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The extent of the floor-plate of His and its significance.

The summary of this paper is as follows: 1. A differentiated floor-plate extends no farther cephalad than the fovea isthmi. Increased morphologic significance is believed to attach to this depression. 2. The plan of arrangement of the longitudinal zones of His as set forth by him and generally accepted is interpreted as giving a wrong morphologic basis for the brain. 3. Theoretic considerations based partly on the 'blastopore theory' indicate: a) that the floor-plate corresponds to a 'sutura neurochordalis' (His); b) that the floor-plate and notochordal plate are primarily coextensive; c) that the neurochordal suture does not extend to the anterior end of the neural plate; d) that the primary motor and sensory zones are continuous from side to side cephalad of the anterior end of the floor-plate. 4. The following interpretations are accepted: a) that the optic chiasma marks the anterior end of the neural plate; b) that the motor zone terminates with the midbrain; c) that the floor-plate terminates at the fovea isthmi; d) that the boundary between motor and sensory zones terminates near the mammillary recess. 5. A rational basis for the division of the brain into epichordal and prechordal portions is afforded by the interpretation presented. 6. A number of facts of cephalic and encephalic morphology may be better interpreted on the basis suggested in this paper.

## THE EXTENT OF THE FLOOR-PLATE OF HIS AND ITS SIGNIFICANCE

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ELEVEN FIGURES

In 1888 Wilhelm His first set forth his well-known interpretation that the neural tube consists of four fundamental longitudinal laminae, plates, or zones—the floor-plate, the roof-plate, and the lateral plates, the last being divisible into the primary sensory zone, dorsal or alar plate, and the ventral, primary motor zone (basal plate), these being demarcated from each other upon the internal (ependymal) surface by a furrow, the sulcus limitans. In the papers by him that appeared in 1892 upon the general morphology of the brain and the divisions of the brain, and in 1893 on the frontal end of the brain tube, His further applied this conception to the brain.

The importance and fundamental character of the analysis of the neural tube in terms of primary longitudinal zones has been generally recognized, as is evidenced from the fact that in nearly every text-book having occasion to present the development of the brain and spinal cord the description is largely based upon the work of His and his figures are reproduced, among them one or more in illustration of the longitudinal zones.

The dorsal and ventral laminae composing the lateral walls of the neural tube are the zones which by their growth furnish the nervous tissue (neurones) of the brain and spinal cord, while the roof-plate and floor-plate are generally interpreted as primarily 'non-nervous,' composed of indifferent (ependymal) cells alone, although this has been frequently tacitly assumed rather than positively stated. Attention has thus been directed rather to the lateral laminae than to the dorsal and ventral medial zones that join them, which have been accordingly rather neglected.

This last statement applies particularly to the floor-plate. The roof-plate, due to the general interpretation that the choroid telas and plexuses express in each instance expansions of it, has received more consideration. Although little attention has been devoted to the floor-plate, the writer believes that the structure, extent, and significance of this portion of the developing brain and spinal cord are matters of marked importance in understanding the fundamental morphological plan of the brain, and it is the purpose of the present paper to emphasize particularly the theoretical significance of this structurally insignificant portion of the neural tube.

Descriptions of its structure are scanty, although its structural appearance is well known to every one working with the vertebrate embryo. The portion of the neural tube that it represents is apparently devoid of neuroblasts, consisting of neuroglial elements alone, which as an ependymal plate are often conspicuously evident. Processes of these cells and subsequently neuroglial fibers extend to the surface of the neural tube. It possesses thus purely negative characters for one interested primarily in the neuronal composition of the nervous system. Streeter ('11)<sup>1</sup> describes it concisely, as also does Strong ('16).<sup>2</sup> It is indeed this differentiation of the lateral wall referred to by Streeter and

<sup>1</sup> (P. 6.) "In the region of the anterior median fissure of the cord and the median raphe of the hindbrain, corresponding to the Boden-platte of His, the neuroglia maintains its primitive ependymal type of simple radial fibers extending from the lumen to the surface of the tube. It is this region that is traversed by the fibers of the anterior white commissure of the cord and the transverse arcuate fibers of the hindbrain. The persistence of this simple type of neuroglia may be explained by the absence of any mantle or nuclear layer with its consequent complications at this place."

(P. 7.) "Thus in the adult we find that the ependymal neuroglia is persistent only as septa in the anterior and posterior median planes of the nervous system and as a lining membrane for its central canal and ventricles."

<sup>2</sup> (P. 453.) "Two points are to be noted: First, that the neural plate is a bilateral structure and the future development of the tube will naturally take place principally in the side walls or lateral plates of the formed tube; second, that the primary connection between the two side walls is the ventral median plate, the dorsal median plate having been produced by a secondary fusion. This being the case, the ventral connection between the two lateral plates will naturally be more extensive and possibly more primitive than the dorsal."

which is lacking in the floor- and roof-plates that sets off both these dorsal and ventral medial zones.

The roof-plate and the floor-plate are comparable structures and this should be borne in mind in the interpretation of the latter. The roof-plate arises from the fusion of the edges of the neural plate when it forms the neural tube. It is thus primarily a bilateral structure, the two halves from the method of its formation united in an ideal dorsal line of concrescence. While in the spinal cord, medulla oblongata, and roof of the third ventricle, it differentiates as non-nervous material—dorsal septum and epithelial tela—in the cerebellum and roof of the midbrain it is so speedily obliterated that it is difficult to say that it exists at any time as a differentiated structure—a septum of non-nervous (neuroglial) elements uniting two primarily nervous plates. This would in no way affect the originally bilateral value of the cerebellum and tectum mesencephali. The same considerations apply to the floor-plate. Theoretical considerations to be discussed subsequently indicate that the floor-plate, like the roof-plate, has its two halves united by an ideal plane. In early stages of the neural tube, it is impossible to determine how much of the floor of the neural tube is non-nervous (ependymal). It is only through the growth and differentiation of the neural tube that the floor-plate becomes clearly demarcated and attains the characteristic structural features above referred to. It is quite possible that it is primarily quite slight. Throughout the extent of the spinal cord and medulla oblongata it remains relatively or completely free from nerve cells, although in certain regions (e.g., as in the pons) what appear as medial migrations of neuroblasts may quite completely transform it.

The histologic structure of the floor-plate and its significance in separating the right and left halves of the spinal cord (as the neuroglial basis of the anterior commissure) and (as the septum medullae) the caudal portion of the brain stem require no additional description or discussion. It is only when the question is raised as to how far forward into the cranial portion of the neural tube it may be traced that we reach questions touching intimately the morphology of the vertebrate central nervous system.

It was clearly the interpretation of His that the floor-plate extended throughout the neural tube and terminated at the 'anterior neuropore' where upon the completion of the closure of the neural tube it was continuous with the comparable structure in the roof. His nowhere, however, as far as I can ascertain, devotes to the question any discussion or gives any full statement. Later descriptions of the development of the neural tube, e.g., particularly the excellent descriptions of Streeter ('11), conform to this interpretation. Thus in the midbrain the existence of a floor-plate is rather tacitly assumed, as requiring indeed no comment, while in the diencephalon the floor-plate is described. If the histologic characteristics of the differentiated floor-plate as they are known in the region of the spinal cord and rhombencephalon are taken into consideration in our conception of a floor-plate, it becomes apparent that the floor-plate has a much more limited extent than is at present the interpretation. In other words, if we define the floor-plate as the medial ventral portion of the neural tube, consisting of neuroglia (ependyma) alone, devoid of neuroblasts and furnishing therefore no neuronal elements, but separating the nervous system (neural plate) into two primary right and left halves, a floor-plate is lacking, as such, in the mesencephalon and diencephalon. The floor-plate would then be recognized as extending throughout the spinal portion of the neural tube and the rhombencephalon, up to a structural feature of considerable morphologic significance, the fovea isthmi, and there rather abruptly terminating. Cephalad of this point, that is, in the floor of the midbrain, we find, not ependyma alone, but differentiation in terms of ependymal, marginal, and mantle zones, such as is encountered in the lateral walls of the neural tube.

The fovea isthmi, to which attention is drawn when seeking the anterior end of the floor-plate, requires brief notice in passing. It was first described by Stieda ('75), Burekhardt ('91) and myself ('95) in the amphibian brain. At that time I referred to it as the mesencephalic pit. His had previously termed it in the embryo the 'Isthmusgrube' ('92, 1), and indicated its presence in frog, shark, salamander, trout, sturgeon, chick, and man.

Corresponding to the medial depression internally, His described a prominence externally to which he gave the name of *eminentia interpeduncularis*. Herrick ('17) has recently reexamined the fovea isthmi in the amphibian brain. It may conveniently be regarded as marking the caudal boundary of the midbrain on the medial floor. Herrick uses the term fovea isthmi, which is here adopted. Von Kupffer ('06) terms it the 'sulcus intraencephalicus posterior.' He figures it in all classes of vertebrates save the cyclostomata and the Mammalia (the latter class was not included in the limits of his presentation). Johnston ('09), who figured the medial plane in the brains of shark, salamander, and mammal, shows the fovea isthmi only in the salamander. In the medial plane reconstructions of the developing brain of shark, bird, and mammal, reproduced here as figures 1, 2, and 3, it is evident in all. The floor of the midbrain anterior to the fovea isthmi is without adequate embryological designation. For the German terms *Haube*, *Haubenwulst* as applied to the mesencephalic floor, 'tegmental swelling,' 'tori tegmentales,' and 'tori semicirculares' have been used. The 'tuberculum posterius' of von Kupffer may be taken as marking the anterior boundary of the mesencephalic floor.

To illustrate the abrupt termination of the differentiated floor-plate at the fovea isthmi, three reconstructions were made of the midsagittal plane, from three classes of vertebrates, the elasmobranch (*Acanthias*), the bird (chick), and the mammal (calf). These are reproduced as figures 1, 2, and 3. It will be seen that the differentiated floor-plate, characterized by the presence of the ependymal layer only and the neuroglial processes (neuroglia fibers), often grouped together in parallel radial bundles, terminates at the fovea isthmi and cephalad of this point, in the floor of the midbrain, the characteristic arrangement of the floor-plate is lacking, while ependymal, mantle, and marginal layers appear. In other words, the differentiation shown is that characteristic of the lateral wall of the neural tube. Cephalad of the midbrain the medial floor thins in the hypothalamic region, to thicken again at the chiasma. Inasmuch as the low magnification for these medial plane reconstructions necessitated

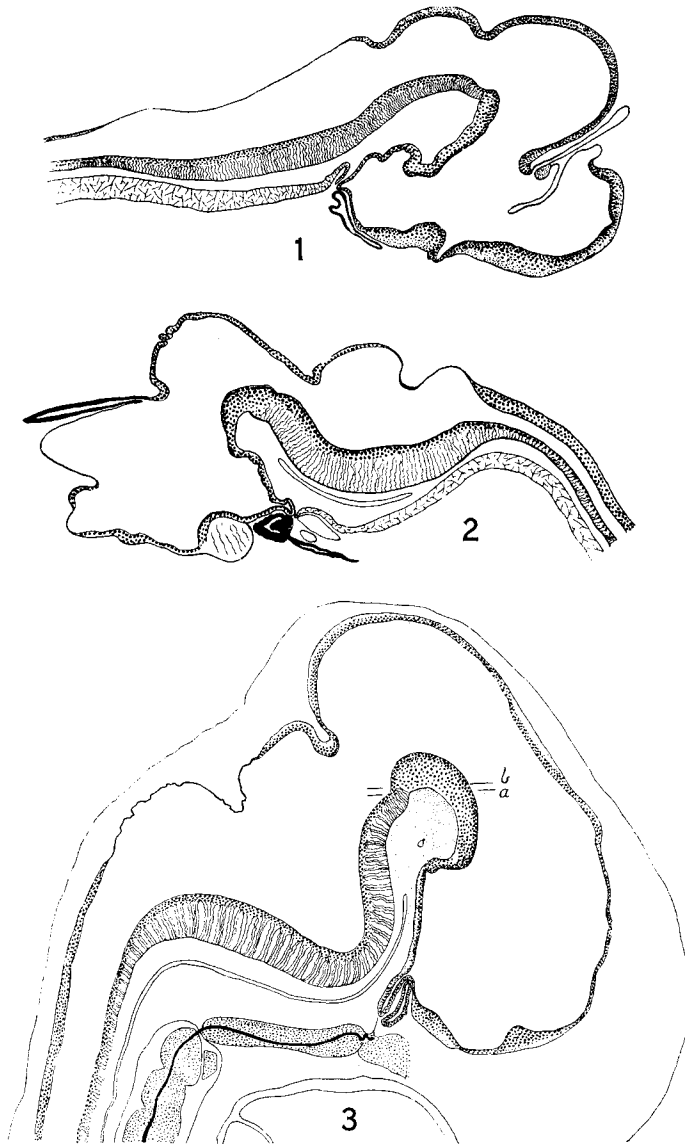


Fig. 1 Reconstruction of the middle plane of the brain, together with notochord and hypophysis, in *Squalus acanthias* embryo, 40 mm. total length.  $\times 10$ .

Fig. 2 Medial plane reconstruction of the brain, notochord, and hypophysis in a chick of seven and one-half days' incubation.  $\times 10$ .

Fig. 3 Medial plane reconstruction of the brain, hypophysis, notochord and basilar plate in a calf embryo of 23 mm. length. (Series C.25, Cornell University Collection.)  $\times 10$ .

In these figures the floor-plate is indicated by the parallel, somewhat irregular lines representing the fibers of the floor-plate.

that the representation of the structure be quite diagrammatic, photographs from the sections showing the median plane at the fovea isthmi are reproduced as figures 7, 8, and 9. Of these, that of the calf embryo shows the median plane throughout, while in figures 8 and 9 only the extent indicated is medial. In figure 9, the pulling away of the neural tube from the mesenchyme has accentuated the 'eminencia,' making it more abrupt, while the outline of the external surface cephalad of it is poorly defined. It will be seen, particularly in the reproductions from the calf and shark embryos (figs. 7 and 8), that the statements made above are fully confirmed by the photographs.

Two additional photographs from frontal sections of a calf embryo (20 mm.), through the summit of the mesenchyme in the plica encephali ventralis<sup>3</sup> and somewhat more dorsally are given for comparison (figs. 10 and 11). The general position of these levels is indicated upon the medial plane reconstruction (fig. 3) by the lines 'a' and 'b.' It may be noted that in figure 10 the floor-plate is shown in the caudal limb of the bend and its absence in the cephalic (mesencephalic) limb or portion. The more dorsal section (fig. 11) is through the cephalic end of the floor-plate where the letter 'c' indicates its limit.

The question of the significance attaching to the termination of the floor-plate anteriorly at the fovea isthmi involves the interpretation of the cephalic portion of the neural tube, and brings up for consideration the much-discussed question of the anterior end of the neural plate and of the neural tube itself. The conclusions reached by His were given in 1888 and particularly in 1892 in his paper on the general morphology of the brain. They are well illustrated by his figure 1 from the latter article, which is reproduced here as figure 4. The anterior end of the floor of the neural tube he placed at the 'Basilarleiste' 'B' (basilar fold) later to become, according to his interpretation, the recessus infundibuli. The dorsal wall of the tube, due to its great curva-

<sup>3</sup> This term introduced by v. Kupffer and meaning, as its composition implies, 'ventral brain fold,' seems to the writer more useful in this connection than 'cephalic flexure' ('head fold') for which it is a partial equivalent.



ture, is more extensive. The floor-plate thus terminates at the basilar fold (*recessus infundibuli*); the roof-plate marks the extent of the medial dorsal wall; while a line of closure at the anterior end of the tube, in the territory of the future lamina terminalis, obliterates the anterior neuropore. "All three medial plates of the brain tube correspond to original seams of closure,"—a dorsal seam (*dorsale Naht*), a ventral or neurochordal seam (*neurochordale Naht*) and an anterior or frontal end-seam (*frontale Naht*).<sup>4</sup> The sulcus limitans, bounding the basal plate from the alar plate, he considered as terminating at the optic recess (i.e., preoptic recess). His conception of the brain tube is thus clear: that in the neural tube there was a dorsal line of closure and an anterior (frontal) line of closure, while the neural plate itself was completely separated into two halves by a floor-plate which itself represents a line of closure in the laying down of the body, by concrescence, hence the term '*neurochordale Naht*' which he used.<sup>5</sup>

The brain-plate was thus interpreted as a completely paired structure, consisting of two separate halves united through con-

<sup>4</sup> His offered no technical designations for these seams of closure which he recognized. These were supplied by Goronowitsch ('93), who termed them '*Sutura neurochordalis seu ventralis, Sutura terminalis anterior, and (by implication) Sutura dorsalis*. He failed, however, clearly to appreciate what His meant by '*Neurochordale Naht*.' His words are (p. 203): "Von der vorderen Grenze der Leisten (*gl*) verläuft ein Spalt (*f*), welcher ventralwärts bis zu der Gegend *a* reicht, wo die ventrale Hirnwand mit den unterliegenden Theilen in Verbindung steht. Diesen Spalt welche ich einfach *Sutura cerebri anterior* bezeichne, da ich eine Zersplitterung dieses Terminus in zwei Termini "*Sutura neurochordalis, seu ventralis und Sutura terminalis anterior* (His) für meine Zwecke überflüssig finde (vergl. 32, pag. 7)."

<sup>5</sup> His ('92, 2), (p. 348): "Alle drei Säume des Medullarrohres entsprechen ursprüngliche Nahtlinien. Am längsten ist die dorsale Naht (*d.N.*) bekannt. Die ventrale oder neurochordale Naht ist zur Zeit noch von Manchen Seiten her bestritten. . . . Ungenügend gewürdigt ist auch die vordere oder frontale Endnaht (*f.N.*, Fig. 1). Sie entsteht durch Verbindung der vorderen Ränder der Medullarplatte und nimmt bei allen Wirbelthieren eine durchaus selbständige und charakteristische Stellung ein. . . . Die Wand des Medullarrohres ist in den an die Nahtlinien anstossenden Strecken in Allgemeinen dünner, als in den beiden Seitenwänden, die verdünnte Strecke der ventralen Röhrenwand ist die sogenannte Bodenplatte, die der dorsalen die Deckplatte. Die verdünnten Nahtstrecken der vorderen Naht liegen im Boden des dritten Ventrikels und in der *Lamina terminalis*."

crecence and joined together by the floor-plate. I shall recur to this later. His figure 8, from his ('93,1) paper on the frontal end of the brain tube, reproduced here as figure 5, illustrates this clearly. Johnston ('09), from a study of the early developmental stages in the shark, the salamander, and the pig, has given valid

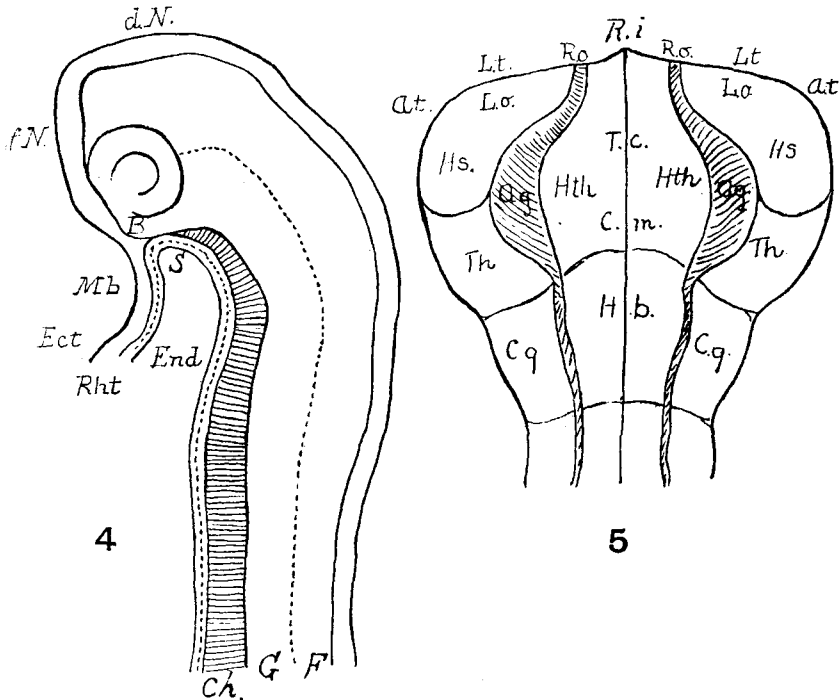


Fig. 4 Copy of figure 1 of Wilhelm His ('92, 2). Schema in explanation of the bent brain tube and its relations to chorda dorsalis (*Ch.*), to Sessel's pocket (*S*) and to the pharyngeal membrane (*Rht.*). *d.N.*, dorsal seam (Naht); *f.N.*, frontal seam; *Mb.*, stomodeum; *G.*, basal plate; *F.*, alar plate; *B.*, basilar fold (Basilarleiste).

Fig. 5 Copy of figure 8 of Wilhelm His ('93, 1). The attempt is made to project the individual brain regions upon the medullary plate of a selachian at a stage in which it is still spread out flat. The regions are indicated as follows: *Ag.*, optic vesicle; *A.t.*, angulus terminalis; *C.m.*, corpus mamillare; *C.q.*, corpus quadrigeminum; *Hb.*, tori tegmentales (Haubenwülste); *Hs.*, pallium cerebri; *Hth.*, hypothalamus; *L.o.*, lobus olfactorius; *L.t.*, lamina terminalis; *R.i.*, recessus infundibuli; *R.o.*, recessus opticus; *T.c.*, tuber cinereum. The region of the optic chiasma would be between *R.i.* and *R.o.*

evidence that the rostral (cephalic) end of the neural plate in the closed neural tube is marked by the anterior boundary of the optic chiasma, that is, is located at the preoptic recess. His termed this recess the optic recess as marking on the middle plane the level of the optic evaginations. Johnston points out that the preoptic recess is secondary and that the basilar furrow of His (Basilarleiste), which he regarded as becoming the recessus infundibuli, in reality marks the level of the optic evaginations. Johnston therefore calls the basilar furrow of His the primitive optic furrow, which he concludes may persist as a postoptic recess. These points of disagreement with the conclusions of His do not particularly concern us here, aside from his conclusion that the anterior end of the neural plate includes the optic chiasma. The experimental results of W. H. Lewis ('12), Spemann ('01) and Stockard ('13), indicating as they do that the anterior end of the neural plate is occupied by the retinal area (or areas), would in a general way confirm this. Johnston further says (p. 462) that "The determination of the anterior end of the brain will fix the extent of the floor-plate and roof-plate of His and will show the point at which the prolongation of the sulcus limitans must end;" and further concludes (p. 504) that "The optic chiasma therefore occupies the anterior border of the floor-plate of the brain." Johnston thus extends the floor-plate farther forward than did His, and apparently, like His, regarded it as completely dividing the cranial portion of the neural plate into two halves. His wording in regard to this is not entirely clear, as appears from the above quotation.

Schulte and Tilney ('15), in a study of the morphogenesis of the neuraxis and the interpretation of the forebrain in terms of the longitudinal zones of the neural tube, have likewise dealt with the problem involved. Their conclusions are based upon the conditions in twenty-six young cat embryos cut in the transverse plane as studied in wax-model reconstructions. They find that the anterior end of the neural plate is marked by a swelling, the 'tubercle of the floor,' which is located at the anterior extremity of the floor-plate. This tubercle, according to their interpretation, becomes the mammillary region. The medial plane of

the floor of the brain cephalad of this point would thus represent a secondary concrescence of the edge of the neural plate. In other words, in terms of the His nomenclature, they would extend the frontal suture caudally in the floor so as to include in its territory not only the optic chiasma (as did His), but the infundibulum as well. Their interpretation thus departs widely from that of Johnston. They approach his interpretation, however, in deriving the infundibular recess from the primitive optic vesicles.<sup>6</sup>

No comment need be made on the interesting conclusions of Schulte and Tilney save to emphasize that the critical point is the interpretation of the 'tubercle of the floor' and to venture the opinion that the figures offered in illustration neither conclusively show that it corresponds to the anterior end of the neural plate nor that it marks the anterior boundary of the mammillary recess. The floor plate, as such, and the question of its extent, they do not specifically discuss.

As is of course well known, His had in a number of articles ('76, '77, '77, '91) proposed and supported the view that the axis of the vertebrate body was established by the concrescence of a 'germ ring.' His last discussion of concrescence ('91) was a paper read at the meeting of the Anatomische Gesellschaft, and in the discussion his conception of concrescence met with considerable adverse criticism. He therefore welcomed the support O. Hertwig ('92) gave to the theory of concrescence through the publication the next year of his classical paper, "Urmund und Spina bifida." Hertwig's conclusion, however, that the 'neurochordal seam' was laid down by the concrescence of the right and left halves of the (dorsal) blastoporic lip, he could not accept.

<sup>6</sup> Schulte and Tilney ('15), (p. 340): "As the tubercle of the floor constitutes the extremity of the floor-plate and at the same time the primitive ventral lip of the neuropore, it is of prime importance to ascertain its position in subsequent stages of development." (P. 341.) "The tubercle of the floor is now losing its demarcation from the parietes with the effacement of the primitive ventral segment of the optic sulcus, and from this period appears as a transverse ridge intervening between the mammillary and infundibular regions. It is, therefore, evident that the mammillary region arises from the cephalic extremity of the primitive floor-plate and that the infundibular region is a derivative of the primitive optic vesicles."

This failure to appreciate the importance of Hertwig's 'blastopore theory' for his own 'conrescence theory' seems to lie mainly in his inability to see how the primitive streak could in any way correspond to a blastoporic lip. Minot ('90, '92), on the other hand, who was an energetic champion of the theory of conrescence, clearly recognized—independently of Hertwig's experimental evidence—that "conrescence is a method of uniting the lips of a greatly elongated gastrula mouth." Since the year 1892 investigations upon the early development of the vertebrate body have contributed fact and interpretation both for and against conrescence. The blastopore theory, however, gives us the more fundamental conception. From the dorsal lip of the blastopore, or the primitive streak that clearly represents it essentially, is formed by differential growth in that region, neural plate, notochord, mesoderm. For this the evidence aside from that experimental and teratological, though largely indirect, is cumulative and conclusive. The growth of the blastoporic lip (primitive streak) essentially constitutes a closure of a primitive blastoporic opening by means of a conrescence, actual or potential. The conrescence theory thus loses all force or application aside from the blastopore theory. The sutura neurochordalis only has significance as a line of conrescent closure if it is conceived as formed along the line of growth of the dorsal blastoporic lip.

It seems a little remarkable that His, entertaining as he did the view that the body axis is laid down by conrescence of a germ ring, should have failed to recognize that there was a high probability at least that anteriorly to the line of conrescence the body material should be primarily continuous and that the neurochordal suture could not extend fully to the secondary line of closure—the frontal suture closing the neural tube anteriorly. Indeed, in his 1891 paper on conrescence, here and there, particularly in his discussion of the formation of the embryo from the primitive streak (p. 76), as well as in his figures, are indications of his recognition of a 'preaxial' portion of the body, but he never apparently saw the import of this for his own theory. Minot ('92) in this respect clearly appreciated that there is a primitive

continuity cephalad of the line of concrescence (closure), as his figures (figs. 64, 66, 67, and 74) show. In terms of the blastopore theory, it is evident that at the anterior end of the line of closure there would be continuity of the blastoporic lip of either side, and that the lateral plates of the neural plate would be continuous across from side to side at this point. Although he did not attempt to determine in what portion of the brain-plate and brain tube such a primary continuity across from side to side cephalad of the neurochordal suture would reside, Hertwig ('92) leaves no doubt of his full recognition of the necessary occurrence of such continuity at this point as an essential part of his interpretation.<sup>7</sup>

His, with his customary acumen, recognized that "it is just in the earliest stages that the key to the understanding of all later manifold complexities in the conformation of the brain must be sought;" that the fundamental plan of arrangement of the brain tube may be mapped out in the neural plate. This he attempted to do ('93, 1) in his figure 8, which has been already referred to and copied in this article as figure 5. The attempt was clearly premature, as the work of Johnston ('09) and others have shown. It is still of course premature to offer a diagram

<sup>7</sup> Hertwig, O. ('92), (pp. 372-373): "Wir erhalten auf diese Weise eine Gas-trula-form bei welcher der noch weit offene Urmund, der vom Kopfe nach dem Schwanzende zu etwas in die Länge gezogen ist, ringsum von der Anlage des Nervensystems eingeschlossen ist. Die Urmundränder selbst bilden eine etwas gekrümmte, nach aussen frei liegende Nervenplatte, einen Medullarring. . . . Das periphere Nervensystem zerlegt sich so ganz naturgemäss nach seiner örtlichen Entstehung in einen sensiblen, von dem äusseren Rande des Nervenrings, und in einen motorischen, von seinem inneren Rand ausgehenden Abschnitt. Indem auch bei den Wirbelthieren das Centralnervensystem, wie unsere Missbildungen so deutlich zeigen, als Ring in der Umgebung des Urmunds zur Anlage kommt, bietet sich eine sehr einfache, von mir (Lehrbuch d. Entw. ges.) schon früher kurz dargelegte, morphologische Erklärung für den Bell'schen Lehrsatz oder die Thatsache des getrennten Ursprungs der sensiblen und motorischen Wurzelfasern." . . . (Pp. 373-374.) "Die Beziehung des Centralnervensystems der Wirbelthiere zum Urmund (Primitivrinne, Blastoporus) sind schon oft erörtert und anerkannt worden. Dabei ist ein Punkt im Unklaren geblieben, die Ausdehnung nämlich, in welcher der Urmund des Centralnervensystem seiner Länge nach gespalten hat. Durch die vorliegende Hemmungsmissbildung ist auch in diese Frage mehr Klarheit gebracht. Die Urmundspalte hat ursprünglich das ganze Centralnervensystem in zwei gleiche, an ihren Enden zu einem Ring geschlossene Hälften zerlegt." Also compare pages 424-452.

alternative to that of His. However, inasmuch as I have in this paper attempted to show that from the actual facts of structure the floor-plate extends no farther forward than the fovea isthmi, and that theoretic considerations strongly speak against its extending to the extreme anterior end of the neural plate as the diagram of His indicates that it does, a simple diagram (fig. 6) will serve to make clear what are the conclusions to which in

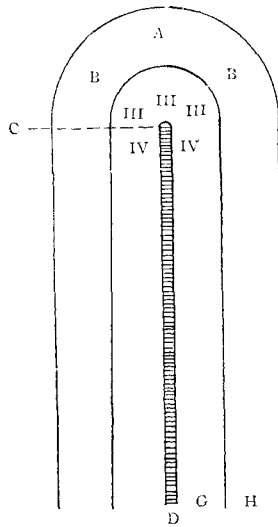


Fig. 6 Diagram to illustrate the interpretation of the cephalic portion of the neural plate. *A.*, the region of the retinal area(s); *B.*, the region of the olfactory lobes (and cerebrum); *C.*, cephalic end of the floor-plate or sutura neurochordalis (fovea isthmi in the neural tube); *D.*, the floor-plate (sutura neurochordalis); *G.*, primary motor zone, lamina basalis; *H.*, primary sensory zone, alar plate; *III*, *N. oculomotorii*; *IV*, *N. trochlearis*.

my opinion one is logically led, both from fact and from theory. In the diagram it will be noted that the alar plate and the basal plate, primary sensory and motor zones, are indicated as extending around from side to side 'anterior' to the cephalic end of the floor-plate or neurochordal suture at whose cephalic end the fovea isthmi appears in the neural tube. The retinal area occupies the more cephalic portion of the alar lamina while the nucleus oculo-

motorius similarly occupies the preaxial portion of the basal plate with the nucleus trochlearis immediately caudad of it. The olfactory areas (and cerebral areas) in the alar plate would occupy positions morphologically caudad of the retinal area. It by no means follows that these areas are more than potentially present in the neural plate. It would be useless, of course to attempt to assign even relative locations for other brain regions without ascertaining the effects that the great growth, in length and breadth, and also the unequal growth, would have.

Certain comments may be made on the relations outlined by the diagram and what they signify.

1. The experiments of W. H. Lewis and Stockard have shown that the retinal area (or areas) occupy the extreme cephalic portion of the neural plate. There is not agreement as to whether the area is primarily single or double, but this has little significance in the present connection, although, if I may state it, my individual opinion is that the evidence supports Stockard's contention of a primarily single medial retinal area in the neural plate. Johnston, from purely morphological studies, has indicated that the cephalic boundary of the neural plate marks the site of the future optic chiasma behind which as the retinal areas separate the primitive optic furrow remains.

2. The closer allocation of the motor and sensory sides of the visual apparatus than would be otherwise possible is also quite suggestive and renders somewhat more comprehensible a feature of head morphology otherwise obscure.
3. The eyes thus would represent the most anterior of the series of sense-organs. This is, I think, no new interpretation, borne out as it is by the reversed relation of eye to olfactory organ in Cyclopia. It also serves to render more comprehensible the seriation of sense organs—retinal, olfactory, otic, etc.—which Duval ('00) so nicely set forth in diagrammatic form in his figure 420.

4. Possibly, though perhaps not probably, the existence of a nucleus centralis n. oculomotorii, effecting a confluence of the oculomotor nuclei of the two sides, may be thus accounted for, as well as the medial position of other nuclei in this region (n. centralis superior, n. centralis raphae, ganglion interpeduncu-



lare). The partial decussation of the oculomotor nerve (crossed origin) might also express a primitive continuity across from side to side in this region.

5. I venture again to call attention to the conclusion of Johnston that what His termed the recessus infundibuli (Basilarleiste) should more appropriately be termed the primitive optic furrow and that the recessus infundibuli was a secondary out-pocketing of the wall of the neural tube. Under the conception of the brain-plate here outlined, this would occur medially between the alar and basal plates separating the sensory zone in the floor (the optic chiasma) from the motor (the floor of the midbrain); but whether at the expense of the sensory zone or of the motor zone or as an essential separation of them, cannot be said. The development of the infundibulum is, I think, unquestionably bound up with the development of the hypophysis, and until the early morphogenesis of the latter is clarified and its morphological significance better estimated, nothing can be added to a mere statement of fact.

6. Such a conception as this of the cephalic portion of the neural plate, it must be conceded, contradicts certain generally accepted doctrines of fundamental brain morphology. Thus, the boundary between primary motor and sensory zones, which appears in the more caudal portion of the neural tube as the sulcus limitans, frequently to be seen, particularly in the mammalian neural tube and in the rhombencephalon, would not terminate at the preoptic recess as is generally thought to be the case, but would terminate in the primitive infundibular recess, primarily continuous across from side to side. In the His models of the developing human brain, as Schulte and Tilney point out, the sulcus limitans does so terminate anterior to the midbrain floor (i.e., in the mammillary region). It is in my opinion a valid objection to the generally accepted interpretation that it includes in the basal, primary motor lamina optic chiasma and hypothalamus—regions which possess no such significance. The motor zone ceases with the floor of the midbrain. This is, I think, more striking in the brain of a lower vertebrate than it is in that of a higher form. The divisions of the brain would lose their

significance as fundamental segments of the neural tube. The telencephalon and diencephalon would then be entirely developed out of alar-plate material. This is the interpretation of Schulte and Tilney ('15).

7. The conception of the floor-plate as marking a line of blastoporic concrescence, and representing the neural portion of a neurochordal suture postulates that when first formed the notochord and floor-plate be coextensive. It would thus be possible to speak of a prechordal portion of the neural plate as a primitive condition, as well as pre- and epichordal parts of the neural tube.

Ahlborn ('83), in the lamprey, so divided the brain into epichordal and prechordal regions, basing the distinction drawn upon three things: 1) The epichordal brain alone possesses nerves comparable to those of the spinal cord; such are lacking in the prechordal portion. 2) It possesses a raphé which is completely lacking in the prechordal brain. 3) It is coextensive with the notochord. Ahlborn thus included only the rhombencephalon in the epichordal brain, the mesencephalon and prosencephalon being prechordal. Strong ('16), doubtless through an appreciation of the force of the first of Ahlborn's points, has likewise divided the brain into epichordal and prechordal parts,<sup>8</sup> but includes the mesencephalon in the epichordal brain, and the reason for this is obvious; to the midbrain belong the oculomotor and trochlearis nerves. The plan of brain morphology here outlined limits the epichordal brain more nearly to the rhombencephalon, essentially as was done by Ahlborn, in the lamprey. The difficulty in recognizing a motor zone cephalad of the chorda is, however, obviated. I also see no reason why the nuclei of the IIIrd and IVth cranial nerves might not vary in position in

<sup>8</sup> (P. 453.) "After closure (of the neural tube), in many Vertebrates at least, a three-fold division can be made out: (1) A caudal part of the neural tube, the spinal cord, which gradually expands cranially into (2) the caudal part of the brain (deuterencephalon v. Kupffer) (fig. 400). These two parts lie above the notochord and all the typical cerebrospinal nerves are connected with them. (3) Cranially, at the anterior end of the notochord, the brain wall expands ventrally forming the third portion (archencephalon). At the forward extremity is seen the anterior neuropore. The deuterencephalon is thus an epichordal part of the brain, while the archencephalon is prechordal."

different vertebrates. It is we who draw sharp boundaries, not nature.

It doubtless will be objected that the notochord originally extends farther cephalad than the point which the present interpretation demands, possibly as His thought to the level of the (his) basilar fold. His ('92, 1), in fact, criticised Ahlborn's division of the brain into epichordal and prechordal parts on the ground that the extent of the notochord in the adult is secondary and varies from stage to stage and in different forms. This objection is of course valid; notochord and neural tube grow markedly after they are first laid down and at different rates, but it applies equally to His' own interpretation. Such figures as his own ('92, 2) figure 4, of the torpedo embryo, as well as such carefully constructed figures as those of Scammon ('12) for *Acanthias*, among others, indicate that the notochord in early stages, when first formed, does not extend forward to the basilar fold as the His interpretation demands.

It is evident, however, that our knowledge of the morphological relations at the anterior end of the notochord is quite inadequate, and any consideration would involve the interpretation not only of the notochord and neural plate, but as well the protochordal or prechordal plate, so-called preoral entoderm (cephalic entoderm), etc.; in fact, all aspects of that intensely interesting portion of the head in the immediate neighborhood of the hypophysis. The present interpretation has the merit of recognizing the distinction of epichordal and prechordal portions of the brain tube as primary and not secondary, and of offering an explanation of the significance of this distinction.<sup>9</sup>

<sup>9</sup> In terminating this paper the writer wishes to acknowledge the helpful editorial comments of Prof. C. J. Herrick.

## SUMMARY

1. A differentiated floor-plate extends no farther forward than the fovea isthmi. Increased morphological significance is believed to attach to this depression.

2. The plan of arrangement of the longitudinal zones of His as set forth by him and generally accepted is interpreted as giving a wrong morphological basis for the brain.

3. Theoretic considerations based partly on the 'blastopore theory' indicate: *a*) that the floor-plate corresponds to a suture neurochordalis (His); *b*) that the floor-plate and notochordal plate are primarily coextensive; *c*) that the neurochordal suture does not extend to the anterior end of the neural plate; *d*) that the primary motor and sensory zones are continuous from side to side cephalad of the anterior end of the floor-plate.

4. The following interpretations are accepted: *a*) that the optic chiasma marks the anterior end of the neural plate; *b*) that the motor zone terminates with the midbrain; *c*) that the floor-plate terminates at the fovea isthmi; *d*) that the boundary between motor and sensory zones terminates near the mammillary recess.

5. A rational basis for the division of the brain into epichordal and prechordal portions is afforded by the interpretation presented.

6. A number of facts of cephalic and encephalic morphology may be better interpreted on the basis suggested in this paper.

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## PLATE 1

### EXPLANATION OF FIGURES

7 Photograph of the median plane in the floor of the brain at the plica encephali ventralis. The section is nearly medial throughout. The floor plate is on the left, extending to the fovea isthmi. Compare with figure 3. Calf, 23 mm.  $\times 37\frac{1}{2}$ .

8 Photograph of the floor of the brain of the shark, *Squalus acanthias*, 40 mm. length, at the fovea isthmi. Only the region included between the two lines is median. Note the sudden cessation of the floor-plate, its characteristic structure in comparison with the floor of the midbrain. Compare with figure 1 and also with figure 7.  $\times 67\frac{1}{2}$ .

9 Photograph of the floor of the brain of the chick, seven and one-half days' incubation, at the fovea isthmi. Only the region included between the two lines is median. The cephalic side, as in figure 2, is toward the left.  $\times 67\frac{1}{2}$ .

10 Photograph of a section cutting horizontally the floor of the brain at the plica encephali ventralis through the summit of the included mesenchyme (i.e., the fossa interpeduncularis). Calf, 20 mm. (Cornell Univ. series C.21).  $\times 37\frac{1}{2}$ .

11 Photograph as in figure 10, but seventeen sections ( $170\mu$ ) farther dorsal, where 'C' marks the upper end of the floor plate. In figures 10 and 11 the cephalic side is up.  $\times 37\frac{1}{2}$ .

