THE ACOUSTIC COMPLEX AND ITS RELATIONS IN THE BRAIN OF THE OPOSSUM (DIDELPHYS VIRGINIANA)

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FOURTEEN FIGURES

The following study of the central acoustic complex has been undertaken by the writer with the primary object of producing by reconstruction methods a simple three-dimensional picture of this apparatus, which would while of specific application to the opossum, yet have a larger value in the development of a clear-cut conception of the morphology of this group of related structures in the mammalian brain as a type. The work of Sabin has established the value of this method of approach in the study of the anatomy of the brain; and it is hoped that this paper may prove a contribution to the field in which she has been so distinguished a pioneer. It may be added that this study is among the first of a series now in progress in this laboratory, whose eventual purpose is to present a morphological survey of the entire brain of Didelphys Virginiana.

As a form in which to study the acoustic complex, the opossum offers several decided advantages, chief among which from the standpoint of this paper is the clearness with which units and relations stand out in a relatively primitive mammalian brain, but little obscured by the massive pontine nuclei and their connections which characterize the higher forms. Differentiation by the method of Weigert being especially satisfactory for a comparatively gross study at low magnification, the models were made from such preparations. The drawings of individual sections serve the double purpose of elucidating the models, and of presenting certain important features whose incorporation in the reconstructions was deemed inadvisable.

In carrying on the present study, the basic work of Held upon the central acoustic path has been constantly referred to; likewise the studies of Cajal and v. Kölliker and the compilation of results given in Barker's text. From the standpoint of reconstruction the work of Sabin upon the medulla of the new-born child has been applied wherever possible as a guide to the region under consideration. The reconstruction work of Streeter upon the cranial nerves and upon the embryology of the peripheral auditory apparatus, that of Essick upon the corpus ponto-bulbare, and the as yet unpublished work carried on in this laboratory by Calhoun upon the cranial nerves of the opossum other than the eighth, have been similarly employed.

As regards the investigation of the brain in Monotremes and Marsupials, the publications of G. Eliott Smith and the work of Ziehen, require mention. Their studies, however, did not extend to the fiber-paths of the hindbrain. Published work on the opossum brain itself has been confined apparently to a paper by Herrick on the olfactory apparatus, giving a brief description and a few typical sections of the region studied. The immediate field of this paper is therefore comparatively virgin. In fact the central acoustic apparatus considered alone, has never been the subject of three-dimensional reconstruction purely for its own sake—so that it is hoped that in this direction the present study will prove a serviceable aid in the visualization and comprehension of this important division of the central nervous system.

It may be stated at this point that the study of the seventh nerve that appears in the reconstructions, is incidental. Morphologically its relations to the eighth makes it a valuable landmark, and it is largely for its value in this direction that it was included in the modelling.

MATERIAL AND METHODS

The material upon which the study was carried out consists of three sets of serial sections, in the transverse, sagittal and horizontal planes respectively, of the entire brain of the adult opossum. These sections are the property of this laboratory and were prepared by Dr. R. R. Pinckard. The sections were cut at

50 microns and stained by the Weigert-Pal method. Two additional transverse series which were prepared by Dr. McCotter and Dr. Kollig, later became available for comparison.

In preparing the reconstructions the Born wax-plate technique has been followed with slight modification. The drawings were made with the projection lantern and corrected from the sections with the binocular microscope. The sheets were incorporated in millimeter plates, the selected structures being then cut out and piled. Models were made from sections in all three planes, and each used as a check upon the other. After making some preliminary models it was found that the best results on the whole were obtained from the transverse sections. Two finished models from this set were accordingly made, and it is from these that the illustrations for this paper are taken. Of the two models, one was made with the parts rigid, the restiform body, the pons and the brachium conjunctivum being included together with the seventh nerve as landmarks. The other is a dissectible model including nothing but the cochlear and vestibular complexes and the seventh nerve. It was found possible to so construct this model that the separate groups could be shown independently. From it the drawings of the two individual systems were made. Reconstruction was carried anteriorly only far enough to include most of the corpus geniculatum mediale. The course of the auditory path anterior to this point was found to be too indefinitely defined to permit of satisfactory rendition by this method. The relation of the superior nucleus of the vestibular to the floor of the cerebellum and its basal nuclei was also rather baffling. In such cases as the latter, where the models do not clearly show the points involved, resort has been made to drawings of the sections themselves, which it is hoped will aid the reader in following the text.

It has become increasingly evident to the writer as this study has progressed that the approaching of the problem from the standpoint of finer histological detail, as obtained by the Golgi and Cajal silver reduction methods, would be essential to the reaching of conclusive results on many of the points of anatomical structure mentioned in this paper. Although a Golgi series is now available in this laboratory, it was finally decided, however, that the scope of the present study might well be limited to the Weigert preparations.

Finally, it should be understood that the drawings of the models herewith presented represent an effort to reduce the apparatus under consideration to something of its simplest terms. Accordingly disputed points and minute details have been largely omitted, and attention called to such omissions in the text. The corpus ponto-bulbare, and the anterior commissural tract in relation with the nucleus lemniscus lateralis are so distinctive in position and relations that they are represented in spite of the fact that they may still be considered as disputed points.

COCHLEAR APPARATUS

In the general topography of the opossum hindbrain, the relatively enormous size and prominence of the primitive sensory and motor groups forming the central apparatus of the cranial nerves, is as striking as is the enormous development of the pons in the human brain. Such sensory groups as the fifth and the eighth stand out with startling distinctness, and the identity of the main units in the structure is seldom in doubt for a moment. Even on the external surface of the brain stem the bulge of the spinal fifth, and the corpus trapezoideum and its offshoot in the form of the lateral lemniscus, are easily made out. The posterior colliculus and the medial geniculate body are even more striking external landmarks. The opossum brain at first glance therefore, impresses one as especially well adapted to the mapping out of large primitive sensory groups by reconstruction.

The general structure of the cochlear apparatus is essentially the same in the opossum as in the more familiar types, and its main divisions may be similarly outlined, somewhat as follows. The chain of auditory conduction begins with the cochlear nerve proper, consisting of the axones of bipolar cells in the spiral ganglion. This cochlear nerve is accompanied by the vestibular nerve, the two together forming the eighth cranial or acoustic nerve of ordinary nomenclature. The cochlear nerve terminates in two nuclei of reception, the dorsal and ventral, the dorsal cochlear nucleus being identical with the so-called tuberculum acousticum. From these two nuclei of reception the auditory path is generally represented as continuing in part by way of the corpus trapezoideum on the ventral surface of the brain stem and in part by way of the striae acousticae on the dorsal, to the nuclear masses associated with the corpus trapezoideum, and to the lateral leminiscus and its associated ganglion mass. The distribution of these centrally directed fibers among the fiber tracts in question and their terminations in the superior olive and the nuclei of the corpus trapezoideum and the lateral lemniscus, are still among the unsettled questions in the finer structure of the central acoustic path. The proportion of acoustic fibers in the striae has also been shown to vary in different mammalian brains. It is now well recognized, however, and the point is of significance in the study of the models, that most of the fibers from the cochlear nuclei of one side of the brain cross the median line and are either interrupted in the superior olive or in the nucleus corporis trapezoidei, or are continued into the lateral lemniscus, of the opposite side. The corpus trapezoideum is therefore essentially a decussating path connecting the cochlear apparatus and more especially the cochlear nuclei of *one* side with the nuclear masses and the lateral lemniscus of the *other*. The value of keeping this relation in mind in studying the model is apparent. In the elongated grey mass of the nucleus of the lateral lemniscus a portion of the fibers which cross by way of the corpus trapezoideum or originate from cells in the nuclear masses of that tract, are interrupted. The fibers of the lateral lemniscus terminate in considerable numbers in the nuclear mass of the inferior colliculus. A portion of the fibers of the lateral lemniscus are prolonged beyond the inferior colliculus, and joined presumably by fibers from cells within the nucleus of the inferior colliculus, proceed by way of the brachium colliculi inferioris to the corpus geniculatum mediale, whose nucleus constitutes the last of the sharply defined stations in the path. From this point the remnants of the lateral lemniscus, and other groups of fibers associated with the eighth apparatus, are prolonged cerebralward.

Before proceeding to the detailed description of the models, certain respects in which they represent conditions peculiar to the opossum may first be pointed out.

The typical situation of the cochlear nuclei in such brains as those of the cat, rabbit and man, is largely external to the corpus restiforme, the tuberculum being lateral to and somewhat above the ventral nucleus, and largely overlying it. In the opossum this is not the case. The tuberculum acousticum lies entirely medial to the corpus restiforme, and all but the more anterior part of the ventral nucleus is similarly placed. The anterior portion of the ventral nucleus escapes from under the corpus restiforme as it ascends into the cerebellum, and extends downward and backward between the entering strands of the cochlear nerve. This arrangement of the nuclei of reception makes it inevitable that the posterior half of the fibers of the N. cochlearis should be obliged to pierce the lower part of the restiform body on their way to the cochlear nuclei. If the opossum brain be regarded as the more primitive type, it is not difficult to conceive that with the crowding of the primary structures in the medulla by the relative increase in size of the cerebellar peduncles, the inferior olive and the pons in higher types of brain, the nuclei of reception of the cochlear apparatus have been forced downward and outward along the root of the cochlear nerve and over the top of the corpus restiforme to their present superficial position.

Discussion of the relations of the dorsal cochlear nucleus calls attention to a second structure in the opossum brain that requires special mention in the description of the model. Essick in 1907 described for the human brain a grey mass on the lateral surface of the medulla in the region of the seventh and eighth nerves, of which he had been unable to find any account in the literature. This he designated the corpus ponto-bulbare, and called attention to its connection with the pons. In his histological description mention is made of certain fibers from it which join the striae acousticae. No other connection with the cochlear apparatus is noted. Streeter ('03) in the figures accompanying his description of the floor of the fourth ventricle labels this mass the nucleus tela chorioidea inferior, presumably from its close association with the choroid plexus of the fourth ventricle. It is mentioned but not described in the text. It has been repeatedly figured in atlases of the brain, but apparently without immediate connection with the tuberculum acousticum. It is easily seen in the gross in the brain of the pig embryo, appearing as a welt-like strip passing from beneath the ventral lip of the lateral recess, downward and forward around the lateral aspect of the corpus restiforme between the roots of the seventh and eighth nerves, forward to the caudal border of the pons at the level of entrance of the fifth nerve. It is continuous dorsally with the tissue from which the ganglion masses of the eighth nerve, and especially the tuberculum acousticum, originate. In the opossum, evidences of connection with the tuberculum acousticum are even more decided (figs. 2, 3 and 5). In the gross it appears as a prominent band beginning at the caudo-lateral border of the tuberculum acousticum and extending over the restiform body downward and forward over its lateral aspect, then almost horizontally forward, immediately above the roots of both the seventh and eighth nerves, to the pons, where it merges with a capsule of grey matter high up on its posterior border. Mention of its appearance in the sections will be made below. The homology between this structure and the one described by Essick may not at first sight appear entirely undoubted, owing to a discrepancy between the positions of the mass in relation to the seventh and eighth nerves in the opossum and in higher mammalian brains. The writer is of the opinion however, that such a difference is readily explained by displacements due to the greater development of the pons in the higher types, and by the difference in position of the cochlear nuclei in the latter as compared with the former.

A third distinctive feature of the cochlear apparatus in the opossum relates to the course of centrally directed fibers from the cochlear nuclei. The close relation of the corpus trapezoideum to the ventral cochlear nucleus is easily made out in the sections and shows quite plainly in the models. This constitutes the ventral conduction path, which however, is not confined exclusively to axones from the ventral cochlear nucleus. The dorsal conduction path in most animals is derived to a considerable extent in similar fashion from the tuberculum acousticum, and in the form of the striae acousticae, which form a variable portion of the so-called striae medullares in different mammalian brains, passes dorsally over the restiform body, across the floor of the ventricle towards the median line and downward in the raphe, or by a more direct route downward on the medial side of the tractus spinalis N. vestibularis, to be distributed to the superior olivary nucleus of the same side or to the corpus trapezoideum to undergo decussation to the opposite side. In the human brain it has been shown that the striae medullares have relatively little to do with the auditory conduction path, though in the cat and rabbit they are largely auditory. In the opossum the dorsal conduction path is a prominent feature, and as in other animals investigated, is apparently largely derived from the dorsal cochlear nucleus. That this is not the exclusive source, however, is readily seen from the numerous fibers having apparently a distinct origin in the mass of the ventral nucleus, which pass upward along the lateral aspect of the tractus spinalis N. vestibularis, and arching over it, join the dorsal path as it passes downward on the medial aspect of the vestibular tract. The opossum brain does not, however, present any definite group of striae medullares passing across the floor of the ventricle. The entire picture is usurped by the dorsal path, the variation in whose course as regards the corpus restiforme is due to the above described relation of that tract to the cochlear nuclei. The corpus restiforme being external to the cochlear nuclei, the fibers of the dorsal path simply collect on the medial border of the tractus spinalis N. vestibularis and without any deflection towards the median line, pass directly downward through the anterior portion of the medial vestibular nucleus to the superior olivary nucleus. While it should remain with histological study by Golgi methods to determine whether this tract represents the exclusive course of fibers of the dorsal path, it is obviously the principal one in the opossum. Since it is at best no more than a homologue of the striae acousticae it was designated in the models for convenience as the olivo-cochlear tract, a name rather more descriptive of its course than that of striae acousticae.

A fourth feature of the model of the cochlear apparatus requiring special mention is the incorporation in it of two groups of fibers not concerned in the main conduction path. The first of these is the so-called peduncle of the superior olive (Stiel der kleinen Olive), which has been repeatedly described, and represents a connection of the auditory path with the nucleus of the sixth nerve. The second is a group of fibers passing from the nucleus lemnisci lateralis towards the median line. This group is present unmistakably in the opossum, has been described especially by von Kölliker, ('96), and mentioned by Held ('93), Cajal ('09) and others, and figured for the cat and the new-born child. In spite of doubt as to their exact origin and distribution it was thought desirable to include them in the model.

Passing now to the detailed description of the cochlear apparatus as modelled, it is easy by reconstruction to distinguish in the root of the eighth nerve its two component parts which with the root of the seventh nerve are somewhat diagrammatically rendered in the figures. All three nerve roots lie at about the same level on the wall of the medulla in the opossum, posterior to the pons and the point of entrance of the fifth nerve. The most posterior division represents the N. cochlearis and appears as a robust fiber tract piercing the corpus trapezoideum at an upwardly directed angle, close to its posterior border. As already pointed out, the most anterior portion of the entering nerve passes entirely below the corpus restiforme as it ascends into the cerebellum. The ventral cochlear nucleus, which is first reached by the fibers, is an irregularly oval mass of cells, flattened dorso-ventrally, lying in part below and in part medial to the restiform body and prolonged laterally and posteriorly into the root of the cochlear nerve, in the form of masses of cells between the entering strands. The posterior portion of this lateral extension is cut off from the mass of the nucleus by the restiform body, but is continuous with the main ganglion mass anteriorly. Part of the fibers of the entering nerve pass directly through the ventral nucleus, still at an upwardly directed angle, to reach the tuberculum acousticum which lies above and medial to the ventral nucleus.

The tuberculum acousticum, or dorsal cochlear nucleus, presents the appearance of an elongated mass of cells uniting the extremities of two peduncle-like fiber tracts, the one lateral and posterior, the other medial and anterior; the former consisting of those entering fibers of the N. cochlearis which are distributed to the tuberculum acousticum, and the latter of the dense strands of fibers constituting the olivo-cochlear tract, which pass downward from the tuberculum acousticum towards the superior olive and the nucleus corporis trapezoidei. The anterior end of the dorsal cochlear nucleus is separated from the ventral nucleus, which at this point lies lateral to it and in the same horizontal plane, by a deep notch, completely filled by the fibers of the nucleo-cerebellar tract of the vestibular nerve, as they pass upward toward the cerebellum. At the point where the N. cochlearis enters the tuberculum, the nuclear mass spreads out in the shape of a mushroom, becoming continuous on the dorsal surface of the restiform body with the corpus ponto-bulbare, already described. The larger part of the ganglion mass of the tuberculum lies at the point of entrance of the cochlear fibers, just lateral to the spinal tract of the vestibular. The remainder of the nucleus forms a bridge over the spinal vestibular tract, merging into the olivo-cochlear tract on the medial side. The tuberculum thus "straddles" the spinal vestibular, so to speak, the nerve forming one leg and the olivo-cochlear tract the other. The long axes of the two cochlear nuclei present a characteristic inclination to each other, that of the ventral nucleus being horizontal and extending antero-posteriorly, that of the dorsal being oblique and extending forward, downward and inward.

Of the central connections of the two cochlear nuclei, the olivo-cochlear tract has been described above. The figures from the model, owing to the necessity of representing a group of strands as a solid tract, give a somewhat exaggerated idea of its calibre, which however, may be corrected from the sections. The corpus trapezoideum or ventral path, is readily seen as a broad strip on the ventral and ventro-lateral surfaces of the unsectioned opossum brain, lying completely exposed posterior to the pons, owing to the comparatively low development of the latter. It is separated from the pons on the lateral aspect of the medulla by an interval occupied by the entering fibers of the fifth nerve. The fibers of the corpus trapezoideum follow the curve of the surface of the medulla, slanting somewhat forward, fibers coursing parallel and the whole tract bulging somewhat immediately below the entrance of the eighth nerve as a result of lateral displacement by the spinal root of the fifth. The main mass of the fibers is anterior to the point of entrance of the cochlear nerve, and even in the gross can be seen to be principally associated with the ventral cochlear nucleus. The seventh and the N. vestibularis pass directly through this thickest portion of the corpus trapezoideum. On the ventral surface of the medulla, the origin of the lateral lemniscus appears as a distinct rounded off-shoot from the anterior margin of the corpus trapezoideum. It is easily identified in the unsectioned brain.

The internal surface of the corpus trapezoideum is shown by reconstruction to present a median rounded elevation extending across it from the posterior to the anterior border, where it becomes indistinguishable from the rounded internal surface of the lower portion of the nucleus lemnisci lateralis. This elevation corresponds to the nucleus corporis trapezoidei and especially in the more prominent posterior portion, to the nucleus olivaris superior. Into the summit of this mass are received the fibers of the olivo-cochlear tract. Attention should be called to the close relation between the nucleus of the superior olive and the nucleus of the seventh nerve, which lies immediately posterior to it, and in actual contact with it. Anteriorly, the bifurcation of the superior olivary nucleus with the formation of median and lateral lobes is better shown in the sections (fig. 7). From the more anterior portion of the superior olive springs also the olivary peduncle already mentioned.

The continuation of the cochlear conduction path into the mesencephalon by way of the lateral lemniscus appears in the opossum as a dense mass of fibers, springing from the anterior border of the corpus trapezoideum. This tract, which at its origin is about half as wide as the corpus trapezoideum, passes rather abruptly towards the roof of the Sylvian aqueduct, following the curve of the outer surface of the brain stem forward, laterally, upward and finally medially towards the nucleus of the inferior colliculus, whose base it enfolds "wei ein Kelch" (von Kölliker). The lemniscus is deeply grooved along its medial surface, the groove broadening and becoming shallower as it ascends. Within this groove covered by a thin layer of fibers lies the elongated cylindrical ganglion mass of the nucleus of the lateral lemniscus. As the fibers of the lemniscus diverge those along the dorsal margin, which constitute the larger proportion, pass almost directly upward toward the nucleus of the inferior colliculus. The more anterior and ventral portion of the tract apparently ascends rather more gradually in the direction of the superior colliculus and the thalamus, the exact destination of the fibers not being determinable from the sections. A portion of them may form a direct extension of the conduction path cerebralward, without interruption in the inferior colliculus. The nucleus of the lateral lemniscus at its lower end can hardly be said to be continuous with that of the superior olive. There is a distinct gap, covering a number of sections in the transverse cuts, between the point where the highly characteristic structure of the superior olivary nucleus entirely disappears, and the point where definite indications of a lateral lemniscus, with its sharply defined nucleus appear. This gap is filled with a reticulated mass containing some ganglion cells apparently, which if anything, partakes of the structural appearance of the nucleus corporis trapezoidei. There appears to be no difficulty in recognizing the anatomical identity of the nucleus lemnisci lateralis in the opossum at least.

The group of fibers extending inward and downward toward the median line from the upper portion of the nucleus lemnisci lateralis has already been mentioned. In the separate model of the cochlear apparatus (fig. 3), the same allowance should be made for its conspicuousness as in the case of the olivo-cochlear tract. It is less prominent in fig. 2, owing to its position along the upper posterior border of the brachium conjunctivum, from which, however, it appears to be fairly distinct.

The inferior colliculus of the opossum brain is a large and conspicuous mass of ganglion cells and fibers forming the wall and roof of the posterior portion of the Sylvian aqueduct. It is of a somewhat uncertainly defined egg shape, the long axis slanting downward and forward at an angle of about 45°. It is divisible into two parts, a medial and a lateral, the medial being the more distinctly nuclear mass and the lateral the more fibrous portion. The medial, nuclear division is roughly bean-shaped, tapering to an indefinite wedge-like lower extremity that becomes indistinguishable from the central grey substance. The lateral division contains the main bundles of fibers of the lateral lemniscus as they pass to their termination in the nucleus colliculi inferioris and to the decussation of the inferior colliculi. It also includes the fibers of the brachium colliculi inferioris and those fibers of the lateral lemniscus whose doubtful destination has already been mentioned. This lateral portion of the colliculus may be regarded anatomically as a capsule-like investment of the medial portion, roughly triangular in shape, with its apex at the middle geniculate body. The brachium colliculi inferioris, uncertainly defined within the colliculus itself, becomes a well-marked group of fiber bundles as it approaches the middle geniculate. The fibers decussating between the two inferior colliculi are gathered apparently from both nucleus and capsule. The decussation is in the roof, well forward in the colliculus.

The corpus geniculatum mediale so far as reconstructed, is an oval mass perhaps one-fourth or one-fifth as large as the nucleus of the inferior colliculus, which forms a distinct protuberance on the external surface of the brain stem, somewhat below the median horizontal plane. Like the nucleus colliculi inferioris it has a partial capsular investment of fibers along its upper and posterior borders, composed largely of strands from the brachium colliculi inferioris, which enters it on its posterior medial surface. Anteriorly and above are other investing strands, whose course and distribution could not be determined.

This completes the description of the general morphology of the auditory conduction path as reconstructed from the opossum brain. Certain points better brought out by the typical sections presented will be taken up after consideration of the vestibular reconstruction.

VESTIBULAR APPARATUS

A reasonably correct understanding of the structure of the central apparatus for the vestibular nerve is a matter of comparatively recent development, and its conduction relations are only beginning to be elaborated with any very great degree of detail. Especially is this true of the cerebellar relations of the vestibular complex, knowledge of which is still in a rather unsatisfactory state. Enough is definitely known, however, about the apparatus as a whole to serve as guide to its reconstruction. This has been done by Sabin ('01) for the human brain in her general reconstruction of the medulla and mesencephalon of the new-born child. As a guide to the present work the following brief résumé condensed from Barker's summary of the conclusions of von Bechterew, Flechsig, Baginski, von Monakow, Sala, Held, Cajal and others, and Sabin's description of her model, may be of service.

With the central vestibular apparatus there are now known to be associated at least four definite nuclei, (1) the medial (Schwalbe's), (2) the lateral (Deiter's), (3) the superior (Bechterew's) and (4) the nucleus of the spinal root. In relation with these are three large groups of fibers, the ascending and descending roots, and the nucleo-cerebellar tract, the latter containing fibers from various parts of the system, passing to the basal nuclei of the cerebellum. The entering fibers of the vestibular nerve bifurcate at once on gaining the interior of the medulla, the descending branches passing downward in the descending limb or spinal root, many of them (according to Cajal, most of them) terminating in this immediate region. All their terminations are not fully known, however. The ascending limb fibers pass upward in the medulla in the ascending root, some of them to terminate in the superior and lateral vestibular nuclei, others to ascend into the cerebellum to terminate in connection with the nuclei of the roof. Of the nuclei, the medial and lateral and the nucleus of the spinal root are quite well defined and easily recognized. The exact limits of the superior nucleus are more doubtful, at least in the opossum. The medial nucleus lies in the floor of the fourth ventricle adjacent to the median line, and in close association posteriorly with the nucleus N. hypoglossi, and below with the nuclei of the N. vagus and the N. accessorius. Anteriorly its relation to the cochlear nuclei varies with the position of these in different brains. The cells of the nucleus of the spinal root as the name indicates, lie among the fibers of the spinal root itself. This brings its position immediately lateral to the medial nucleus, the adjoining borders of the two not being sharply differentiated from each other. The lateral nucleus (Deiter's) apparently consists of two parts as described by Sabin for the human brain, one medial and the other lateral to the spinal root of the vestibular nerve, and both approximately opposite, the point of entrance of the nerve. The division is only apparent however, since typical Deiter's cells can be recognized among the strands of the spinal tract, uniting the two divisions of the nucleus. The superior nucleus of the vestibular nerve lies in the line of continuation anteriorly of the vestibular spinal and ascending roots, in close association with Deiter's, and so wedged between it and the nucleo-cerebellar tract in higher mammals that it was at first regarded as an appendage of that nucleus. Whatever may be said for its definiteness in brains like the human, in the opossum it is outlined with difficulty. The ascending tract is distributed in part to the superior nucleus, as already mentioned, and in part to the basal nuclei of the cerebellum, especially the nucleus fastigii.

Decussation between the vestibular complexes of the two sides of the brain occurs between the fibers of the nucleo-cerebellar tract by way of the decussation of the two fastigial nuclei, and anteriorly between fibers from the two superior nuclei, opposite the point of origin of the brachium conjunctivum.

The nucleus cerebello-acousticus is the name under which Cajal has called attention to the existence of a group of cells in the lateral wall of the ventricle, in the margin of the ascending limb of the spinal tract as its cerebellar fibers ascend towards the ventricular roof, which receive collaterals from the ascending root. Such a structure cannot be definitely determined in Weigert preparations of the opossum hindbrain.

Three other groups of vestibular connections are usually described, namely, the internal arcuate fibers from the medial and spinal nuclei, a bundle from Deiter's nucleus to the spinal cord, and two groups of cerebellar connections, the medial and lateral bundles. These groups are not capable of satisfactory reconstruction in the opossum, and in fact distinct cerebellar groups could not be definitely identified.

In general the vestibular complex of the opossum corresponds quite closely to the general conception outlined above. Several points, however, require special notice.

From time to time in the literature relating to the nuclei of the floor of the fourth ventricle, stress has been laid upon the separate anatomical identity of the nucleus intercalatus, and its relation to the medial vestibular nucleus. A considerable number of authorities regard the former as part of the latter. In a recent paper ('03), already referred to, on the floor of the fourth ventricle, Streeter in endeavoring to correlate external and internal topography, discusses the status of the nucleus intercalatus. After reviewing the opinions since Staderini and van Gehuchten, he directs attention to the fact that Weigert preparations of the human brain give no ground for differentiating the two. Other methods of investigation however, show the question to be less easily settled. He advances as evidence for giving the nucleus intercalatus an identity of its own, among other things the existence of a neuroglia partition between it and the medial vestibular nucleus, demonstrable by special neuroglia stains, and also certain evidence from a brain in which one half of the cerebellum was congenitally absent, in which degenerative changes tending to establish the separateness of the two nuclei could be demonstrated. This same question came up at the outset in the reconstruction of the medial vestibular nucleus in the opossum. The use of Weigert preparations may of course lay the work open to the objection pointed out by Streeter, and the writer makes no pretence of urging the finality of his conclusions on this point from such evidence. None the less, he is obliged to confess that the preparations upon which this work has been done offer not the slightest excuse for differentiating the nucleus intercalatus from the nucleus medialis N. vestibularis. From the median line to the border of the spinal tract, the uniformity of the structure and staining reaction are absolutely unbroken, there is not the slightest sign of a partition, the felt-work of fibers is characteristic throughout, and even a significant dividing groove in the ventricular floor is apparently lacking. If the nucleus intercalatus is to be distinguished from the medial vestibular nucleus, it becomes impossible to reconstruct the latter in the opossum from Weigert preparations. The writer therefore followed what seems a legitimate conclusion from this material, and included all the area labelled as such in fig. 10, in the medial nucleus.

A second feature of the opossum brain that has to be reckoned with in the reconstruction of the anterior portion of the vestibular complex, is the imperfect differentiation of the basal structures of the cerebellum, especially the nuclei; and the confusing intimacy of the vestibular relations with these nuclei. The opossum cerebellum has no dentate nucleus, a fact which probably has its influence upon the primitive confusion of the base, since the functions and connections thus differentiated fall presumably at least in rudiment to the basal nuclei. The nucleus fastigii is a rather indefinitely defined structure, the chief clue to whose identity is its relation to the superior peduncle anteriorly. One other nuclear mass, medial to the nucleus fastigii and below, can be recognized in some of the sections. Figs. 6, 7 and 8 may serve to convey some idea of the difficulties of reconstructing in this region. The decussation in the roof seems to offer an exception to this rule, its parts standing out with considerable clearness.

A third point requiring brief mention in the same connection relates to the intimacy of the association between the superior nucleus of the vestibular nerve and the sensory nucleus of the fifth nerve, below it. The commissural connection of Bechterew's nucleus seems to be associated with a decussation between the two fifth nuclei, rather than with that of the superior peduncle as described by Sabin ('01) for the human brain. In the cross sections, boundaries for Bechterew's nuclei cannot be assigned, but the horizontal sections are somewhat more satisfactory in this respect.

Finally, in studying the figures of the models, the following points should be remembered: (1) certain connections of a minor nature or requiring special consideration are dealt with in discussing the typical sections shown; (2) all of the vestibular above the level of Deiter's may be regarded as in the cerebellum, not the medulla; (3) the view of the apparatus from above (fig. 4) represents it with a piece cut from the nucleo-cerebellar tract in order to give a better conception of the position and relation of Deiter's nucleus, and the connection between its two apparently separate parts.

Passing now to the detailed description of the vestibular system as reconstructed for the opossum, the N. vestibularis appears as a fiber bundle of somewhat smaller size than the N. cochlearis, the root being composed of a number of separate fasciculi, easily demonstrated in careful examination of the gross specimen, in contrast to the single solid bundle of fibers presented by the cochlear root before it reaches the lateral surface of the medulla. The vestibular root enters just anterior to the cochlear, at a slightly sharper angle, some of its strands underlying those of the latter nerve. The restiform body passes up into the cerebellum so far posterior as to lie entirely above the level of entrance of the vestibular nerve, and so forms no part of the picture in this immediate area. As soon as the root has pierced the corpus trapezoideum, bifurcation into ascending and descending roots occurs. This bifurcation takes place in a region rather closely confined by surrounding structures. Laterally the larger part of the root and its divisions is overlaid by the anterior part of the ventral cochlear nucleus. The root of the seventh nerve is closely applied to the anterior and lower border of the vestibular, the ascending root of the latter passing into the superior nucleus and the cerebellum above the anterior limb of the genu. Just medial to the point of bifurcation the olivo-cochlear tract passes downward through the medial vestibular nucleus to the superior olive. In the same way the cerebellar part of the ascending tract is surrounded medially, posteriorly and postero-laterally by the cochlear nuclei and on its antero-lateral aspect bears a shallow depression in which lies the corpus restiforme. Just as the dorsal cochlear nucleus may be said to "straddle" the spinal vestibular, so the spinal vestibular in the region of origin of its two divisions may be said to be squeezed between the two peduncle-like fiber tracts associated with the cochlear reception nuclei. No sooner is the pressure relieved than both the vestibular fiber-tracts expand considerably, the anterior to its distribution in the cerebellar nuclei and the superior vestibular nucleus, and the posterior to accommodate the cells of the spinal nucleus.

Of the nuclear masses, the medial possesses perhaps the most characteristic shape. It lies as previously remarked in the floor of the fourth ventricle, its lateral border fused with the spinal tract. The triangular area, apex posterior, which corresponds to it, just lateral to the elevation marking the spinal tract is easily recognized in the floor of the ventricle in the unsectioned brain. The form of the dorsal surface and the longitudinal groove in the ventral surface made by the sensory fifth, together with the deep notch medial to it for the nucleus N. vagi and the tractus solitarius are well shown in figs. 2 and 4. Anteriorly the medial nucleus is pierced by the olivo-cochlear tract in the manner described above. The slender tongue extending horizontally forward along the medial side of the olivo-cochlear tract toward the region of the superior nucleus, will be noted again in connection with the sections.

The nucleus of the spinal tract of the vestibular nerve takes its form from that of the tract among whose fasciculi it lies. The combined mass is therefore roughly a long cone, tapering towards a blunt point posteriorly, but represented as cut across to allow for as yet undetermined caudal extension. The cross section posterior to the tuberculum acousticum is round or an oval slightly flattened dorso-ventrally. In the region of greatest constriction, the flattening of the dorso-medial and dorso-lateral surfaces and the greater compactness of the mass is gained largely at the expense of the grey matter, which is relatively small in amount here, though most abundant just posterior to this region. The boundaries of the medial and spinal nuclei and the spinal tract are not as distinct in the model as in the sections. Their form, however, can be made out in figs. 5, 10 and 12.

The ascending tract of the spinal vestibular runs a comparatively short course from the bifurcation, beginning almost at once to break up into its component parts for distribution. Some strands continue horizontally forward into the substance of the superior nucleus. Another portion breaks up in Deiter's nucleus. A large number of strands, however, turn abruptly upward in a vertical direction, forming a flattened column in a depression in whose lateral surface lies the upper and outer part of Deiter's nucleus. The posterior and medial fibers of this column fill the notch separating the anterior extensions of the two cochlear nuclei. On reaching the level of the nucleus fastigii in the base of the cerebellum, these fibers, in company with others forming the nucleo-cerebellar tract, bend sharply medially and spread out like a fan into the nuclear masses of the base of the cerebellum, a well-defined portion participating in a decussation with fibers from the opposite side. This decussation is very easily distinguished from that of the restiform body, the complete separation of the two being very beautifully shown in horizontal sections through the base of the cerebellum. The restiform body appears as a dense compact mass, lying lateral to the ascending nucleo-cerebellar tract, and passing upward at an inclination which brings its point of decussation well anterior to that of the vestibular group. The discrete smaller bundles and ribbon-like strands constituting the latter are totally different in appearance from the compact solidity of the former.

The distribution of fibers of the ascending path to the superior nucleus follows the same general arrangement of ribbon-like strands, curving around towards the medial side in the anterior end of the superior nucleus, in a manner which serves to some extent as an index to the boundary of the nucleus in this direction.

The outlines of the superior vestibular nucleus as previously noted, are not very definite. The mass lies in the lateral wall of the ventricle and forms in a general way a blunt prolongation of the long axis of the descending root. It is much cut up by strands of fibers ascending towards the cerebellum or terminating in its substance. Its close relation to the nucleus of the fifth nerve, especially the sensory division, which lies immediately below it, corresponds to that noted in the general description. Externally it is of course entirely concealed from view by the middle and posterior cerebellar peduncles and the overhanging mass of the great flocculus-like lateral extension of the opossum cerebellum itself. Internally the point of origin of the commissure from the superior vestibular nucleus, in association with fibers from the sensory nucleus of the fifth, is suggested in fig. 4. The slender anterior projection of the medial nucleus, which is also suggested, and its connection will be referred to in discussing the sections.

The lateral nucleus of the vestibular nerve as contrasted with the superior, is easily recognized and outlined, owing chiefly to the highly characteristic large ganglion cells of which it is composed. It lies opposite and above the point of entry of the nerve and corresponds in its apparent division into two parts, to the outline description already given. The continuity of the two can be readily made out, however, in the horizontal sections especially. The upper part of Deiter's therefore appears as a bulge in the side of the nucleo-cerebellar tract while the central part lies within the ascending limb of the spinal tract itself, and the lower forms a tongue or wedge-like piece inserted between the olivo-cochlear tract and the descending vestibular root.

DISCUSSION OF SECTIONS

(FIGS. 5–14)

The closing part of this paper is devoted to a discussion of the sections selected as illustrative of the topography of the two divisions of the central acoustic complex in the opossum, as previously discussed. While the sections have also a general interest from the standpoint of other groups of structures in the medulla, the intention in the present case is to confine the discussion to salient points connected with the eighth and incidentally the seventh nerves, and to direct attention to their bearing on the models and to particulars in which they fill out deficiencies in the plastic work.

The drawings constituting the figures under consideration were made by the use of the projection lantern, every possible detail obtainable being filled in in this way. The pen and ink work was then done on the projected outline, additional detail being obtained by the use of the binocular microscope, and every effort being made to make both detail and general effect correspond as closely to the original as the medium in use would permit. The diagrammatic has been studiously avoided, especially in connection with doubtful points. A system of abbreviated labelling was adopted, which it is hoped will be intelligible practically on first inspection, without the use of a key. Where conventional labelling appeared unsatisfactory, letters were used and referred to in the legend.

Inasmuch as the models were developed primarily from the transverse sections, consideration of the topographical detail may appropriately begin with them.

Fig. 5. Series A, slide 98, row 2, section 2. This section is taken at the level of the posterior part of the radix N. cochlearis (see figs. 1 and 2). It presents very satisfactorily the manner in which the fibers of the cochlear root pierce the corpus restiforme, and the medial situation of both cochlear nuclei as regards that tract. Indications of the imbricated character of the strands in the ventral nucleus, a very characteristic appearance in the region of entrance of the nerve in all the sections, and of the extension of the grey matter downward between the strands of the nerve, are apparent. The corpus ponto-bulbare and its connection with the tuberculum are prominent in this region. The connection with the tuberculum consists of a distinct band of fine fibrils arching over the dorsal surface of the corpus restiforme. In these preparations no signs of ganglion cells associated with them, either in the tuberculum or in the corpus ponto-bulbare could be made out. It may be noted incidentally that one of the newer series mentioned under the heading of Materials and Methods, owing to a more intense Weigert staining, exhibits this connection between the tuberculum and the corpus ponto-bulbare in a more striking fashion than does the section figured. As regards the vestibular, the close relation between the descending root and its

nucleus, and the medial nucleus is apparent, and the surface markings in the floor of the ventricle outlining their position can be inferred. Internal arcuate fibers are abundant in all sections involving this part of the vestibular complex, strands of them emerging from between the fasciculi of the descending root and passing toward the median line, or more directly downward among the bundles of the formatio reticularis. An interesting group of fibers is indicated by the letter *A*. This group appears in a series of eight or ten sections of which the most anterior ones begin to show the fibers of the corpus trapezoideum, from which however, it appears to be entirely distinct. The apparent origin is among the fasciculi of the descending vestibular root, and its termination in the nucleus of the seventh nerve, at whose lateral border the fibers scatter. Such scattering of course may be due to the interposition of an obstacle, and may not indicate an interruption in the path. I have not been able to find in von Kölliker's or Cajal's descriptions or figures any reference to such a bundle among the connections of the seventh nerve. It is of course possible that this represents a collateral of the vestibular system passing by way of the medial lemniscus to other levels in the mesencephalon or the cord. This section also shows the position and bilobed form of the seventh nerve nucleus, and the characteristic arrangement of the fine strands passing upward toward the genu. Throughout this and other sections more or less characteristic differences in size of ganglion cells may be made out without special staining. Those of the medial and spinal vestibular nuclei for example are quite small, those of Deiter's nucleus or the nucleus of the seventh nerve very large. The two latter are so conspicuous as to make the nuclei in question recognizable at first glance.

Fig. 6. Series A, slide 90, row 2, section 1. This and the following section are through the most complicated part of the opossum medulla, and present especially interesting pictures. This section is taken through the middle of the radix N. vestibularis and the genu of the facial nerve. The anterior part of the ventral cochlear nucleus is still prominent, but the tuberculum is represented only by a bit of grey matter from the anterior end. The

lower portion of the olivo-cochlear tract is conspicuous, and the contribution of the ventral nucleus to the dorsal path by way of this bundle is well shown. The principal origin of the tract in the tuberculum is more posterior, but is shown quite as satisfactorily in sagittal section (fig. 13). The corpus trapezoideum appears from origin to decussation. The origin in the substance of the ventral nucleus and the button-holing with the entering strands of the vestibular root are well shown. The lateral half of the bilobed superior olive and the termination of the ventral end of the olivo-cochlear tract in connection with it, can be better made out in the sections themselves, owing to the impossibility of doing justice in pen and ink work to the whorls and coils of delicate fibrils which give the nucleus a characteristic appearance. The posterior end of the medial half is just suggested and with the nucleus corporis trapezoidei appears to better advantage in the next section. The division of the decussation into a dorsal and a ventral part, the dorsal apparently concerned largely with fibers from the olives, and the ventral a more direct long-path decussation, can be well made out. The fibers of the sixth nerve should not be confused with olivary connections in this section. As regards the vestibular, the distribution of the main mass of fibers direct to the region of the spinal tract, along its ventral surface is apparent. Deiter's nucleus, with its large ganglion cells, easily the largest in this part of the brain, looms up, a conspicuous landmark in the field, above and medial to the division of the entering strands. The medial part is easily made out in this section. The most posterior strands of the nucleo-cerebellar tract of the vestibular nerve are also seen, and the dense strands cut at an angle which represent the more anterior fasciculi of the same tract as they bend back towards the more posterior parts of the nucleus fastigii. The restiform body in its groove on the outer side of the nucleo-cerebellar tract, stands out clearly. On the medial side in the roof of the ventricle, the characteristic appearance and relations of the vestibular decussation, especially its independence of the corpus restiforme, are apparent. Of the medial vestibular nucleus, nothing but the anterior tongue-like mass of fibers and grey matter lateral to the olivo-cochlear tract remains. This group of fibers can be better traced in horizontal sections. The region in the angle between this and the spinal vestibular tract is a matted mass of fibers which cannot well be represented in low power pen and ink work. Such a complex well deserves Golgi analysis. A portion of these fibers are undoubtedly a part of the connections of Deiter's with the vestibular tracts. Another part can be shown to be aberrant strands of the seventh nerve, which appears in the next few sections. A considerable number of them probably represent internal arcuates, and the connections of Deiter's with the median longitudinal fasciculus. Still others are fibers to the olivo-cochlear tract. An appearance perhaps striking enough to deserve mention, is found in the other half of this section. One coarse strand of fibers presents every appearance of being an olive-cerebellar connection, lying somewhat lateral to the remnants of the main band of olivo-cochlear fibers, and joining the nucleo-cerebellar path of the vestibular above. On going back and forth through this region repeatedly comparing sides, the writer has inclined to the conclusion, however, that this is merely an aberrant strand of the olivo-cochlear system, whose close relation to an ascending strand of the vestibular spinal tract produces the deceptive appearance.

Fig. 7. Series A, slide 88, row 2, section 2. This section is somewhat anterior to the previous one, and involves the radix N. facialis. The features of special interest center around the corpus trapezoideum and the olive and its connections.

The region marked *A* in this section represents the principal feature for discussion. In reviewing the descriptions of the corpus trapezoideum given by Cajal, von Kölliker, Edinger and Held, the writer has been unable to find any reference to a possible connection of the corpus trapezoideum and the ventral cochlear nucleus, with the cerebellar nuclei. In fact the absence of connection of the cochlear apparatus with the cerebellum seems to be emphatically pointed out by a number of writers as a main distinction between vestibular and cochlear systems. With this weight of opinion against it, the writer calls attention to this and other sections through this portion of the opossum brain with considerable diffidence, and with the full realization that Weigert preparations are no final settlement of the question, and that their most convincing appearances may be deceptive. The grey matter between the strands of the corpus trapezoideum in sections somewhat posterior represents to all appearances the extreme anterior limit of the ventral cochlear nucleus, traceable back to the main mass without a break. Those familiar with Cajal's figures will recognize in fig. 359 on page 819 of the Histologie du Systeme Nerveux, Tome 1 (Azoulay), on the right hand side of the section, approximately the same region, as he pictures it for the cat. Comparison of the figures here given (figs. 6 and 7) with Cajal's is very instructive as regards the differences between the opossum and higher mammalian brains in this region. The cerebello-acoustic or nucleo-cerebellar path is the only group of fibers in this region labelled in his figure. In the opossum, another group is apparent, consisting of fine fibrils from the grey matter of the before-mentioned anterior part of the ventral cochlear nucleus, which apparently pass upward on the lateral side of the vestibular nucleo-cerebellar tract, gathering into slender strands which closely skirt the medial border of the inferior brachium, but are always perfectly distinct from it. These fibers follow the general direction of the ascending vestibular fibers although apparently distinct from them also and turn medianward to be lost among the fibers of the roof. Somewhat more anteriorly these slender stands are replaced by the coarser ones shown in fig. 7—absolutely identical in appearance with the perfectly characteristic root bundles of the corpus trapezoideum, sharply defined, standing out clearly against a paler background, and in one section appearing as an almost continuous strip of fibers from above the level of the highest part of Deiter's to the middle of the dense mass of the undoubted corpus trapezoideum. The section drawn is only averagely good in showing this relation. It however brings out the entire difference in direction of the fibers from those of the spinal tract, and their striking individuality as regards origin at least. In the face of these appearances, which are confirmed by the newer series of transverse sections prepared in this laboratory since this work was begun, and of the apparent impossibility of confusing the fiber-group in question with any other structure described for this region, the writer feels obliged to contend that so far as such preparations will support a contention, this represents some form of connection, at least of the corpus trapezoideum and probably of the anterior part of the ventral cochlear nucleus, with the cerebellum.

The remaining features of the section concern the superior olive and the nucleus corporis trapezoidei. The two are easily differentiated and the bilobed structure of the former made out. The differentiation of the parts of the nucleus corporis trapezoidei is not very satisfactory. Of the three groups of fibers passing dorso-ventrally through the formatio reticularis, the one nearest the raphe is the sixth nerve, and the middle one of the three can be followed through several sections as the peduncle of the superior olive, connecting it with the nucleus of the sixth.

Fig. 8. Series A, slide 85, row 1, section 1. This section is through the sensory and motor roots of the fifth nerve, and presents the anterior limits of the vestibular apparatus and the decussation of fibers from Bechterew's nuclei, in association with a similar set of fibers from the fifth. As regards the cochlear apparatus, the anterior part of the corpus trapezoideum can be seen, and the beginning differentiation of the lateral lemniscus and the nucleus of the lateral lemniscus. Primarily as regards the topography of the region as a whole, the section serves to indicate the indefiniteness of boundaries between the fifth, the superior vestibular and the fastigial nuclei in the wall of the ventricle. The group of fine fibers marked *A* appearing in cross section are apparently continuations of the fibers of the anterior portion of the medial vestibular nucleus, which have already been referred to.

Fig. 9. Series A, slide 77, row 1, section 1. This section is taken through the posterior median portion of the inferior colliculi, just short of the decussation between the two. The fact that in the same section so much of the lateral lemniscus and its distribution, and the nucleus of the colliculus can be shown, illustrates the abrupt upward sweep of the tract. The capsule of lemniscus fibers on the lateral aspect of the nucleus is also well

shown. The section also pictures very satisfactorily the groove in the medial surface, in which lies the nucleus with its covering of scattered strands and explains its failure to show in the figure of the lateral aspect (fig. 1). The letter *B* directs attention to the group of fibers from the nucleus lemnisci lateralis towards the median line, which was mentioned above among the details included in the model of the cochlear apparatus. The fibers can be traced quite definitely to the median line and a part of them at least show every indication of connection with the median longitudinal fasciculus. In the sections where this structure is most conspicuous, decussation of most of its fibers with those of the opposite side undoubtedly occurs. Attention may also be called to a somewhat similar but smaller and shorter group of fibers from the region of the lateral lemniscus itself, marked *A* in the figure. They are lost in the central grey and show no signs of any relation to those of the opposite side. In Weigert preparations at least, they appear to be quite distinct from the group just described.

As regards the association of the first-mentioned group of fibers with any definite group of cells in the nucleus lemnisci lateralis the sections somewhat anterior to the one shown, present every indication that such is the case. In one of these sections a definite almond-shaped mass of cells, probably the anterior superior end or superior division of the nucleus lemnisci lateralis appears as the point of origin of the fine fibrils uniting to form the strands in question. Of the relation of the tract to the brachium conjunctivum little can be said from these preparations except that the fibers under discussion appear coincidently in the section with the first signs of an approaching decussation of the brachium, but are readily distinguished from these latter by their greater delicacy and the relative absence of clumping into strands. Before the decussation of the brachium has reached decided proportions the tract in question has completely disappeared from the field. The general impression gained from these preparations is that any relation to the brachium conjunctivum is incidental rather than fundamental.

Passing now to the horizontal sections, we find them rather better adapted than the transverse to the picturing of the general relations and structure of the vestibular system in the medulla.

Fig. 10. Series B, slide 75, section 1. This section is taken at the level of the broadest part of the combined medial and spinal nuclei of the vestibular nerve, and presents the arrangement of the structures in the right wall and floor of the fourth ventricle. The picture of the medial vestibular is one of the best in the series. In the general topography the brachium conjunctivum, the restiform body and the pons are conspicuous landmarks. The two cochlear nuclei appear in typical relation to each other and to the corpus restiforme, the anterior part of the ventral nucleus being also clearly shown in its association with the region of Deiter's and the nucleo-cerebellar tract. The corpus ponto-bulbare on the lateral aspect of the corpus restiforme is better shown in the following section. In drawing the medial and spinal vestibular nuclei an attempt was made to convey the effect of uniformity in staining reaction, which is so striking a feature of this mass, even in the best differentiated sections. The absence of any visible division into nucleus intercalatus and medial vestibular nucleus is apparent, the peculiar brownish background and the felt-work of exceedingly delicate fibers and small ganglion cells being uniform throughout. There is however, a marginal concentration of fibers along the inner border of the medial nucleus. Some of these pass posteriorly as a slender tail-like extension towards the anterior end of the hypoglossal nucleus. The larger part, however, appear better in the following figure, as the anterior tongue or extension already mentioned as lying on the medial side of the olivo-cochlear tract. The caudal indentation in the medial nucleus due to the nucleus N. vagi and the tractus solitarius, and the position of the fifth on the postero-medial border, are well shown. Of Deiter's only the lateral portion can be seen, among the strands of the nucleo-cerebellar tract. The typical inward curve of those strands of the spinal tract which pass into the nucleus superior N. vestibularis (the tract itself lies ventral to this section) gives an index to the anterior limits of the

nucleus, while the close association of the nucleus itself with the structures of the cerebellar base can be inferred from the proximity of the fibers of the superior brachium, originating in the nucleus fastigii.

Of the special features of this section, the one marked *A* is taken up with the next figure. *B* is also better shown in that connection. Particular attention is however, directed to *C*. This band of fine parallel fibers is a conspicuous object in five sections in this region, and can be made out in two or three more. In two or three of the best sections it can be traced definitely into the substance of the ventral cochlear nucleus, separating into fine strands in the nuclear mass. Ultimate origins or terminations could not be determined. The fibers follow the curve shown in the figure cerebralward scattering fan-like among the bundles and grey matter of the superior vestibular nucleus and the nucleo-cerebellar tract. The close association of this group of fibers with other more doubtful ones apparently forming cerebralward connections of the vestibular makes interpretation of them difficult, and in any case Golgi analysis would appear essential. In these preparations the group, however, presents every appearance of a cochlear-vestibular connection possibly uniting the ventral nucleus of the former with the superior of the latter. While a connection of the ventral cochlear nucleus with the cerebellum or midbrain by this route might be considered among the possibilities, such connection is hardly apparent in these sections. In the opinion of the writer, this fiber group corresponds to the one marked *B* in fig. 6, and should not be confused with the possible cochlear-cerebellar group mentioned under fig. 7, page 426, which lies lateral to it. See also fig. 6, where the latter group lies close against the medial surface of the restiform body.

Fig. 11. Series B, slide 79, section 2. This section is ventral to the one shown in the preceding figure, and with the following one is given primarily for the sake of certain special features of the vestibular system. The two parts of Deiter's nucleus are well shown, the large ganglion cells being inserted somewhat schematically in black. The anatomical connection of the two parts by scattered cells among the strands of the spinal

tract of the vestibular is also apparent. These cells are conspicuous in the sections owing to the brownish color they take from the mordanting and staining, so that the nucleus is usually easily defined. Under *A* in all three horizontal sections attention is directed to a prominent nuclear mass in the central grey substance, to which a majority of the fibers of the anterior extension of the nucleus medialis N. vestibularis, apparently lead. The region does not differentiate entirely satisfactorily in these Weigert preparations, and the fibrils are very delicate, which tend to make conclusions about them rather vague. The connection of the band of fibers with the medial vestibular nucleus is the more apparent of the two terminations of the group. The writer has not encountered any description of such a structure as this path or such connection with the central grey substance as it apparently presents, in any account of the vestibular system that he has seen. The nuclear mass in the neighborhood of the point of entrance of the fibers presents a considerable clump of fairly large ganglion cells. More medially the mass presents somewhat the appearance of the substance of the medial vestibular nucleus, the cells in this portion being very much smaller. The relation to the mesencephalic fifth is seen in fig. 10.

Fig. 12. Series B, slide 82, section 2. This section is taken still more ventral to the two preceding. The spinal tract and Deiter's are again conspicuous and the olivo-cochlear tract is seen in cross section as in the preceding figure. The chief feature of interest is the decussation between fibers from Bechterew's nuclei (marked *A*) in connection with a decussation of fibers from the fifth (marked *B*), posterior to it in the main, though in the transverse sections (fig. 8) the two are seen in the field at the same time. In the human brain, according to Sabin, this Bechterew decussation is as closely associated with the brachium conjunctivum as it is with the fifth in the opossum. This section also illustrates very satisfactorily the connection of the corpus ponto-bulbare with the posterior border of the pons. The presence of large numbers of delicate fibrils can only be indicated in the drawing. No ganglion cells can be distinguished in these preparations.

Finally we pass to a short consideration of the sagittal sections shown, which serve the purpose of presenting in panoramic style many of the features of the foregoing discussion.

Fig. 13. Series C, slide 80, section 2. This section is taken approximately midway between the raphe and the side of the brain stem. It is too far medial to show much of the cochlear nuclei, but presents in especially satisfactory manner the antero-posterior relations of the seventh nerve nucleus, the nucleus of the superior olive and the origin of the lateral lemniscus and its nucleus. The nucleus colliculi inferioris is also especially well shown, together with its decussation in cross section, which has not appeared in the preceding figures. The antero-posterior dimension of the vestibular system in the medulla is also given, including the piercing of the medial nucleus by the strands of the olivo-cochlear tract. The decussation of fibers from the superior nucleus of the vestibular in association with those from the fifth is seen in cross section anterior to the radix N. facialis. Some idea is also given of the sagittal section of the cerebellar base.

Fig. 14. Series C, slide 93, section 1. This section is taken lateral to the preceding one and is intended primarily to present the mesencephalic portion of the cochlear apparatus. The arrangement of the fibers of the lateral lemniscus, the nucleus lemnisci lateralis, the brachium colliculi inferioris and the medial geniculate body are ideally presented. Posteriorly the tuberculum acousticum is prominent and a good cross section of the corpus trapezoideum forms the ventral boundary of this part of the medulla. The close association of the anterior part of the vestibular complex and the sensory nucleus of the fifth is again apparent. The ascent of the nucleo-cerebellar tract to its distribution and descussation in the base of the cerebellum is not as well shown as in some of the preceding figures.

SUMMARY

1. The cochlear reception nuclei lie internal to the restiform body.

2. The corpus ponto-bulbare apparently is structurally connected with both the tuberculum acousticum and the pons. Its failure to follow the course between the seventh and eighth nerves described for other brains can be explained by the low development of the pons in the opossum, and the position of the cochlear nuclei, as compared with other mammalian brains.

3. No distinct striae medullares were recognized, the dorsal path of impulses from the cochlear nuclei being by way of an olivo-cochlear bundle to the region of the superior olive of the same side. This bundle receives fibers from both nuclei, but principally from the dorsal.

4. The ventral path is by way of the corpus trapezoideum, which originates largely in the ventral cochlear nucleus.

5. The corpus trapezoideum presents indications in these preparations of a connection with the base of the cerebellum anteriorly.

6. The anterior part of the ventral cochlear nucleus presents evidence of a connection with the base of the cerebellum in the region of the before-mentioned trapezoidal connection.

7. The ventral cochlear nucleus apparently presents a connection with the region of the superior nucleus of the vestibular system.

8. The superior olive in the opossum is distinctly bilobed, and is not anatomically continuous with the nucleus lemnisci lateralis.

9. The peduncle of the superior olive and the fibers passing to the median line from the superior end of the nucleus of the lateral lemniscus are easily recognizable in the opossum.

10. Of the vestibular system the superior, the lateral, and the medial nuclei, and the nucleus of the descending root, together with the bifurcation of the entering fibers into ascending and descending paths, and the nucleo-cerebellar tract, can be identified.

11. The comparatively undifferentiated cerebellar base makes the cerebellar relations of the vestibular apparatus uncertain.

12. The superior nucleus is poorly defined and differentiated with difficulty from surrounding structures, namely the nuclei of the base of the cerebellum above, and the sensory nucleus of the fifth nerve below and anteriorly.

13. The decussation between fibers from the two Bechterew's nuclei occurs in association with a decussation of fibers apparently from the sensory nucleus of the fifth nerve, rather than with the brachium conjunctivum.

14. The nucleus lateralis N. vestibularis (Deiter's) presents a medial and a lateral portion, separated by strands of the vestibular spinal tract, but characteristic Deiter's cells are found among the strands, showing the two parts to be essentially one nucleus.

15. So far as these preparations indicate, there is no nucleus intercalatus separate and distinct from the nucleus medialis N. vestibularis.

16. A band of fine fibers passing cerebralward from the medial vestibular nucleus along the floor and wall of the ventricle, medial to the olivo-cochlear tract, apparently connects this nucleus with a ganglion mass in the central grey substance in the floor of the ventricle anterior and medial to the superior vestibular nucleus.

17. A connection apparently exists between the spinal vestibular nucleus and the seventh nerve nucleus.

18. The strands of the nucleo-cerebellar tract are distributed to the large nuclear mass in the base of the cerebellum that apparently corresponds to the nucleus fastigii of the human brain. Decussation of these fibers takes place in the roof of the ventricle, and is easily distinguished from the decussation of the corpus restiforme.

The writer desires that the concluding paragraph of this paper shall be an expression of his sense of obligation to Professor Streeter, at whose suggestion this work was undertaken, and who with generous coöperation has made his own and the laboratory's resources freely accessible for its advancement.

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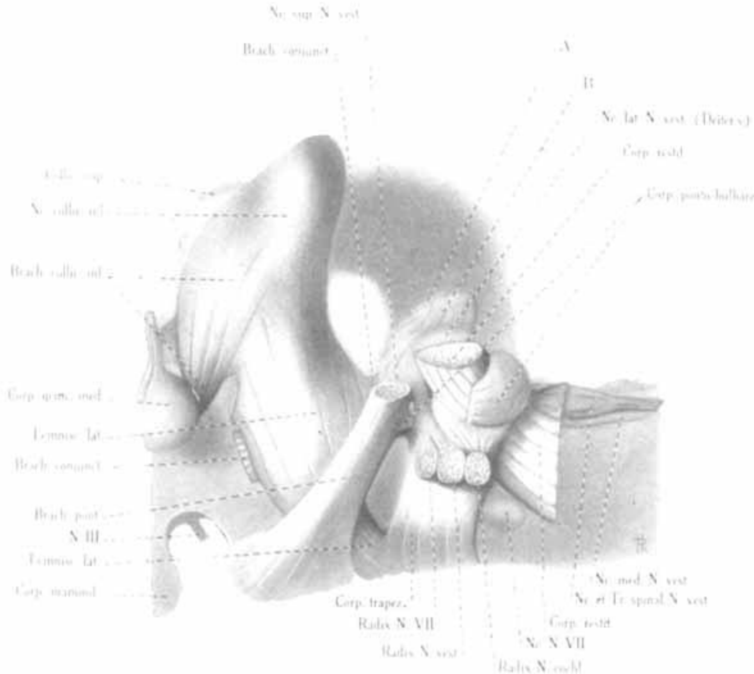
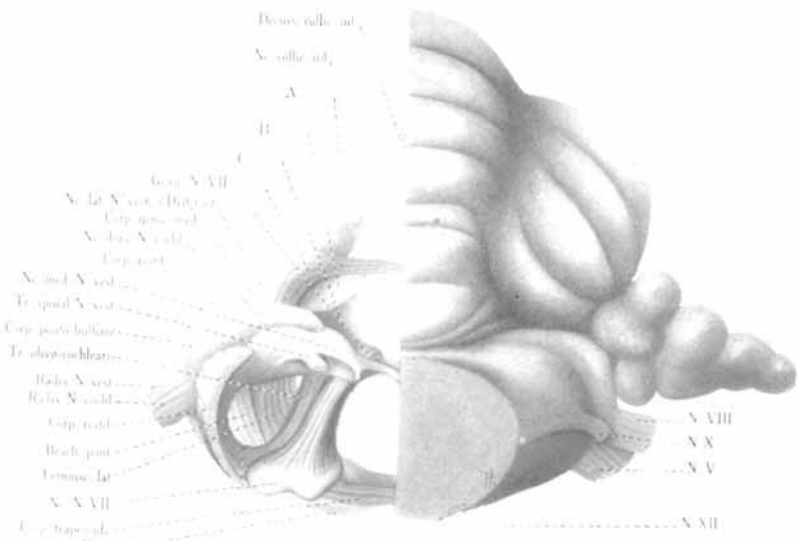
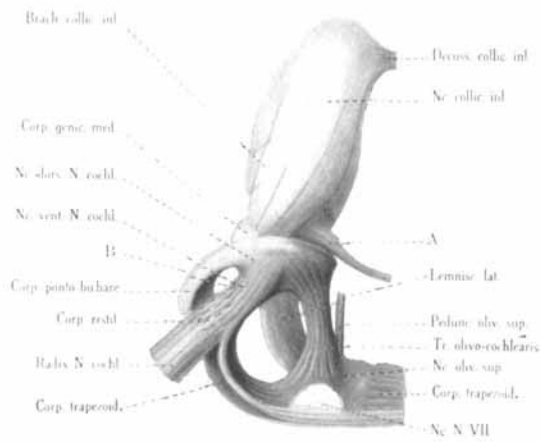
Fig. 1 Left lateral aspect of a wax-plate reconstruction of the cochlear and vestibular systems of the opossum brain. Enlarged 5 diameters. The corpus *restiforme, the pons, the brachium conjunctivum* and the seventh nerve are included as landmarks. *A*, decussating vestibular fibers from the nucleus fastigii and the nucleo-cerebellar tract; *B*, nucleo-cerebellar tract.

Fig. 2 Posterior aspect of reconstruction shown in fig. 1. *A*, cut surface of the nucleus fastigii. *B*, fibers passing from the superior end of the nucleus lemnisci lateralis to the median line, showing close relation with the decussation of the brachium conjunctivum; *C*, nucleo-cerebellar tract of the vestibular system and decussating strands.


Nc. sup. N. vest.
Brach. conjunct.
A
B
Nc. lat. N. vest. (Deiters)
Corp. restif.
Corp. ponto-bulbare
N. collic. inf.
Brach. collic. inf.
Corp. genic. med.
Lemnisc. lat.
Brach. conjunct.
Brach. pont.
N. III
Lemnisc. lat.
Corp. mamml.
Corp. trapez.
Radix N. VII
Radix N. vest.
Nc. med. N. vest.
Nc. et Tr. spinal. N. vest.
Corp. restif.
Nc. N. VII
Radix N. cochl.


Decuss. collic. inf.
Nc. collic. inf.
A
B
Genu N. VII
Nc. med. N. vest.
Tr. spinal. N. vest.
Corp. ponto-bulbare
Tr. olivo-cochlearis
Radix N. vest.
Radix N. cochl.
Corp. restif.
Brach. pont.
Lemnisc. lat.
Nc. N. VII
Pons
N. VIII
N. X
N. V
N. XII

2



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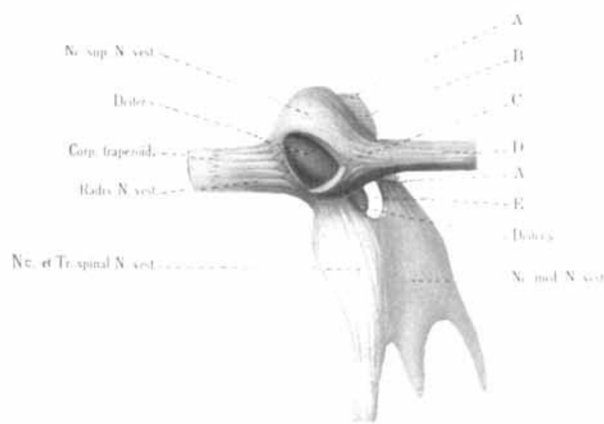

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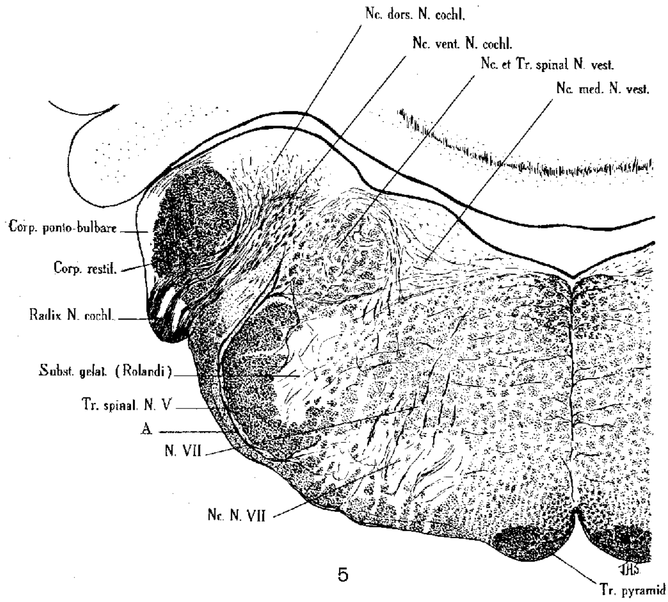
Fig. 3 Posterior aspect of a wax-plate reconstruction of the cochlear apparatus of the opossum brain. Enlarged 5 diameters. *A*, fibers passing from the superior end of the nucleus lemnisci lateralis to the median line (see *B* in fig. 2); *B*, opening through which passes the main mass of the corpus restiforme; *Corp. restif.* indicates the region in which the cochlear root is pierced by strands of the corpus restiforme.

Fig. 4 Dorsal aspect of a wax-plate reconstruction of the left vestibular complex of the opossum brain. Enlarged 5 diameters. *AA*, fibers passing from the medial nucleus cerebralward towards a nuclear mass in the central grey substance; *B*, fibers forming a decussation with similar ones from the superior vestibular nucleus of the opposite side; *C*, cut surface where a piece of the nucleo-cerebellar tract has been removed to expose Deiter's nucleus; *D*, decussation of vestibular fibers from the nucleo-cerebellar tract and the nucleus fastigii; *E*, opening through which pass the fibers of the olivo-cochlear tract or dorsal path of the cochlear system.



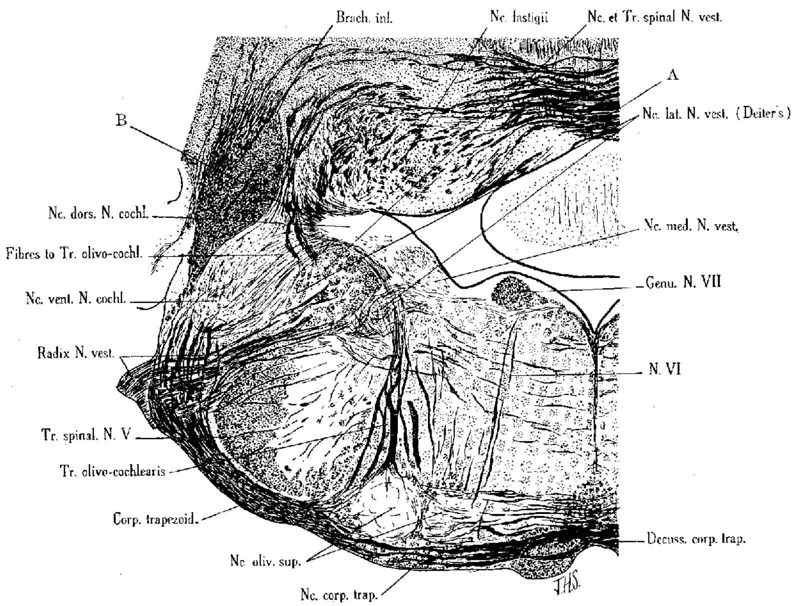
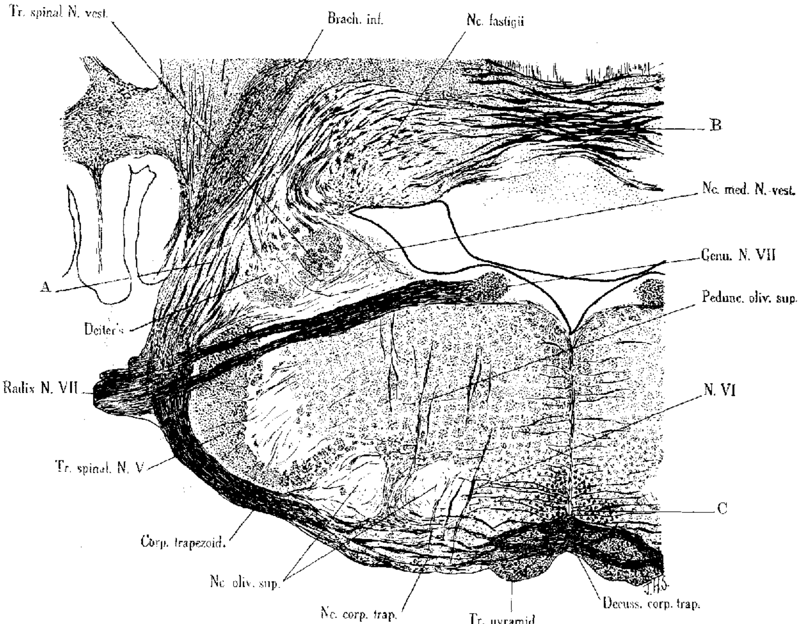


Fig. 5 Transverse section at the level of the Radix N. Cochlearis. Series A, slide 98, row 2, section 2. Enlarged 10 diameters. *A*, possible connection of N. vestibularis with N. facialis. For description of section, see page 422.

Fig. 6 Transverse section at the level of the Radix N. vestibularis. Series A, slide 90, row 2, section 1. Enlarged 10 diameters. *A*, vestibular decussation in the base of the cerebellum; *B*, cochlear-vestibular connection. For description of section, see page 423.



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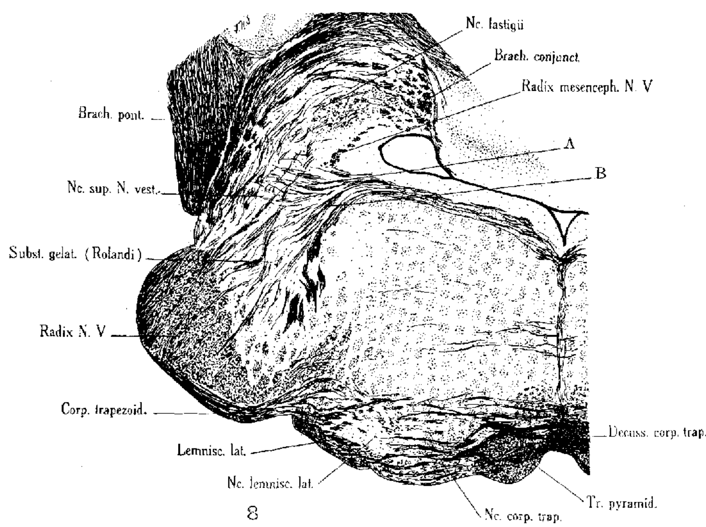

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Fig. 7 Transverse section at the level of the N. facialis. Series A, slide 88, row 2, section 2. Enlarged 10 diameters. *A*, possible cerebellar connection of corpus trapezoideum; *B*, vestibular decussation in the base of the cerebellum; *C*, possible inter-olivary portion of the decussation of the Corpus trapezoideum. For description of section, see page 425.

Fig. 8 Transverse section at the level of the radix N. trigemini and the superior vestibular nucleus. Series A, slide 85, row 1, section 1. Enlarged 10 diameters. *A*, decussating fibers from Bechterew's nucleus; *B*, decussating fibers from the nucleus N. trigemini. For description of this section, see page 427.

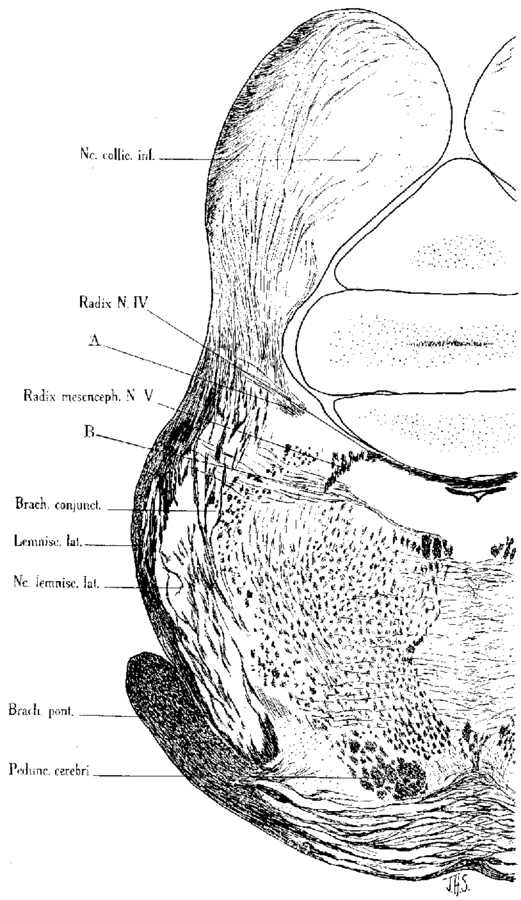


Fig. 9 Transverse section through the posterior part of the inferior colliculus. Series A, slide 77, row 1, section 1. Enlarged 10 diameters. *A*, see page 428; *B*, fibers from nucleus lemnisci lateralis to median line. For description of section, see page 427.

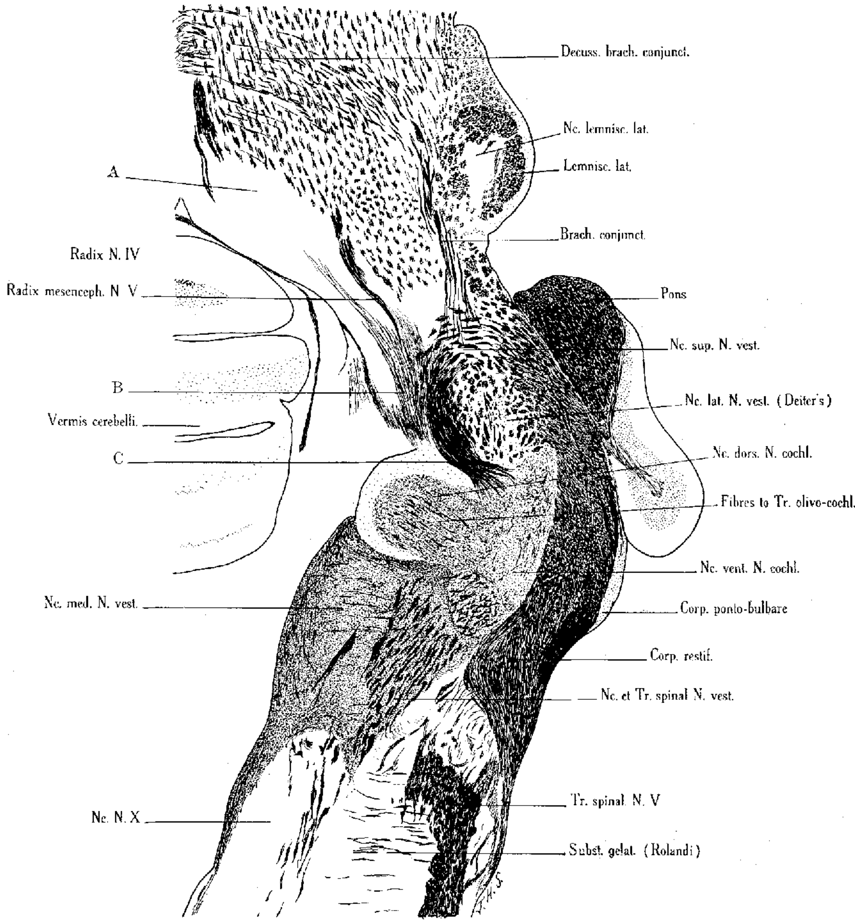
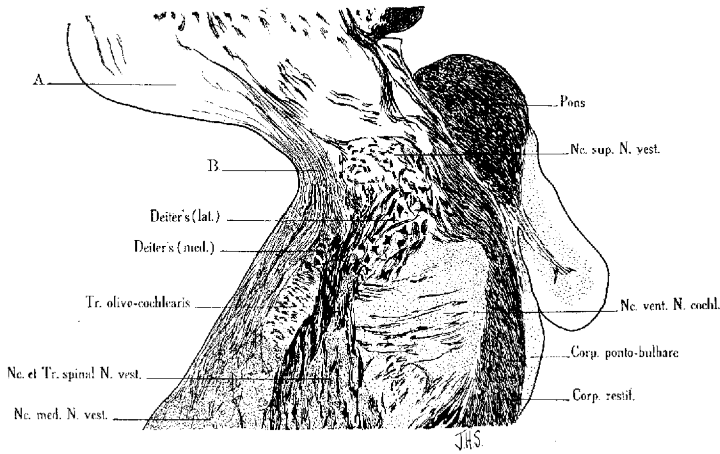


Fig. 10 Horizontal section somewhat above the level of the bifurcation of the fibers of the right radix N. vestibularis into ascending and descending roots. Series B, slide 75, section 1. Enlarged 10 diameters. *A*, ganglion mass connected apparently with the nucleus medialis N. vestibularis (see fig. 11); *B*, marks the fibers connecting the two; *C*, possible cochlear-vestibular connection. For description of section, see page 429.



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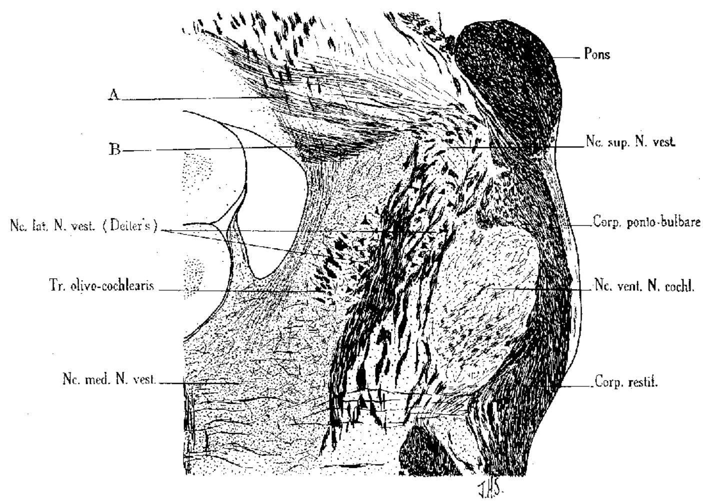

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Fig. 11 Horizontal section taken somewhat ventral to that in fig. 10, showing the relation of Deiter's nucleus to the radix descendens N. vestibularis. Series B, slide 79, section 2. Enlarged 10 diameters. *A* and *B*, as in the preceding figure, represent a possible connection of the medial vestibular nucleus with the central grey substance. For description of section, see page 430.

Fig. 12 Horizontal section at the level of the decussation of fibers from Bechterew's nuclei. Series B, slide 82, section 2. Enlarged 10 diameters. For description of section, see page 431.

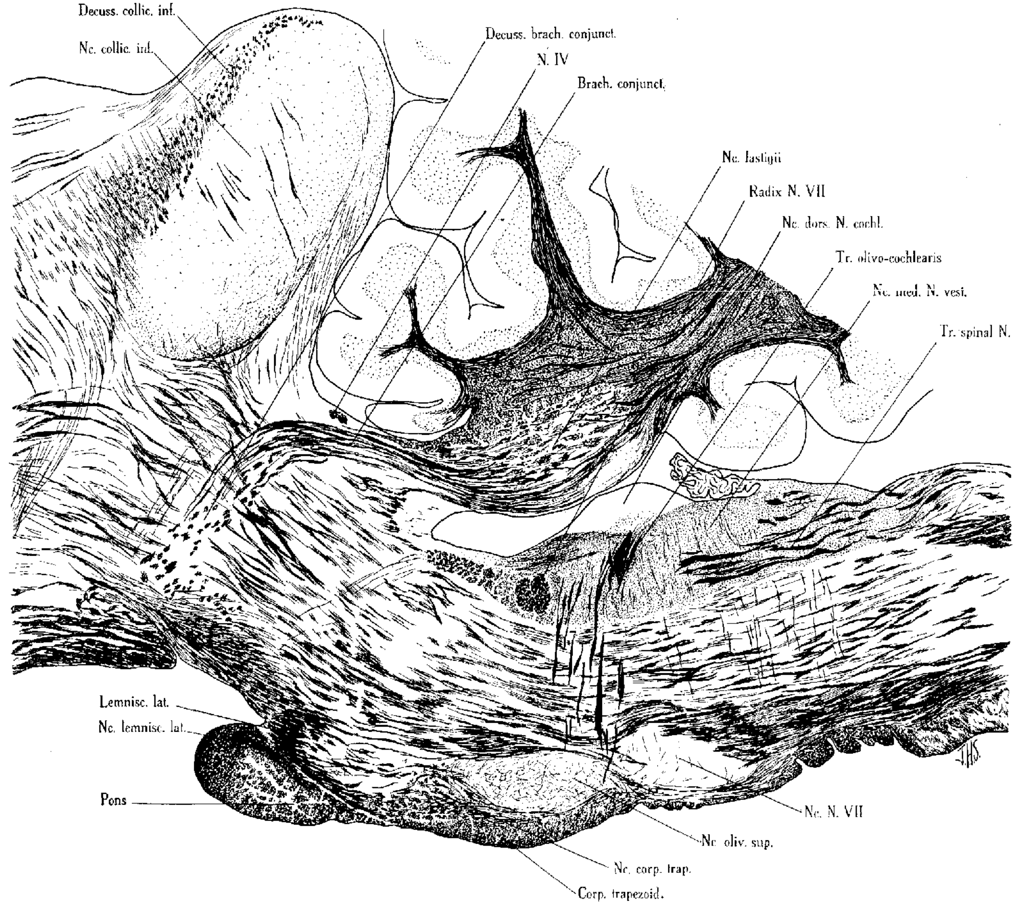

Fig. 13 Sagittal section taken midway between the raphe and the lateral surface of the brain stem. Series C, slide 80, section 2. Enlarged 10 diameters. For description of section, see page 432.

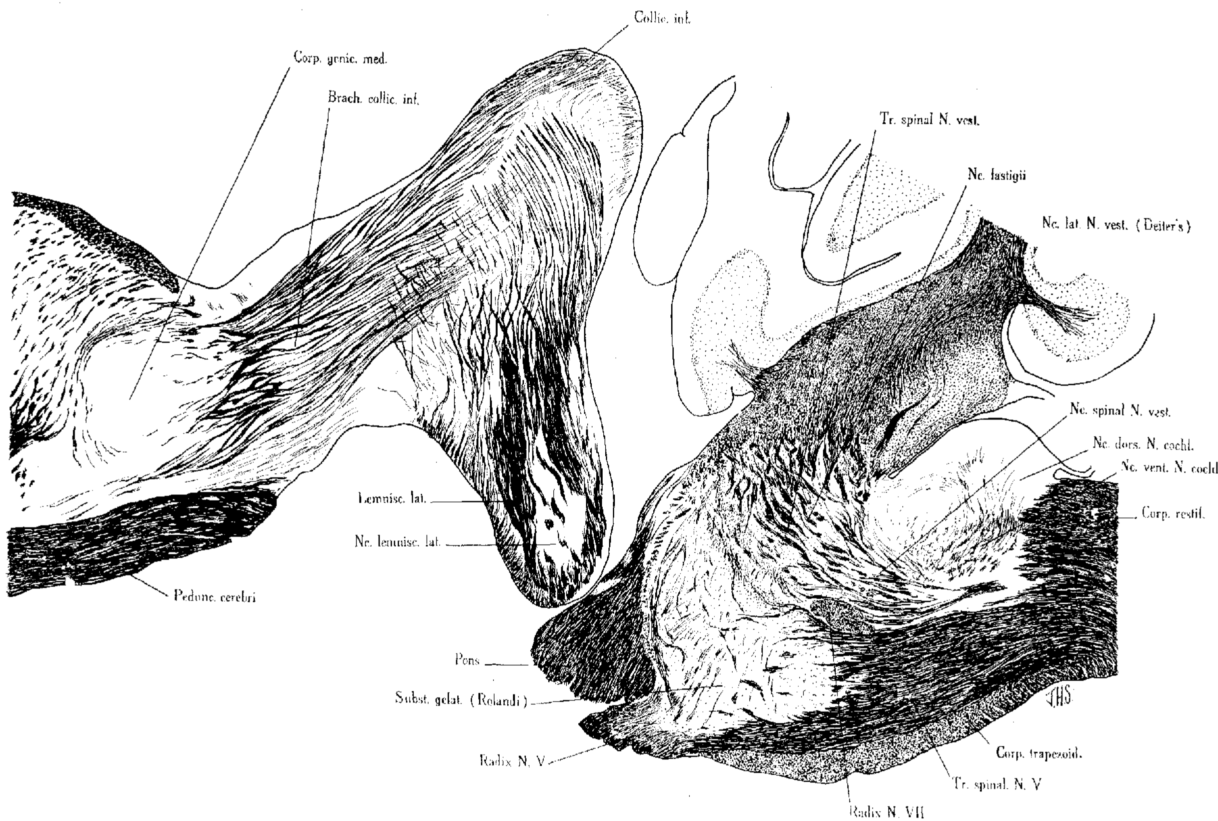

Fig. 14 Sagittal section through the corpus geniculatum mediale, the lemniscus lateralis and the tractus spinalis N. vestibularis. Series C, slide 93, section 1. Enlarged 10 diameters. For description of section, see page 432.