

THE MEDIAL GENICULATE BODY AND THE NUCLEUS ISTHMI

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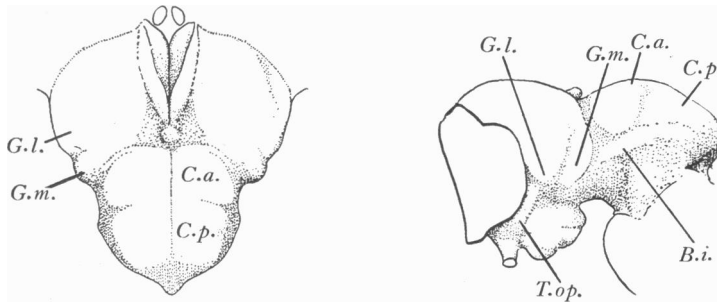
IN the small brains of primitive Mammals such as insectivores, the medial geniculate body forms a conspicuous rounded tubercle projecting from the lateral aspect of the caudal end of the thalamus. Topographically it appears to be essentially a part of the latter, for while it is marked off from the mid-brain by a relatively deep furrow, it is separated from other thalamic elements such as the lateral geniculate body and the pars posterior of the lateral nucleus (pulvinar) superficially by quite shallow grooves. It is held by many authorities, however, on the basis of comparative anatomical studies, that the medial geniculate body is rather to be regarded as a mesencephalic element which has become secondarily approximated to the diencephalon during the course of evolutionary differentiation of the fore-brain, and it is one of the aims of this paper to consider this interpretation.

Coronal sections through the medial geniculate body of insectivores (e.g. *Erinaceus* and *Sorex*) show that in its cyto-architecture it consists mainly of a homogeneous group of rounded and fairly large polygonal cells of uniform size which are scattered evenly throughout the nucleus. This may be called the principal nucleus of the medial geniculate body. It marks the termination of the bulk of the fibres forming the brachium inferius of the posterior colliculus and it gives off contributions to the thalamic radiations which at first pass forwards medio-ventral to the optic radiations emerging from the lateral geniculate body, and then turn laterally to reach the cortex. There is experimental evidence to indicate that these cortical connections conduct in both directions and are essentially related to the area temporalis of the neopallium.

If coronal sections of the insectivore brain are traced rostrally, the principal nucleus of the medial geniculate body is found to pass without any demarcation or interruption directly into the ventral nucleus of the thalamus, which is made up of precisely the same type of cell. This broad continuity of the medial geniculate body with the ventral nucleus is well shown in horizontal sections through the diencephalon of *Sorex*. In this primitive brain, therefore, the geniculate body is merely the latero-caudal part of the main sensory nucleus of the thalamus, and is not to be distinguished from the latter except by its topographical position and its fibre connections (especially with the inferior brachium). In the brains of larger Mammals the medial geniculate body undergoes a caudal displacement consequent mainly upon the expansion of the lateral

nucleus of the thalamus. A study of a graded series shows that in this way it becomes extruded caudo-ventrally and finally "pinched off" from the main part of the ventral nucleus, and its connection with the latter thus becomes increasingly indistinct. Nevertheless, such a connection has been noted in higher mammalian brains. Thus Rioch (20), and later Ingram, Hannett and Ranson (9), note a continuity between the medial geniculate body of Carnivora and the pars arcuata of the ventral nucleus, and Papez (16) has recently indicated a similar relation in the armadillo.

The common origin of the principal nucleus of the medial geniculate body and the ventral nucleus of the thalamus is indicated clearly enough in the brain of the human embryo. Thus, Plate I, fig. 1 represents a horizontal section through the diencephalon and mid-brain of a human embryo of 92 mm. C.-R. length, in which the cells of the medial geniculate body merge with those of the ventral thalamic nucleus to form a common mass which extends caudo-



Text-fig. 1. Dorsal and lateral views of the diencephalon and mid-brain of a 92 mm. human embryo. $\times 3$.

B.i. inferior brachium. *C.a.* anterior colliculus. *C.p.* posterior colliculus. *G.l.* latera geniculate body. *G.m.* medial geniculate body. *T.op.* optic tract.

laterally to the surface of the thalamus. It may be noted, further, that the superficial cells of both lateral and medial geniculate bodies form a continuous stratum although the former (which is also derived from the common ventral nuclear mass) is otherwise well defined at this stage of development by medullary laminae. In the section, fibres of the brachium inferius can be seen entering the caudal extremity of the medial geniculate body. The dorsal and lateral aspects of the diencephalon and mid-brain of the embryo from which this section was taken are illustrated in text-fig. 1. From this, it will be seen that in the 92 mm. stage the two geniculate bodies occupy the primitive position which is found in Insectivora, that is to say, they form low elevations on the lateral wall of the thalamus proper and are not yet overhung by a caudally projecting pulvinar. The medial geniculate body occupies a rostral position relative to the mid-brain, and passing forwards and downwards to it on the lateral aspect of the latter is to be seen very distinctly a broad white band, the inferior brachium.

Ventral to the principal nucleus of the medial geniculate body in the insectivore brain and extending to its caudal margin is a flattened plate of spindle-shaped cells which may be called the ventral nucleus of the medial geniculate body. It runs into direct continuity medially with the zona incerta of the subthalamus, and rostrally it is continuous with the nucleus reticularis thalami (which, incidentally, should not be included among the nuclei of the thalamus proper for it is nothing more than an extension dorso-laterally of the subthalamus to form a thin shell covering the lateral surface of the thalamus and penetrated everywhere by the thalamic radiations). It represents the *noyau suspédonculaire* of Cajal (1) in the mouse brain, the *noyau caudal gris* of Vogt (27) in the medial geniculate body of *Cercopithecus*, the caudo-ventral element of Friedemann (5), Pines (17), and Clark (2) in *Cercopithecus*, *Lemur*, and *Tarsius* respectively, the *nucleus infrageniculatus* of Prěchechtěl (19) in the elephant, the *c* nucleus of Winkler and Potter (25, 26) in the rabbit and cat (in which these authors note it is united with the ventral part of the formatio reticularis), and the marginal nucleus of Winkler (24). It is with the ventral nucleus of the medial geniculate body that the commissure of Gudden appears to be principally related. Winkler states that after removal of the hemisphere in the rabbit, while the main part of the medial geniculate body undergoes complete atrophy, this is not the case with his marginal nucleus. Meyjes (14) found no degeneration in the *c* nucleus after lesions involving the area temporalis of the cortex in the rabbit.

By Rioch (in carnivores) and Papez (in *Tatusia*), this element is not distinguished from the reticular nucleus. It should, however, be included in the medial geniculate body, for in many Mammals it becomes incorporated with the principal nucleus (and intimately related to it) in the eminence of the medial geniculate body. Its connections with the zona incerta become much less obtrusive in the brains of higher types (in association with the displacement of the body ventro-caudally in these forms), and sagittal Weigert sections in *Erinaceus* and *Tarsius* show that it receives a contribution from the inferior brachium. In these animals, also, the ventral nucleus of the medial geniculate body is connected with the subthalamus by fine myelinated fibres (see text-fig. 2), the ultimate destination of which cannot be determined by normal Weigert material.

Thus the medial geniculate body in its simplest form is found from a study of mammalian brains to consist essentially of two diencephalic elements which are differentiated respectively from the ventral nucleus of the thalamus proper and the subthalamus. These divisions are, moreover, directly comparable with the two elements of the lateral geniculate body. The dorsal nucleus of the latter (corresponding to the nucleus principalis of the medial geniculate body) is delaminated off from the lateral aspect of the main sensory nucleus of the thalamus in association with its optic connections (4) and gives off cortical projection fibres, while its ventral nucleus I have shown (3) to be really a differentiated lateral portion of the subthalamus (which was confirmed later by

Papez⁽¹⁶⁾. There is no evidence in the mammalian series of a phylogenetic shifting forwards of the medial geniculate body relative to the mid-brain. Gurdjian's statement⁽⁶⁾ that in the rat's brain the body is situated more caudally than in the brain of higher Mammals rests on an error of interpretation related to the fact that in the rat there is no caudally projecting pulvinar.

The relation of the medial geniculate body to other nuclear elements in the caudal part of the thalamus, especially the pars posterior of the lateral nucleus (pulvinar), requires emphasis. It has been pointed out in previous papers^(2, 4) that in primitive mammalian brains the pars posterior of the lateral nucleus extends back in a caudo-ventral direction and that its caudal extremity intervenes between the medial geniculate body ventro-laterally and the pretectal nucleus dorso-medially. It appears that this caudal extremity has been described by some authorities as an integral part of the medial geniculate body. Cajal⁽¹⁾ described dorsal and ventral lobes in the medial geniculate body of the mouse. The ventral lobe is the principal termination of the lateral lemniscus and gives off auditory radiations, and it evidently corresponds to the principal nucleus as described above. On the other hand, the afferent connections of the dorsal lobe are uncertain, though Cajal thinks they may be derived from the posterior colliculus. Further, Cajal quotes von Monakow to the effect that while ablation of the auditory cortical area in Mammals is followed by atrophy of the ventral lobe, the superior lobe remains unaffected. Cajal's figures (which I have compared with serial sections through a mouse brain) confirm the supposition that, in its topographical position, and especially in its relation to the lateral geniculate body and the optic tract, his superior lobe is really the caudal end of the pars posterior of the lateral nucleus. In 1902, Munzer and Wiener mistook this element for the medial geniculate body in the rabbit (as, indeed, has already been pointed out by Rioch), and the same interpretation applies to the dorsal nucleus of the medial geniculate body of Winkler, or the *b* nucleus of Winkler and Potter in the rabbit. Yoshida⁽²⁸⁾ found that after lesions involving the cortex of the temporal lobe in the rabbit, cell degeneration was practically confined to his ventral nucleus of the medial geniculate body. On the other hand, the dorsal nucleus was intact except for its extreme medio-ventral angle where there was also some cytolysis, and it seems probable that this atrophy was due to the slight involvement of the cortex immediately adjacent to the area temporalis superior. In a recent and admirable monograph by Posthumus Meyjes⁽¹⁴⁾, a similar error in identification is made. The excellent photographs in this paper show that the *b* nucleus of this author is a direct extension of the pulvinar, being covered by the main mesencephalic root of the optic tract and penetrated by many of its fibres, while the cell group which lies on the tectal side of the nucleus limitans and which recent studies of the mammalian thalamus have shown to be the nucleus pretectalis, has been labelled the pulvinar. Meyjes applies the term nucleus suprageniculatus to the caudal extremity of his nucleus *b*, but, again judging from his figures, it seems certain that his nucleus profundus represents the nucleus suprageniculatus as it has

been defined in recent literature. This author found only a simple general atrophy of the medial geniculate body in rabbits after cortical lesions involving the temporal areas, without the cell loss and gliosis which is exhibited in the lateral geniculate body after lesions of the visual cortex. According to his account, the general appearance of the medial geniculate body was normal in these experiments, and the simple atrophy could only be recognised by careful comparison with the normal side. This was not the experience of Yoshida who states that, after similar cortical lesions "sind die meisten Zellen schon verschwunden, und die Gliawucherung ist sehr deutlich." The results of Meyjes' first series of experiments are difficult to assess, partly because the cortical lesion was only in one case limited to the area temporalis proper, and partly because the staining method which he used (Weigert-Pal and van Gieson) is not very suitable for determining the precise origin of fibres which had been involved by the experiment. In the case in which the lesion was limited to the area temporalis, it is observed that while very little difference was found between the geniculate bodies of the two sides, there was a slight indication of a simple atrophy affecting mainly the *a* nucleus (i.e. the nucleus principalis of the present description) of the operated side. The Marchi experiments of this author, however, demonstrated that degeneration in the *b* nucleus only occurred after lesions which were situated at the upper corner of the area temporalis, i.e. which involved to some extent the immediately adjacent visual cortex.

It appears, therefore, that, on the basis of cortical connections, there is no convincing experimental evidence for the inclusion of the pars posterior of the lateral nucleus (nucleus *b*) as an integral element of the medial geniculate body. It may be further noted, also, that there is no evidence that this element receives lateral fillet fibres or is in direct relation with the brachium inferius.

Apart from these misinterpretations, however, there is evidence that in higher mammalian forms, the lateral thalamic nucleus does contribute an element which becomes incorporated in the structure and the eminence of the medial geniculate body. In *Tarsius* (2) the dorsal and lateral surfaces of the body are formed by a layer of cells rather larger and more deeply stained than those in the central part, and this element has been termed the pars lateralis. It is found to be directly continuous rostrally with the nucleus suprageniculatus which, appearing as a condensation of the cells of the caudal end of nucleus lateralis *b* of the thalamus near the dorsal surface of the latter, extends downwards, backwards and outwards to reach the medial geniculate body. Text-fig. 2 represents a sagittal section of the medial geniculate body of *Tarsius* at the level of which the nucleus suprageniculatus becomes incorporated in its dorsal part. It will be observed that the nucleus does not appear to be related terminally with the inferior brachium. On the other hand, it emits cortical fibres which pass forwards to the internal capsule immediately dorsal to the auditory radiations emerging from the central part (nucleus principalis) of the medial geniculate body. This disposition of the nucleus suprageniculatus, which is so diagrammatically clear in the simple brain of *Tarsius*, becomes consider-

ably obscured in higher Primates. The line of demarcation between the medial geniculate body and the pulvinar also becomes less clear in Nissl preparations in association with the development of rich internuclear connections which tend to break up the outlines of these two elements where they come into contact. Friedemann⁽⁵⁾ describes and figures a lateral large-celled element in the medial geniculate body of *Cercopithecus* which is similar to the pars lateralis of *Tarsius*. In the monkey, however, its direct connection with the lateral nucleus of the thalamus seems to be broken and represented by more or less isolated groups of cells in the nucleus limitans and especially the pars suprageniculata nuclei limitantis. The nucleus limitans of the higher Primates is probably a composite structure into which several distinct thalamic elements enter. Its elementary composition is shown clearly in fig. 8 of my paper on the thalamus of *Tarsius*, and a comparison of this with the figures of Friedemann (*Cercopithecus*) and Pines (*Lemur*) shows that in the higher Primates it is formed by a compressed lamina of cells involving from above downwards the large-celled nucleus of the optic tract, the nucleus suprageniculatus, and the nucleus parafascicularis. Rioch describes in Carnivora a direct connection between a part of the medial geniculate body and the nucleus suprageniculatus, and this is confirmed by Ingram, Hannett and Ranson. It should be noted, however, that in its intrinsic structure, the topographical disposition and cyto-architecture of the nuclear elements of the medial geniculate body in this specialised mammalian group do not appear to be directly comparable with those found in the Primates.

Another element has been described by Vogt, Friedemann, and Pines, under the name of the *noyau basal* or nucleus parageniculatus, which is topographically closely related to the medial geniculate body in the monkey and lemur. These authors regard it as equivalent to the nucleus parageniculatus of Lewandowsky and as a part of von Monakow's nucleus ventralis *c*. Possibly, also, it may correspond to the corpus geniculatum mediale accessorium of Marburg in the human thalamus. The significance of this element still remains obscure, but it seems fairly clear that it cannot be regarded as a part of the medial geniculate body.

THE NUCLEUS ISTHMI

In the reptilian brain, there is a conspicuous group of cells which bears an intimate relation to the lateral fillet called the nucleus (or ganglion) isthmi. It is commonly held by those observers who have made a study of this nucleus that it is the reptilian homologue of the medial geniculate body in Mammals. Joustra's study⁽¹⁰⁾ of the nucleus isthmi in the crocodile and chameleon led him to this conclusion and, three years later, Kappers and Fortuyn, in their classical treatise on the comparative anatomy of the nervous system⁽¹¹⁾, reviewed the evidence in great detail. They note that in many Reptiles the nucleus forms a macroscopic swelling and lies at the edge of the anterior medullary velum immediately in front of the superficial origin of the trochlear nerve. They describe connections of the nucleus with the lateral fillet, tectum, corpus

posticum (which is probably the equivalent of the posterior colliculus), and probably with the commissure of Gudden (commissura transversa, dorsal part of the ventral supra-optic decussation). The nucleus isthmi in the frog was described in detail by Larsell (13) who first distinguished clearly between this nucleus and the secondary visceral nucleus of Fishes and Amphibia (with which the nucleus isthmi had been confused by some earlier writers). Larsell records that the nucleus isthmi is a mesencephalic element and receives fibres from the lateral lemniscus which accompanies the spino-tectal tract on its way to the tectum. He found also the following connections: tractus tecto-isthmi, tractus quadrigemino-isthmialis (from the posterior colliculus), tractus isthmio-tectalis (ending in the deeper layers of the tectal cortex), tractus isthmio-thalamicus, commissural fibres running through the anterior medullary velum, and commissural fibres forming Gudden's commissure. Huber and Crosby (8) found similar connections in the alligator (but do not mention an isthmio-thalamic tract). They state that the fibres of the lateral fillet end mostly in the posterior colliculus, a smaller number terminating in the optic tectum and the nucleus isthmi, and they mention groups of cells intermingled with the fibres of this bundle which they regard as the nucleus of the lateral lemniscus. Shanklin (22) deals with the nucleus isthmi in the chameleon in which it is unusually large, bulging over the superficial origin of the fourth nerve. Besides many of the connections already noted, he describes a connection with the nucleus profundus mesencephali and also figures a tract running from the nucleus to the trochlear nucleus and the posterior longitudinal bundle. In *Sphenodon*, Hindenach (7) describes a dorso-lateral pars magnocellularis of the nucleus isthmi, and a medio-ventral pars parvicellularis. The nucleus is crossed dorsally by the trochlear nerve and is separated medially from the posterior colliculus by the mesencephalic tract of the fifth nerve. It receives caudally fibres from the lateral lemniscus and is connected with the optic tectum and posterior colliculus, as well as with the opposite nucleus by commissural fibres crossing in the anterior medullary velum. Ventral to it is a flattened nucleus lying in the stream of the lateral lemniscus which is called the nucleus of the lateral lemniscus.

It will be apparent that there are very serious objections to the common conception that the nucleus isthmi of the reptilian brain is homologous with the medial geniculate body of Mammals. The former is without doubt a mesencephalic element, situated indeed in the caudal region of the mid-brain, while the principal nucleus of the medial geniculate body—as has been shown above—is just as clearly a diencephalic element derived from the main sensory nucleus of the diencephalon. Further, the relation of these two structures to the lateral fillet is different, for in Reptiles the nucleus isthmi lies in the course of this tract on its way up to the roof of the mid-brain. Kappers has pointed out that it would be surprising if an element such as the nucleus isthmi, which is so constantly to be found in the reptilian brain, were not also represented in Mammals. If it is so represented, however, it is most likely to be found in

relation to the lateral fillet in the region where this tract is running to its main termination in the nucleus of the posterior colliculus.

In Plate I, fig. 3 is shown a photograph of a coronal section through the mid-brain of *Lacerta viridis* at the level of the nucleus isthmi, stained by the Weigert-Pal method and counter-stained with neutral red. In Plate I, fig. 4 is shown a section through the mid-brain of the primitive insectivore *Macroscelides*, stained by the same method. A comparison of these two specimens is instructive. In the lizard, the nucleus isthmi stands out as a group of intensely stained cells lying at the ventro-lateral margin of the tectum close to the trochlear nerve and related medially to a stream of the lateral lemniscus fibres which are passing dorso-medially towards the posterior colliculus. In *Macroscelides*, a conspicuous group of closely packed cells with similar staining properties is seen in a corresponding position lying immediately ventral to the cross-section of the caudal end of the brachium inferius and related in the same way to the fourth nerve and the fibres of the lateral lemniscus system. This nucleus has been variously labelled by other authors as the dorsal nucleus of the lateral lemniscus, the parabigeminal nucleus, and the nucleus bigeminalis (*vide infra*). Here, for reasons which will be advanced, it is termed the nucleus isthmi.

The lateral fillet in *Macroscelides* forms a broad and dense fasciculus running up on the lateral surface of the mid-brain. In the ventral part of its course it encloses an elongated strip of grey matter formed of small and somewhat scattered cells, which is evidently the ventral nucleus of the lateral fillet. More dorsally, the main part of the lemniscus runs straight on into the nucleus of the posterior colliculus, but where it comes into relation with the deep aspect of the nucleus isthmi it appears to contribute some fibres which end here. Thus it seems certain that the nucleus isthmi in this insectivore receives afferent fibres from the octavus system. It has been established (de Lange (12), Winkler (24), Poliak (18)) that the most superficial fibres of the lateral fillet system are tectopontine fibres which degenerate after lesions involving the posterior colliculus and which pass down to the nucleus lateralis pontis. This component of the lateral fillet can be recognised in the *Macroscelides* material and a large proportion of its fibres appear to take origin in the nucleus isthmi. They are more finely medullated than the main part of the fillet and can be traced down in a circumscribed bundle to the lateral nucleus of the pons. Diffuse fibre connections are also to be seen linking the nucleus isthmi with the posterior colliculus, and running medially towards the mid-line where they enter the posterior longitudinal bundle, or cross to the opposite side as the commissure of Probst.

The nucleus which has thus been briefly described in *Macroscelides* is also quite as obtrusive in the brains of *Tupaia*, *Microcebus*, and *Tarsius*, but much less conspicuous in the brains of such insectivores as *Erinaceus* and *Sorex*. In the former examples the tectum is relatively large, while in the latter it is much reduced. There appears, in fact, to be a relation between the size of the tectum and the degree of development of the nucleus isthmi in Mammals. This corre-

sponds with the fact that in Reptiles, in which the tectum is a highly elaborate structure, the nucleus isthmi is particularly well differentiated. In *Erinaceus* and *Sorex*, the nucleus is continuous with little interruption with the cells loosely scattered among the fibres of the dorsal part of the main portion of the lateral lemniscus. This relationship leads to the supposition that the nucleus isthmi is but a differentiated part of the dorsal nucleus of the lateral lemniscus, which has been frequently described in the mammalian brain. It is in the primitive *Tarsius* that the nucleus isthmi is best developed, and as there are available to me series of sections of this brain cut in three planes, I have used this material for making a more complete study of it.

If the lateral aspect of the mid-brain of *Tarsius* is examined macroscopically, the nucleus isthmi is quite apparent as an oval grey eminence 1.5 mm. in length lying over the lateral fillet immediately behind the caudal end of the inferior brachium and in close relation with the superficial origin of the trochlear nerve (Plate I, fig. 2). In Nissl preparations, this tubercle is found to consist of a clearly circumscribed nucleus of closely packed cells, triangular and polygonal in shape and of medium size. It is in immediate relation with the main part of the lateral fillet the lateral fibres of which separate it from the diffusely scattered cells which stream in linear arrangement along the course of the fillet and which constitute the nucleus proper of the lateral lemniscus. Weigert preparations demonstrate the connections of the nucleus isthmi very clearly. In *Tarsius* the octavus system is highly developed, and the whole course of the lateral fillet stands out with unusual distinctness. In text-fig. 2 is shown a sagittal section taken through the lateral part of the diencephalon and which cuts through the elevated tubercle of the nucleus isthmi. Here the nucleus is seen to be in direct connection with the caudo-ventral fibres of the inferior brachium through which it is brought into fibre relation with the medial geniculate body. In its posterior margin is seen the termination of the most rostral and lateral fibres of the lateral lemniscus system. These fibres can be traced ventrally in the more medial sections of this sagittal series, and while some of them—from the deeper part of the nucleus—are undoubtedly derived from the trapezoid system (the bulk of which passes up behind the nucleus isthmi to the posterior colliculus), the majority are related below to the nucleus lateralis pontis and thus form a part of the tecto-pontine system. These sections also demonstrate a fibre connection between the deep aspect of the nucleus isthmi and the posterior colliculus.

In text-fig. 3 is shown a section—taken from a horizontal series of Weigert preparations—through the diencephalon and mid-brain of *Tarsius*. The prominence of the nucleus isthmi is well shown here, as well as its close topographical relation to the superficial origin of the trochlear nerve. The nucleus is partly encapsuled by the most anterior fibres of the lateral lemniscus system and is richly permeated by a fine network of medullated fibres derived from this. Fine fibres can also be seen coursing directly medially from the nucleus into the tegmental part of the mid-brain. This section displays particularly well the

course of the fibres of Gudden's commissure. The more lateral of these fibres penetrate the rostral margin of the medial geniculate body. The medial fibres, however, form a fine stream which runs back medial to the ventral part of the geniculate body and which can be traced caudally as far as the nucleus isthmi. There is little doubt that these fibres have a direct relation with the nucleus.

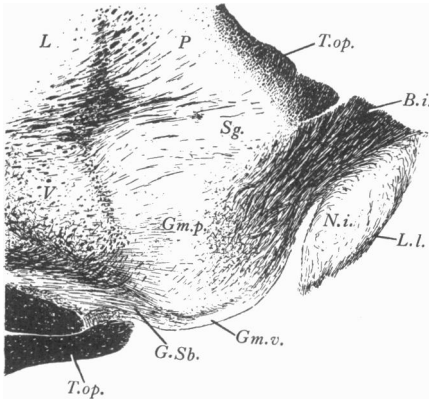


Fig. 2.

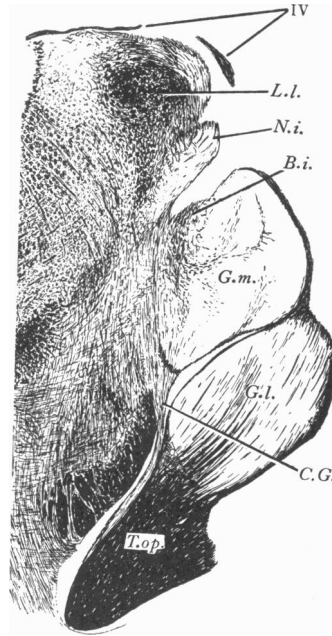


Fig. 3.

Text-fig. 2. Sagittal section through the medial geniculate body and nucleus isthmi of *Tarsius*. Weigert-Pal. $\times 14$.

B.i. inferior brachium. *Gm.p.* principal nucleus of medial geniculate body. *Gm.v.* ventral nucleus of medial geniculate body. *G.sb.* geniculo-subthalamic tract. *L.* lateral nucleus of thalamus. *L.l.* lateral lemniscus. *N.i.* nucleus isthmi. *P.* pulvinar. *Sg.* nucleus suprageniculatus. *T.op.* optic tract. *V.* ventral nucleus of thalamus.

Text-fig. 3. Horizontal section through the diencephalon and mid-brain of *Tarsius*. Weigert-Pal. $\times 12$.

B.i. inferior brachium. *C.G.* commissure of Gudden. *G.l.* lateral geniculate body. *G.m.* medial geniculate body. *L.l.* lateral lemniscus. *N.i.* nucleus isthmi. *T.op.* optic tract. *IV*, trochlear nerve.

Coronal sections of the *Tarsius* brain show similar fibre relations. Here, again, the most rostral fibres of the lateral fillet system are linked up with the medullary plexus which pervades the nucleus isthmi and partly enclose the latter to form a medullary capsule. Following the sections caudally, it appears that many of these fibres form a part of the tecto-pontine system, while at least a proportion of them are derived from the main part of the lateral lemniscus which is continued up from the trapezoid body. Some fibres are also seen

running medially from the nucleus isthmi and disappear in the tegmental region of the mid-brain, and there is a connection by diffuse fibres running dorso-medially with the deep strata of the anterior colliculus.

A survey of the literature shows that in many mammalian brains the nucleus isthmi as here defined has been included under the term nucleus dorsalis lemnisci lateralis. Winkler and Potter have thus figured it in their atlases of the cat and rabbit brain, and note that it is characterised by large cells. Winkler states that this dorsal nucleus of the lateral lemniscus receives a large proportion of the fibres of the lateral part of the lateral fillet, which are derived from the superior olivary nuclei through the trapezoid system. Unilateral extirpation of the tuberculum acusticum and the ventral cochlear nucleus in the rabbit leads to some atrophy of the nucleus, and after a superficial lesion in the posterior colliculus Marchi degeneration demonstrates that some of the tecto-pontine and tecto-reticular fibres end in it. It is held that the nucleus transmits impulses to the motor nuclei in the brain stem by way of the posterior longitudinal bundle and the fasciculus praedorsalis. Stokes⁽²³⁾ also describes in the opossum connections from the nucleus of the lateral fillet to the posterior longitudinal bundle, some of which are believed to decussate (Probst's commissure).

The nucleus isthmi of the mammalian brain which has been described in this paper is evidently a differentiated portion of what has usually been called the dorsal nucleus of the lateral fillet. In its topographical position relative to the lateral fillet, the posterior colliculus, and the superficial origin of the trochlear nerve, in the staining properties of its cells, and in its fibre connections with the lateral fillet, posterior colliculus, optic tectum, and Gudden's commissure, this nucleus is clearly the homologue of the nucleus isthmi of reptiles. In a private communication, Prof. Ariëns Kappers has informed me that, following Prěchechtěl's observations on the structure of the elephant's brain (19), he is now of opinion that the magnocellular element of the ganglion isthmi of sub-mammalian forms is represented in Mammals by the nucleus lemnisci lateralis dorsalis. Prěchechtěl notes that this nucleus occupies a position which corresponds with the ganglion isthmi of Reptiles, but he believes also that the medial geniculate body may represent the chief part of the ganglion isthmi of lower vertebrates, "having shifted in a frontal direction." Papez⁽¹⁵⁾ briefly mentions the nucleus isthmi in a macroscopical description of the dog's brain, and also figures it in the cat's brain. He calls it the nucleus bigeminus, but this term should be discarded, since it has previously been employed by Kappers for quite a different element in the hind-brain. Papez records a bigeminopontine tract of fibres arising from the nucleus, and as he uses the same name for a tract passing from the nucleus isthmi of birds to the region of the pons, he implies a homology between his bigeminal nucleus and the nucleus isthmi. He does not, however, discuss this matter specifically.

CONCLUSIONS

A study of the brains of primitive Mammals in which the tectum is large shows that the nucleus isthmi of Reptiles is also present and well developed in these forms, and is represented by a part of what has usually been called the dorsal nucleus of the lateral fillet. In higher Mammals, the nucleus is much less obtrusive in association with the diminished importance of mesencephalic centres generally. It is probable, also, that the ventral nucleus of the lateral fillet of mammals is the equivalent of the diffuse collection of cells found among the fibres of the lateral fillet in Reptiles and which has there been termed the "nucleus of the lateral fillet." The main part of the medial geniculate body of Mammals is developed as a caudo-ventral extension of the main sensory nucleus of the thalamus, drawn out, it would appear, under the neurobiotactic influence of auditory impulses which pass up to it from caudal levels.

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EXPLANATION OF PLATE I

- Fig. 1. Horizontal section of the diencephalon of a 92 mm. human embryo. $\times 20$.
B.i. inferior brachium. *C.m.* centre median nucleus. *C.p.* posterior colliculus. *G.l.* lateral geniculate body. *G.m.* medial geniculate body. *V.* ventral nucleus of thalamus.
- Fig. 2. Lateral view of mid-brain and diencephalon of *Tarsius*. $\times 5$.
C.a. anterior colliculus. *C.p.* posterior colliculus. *Cr.* crus cerebri. *G.l.* lateral geniculate body. *G.m.* medial geniculate body. *N.i.* nucleus isthmi. *T.ac.* tuberculum acousticum.
- Fig. 3. Coronal section of mid-brain of *Lacerta viridis*. $\times 25$.
C.p. posterior colliculus. *L.l.* lateral lemniscus. *N.i.* nucleus isthmi. *T.* tectum. *IV*, trochlear nerve.
- Fig. 4. Coronal section of mid-brain of *Macroscolides*. $\times 18$.
B.i. inferior brachium. *C.a.* anterior colliculus. *C.p.* posterior colliculus. *L.l.* lateral lemniscus. *N.i.* nucleus isthmi. *IV*, trochlear nerve.

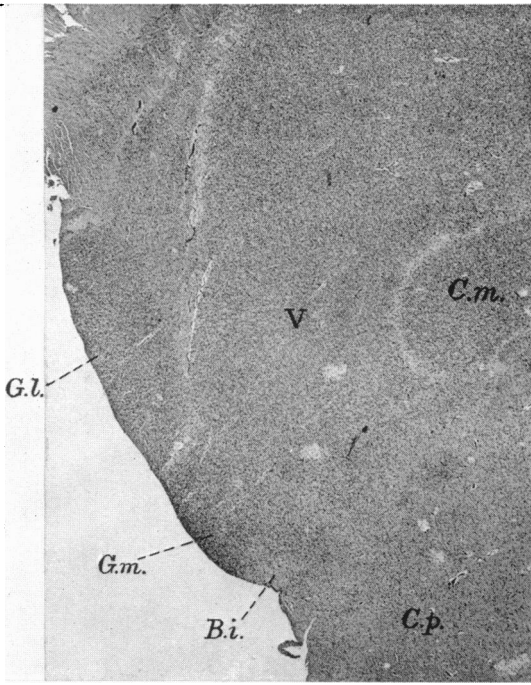


Fig 1.

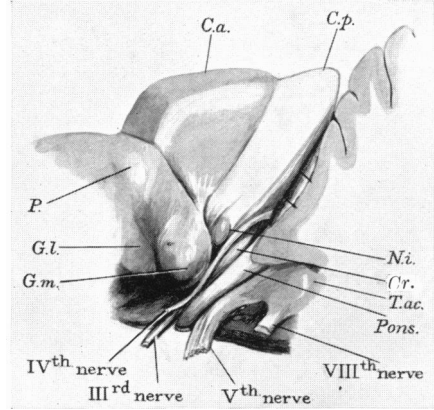


Fig. 2.

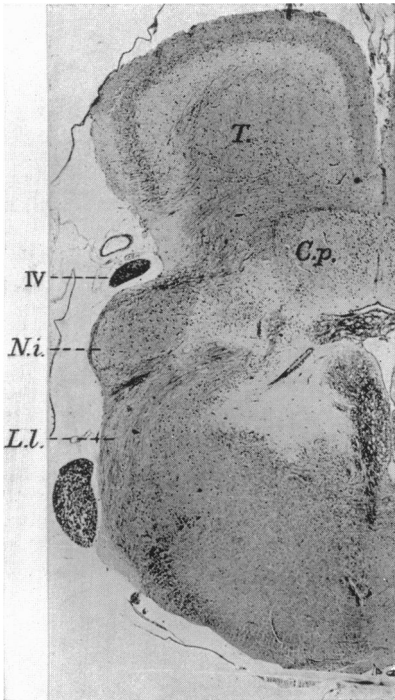


Fig. 3.

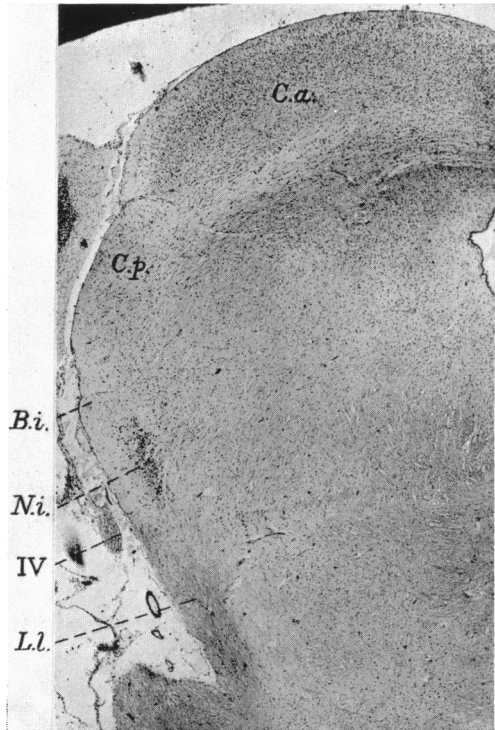


Fig. 4.