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ABSTRACTS OF THREE LECTURES

ON

THE BRAIN-MECHANISM OF SIGHT AND SMELL.

Delivered at the Royal College of Surgeons.

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THE BRAIN-MECHANISM OF SIGHT AND SMELL.

LECTURE I.

THE HISTORY OF SENSORY NERVES, AND THEIR RELATION TO THE CENTRAL SYSTEM.

NOTHING in the progress of science is more conspicuous than the frequency with which the standpoint of investigation is changed. For a time, the assault of a difficult problem is carried on from a certain point; and it may be that, for a generation, observers are content with the slowly widening breach produced by their successive blows. But when a more commanding position is discovered, it is soon occupied by the reorganised forces, each man eager to discharge his shot at the stronghold, from the new vantage ground. Never before, in the history of science, has the whole plan of attack been so completely changed as by the doctrine of evolution. Before Darwin, our intellectual reflection of the universe showed but stationary forms. Plants and animals, arts and creed, stood still—each a final and completed form. The man of science and the man of letters, each alike viewed the object of his study as a thing at rest. At the master's word, all was changed. The inhabitants of the mind's realm began to move; every creature in it bore a history—emerging from the past, and growing from a minute simple form, it was tending towards perfection and complexity. Before Darwin, the universe appeared immutable; since Darwin wrote, it is seen to be mobile. The recognition of this great fact has penetrated every science; fresh impetus has been given to research, fresh aims to study, and, in those branches of science to which we more especially devote ourselves, inquiry has entered upon new ground. Anatomy still deals with structure, and the final aim of the study of structure is to discover function. But the anatomist no longer regards his material as fraught with teleological lessons only; it discourses to him of the past; it suggests the future. No longer does the structure just exposed by his scalpel stand alone, but attracts to itself out of the gloom forms that have passed, and is linked in relationship with all that now exist. And so, while the exigencies of knowledge are enormously increased, the aims of study are more sharply defined. We want to know of every animal, of every organ, even of every cell, how it came by its present form. Nor does it impress upon our minds an image, until we can, as it were, see it move; until we can trace its path. Like a solitary stone standing upright on a plain, it only satisfies our mental grasp when, by comparing it with other forms, by observing on it traces of the tool-marks, by painful interpretation of its inscribed signs, we realise the forces under the influence of which it assumed its outline and position. The scientific standpoint of to-day might thus be defined. We study the History of the forms around us.

Such historical study, however, is no mere intellectual pastime; it has come to be a practical necessity that we should know something of the changes through which structures have passed, in order to distinguish between the immediate suitability to perform function, and historical continuity of form. In no case is this so obvious,| as when our attention is directed to the central nervous system. For, among the organs of the body, the nervous system is the real aristocrat. First to be formed in the embryo, first to be considered when the supply of food for the organism runs short, it is last to adapt itself to altering circumstances. Muscles may come and go in obedience to the needs of the race; bones change in form to bear the altered strain of the muscles; blood-vessels strike out new paths for themselves to supply them more expeditiously and with less risk of compression; but nerves still keep on in the old paths, content with the simple reason that these it was their ancestors were wont to use. Forearm and leg have twisted on their axes; posterior interosseous, and anterior tibial arteries long since have learnt to take a short and sheltered course between the bones; but ulnar and peroneal nerves still pass to their destinations round the postaxial border of the limb, nor can generations of suffering "funny bones" induce them to adopt any less dignified course. The nervous system is full of archaisms, and its evolution must be understood before its structural peculiarities can be correlated with their use.

Although our knowledge still presents several gaps, the origin and growth of the nervous system can be worked out with remarkable completeness, owing to the constancy with which it adheres to the original lines of its growth, and to the primitive cell-layer in which it first appeared.

Unicellular animals present no trace of a nervous system, nor is any to be found in such compound animals as consist of two cell-layers only. It is with the appearance of a third layer (the mesoderm or mesoblast) that it first arises. The mesoblast is derived from the outer layer, the epiblast; and partly also, perhaps, from the inner layer, or hypoblast. Its most characteristic elements are muscle-fibres, by which the power of withdrawing from danger is given to the animal. The muscle-fibres are at first processes of the ectodermal cells; and, in order that their contractility may be of use to the animal, it is necessary that the ectoderm should be sentient, so that the intimations of danger which it receives may cause the muscle-fibres to contract. To conduct these impulses from the sentient epiblast to the contractile mesoblast, a continuity between the two is kept up by means of protoplasmic strands or nerves; and long after the process of development has been abridged, and the mesoblast become a separate layer, some of the cells of which develop into muscular fibres, the conducting strands still grow to meet the muscles from the epiblast. As far as we know, it is only from this latter layer that the nervous system is developed.

The next step in development consists in the grouping together of such ectodermal cells as, owing to their containing pigment or crystals, are peculiarly suitable for the reception of sensory impressions, into distinct sense-organs. At the same time, instead of each cell being connected only with its own muscle-fibre, such junctions between the nerve-fibres are introduced as will enable the impulses received by a few cells to be conveyed to a number of muscle-fibres or to various groups of fibres, according to the nature of the movement it is desirable to produce. Such junctions are effected by means of ganglion-cells, which hence may best be termed *distributive*. These are obtained from the sensory ectoderm, certain cells losing their distinctive characters, and sinking into the mesoderm to serve as nodes of the nerve-plexus. In the covered-eyed Medusæ, the plexus presents no tendency to centralisation, except such as occurs at the bases of the sense-organs. In the naked-eyed Medusæ, commissures are developed, and distinct nerve-rings produced. Thus appears, for the first time, what one may regard as a central nervous system. This system is variously disposed, and presents different degrees of aggregation throughout the animal kingdom; but it is important to remember that it always remains a plexus, the primary function of which is to distribute the stimuli received by sense-organs to appropriate combinations of muscles.

Among invertebrate animals, the central system comprises two parts, which might be termed head-ganglia and body-ganglia respectively, united together by a commissure which surrounds the œsophagus. In vertebrate animals, the system lies entirely dorsal to the alimentary canal, and no traces of a primitive duality are to be discovered. In Amphioxus, appearances are to be found which indicate that, in its earliest stage, the vertebrate central nervous system consisted of a solid plate of epiblast, but in all other forms it constitutes from the first a tube which extends from behind forwards; its posterior extremity communicating originally with the hinder end of the gut. The single layer of cells, of which its wall is formed, proliferates, and of the new layers thus produced, the innermost becomes the epithelium of the central canal; the others, ganglion-cells of the grey matter. From the ganglion-cells, processes grow out as nerves. Some of the processes extend outwards to the muscles, others extend up and down the central tube, bringing its various cells and groups of cells into connection; these latter constitute the white matter of the cord and brain. The origin of the sensory nerves is not by any means so clear. Certain it is that they, and the cells in the spinal cord with which they are in connection, appear much later than the motor nerves and cells. At the time of their origin, the posterior root-ganglia are already large and well developed. These root-ganglia grow, not from the central system, but from separate thickenings of the epiblast, each of which gives origin at the same time to a segmental sense-organ. Most of these sense-organs disappear as development proceeds. It also appears certain that a part, if not the whole, of the nerves on the distal side of the ganglion, grow from its cells, and not from cells of the central tube; and it appears to the lecturer probable that the fibres of the posterior roots also grow from the cells of the ganglion centralwards into the cord, instead of from the cord to the ganglion, as usually supposed. A consideration of the effects of cutting nerves in such cases as have been hitherto deterior roots are cut, the fibres which remain attached to the root-scribed, leads him to formulate the law that *nerve-fibres die when cut off from the cells of which they are processes, and from which they derive their nutrient supply.* It is well known that, when the pos-ganglia live, those entering the cord die. As the result of his attempts to trace the distribution of these fibres within the cords of lower vertebrates, the lecturer concludes that they break up into the plexus known as the gelatinous substance of Rolando, from which filaments are reassociated, to form the processes of the spindle-shaped cells of the posterior cornua of the cord. The cells of the root-ganglion, which in lower vertebrates are fusiform, bipolar, become in higher vertebrates so folded on themselves, that the poles are brought together, the cell being, as it were, connected with the fibre by the vertical limb of a **T**; while the afferent and efferent nerve-fibres, as the two horizontal limbs, are directly continuous, and the passage of the impulse through the cell is thus avoided. If this view be correct, every sensory nerve, in its passage to the Central Tube, is interrupted in (1) a bipolar cell, and (2) a process-plexus, before it reaches a nerve-cell of the cord. Bateson's observations on Balanoglossus, which he considers to represent the ancestors of the vertebrate stock, taken in conjunction with appearances described in the development of other forms, render it probable that the posterior root, as well as the ganglion, arose at first by delamination from the epiblast. The sensory nerve was thus at first an ectodermal path between the single sense-organ of each segment, and its centre in the cord. Its homological value is very different from that of the motor nerves, which consist of the processes of the cells of the anterior cornua, and pass without interruption to the muscles, at first separately, but collected in later forms into one or more bundles for each segment.

LECTURE II.

The History of the Sense Organs.

All vertebrates exhibit a distinct tendency to body-segmentation. From head to tail, there is a repetition of similar structures. Vertebræ and spinal nerves follow one another in unbroken succession ; and not only do such axial structures serially recur, but other organs also tend to be repeated in numerical harmony with the vertebræ and nerves. In fishes, the muscles are disposed in myotomes, their fibres not passing the boundaries of the segment. In the embryo, the mesoblast splits into somites, from parts of each of which arise the bones, muscles, and other tissues of the segment. All these facts point irresistibly to the conclusion that the vertebrate ancestor was constructed of a series of similar segments, in each of which the same elements were to be found ; separate joints, as it were, each containing a sense-organ, with its afferent nerve and clump of central plexus, a group of efferent nerves with their muscles, its skeletal framework, and a piece of gut. At least, morphologists believe that the key to vertebrate structure is to be found in such a scheme. It does not follow that the ancestor was definitely segmented, or that all the elements belonging to each segment were contemporaneous. Serial repetition of similar structures was the goal towards which development tended.

According to this plan, each segment contained a sense-organ; and, as will be shown, there is ample evidence that, in this respect, the plan was actually carried out. In the lowest vertebrates, all the sense-organs were probably of equal value. Very soon, however, a division of labour took place. While the greater number of the sense-organs retained the common form, certain of those situate in the anterior extremity of the body became specialised. Of these, the first to advance along a new line was the eye; and so important an organ did this become, that its relation to the central system was extensively modified. Then the ear and nose assumed independent positions; and these three alone, unless the organs of taste also are derived from segmental organs, obtained a sufficient degree of development to secure their retention in higher vertebrates. There is, however, sufficient evidence to prove that in each of the other segments a sense-organ once existed ; for, leaving out of consideration the fact that in certain worms (the capitellidæ), the claim of which to find a place in the vertebrate pedigree is problematical, a sense-organ, in structure resembling those of higher forms, is to be found in each segment, such organs exist in the embryos of all bony fishes, while they persist throughout life in some (for example, *Gobius Esox*). They present the form of a bulb of hair-cells, on the same plan as taste-bulbs. As the organs of special sense diverged from these of common type, it became advantageous that all these common ones should be supplied by a single diametameric nerve, the nerve of the lateral line. The nerve extends from before backwards, apparently by delamination from the epiblast. In cartilaginous fishes, the nerve and its sense-organs extend no farther backwards than the gill-bearing region, in which their reports as to the character of the surrounding water are especially important. The only vestige of this series which remains in man is the remnant of the nerve of the lateral line, which persists as the auricular branch of the vagus.

The ear is commonly regarded as derived from a member of this series, but the eye and nose are always excluded. The first and second nerves are treated as parts of the brain, and excluded from the segmental scheme ; either because they, and the part of the brain with which they are connected, are regarded as homologous with the cephalic ganglia of invertebrates (occurring in a region into which segmentation does not extend); or because of their hollow outgrowth from the neural tube; or, lastly, because the retina and olfactory bulb contain elements which elsewhere are rightly considered to be comprised within the brain and spinal cord. The first of these reasons has been already discussed. The second appears, to the lecturer, to be of no morphological importance, for the whole central nervous system was at first solid, and only subsequently became hollowed out and lined with cilia (as Mr. Sedgewick has suggested), for the safer location of its cells and for convenience of respiration. It is no wonder that this hollowing out is extended into the optic nerve, which contains probably more fibres than all the spinal sensory nerves put together.

With regard to the structure of the retina and olfactory bulb, there is, in the first place, an entire homology between the two; for, although the cylindrical form of the olfactory bulb does not favour stratification, and the arrangement of its elements varies considerably in different animals, their resemblance to the structures found in the retina is unmistakable. The interruptions in the course of the nerve-filaments, as they pass centrally from the epithelial cells, is probably the same in the two cases. First, they are connected with bipolar cells (the "inner nuclei" of the retina and cells of the glomerular layer of the bulb), secondly, in a process-plexus (the molecular layer of the retina and stratum gelatinosum of the bulb), and, thirdly, with multipolar cells. Further, the lecturer is of opinion that every sensory nerve of the body, on its way to the central plexus, passes through the same series of interruptions; the spinal sensory nerve being connected first with a (primitively) bipolar cell of the spinal ganglion, upon which it depends for its nutrition. Secondly, they are broken up in the gelatinous substance of Rolando, from which again filaments are reassociated as the processes of the multipolar cells of the cord. There is no greater difference in size between the cells of the spinal ganglia and the bipolar cells of the retina and bulb, than there is between the nerve-fibres which depend upon these cells for their nutrition in the two cases respectively.

It is not because of any differences in the character of the epithelial cells with which the nerves are in the several cases united, that morphologists have introduced such a broad distinction between the first two sense-organs and the rest. The columnar and fusiform cells of the olfactory epithelium, the rods and cones of the retina, the cells of Corti and the cells of Deiters in the ear, make up couples which remarkably resemble one another. It is because they claim for the first two nerves that they are parts of the brain, that they draw the line, and only commence the segmental arrangement behind them. Professor Milnes Marshall has proved that the olfactory nerve arises, like any other, from the neural crest, but still considers its sense-organ, the nose, to be not a segmental sense-organ but a gill-cleft. Van Wijhe recognises that the origin of the first nerve throws it into the segmental series; but, as the second nerve does not likewise arise in any animal from the neural ridge, he supposes that a displacement has occurred, and that the optic nerve is really the first, an inference opposed to all that is known of the history and development of the nerve. Beard recognises the necessity of making the nose a segmental sense-organ, but still excludes the eye. It appears to the lecturer that nose, eye, and ear, must "swim in the same boat;" and that, while it is in a sense true that the olfactory and optic nerves are parts of the brain, the modification of the system by which this comes about is, after all, remarkably slight. Indeed, it is the other sense-organs which have undergone modification, while the nose and eye perpetuate an older and more primitive arrangement. It has already been shown that in its first inception the nervous system was wholly peripheral. Then a part of the plexus assumed a central position, the rest remaining in the vicinity of the sense-organs; of this latter portion all, except the bipolar cells of the spinal ganglia, has in the posterior segments drifted into the central system ; while in the case of the first two segments, the older arrangement is still preserved.

LECTURE III.

The Relation of the Olfactory and Optic Nerves to the Central Grey Tube and Cerebral Cortex.

In the scheme of the central nervous system submitted in the two preceding lectures, the neural axis was represented as exhibiting an uniform plan of structure throughout its whole extent. The large cells of which the peripheral nerves are the axis-cylinder processes, accumulate at the point of exit of these nerves ; in the same way, the small-celled tissue with which the sensory nerves, after breaking up in the gelatinous substance of Rolando, terminate, exhibits a similar segmental arrangement. The key to the constitution of the system is to be found in its metameric division. Most anatomists are willing to concede this proposition for the whole of the neural axis behind the optic thalamus. At this level, however, a complete alteration in the plan of the system is supposed to occur. On the one hand, two nerves, the olfactory and optic, are left without primary centres in the neural tube ; on the other hand, a mass of small-celled grey matter, the optic thalamus, directly continuous with that surrounding the aqueduct of Sylvius, and developed in the same relation to the primitive neural canal, as the rest of the æsthesodic portion of the central tube, is excluded from it. No motor nerves arising from the mid-brain, small-celled plexus only should be formed from its wall. It is impossible to determine the amount of this plexus needed to constitute the primary centres of these two large nerves, for there is no evidence to show that a sensory nerve is connected with only one cell of the neural axis ; rather does it seem that the sensory fibre, after its division, is brought into connection with as many cells of the plexus as may be needed for the distribution of its impulses to their appropriate motor apparatus. It is not on account of its structure, its connections, or its mode of growth, that the optic thalamus has been severed from the rest of the grey tube, but because physiologists require centres intermediate between the cortex and the cord, to carry out a certain class of reflex actions. The optic thalamus is therefore allied with the corpus striatum to form a subordinate *bureau*, in which the messages from the front may be submitted to an official censorship before being forwarded to the cortex, and the mandates of the Will be put into proper form for transmission to the seat of action. The two ganglia so allied are developed from different cerebral vesicles, and have very different phylogenetic records ; but this is overlooked in the desire to satisfy what the lecturer can only term the pernicious doctrine of "centres." Not physiologists only, but also anatomists, have come to regard the nervous system as consisting of a series of centres of ascending grades of authority ; societies of cells, differing from one another in structure, but bound together for a common object. It is almost a revelation to find, on submitting the central nervous system to section-cutter and microscope, that, from filum terminale to lamina terminalis, no collection of cells, which could be regarded as a centre in this sense, exists. There is no reason for separating the optic thalamus from the remainder of the central grey tube.

Turning now to the two nerves which are left without primary centres, the lecturer explained, with the aid of diagrams, how it is easily to be seen (at any rate, in the brains of ungulates) that the optic nerve grasps the posterior end of the thalamus very much in the same way as the auditory nerve its æsthesodic portion of the medulla oblongata.

The route by which the olfactory nerve reaches its primary centre in the anterior end of the thalamus is a circuitous one. The fibres from the olfactory bulb stream centralwards in three divisions; of these, the inner is inconsiderable. The middle, a thick bundle, grooving the head of the nucleus caudatus, curves inwards to the anterior commissure. This commissure is not wholly made up of olfactory fibres, since it is found in animals devoid of smell. Like the optic chiasma, it is taken advantage of by crossing fibres of the great brain, its size varying inversely as that of the corpus callosum. By this root, the fibres of the olfactory nerve reach the extremity of the temporo-sphenoidal lobe, presenting, in their decussation, a close analogy to the optic nerves. The outer, larger, and more important root, lying on the under surface of the brain, passes backwards into the pyriform lobe. Here it divides into two parts, an outer thin expansion, which spreads over the surface of the lobe, and an inner thicker portion, which, passing to the inner side of the lobe, tucks itself in under the edge of the cortex-mantle. Omitting, for the moment, any account of the relation of these fibres to the hippocampus, the lecturer stated that the olfactory nerve was to be traced through the fimbria, posterior pillars, body, and anterior pillars of the fornix, into the corpus mammillare (corpora albicantia), in which it turns up as the bundle of Vicq d'Azyr, into the anterior end of the optic thalamus. The anatomical connections of this root were explained, and its functional continuity was proved by an appeal to what might be termed one of nature's experiments. In all aquatic mammalia, the sense of smell is either deficient or absent. In the porpoise, it is completely abrogated. The olfactory bulb is reduced to a mere cord, and all the other portions of the olfactory tract just indicated show a corresponding want of development. The cross section of the body of the fornix of a specimen examined, with a view to deciding this question, was less than one ninth as great as that of an ox brain of the same weight. It contained only those fibres termed by Huxley "precommissural."

Returning to the hippocampus, the lecturer stated it as his belief that the special structures here attached to the folded-over edge of the cortex, that is to say, the cord of large multipolar cells and its cap of fascia dentata are portions of the olfactory bulb. The microscopic appearances of the cells of the fascia dentata are precisely similar to those of the cells of the glomerular layer of the bulb. In the porpoise brains as yet examined, of which none, unfortunately, were in good condition for the purpose, no fascia dentata could be found. The edge of the cortex was simply folded over, and the posterior pillars of the fornix spread out into the medullary lining of the ventricle, without forming a true corpus fimbriatum.

Relation of the Cerebral Cortex to the Central Grey Tube.—In the wall of the neural tube, where it is dilated at its anterior end to form the primary cerebral vesicles, a second layer of grey matter is developed on the outer side of the sheath of white fibres. This may be conveniently referred to as the peripheral grey tube. As the key to the central grey tube was to be found in its segmentation, the question arises as to whether the outer tube is similarly divided up into areas; and if so, what is the relation of its segments to those of the central tube? There is no reason for believing that any sensory nerve-fibres end directly in the cerebral cortex, or motor fibres take origin there, to pass to their destination without interruption in the central grey tube. On the other hand, there is abundant evidence that the areas into which the lower tube is divided are represented in the higher one. Experimental stimulation and ablation of cortical areas, as well as pathological observation, have thrown much light upon this subject. The evidence with regard to cortical localisation, submitted in this lecture, was obtained from the comparison of the brains of animals endowed with different degrees of motor and sensory development. It was shown that all mammals might be divided into two classes; the hunting and the hunted. Herbivora depend for safety on the eye, their sense of smell being of little use in helping them to escape from the neighbourhood of their foes; carnivora seek their prey with the nose, it being of little consequence, apparently, as may be inferred from the habits of young dogs, and from the strong smell of the carnivorous quarters of the Zoological Gardens, whether or not their own bodies emit a powerful odour. More common, however, than exceptional sensory development, is marked deficiency; and, amongst other brains, the otter's was pointed out as that of an animal in which the sense of smell is reduced to a minimum.

It was shown how the development of the temporo-sphenoidal lobe varies as the sense of smell; that of the postero-internal part of the occipital lobe, as the sense of sight. The location of the other senses may, in like manner, be discovered by observing the brains of animals in which they are unusually well or badly developed. The general result arrived at confirms, in the main, the allocations of experimental physiologists.

The lecturer then proceeded to show how, while the first nerve has its secondary centre in the temporo-sphenoidal lobe, the area for the second nerve lies above and behind this, and such others as have already been determined occupy a reversed position from behind forwards on the cerebrum. This is only to be explained by supposing that the great brain has in its growth twisted over in a single spiral coil.

Although, in such a plastic tissue, developmental markings are soon obliterated, observations of the changes in form of the fœtal brain entirely confirm this conclusion. At first, the cerebral hemisphere is directed forwards, the foramen of Monro leading into the back of its cavity. Then, first of external markings, the rhinal fissure appears, separating the pyriform lobe from the rest of the hemisphere. Being attached at its anterior end, the olfactory nerve soon asserts a traction on the growing brain, causing its outer wall to sink in as the fossa of Sylvius, which later on is closed over, and reduced to the fissure of Sylvius. The foramen of Monro enters now the lateral ventricle near the front. In certain stages of its growth, the cerebrum has all the appearance of a coil. Only in this way, too, the lecturer contended, can the circuitous route of the olfactory nerve be explained. Arising from the neural ridge of the first vesicle, it is at first pushed down forwards by the budding cerebral hemisphere. Becoming then adherent to the hemisphere, it is lifted up again, and carried round with it over the upper margin of the foramen of Monro. The advantage of this twisting over is to be found in the globular form afforded to the brain. One may conjure up a ludicrous picture of what a man's head would be like, were space no object, and all the secondary centres of the cortex arranged, as in an alligator, in a rectilinear series.

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