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VESTIBULO-OCULAR REFLEX PATHS

BY

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THE present paper is in the nature of an addendum to the Presidential Address, which was published in Vol. L of the *Transactions of the Ophthalmological Society*. Its aim is to describe the anatomical paths by which the labyrinth is able to establish the controls described in that paper. On that occasion, I spoke of the unceasing control exercised by the labyrinthine structures on the eyeballs, and I tried to indicate that, while there was evidence of a differentiation of function in the various parts of the labyrinth, the differentiation was not, by any means, complete, and it was possible that, after destruction of one portion of the labyrinth, other portions might vicariously take up the function of the destroyed portion. Beyond the acoustic functions and the ocular controls the labyrinth has a control over the muscle tone of the whole body, and on these controls depends the preservation of the body equilibrium. The anatomical paths concerned in the conduction of these various reflexes are naturally numerous and complex, and in many cases have not been fully worked out.

The labyrinth is the receptor organ for three types of impulse:—

(1) Gravistatic, resulting from variation in pressure on the maculae of the sacculus and utriculus produced by changes in the position of the head in space.

(2) Gravikinetic, produced by variations in pressure on the ampullae of the semicircular canals resulting from movements of the head.

(3) Rhythmical variations in pressure on the organ of Corti transmitted usually to the endolymph through the intermediary of the tympanic mechanism and giving rise to the sensation of sound, *i.e.*, mainly epicritic in character, but also having important dyscric factors.

Our task would be greatly simplified if we could separate with any certainty the paths that these different impulses follow in the central nervous system. As far as the control of eye positions and movements is concerned, the simple gravistatic and gravikinetic controls are the two which really matter, but, in the present state of our anatomical knowledge, they cannot be, in any satisfactory way, separated from the paths of the impulses emanating from the cochlea. So we are compelled to consider the whole complex of paths and indicate only probabilities.

Diagram No. 1 from "*Körperstellung*" by Magnus represents the physiological connections of the sacculus and the utriculus with the various ocular muscles in the apes and man, and it is the anatomical paths by which these are linked up which we have to trace out.

COCHLEAR PORTION OF VIIITH NERVE

The cochlear root from the labyrinth enters the central nervous system distally, laterally and dorsally. The vestibular root is proximal, mesial and ventral. The cochlear root consists mainly of fibres from the cochlea which have passed through the ganglion spirale, but also may contain afferent fibres from the vestibule (especially macula sacculi) and efferent autonomic fibres from autonomic cells in the ventral nucleus of the VIIIth.

CONSTITUTION OF DORSO-MESIAL PORTION OF OCTAVO-MESENCEPHALIC TRACT (Diag. II)

The cochlear nerve entering the central nervous system sweeps up through the outer part of the ventral nucleus of the VIIIth. Some fibres pass into the ventral nucleus on its inner side. Above, it is capped by the tuberculum acousticum into which the bulk of the remaining fibres pass. A few fibres pass on in the striae acousticae to the proximal end of the nucleus triangularis. These latter fibres arise, in all probability, from the sacculus, and not from the cochlea. The main secondary acoustic tracts arising from the two primary nuclei, the ventral nucleus and the tuberculum

acousticum, pass into the dorso-mesial portion of the octavo-mesencephalic tract, which leads by way of the striae acousticae, the decussations of Monakow and Held and the lateral fillet to the posterior corpus quadrigeminum and the mesial geniculate of the opposite side. The bulk of the fibres cross by the dorsal decussation of Monakow and the mesial decussation of Held to the lateral fillet of the opposite side, *i.e.*, form a crossed vestibulo-mesencephalic tract, but a small bundle remains uncrossed, and passes up to the posterior corpus quadrigeminum of the same side. In this part of the octavo-mesencephalic tract, there are no nuclei intercalated between the two main primary nuclei and the posterior corpus quadrigeminum, and the mesial geniculate. With the fibres passing on to the auditory cortex we are not concerned, but the connection of the posterior corpus quadrigeminum with the anterior corpus quadrigeminum, and of the whole tectum by means of the *fibrae radiales* and the posterior longitudinal bundle with the oculo-motor nuclei, and by the pre-dorsal bundle of Held with the motor nuclei for the head and neck muscles supplies one of the centrifugal reflex paths with which we are concerned. Furthermore, from cells in the posterior corpus quadrigeminum fibres arise which pass downwards to the nuclei of the lateral fillet and from both the dorsal and ventral nuclei of the lateral fillet fibres pass to the posterior longitudinal bundle of the opposite side, forming a link with oculo-motor nuclei and the motor nuclei of the cord. Some of these centrifugal fibres from the colliculus carry on to the superior olive.

Mixed up in the striae acousticae with these fibres are also fibres going to and coming from the nuclei of the cerebellum. The consideration of these is best deferred until the course of the fibres of the vestibular branch has been described.

THE VESTIBULAR PORTION OF VIIITH NERVE

The vestibular nerve is the proximal and ventral and mesial branch of the octavus. It carries fibres from the semicircular canals, the utricle and the anterior part of the saccule. It passes into the medulla below the ventral nucleus of the VIIIth to which it sends fibres. Some fibres also pass directly into the trapezoid body, but the main bulk of fibres pass between the corpus restiforme and spinal tract of the Vth to reach the nucleus triangularis. At the level of the corpus juxta-restiforme a number of fibres turn sharply downwards to form the descending root of the VIIIth and these are accompanied by the nucleus triangularis and can be traced as far down as the level of the nuclei gracilis and cuneatus. Another group of cells also accompanies this descending tract, the nucleus of the descending root.

An ascending root can also be traced to a group of oval or round cells in the lateral wall of the IVth ventricle, the nucleus of Bechterew.

The primary nuclei of the vestibular branch are the ventral nucleus of the VIIIth, the triangular nucleus and the nucleus of Bechterew. With regard to this last nucleus, while most authors regard it as one of the primary nuclei of reception of afferent fibres of the VIIIth, there is much evidence in favour of looking on it as a nucleus for efferent fibres of an autonomic nature. The importance of the autonomic control in a system whose receipts depend on variations in fluid pressure must be fully recognized. The mechanism for maintaining the balance of pressure between the endolymph and the perilymph must be of the most delicate description and the importance of this demands a well-developed autonomic centre. Winkler regards Bechterew's nucleus as the centre for autonomic control and its position in regard to the walls of the IVth ventricle and the shape of its cells are points in favour of its relationship to the intermedio-lateral tract in the cord. Paul van Gehuchten, on the other hand, follows most of the older authorities in regarding Bechterew's nucleus as a primary afferent nucleus of the vestibular system and places the autonomic control in a nucleus lying close to the raphe inside the fibres of the VIIth as they pass up to the genu.

CONSTITUTION OF VENTRO-LATERAL PORTION OF OCTAVO-MESENCEPHALIC TRACT (Diag. III)

We have seen that the ventral nucleus (cochlear nucleus of many authors) receives fibres from both roots of the nerve and also probably gives rise to efferent autonomic fibres. We have already traced the course of the fibres which pass from it into the striae acousticae. We must now trace the fibres which pass down and in from it to form the main part of the trapezoid body and the ventro-lateral portion of the octavo-mesencephalic tract. Into the trapezium there also enter direct fibres from both branches of the nerve. In describing the dorso-mesial portion of the lateral fillet, we found no intercalated nuclei between the primary nuclei and the posterior colliculus and the mesial geniculate. In this other portion of the octavo mesencephalic tract, however, we find several important intercalated nuclei and only a few of the fibres reach the posterior colliculus. The first nuclei met with are the nuclei of the corpus trapezoides, lateral and mesial. The direct radicular fibres end in the mesial nucleus. Those which have been relayed in the ventral nucleus end in the lateral nucleus. These nuclei seem to be only a relay on the way to the superior olive and they are connected up with trapezoidal fibres, both crossed and uncrossed. The main

Labyr and Neck Reflex Paths to Oculo Mot. Nuclei in Apes.

DIAGRAM I.

DIAGRAM II.

Reflex Paths from Mac. Sacc. and Mac. Utric.

DIAGRAM III.

Connections of Superior Olive.

DIAGRAM IV.

Macular Connections
with Nucl. Triang.

DIAGRAM V.

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Cerebellar Connections of VIII Nerve.

DIAGRAM VII.

bulk of the fibres cross at the decussation of Flechzig and form the ventro-lateral portion of the lateral fillet. On this there are two nuclei, the ventral and dorsal nuclei of the lateral fillet, in which many of the fibres of this part of the tract end. A few pass on to the posterior corpus quadrigeminum. The nerve fibres arising from the nuclei of the fillet pass inwards towards the raphe and help to build up the posterior longitudinal bundle, both crossed and uncrossed, and so form one of the links in the reflex chain between the labyrinth on the one hand, and the oculo-motor nuclei and the anterior horn cells of the spinal cord, on the other. Both nuclei also receive fibres from the posterior colliculus.

CONNECTIONS OF SUPERIOR OLIVE (Diag. IV)

Closely connected with the trapezium is the superior olive. Great variations are found in the development of this structure. In man, it is insignificant in its development, but in animals where the labyrinthine control of ocular movements is predominant, the superior olive is fully developed. Its importance as a co-ordinating centre in these animals is shown by the number of different parts from which it receives fibres:—

1. Secondary fibres from the ventral nucleus of the VIIIth, both crossed and uncrossed.
2. Secondary fibres from the mesial nucleus of the trapezoid.
3. Tecto-reticular fibres from the anterior corpus quadrigeminum linking up with the optic system, and from the posterior corpus quadrigeminum linking up with the acoustic system.
4. Kinaesthetic impulses from the spinal root of the Vth by a path which passes into the trapezoides.
5. An important bundle of fibres from the collateral lobe of the cerebellum.

Of the fibres passing out from it, some pass directly to the VIth nucleus of the corresponding side. Others pass in an ascending direction to the posterior longitudinal bundle of both sides, and so link the superior olives with all the oculo-motor nuclei of both sides.

The function of the superior olives would seem to be to collate auditory, gravistatic, gravikinetic, kinaesthetic and ocular impressions and utilize them in the control of eye movements. In cases of complete anophthalmos, no cells are found in the superior olives.

CONNECTIONS OF NUCLEUS TRIANGULARIS AND NUCLEUS OF DESCENDING ROOT (Diag. V)

The nucleus triangularis is the most important primary nucleus of the vestibular branch. It lies in the floor of the IVth ventricle, ventral to the nucleus of Bechterew and between it and the genu of

the VIIth. At this level it is at its broadest and it tails off distally, reaching to the level of the nuclei gracilis and cuneatus. At its distal end, it forks, and the mesial fork lying close to the nucleus of the XIIth is called the nucleus intercalatus. It is accompanied on its outer side by the nucleus of the descending root. It probably gives some direct fibres to the nucleus of the VIth lying closely mesial to it at its proximal end, and to the nucleus of the XIIth at its distal end, and also to nucleus prepositus, but, in the main, it is a relay station on the way to the secondary nuclei, the nucleus of the descending root, Deiter's nucleus and the nuclei in the base of the cerebellum.

The nucleus of the descending root also receives fibres from the cerebellar nuclei. These we shall leave till later, when we can deal with the cerebellar connections in general. The emissary fibres from the nucleus of the descending root, apart from a few which pass directly to the VIth nuclei of both sides, pass into the posterior longitudinal bundle, both crossed and uncrossed, and so link up with all the oculo-motor nuclei of both sides and with the motor cells of the anterior horn in the cord.

In all probability, this nucleus forms an important relay on the reflex path linking up labyrinthine receipts with movements of the eyes and of the limb muscles. (The posterior longitudinal bundle and the predorsal bundle of Held are mainly linked with ocular muscles and limb muscles. The Deitero-spinal tract, which we come to anon, links mainly with neck and trunk muscles.)

DEITER'S NUCLEUS AND THE VESTIBULO MESENCEPHALIC AND VESTIBULO SPINAL TRACTS, AND POSTERIOR LONGITUDINAL BUNDLE (Diag. VI)

Deiter's nucleus, from the large size of its cells, forms a fairly conspicuous land-mark in a complex bit of country. It lies in the mesial portion of the corpus juxta-restiformis down from the level of the VIth nucleus to which it sends direct fibres. Its main bulk of entering fibres comes from the nucleus triangularis, but it also receives fibres from the cerebellum. It gives rise to two important direct tracts, the direct Deitero-mesencephalic tract, or vestibulo-mesencephalic tract to the oculo-motor nuclei and the Deitero-spinal tract, or vestibulo-spinal tract, which forms a main link with the neck and trunk muscles. In addition to these two direct tracts, it is the main nucleus of origin of the ascending and descending fibres of the posterior longitudinal bundle, both crossed and uncrossed. In this way, it has a double link with the oculo-motor nuclei by the direct vestibulo-mesencephalic tract and by the posterior longitudinal bundle, and it links up by the Deitero-spinal

tract with the neck and trunk muscles and by the posterior longitudinal bundle with the limb muscles.

CEREBELLAR CONNECTIONS OF VIIITH NERVE (Diag. VII)

We have still left for consideration the cerebellar connections of these various nuclei, which we have only, so far, mentioned incidentally.

From the dorsal portion of the ventral nucleus of the VIIIth and from the nucleus triangularis, fibres pass to the tectal nuclei of the cerebellum. In the main, those from the ventral nucleus of the VIIIth seem to pass to the nucleus dentatus and those from the nucleus triangularis to the other three roof nuclei, emboliformis, globosus, and fastigiosus. From the nucleus dentatus fibres originate which pass into the anterior cerebellar peduncle, the brachium conjunctivum cerebelli, and cross at the decussation of Wernekink. Some of these end in the red nucleus and others pass to the optic thalamus. From the red nucleus, fibres arise which, crossing again at the decussation of Forel, pass into the lateral column of the cord as the rubro-spinal tract.

The close association in position of the red nucleus with the oculo-motor nuclei leads one to surmise that it may have some direct relationship with them. If so, it would be of great interest in correlating some forms of nystagmus with the forms of tremor which result from lesions of the red nucleus. But that is pure surmise, and I do not know of any cases of nystagmus in which the condition of the red nucleus has been examined, nor of any evidence of the surmised connection with the oculo-motor nuclei.

To return to the other cerebellar nuclei; the fibres arising from the nucleus emboliformis pass backwards to the medulla and passing as *fibrae perforantes* through the corpus juxta-restiforme, reach the superior olive. Of these, we have already spoken and of their importance in animals, where the labyrinthine control of eye movements is predominant. Some fibres also from the nucleus globosus join this same cerebello-olivary tract. The remaining fibres from the globosus and the fibres from the fastigiosus cross the mid-line, turn upwards for a short distance and then hook round the brachium conjunctivum cerebelli and pass backwards into the posterior peduncle of the cerebellum to reach the corpus juxta-restiforme. This tract is the tractus uncinatus of Risien Russell and it links up with the nucleus of Deiters and then forms a descending tract which links with the nucleus of the descending root. With the further connections of these two nuclei, we have already dealt.

I am not going to attempt, at the moment, to trace the cortical

connections, the thalamic connections, the cortico-pontine connections and the ponto-cerebellar connections.

The important point which, alone, can justify my dwelling so much on these complex and, in part, conjectural anatomical descriptions is to show in how many different ways the labyrinthine impulses can reach and affect the oculo-motor controls and how intimately they are linked up with other muscular controls of head, neck, trunk and limbs. It is unnecessary, for my immediate purpose, to discuss the further controls in which a gnostic or more fully epiritic element is involved.

A MORPHOLOGICAL STUDY OF THE LATERAL GENICULATE BODY

BY

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IF, in the brain of a simple type of mammal, the optic tract is followed on its course from the chiasma to the roof of the mid-brain, it will be found to extend up along the side of the thalamus and to come into relation here with an ill-defined eminence called the lateral geniculate body. This eminence is a local swelling on the dorso-lateral aspect of the thalamus and, in fresh specimens, is white in appearance by reason of its covering of optic tract fibres.

The lateral geniculate body in mammals is one of the main terminal centres of the optic tract and is to be regarded fundamentally as a group of cells differentiated from the main mass of the diencephalon in association with its retinal connections. In the lowliest vertebrates all the fibres of the main part of the optic tract are believed to terminate in the midbrain, but, even in these forms, collaterals of these mesencephalic fibres branch off to end in the optic thalamus. Thus it may be said that in all vertebrates the thalamus is concerned to a greater or lesser degree with the direct reception of visual impulses and, indeed, such a conclusion is to be anticipated from a consideration of the diencephalic origin of the retina and optic nerve and tract in the course of embryological development.

The basic structure of the lateral geniculate body in mammals may best be understood from a section taken through this structure along the line of the optic tract in the brain of a simple insectivore, and such a section is illustrated in Fig. 1, which is taken from the brain of *Macroscelides*, one of the small elephant shrews.