IX. Observations on the Anatomy, Physiology and Degenerations of the Nervous System of the Bird.*

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[Plates 25–31.]

INTRODUCTION.

This research was originally undertaken as a continuation of the studies on the pyramidal system made by one of us in Professor Horsley’s laboratory in 1894. This early led to the discovery of the fact, which was demonstrated at the time, that in birds the pyramidal system, as such, does not exist, and that after complete removal of one hemisphere the resulting degeneration in no case extends lower than the mesencephalon.

All workers, with the exception of Sandmeyer,† are now agreed upon this point.

In this communication we wish to give a general account of the nervous tracts in the bird, and to consider their functional significance.

Our observations have been made exclusively upon the fowl and pigeon, the anatomy of which does not differ, except in insignificant points.

Complete series of sections have been cut in the transverse, sagittal and horizontal planes and stained by Weigert’s method or the acid hæmatoxylin stain of Schäfer. The sections in the horizontal plane appear to us to be especially valuable in completing the information derived from those in transverse and sagittal section.

Various parts of the central nervous system have been injured, and the resulting degenerations in the nervous system followed by means of the Marchi method of staining. The bird is a favourable subject for such operative interference; a very

* Part of the expenses of this research were defrayed by the Scientific Grants Committee of the British Medical Association.
† Sandmeyer, ‘Zeits. f. Biologie,’ vol. 10.

17,10,99
slight amount of anaesthetic is sufficient, and recovery is almost invariable. Strict antiseptic precautions are not necessary, the chief obstacle to a successful operation is the large amount of haemorrhage which takes place should a sinus be injured. If such an accident occurs the use of a soft wax is generally sufficient to arrest the haemorrhage.

PREVIOUS LITERATURE.

The literature directly referring to the subject is comparatively scanty. The first account of the microscopic structure of the brain of the bird was given by Stieda,* in 1869, whose paper on the subject contains some excellent figures which, though unstained, plainly indicate the position of the great tracts running from the cerebral hemispheres to the thalamus and mesencephalon. Stieda also describes and figures the large cells in the roof of the aqueduct, which are now believed to be the mesencephalic nucleus of the trigeminus.

In 1883 Bumm† published his paper on “Das Grosshirn der Vogel.” The first part of this communication is devoted to a consideration of the general morphology of the Avian brain. The second portion describes some features of the microscopical anatomy. His descriptions are strictly limited to the cerebral hemispheres.

Using the older methods of staining, he described in detail the course and origin of that large bundle of white fibres seen on the mesial surface of the hemispheres, which he named “Markbündel der strahligen Scheidewand.”

All writers agree in the main with his description of this tract. He also pointed out the existence of the large tracts passing from the cerebral hemispheres to the thalamus and mesencephalon, and of the great associational system of fibres on the base of the brain, now called the tractus occipito-frontalis, and named by him the “Basal-Markbündel.” Bumm’s valuable contribution outlined the main facts of the anatomy of the cerebral hemispheres.

In 1891 a series of papers by C. H. Turner‡ appeared on the morphology and histology of the Avian brain. That part of it which deals with the subject which we have especially studied, viz., the course of the various tracts, is less complete than the remainder of the paper which describes the cell-groups. Unfortunately, the methods and staining employed by the writer do not give results which can be compared with those obtained by means of the Weigert method.

Edinger§ has included the structure of the bird’s brain in his researches on Comparative Neurology, and has employed the methods now universally used in tracing the course of nerve tracts, viz., those of Weigert and Marchi. His researches on the allied brain of the reptile have also been particularly valuable to

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‡ ‘Journal of Comparative Neurology.’
us, and we have adopted, where comparable, the nomenclature used by him in describing the nervous tracts in this class of animals.

**Bellonci** and **Perlía** have contributed to our knowledge of the optic tracts, and quite recently, while this paper was in progress, communications have appeared by **Friedländer**, **Wallenberg**, and **Münzer and Wiener**.

**Münzer** and **Wiener**'s work is a complete and important contribution to the study of the tracts of the central nervous system and the degenerations they undergo. In most essential points the independent conclusions arrived at by these writers and ourselves are in agreement.

In this place it is unnecessary to mention the older observations, to which a complete reference is given by **Friedländer**, or the researches on the fine cellular anatomy of **Ramon y Cajal**, **van Gehuchten**, and **Köllikér**.

**NAKED EYE LANDMARKS OF THE BIRD'S BRAIN.**

The paramount importance of the visual apparatus in the bird is indicated by the size of the optic nerves and chiasma; the transverse section of an optic nerve being as large as that of the dorsal region of the spinal cord. On the other hand, the olfactory lobes are very small.

The cerebral hemispheres are well developed, and for purposes of description may be roughly divided into anterior, middle, and posterior lobes (Plate 25, fig. 7). As we shall see, these lobes give origin respectively to different groups of nerve fibres.

Fissures on the surface of the brain are not well marked. We draw attention, however, to one which runs from before back on the dorsal surface about 1/16th inch on each side of the median plane, and forms the external boundary of an area which is excitable by the faradie current, the stimulation resulting in well-marked pupillary contractions (Plate 31, fig. 51).

The main tracts of nerve fibres are fairly obvious as prominent white strands of tissue. On carefully separating the hemisphere there is seen—

(1) On the mesial aspect, the fan-shaped tractus septomesencephalicus, disappearing just in front of the transversely running anterior comissure (fig. 15, Plate 27).

(2) Beneath this comissure, the united fibres of the tractus striothalamicus and striomesencephalicus (fig. 40, Plate 30).

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† Perlía, 'Graefe's Arch. für Ophthalm.,' Bd. 35, 1889.
‡ Friedländer, 'Neurolog. Centralblatt,' April, 1898.
§ Wallenberg, 'Neurolog. Centralblatt,' June, 1898.
|| Münzer and Wiener, 'Monats. f. Psych. und Neurol.,' Bd. 3 and 4, 1898.
¶ Since this paper was read Edinger and Wallenberg have published in the 'Anatomischer Anzeiger,' Band 15, 1899, a communication, entitled "Untersuchungen über das Gehirn der Tauben." In this the various tracts and cell nuclei are described in detail and the previous work of the authors incorporated.
When the brain is placed with the ventral surface uppermost there appear:—

1. The superficial termination of the tractus septomesencephalicus, a well-formed strand of fibres situated along the junction of the cerebral hemispheres with the optic lobes and thalamus (fig. 52, Plate 31).

2. Laterally, on the hemisphere, the great associational system between the posterior and anterior parts of the brain (fig. 52, Plate 31).

3. The prominent white fibres covering the surface of the optic lobes.

On transverse section of the hemispheres the origin of the striothalamic tract and anterior commissure is well seen (fig. 40, Plate 30).

DESCRIPTION OF TRACTS.

The various tracts of the central nervous system fall into the following groups:—

1. Tracts in connection with the great cell mass of the hemisphere.
2. Optic chiasma and tracts in connection with it.
3. Posterior commissure and lamina commissuralis mesencephali.
4. Transverse fibres of the optic vesicle.
5. Mesencephalic system of fibres.
6. Tracts of the spinal cord.

I. THE TRACTS IN CONNECTION WITH THE GREAT CELL MASS OF THE HEMISPHERE INCLUDE:—

(a) Tractus septomesencephalicus or pallial system.
(b) The striate tracts (tr. strio-mesencephalicus and tr. strio-thalamicus).
(c) Tractus occipito mesencephalicus.
(d) Tractus occipito frontalis.
(e) Commissura anterior.

(a) Tractus Septomesencephalicus or Pallial System.*

The great mass of the cerebral hemisphere is formed by the corpus striatum, a ganglionic mass of densely-packed cells of ovoid shape. The cells are grouped in clusters, and, as shown by the Nissl method, each cell contains a very large nucleus (fig. 54, Plate 31).

The pallium which lies over the corpus striatum consists of a thin plate of nervous matter forming the mesial and dorsal wall of the ventricle; laterally it gradually loses itself in the substance of the corpus striatum. It contains the fibres of an important tract described by Bümm under the name of Markbündel der strahligen Scheidewand or Tractus Septomesencephalicus (Edinger). This fan-shaped tract is superficial, and covers a large part of the posterior and mesial aspect of the surface of the brain (Plate 25, figs. 1, 2, 3, &c.).

* This tract is lettered Α in the figures, and appears in a very large number of the sections.
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The main mass of the tract converges in front of the anterior commissure (fig. 15, Plate 27), then turns sharply outwards to become superficial, and bends round the tractus striothalamicus (figs. 9, 10, 11, Plate 26). It remains superficially situated in the dorsal and lateral aspect of the thalamencephalon. Transverse sections show that it can be traced down as far as the junction of the thalamus with the optic lobes (fig. 27, Plate 28; figs. 35–37, Plate 29). Bumm,* in his original description, states that the tract ends in the region between the lateral part of the cortex of the corpus bigeminiun and the corpusopticum. Edinger† states that it disappears in the most frontal section of the roof of the middle brain. We have not succeeded in tracing the tract quite so far as these authors, and incline more to the view of Munzer and Wiener, who were unable to follow it further than the epithalamic region. Horizontal sections show that, although the great mass of fibres composing the tract are contained in the pallium, there is a special group which is in connection with the anterior part of the cell mass of the hemisphere (figs. 3 and 4, Plate 25).

Whilst the major part of the tract converges to pass in front of the anterior commissure, a definite and smaller portion passes posteriorly to this commissure (figs. 13 and 16), and enters the thalamic region.

The homologies of the tracts in the mesial wall of the hemisphere are of great interest. Phylogenetically they are the most ancient. As Elliot Smith‡ says: "The cerebral cortex of the reptile becomes relegated in the mammal to the region immediately surrounding the hilum of the hemisphere, and constitutes the true 'limbic' lobe. Similarly, in birds, the greater part of the mesial wall represents the precommissural body—a small part dorsal to this the hippocampus."

The greater part of the pallial tract described above as passing toward the base of the brain in front of the anterior commissure, is represented in the precommissural fibres of the mammal and in that part of the fornix which lies in the septum lucidum (figs. 15 and 16, Plate 27). The smaller part, which passes posteriorly to the anterior commissure, and which is more strongly developed in reptiles, forms, as shown in Edinger's figure of the Eidechse,§ a tr. cortico-habendularis, and corresponds to the anterior pillar of the fornix.

In transverse sections, two fine bands of fibres are seen, dorsal to the anterior commissure (fig. 23, Plate 28). In reptiles they are much more strongly marked, and are figured by Edinger (p. 149), and described as commissura anterior and posterior pallii—a psalterium system. We have not been able to ascertain the exact origin of these two fine strands. They have been described by other writers, e.g. Meckel and Turner,|| under the name of the corpus callosum, but if by that we understand

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* Loc. cit.
† Loc. cit.
‡ 'Journ. of Anat. and Physiology,' vol. 30, p. 484.
|| Loc. cit.
a dorsal commissure of the pallium—the corpus callosum of man—the term is inaccurate; such a commissure is limited to the eutheria, and develops pari passu with the great cortical formation of higher mammals. They can be better described as commissural fibres of the precommissural area and hippocampus. In the sagittal sections (figs. 15 and 17, Plate 27), pallial fibres are seen to pass ventrally between the anterior and posterior divisions of the tr. septomesencephalicus, and in transverse sections (fig. 27, Plate 28), they appear to enter the optic chiasma. The large system of fibres just described above is probably both an associational and projectional system. It connects corresponding parts of the fore brain with the thalamencephalon and mesencephalon, and perhaps, as indicated above, directly with the optic tract. After removal of the hemisphere, the Marchi method of preparation shows that a limited degeneration takes place.

We do not think that this can be doubted, though Münzer and Wiener expressly state the contrary.

(b) The Striate Tracts.

Series of horizontal sections through the brain show that the great cerebral tracts are connected respectively with cells situated (a) in the anterior lobe, (b) in the middle lobe, (c) in the posterior lobe. The striomesencephalic and thalamic tracts and the occipito-mesencephalic tract are descending tracts with well-marked fibres, and after section in the hemispheres, degenerated fibres can be readily stained by the Marchi method. They connect the cell masses in the cerebral hemispheres with the thalamencephalon and mesencephalon.

i. Tractus Strio-mesencephalicus.—The anterior lobe of the brain as seen in horizontal section gives rise to three groups of fibres: (1) most superficially and internally to fibres which go to form the pallium, fig. 4; (2) externally to the fibres of the occipito-frontal tract, figs. 5 and 6; and (3) to fibres between the last two which plunge deeply to the base of the brain, figs. 5-10. The latter fibres appear to have an extended origin from the anterior portion of the brain; they collect together as they pass downwards and backwards and join the other bundles formed by the strio-thalamic and occipito-mesencephalic fibres. It appears to be the most ventrally placed of the bundles, and with the strio-thalamic tract passes beneath the anterior commissure, fig. 40, Plate 30, into the thalamus and proceeds as far as the mesencephalon. It is the longest of the three cerebral descending tracts.

By the degeneration method, after removal of the anterior portion or of the whole of the hemisphere, it can be readily demonstrated as it passes through the thalamus to the mesencephalon. It terminates in cells in the substance of the optic lobes at a level a little above and more lateral than those of the oculomotor nucleus (figs. 29 and 32 to 39, Plate 29). Closely associated with the tract, on its ventral aspect in the mesencephalon and thalamus, is a well-marked group of fibres, which are found to undergo ascending degeneration; this tract will be described later on as the tractus mesencephalicus striatus (see figs. 39-42, Plates 29 and 30).
ii. Tractus Strio-thalamicus.—This tract was first seen by Bumm and afterwards described by Edinger. It arises chiefly from the middle mass of the hemisphere, and is well seen in figs. 6 and 7. It joins with the preceding tract, but remaining more dorsal, passes beneath the anterior commissure (fig. 40, Plate 30), and terminates in the nuclei of the thalamus (figs. 35 and 36, Plate 29). It degenerates after removal of a hemisphere, and the course of its fibres can be well traced by using the Marchi method (figs. 32–38, Plate 29).

(c) Tractus Occipito-mesencephalicus.

This tract, represented in the reptiles, is especially large in birds, and can be traced from the posterior segment of the hemisphere (figs. 5–8, Plates 25 and 26), where it has a wide origin in close connection with that of the anterior commissure and occipito-frontal bundle. The tract passes inwards and backwards on a level with the anterior commissure, and sweeps into the thalamus where some of its fibres cease.

Others may proceed as shown in figs. 17 and 19 E., Plate 27, into the mesencephalon. According to Edinger it ends in the roof of the middle brain, close to the termination of the optic nerve. It degenerates completely after removal of a hemisphere, and can be traced in transverse sections (figs. 33–35, Plate 29).

(d) Tractus Occipito-Frontalis (Bumm and Edinger).

A large superficial associational tract, extending from the posterior to the anterior part of the brain, which is beautifully shown in horizontal section (figs. 5, 6, 7, Plate 25). As described above, it has an origin in the posterior lobe, closely associated with that of the anterior commissure and occipito-mesencephalic tract. The posterior lobe, which is exceedingly well developed in the pigeon, has thus an extensive connection with the frontal lobe, with the occipital lobe of the opposite side, and with the optic thalamus.

(e) Commissura Anterior.

A large well-formed tract connecting the posterior lobes of opposite sides (figs. 8, 9, Plate 26; figs. 15, 16, 17, Plate 27; fig. 40, Plate 30). It is comparatively simple as compared with the reptiles, but is very large, and no trace of a pars olfactoria can be seen. Through its common origin with the tr. occipito-frontalis it is in connection with the anterior lobe of the brain; the two combined systems thus encircling the hemisphere. Some of its fibres are seen in the Marchi preparations to degenerate after removal of the hemisphere.

II. The Optic Chiasma and Tracts in Connection with It.

Optic Chiasma.

The very extensive origin of the optic tract is best demonstrated in horizontal sections (figs. 13 and 14, Plate 26). It is seen as a large band of fibres sweeping round
the external geniculate body to spread over the cortex of the optic vesicle. In fig. 13, Plate 26, a large number of fibres are seen to pass from the optic chiasma immediately internal to the geniculate body and to terminate in the roof of the ventricle of the optic lobe. In fig. 14, Plate 26, the external geniculate bodies are seen to be embedded in the fibres of the optic chiasma, the great mass of which lie on their outer side, and the smaller mass described above on the inner side. The anatomical arrangement shows the close relationship of the geniculate bodies and the optic tract. The central ending of the optic nerve in the bird has been described and beautifully illustrated by Belloni,* with whose account of the optic chiasma this description practically agrees. This author also alludes to certain fibres in connection with the two bundles into which, as mentioned above, the optic chiasma divides; these are:

(a) Inferior optic fibres, which pass from the chiasma to end in the grey matter of the third ventricle.

(β) Superior and anterior fibres, which pass through the geniculate body and unite with the external bundle of the optic tract.

(γ) Superior and superficial fibres lying directly above the corpus geniculatum passing through the grey substance of the thalamus and uniting with the external bundle of the optic tract.

All these fibres are shown in our figures.

In close association with the optic chiasma there are the following tracts:

1. Gudden's commissure.
2. Commissura post chiasmatica.
3. Commissura supra infundibularis.
4. Epithalamic connection.
5. Pallial connection.
7. Connection with the hemispheres and thalamus.

1. Gudden's Commissure or Commissura Inferior (Belloni).—This commissure is seen in the horizontal sections (figs. 13 and 14, Plate 26), and in sagittal sections (figs. 16 and 17, Plate 27). In the former plane it appears as a distinct band of fibres immediately behind the optic chiasma, internal to the deep branch of that tract. In fig. 15, Plate 27, it is cut in tranverse section and appears to give fibres to the optic chiasma.

Fig. 13 shows that it has an origin in the grey matter of the interior of the optic vesicle, and in sagittal sections (figs. 16 and 17, Plate 27) fibres are seen coming down from the nuclei of the thalamus.

In fig. 15, Plate 27, where it is cut in transverse section, it appears to give fibres to the optic chiasma.

2. Commissura Post-chiasmatica (described by Edinger in the Reptiles.)—This

* Belloni, loc. cit.
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commissure is well seen in fig. 14, Plate 26, and consists of a well-marked band of fibres which sweeps round the ventricle anteriorly, closely applied to the optic chiasma, and to which it appears to give fibres (fig. 15, C.p.c.). It is immediately posterior to Gudden's commissure. Its fibres pass backwards on each side (fig. 14, Plate 26) in a horizontal plane to the ganglion ectomammillare, or nucleus peduncularis (Bellonci). It will be observed that this tract in horizontal sections makes a considerable angle with Gudden's tract, the latter is much more external than the former. Bellonci figures a tract having a very similar position to this and describes it under the name of the Decussatio Inferior. As this writer suggests, it is probably the representative of the Fibre Ansulate of other types, a decussating system existing in the Reptiles and Amphibians, and regarded by Bellonci as corresponding to Meynert's commissure in Mammals.

Their termination in the ganglion ectomammillare is well seen in our figures; whether they pass after decussating to the upper part of the thalamus, as stated by Bellonci, is uncertain.

3. Commissura Supra Infundibularis.—This commissure is also well seen in fig. 14, Plate 26, having an opposite position to the previous commissure and decussating behind the third ventricle. Its fibres appear to arise in the lateral walls of this ventricle.

4. Epithalamic Connection.—In sagittal sections (figs. 17 and 18, Plate 27) a scattered band of fibres are seen to come down from the roof of the thalamus, perhaps from the ganglion habendulae, and to pass forward, behind the anterior commissure, to a position in front of the optic chiasma, to which place also fibres from the pallial tracts converge, as described in the next paragraph.

5. Pallial Connection.—The middle group of pallial fibres, which pass backwards in front of the anterior commissure to a spot immediately in front of the chiasma, have already been described, and are seen in figs. 16 and 17, Plate 27.

6. Connection with the Ganglion Isthmi.—This tract, which will be described later on, is a well-marked tract which, after lesion of the medulla in the region of the ganglion isthmi, undergoes degeneration and can be traced into the optic tract (figs. 40-45, Plate 30).

7. Connection with the Hemispheres and Thalamus.—Bellonci describes bands of fibres passing from the region of the ganglion ectomammillare and the interior of the optic lobes to end respectively in the fore brain and in the thalamus. Our sections do not afford sufficient evidence as to the exact origin and termination of certain fibres which appear to correspond to those indicated by this observer.

III. POSTERIOR COMMISURE AND LAMINA COMMISURALIS MENSEcephali.

(a) Posterior Commissure.—This is seen as a large bundle cut transversely in sagittal sections (figs. 15 and 18, Plate 27). In fig. 17 the fibres are seen curving backwards to join the posterior longitudinal bundle. In horizontal sections (fig. 7, Plate 25) it is seen in the roof of the mesencephalon, and in transverse sections
(fig. 28, Plate 28) the deeper portion can be seen curving inwards around the aqueduct to the region of the descending fibres of the posterior longitudinal bundle.

(b) Lamina commissuralis mesencephali.—A wide commissure limited in front by the posterior commissure and behind by the decussation of the fourth nerves.

It is seen in sagittal sections (figs. 15–18, Plate 27) cut transversely, and its great width is obvious in horizontal sections (fig. 7, Plate 25). It is a lamina of white fibres extending between the two optic lobes, the fibres reaching far into the roof of the ventricle of the vesicle (fig. 28, Plate 28). In this commissure lie the large ganglion cells of the roof of the aqueduct, which were originally described by Stieda.* Stained by Held's modification of the Nissl method, we have found that they are grouped as parallel rows of large oval cells as large as those forming the nucleus of the IIIrd nerve. Their nucleus is large, and their protoplasm contains numerous Nissl bodies (fig. 55, Plate 31); it is believed that they give origin to the radix mesencephali of the trigeminus. Brandis† describes in considerable detail certain fibres in the region of the medulla oblongata turning round so as to surround the Vth nucleus, and giving off branches which pass into that nucleus, and states that this tract can be traced upward into the region of the roof of the middle brain, and in some of our Marchi preparations, after lesion of the optic lobe, certain degenerated fibres can be seen passing from the region of these cells downwards into the medulla.

IV. Transverse Fibres of the Optic Vesicle.

(a) The commissure of the optic vesicle described as above.

(b) Deeper transverse fibres from the interior of the optic vesicle which arise much anterior to the previous group, and pass across to the wall of the aqueduct (figs. 9 and 10, Plate 26).

(c) Tractus tecto-spinalis.—Fibres arising in a similar position to the preceding, and passing more obliquely than the transverse fibres; they form part of the descending mesencephalic fibres, extending downwards to the cord (fig. 11, Plate 26).

(d) The diagonal tract.—A well-marked bundle more ventrally situate to any of the preceding, and passing in a diagonal region to the region of the oculomotor nucleus (figs. 12 and 13, Plate 26).

We have not found any description of fibres corresponding to these, which may represent tracts connecting the sensory with the motor side of the visual apparatus.

V. Mesencephalic System of Fibres.

A system of efferent fibres from the mesencephalon to the cord was described in the cat by one of us‡ and by Held.§ In the cat it was shown that Forel's decus-

* Stieda, loc. cit.
† Brandis, 'Arch. für Mikr. Anat.,' 30, 43, 1894.
‡ Boyce, 'Phil. Trans.,' B, 1835.
§ Held, 'Arch. f. Anat. und Phys.,' 1892.
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sating fibres formed the efferent lateral columnar fibres, whilst anterior columnar fibres degenerated in the posterior longitudinal bundle. A similar system was shown by us to exist in the bird at the Neurological Society's meeting (June, 1897), and this is also described in their recent paper by Münzer and Wiener.

These observers distinguish after lesion of the optic vesicle as degenerating tracts, the

(a) Tractus tecto-bulbaris profundus cruciatus.—Forel's fountain decussation, which, crossing over the median line to a position ventral to the posterior longitudinal bundle, can be traced caudalwards into the medulla oblongata.

(β) Tractus tecto-bulbaris superficialis non-cruciatus, which passes ventrally, remaining superficial, and loses itself in a ganglionic mass, which corresponds to the trapezius nucleus of rabbits.

They also succeeded in obtaining degeneration of the descending Vth root.

(γ) Tractus tecto-cerebellaris, which passes from the ventral and posterior part of the optic lobe and ends in the cerebellum, partly in the nucleus of the "Kleinhirnkörper," partly in the ventral lobules of the middle of the cerebellum.

Our own observations agree in the main with those of these writers, and the investigation of the origin and destination of these tracts shows the marked resemblance which exists between this system in birds and Mammals. After injuries to the mesencephalon we find that there arise a system of arciform fibres which sweep across the formatio reticularis, and for the most part decussate in the middle line. The commencement of this system is shown in fig. 28, Plate 28, where fibres can be seen streaming in from the mesencephalon to cross the raphe. This origin corresponds to that of the "fountain decussation" of Forel. In the series of transverse sections (figs. 41–44, Plate 30) extending from the upper level of the origin of the IIIrd nerve to the origin of the IVth nerve, the degeneration which these fibres undergo after lesion of the mesencephalon is well shown. They occupy especially two regions of the formatio reticularis, (1) a deeper dorsal position, (2) a more superficial ventral position, and correspond respectively with the antero-lateral and lateral columnar fibres described by one of us, i.e. with the fountain decussation of Meynert and Forel. After their decussation they form a descending system of fibres, and are seen in all sections below this level, extending as far as the cervical region of the cord (figs. 47–50, Plate 30). In those cases in which the lesion was made at a lower level of the mesencephalon, and involved also the lateral region of the medulla, a third system of decussating fibres appears, which is situated dorsally, and apparently supplies fibres to the posterior longitudinal bundles (fig. 46, Plate 30).

The degeneration of these fibres is very well marked (fig. 47, Plate 30), and they probably in part go to form the ventral fibres of the cord (fig. 50, Plate 30), being supplemented by those derived from the higher origin.
Russele, in the case of the dog and monkey, after severing Deiters nucleus from its connection with the medulla, has found a degenerated band of fibres almost in an identical position to that now described by us. Many of the fibres enter the posterior longitudinal bundles of both sides, where they pursue an ascending and descending course. The descending fibres can be traced into the cord as far as the thoracic region. The tracts thus described in the bird and mammal therefore resemble each other in their course and destination.

Russele has also described efferent lateral tracts resulting from a lesion of the medulla. We agree with this author in maintaining that they belong to the same system as the efferent mesencephalic fibres. That Russele's tract is an uncrossed one is easily explained by the view that the decussation has occurred higher up.

Throughout the medulla and pons uncrossed internuncial fibres exist, entering the formatio reticularis and receiving additions from various levels. In some of our experiments the cerebellum and restiform body were involved, and sections (figs. 46, 47, Plate 30) show that there results a well-marked degeneration in fibres which occupy the periphery and ventral aspect of the medulla—many of them cross to the opposite side, others end in the formatio reticularis or olive of the same side.

The position assumed by these fibres is identical with that described by Russele as resulting from ablation of the middle lobe of the cerebellum and after section of the restiform body. Friedländer states that in the bird, after lesions of the cerebellum, a degenerated tract of fibres can be traced into the spinal cord as far as the lumbar region. Our observations are opposed to this view; lesions limited to the cerebellum do not in our experience give rise to degenerations descending into the spinal cord.

VI. Ascending Tracts after Lesion of the Mesencephalon.

1. Median Optic Bundle (Perlia).

In 1889, Perlia † enucleated the eyeball of a chicken. In addition to the resulting atrophy of the opposite tract, he described as the median optic bundle an atrophied strand of fibres, which lie just median to the optic tract, and which, traced upwards, are found to terminate in the ganglion isthmi in the roof of the middle brain. This ganglion he consequently regarded as a reflex centre between the retina and the sphincter iridis. In lesions of the corpus nigrominum we have found a bundle of fibres occupying identically the same position as described by Perlia. This degenerated bundle makes its appearance at the level where the IVth nerve becomes superficial, at the angle formed by the pons, cerebellum, and optic vesicle.

It is situated just internal to the most dorsal part of the optic tract, and can be traced ventrally into the thalamic region as far as the foremost part of the optic tract.

* 'Brain,' Part LXXX., p. 427, 1898.
† Perlia, loc. cit.
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It thus contains fibres which degenerate in both an ascending and descending direction. This fact was demonstrated by us at the meeting of the Neurological Society in June, 1897, and has quite recently been made the subject of a special paper by Wallenberg,* who succeeded in injuring the ganglion isthmi, or "ganglion opticum dorsale" (Jelgersma), by a needle passing through the neighbouring part of the cerebellum. He describes the resulting degeneration as existing in the thalamic region in an identical position to that noticed by us, but further states that the tract passes into the opposite optic nerve and can be traced to end in the retina around the cells of the ganglionic layer. The same author has also observed a tract of fibres which degenerate towards the region of the ganglion isthmi after a lesion of the outer part of the cortex of the optic vesicle. This tract he names the tractus isthmo-tecalis. Hence we have a reflex arc, whose afferent system conducts from the complicated cortex of the optic lobe and whose efferent trunk terminates in the retina. Wallenberg regards this system as of great importance, whose function is a regulation or accommodation of the retina.

2. Tractus Mesencephalicus Striatus.

Series of transverse sections extending upwards from the mesencephalon always show, after lesion of the optic lobe, a well-marked band of degenerated fibres. These commence as a scattered system about the level of the IIIrd nerves, and soon collect into a distinct strand which passes upwards into the thalamic region, where it occupies a position immediately ventral to the tr. striomesencephalicus. It can be traced to end in the striate region. Thus, between the corpus striatum and optic lobes there exist distinct ascending and descending tracts.

Münzer and Weiner have arrived at the same conclusion; they moreover state that the tr. mesencephalicus striatus is partly crossed, the crossed part deriving some of its fibres at least from the commissura inferior of Gudden. We have seen certain degenerate fibres in the commissura inferior, but in our sections of the thalamic region after lesion of the optic lobe, Marchi preparations show degeneration only on the side of the operation. Wallenberg* has described, under the title tractus isthmo-striatus or bulbo-striatus, a tract which in the thalamic region certainly has an identical position to the tr. mesencephalicus striatus. According to this observer, it takes origin about the level of the ganglion isthmi, and in part crosses to a similar position on the opposite side; from these two foci the tracts can be traced up to and into the ventral part of the corpus striatum.

We do not think the evidence is sufficient to separate this tract of Wallenberg's from the tr. mesencephalicus striatus; a crossing, such as the author describes, is always found after lesion of the optic lobe, but it may be part of the "fountain decussation" characteristic of this region, and not a special decussation of an

* Loc. cit.
ascending system, whilst its course and termination again correspond to that of the mesencephalicus striatus.

VII. Tracts of the Spinal Cord.

These are:

*Ascending* in the posterior columns as far as the upper extremity of the cord.

In the lateral region, a very well marked direct cerebellar tract passing by the corpus restiformis into the cerebellum.

A short tract in the anterior columns which does not quite reach the middle line; this system is probably internuncial in nature, connecting different levels of the spinal cord.

*Descending.*—The descending tracts occupy both the anterior and lateral columns, in the same relative position as the direct and crossed pyramidal system of mammals, and extending downwards into the lumbar region. This description agrees in all respects with that of Münzer and Wiener.

A. Friedländer,* who has recently studied the degenerations following lesions of the spinal cord in the bird, takes a different standpoint.

He holds that there are no distinct system tracts in the cord, but that fibres of an internuncial nature ascend and descend in the same region. As however indicated, we cannot accept this opinion.

**Physiological.**

The anatomical features which we have described bring out four salient facts:

1. The absence of any tracts extending to the spinal cord from the cerebral hemispheres.
2. The paramount importance of the tracts from the cerebral hemispheres to the mesencephalon.
3. The extensive connection existing between the corpus striatum and the thalamus.
4. The importance of the mesencephalon both as a reflex centre and as the seat of origin of important spinal tracts.

1. *The Absence of Tracts extending from the Hemisphere to the Cord.*—Such a system of fibres, according to Edinger, first makes its appearance in mammals. This author remarks, "Der Fuss ist ein novum additum, das erst sehr spät in dem Thierreiche erscheint" ('Vorlesungen,' 1896). No trace is found in fishes, reptiles, or birds, it appears *pari passu* with the great development of the cortex, and the

* Friedländer, loc. cit.
entire absence in these animals of any noted defect of movement after removal of one hemisphere, accords with this anatomical fact. That the cerebral hemisphere, however, does exercise a great influence over the rest of the nervous system is shown by the condition of pigeons in which both hemispheres have been removed. This has been made the subject of an elaborate study by Schrader.*

We can fully confirm the description this observer gives of the symptoms, which vary according to the time which has elapsed since the operation. After recovering from the operation the animal is markedly inert, standing with ruffled feathers and bent head; its eyes are shut and the animal pays no attention to noises, nor when the eyelids are open does the movement of objects in the field of vision produce any effect; when touched the animal makes a few steps forward and then comes to a standstill. There is complete loss of initiative; when thrown into the air it obtains some kind of support from its wings, but the appearance is more of falling than flying. It does not pick corn and must be fed. After several days this condition of lethargy passes away and is replaced by constant walking aimlessly about, as Schrader says the animals wander ceaselessly to and fro. They are capable of perching, and adjust their balance when placed in a position opposed to gravity. Since they never run into obstacles the movements of the animal are always under some guidance.

It is probable that we are dealing here with symptoms resulting from the activity of the remaining parts of the central nervous system relieved from the control of the cerebral hemispheres.

2. The function of the striothalamic tract is unknown; it may be noted, however, that of the two parts of the surface of the brain which are excitable by the faradic current, one is situated on the lateral aspect of the hemisphere, in a position corresponding to the junction of the strio-thalamic with the common origin of the occipitomesencephalic and occipito-frontal tracts (figs. 51, 52, 53). We here found that stimulation of this area was followed by rotation of the head and neck to the opposite side and a simultaneous movement of pecking and deglutition, and Schrader, from his experiments, came to the conclusion that injury in the thalamus deprived a falcon of the power of swallowing—that is, of getting meat placed in its beak into the pharynx.

Observations and Experiments in Connection with Vision.

The tractus occipito-mesencephalicus may be regarded as the earliest representative in the animal series of the important system of fibres existing in the higher vertebrates which connect the primary optic centres—the optic lobes—with the cerebral hemispheres, though it is possible, according to Edinger,† that the higher reptiles possess in a much less developed form such a tract.

* Schrader, 'Pflüger's Arch.,' vol. 55, pp. 44, 175.
In the bird the occipital lobes are largely developed, and in addition to their connection with the optic lobes are brought into relation with the frontal regions by the associational tracts, and with each other by the anterior commissure.

Our experiments show that the constant result of interference with one hemisphere is marked deficiency of vision in the opposite eye. This result occurs after removal of the anterior or posterior portion of the cerebral hemisphere, after removing the pallium or destruction of the great cell mass of the hemisphere, leaving the pallium intact, thus demonstrating the complicated and extended relations of the visual tracts.

No alteration is seen in the pupils after such operations; they remain of equal size and re-act promptly to light. This observation is also made by Münzer and Wiener. Injury to one optic vesicle also causes deficiency of vision in the opposite eye.

Several further questions arise; Munk removed one hemisphere and enucleated the eye of the opposite side, and showed that the animals were still able to avoid obstacles, and that they thus possessed a visual guidance independent of the hemisphere. The observation has been confirmed by Steffani,† Münzer and Wiener,‡ and ourselves. This result probably depends on the integrity of commissural fibres connecting the two opposite lobes by means of which the eye is placed in connection with the hemisphere of its own side. Steffani maintains that permanent complete blindness results if, when one hemisphere is removed, together with the opposite optic lobe, the eye of the same side as the injured hemisphere is enucleated. Münzer and Wiener, however, found that blindness did not occur in such cases when a newly-fledged bird was made the subject of the operation. One explanation of this difference is that the resulting affection of sight after injury to an optic lobe depends on the extent of the lesion. If the lesion is very severe, involving the nuclear masses of the optic vesicle, then the animal presents marked deficiency of sight in the opposite eye. In a comparatively slight lesion, when the connection between the two optic vesicles is maintained to some extent, the animal is still capable of seeing. The question of the relation of the pallial tract to vision is important; we have seen that a superficial brain lesion produces symptoms similar to one involving the posterior part of the brain, and by the following experiment Münzer and Wiener seem to have demonstrated the importance of the tract in vision.

In a newly-fledged bird the left hemisphere was removed, the bird apparently seeing clearly with the right eye.

In six weeks the right hemisphere was removed, but the mesial surface left intact. The left eye now became blind, the right remained capable of seeing, and this integrity of vision could alone depend on the remaining pallium.

‡ Münzer and Wiener, loc. cit.
Has the pallial tract any other connection with vision?

Ferrier long ago described, from stimulating the mesial aspect of the hemisphere, contraction of the opposite pupil, a result which we have fully confirmed. Such stimulation, as the position indicated in fig. 51, Plate 31, shows, is applied directly to the superficial fibres of the tractus septomesencephalicus, and we found a certain number of degenerated fibres in the tract after removal of the corresponding part of the cortex, but we cannot trace any connection with the oculomotor nuclei nor any decussation in the mesencephalon.* The vast importance of the mesencephalon becomes apparent if we enumerate its various connections with the rest of the centre nervous system:

1. With the corpus striatum of the same side by the tr. mesencephalicus striatus and tractus striomesencephalicus, which latter affords an indirect connection with the thalamus.
2. With the pallium of the same side by means of the tr. septomesencephalicus.
3. With its fellow of the opposite side by the posterior commissure.
4. With the medulla by internuncial fibres.
5. With the cerebellum by the tr. tecto-cerebellaris, and by the superior peduncle of the cerebellum.
6. With the spinal cord by the efferent mesencephalic tracts, and by fibres in the posterior longitudinal bundle.
7. The peculiar retinal connection by the median optic bundle (Perlía, Wallenberg).

In cats, no motor symptoms other than the occurrence of forced movement of rotation are noticed after lesion of the corpora quadrigemina. In birds the mesencephalic pyramidal system is functionally more developed, and we have been able to satisfy ourselves that after a lesion of moderate severity to one optic lobe, a certain amount of weakness in the opposite limbs occurs, so that the animals tend to fall to that side.

* Wesley Mills, in a communication to the Royal Society of Canada, 1898, does not agree with these observations.
DESCRIPTION OF PLATES.

The figures have been drawn by one of us (R. B.) by means of Edinger's camera lucida, and are all of nearly equal magnification.

PLATE 25. Figs. 1-7.

Fig. 1. Pigeon. Horizontal section through cerebral hemisphere. Very superficial. Weigert stain. Left hemisphere.

A. Pallial tract. Origin seen on mesial surface of section.

Fig. 2. Pigeon. Horizontal section through cerebral hemisphere. Slightly deeper than fig. 1, and showing the ventricle. This and the succeeding sections are through the right hemisphere.

A. Pallial tract, taking origin from the fore part of the brain, from the mesial surface, and extending laterally.

Fig. 3. Pigeon. Horizontal section, deeper than preceding figures.

A. Pallial tract, taking origin from fore part of brain and from the mesial and lateral aspect.

Fig. 4. Pigeon. Horizontal section, at a deeper level than the preceding.

A. Pallial tract. E. & F. Origin of Tr. occipito-mesencephalicus and Tr. occipito-frontalis.

Fig. 5. Pigeon. Horizontal section. Deeper level than preceding figures.


Fig. 6. Pigeon. Horizontal section, at a deeper level than preceding figures.

Letters as above.

Fig. 7. Pigeon. Horizontal section, at a deeper level than preceding. Weigert stain.


PLATE 26. Figs. 8-14.

Fig. 8. Pigeon. Horizontal section, at a deeper level than preceding. Weigert stain.

Fig. 9. Pigeon. Horizontal section through the base of brain. Weigert stain.
Letters as above. Th.n. Thalamic nuclei. tr.fr. Transverse fibres of mesencephalon. IV. Fourth nerve.

Fig. 10. Pigeon. Horizontal section, at a deeper level than preceding. Weigert stain.
Letters as above. n.1.n2. Thalamic nuclei.

Fig. 11. Pigeon. Horizontal section through deeper plane than preceding. Weigert stain.
Letters as above. Ax.C. Striomesencephalic and deep descending tracts. Tr.tect.sp. Tr. tecto-spinalis.

Fig. 12. Pigeon. Horizontal section through optic chiasma and optic vesicle. Weigert.

Fig. 13. Pigeon. Horizontal section, deeper than preceding section, and showing optic tract and tracts in connection with it.
Letters as in above fig. 12. Inf.tr. Tr. Infundibularis.

Fig. 14. Pigeon. Horizontal section, deeper than figs. 12 and 13, showing optic chiasma and tracts in connection with it.

PLATE 27. Figs. 15–22.

Fig. 15. Pigeon. Sagittal section, median plane. Weigert stain.

Fig. 16. Pigeon. Sagittal section, lateral to fig. 15.
Letters similar to fig. 15. G.Hb. Ganglion habendule. Inf.tr. Tractus infundibularis. IV. Fourth nerve.

Fig. 17. Pigeon. Sagittal section, lateral to last. Weigert stain.
Letters similar to preceding figures. Epith.fb. Epithalamic fibres. Lm.cm.ms. Lamina commissuralis mesencephali. E. Tr. occipito-mesencephalicus.

Fig. 18. Pigeon. Sagittal section, lateral to last. Weigert stain.
Fig. 19. Pigeon. Sagittal section, lateral to last. Weigert stain.

Fig. 20. Pigeon. Sagittal section, lateral to last.
Letters similar to preceding figures. n. Thalamic nuclei.

Fig. 21. Pigeon. Sagittal section, lateral to last. Weigert stain.
Letters similar to preceding figures.

Fig. 22. Pigeon. Sagittal section, lateral to preceding figure. Weigert.
Letters as above.


Fig. 23. Pigeon. Transverse section through fore part of brain. Shows origin of tracts. Weigert stain.

Fig. 24. Pigeon. Transverse section, slightly behind preceding figure. Weigert stain.
Letters as above.

Fig. 25. Pigeon. Transverse section, behind preceding. Weigert stain.
Letters as above.

Fig. 26. Pigeon. Transverse section through hemisphere and optic thalamus.

Fig. 27. Pigeon. Transverse section, behind level of preceding. Weigert.
Letters as above. A' = chiasmal fibres of Tr. striaomesencephalicus.

Fig. 28. Pigeon. Transverse section through hemisphere and optic vesicle. Weigert.

PLATE 29. Figs. 29–39.

Fig. 29. Hen. Transverse section through hemisphere. Slight lesion of hemisphere near mesial surface. Marchi stain.
A. Tr. striaomesencephalicus. B. Tr. striaothalamicus.

Fig. 30. Hen. Transverse section through hemispheres. Marchi stain.
A. Tr. striaomesencephalicus.

Fig. 31. Hen. Transverse section through hemisphere. Marchi stain.
A. Tr. striaomesencephalicus.
ON THE NERVOUS SYSTEM OF THE BIRD.

Fig. 32. Hen. Transverse section through hemispheres. Marchi stain. Removal of one hemisphere.


Fig. 33. Hen. Transverse section through hemisphere and optic thalamus. Removal of one hemisphere. Marchi stain.


Fig. 34. Hen. Transverse section through hemispheres and optic thalamus. Removal of one hemisphere. Marchi stain.

Letters as in above.

Fig. 35. Hen. Transverse section through hemispheres and optic thalamus. Removal of one hemisphere. Marchi stain.

Letters as above.

Fig. 36. Hen. Transverse section through hemisphere and optic thalamus. Removal of one hemisphere. Marchi stain.

Letters as above.

Fig. 37. Hen. Transverse section through hemispheres and optic thalamus. Removal of one hemisphere. Marchi stain.

Letters as above.

Fig. 38. Hen. Transverse section behind level of preceding, showing termination of degenerated tracts, after removal of one hemisphere. Marchi stain.

Letters as above.

Fig. 39. Hen. Transverse section through mesencephalon, showing termination of degenerated tract, after removal of one hemisphere.

C. Tr. striomesencephalicus. G. Tr. mesencephalicus striatus (undegegenerated). P.C. Posterior commissure.

PLATE 30. Figs. 40–50.

Fig. 40. Hen. Transverse section through hemispheres and optic thalamus, showing ascending degeneration after lesion of the right optic lobe. Marchi fluid.


Fig. 41. Hen. Transverse section through mesencephalon. Lesion of the right optic lobe slightly below this level. Marchi stain.

Antero-lateral columnar fibres degenerating in a descending direction. 
Lamina commissuralis mesencephali, showing the cells of Stieda.

Fig. 42. Hen. Transverse section through mesencephalon. Lesion of right optic lobe just behind this level. Marchi stain.
Letters as in preceding figure. P.C. Posterior commissure.

Fig. 43. Hen. Transverse section through mesencephalon. Lesion of right optic lobe. Resulting ascending and descending degenerations.
Letters as in preceding figures.

Fig. 44. Hen. Section through mesencephalon, showing resulting degenerations after lesion of the mesencephalon. Marchi stain.


Fig. 45. Hen. Transverse section through cerebellum, optic lobe and pons. Lesion at level of section. Resulting degenerations. Marchi stain.
Letters as above.

Fig. 46. Hen. Transverse section through cerebellum and pons. Lesion in the neighbourhood. Resulting degenerations. Marchi stain.


Fig. 47. Hen. Transverse section at a level slightly below the preceding section. Marchi stain.

P.l.l. Degenerated posterior longitudinal bundle.

Fig. 48. Hen. Transverse section through the upper part of the pons, showing descending degenerations in the columnar fibres resulting from a lesion higher up. Marchi stain.

Lateral columnar fibres.

Fig. 49. Hen. Transverse section through pons, showing descending degenerations from lesion at a low level of the mesencephalon on the same side. Marchi stain.
Letters as above.

Fig. 50. Hen. Transverse section of cervical region of spinal cord, showing the anterior and lateral degenerations from a lesion at a low level of the mesencephalon of the same side. Marchi fluid stain.

PLATE 81. Figs. 51–55.

Fig. 51. Brain of Pigeon seen from dorsal aspect.
c.p. Position of excitable area which produces contraction of pupil of opposite eye. Pec. Position and excitable area which produces
complex movements of rotation of head, pecking, and deglutition.  

Fig. 52. Brain of Pigeon seen from ventral aspect.  
A. Tr. septomesencephalicus. F. Tr. occipito-frontalis. A.C. & E.  
Anterior commissure and Tr. occipito-mesencephalicus.

Fig. 53. Brain of Pigeon seen from the lateral aspect, showing position of  
excitable areas, cp. & Pec.

Fig. 54. Cells of the pallium. Nissl stain. Showing cell clusters, \( \frac{1}{3} \) in. obj.

Fig. 55. Transverse section through the mesencephalon, showing the position of the  
large cells described originally by Stieda in the lamina commissuralis  
mesencephali.

a. These cells highly magnified, \( \frac{1}{5} \) in. obj.
Boyce and Warrington.