AN ADDRESS ON THE ORIGIN OF THE VERTEBRATE NERVOUS SYSTEM.

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The Peculiarities of the Central Nervous System in Vertebrates.

—In the course of my researches on the nervous system of the higher vertebrates, my attention was directed to the evident metameric arrangement of the elements of the central nervous system, and to the large amount of non-nervous epithelial membrane which forms so conspicuous a part of that nervous system; and I was led to put forward the view that the nervous system of the higher vertebrates has been formed by the continual increase and growth of a segmentally arranged nervous system situated on the outside of, and in close connection with, a non-nervous unsegmented tube. This non-nervous unsegmented tube forms the lining epithelium of the central cavities of the brain and spinal cord; it exists on the dorsal side, free from nervous matter, as the epithelial linings of the choroid plexuses; it comes to the surface on the ventral side as the lining of the infundibulum, being especially conspicuous in the lower vertebrates, where it forms a large non-nervous bag known as the saccus vasculosus. In the embryo it passes free from nervous material as the neurenteric canal directly into connection with the alimentary canal, and so with the anus. Further, the development of the nervous system shows that, although it is clearly segmented both anatomically and physiologically, yet it is developed as a straight tube, the anterior extremity of which is at first dilated and afterwards constricted in such a manner as to form the cerebral vesicles. Any attempt, then, to discover the origin of the central nervous system of vertebrates must take these peculiarities into account, and must therefore give a satisfactory reason for what has hitherto been without explanation, namely, the extraordinary shape of the central cavities; the tubular formation of the nervous system; the presence of so large an amount of non-nervous material, especially on the dorsal side of the brain cavities; the formation of the cerebral vesicles; and the presence of a neurenteric canal.

The Central Nervous Tube an Invertebrate Alimentary Canal.—Every one of these difficulties vanishes and receives a perfectly natural and simple explanation if we look upon this epithelial tube as representing the alimentary canal of the invertebrate, from which the vertebrate sprang. If, further, we take as the type of invertebrate alimentary canal that of the crustacean, we see that the straight narrow intestine leading to the anus, with its simple non-glandular epithelial walls, represents the central tube of the spinal cord, terminating in the anus by means of the neurenteric canal; while the large globular cephalic stomach, with its simple non-glandular epithelium, represents the ventricular cavities of the brain with their simple epithelial roofs, as seen in the choroid plexuses of the third and fourth ventricles, the formation of the cerebral vesicles being explained in the simplest manner, as caused by the growth of nervous material in the position of the constrictions.¹

Further, the cavity of the infundibulum is prolonged on the very surface of the tuber cinereum as a fine tube which is much more conspicuous in the lower vertebrates, and is known in amphibia and lampreys as the impaired lobus infundibuli. This tube, which is the anterior termination of the cavities of the central nervous system, is in the position of and represents the oesophagus of the invertebrate ancestor. Here, then, we see that the topographical arrangement of the lining epithelium of the central cavities of the nervous system of vertebrates corresponds in every respect to the assumption that these cavities represent the alimentary canal of the crustacean-like ancestor of the verte-

brate—oesophagus, globular stomach, straight intestine leading to the anus—all are there.

The Vertebrate Nerve Substance Represents the Invertebrate Ganglionic Masses.—Further, the nervous material which surrounds this epithelial tube is the same, both in its topographical and in its physiological relations, as that which forms the ganglionic chain of arthropods.

The Arthropod and Vertebrate Brains Compared.—It is strange that the striking resemblances existing between the brains of arthropods and vertebrates, which were recognised and well described between twenty and thirty years ago, should have been allowed to fall into comparative oblivion just because embryologists found out that the nervous system was a tubular formation, and the attempts to pierce the brain with an oesophagus proved a failure. In reality, the evidence of the complete homology between the two kinds of nervous systems has been accumulating slowly all the time, and it is possible now, as I have pointed out in my paper in *Brain*, vol. xii, p. 1, to speak much more confidently than Leydig was able to do in 1864.

We see that, if we look upon the crura cerebri as representing the oesophageal commissures, we should have as supracerebral ganglia the brain proper, with its olfactory lobes and olfactory nerves, together with a separate optic portion forming the optic thalamus and the other centres of the optic nerves, while the infracerebral ganglia, with their special association with mechanisms for the maintenance of equilibrium, form the hind brain and cerebellum; and the thoracic and ventral chain of ganglia in connection with respiratory and locomotor mechanisms are found as the medulla oblongata and spinal cord. Even the function of the semicircular canals in assisting to maintain equilibrium has been shown to have its counterpart in the otocysts of crustaceans. We see, then, that the grouping of the nervous material around the central tube corresponds in every respect to that of an arthropod around the alimentary canal, if we suppose that the nervous system, in consequence of the great development which has taken place, has largely surrounded the original alimentary canal.

Comparison of Typical Brains in the Animal Series.—Whether this supposition is true or not can be determined by the comparison of the brains of vertebrates from the lowest to the highest. We have two alternatives to choose between: either the central tube is a nervous tube, and therefore the thin membranous portions are of the nature of nervous material, although non-nervous in function, or else the true nervous material has grown over a pre-existing epithelial tube in the manner already suggested. In the first case we ought to find evidence that the membranous portions have at some time or other resembled the purely nervous walls more closely than they do now; in the other case we ought to find that the lower we descend in the vertebrate scale the more do the non-nervous walls become conspicuous and the less are they covered with the nervous material—that, in fact, the proportion between nervous and non-nervous walls more nearly approaches to the condition found in a crustacean-like animal.

In Figs. 1, 2, 3, and 4 I give you a series of sketches, taken from Edinger, of the brains of mammalia, reptilia, amphibia, and teleostea, which show how the nervous matter of the cerebral hemispheres has been gradually built up from a simple nervous mass in the position of the corpus striatum, and that the great growth of the cerebral matter has taken place by extension from the basal ganglion over the membranous pallium.

So, too, with the cerebellum, in its passage upwards from a slender strip of nervous tissue in lampreys and amphibians to its full complexity in man of vermiform appendix and cerebellar hemispheres, we see how at first the nervous material encloses a portion of the membranous walls and so forms the "worm," while the cerebellar hemispheres are still for the most part membranous, then the place of this membranous portion is taken up by the invading nervous material and the cerebellum of the mammal becomes perfected. Further, we see in all these figures given by Edinger that the optic lobes roof over the mid-dorsal portion of the brain, forming a varying mass of nervous matter, known as the roof of the aqueductus Sylvii; and yet, if we go a little lower and look at the brain of the lowest vertebrate, namely, the ammocoetes stage of petromyzon, we find that here, too, the roof of the aqueductus Sylvii (Fig. 6; and CH₂ in Fig. 7) is membranous, and that the optic lobes do not meet together in the mid-dorsal line until the transformation of the ammocoetes into the petromyzon has taken place. In this, the lowest vertebrate brain, we see—as is natural, if my theory is true—the clearest evidence that the

¹ Cf. *Journ. of Physiol.*, vol. x, p. 227.

Fig. 1.

Fig. 2.

AMPHIBIA

Fig. 3.

lower we go in the vertebrate scale the more evident is the pre-existence of a large membranous folded cephalic bag around which the nervous material is grouped.

In Figs. 7, 8, and 9 I give the appearance of the brain of ammocoetes from the dorsal, lateral, and ventral aspects. In Fig. 9, which is copied from Ahlborn's paper, the membranous saccus vasculosus has been removed.

The whole of the dorsal surface of the brain up to the posterior commissure and ganglia habenulæ is seen to be composed of a large mass of membranous folds which are interrupted only in one place where the fourth nerve and the thin strand of nervous matter which forms the cerebellum cross over from one side to the other. These folds are known as the choroid plexuses I and III, CH_2 , forming the roof of the aqueductus Sylvii, the cavity of which in this animal is large, and CH_3 , the roof of the fourth ventricle. Choroid plexus I is shown in the diagram Fig. 5, and roofs over the space between the optic thalami, being continuous with the membranous lamina terminalis between the two cerebral hemispheres.

The Evolution of the Vertebrate Brain around the Cephalic Stomach.—Such a brain is the most striking evidence of the manner in which the vertebrate brain originated. A comparison of the diagrams Figs 5 and 6 show how the folding of the free parts of the membranous walls of the cephalic stomach is all that is required to produce the appearance of a brain such as is drawn in Fig. 7, where the supracæsophageal ganglia at the anterior extremity of the cephalic stomach are represented in their natural position, in their natural relations, and with their natural functions, by the basal ganglia C E R and the right ganglion habenulæ G H R. In front of the right ganglion habenulæ and between the two cerebral ganglia the median pineal eye P N, which, as we shall see, is distinctly arthropodan in type, forms a conspicuous object: the rest of the supracæsophageal ganglia, namely, the optic thalami and the small left ganglion habenulæ are hidden in this drawing.

The Invertebrate Mouth and Oesophagus.—We see then that the evidence of the pre-existence of a large globular cephalic stomach, around which the nervous system has been built up, is strongest

when we examine the lowest vertebrate brain. We find the same thing is also true of the remains of the invertebrate mouth and oesophagus. In the ammocoetes the folded down tube, which was the original oesophagus, is called by Ahlborn the impaired lobus infundibuli; and it is a backward continuation of the membranous saccus vasculosus, and lies most conspicuously on the ventral surface of the brain in the infundibular region just in front of the termination of the notochord. It is interesting to note that the lumen of this tube is either fairly round, or, if compressed, it is flattened so as to form a horizontal and not a vertical slit, as would naturally be the case if the pressure to which it was subjected was due to the growth of the infracæsophageal ganglia ventral to which it is lying.

The Ependyma a Primitive Epithelium.—So also we find here more conspicuously than in any other vertebrate that the lining membrane of the cavities of the brain is a structure distinct from the nervous material lying in close contiguity to it. By the use of osmic acid the cells of this lining membrane are most sharply differentiated; by the manner of their staining they are found to be full of fat globules, which stain black with the osmic, while the nervous material takes on only a greyish colour. This accumulation of fatty material in these cells not only points to a fatty change in the protoplasm of the cells, but also enables us to trace with ease the limits of the original cavity, even when that cavity has been partially or wholly occluded by the coming together of its walls. Thus we see that in the whole region of the medulla oblongata the central cavity in reality extends close to the ventral surface of the brain, but its walls have been compressed together by the nervous material on each side, so that the epithelial cells, with their interlacing cilia, form a median seam or slit which expands dorsally into the open cavity of the fourth ventricle. In other words, the raphé which is so characteristic of this portion of the brain in all vertebrates owes its origin to the nipping of the ventral portion of the cephalic stomach in consequence of the growth dorsalwards of the infracæsophageal and thoracic ganglia on each side of it, the natural effect of which is to form a vertical slit instead of a horizontal slit, as already mentioned in the case of the oesophagus.

Fig. 4.

Fig. 5.

Fig. 6.

So far it is clear that a simple straightforward explanation of all the difficulties connected with the peculiarities of the cavities of the central nervous system in vertebrates is given by the theory that these cavities are formed by the alimentary canal of the invertebrate from which the vertebrate arose.

The Fate of the Invertebrate Liver.—A new difficulty now arises; the alimentary canal of crustacean-like animals is free from digestive glands, and the function of digestion is performed by a large and most important organ—the liver—a bilateral organ which is situated in the cephalic region of the body, and which opens into the pyloric end of the stomach on its ventral side, either by a number of separate ducts or by a single duct. The liver, then, is the most important organ of the alimentary system of the crustacean, and we can hardly speak of any comparison with that system unless we find some evidence of the existence of a cephalic liver. Now the comparison of the brains of different vertebrates brings to light an extraordinary fact, which has hitherto been without sufficient explanation, that in the lowest vertebrates the brain is much too small for its case; so that whereas in the human brain the nervous matter fills up the cranium very completely, in the brains of fishes a very large portion of the cranial cavity is occupied by a gelatinous cellular mass within which the small brain is, as it were, packed. The only suggestion that has been made to account for the presence of this cellular material around the brain in the lowest vertebrates is that it is a kind of fat material which is interspersed between the brain and the skull walls, for the purpose of steadying a brain which is too small for its case. Such an explanation is clearly no explanation at all; and it is much more rational to suppose that this material exists between the brain and brain case in the lowest vertebrates, because it represents something of importance to the animal from which the vertebrates sprang; that it is there, not in order to steady a brain which is too small, but because it is the remains of a pre-existing organ which is only gradually eliminated as we pass upwards in the scale of vertebrate evolution; such an organ as is demanded on this hypothesis is clearly the cephalic liver; and when we come to examine this tissue in the ammocoetes we find that it is quite

possible to look upon it as the degenerated bilaterally situated liver belonging to the alimentary canal already treated of. In the first place, it is not fat tissue, it does not stain like fat with osmic; the degenerated nucleus is in the centre of the cell, and is not pushed to one side; the cells are closely packed against each other, being separated from one another in places by lines of pigment. In whatever direction the section is made the same appearances are seen, showing that each cell is not plate-like, but solid. The tissue is arranged as a bilateral organ on each side of, and in front of, the brain, but does not extend to the dorsal side in the region of the choroid plexuses, or to the ventral side in the region of the infundibulum. Its two lobes converge together in the middle line ventrally at the termination of the epichordal portion of the brain where the notochord begins, and where the marked projection known by the name of the conus postcommissuralis, which marks out the region of the ganglion interpedunculare, forms such a conspicuous prominence on the ventral aspect of the brain (see Figs. 8 and 9). Here at this very place, where alone there is any appearance of a hilum, osmic specimens show the presence of an occluded and bilaterally compressed tube, which comes to the very surface of the conus postcommissuralis. This tube is formed by the ventral portion of the slit of the raphé, which abruptly terminates at the extremity of the conus postcommissuralis, while the more dorsal part of the raphé, separated from it by nervous matter, continues onwards past the deep ventral furrow as the raphé of the aqueduct. We see, then, on my theory another mystery of the vertebrate brain is cleared up, and the reason why the brain of the lower vertebrates is much too small for its case is because it is surrounded by the remains of the cephalic liver of the invertebrate ancestor, the duct of which enters into the pyloric end of the stomach on the ventral side just as the oesophagus enters into its anterior end.²

² Microscopic specimens were exhibited on the screen to show the tube of the old oesophagus, the fat globules in the central epithelium, the formation of the raphé, the nature of the old liver tissue, and the presence of the liver duct. All the specimens which were exhibited are figured in my paper "On the Origin of Vertebrates from a Crustacean-like Ancestor," *Quarterly Journal of Microscopical Science*, August, 1890.

The Pineal Eye of Vertebrates.—Finally, to turn from the arthropod alimentary canal to the arthropod nervous system, I could tell you how great is the agreement not only between the topographical anatomy and physiology of the arthropod and vertebrate systems, but also in the histology of their several parts; the limits of time, however, warn me that I cannot enter upon every question connected with this theory of mine, and I therefore I will confine the rest of my remarks to the consideration of one most important point, which forms indeed the keystone of the structure I have been building up before you, which is the one clue to the past history of the vertebrate nervous system brought clearly into light by the work of recent years, and which must receive a satisfactory explanation before any theory of the origin of that system can be accepted. I mean of course the question: Why does the vertebrate possess a pineal eye? I will show you that the answer to this question harmonises so thoroughly with

sion to which I have come upon careful investigation of this eye is that it represents an arthropodan eye of an ancient type such as is found in *artemia*; the central cavity is tripartite, its posterior wall forming the retina composed of large nerve-end cells covered with pigment, the terminations of which projecting into the central cavity are free from pigment and have attached to them simple little curved rods or rhabdites. The anterior wall of the eye forms the vitreous layer or corneagen composed of large cells with large nuclei which are arranged just like the corneagen cells of arthropod eyes. In front of the corneagen layer the cuticular lens is placed in the eye of the arthropod, and we find in the pineal eye of ammocoetes that the tissue forming the cranial wall (CR) is thickened at the spot where the eye is attached to it, so that when the cranial wall is removed, a shallow depression is seen in the anterior portion of the eye, where it is fitted into this projecting knob of the cranial wall. As far then

Fig. 7.

the theory which I have put before you as to form almost the last link in the chain of evidence necessary to complete the proof of its truth. The nature of the pineal eye of ammocoetes, with its nerve and the right ganglion habenulae (GHR), is shown in Fig. 10, which represents semi-diagrammatically the appearance of a series of horizontal sections through the most anterior portion of the brain case. Such a series of sections, as can be imagined from Fig. 7, cuts through the pineal eye (PN), the right ganglion habenulae (GHR) and the membranous folds of the choroid plexuses (CH_2 , CH_3) over the aqueductus Sylvii and the fourth ventricle. No other structure is seen in these sections, except the large cells (L) which I have already spoken of as the remains of the old liver. The eye itself on the left hand side is represented as it is seen in osmic preparations, where the pigment remains unaltered. On the right side the pigment has been removed and the structure of the eye restored. The conclu-

Fig. 8.

as the eye itself is concerned it agrees perfectly in its structure with an ancient or larval type of arthropod eye.

Further, we see that a very common method of connection of the eye with the rest of the nervous system is as follows: The nerve-end cells pass into the nerve fibres of the optic nerve, which enters into a special structure called the optic ganglion, the latter being connected with the rest of the supracerebral ganglion by intermediate nervous material which has been called the medullary stalk. The optic ganglion itself is always composed of thick cortical masses of small, closely set cells around an internal medullary mass of fine nerve fibres which are connected on the one hand with the optic nerve, and on the other with the medullary stalk, and so with the rest of the nervous system.

Precisely the same arrangement, even to the finest details of structure, is seen in the connections of the pineal eye of ammocoetes. A well-defined optic nerve is formed, which passes round

the right ganglion habenulæ to dip downwards into its substance at its posterior border; the right ganglion habenulæ presents all the appearances of an optic ganglion, being composed of a cortical layer of closely-set small cells, with a medullary mass of fine fibres. These fine fibres are not only connected with the nerve of the pineal eye, but also with the basal ganglion, or cerebrum, by

Fig. 9.

means of the fibres forming the tænia thalami, which reach the brain proper by way of the optic thalamus, or medullary stalk.

In addition to the large right ganglion habenulæ, there exists a small insignificant left ganglion habenulæ; this, also, is in connection with a much degenerated median eye, which is situated ventrally to the large, much more perfect eye commonly called the pineal eye.

Summary.—I will not, however, trespass upon your patience longer, as I have now put before you all the most important points upon which I base my theory of the manner in which the vertebrate nervous system has arisen, and have shown you how the single conception that the central nervous system has been formed by the growth of nervous material around the pre-existing inver-

Fig. 10.

tebrate alimentary canal explains the presence of the choroid plexuses, explains the shape of the central cavities of the brain and spinal cord, gives a meaning to the formation of the cerebral vesicles and of the neurenteric canal, gives an adequate reason for the discrepancy between the size of the brain and its case in the lowest vertebrates, and, finally, in the most natural manner accounts for the presence of the pineal eye.

AN ADDRESS ON CERTAIN POINTS IN THE PROGNOSIS AND TREATMENT OF DISEASES OF THE HEART.

Delivered before the Hunterian Society.

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WHEN we say that a patient has "disease of the heart," we generally mean, and are understood to mean, that he has an organic lesion of the valves. If dilatation or hypertrophy of the cardiac cavities, with the effects they produce on the circula-

tion, are secondary to disease of the lungs or the kidneys, we speak of the patient suffering from chronic bronchitis or Bright's disease, as the case may be, with cardiac complications. If again we find that palpitation, irregular pulse, and other signs of disordered circulation are not accompanied by the physical signs which denote a valvular lesion, we seek for the explanation of the symptoms in derangements of the stomach, or nervous system, or in some injurious habit, such as excess in the use of alcohol, of tea, or of tobacco, and call the cardiac disorder a symptom.

Excluding these secondary and functional disorders, what proportion of cases of primary and organic disease of the heart are of valvular origin?

When Laennec introduced the practice of mediate auscultation, the answer would have been that the proportion was small. In the second volume of his great work, the chapter on Valvular Disease, its Anatomy and Physical Signs occupies only thirteen pages. It is preceded by six chapters on Hypertrophy and Dilatation of the Heart and five more on Atrophy, Softening, Indura-