Physiology. — *An Anatomo-physiological study of the Supra-vestibular Tractus in Columba domestica.* By L. J. J. MUSKENS. (Communicated by Prof. J. W. VAN WIJHE).

(Communicated at the meeting of March 26, 1927).

§ 1. *The function of the tr. strio-mesencephalicus and of the nuc. spiriformis.*

In pursuing the line of research of LONGET, SCHIFF, and others we established in a previous publication [1]), that the commissura posterior in mammals (cat, dog, rabbit) marks the point, at which the physiological effect of the hemisection of the brain-stem is reversed. This may be observed best when, performing in a rabbit a series of hemisections of the brain-stem, starting in the vestibular region, and terminating in the thalamus; then it will be seen that e.g. after severance of the right side of the brain-stem the animal performs a circus-movement towards the left, while the rolling-movement (and also the so-called Magendie Hertwig strabismus, and the tendency to fall down) takes place towards the impaired side. With hemisection, oral to the posterior commissura, the circus-movement takes place towards the unimpaired side. By comparative experiments with subsequent osmic acid staining of the preparations it could be determined in quadrupeds, that only the middle-, and the lateral part of the posterior longitudinal bundle represents the anatomical substrate of these forced movements. However, with lesion oral to the commissura posterior these forced movements and positions occur only if the tertiary vestibular tracts, demonstrated by the present writer. (which connect the supravestibular-commissural nuclei with the globus pallidus and other palaeostriatal nuclei) have been injured. MARCHI's staining presents great difficulties for a precise decision as to which of the superposed nuclei from the region of the commissura-posterior, are the carriers of these functions. These nuclei had been examined purely anatomically by CAJAL, KÖLLIKER, KAPPERS, MESDAG, BECCARI, CASTALDI. In virtue of a number of lesions in the commissural-region in the cat, the present writer established with such a lesion the regular occurrence of bundles descending into the longitudinal bundles, viz. 1°. of the tr. commissuro-medullaris and 2°. of the tr. interstitio-spinalis.

A comparative study of the consequences of a number of lesions induced us to correlate the lesion of the first tract with the circus-movement (to

[1]) Verhandelingen der Koninkl. Akad. van Wetensch. 1902, Deel 8, N°. 5; BRAIN, 1914 and 1922.

the impaired side), that of the second with the rolling-movement (towards the unimpaired side).

These data, which were in part new, postulating *inter alia* a vestibular function of the globus pallidus, necessitated a more extensive study of the commissuro-pallidal tracts, as well in their anatomical as in their physiologico-anatomical aspects. As to the former RIESE issued from the Senckenberg Institute at Frankfort an inquiry into the relations in aquatic mammals. The connection of the globus pallidus with the nuclei in the region of the posterior commissure, which had been demonstrated by dint of painstaking physiological experiments in the rabbit, the dog and the cat, was found very distinctly in these animals in the bundle H. 2. As RIESE has it, RIESE's finding in the aquatic mammals supports "vom vergleichend-anatomischen Gesichtspunkt, die neueren Ergebnisse, zu den MUSKENS auf Grund experimenteller Untersuchungen gelangt ist" [1]).

On this ground pursuance of the same anatomo-physiological research into the bird's brain promised a priori to be successful, because in this group of animals with their double mode of locomotion the system of superposed vestibular nuclei in the neighbourhood of the commissura posterior must be extremely developed. I was all the more inclined to do this, because the very accurate investigations by WALLENBERG, and MESDAG's painstaking degeneration work, served as a guide for my experimentation.

While passing by in silence lesions in various parts of the corpus striatum, which did not reveal forced movements, I intend to report my findings with a pigeon that displayed until death circus-movements towards the impaired side. In this animal I had injured the occipito-parietal portion of the forebrain [2]) (Fig. 1 and 2 top on the right hand) the portion, that, according to FERRIER, BOYCE and WARRINGTON [3]) and KALISCHER [4]), MAC KENDRICK, JASTROWITZ, GALLERANI and LUSSANNA, elicits on an electric stimulus an eye-movement towards the opposite side. It was especially the tr. strio-mesencephalicus that was found thickly degenerated, (Fig. 1—4) [5]).

The degenerated bundle helps to constitute the ventral part of the brain-stem, bends in the oral part of the thalamus in dorso-lateral direction round the tractus thalamo-tectalis and the round nucleus. It is made up of rather thick fibres, and soonest develops medullary sheaths (SCHROEDER).

Already on this level degeneration is more extensive in the lateral (macrocellular) portion of the nuc. spiriformis, into which nucleus the

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1) Zeitschr. f. d. Ges. Neur. u. Psych. **90**, 1924, p. 597.

2) The small lesion at the bottom fig. 1 marks the most caudal point of the lesion.

3) Philos. Transactions Royal Society London B, 1899, Vol. **191**, p. 308.

4) Abhandl. der Akad. der Wissenschaften, Berlin 1905, p. 69.

5) This case instances a whole set of experiments. Similar results were achieved in other pigeons, in which a puncture in the forebrain had pierced only or principally the tr. strio-mesencephalicus.

degenerated bundle merges there where the round nucleus begins to disappear, at the oral side of the commissura posterior. In the same areal weak products of decomposition may be found distad, as far as the level

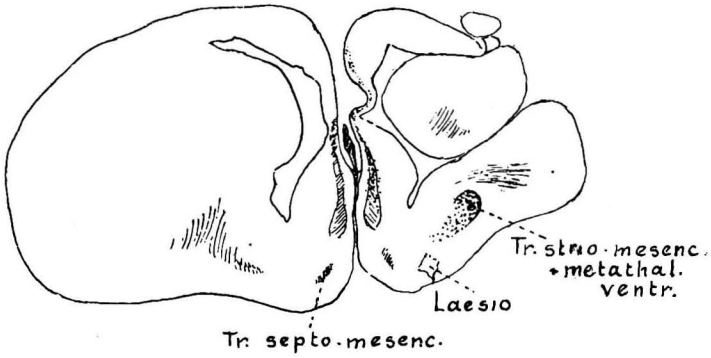

Fig. 1.

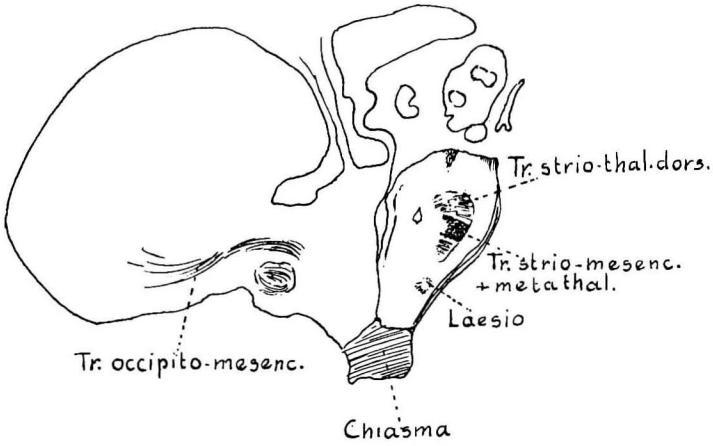

Fig. 2.

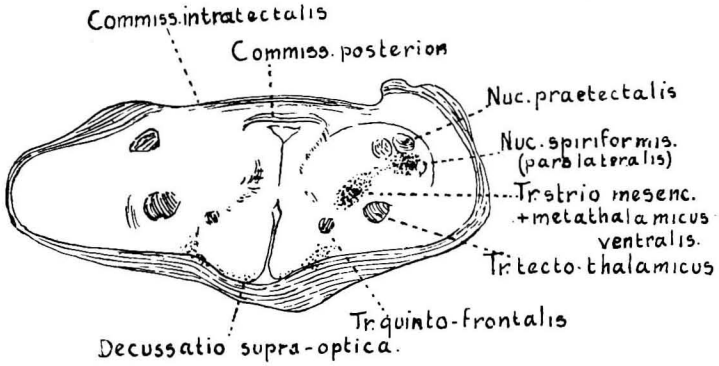

Fig. 3.

of the sensible Trigeminus nucleus, while some of them seem to disappear into the tectum. This descending degeneration (tr. strio-reticularis) was described also by WALLENBERG.

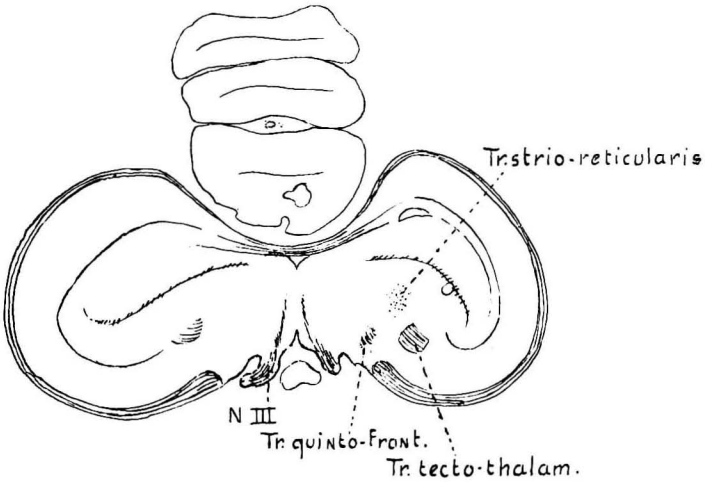

Fig. 4.

In a pigeon (273) the right nuc. spiriformis itself was punctured by a needle. For four days this animal showed a tendency to turn to the right. In the posterior longitudinal bundle no descending degeneration-fibres were encountered.

If this conjecture is correct (partial identity of the nuc. spiriformis of birds with the nuc. commissurae posterior of mammals), this case would warrant the conclusion, that the origin of the fibres in the longitudinal bundle, descending down to the nuc. abducens, is not to be found in the lateral portion of the nucleus.

Neither in my MARCHI-material, nor in the CAJAL-preparations, placed at my disposition by my colleague BOK, do I possess material to disprove WALLENBERG's hypothesis, that also from his nucl. dorso-ventralis (JELGERSMA's nucleus anterior) longitudinal bundle fibres take their origin. Nor is it altogether impossible, that contrary to the quadrupeds, birds with their double mode of locomotion, should have at their disposition two separate mechanisms for these functions.

It seems to me that these findings are to be interpreted in the way alluded to by WALLENBERG and MESDAG (if I am not mistaken), though they do not express that supposition, viz. that the nuc. spiriformis forms part of the system of commissural nuclei.

In birds these nuclei take up a much larger space than in quadrupeds, which tallies with the observation by EDINGER [1]), and WALLENBERG that the fibres of the posterior longitudinal bundle disappear into the nucleus spiriformis. It may be remembered here that already long ago KAPPERS

[1]) Anat. Anzeiger **33**, 1908, p. 329. EDINGER thought of a connection with the visual function, which may be deemed reasonable.

suspected, that in birds the eye-movements are regulated in the palaeostriatum (mesostriatum).

In conclusion I think that it may reasonably be assumed that the tractus mesostriato-spiriformis represents one of the two tertiary vestibular bundles, alluded to above, which have been recognized in quadrupeds, namely in their function, and in their descending and ascending fibres, not yet exactly in their initial-, and terminal nuclei in the globus pallidus and in the commissural region.

According to my personal observations made on the cat the fibres of the nuc. posterior thalami (where according to D'HOLLANDER in the rabbit most cortico-thalamic fibres terminate), are directly connected with the two sources of the tractus, which descend in the posterior longitudinal bundle, (viz. nucleus commissurae posterioris and nuc. interstitialis). If, thus, the nuc. spiriformis in birds should occupy partly the place of the nuc. commissurae posterioris of mammals, the question arises, whether in that case the nuc. posterior thalami of mammals may be a newly acquired property of mammals, as a motor nucleus inserted into the cortical tract, (especially subservient to the voluntary eye-movements).

Just as the pallido-commissural bundle in quadrupeds the tr. striomesencephalicus of birds degenerates as well in ascending (but in a smaller degree) as in descending direction, which fact had already been established by EDINGER in 1903 and by GROEBBELS. My preparations do not furnish evidence for a partial crossing of this tractus, neither for a connection with the tectum (GROEBBELS).

The wider extent of the area of the commissural vestibular nuclei seems to render it possible that further experiments with various birds may be of use exactly for this more extended analysis, for further localisation of the superposed vestibular nuclei and further homologizing of the mesostriatum and of the commissural region in birds and quadrupeds.

As for our knowledge of the functions of these nuclei, after the function of one of the most significant nuclei has been identified, a way is opened up along which step by step progress can be expected, also with respect to the "Stell reflexe" or righting-reflexes. For it has become evident that a lesion of the secondary, and also of the tertiary ascending vestibular tractus in mammals, as well as in birds entail symptoms, that are comparatively easy to recognize.

§ 2. *Significance of the tracts descending from the mid-brain into the posterior longitudinal bundle, and their relative position in the areal.*

Forced movement in the horizontal plane (circus-, and clock-hand movement with lateral conjugated deviation of the eyes) and forced movement in the plane normal to the long-axis of the animal (rolling movement and skew-deviation of Magendie-Hertwig, tendency to fall down and to lie on one side) are in all animals commonly found to appear

coincidently after lesion of secondary and tertiary vestibular tractus (just as with insects and octopods [1]) after otolith-excision and lesion of the supra-oesophageal ganglion).

This coincidence consists in the circus-movement towards the one side occurring simultaneously with the rolling movement to the other [2]; this is very evident in frogs and tadpoles, and also in fish. As to the latter this may be ascribed to a mechanic, internal connection, (centrifugal force in connection with the labile equilibrium of these animals), for also steamers, when taking a turn on their path to the one side, may be seen to heel over to the other.

The investigation of warm-blooded animals has taught us, that the ascending vestibular tracts, are so disposed within the posterior longitudinal bundle in the areal of this bundle that the fasciculus vestibulo-mesencephalicus homolateralis and cruciatus in the middle-third part, the fasc. vestibulo segmentalis med. and lat. in the lateral part runs upwards. The middle third part, and that the most medial zone of the areal, is occupied by the descending tr. commissuro-medullaris and the tr. interstitio-spinalis.

When comparing WALLENBERG's [3]) classic description of the composition of the posterior longitudinal bundle in pigeons with the later descriptions of that in the rabbit by VAN GEHUCHTEN [4]), and of the same in the cat by the present writer [5]), one is struck by the great similarity e.g. with respect to the increase and the decrease of the bundle in various regions, by the comparative strength of the crossed and the uncrossed bundles, by the ratio of the number of descending fibres from the acusticus-field, even by the shifting of the bundles in the medulla more ventrad, and by the relative position of the bundles (the longest excentric).

However, there is one considerable difference between quadrupeds and birds, in that in birds no trace has yet been found of the absolutely medial position, in quadrupeds, of the bundles descending from the mid-brain.

In connection with the termination of the tr. strio-mesencephalicus in and near the nuc, spiriformis, which on physiological grounds we consider to perform a similar function to that of the nuc. commissurae posterioris in quadrupeds, and in connection with the most lateral position of that nucleus in the formatio reticularis of the mid-brain in birds, an other light is thrown on this discordance. This is borne out by the fact that, whereas in quadrupeds the nuc. commissurae posterioris and the nucleus interstitialis (the two principal sources of the fibres descending into the longitudinal bundle), relative to the smaller extent of this region, are not lying far from the raphe, this is, at least partly, quite different in birds.

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1) Archiv. f. (Anat. u.) Physiol, 1904, p. 51,

2) Journal of Physiology, **31**, 1904, p. 205.

3) Anatomischer Anzeiger, **24**, 1903, p. 142.

4) Neuraxe, **4**, 1904, p. 63.

5) Cf. BRAIN, 1914, fig. 7 and 8, p. 370—373; Verslag der zittingen van de Koninkl. Akademie Amsterdam, 19 April 1913, p. 1474.

Here the nuclei in question are larger, and owing to the excentric position of some primary nuclei the fibres descending from them cannot possibly reach in the higher regions the most medial zone in the longitudinal bundle, and only on a lower level do they appear immediately beside the raphe. Figs. 5—9 have been derived from a pigeon, in which the rather considerably lateral incision severed the origin of a bundle, descending into the posterior longitudinal bundle, 10 days before death. They illustrate the anomalous dorsal position of these descending bundles in the pigeon.

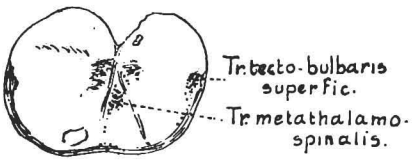

Fig. 5.

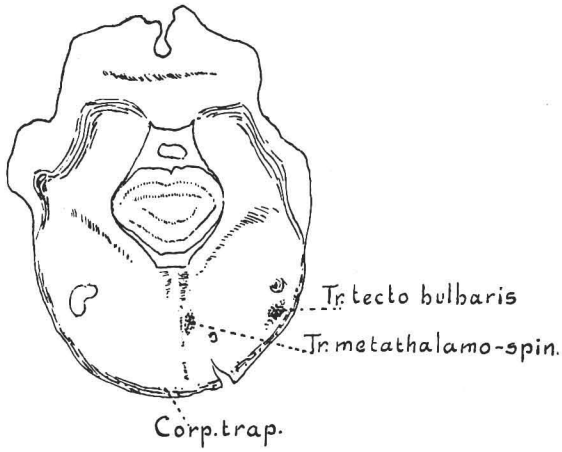

Fig. 6.

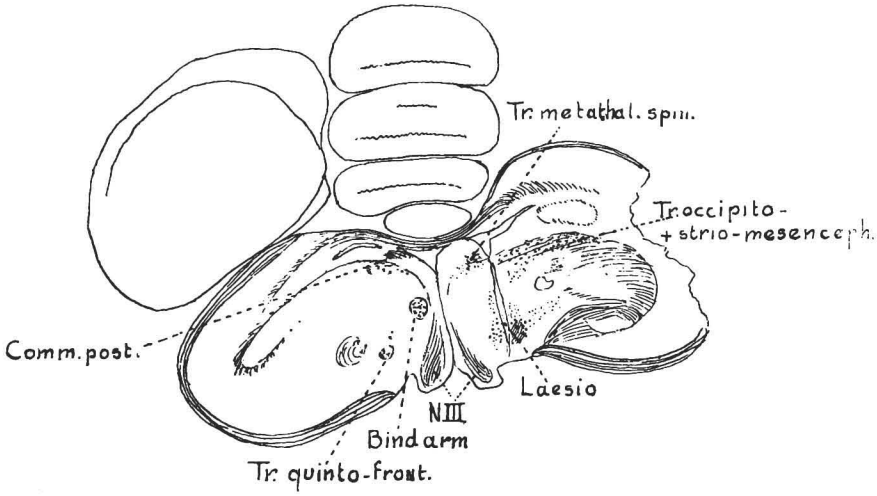

Fig. 7.

From this observation we infer an extremely lateral source of thick longitudinal-bundle fibres. They descend far into the spinal cord just as the tr. interstitio-spinalis, and emanate from a nucleus situated near the

nuc. spiriformis. This, however, cannot take away from the fact, that there exists near the median line a source of similar thick fibres, according to CAJAL.

This is substantiated by BOK's preparations of very young chick-embryos, in which I could verify this latter source of descending bundles-

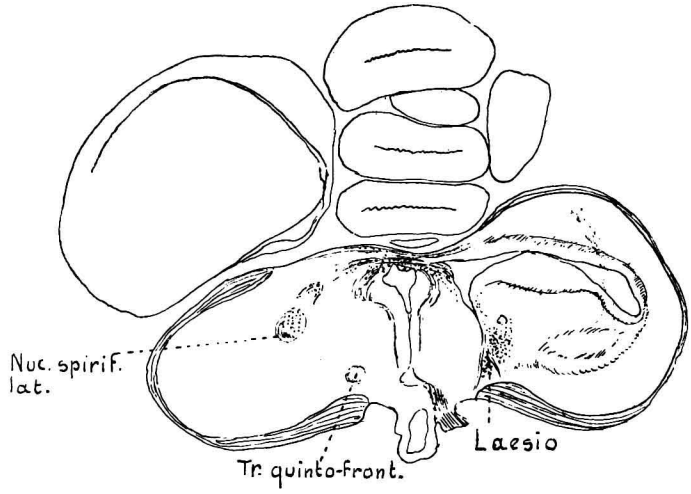

Fig. 8.

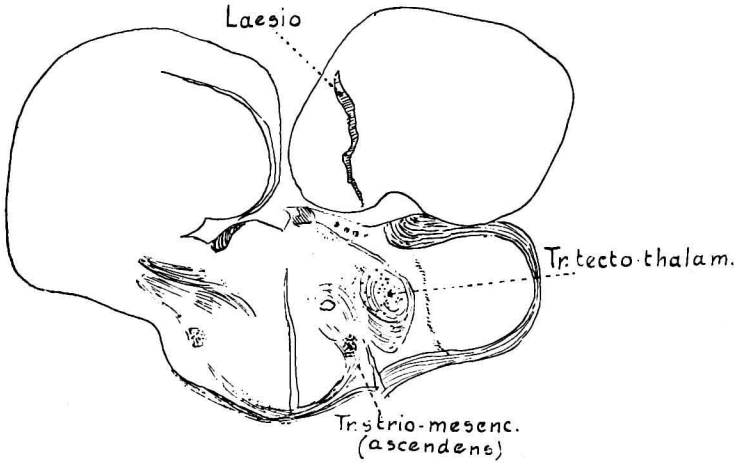

Fig. 9.

called also nuc. interstitialis in birds. This observation also unmistakably bespeaks in birds a double source of descending longitudinal bundle fibres, in connection also with their twofold mode of locomotion.

In connection with the greater extent of these commissural-nuclei in birds there is another physiological point of importance. Theoretically speaking, it should be possible also in warm-blooded animals to make

a lesion in the commissure-region in such a way, that the two forced movements, discussed above, should appear separately, or also in such a way that not the ordinary difference in direction should appear, so that circus-movement to the one side and rolling movement to the *same* side should coincide. Experience, however, teaches, that this does not practically occur in animals, very likely on the one hand because the discussed, ascending vestibular tractus in the longitudinal bundle are lying in the same areal, on the other hand, because the nuc. commissurae posterioris and the nuc. interstitialis are, like their descending bundles, disposed very medially at a short distance from each other. We are justified in assuming that an antero-posterior stab in birds can cut one of the commissural-nuclei, as well as (more caudad) one of the ascending bundles.

This is really the case in the above-named pigeon 22, which received a stab in the commissure from above on the right side. The animal succumbed after 10 days, after it had continually displayed a tendency to move *and* roll towards the left. The sections were stained with osmic-acid, and cut in orderly series.

In consequence of the operation under consideration we find, (figs 7, 6, 5) degenerated at the side operated upon, the bundle (whose course agrees with the tr. interstitio-spinalis (Boyce's bundle), to be much richer in fibres in the pigeon than in the cat. This degeneration proves that, in spite of the extremely lateral lesion, still a nucleus, partly homologous to nuc. interstitialis in the cat, has either been injured through the incision, or is situated more lateral than the lesion, anyhow is severed by the stab into the longitudinal bundle. Quite in keeping with the consequence of such an operation on the right side in cats, the animal invariably rolled towards the left after the dextrolateral operation.

Until the site of origin is exactly determined, this bundle in the pigeon we propose to designate by the name of tr. metathalamo-spinalis.

Whereas after a similar lesion in the cat and in the rabbit circus-movement towards the *impaired* side takes place, as a rule, concomitantly with the rolling towards the *unimpaired* side (and degeneration of the tr. commissuro-medullaris), with this pigeon the circus-movement (and the conjugate deviation of the eyes) had likewise been observed towards the *healthy* side, at the same time no proof was afforded of an injury done to the left tr. commissuro-medullaris. Still, here no doubt that part of the commissura posterior (middle layer) has been severed, in which according to the experiment, as well in birds as in mammals, those secondary ascending vestibular bundles are running of which a lesion always engenders circus-movement towards the uninjured side.

These degenerated commissural bundles can be traced out in the preparations towards the left up to the region of the nuc. spiriformis and the nuc. praetectalis.

From the region of the scar a bundle runs orally to the mesostriatum in the areal of tr. strio-mesencephalicus. In the light of what has been

said in the first paragraph, it is quite natural that we should suppose to have to do here with degeneration of the tr. strio-mesencephalicus, but now of the ascending fibres. These fibres are thinner, less numerous and slightly more ventral in the areal (MUNZER and WIENER) than the descending ones.

As to fish it should be borne in mind, that WALLENBERG [1]) recognized in Selachians termination of the tr. strio-mesencephalicus near the oral end of the fasc. longitudinalis posterior. In cyprinus auratus he traced out a descending bundle from the nuc. lentiformis thalami [2]) down to the caudal part of the medulla oblongata.

About the relations in man of the ascending and the descending vestibular bundles in the longitudinal bundle and in the commissure, little is known thus far. We do know that here also, in contradistinction to the quadruped vertebrates, the bundles descending from the commissural nuclei are not disposed medially. As the assumption is warrantable of the existence, also in man, of a wider development of the superposed, vestibular nuclei, and of the commissural region (erect posture, complicate relations of the eye-movements), it is also reasonable to suppose, that here also considerable extension is answerable for the anomalous position of the descending bundles in the longitudinal bundle.

§ 3. *Some of the principal connections of the nuc. spiriformis.*

In the pigeon we have identified the nuc. spiriformis as the nucleus, at least as one of the nuclei, that have been inserted into the centrifugal bundle originating in the forebrain and governing the unilateral movement (section of the bundle causes movement towards the side of the lesion). It will now be worth while ascertaining what the anatomical pioneers of the bird's brain have to say about the morphological features of the nucleus, round which our interest has centred in this experiment. Whereas WALLENBERG was struck only by the fact, that the nuc. spiriformis is a terminal stage of longitudinal bundle fibres as well as of a majority of the fibres of the tr. strio-mesencephalicus, it is interesting to observe that MESDAG was obviously struck by the large quantity (6) of the connections of this nucleus found by him, so that he devotes more space to the description of that nucleus than to any of the others, and gives us many particulars concerning them by photographs, and by pictures [3]). The sand-glass-shaped nucleus, then, "consists of medium-sized, triangular or multangular ganglion-cells with exceedingly ramified protoplasm-processess. The cells are packed closely. The axis-cylinders in the centre of the nucleus are not distinguishable from the protoplasm-processes. The nucleus stains very deep with the Cajal method, so that it is very

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1) Anatomischer Anzeiger, **31**, 1907, p. 395.

2) This term is applied to a meta-thalamic nucleus of fishes.

3) Loc. cit, p. 107.

conspicuous in all sorts of series (see photographs 5 and 6). The cells with the deepest stain lie on the anterior margin. The nucleus is joined by all sorts of fibre-tracts to various parts of the mid-brain".

And further on MESDAG says: "There is no doubt but that the Nuc. Spiriformis is extremely significant for the mid-brain. In the paragraph on the optic tract this point will be resumed".

I have devised a diagram exclusively of the tracts, that could be verified by MESDAG after CAJAL's method in chick-embryos, and by WALLENBERG after the MARCHI method in pigeons, and by myself after either method.

Undoubtedly the tracts for the vestibular- and the optic impressions are foremost among the reflex-forming connections which govern the direction of the eyes and of the movement to one side, i. e. the movement in the horizontal plane. As regards the former we see for instance rising out of the left vestibular nucleus into the longitudinal

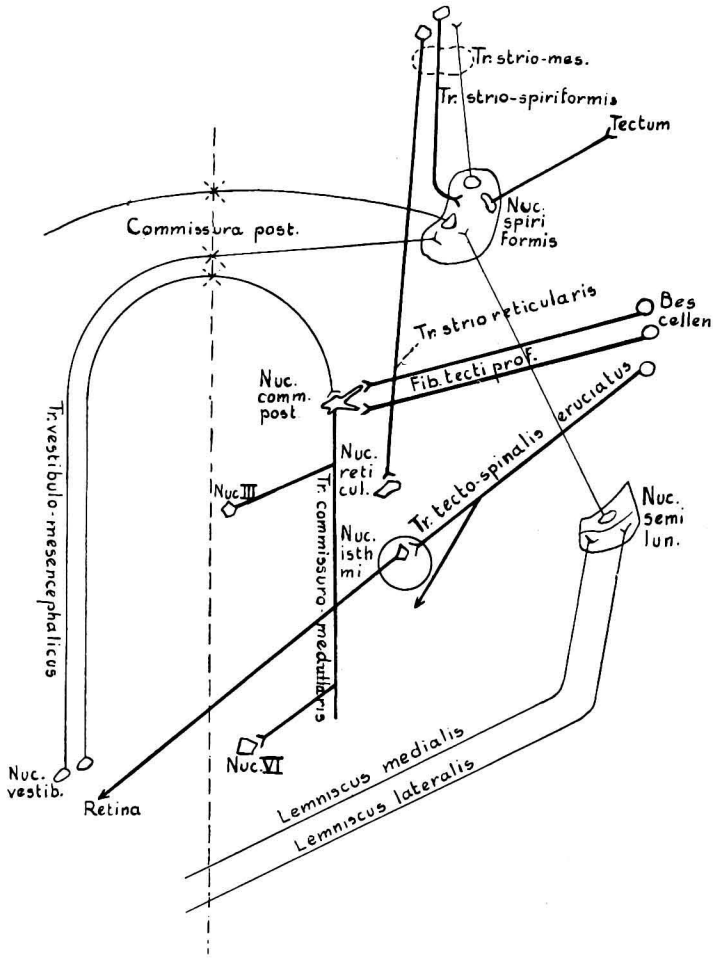

Fig 10.

bundle, a tract that (according to CAJAL-preparations of a six-day-old chick embryo) crosses in the commissura posterior, and terminates in the right nuc. spiriformis, and the right nuc. commissurae posterioris. Severance of that bundle (section of the left longitudinal bundle) will render the stimulation of the nuclei concerned insufficient, and will on that account induce circus-movement to the one side, which fits in with the physiological observation (section of the left longitudinal bundle yields circus to the right.

As for the optic stimuli, we know a tractus of the deep tectum fibres, whose axis-cylinders, according to MESDAG are disposed towards the protoplasm-processes of the ganglion-cells, that constitute the origin of descending fibres in the longitudinal bundle. Where we know, that *lesion* of that nucleus (homologon of the nuc. commissurae post. of mammals) causes the animal to move and look towards the operated side — so mutatis mutandis a *stimulation* of that nucleus: moving and looking towards the other side, thus towards the illuminated field of vision — so here also the anatomical connections tally with the physiological observation, for blinding of one eye yields for a short period a deviation towards the seeing side. We should not omit mentioning here the ganglion Isthmi-retina connection (reflex cone-movements of VAN GELDEREN STORT [1]) according to the amount of illumination. The ventral part of the ganglion isthmi is *pierced* by the tr. tectospinalis non cruciatus, whereas, according to WALLENBERG the Isthmoretinal bundle ends in the crossed retina. So, no contrast here either.

As to the acoustic tractus, CAJAL and MESDAG see the lemniscus medialis terminate at the caudal wall of the tectum opticum, imparting fibres to the nuc. semilunaris medialis. The lemnicus lateralis also enters the nuc. semulinaris medialis, so that given the known tractus of the lobus opticus with the commissural nuclei, the acustical stimuli and tactile stimuli to one side of the body will induce the head and the eyes to move by reflex towards the side of the stimulation.

Anyhow, so far as we know, there is for the moving of head and eyes in the horizontal plane — the only one considered here — no contradiction between the anatomical and physiological data that have thus far been published.

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[1]) Archiv. Néerlandaises T., **21**, 1883.