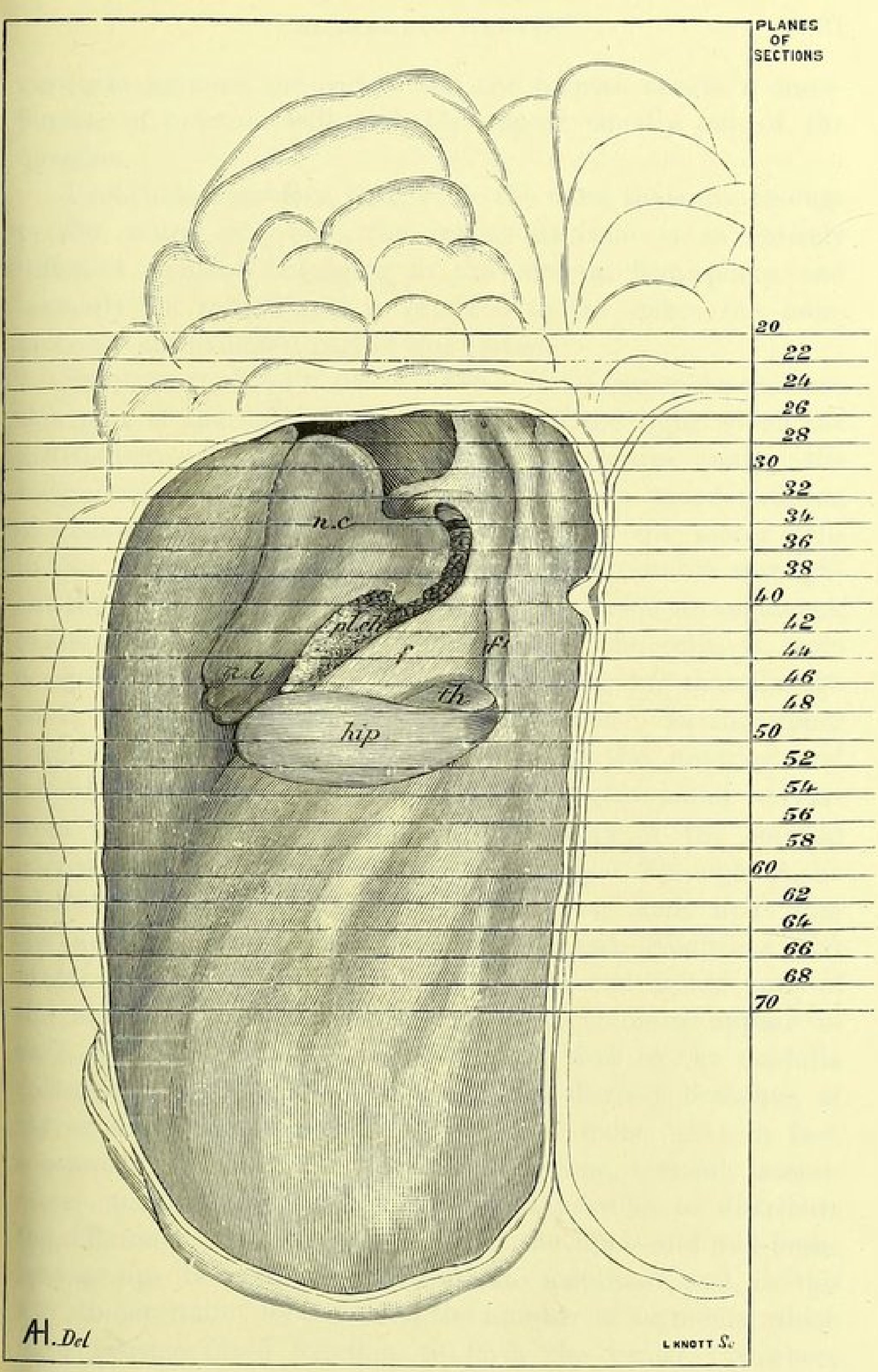


FIG. 17. Upper surface of the hydro-microcephalic brain of an idiot, as seen after the removal of the membranous undeveloped part of the cerebral wall. *n.c* nucleus caudatus; *n.l* nucleus lenticularis; *pl.ch* plexus choroideus; *th* optic thalamus; *f* fornix. (By kind permission of the Editors of the *Journal of Anatomy and Physiology*.)

structure between the cortex and the corpora striata a transference of function will probably appear equally out of the question.

I conclude, therefore, that, while the optic thalamus belongs to the central grey-tube, the corpus striatum is an entirely different element, belonging to the cerebral hemisphere, and certainly not subordinate in function to the cortex, but more probably an involuted part of this system.

SEGMENTAL VALUE OF NERVES. It is impossible to leave this part of the subject without noticing the light which the distribution of the primary metameric centres among the several columns, may perhaps throw upon the vexed question of cranial segmentation. A distribution of the motor cells in two columns, the anterior and lateral, is noticeable throughout the greater portion of the cord. This double arrangement, exhibited from the first differentiation of the cells, is more conspicuous (as shown by Vignal) in the foetus than in the adult, and can hardly be without significance. In the upper part of the cervical region, the cells of the anterior and lateral columns appear to give rise to different motor nerves; from the former spring the anterior roots of the cervical nerves, from the latter, the Spinal Accessory. Throughout the whole of the hind-brain, this distinction is kept up: from the anterior column arise the Hypo-glossal, Abducens, and Motor Oculi, from the lateral the Facial and motor part of the 5th. As portions of each of these columns appear in each metamer, the idea suggests itself that in the medulla oblongata, we have the separation into distinct branches, of nerves which run together in the spinal roots; that in fact, a complete cranial nerve consists of sensory, visceral, lateral-motor and anterior-motor parts. Is it possible to distribute the different nerves, which arise from the hind- and mid-brain, into groups belonging to the separate metamers, and, in this way, to determine, by their aid, the number of segments, which have become fused together to form the head? Nowhere in the vertebrate series do we find an animal, the central nervous system of which presents any likelihood of having retained its primitive form. It is only by piecing together the scattered fragments of our ancestral records, which are dispersed throughout the sub-kingdom, that we can hope to write the history of the head and picture to ourselves its condition in the vertebrate prototype. Various changes have occurred in the primary segments and their nerves, fusions of originally separate elements, dissociation of primitively single ones; while, in the struggle for existence among the different parts of which the body is composed, some may either have become obliterated or reduced to merely vestigial proportions. We must not therefore expect that it would be possible, according to any plan, to distribute the several cranial nerves into groups belonging to the several segments. This quadripartite arrangement however appears to me to fit in with what little we do know about the segmentation of the head better than any other.

Balfour discovered that the splitting of the mesoderm is continued into the head forming three cavities, the hyoid, mandibular and praemandibular, serially homologous with the portions of the body-cavity found in post-cephalic segments. From the mesoblast bordering these cavities the muscles are formed. The cavities throughout the body are divided into two parts by the fusion of the mesoblast in the middle of each of them. There is therefore a primitive distinction of the musculature into that arising from the dorsal and that from the ventral portion of the muscle plate. The various muscles derived from these portions respectively have never been determined, nor the relation of this primitive distinction to the permanent division into dorso-lateral and ventro-lateral muscles; but it is possible that upon it depends the separation of the motor cells into lateral and anterior groups. In the absence of further evidence this is however mere conjecture as far as the trunk-muscles are concerned. In the case of the head-muscles the question appears to assume a somewhat more substantial form.

Marshall[1] has shown that from the walls of the anterior (praemandibular) head-cavity are formed the muscles of the eye-ball supplied by the third nerve. The superior oblique muscle has not been observed in direct connection with the

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[1] *Quart. Journ. Micr. Sci.*, 1881, p. 94.

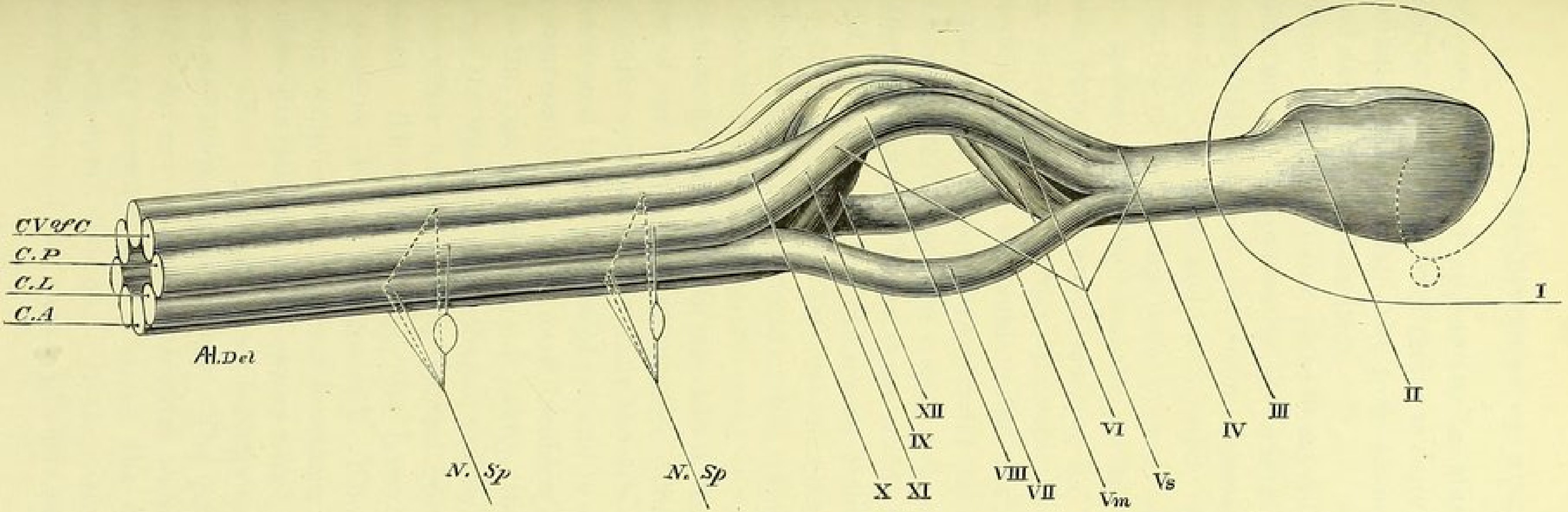

Fig. 18. Diagram of the central grey tube, showing the eight columns of which it is composed in the cord and their separation in the medulla and pons, its simple tubular character in the mid-brain, and termination anteriorly in the grey matter surrounding the third ventricle (optic thalami). Each of the spinal nerves contains fibres from all the columns. The cranial nerves of the hind-brain except *V* arise from a single column only. The second nerve has its primary centre in the posterior part of the thalamus. The first nerve reaches the anterior part of the thalamus after travelling in the fornix and forming a loop in the corpus mammillare.

CV of C columna vesicularis of Lockhart Clarke (visceral column of Gaskell); *CP* posterior column or horn; *CL* lateral column; *CA* anterior column; *N.Sp* spinal nerves.

cavity; from its first appearance in Marshall's sections it lies dorsad to it. The external rectus is derived not from the praemandibular muscle plate but from tissue in the region of the second and third head-cavities.

From the mandibular plate must be developed the mandibular muscles (supplied by the motor division of the fifth) although this has not yet been observed. The position of the rectus externus and its double origin are extremely suggestive of its having been pushed in through the sphenoidal fissure from the ventral portion of the mandibular muscle plate. This would account for the existence of the fissure in animals in which the orbit is otherwise completely separated from the temporal fossa. At any rate we have in the mandibular segment two motor nerves derived from the lateral and anterior columns respectively and supplying muscles of different groups. There is no reason for supposing that the 6th is a branch of the 5th, or as Marshall supposes, of the 7th. It is one of the two motor elements of equal value which belong to every metamer but which in the spinal nerves run together in the anterior root; it contains the processes which have grown out from the cells of the anterior horn for the supply of the ventro-lateral muscle. The sensory nerve of the mandibular segment is obviously the 5th. The visceral branch is distributed to the parotid gland and is either a branch of the pars intermedia of the 7th or of Jacobson's nerve.

In the case of the hyoid cavity, the hypo-glossal nerve supplies the muscles of the tongue and, by its descending branch, certain other muscles of the ventral group of this and other segments. The 7th supplies the lateral muscles (stylohyoid and posterior belly of digastric). The pars intermedia of Wrisberg supplies the visceral branches, the 5th the sensory. The glossopharyngeal is the sensory nerve of the first post-hyoid segment. The vagus obviously belongs to post-hyoid segments, as does also the spinal accessory. The question now arises as to whether the nerves of special sense were primitively branches of ordinary sensory nerves, or, on the other hand, complete sensory segmental divisions. If they were originally the only sensory divisions of the nerves of their segments, the wide distribution of the 5th nerve and its extended origin in the hind- and mid-brain are secondary and supplementary only. If they were originally branches of segmental sensory nerves, the remainders of these nerves are fused together into the 5th. The 4th, as I have already pointed out, appears to be a nerve, which has suffered severely in the struggle for existence and become reduced to its present insignificant size from a perhaps originally compound nerve.

That the nerves of special sense are to be regarded as complete sensory elements of segmental nerves appears to me improbable; rather were they originally but branches of the sensory nerves supplied to a series of sense organs of equal low value, certain members of which have since become highly specialized. The specialization of the sense organ has induced a corresponding development of the nerve and even eventually affected profoundly its mode of growth and its relation to the brain.

Balfour regarded all cranial nerves as segmentally equivalent, as preserving the primitive dorsal origin, and thus differing from spinal nerves in not having given way to the division into anterior and posterior roots.

Marshall has claimed for the olfactory the position of "a segmental nerve" and yet writes of the optic that it "must therefore be regarded as one *sui generis*, and as one which can accordingly have no claim to be considered of segmental value" and of the auditory that "neither its development nor its anatomical relations afford the slightest ground for thinking it to be of segmental rank." Had Marshall not examined the developing brain of the chick prior to the seventh day he would never have discovered that it arises as an outgrowth from the neural ridge and not as, *ab initio*, a hollow prolongation of the cerebral hemisphere. Ontogeny is the recapitulation of phylogeny. How can Marshall tell that in the more highly specialized optic nerve the early stages which connect it with other sensory nerves have not been dropped out in the development of the individual just as their permanent illustration has been annihilated in the race? In the first seven days of the chick's development we have an abstract of the history of the olfactory nerve through geological epochs. In the case of the optic nerve this abstract has been still further abridged and the remote period at which it arose as a solid outgrowth of the fore-brain is no longer represented. In any case it would appear to me that olfactory optic and auditory nerves must be treated alike, the differences between them being questions of degree only—the optic being the most specialized in structure and development just as the eye was the first of the primitive segmental sense organs to outgrow its fellows and has since progressed more rapidly than the others.

The mistake has been made of supposing that in each segment the central nervous system could give off but *one segmental* nerve whereas the columns of cells teach us that a true segmental nerve consists of four elements. In Petromyzon the anterior and posterior roots into which they are grouped appear to run separately throughout their whole extent, not united into a single nerve as in other vertebrates. In the case of the cranial nerves these four elements run separately but are to be taken together in considering the segmental value of nerves; not one chosen and the others left over as branches. No nerve of special sense is to be regarded as primarily a segmental nerve, although it may be the only remaining representative of the sensory element of which it was primarily but a lateral branch, possibly the only representative of all the four elements which at one time arose from its segments, or would have arisen from it had specialization ever been carried thus far. To see in the double origin of the olfactory nerve in Epicrium and some other of the Gymnophiona, as Widersheim[1] does, evidence of the homology of the olfactory with a complete spinal nerve, appears to me to be to mistake still farther the meaning of these nerves of special sense.

Guided by the principles enunciated above I should attempt to piece together the monumental fragments which remain to us into the following scheme.

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[1] *Die Anatomie der Gymnophionen*, p. 60.

	2nd and subsequent post-hyoid segments	1st post-hyoid segment	Hyoid segment	Mandibular segment	Prae-mandibular segment	
Posterior column	X	IX	V			Sensory
Meso-dorsal column	X	IX	pars intermedia	parotid branch of (?) VII	lachrymal branch of V	Visceral
Lateral column	XI		VII	V (motor)	IV (reduced)	Dorso-lateral muscles
Anterior column	XII			VI	III	Ventro-lateral muscles
	Branchial body-cavities		3rd head-cavity	2nd head-cavity	1st head-cavity	

THE CORTEX.

In the anterior part of the body the involuted tube is dilated into vesicles. This alteration in form is accompanied by a marked change in intimate structure. The white fibres are now included between two concentric layers of grey matter. In other words, there is added to the arrangement which obtains in the spinal cord a *peripheral grey tube* constituting the cortex of the cerebellum, corpora quadrigemina and cerebral hemispheres (fig. 19). It is not yet certain that any part of the thalamencephalon is thus invested.

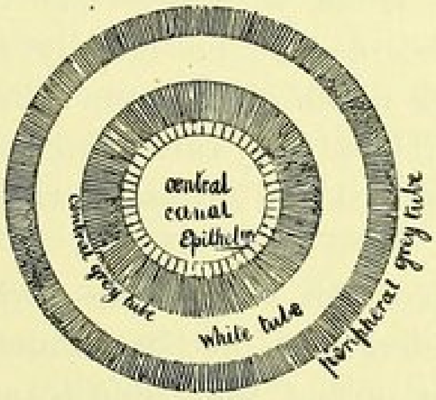

FIG. 19. Scheme showing the differentiation of the involuted tube of epiblast into lining epithelium, central grey, intermediate white and peripheral grey tubes.

The differences in the characters of the tissue forming the central and peripheral grey tubes justify us in believing that the latter is a new tissue peculiar to the cerebral vesicles and not merely a layer of the grey tube of the spinal cord split off by the white tube. This question now arises:—What is the relation of the peripheral to the central grey tube? We found reasons for believing that certainly all the motor, and probably all the sensory fibres, have their primary connection with cells of the central grey tube of their own metamer. None of them, that is to say, pass through the segment of the cord to which they belong, on their road from or to higher grey matter without interruption in its cells. It is impossible to speak thus positively of the nerves of the anterior vesicle, the olfactory and optic. The tubular prolongation of this vesicle in the formation of the optic nerve, and of the cerebral vesicles in the formation of the olfactory nerve, as well as the course of their fibres in the adult, indicates that by a secondary process of adaptation, a portion of each of these nerves, which play such an important rôle in conscious life, may have become directly united to the cortex without the intervention of the cells of the central grey tube. Their fibres are however outgrowths of these cells, with them therefore they were primitively connected and this connection must permanently be the more important; indeed it must be remembered that it is not yet proved that they have any other. The question therefore may be broadly stated thus:—What course do the fibres which connect the cells of the central with the cells of the peripheral grey tube take, and which parts of the latter are connected with the several metameric elements of the former?

Our opinion upon this subject has always been based upon physiological considerations, neither minute nor gross anatomy having as a matter of fact been able to answer the question. Hitherto the basal ganglia have been considered as middle men between the two tubes, as constituting a kind of intermediate bureau in which the messages from the front are submitted to an official censorship before being forwarded to the seat of consciousness, and the mandates of the will in like manner put into proper form for transmission to the executive staff. Consciousness and volition removed, applications from the seat of action might be answered in this office. We have shown that no analysis of reflex actions justifies the introduction of a class intermediate between the common reflexes of the cord, and reflexes which we may suppose to be carried out by the cortex. Reflex actions cannot be arranged in three distinct categories. Again, the behaviour of an animal deprived of its cerebral hemispheres only does not justify us in supposing that a machinery is at work which carries out actions, intermediate in kind, between ordinary reflex actions and volitions. If we remember the enormous importance of the sensations of smell and sight in determining the events of an animal's daily life we shall see at once that the reflex exhibition of the signs of emotion by an animal deprived of its cerebral hemispheres is fully accounted for, by the fact that the primary metameric centres of the optic and olfactory nerves are still in connection with the rest of the central grey tube. The differences in the character of the actions performed by an animal retaining its optic thalami and an animal deprived of them are not by any means greater than one would expect from the differences in the amount and importance of the grey matter by which they are carried out in the two cases.

We have allotted the optic thalami to the central grey tube and shown that there is no evidence of the interruption of the fibres connecting the two tubes in the corpora striata. In opposition to Wernicke's hypothesis and in support of Meynert's Kowalewsky[1] brings forward evidence derived from the observation of the brains of numerous animals. But it is time that we learnt to look with utmost distrust on naked eye observations of the course of fibres—and further, Kowalewsky's observations only prove at the most, that in certain animals in which the corpora striata are fully developed, the fibres of the corona radiata pass through them on the road to the cortex Indeed these observations rather favour the belief already supported by evidence of the most cogent kind that no break in the fibres, connecting the two tubes, occurs. In the case of the cerebrum therefore the question resolves itself into this:—*which segments of the cortex are connected with the several metamers respectively?*

This question can only be answered as I believe, by supposing that THE CEREBRAL HEMISPHERES HAVE UNDERGONE A ROTATION BACKWARDS INTO A SINGLE SPIRAL COIL.

The direct evidence of this is by no means complete. Nevertheless I doubt whether evidence of a more conclusive kind is likely soon to be obtained, for, owing to the plasticity of the brain tissue, the markings and contours by which the history of the changes which it has undergone might be expected to be

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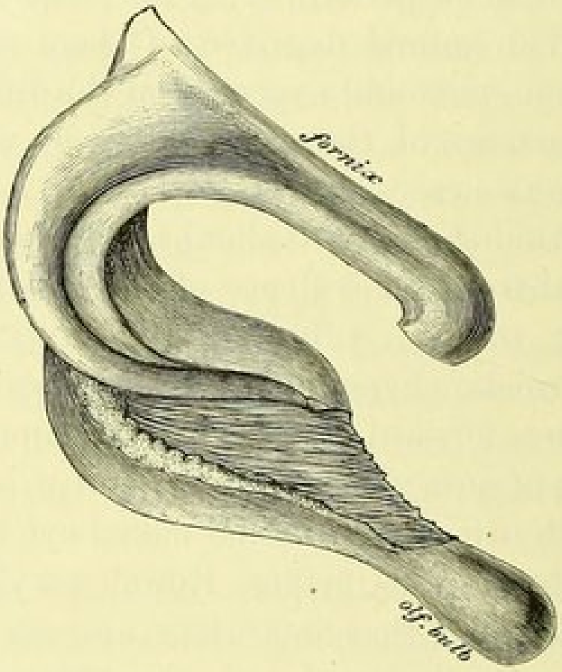
[1] *Sitzb. der k. Akad. der Wissensch.* Bd. LXXXVI. III. Abth. Dec. 1882.

taught, are rapidly obliterated both in the growth of the individual and in the race. Nevertheless there are appearances in adult anatomy, strongly suggestive of this folding over; for instance, the direct continuity of the olfactory tract, pyriform lobe and fornix, as seen in fig. 12, constituting one turn of a spiral. This twisting is seen also when the upper part of the hemisphere is cut away from the brain of a rabbit (fig. 20).

Fig. 12.



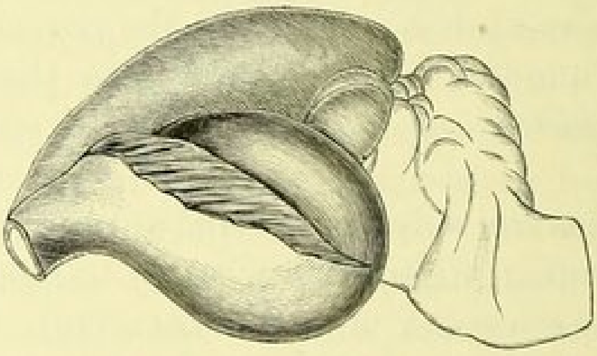


Fig. 20. Brain of rabbit. The upper part of the cerebrum has been cut away so as to expose the hippocampus.

It is not quite certain in what way the anterior pillars or columns of the fornix are connected with the thalamus. By Vicq d'Azyr they were described as turning over in the corpus mamillare to pass up to the thalamus in the bundle which bears his name. This view was adopted by Meynert. It has been denied by Forel on anatomical grounds and by Gudden on the results of section. It has been reasserted by Luys and again denied by Randacio; for my own part I am disposed to abide by the original description for the following reasons:—a corpus mammillare or corpora albicantia are only found in mammals. They are absent, that is to say, in all animals destitute of a fornix. Among mammals they are very small in those in which the fornix is feebly developed (the aquatic mammalia), while in those in which the fornix is large they project freely backwards into the inter-peduncular space. To appreciate this properly, a fresh brain should be observed; like all other prominences they subside under the influence of the hardening re-agents[1]. The corpus mammillare of the ox and sheep is composed almost entirely of white matter and it is difficult to account for its existence at all if it does not contain a loop or knot of fibres. The columns of the fornix pass under the optic tracts and skirting round the infundibulum reach the middle line in the corpus mammillare of which they constitute therefore the anterior, ventral and mesial parts, while the bundle of Vicq d'Azyr ascends from the anterior and outer part. At the time therefore that it reaches the corpus mammillare the column of the fornix is taking a course which would land it if continued in the middle of the interpeduncular space. It is difficult to conceive what next becomes of it, if it does not turn up again in the bundle of Vicq d'Azyr. I was unable in the porpoise brain which I examined to find any bundle of Vicq d'Azyr, the brain was however as already stated in an unsatisfactory state. It may be remarked here that it is rendering the problem needlessly difficult of solution to attempt to settle it by means of microscopic sections through the human brain, when in the brain of such an animal as the ox the structures are of a size which allows them to be observed most easily with the naked eye, and the amount of grey matter in the tubercle is small.

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[1] I came to the conclusion that no corpus mammillare was to be found in a fresh specimen of Delphinus delphis which I recently examined; it is however difficult to be certain of this owing to the fulness of the posterior part of the infundibulum.

Among fishes the brain is subject to very great variations in form. The cerebral hemispheres may be single or paired and very frequently are so far blended with the olfactory nerves and their enlargements that it is impossible to recognize their limits. In some cases however as among the Squalidæ the olfactory nerves although very large present no ganglionic swelling and pass to the base of the brain almost independently of the small unpaired cerebrum. We may safely conclude that such is the primitive arrangement, that the olfactory nerves were originally connected with the thalamencephalon, and that the connection with the prosencephalon is secondary.

Among reptiles the brain assumes a stable form. All the elements found in mammalian brains are present. The optic thalami obviously belong to the thalamencephalon, the corpora striata to the prosencephalon. The hemispheres are directed forwards. The olfactory nerves are connected with the anterior extremities of the hemispheres. The foramen of Monro is situate posteriorly. The well known diagram of the foetal brain in Huxley's "Vertebrata" might well be taken as representing the typical reptilian structure.

In birds on the other hand the cerebrum is highly specialized and exceedingly different from that of other vertebrates. As Cuvier remarked it consists almost entirely of corpus striatum. The foramen of Monro is situate posteriorly and leads into a lateral ventricle which separates the solid corpus striatum from the almost membranous dorsal and mesial wall of the cerebrum. The two olfactory nerves are in direct apposition and connected with the anterior extremity of the hemispheres.

It is only among mammals that we find appearances suggestive of a rotation backwards; the anterior situation of the foramen of Monro, the connection of the olfactory nerves with the posterior and inferior part of the cerebrum, the spiral twist of the fornix, and the fissure of Sylvius; and it is extremely noteworthy that the lower we descend in the mammalian scale the more marked do these appearances become. In Monotremes and Marsupials the head of the nucleus caudatus causes a considerable prominence on the under surface of the brain and deflects the whole of the olfactory tract into the pyriform lobe.

The olfactory stria is very large and prominent and passes to the inner side of the pyriform lobe, that is to say, into the region in which the fornix terminates—possibly directly over into this structure. This external stria would appear to me to be the true olfactory nerve and in many animals, the rat for instance, there is no distinct interruption between it and the white matter lining the descending horn of the lateral ventricle; of which white matter the fornix is but the thickened inner border. The posterior pillars of the fornix are almost transverse in Monotremes and Marsupials and the body of the fornix can hardly be said to exist, indications that the folding over is much less extensive than in higher mammals[1].

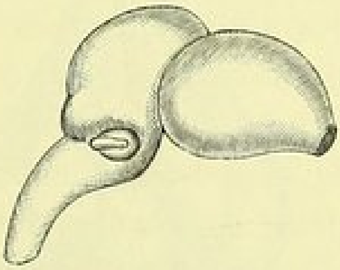

Fig. 21. Brain of foetal rabbit after Löwe.

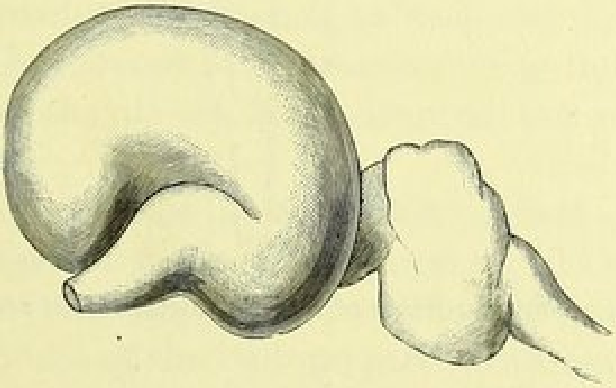

Fig. 22. Brain of foetal sheep, drawn from specimen in Museum of Comparative Anatomy at Cambridge. The distinctness of the pyriform lobe is unintentionally somewhat exaggerated.

Ontogenetically the folding over, although it cannot be traced in a series of stages, is strongly suggested. At first the hemisphere is directed forwards, the foramen of Monro is posterior, the olfactory vesicle anterior (fig. 21). Then appears, first of all external markings, the rhinal fissure (fig. 22). The olfactory

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[1] See in this connection the admirable plates with which Prof. Flowers' article in the *Phil. Trans.*, 1865, is illustrated.

tract passes continuously into the pyriform lobe, from which the temporo-sphenoidal lobe is subsequently separated, at the back and base of the hemisphere (fig. 23). Above the rhinal fissure appears, as the folding over increases, or rather as the tension exerted by the olfactory nerves is first felt, the fossa of Sylvius, subsequently contracted into a fissure. The fornix when it first appears is almost transverse, as it is permanently in the Monotremes and Marsupials. The olfactory stria is very strong (fig. 23) and passes to the inner side of the pyriform lobe.

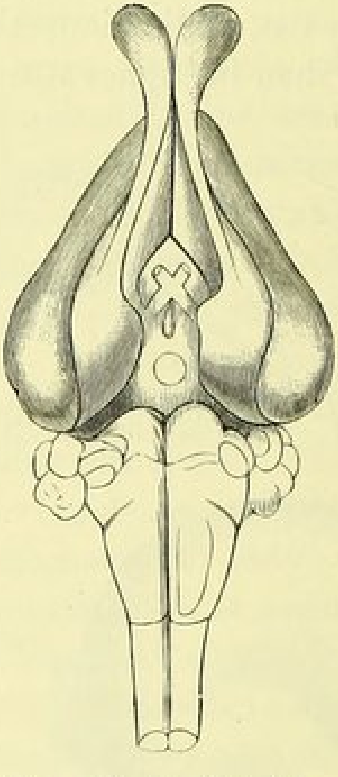

FIG. 23. Ventral surface of brain of foetal rabbit after Löwe.

The principal difficulty in the anatomical proof which has presented itself to me is the following:—In those animals in which the olfactory bulb remains vesicular and its cavity connected with the lateral ventricle, the hedgehog, horse and ox for example, the communication is by means of a slit-like opening in the floor of the ventricle, on the inner side of the head of the nucleus caudatus. The following considerations however show that this fact is by no means fatal to the hypothesis: (1) The folding over must occur at a very early period, before the division of the ventricle into anterior and posterior parts by the growth in its floor of the crura cerebri. (2) Although the olfactory ventricle is pyriform, the opening into the lateral ventricle is not at its apex but in its dorsal wall, simply causing a separation, not a deflection, of the longitudinally-running fibres with which it is lined; the ventricle is obviously prolonged backwards towards the pyriform lobe. (3) We have many instances of the shifting of such an aperture, and its situation immediately in front of the crura cerebri, taken in conjunction with the backward prolongation of the olfactory ventricle, strongly suggests that these structures have, during their growth, pushed it forwards. (4) The relation of the olfactory vesicle to the external stria is by no means clear. In my opinion this latter, the *external stria* or root of anthropotomy is the *true olfactory nerve,* but this view will only be intelligible after a description has been given of the structures to be found in the olfactory bulb. This organ has, as I believe, been hitherto completely misunderstood. Generally it is regarded as a portion of the brain, a "rhinencephalon." Krause believes that it is partly homologous with a spinal ganglion, and with this view Schwalbe is inclined to agree. I prefer not to enter at the present moment into a detailed account of its structure in different animals and different stages of development but merely to summarize, owing to their important bearing upon the theory here advanced, the results of my own observations.

The elements contained in the olfactory bulb are identical with those contained in the four outer layers of the retina.

It is most conveniently studied in the rat by means of extremely thin sections of the bulb prepared with osmic acid. In such a preparation the following layers are to be recognized:—

1. The grey fibres from the olfactory mucous membrane. These pass directly into the ventral surface of the bulb, and form a tangled plexus around,

2. the glomeruli or groups of granules. The granules are spherical nuclei, each with a central nucleolus and scanty surrounding protoplasm. The protoplasm can occasionally be seen to tail off into a fibre, with which there can be little doubt it is connected on either side. In the rat the granules have a diameter equal to one and a half times that of a blood cor-

puscle, and are therefore a trifle larger than the inner granules of the retina, in other respects it appears to me to be impossible to distinguish the one from the other.

3. The so-called stratum gelatinosum contains precisely the same elements as the inner molecular layer, viz. (*a*) A granular basis which appears to me, in preparations made as above described, as a felt-work of fibres[1]. (*b*) Fibres entering from the side of the glomeruli which break up and become lost in its substance, and fibres issuing on the side of the ganglion cells. (*c*) Small darkly staining stellate cells with round nuclei, similar to the cells of the molecular layer of the retina, which are commonly regarded as supporting.

4. The layer of ganglion cells. These appear in hardened preparations as long cones, but are no doubt oval or caraffe-shaped when uncontracted. From the base of the cone are seen to stream from three to six fine filaments towards the stratum gelatinosum in which they become lost. From the apex of the cone is derived a single, for a grey fibre, stout process. This, after running a short distance into the next layer, turns backwards at a right angle to acquire, no doubt, a medullary sheath.

5. The layer of medullated fibres running, as above noticed, from before backwards at right angles to the cell processes.

The probable relation of these several elements to one another is expressed schematically in fig. 24.

Broca (*loc. cit.* pp. 408 and 410) speaks of the granules of layer 2 as presenting " tous les charactères des cellules nerveuses sensitives," and as " semblables à celles de la corne postérieure de la moelle "; a description against which Schwalbe most justly protests.

Writing of the ganglion cells Broca says (p. 405), that they are of a kind which "la physiologie actuelle nous permet de considérer comme motrices." I should wish on the contrary to insist most strongly that we have not at present the slightest clue to the nature of a *cortical* motor cell. In the earlier part of this paper I have urged that we are sufficiently well ac-

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[1] This is also the opinion of Prof. Babuchin who recognizes its similarity to the molecular layer of the retina. Cf. Stricker's *Handbook*.

quainted with the characters of a *primary* metameric motor cell to recognize it in any part of the basal system. Neither observation nor experiment has yet helped us in any degree to form an opinion as to the elements in the cortex which are in connection with the motor cells of the central grey tube. The pyramidal cells of the sigmoid gyrus and the paracentral lobule are neither larger nor more numerous than those of the hippocampus, and any attempt to deduce the functions of portions of the cortex from the analogy in form and size of its cells with those of the motor region of the cord is premature. It should be distinctly understood that we have two kinds of elements to

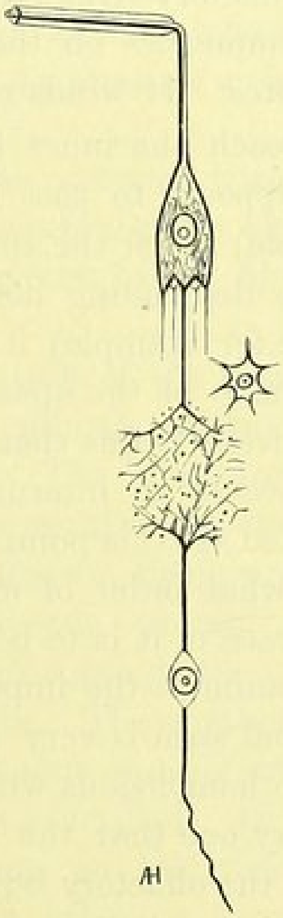

Fig. 24. Scheme of the connections between the elements of which the olfactory bulb is composed. The grey fibre from a cell of the olfactory epithelium enters the ventral surface of the bulb, is connected with a "nucleus" of the "glomerular layer" and passes on to break up in the reticulum of the "gelatinous layer." The basal processes of the ganglion cell are derived from this reticulum. The apical process of the cell turns back at a right angle and acquiring a medullary sheath constitutes a fibre of the olfactory root. One of the stellate cells of the gelatinous layer is also shown.

deal with; firstly, the cells of the central grey tube, the connections of which we know; and secondly, the cells of the peripheral grey tube, the connections of which are as yet involved in obscurity.

With regard to the olfactory stria, root or, as I should prefer to term it, nerve. It commences on the dorsal surface of the bulb, in the layer of fibres. It winds round the outer side of the olfactory tract to reach the inner border of the pyriform lobe. At this spot it appears to pass in certain animals (the rabbit and rat for example) under the inner edge of the mantle to the fibres lining the descending horn of the ventricle; in others (the sheep and ox for example) it divides and part of it spreads over the outer side of the apex of the pyriform lobe. It is only by examining fresh brains that one can make certain of the presence or absence of an internal stria, and my attention has not been directed to this point for a sufficiently long time for me to state in what order of mammals it first makes its appearance. Not a trace of it is to be seen in the hedgehog, rat, or rabbit, in which animals the importance and nerve-like appearance of the external stria is very marked. The external stria appears to me to be homologous with the optic nerve.

It must occur to every one that the similarity in structure between the retina and the olfactory bulb is in harmony with their common development as hollow outgrowths of the brain, and it can hardly be without significance that the layers of the retina unrepresented in the olfactory bulb are those which are commonly regarded as non-nervous. This view of the twofold structure of the retina is based upon Kölliker's observation that the rods and cones and outer granules are developed from the single layer of cells which elsewhere becomes the epithelium lining the ventricles. There are some difficulties in the way of this view, both developmental (see *contra* Löwe), and comparative (the pointing of the rods and cones *towards* the centre of the eyeball in the typical molluscan eye), it is nevertheless a curious fact, that, except of course in size, the two kinds of element found in the olfactory epithelium and their nuclei, so closely resemble the missing retinal layers. Further it appears to me highly probable that the same arrangement of the fibres coming from peripheral sense organs obtains in all cases, that is to say the sensory fibre is connected in the first instance with a bipolar cell, then breaks up in a process-reticulum and finally joins a multipolar nerve cell.

That the substantia gelatinosa Rolandi is the same substance that occurs in the retina under the name of molecular layer and in the olfactory bulb as stratum gelatinosum appears to me obvious.

That the cells of the posterior horn receive fibres from the substantia gelatinosa appears to me equally obvious. In fishes again the story is completed by the fibres of the posterior root bearing bipolar cells.

The relation of the cells of the root ganglion to the fibres of the posterior root in animals above fishes is a difficult and much disputed matter. The literature of the subject has been recently summed up in so many papers that it is unnecessary to repeat it. As is well known, Beale and Arnold saw two fibres issuing from the cell—one straight and the other coiled. Kölliker[1] followed fibres through the ganglion without observing any cell connection. The method of counting has given various results in the hands of different observers, depending no doubt upon the animal examined. In some no increase in the number of fibres occurs on the distal side of the ganglion (Rudolf Wagner[2]). In others a very considerable increase is found. Again, the opinion formed as to the nature of the cells evidently depends upon the animal chosen. Wagner, Kölliker, Stannius, Stieda, Holl, Freud described them as bipolar. Schwalbe and Fräntzel as unipolar. Schramm as apolar, unipolar and bipolar. Rawitz[3] shows that they are bipolar in cartilaginous fishes and unipolar in all higher animals.

Ranvier[4] described the single process as having a T form, the cross of the T resting upon the sensory fibre. Retzius[5] in his elaborately illustrated paper maintained that the true inter-

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[1] *Microscop. Anat.* Vol. II. p. 202.

[2] *Handwörterbuch der physiologie*, Vol. III. Part 1.

[3] *Archiv für Microsc. Anat.* 1882, p. 244.

[4] *Comptes rendus*, 1875, T. LXXXI. No. 25.

[5] *Archiv für Anat. u. Physiologie*, 1880, Anat. part.

pretation of the appearances which Ranvier saw is, that the short process springing from the single pole bifurcates into one fibre which runs centrally and another running peripherally.

Strongly confirmatory of my conclusions with regard to the homology of the bipolar cell layers of the olfactory bulb and retina with the spinal ganglia are the recently published results of Froriep[1] and Beard[2]. Approaching the question from the opposite standpoint to mine, these observers find that the ganglia of certain cranial nerves are developed in immediate contact with the ectoderm and that the cells of the ectoderm which overlie the ganglia are enlarged, constituting the rudiment of a sense organ not subsequently developed. If the same arrangement obtains in the case of the ganglia of the spinal nerves they must primitively have occupied with regard to the sense organs of their segments a position exactly similar to that permanently borne by the bipolar cell layers of the olfactory bulb and retina to the nose and eye. The homologies of the constituents of the retina, bulb and a spinal ganglion are shown in the accompanying diagram (Fig. 25).

Whatever may be the exact mode of connection between the sensory fibres of the posterior root and the ganglion cells in mammals it appears to me that the fact that a connection exists is placed beyond doubt by the death of the fibres which follows their section.

A nerve fibre dies when it is cut off from the cell of which it is a process.

That fibres commence in the ganglion cells to run a peripheral course without central connection appears to me to be a suggestion beyond the pale of serious discussion; rather do I consider that the simple arrangement which obtains in the fish has been modified into some such arrangement as Retzius has described in mammals. The assumption of Rawitz that the ganglia of the mammal are not homologous with those of the fish is unnecessary and not supported by evidence.

The hypothesis of the rotation of the cerebrum finds its strongest support in the results of experimental research. If

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[1] *Archiv für Anat. u. Physiologie*, 1885, p. 1.

[2] *Zoologische Anzeiger*, April 20, 1885.

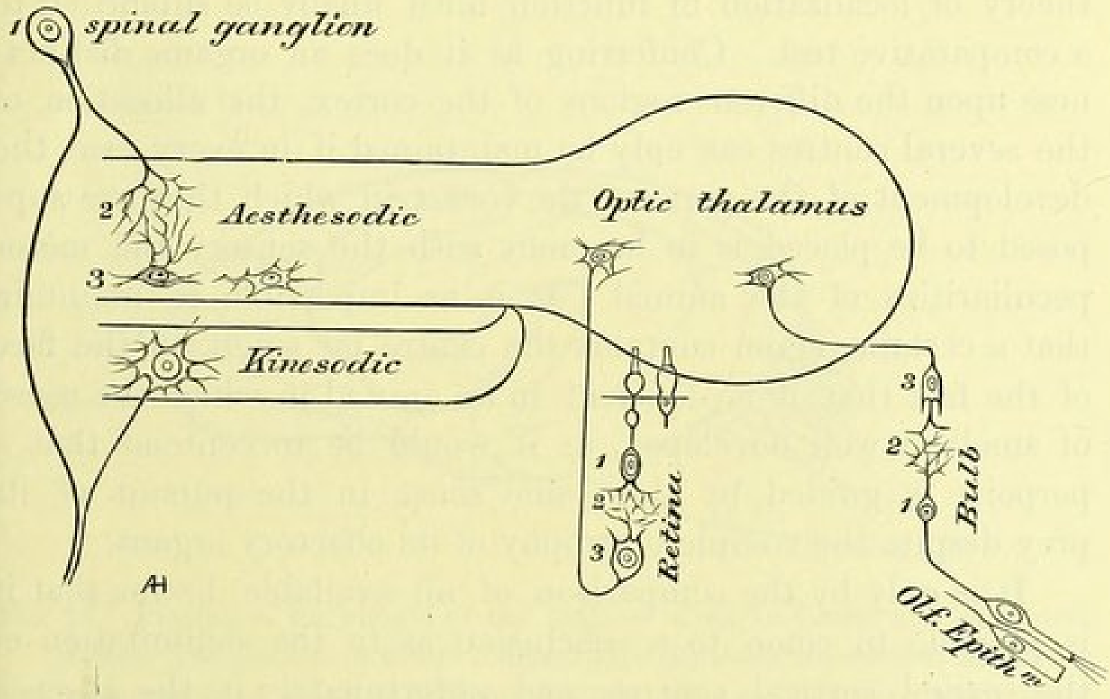

Fig. 25. Diagram of the anterior extremity of the central grey tube, showing the homologous elements of the olfactory, optic and spinal nerves. In the case of the spinal nerve only 1, the ganglion cell is outside the aesthesodic region of the cord; 2, the reticular layer (substantia gelatinosa) and 3 the cells of the posterior horn are included in the neural axis. In the case of the olfactory nerve all three elements are situated peripherally. The epithelial elements connected with the olfactory and optic nerves are shown, but not those in which the sensory fibres of the spinal nerve terminate.

the situation of the several regions which are in connection with different segments of the central grey tube, as determined by stimulation and ablation, be noted, it will be seen that they occupy reversed positions on the spiral, commencing with the frontal lobe and terminating at the apex of the temporo-sphenoidal. First come the centres for the trunk and tail, then those for the limbs, for the 5th nerve, the 2nd nerve, and lastly the 1st. This arrangement is shown in Munk's diagram, which however I have purposely refrained from reproducing, for I cannot, on comparative grounds, believe that physiologists have yet rightly determined the centres for smell and hearing. The discrepancies and ambiguities in the accounts hitherto published show that the matter is still unsettled. In the lectures delivered by me at the Royal College of Surgeons, to which I have already referred, I pointed out that the theory of localization of function must finally be submitted to a comparative test. Conferring as it does an organic distinctness upon the different regions of the cortex, the allocation of the several centres can only be maintained if, in every case, the development of the parts of the cortex in which they are supposed to be placed is in harmony with the sensory and motor peculiarities of the animal. It is as impossible to maintain that a certain region contains the centre for smell, in the face of the fact that it is deficient in an animal in which the sense of smell is well developed, as it would be to contend that a porpoise is guided by this same sense in the pursuit of its prey despite the complete atrophy of its olfactory organs.

It is only by the comparison of all available brains that it is possible to come to a conclusion as to the delimitation of the several cortical centres, and unfortunately in the absence of a satisfactory system of measurement, it is impossible to produce statistics in support of the opinion so formed. Personally, however, I am convinced that the development of the temporo-sphenoidal lobe varies as the sense of smell, and that the centre for hearing is situate higher on the brain, above the processus acuminis of the fissure of Sylvius, and I believe that the three brains reproduced below (figs. 26, 27, 28) may be accepted as typical of all animals presenting similar sense characteristics. In the dog the sense of smell is paramount, in the cat it is largely replaced by hearing and sight, in the otter (Lutra) it is extremely deficient. Were it possible for me to reproduce long series of diagrams I believe this position would be rendered secure. The three figures (26, 27, 28) with which this is illustrated are tracings from the beautiful drawings in Leuret and Gratiolet's Atlas, mechanically reproduced and reduced to about the same absolute size by the Typographic Etching Company. These drawings were made, it is needless to remark, long before there was any thought of the localization of function in the cortex. The numbers which I have marked upon them indicate in the roughest way the situation of the areas connected with the several peripheral nerves. No doubt the distribution in the cortex of the fibres derived from the primary centre of the 5th nerve is as extended as is this pri-

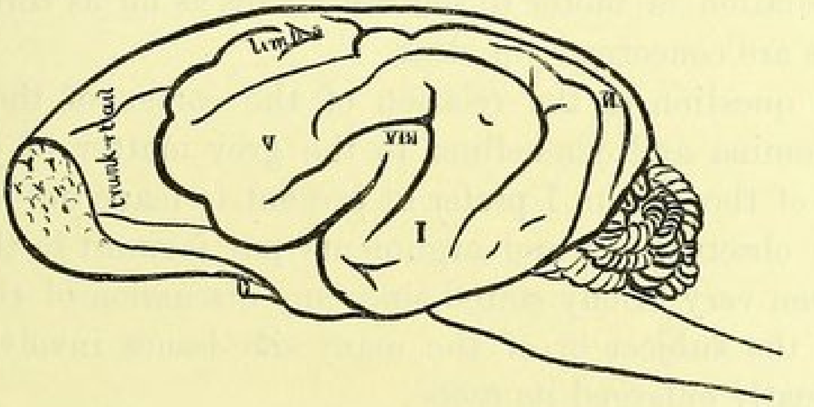

Fig. 26. Tracing of the picture of the brain of a dog in Leuret and Gratiolet's Atlas. The Roman numbers indicate approximately the cortical areas, the development of which in different animals varies as the cross section of the several sensory nerves.

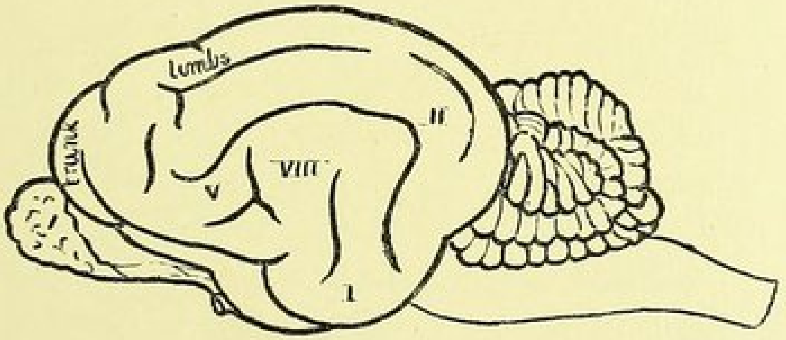

Fig. 27. Brain of cat.

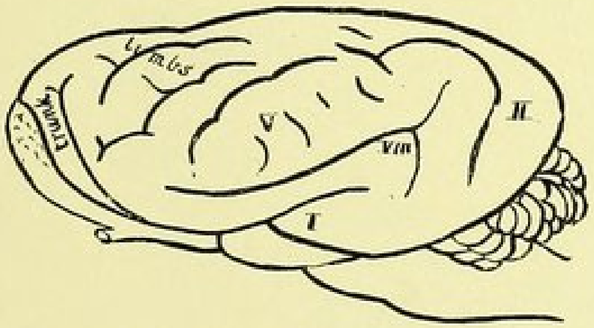

Fig. 28. Brain of otter.

mary centre in the central grey tube; it probably overlaps the area of the 8th nerve on either side. To the vagus and glossopharyngeal nerves no centres have yet been allotted, nor is the relation of motor to sensory nerves as far as cortical connections are concerned yet clear.

The question of the relation of the cortex of the corpora quadrigemina and cerebellum to the grey matter of the basal portion of the system I prefer at present to leave untouched.

The observations and arguments put forward in this thesis have been very briefly stated since any discussion of the literature of the subject or of the many side-issues involved would have greatly enlarged its scope.

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