

STUDIES ON THE DIENCEPHALON OF CARNIVORA

PART II. CERTAIN NUCLEAR CONFIGURATIONS AND FIBER CONNECTIONS OF THE SUBTHALAMUS AND MIDBRAIN OF THE DOG AND CAT

DAVID MCKENZIE RIOCH

National Research Fellow, Laboratory of Comparative Neurology, Department of Anatomy, University of Michigan

FOUR PLATES (NINE FIGURES)

CONTENTS

Introduction	121
Description of nuclear masses and fiber connections	122
Entopeduncular nucleus	122
Zona incerta	123
Zona incerta proper	124
Zona incerta caudalis	125
Nucleus subthalamicus	126
Field H ₁ of Forel	127
Field H ₂ of Forel	129
Nucleus ruber	130
Substantia nigra	132
Discussion	137
Bibliography	143
Plates	145

INTRODUCTION

In the first paper of this series a description was given of the dorsal thalamus, epithalamus, and hypothalamus of the dog on the basis of nuclear pattern. In the present paper a similar account of the subthalamus of both the dog and cat, together with a description and discussion of their fiber connections, is presented. This investigation was carried out on the same material as that used for the previous paper. The pertinent literature will be considered in connection with the discussion of the fiber connections.

I wish to take this opportunity of thanking Prof. G. Carl Huber, who supervised this work, for his help and for the material which he kindly prepared. I also wish to thank Dr. Elizabeth Crosby for her assistance and guidance throughout the problem.

DESCRIPTION OF NUCLEAR MASSES AND FIBER CONNECTIONS

The general structure and arrangement of the corpus striatum, entopeduncular nucleus, zona incerta, nucleus subthalamicus, substantia nigra, and nucleus ruber resemble the configuration found in lower mammals (fig. 4). The system, as a whole, is elongated in a cephalocaudal direction, the nuclei lying one behind the other in relation with the descending motor paths from the cortex. The nucleus caudatus lies almost entirely in front of the thalamus and has a very short tail. The putamen and globus pallidus lie ventrolaterally to the anterior portion of the thalamus, separated from it by the internal capsule. The globus pallidus and putamen are separated from each other by the lateral medullary lamina, which is a well-developed structure, but the two parts of the globus pallidus are more or less fused together, the internal medullary lamina being quite indistinct, more so in the cat than in the dog. The caudate nucleus, the putamen, and the globus pallidus belong to the striatum. The other nuclei mentioned at the beginning of this paragraph are the main nuclear constituents of the subthalamus, which lies ventral to the dorsal thalamus and to a plane through the sulcus medius, lateral to the hypothalamic areas, dorsomedial to the cerebral peduncle, and which is directly continuous caudally with the tegmentum of the midbrain.

Entopeduncular nucleus

The entopeduncular nucleus consists of cells scattered between the fibers of the ansa lenticularis as the latter swing across the internal capsule and first part of the peduncle to enter the dorsally lying nuclei. The entopeduncular nucleus in cat (fig. 4) is in direct continuity with the medial portion

of the globus pallidus, and the only differentiations seen are the more scattered arrangement and the slightly smaller size of the cells. In the dog (fig. 8; Rioch, '29, figs. 1 to 8) there is an indefinite separation between the entopeduncular nucleus and the globus pallidus. In both these forms the cells lie adjacent to the supra-optic and optic fibers as these fibers swing along the surface of the brain outside of the peduncle. The caudal pole of this group of cells lies in the lateral portion of the peduncle, maintaining the same relation to the optic and supra-optic systems. The cells of this nucleus are elongated triangular to fusiform in shape, with two to three long cytoplasmic processes. The cytoplasm contains coarse, deeply stained granules, densely arranged and extending into the processes. The cellular nucleus is small, oval to round, and contains a coarse chromatin network and a single, deeply stained nucleolus.

The entopeduncular nucleus receives large numbers of short connections from the medial end of the globus pallidus and also from the lateral medullary lamina. These end, in part at least, in pericellular synapses around the cells of the entopeduncular nucleus. Bundles of finer fibers come into the nucleus through its dorsolateral border out of the internal capsule. It is to be understood that this latter relation does not necessarily imply cortical connections, because in the more anterior sections a large portion of the superior thalamic radiations together with fibers from the caudate nucleus are seen to cut across the internal capsule directed toward the lenticular nucleus.

As the nucleus is followed downward in relation with peduncular fibers it receives connections from the dorsal supra-optic decussation, the synapse being again pericellular. The direction of the neuraxes is in large part dorsomedial toward the inferior thalamic peduncle.

Zona incerta

The *zona incerta* is an area in the dorsal part of the sub-thalamus which is characterized by the numerous fibers of

passage rather than by its intrinsic nuclei. In the cat it can be divided into two main zones: 1) the zona incerta proper, 2) the zona incerta caudalis.

Zona incerta proper. The zona incerta proper is a more or less circumscribed nucleus, shaped like a cylindrical lens, lying on the dorsal surface of the peduncle rostral and dorsal to the nucleus subthalamicus. Its rostral margin lies at the level of the posterior border of the chiasm and it extends caudally a little past the rostral pole of the nucleus subthalamicus. The field H_1 of Forel is medial to it; the field H_2 lies ventromedial to its caudal surface. The ventral boundary is formed by the peduncle, except at the caudal pole, where the nucleus subthalamicus and fibers of its capsule extend between the two. The lateral boundary is formed by the ventral part of the nucleus reticularis, with which in places the zona incerta appears to be almost continuous. The dorsal boundary is formed at first by the lamina medullaris externa and through its caudal half by the zona incerta caudalis. Caudally, also, it is separated from the zona incerta caudalis by a thin fiber layer and is easily distinguished from the latter by its deeply staining ground-substance.

The cells of the zona incerta proper are arranged transversely between fibers. They are medium to small in size, elongated triangular to fusiform in shape, with two to three moderately long, thick, branching cytoplasmic processes. The cytoplasm contains diffusely scattered, coarse, well-stained granulations, which extend for a short distance out into the processes. The cellular nucleus is large, oval, pale, with a faint, rather coarse chromatin network and a single deeply staining nucleolus.

The fibers coming into the zona incerta may be divided into certain groups. Two forebrain components are present: striatal connections through the ansa lenticularis and cortical connections from the internal capsule. The ansa is distributed mainly through the thalamic fasciculus of Forel (H_1) and to a less extent through the lenticular fasciculus (H_2).

The internal capsule connections come from the retrolenticular portion of the internal capsule in the dog and cat (homologous with the sublenticular region of human).

There are numerous connections with fibers of the dorsal supra-optic decussation (fig. 5). Some of these cross the hypothalamic area to the medial end of the zona incerta; a greater number run parallel with the optic tract, along the base of the peduncle, and turn dorsalward, running through the peduncle or around its lateral margin to enter the ventrolateral surface of the zona incerta. Many of these are fibers of passage on their way to the tectum and are accompanied in their further course by incerto-tectal fibers.

There are apparently connections between the zona incerta and the nucleus geniculatus lateralis ventralis and also between the zona incerta and the ventral nucleus of the thalamus. The exact termination of these fibers was not found in the material available. There are also connections of the zona incerta with both the ventral and lateral hypothalamus, especially with the nucleus hypothalamicus ventromedialis. Conduction is in both directions, but with the emphasis on the hypothalamico-incertal paths. There are quite numerous fiber bundles which run caudally between the zona incerta and the tegmental areas of the midbrain. The assumption is justified that this latter area and the tectum provide the main efferent path for the zona incerta.

Zona incerta caudalis. The zona incerta caudalis (fig. 1) lies around the dorsolateral margin of the peduncle, separated from the zona incerta proper by a band of fibers largely the dorsal supra-optic decussation. Laterally, it is continuous with the caudal pole of the nucleus reticularis; medially, it fuses with the field H_1 of Forel; ventrally, it lies on the surface of the peduncle, and dorsally, it is limited by the most caudal portion of the external medullary lamina. It is continuous with a group of cells extending among tecto-tegmental fiber systems dorsocaudally and intermingles with the lateral portion of the substantia nigra ventrocaudally. The cells are slightly larger than those of the zona incerta proper, but are otherwise similar.

The zona incerta caudalis, as the zona incerta, is in relation with the dorsal supra-optic commissure and with the optic tectum and receives connections from the striatum by way of the lenticular fasciculus of Forel (H_2). It also has hypothalamic connections, some of which consist of fibers which turn laterally out of the combined mammillo-thalamic and mammillo-tegmental tracts. Many fibers from the decussation of Forel can be traced to the zona incerta caudalis. They have the appearance of being true commissural fibers. Aberrant pyramidal tracts on the lateral side of the peduncle turn dorsomedialward through this region, but any connection of these with the cells cannot be determined.

Nucleus subthalamicus

The nucleus subthalamicus (figs. 1, 4, and 8) is a lens-shaped mass of cells lying on the dorsomedial surface of the peduncle, extending from the level of the infundibulum to that of the middle of the mammillary nuclei. The mass of cells curves around the medial surface of the peduncle, forming a cap. Laterally, along the dorsal surface of the peduncle, it continues as a narrow band of cells almost to the dorso-lateral corner.

The rostral boundary is formed by the zona incerta, with fibers of the ansa forming the rostral portion of the field H_2 of Forel lying medially. The dorsomedial boundary also is formed by the field H_2 of Forel. Ventromedially, there is some fusion with the cells of the lateral hypothalamic area. The pedunculus cerebri forms the lateral and ventrolateral boundary. In the caudal portion the ventromedial part of the nucleus subthalamicus extends toward the lateral mammillary nucleus. Caudally, it is separated from the substantia nigra by an area consisting mainly of fibers with scattered cells which are continuous with the lateral mammillary nucleus ventrally, the zona incerta dorsally, the lateral hypothalamic area rostrally, and the reticular substance of the tegmentum caudally. The fibers in this area consist of the anterior connections of the red nucleus and

substantia nigra, with the dento-rubro-thalamic bundle and with other less-known groups.

The cells of the nucleus subthalamicus are arranged for the most part between fibers running in a lateromedial plane, following the curve of the surface of the peduncle. The cells are large, polygonal to triangular in shape, with moderately long cytoplasmic processes, quite thick with a few branches. The cytoplasm is filled with large, coarse, rod-shaped granules which stain deeply and extend along the processes. The cellular nucleus is large, well outlined, and shows a coarse, well-stained, granular chromatin network and a single, moderately large, deeply staining nucleolus.

Numerous fibers turn dorsally out of the peduncle into the nucleus subthalamicus, some of which end there and others of which are fibers of passage. Most of the latter rejoin the peduncle. Fibers from the ansa lenticularis enter the ventral surface of the nucleus subthalamicus by cutting directly through the peduncle, and others enter the medial surface by the lenticular fasciculus of Forel (II_2). Many of these fibers come into synaptic relation with cells of the nucleus (fig. 5). The larger number accumulate in a layer between the nucleus and the peduncle and continue in that position caudalward to enter the anterior end of the substantia nigra (fig. 5). These bundles are joined on the dorsal side by neuraxes of neurones of the nucleus subthalamicus which follow the same course. There are commissural connections through the commissure of Forel with the nucleus of the opposite side. There are also connections with the dorsal supra-optic decussation, lateral portion, which are certainly not entirely commissural. The adjacent hypothalamic regions and the zona incerta are in relation with the nucleus subthalamicus by internuclear fibers.

Field H_1 of Forel

The field H_1 of Forel (figs. 1 and 8) is an area of fibers of passage lying dorsolateral and then directly caudal to the medial hypothalamic area. Laterally, it is bounded by the

zona incerta and then fused with the field H_2 of Forel; dorsally, it is bounded by the caudal portion of the external medullary lamina; medially, it adjoins a region containing large polygonal cells which form the extreme rostral pole of the tegmental area of the midbrain; ventrally, it is bounded by the mammillary nuclei, and caudoventrally, by the interstitial nucleus of the decussation of Forel. The cells of the region are similar to the cells of the zona incerta, but are more scattered and elongated between fibers. There are also a few larger elements.

The term H_1 is used here to designate an area containing numerous fascicles, one of which is the thalamic fasciculus of Forel. This latter fasciculus separates from the ansa lenticularis at the medial boundary of the peduncle just rostral to the nucleus subthalamicus and the field H_2 of Forel. It passes a short distance caudalward and medialward to join with the fascicles from the anterior capsule of the red nucleus. Here some of the fibers turn rostrally and accompany the dento-rubro-thalamic group, following a rostro-dorsolateral course to the external medullary lamina. A few fibers of the fasciculus turn caudally toward the red nucleus. The largest number of fibers in the field H_1 of Forel consists of the fascicles of the dento-rubro-thalamic tract from the anterior capsule of the red nucleus. Fibers, the origin of which cannot be determined definitely, turn out of this region in small compact bundles to the nucleus parafasciculus, beyond which they could not be traced. There are numerous connections medially, especially just in front of the decussation of Forel, with the anterior pole of the central gray of the aqueduct. The region also receives fibers from the decussation of Forel and from the medial part of the dorsal supra-optic decussation. The relation of these fibers to the cells could not be determined. Rostrally, the region is connected by internuclear fibers with the zona incerta and hypothalamic areas and, caudally, with the tegmentum.

Field H₂ of Forel

The term field H₂ of Forel (figs. 1 and 8) is used to designate the region medial to the nucleus subthalamicus, bounded rostrally and rostroventrally by the lateral hypothalamic area and rostradorsally by the zona incerta proper. Medially, it fuses with the field H₁ of Forel and extends caudally into the lateral capsule of the red nucleus. The cells of the region, on the whole, resemble those of the field H₁ of Forel.

The so-called nucleus of the field of Forel (fig. 1) consists of moderately large elements scattered mainly through the field H₂ and grouped in the region of juncture of the two fields of Forel. These cells are polygonal to triangular in shape, with long cytoplasmic processes. The cytoplasm contains scattered, rod-like granulations which extend into the dendrites. The cellular nucleus shows a coarse chromatin network and a single deeply stained nucleolus.

The main fiber groups of the region consist of the lenticular fascicle H₂ of Forel and fibers from the lateral capsule of the red nucleus. The former bundle (fig. 6) consists of fibers from the ansa lenticularis, which reach the area either through the nucleus subthalamicus or around its lateral or medial borders, the majority of the fibers following the latter course. The lenticular fascicle as a whole runs directly caudalward to the red nucleus, losing some fibers on the way to the reticular areas of the tegmentum and to the substantia nigra. The majority of the fibers enter the red nucleus and come into synaptic relation with its cells. The dento-rubrothalamic group from the lateral capsule of the red nucleus turns dorsally out of the field H₂ of Forel at the level of the zona incerta caudalis to enter the most caudal part of the external medullary lamina. The dorsal supra-optic fibers cross the rostral part of the area. Fibers of the decussation of Forel cross the area more caudally. Included with these are ansal fibers which interdigitate in the midline, just above the decussation of the fornix, with the commissural fibers of the decussation of Forel. They thus run from a ventrolateral to a dorsomedial position to reach the field H₂ of Forel of the

opposite side. There are internuclear connections with the lateral hypothalamic area, the nucleus subthalamicus, substantia nigra, and the tegmentum.

Nucleus ruber

The red nucleus (fig. 2) is one of the most prominent structures in the mesencephalon. Rostrally, it is more or less continuous with the cells of the reticular formation of the midbrain, which consists of large cells, scattered singly or in groups among the fibers running forward from the anterior capsule of the red nucleus. Such cells extend forward in conjunction with these fibers (*n.interst.teg.*, fig. 2, also figs. 11 and 12, Rioch, '29) and border medialward on cells intermingled with the median longitudinal fasciculus apparently there becoming part of a dorsal nucleus interstitialis, which nucleus is included under *n.interst.teg.*, in figures 9 and 10, Rioch ('29).

The rostral pole of the red nucleus lies just in front of the root of the oculomotor nerve, the large cells here forming a more or less circumscribed group in a moderately deeply stained ground-substance. The nucleus is surrounded by a capsule of fibers separating it dorsomedially and dorso-laterally from the tegmentum; medially, from the central nucleus of the tegmentum; ventromedially, from the interpeduncular nucleus; ventrally and ventrolaterally, from the substantia nigra; caudally, it is continuous with the superior cerebellar peduncle. The caudal boundary is sharp, lying a few sections rostral to the rostral margin of the pons.

A rather indefinite division of the red nucleus into two parts can be made: 1) a compact, caudal portion, the cells being mostly of the very large type (see below); 2) a more loose, oral portion, the cells being both of the very large and the less large types. In the oral portion the cells are grouped somewhat in the form of a thick crescent, with the convex surface facing ventrolaterally.

The cells of the red nucleus are moderately widely separated with fibers running between them. There is no par-

ticular arrangement with regard to the direction of the fibers. The neurones are of three types, with some transitional forms: 1) Very large cells (fig. 9), larger than any in the thalamus, polygonal in form, with numerous long processes. The processes are thick at the base and contain scattered granules, but rapidly become fine and clear. They give off several branches. The cytoplasm is voluminous and is packed with large, deeply staining, rod-shaped and round granulations. The nuclei are round to oval and are relatively small. They are pale, well outlined, and show coarse chromatin network. 2) Less large cells (fig. 9). Most of the other cells of the red nucleus are about half the size of the very large cells, although elements of all sizes between the two are present. These smaller cells are similar in all respects in structure to the very large cells. 3) Scattered small cells (fig. 9). A few scattered small cells, of an undifferentiated type, are intermingled with the larger elements. These are more numerous rostrally than at the caudal pole of the nucleus.

Obviously, the red nucleus receives crossed fibers from the superior cerebellar peduncle. It is connected with the tectum by three groups of fibers. The most medial of these accompany the tecto-oculomotor and medial tecto-spinal bundles in the stratum profundum and cross in the dorsal tegmental decussation to the red nucleus of the opposite side (fig. 7). Lateral to these are similar bundles crossed and uncrossed, connecting the whole midbrain roof with the red nuclei (fig. 7). The third group of tectal bundles consists of a tract of much finer fibers connecting the rostral portion of the red nucleus and the reticular formation of the tegmentum, on the one hand, with the superior collicular portion of the midbrain, on the other hand. These are accompanied by posterior commissure components.

The red nucleus is connected with the striatal areas of the forebrain by way of the lenticular fasciculus of Forel (fig. 6), which is that part of the ansa lenticularis described above as passing through the field H_2 of Forel. There may be a further connection of the ansa with the red nucleus by fibers

which turn caudalward out of the thalamic fasciculus of Forel (H_1) to enter the anterior capsule of the red nucleus. Definite cortico-rubral connection could not be recognized in the material available, although fibers were seen to leave the medial border of the peduncle at the level of the caudal third of the nucleus subthalamicus and to join the ventral bundles of the lenticular fasciculus of Forel.

The red nucleus is connected with the surrounding tegmental area by internuclear fibers. Numerous neuraxes of cells of the nucleus can be traced into these areas (fig. 9). This provides for a discharge path by way of tegmental centers. The major path is the crossed rubro-spinal tract (von Monakow), which has been repeatedly described.

Substantia nigra

The substantia nigra (figs. 2 to 4) is a large, cellular structure, roughly ellipsoid in shape, covering the dorsal and medial surfaces of the peduncle. It extends from the level of the rostral end of the posterior third of the mammillary nuclei caudalward to the level of the rostral margin of the pons. It reaches its greatest dimensions in the caudal half of its rostral third, consisting only of scattered cells anteriorly and becoming a narrow band posteriorly. The substantia nigra may be divided into the following portions: 1) zona reticulata, 2) zona compacta, 3) pars lateralis.

The zona reticulata (figs. 2 and 4) first appears in the cross-sections as scattered cells in the dorsomedial margin of the peduncle. It remains as a small, indefinite group ventral to the rostral pole of the zona compacta until about the level of exit of the oculomotor nerve, where it becomes considerably larger, the cells extending through the peduncle almost to its ventral boundary. This increase in size takes place at first medially and later laterally. At the level of the rostral half of the nucleus interpeduncularis, the zona reticulata diminishes in size and finally disappears about the level of the middle of said nucleus.

The cells are irregularly scattered along fibers which run diagonally through the peduncle, at times perpendicular to the peduncular fibers. At places these fibers with the cells form a sort of coarse reticulum. The cells are medium-sized, slightly smaller, on the whole, than those of the zona compacta, and fusiform to triangular in shape. They have long, thick cytoplasmic processes which give off occasional finer branches. The cytoplasm contains numerous rod-like granulations, deeply stained, which are diffusely arranged and extend for a short distance out into the processes. The cellular nucleus is moderately deeply stained and shows a coarse chromatin network and a single deeply stained nucleolus.

The *zona compacta* (figs. 2 to 4) lies on the medial and dorsomedial surface of the cerebral peduncle, more or less separated from the *zona reticulata* by the *stratum intermedium*. Its rostral pole lies at the level of the caudal end of the mammillary nuclei. The caudal pole of the *zona compacta* is at the level of the anterior margin of the pons. Ventrolaterally, throughout its extent this zone is in relation with the peduncle; medially and dorsally, it is in relation with several fiber systems, which are as follows: dorsomedially, the field H_2 of Forel; laterally, the lateral tectal systems; dorsocaudally, the medial lemniscus, and caudomedially, the mammillary peduncle. Through its rostral half the *zona compacta* has a comma-shaped appearance, as described by Morgan ('27). It extends medially to the midline and to the border of the interpeduncular nucleus through a zone of scattered cells. In this region at first it fuses laterally with the *zona incerta caudalis* and then with the *pars lateralis* of the *substantia nigra*. Gradually throughout its caudal half it becomes a band of characteristic cells along the dorsal surface of the peduncle from which scattered cells continue dorsolaterally into the lateral system of tectal fibers. The medial lemniscus, in turning dorsalward in the lower levels of the midbrain, passes through the caudal pole of the *zona compacta*.

The cells of the zona compacta are moderately densely and quite irregularly arranged. They vary in size, being small anteriorly and at the extreme medial and lateral boundaries, and large, mainly in the dorsomedial and caudal portions. They are polygonal, triangular, and fusiform, with long cytoplasmic processes. The cytoplasm and nuclei otherwise resemble those of the cells of the zona reticulata, except that they stain more deeply.

The pars lateralis of the substantia nigra (Rioch, '29, figs. 10 to 12) consists of a group of cells lying among diagonally directed fibers in the dorsolateral corner of the peduncle, dorsolateral to the other two parts of the substantia nigra. Rostrally, it extends as far as does the zona reticulata and is bounded rostrally, dorsally, and laterally by the zona incerta caudalis. Medially, it connects with the zona reticulata and then fuses with the zona compacta through a narrow band of elongated cells. It fuses medially with the zona compacta about the level of the posterior portion of the root of the oculomotor nerve. Laterally, at about the same level it extends as intercalated cells into the lateral tectal systems.

The cells are irregularly arranged and are as large as any in the substantia nigra. They resemble the cells of the zone reticulata in all respects, except that they are larger and slightly more elongated.

The substantia nigra is connected with a number of functionally different centers within the brain, among which may be mentioned cortical, striatal, tectal, and cerebellar areas, subthalamic, hypothalamic, and tegmental regions, and secondary afferent centers of the brain stem and cord.

Throughout the whole extent of the substantia nigra, fibers turn dorsally from all levels of the peduncle to distribute to the zona compacta (fig. 7). The cells of the zona reticulata lie in relation with these fibers.

The strio-nigral connections are through the ansa lenticularis. These fall into two groups. The first consists of bundles which accumulate between the nucleus subthalamicus and the peduncle and enter the zona compacta through its

rostral pole (fig. 5). These are accompanied by fibers from the nucleus subthalamicus (p. 127). The second group continues in the medial margin of the peduncle, swinging into the medial portion of the zona compacta in its rostral third (fig. 7). There are also fibers out of the lenticular fasciculus of Forel which turn lateralward into the substantia nigra.

The tectal connections of the substantia nigra may be divided into four groups. The first of these is via the so-called 'courant de la calotte,' which is a diffuse group of fibers leaving the dorsal surface of the substantia nigra throughout its whole extent and running into and through the tegmentum (fig. 7). Fibers from the rostral portion of this group run into the posterior commissure, others are directed medially toward the central gray of the aqueduct, and still others dorsolaterally toward the deep layers of both superior and inferior colliculi. The second group of connections with the tectum runs with the lateral fibers of the stratum profundum. Some swing ventrally and then medially through the tegmentum and red nucleus, to cross in the middle tegmental decussation and enter the ventromedial margin of the substantia nigra of the opposite side (fig. 7, *tr.tect.nigr.*). Others swing more laterally and pass between the bundles of the medial lemniscus to enter the dorsolateral surface of the substantia nigra of the same side (fig. 7, *tr.tect.nigr.*). The third and fourth groups of connections consist of two layers of vertically running fibers which lie at the lateral margin of the mesencephalon (fig. 7). The most rostral of both these groups of fibers connect with the superior colliculus, but the majority of the fibers connect with the inferior colliculus. The more superficial of these two layers (*tr.nigro-tect.lat.*) connects with the more superficial portions of the colliculi, passes laterally to the lateral lemniscus and to the brachium of the inferior colliculus, and enters the lateral portion of the dorsolateral surface of the substantia nigra. Some of the lateral fibers of this group pass between the fibers of the peduncle and enter the substantia nigra from its ventral surface (fig. 7). More caudally, a large number of the most

superficial fibers of this layer continue ventrally, round the ventral surface of the peduncle, into the pontine gray, the medial fibers maintaining their relations with the substantia nigra. In planes through the brachium of the inferior colliculus fibers are seen running out of the latter into this layer. The deeper of the two superficial layers (*tr.nigro-tect.med.*) connects with the deeper layers of both the superior and inferior colliculi. It extends vertically downward medial to the lateral lemniscus and the brachium of the inferior colliculus and reaches the medial portion of the dorsolateral surface of the substantia nigra. In the caudal planes these fibers interdigitate between the bundles of the lateral and medial lemniscal systems.

The cerebellar connections are by fibers of the superior cerebellar peduncle which cross in the ventrocaudal portion of the superior cerebellar decussation and end around the ventromedial cells of the substantia nigra. These fibers accompany the cerebello-tegmental fibers which run between the substantia nigra and the red nucleus to pass forward and lateralward to the tegmentum.

As the medial lemniscus passes through the caudal pole of the substantia nigra fibers, some of which are probably collaterals, are seen to leave the larger bundles and end in synaptic relations with the cells of the nucleus (fig. 3). There are rather dense internuclear connections with the following midbrain nuclei: the nucleus tractus peduncularis transversi, the nucleus interpeduncularis, and the nucleus of the lateral lemniscus. The nucleus tractus peduncularis transversi could not be differentiated as separate from the medial portion of the substantia nigra in the cell preparations (see also Friedemann, '12). However, the position of the nucleus is easily determined by the distribution of the fibers of the tract, which are seen to leave the optic tract just ventral to the nucleus geniculatus lateralis. They then turn caudally and ventrally, over the surface of the peduncle, and finally swing dorso-medially (fig. 2) round its medial margin at the level of the oculomotor nerve. The connections with the interpeduncular

nucleus pass directly laterally from that nucleus to the ventromedial margin of the substantia nigra throughout the extent of the former nucleus. The fibers connecting the nucleus of the lateral lemniscus with the substantia nigra enter the latter with the tectal connections in its dorsolateral portion. The rostral portion of the substantia nigra is connected with the nucleus of the opposite side through the rostral fibers of the decussation of Forel.

Reference has already been made to the 'courant de la calotte,' or tegmental radiations of the substantia nigra (fig. 7). This consists of large numbers of irregular bundles of fine fibers running dorsally from the surface of the substantia nigra throughout its whole extent. These enter into the reticulum around the large bundles of the ascending tract and as a system connect with the posterior commissure, with both superior and inferior colliculi, and with the central gray around the aqueduct. The direction of conduction could not be determined in the available material. The evidence in the literature, however, is that this is an efferent system.

The present material yields no evidence for the presence of nigro-fugal fibers entering the peduncle.

DISCUSSION

In this discussion each nucleus with its fiber connections and the pertinent literature will be considered and then the interrelation of the groups will be summarized briefly.

The entopeduncular nucleus is phylogenetically very old, being present in submammalian and mammalian forms. This has been described under the name of *noyau du capsule interne* by Ramón y Cajal ('11) for mouse and by Morgan ('27) for cat and as the entopeduncular nucleus by Gurdjian ('27) for rat and by Le Gros Clark ('29) for *Tupaia minor*. Ramón y Cajal described cortico-thalamic fibers to this nucleus and efferent fibers from it running caudalward. Gurdjian and Morgan related it to the striatum, the latter specifically to the globus pallidus. The present account indicates that the nucleus receives fibers from the globus pallidus and

the putamen, and that it also receives fibers out of the internal capsule. These latter may be cortical or may be from the caudate nucleus or the thalamo-striate radiations. The entopeduncular nucleus contributes a large contingent of fibers to join the ansa. There are two groups of fibers which have a special interest from a phylogenetic standpoint, having been previously described only in reptiles (Huber and Crosby, '26) and birds (Huber and Crosby, '29). These groups consist of the connections of the dorsal supra-optic system with the nucleus entopeduncularis, on the one hand, and the connection of this nucleus with the dorsal thalamus by way of fibers joining the inferior thalamic peduncle, on the other.

The zona incerta has been described by practically all observers studying this region, but the nucleus has been so poorly delimited that it is difficult to compare their descriptions of the fiber connections. Several recent workers (Malone, '10; Morgan, '27; Papez, '29) called it the peripeduncular nucleus. It should be noted that in the Winkler and Potter ('14) atlas on cat, the area labeled corpus subthalamicus belongs to the zone incerta. Papez described a reticular subthalamic nucleus medial to the peripeduncular nucleus which is comparable to the fields H_1 and H_2 of Forel of the present account and which has been regarded as the medial part of zona incerta by several authors (Kölliker, '96; Dejerine, '01; Foix and Nicolesco, '25; Gurdjian, '27; Le Gros Clark, '29). Most authors (Dejerine, '01; Foix and Nicolesco, '25; Tsai, '25; Morgan, '27) relate the zona incerta to descending striatal paths, including the bundles of Forel. Papez described strio-oculomotor and strio-peduncular fibers to the zona incerta. Several authors (Dejerine, '01; Ramón y Cajal, '11; Papez, '29) described connections with the superior cerebellar peduncle. Ramón y Cajal ('11) also found fibers into the region from the lemnisci systems. This latter author and Gurdjian ('27) mentioned connections from the internal capsule. von Monakow ('95) thought that the cortical region related to this center included the temporal

lobe, the operculum, and the island, but that the cortical area was not sharply definable. Connections with the dorsal supra-optic decussations were described by Tsai ('25) and Gurdjian ('27) and with the supramammillary decussation by the latter observer. Incerto-tectal connections were described by Gurdjian ('27) and Papez ('29), both of whom also found efferent fibers to the tegmentum. Other connections described are mammillo-incertal by Kölliker ('96) and hypothalamico-incertal by Gurdjian ('27).

By limiting the zona incerta to the lateral part of the region, as has been done in the preceding account of the area in dog, the connections place it definitely on the efferent side of the arc. It is seen to be a way station between the striatal and possibly the cortical areas of the hemisphere and efferent centers of the midbrain as represented in the tectum and tegmentum.

One connection of considerable interest to comparative neurologists, which has been described previously for rat (Gurdjian, '27) and apparently is present in the cat material, is a bundle which extends from the ventromedial border of the nucleus geniculatus lateralis ventralis into the zona incerta. Whether the main bundle terminates here or passes to lower centers it is impossible at present to determine. It represents the fasciculus geniculatus descendens of reptiles (Beccari, '23; Huber and Crosby, '26).

The fields H_1 and H_2 of Forel are intimately associated with the zona incerta and have been included with this area by many observers. Practically all investigators agree as regards the distribution of the thalamic and lenticular fasciculi to these fields. Papez ('29) included this area in his reticular subthalamic nucleus and described to it terminals of the *brachium conjunctivum*, fibers from the mammillo-thalamic tract, and efferent fibers to the corpus striatum which, according to his account, ran in the thalamic fasciculus. The hypothalamico-incertal connections described by Gurdjian and connections with the mammillary body described by Kölliker ('96) and Dejerine ('01) probably belong to this area.

From the observations recorded here and from the literature, it appears that this region is mainly one of fibers of passage, both ascending and descending systems being represented. The most important neurones of the region are the large cells forming the nucleus of the field of Forel. These apparently provide for synapses of the lenticular bundle of Forel. The most specific connections to the area appear to be from the hypothalamic region. This offers a means of connecting the hypothalamic areas with the striatal system to the red nucleus and substantia nigra.

The zona incerta caudalis has been differentiated cyto-architectonically and is associated apparently with the lateral aberrant pyramidal tracts, although the available material does not show definite synapses. In other respects it resembles the zona incerta proper.

The nucleus subthalamicus, or the corpus Luysii of most authors, has been described frequently. In Winkler and Potter's atlas of the cat it was termed the nucleus pedunculus proprius cerebri. There is general agreement as to the connections from the striatum by strio-luysian fibers from the globus pallidus, by the ansa lenticularis, and by the lenticular fasciculus of Forel (H_2). Cortical connections were described by Dejerine ('01) and Foix and Nicolesco ('25). Several authors (Tsai, '25; Gurdjian, '26; Kölliker, '96) have related the nucleus with the dorsal supra-optic system. Kölliker ('96), Dejerine ('01), and Foix and Nicolesco ('25) described inter-nuclear connections with the nucleus of the opposite side by way of the supramammillary decussation of Forel. Bochenek ('08) and Tsai ('25) carried fibers of the optic tract to this nucleus. Very few authors have identified efferent tracts from the nucleus subthalamicus. Morgan ('27 a) found a large fasciculus to the medial part of the substantia nigra and the region ventral to the red nucleus, a few fibers of which crossed to the nucleus subthalamicus of the other side. Papez ('29) mentioned efferent fibers into the cerebral peduncles and into the reticular formation, probably passing to pons and cerebellum.

In the material presented here the striatal connections via the ansa and the lenticular fasciculus (H_2) of Forel, peduncular connections, commissural connections with the nucleus of the opposite side through the supramammillary decussation, and connections with the supra-optic decussation were found. The efferent tract described by Morgan was not identified in this material, but a large number of non-myelinated fibers were seen to leave the caudal pole of the nucleus subthalamicus and to accompany fibers from the ansa which had accumulated between the nucleus subthalamicus and the peduncle. The two components formed a single group running along and through the medial margin of the peduncle to enter the dorsal pole of the substantia nigra and distribute around the cells of the zona compacta. No efferent fibers from the nucleus subthalamicus into the peduncle, as described by Papez ('29), could be traced in the material. Obviously, the nucleus subthalamicus is an important way station in the passage of impulses in the efferent path from striatal areas to lower centers of the same and opposite sides.

The relations of the red nucleus with the superior cerebellar peduncle, the lenticular fasciculus of Forel, and the rubro-spinal path are agreed upon by most observers. Connections through the posterior commissure with the contralateral nucleus were described by Foix and Nicolesco ('25) and internuclear commissural fibers by Gurdjian ('27). Definite evidence is presented in the present account for the tectal connections hypothesized by Foix and Nicolesco ('25). The neuraxes found connecting the red nucleus to the tegmentum indicate that the rubro-spinal is not the only discharge path for this nucleus.

The substantia nigra, as a nuclear mass, has been recognized for a long time and usually has been divided into a zona reticulata and a zona compacta. Recently, Morgan ('27), following Malone ('10), described a medial group of cells, a lateral group (the intrapeduncular nucleus of Jacobson), both motor in type, and a central group (corresponding to the reticular zone), sensory in type. It was not possible in

the available material to confirm this differentiation into motor and sensory portions.

Most observers are agreed that the striatum discharges to the substantia nigra by way of the ansa lenticularis. von Monakow ('95), Dejerine ('01), Ramón y Cajal ('11), and Foix and Nicolesco ('25) described cortico-nigral fibers. Other afferent connections are the subthalamic fasciculus of Morgan ('27) and fibers from the lateral border of the medial lemniscus mentioned by Papez ('29). Tsai ('25 a, fig. 4) showed four systems of fibers connecting with the substantia nigra, but did not describe them: tractus tecto-nigralis, tractus pretecto-tegmentalis, tractus cerebello-tegmentalis, and tractus strio-nigralis. On the efferent side, Ramón y Cajal ('11) described fibers to the tegmentum and to the posterior commissure; Foix and Nicolesco ('25) mentioned this latter as the main efferent system and hypothesized a descending tegmental path. The latter authors and also Kawata ('27) described fibers from the substantia nigra descending in the peduncle to lower centers, probably to the pons.

The substantia nigra is usually recognized as one of the centers related with the striatum by way of the ansa, but its fiber connections suggest that it has other, and possibly even more important, functions. The relations of the tectal connections of the substantia nigra indicate that the most superficial group is nigro-tectal as it enters the surface layers of both colliculi. The two deeper groups are probably tecto-nigral, since they are associated with the efferent bundles of the tectum. The presence of nigro-tectal connections suggests that the substantia nigra is a way station between the cortical centers of the hemisphere and the roof of the midbrain. This resembles the intermediating position of the pontine gray between the cortical areas of the forebrain and the cerebellar cortex. The nigro-tectal connections provide a discharge path for the area by way of the tectum and then tecto-spinal paths. The strio-nigral, cortico-nigral, and tecto-nigral bundles indicate that the substantia nigra is a correlation

center for efferent impulses from these areas. The connections with the nucleus tractus peduncularis transversi, interpeduncular nucleus, the nucleus of the lateral lemniscus, and with the medial lemniscus suggest further possibilities of the modification of these impulses. The unquestioned presence of a final common path from substantia nigra to motor neurones has not been established as yet, the widely distributed 'courant de la calotte,' or nigro-tegmental fasciculus, being the most generally recognized efferent system.

The entopeduncular nucleus, the zona incerta, the fields of Forel, the nucleus subthalamicus, the red nucleus, and the substantia nigra fall into a common group through their relations with the ansa lenticularis. Consequently, their differentiation from each other depends upon their fiber relations with other than striatal areas. In this respect certain connections may be said to be characteristic for each nuclear mass: for the entopeduncular nucleus, the dorsal supra-optic system in relation with the connection of the nucleus with the dorsal thalamus; for the zona incerta, the dorsal supra-optic system in relation with the tectal connections; for the fields of Forel, a possible hypothalamico-rubral pathway; for the nucleus subthalamicus, commissural connections and the dorsal supra-optic system in relation with the subthalamico-nigral fasciculus; for the red nucleus, the dominating cerebellar connections with some fibers from the tectum; and for the substantia nigra, a preponderance of tecto-nigral and nigro-tectal paths.

BIBLIOGRAPHY

- BECCARI, NELLO. 1923 Il centro tegmentale o interstiziale ed altre formazioni poco note nel mesencefalo e nel diencephalo di un rettile. *Arch. Italiano di Anat. e di Embr.*, T. 20, p. 560.
- BOCHENEK, A. 1908 Ueber die zentrale Endigung des Nervus opticus. *Anz. d. Akad. Wiss. z. Krakau.* (Quoted from Tsai, '25.)
- DEJERINE, J. 1901 *Anatomie des centres nerveux*, T. 2. Rueff, Paris.
- FOIX, C., ET NICOLESCO, J. 1925 *Les noyaux gris centraux et la région mésencéphalo-sous-optique.* Masson et Cie, Paris.
- FRIEDEMANN, M. 1912 Die Cytoarchitektonik des Zwischenhirns der Cercopithecen mit besonderer Berücksichtigung des Thalamus opticus. *Jour. f. Psychol. u. Neur.*, Bd. 18, S. 309, *Ergänzungsheft 2.*

- GURDJIAN, E. S. 1927 The diencephalon of the albino rat. Studies on the brain of the rat. No. 2. *Jour. Comp. Neur.*, vol. 43, p. 1.
- HUBER, G. CARL, AND CROSBY, ELIZABETH CAROLINE 1926 On thalamic and tectal nuclei and fiber paths in the brain of the American alligator. *Jour. Comp. Neur.*, vol. 40, p. 97.
- 1929 The nuclei and fiber paths of the avian diencephalon, with consideration of telencephalic and certain mesencephalic centers and connections. *Jour. Comp. Neur.*, vol. 48, p. 1.
- KAWATA, A. 1927 Über die Fasersysteme der Substantia nigra und der Stammganglien nach Untersuchungen bei Parkinsonismus. *Arb. a. d. neur. Inst. a. d. Wiener Univ.*, Bd. 29, S. 265.
- KÖLLIKER, A. 1896 *Handbuch der Gewebelehre des Menschen*. 6. Aufl., Bd. 2. Engelmann, Leipzig.
- LE GROS CLARK, W. E. 1929 The thalamus of *Tupaia minor*. *Jour. of Anat.*, vol. 63, part II, p. 177.
- MALONE, EDWARD F. 1910 Über die Kerne des menschlichen Diencephalon. *Abhandlungen der Königlichen Academie der Wissenschaften zu Berlin, Physicalisch-mathematische Classe*.
- VON MONAKOW, C. 1895 Experimentelle und pathologisch-anatomische Untersuchungen über die Haubenregion, der Sehhügel und die Regio subthalamica. *Arch. f. Psych. u. Nervenkr.*, Bd. 27, S. 1 and 386.
- 1905 *Gehirnpathologie*. Hölder, Wien.
- MORGAN, L. O. 1927 A study of secondary degenerations following lesions of the corpus striatum in man and symptoms and acute degenerations following experimental lesions in the corpus striatum of cats. *Arch. of Neur. and Psychiat.*, vol. 18, p. 495.
- 1927 a Symptoms and fiber degeneration following experimental lesions in the subthalamic nucleus of Lays in the dog. *Jour. Comp. Neur.*, vol. 44, p. 379.
- PAPEZ, JAMES W. 1929 *Comparative neurology*. Thomas Y. Crowell Co., New York.
- RAMÓN Y CAJAL, S. 1911 *Histologie du système nerveux de l'homme et des vertébrés*, T. 2. Maloine, Paris.
- RIOCH, D. MCK. 1929 Studies on the diencephalon of Carnivora. Part I. The nuclear configuration of the thalamus, epithalamus, and hypothalamus of the dog and cat. *Jour. Comp. Neur.*, vol. 49, p. 231.
- TSAI, CHIAO 1925 The optic tracts and centers of the opossum, *Didelphis virginiana*. *Jour. Comp. Neur.*, vol. 39, p. 173.
- 1925 The descending tracts of the thalamus and midbrain of the opossum, *Didelphis virginiana*. *Ibid.*, vol. 39, p. 217.
- WINKLER, C., AND POTTER, ADA 1914 An anatomical guide to experimental researches on the cat's brain. Versluys, Amsterdam.

PLATES

PLATE I

EXPLANATION OF FIGURES

1 Transverse section through the level of the nucleus subthalamicus. Adult cat. Toluidin-blue preparation (1928.143:1). $\times 7$. *acq.*, aqueductus; *a.pretect.*, arca pretectalis; *com.post.*, commissura posterior; *f.*, fornix; *H₁*, field H₁ of Forel; *H₂*, field H₂ of Forel; *l.m.e.*, lamina medullaris externa; *l.m.i.*, lamina medullaris interna; *n.com.post.*, nuclei commissurae posterioris; *n.g.l.d.parr.*, nucleus geniculatus lateralis dorsalis, lamina parvocellularis; *n.g.l.d.pr.p.*, nucleus geniculatus lateralis dorsalis, lamina principalis posterior; *n.g.m.m.*, nucleus geniculatus medialis, pars magnocellularis; *n.g.m.pr.*, nucleus geniculatus medialis, pars principalis; *n.H₂*, nucleus of the field H₂ of Forel; *n.lent.mes.*, nucleus lenticularis mesencephali; *n.mam.lat.*, nucleus mamillaris lateralis; *n.mam.med.*, nucleus mamillaris medialis; *n.paraf.*, nucleus parafascicularis; *n.sub-paraf.*, nucleus subparafascicularis; *n.subthal.*, nucleus subthalamicus; *n.supra-gen.*, nucleus suprageniculatus; *n.supra-mam.*, nucleus supramamillaris; *n.vent.arc.*, nucleus ventralis, pars arcuata; *n.vent.ant.*, nucleus ventralis, pars anterior; *n.vent.ext.*, nucleus ventralis, pars externa; *ped.cer.*, pedunculus cerebri; *periv.gr.*, periventricular gray; *tr.hab.ped.*, tractus habenulo-peduncularis; *tr.mam.thal.*, tractus mamillo-thalamicus; *tr.opt.*, tractus opticus; *vent. III.*, ventriculus tertius; *zinc.caud.*, zona incerta caudalis; *zinc.pr.*, zona incerta proper.

2 Transverse section through the level of the root of the oculomotor nerve. Adult cat. Toluidin-blue preparation (1928.105:1). $\times 7$. *acq.*, aqueductus; *br.col.inf.*, brachium colliculi inferioris; *col.sup.*, colliculus superior; *com.col.sup.*, commissura colliculi superioris; *f.l.m.*, fasciculus longitudinalis medialis; *l.m.*, lemniscus medialis; *n.cent.teg.*, nucleus centralis tegmenti; *n.com.post.*, nuclei commissurae posterioris; *n.Dark.*, nucleus of Darkschewitseh; *n.E.-W.*, nucleus of Edinger-Westphal; *n.f.l.m.*, nucleus fasciculi longitudinalis medialis; *n.inter-ped.*, nucleus interpeduncularis; *n.interst.teg.*, nucleus interstitialis tegmenti; *n.lat.teg.*, nucleus lateralis tegmenti; *n.N.III.*, nucleus nervi oculomotorii; *n.rub.*, nucleus ruber; *n.tr.ped.tr.*, nucleus tractus peduncularis transversi; *n.vent.teg.*, nucleus ventralis tegmenti; *N.III.*, nervus oculomotorius; *ped.cer.*, pedunculus cerebri; *s.n.comp.*, substantia nigra compacta; *s.n.ret.*, substantia nigra reticularis; *str.alb.med.*, stratum album mediale; *str.alb.pro.*, stratum album profundum; *str.gr.cent.*, stratum griseum centrale; *str.gr.med.*, stratum griseum mediale; *str.gr.pro.*, stratum griseum profundum; *str.gr.sup.*, stratum griseum superius; *str.opt.*, stratum opticum; *str.z.*, stratum zonale; *tr.hab.ped.*, tractus habenulo-peduncularis; *tr.ped.tr.*, tractus peduncularis transversus.

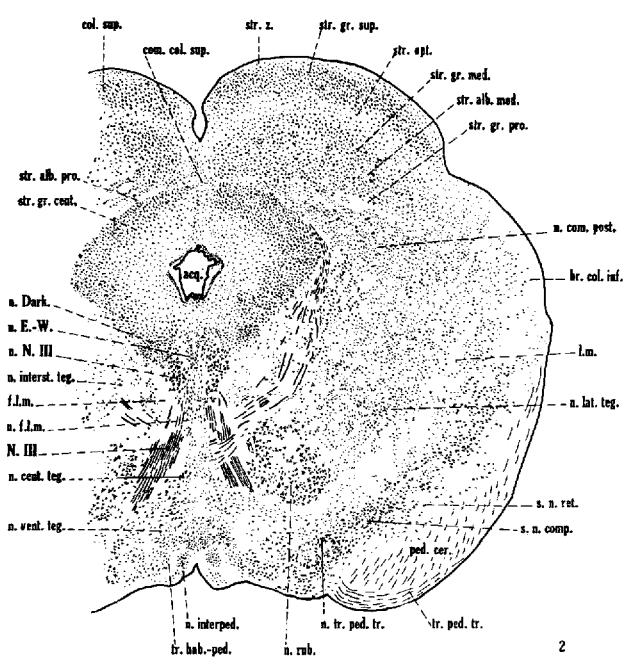
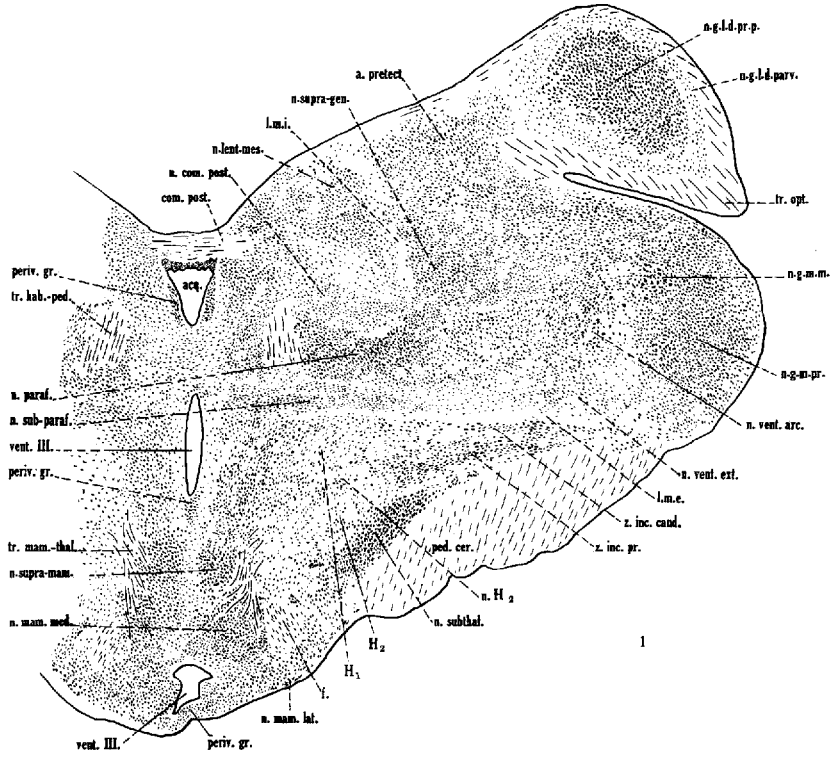


PLATE 2

EXPLANATION OF FIGURES

3 Transverse section through the level of the anterior margin of the pons. Adult cat. Toluidin-blue preparation (1928.90:1). $\times 7$. *acq.*, aqueductus; *br.col.inf.*, brachium colliculi inferioris; *br.pont.*, brachium pontis; *col.inf.*, colliculus inferior; *com.col.inf.*, commissura colliculi inferioris; *dec.ped.cer.sup.*, decussatio pedunculi cerebelli superioris; *dec.teg.dor.*, decussatio tegmenti dorsalis; *f.l.m.*, fasciculus longitudinalis medialis; *l.l.*, lemniscus lateralis; *l.m.*, lemniscus medialis; *n.cent.teg.*, nucleus centralis tegmenti; *n.f.l.m.*, nucleus fasciculi longitudinalis medialis; *n.interped.*, nucleus interpeduncularis; *n.lat.teg.*, nucleus lateralis tegmenti; *n.l.l.*, nucleus lemnisei lateralis; *n.N.IV.*, nucleus nervi trochlearis; *n.N.V.mes.*, nucleus nervi trigemini mesencephalici; *n.pont.lat.*, nucleus pontis lateralis; *ped.cer.*, pedunculus cerebri; *pons*, pons; *s.n.comp.*, substantia nigra compacta; *str.gr.cent.*, stratum griseum centrale; *tr.rub.sp.*, tractus rubro-spinalis; *tr.tect.sp.med.*, tractus tecto-spinalis medialis.

4 Sagittal section passing through diencephalon just medial to the geniculate bodies. Adult cat. Toluidin-blue preparation (1928.80:2). $\times 7$. *a.prcopt.*, area preoptica; *a.prectect.*, area pretectalis; *ch.opt.*, chiasmum opticum; *col.inf.*, colliculus inferior; *col.sup.*, colliculus superior; *com.ant.*, commissura anterior; *com.post.*, commissura posterior; *H₁*, field H₁ of Forel; *H₂*, field H₂ of Forel; *l.l.*, lemniscus lateralis; *l.m.*, lemniscus medialis; *n.caud.*, nucleus caudatus; *n.entoped.*, nucleus entopeduncularis; *n.lat.ant.*, nucleus lateralis anterior; *n.lat.inter.*, nucleus lateralis intermedius; *n.lat.post.v.*, nucleus lateralis pars posterior, portio ventralis; *n.lat.teg.*, nucleus lateralis tegmenti; *n.pont.lat.*, nucleus pontis lateralis; *n.post.*, nucleus posterior; *n.ret.*, nucleus reticularis; *n.subthal.*, nucleus subthalamicus; *n.supra-gen.*, nucleus suprageniculatus; *n.tang.*, nucleus tangentialis; *n.vent.ant.*, nucleus ventralis, pars anterior; *n.vent.arc.*, nucleus ventralis, pars arcuata; *n.vent.ext.*, nucleus ventralis, pars externus; *ped.cer.*, pedunculus cerebri; *ped.cer.sup.*, pedunculus cerebelli superioris; *pons*, pons; *pul.*, pulvinar; *s.n.comp.*, substantia nigra compacta; *s.n.ret.*, substantia nigra reticularis; *z.inc.pr.*, zona incerta proper.

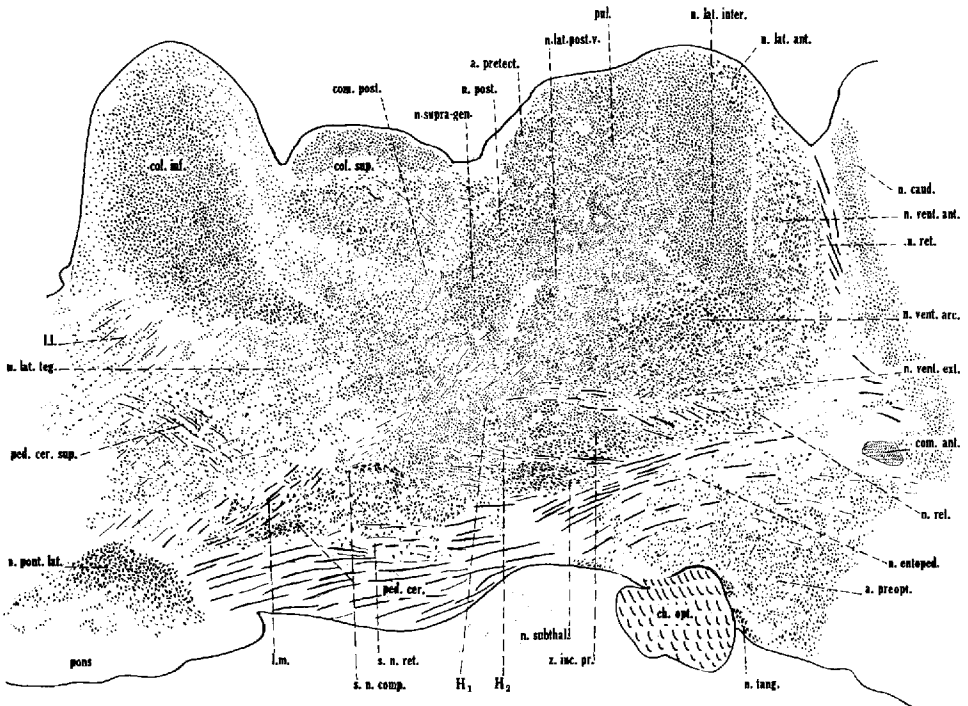
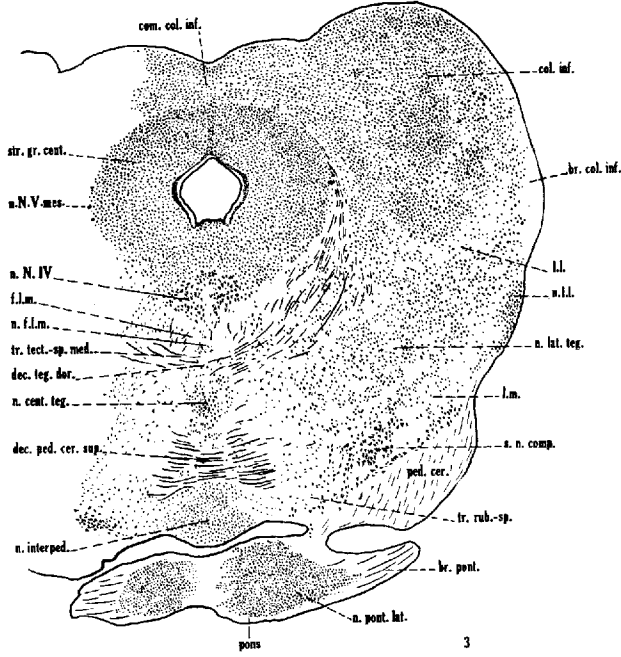
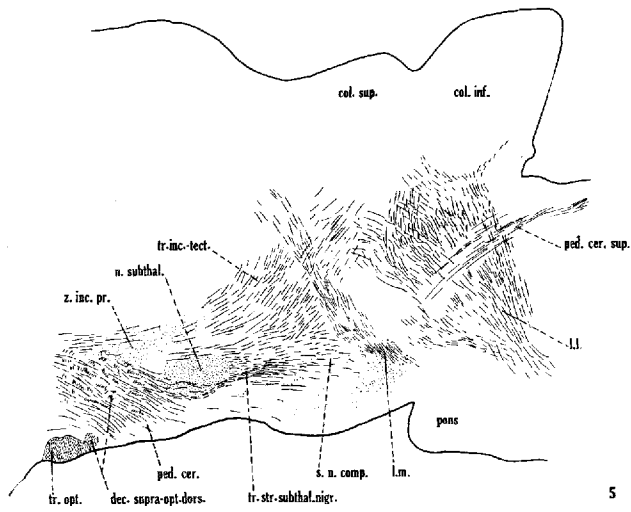


PLATE 3

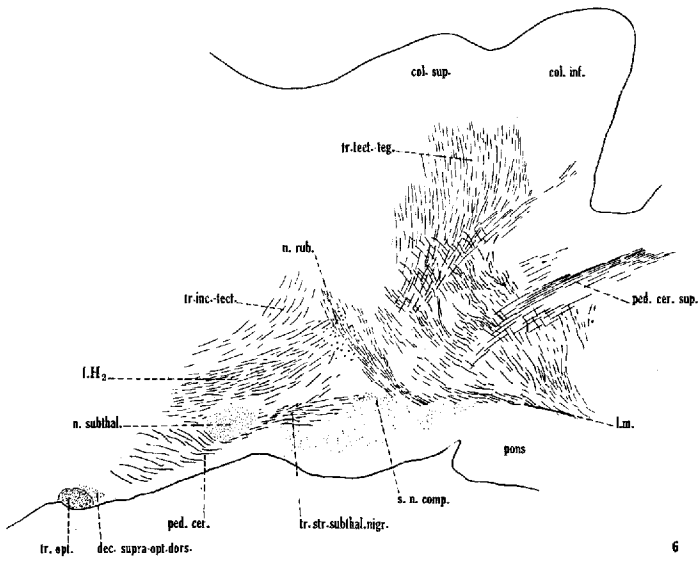
EXPLANATION OF FIGURES

5 Sagittal section in a plane through the lateral margin of the superior cerebellar peduncle. Three-day-old puppy. Pyridine-silver preparation (1929.77:5). $\times 10$. *col.inf.*, colliculus inferior; *col.sup.*, colliculus superior; *dec.supra-opt.dors.*, decussatio supra-optica dorsalis; *ll.*, lemniscus lateralis; *lm.*, lemniscus medialis; *n.subthal.*, nucleus subthalamicus; *ped.cer.*, pedunculus cerebri; *ped.cer.sup.*, pedunculus cerebelli superioris; *pons*, pons; *s.n.comp.*, substantia nigra compacta; *tr.inc.tect.*, tractus incerto-tectalis; *tr.opt.*, tractus opticus; *tr.str.subthal.nigr.*, tractus strio-subthalamico-nigralis; *z.inc.pr.*, zona incerta proper.

6 Sagittal section in a plane through the lateral margin of the red nucleus. Three-day-old puppy. Pyridine-silver preparation (1929.37:1). $\times 10$. *col.inf.*, colliculus inferior; *col.sup.*, colliculus superior; *dec.supra-opt.dors.*, decussatio supra-optica dorsalis; *f.H₂*, fasciculus lenticularis of Forel; *lm.*, lemniscus medialis; *n.rub.*, nucleus ruber; *n.subthal.*, nucleus subthalamicus; *ped.cer.*, pedunculus cerebri; *ped.cer.sup.*, pedunculus cerebelli superioris; *pons*, pons; *s.n.comp.*, substantia nigra compacta; *tr.inc.tect.*, tractus incerto-tectalis; *tr.opt.*, tractus opticus; *tr.str.subthal.nigr.*, tractus strio-subthalamico-nigralis; *tr.tect.teg.*, tractus tecto-tegmentalis.



5



6

PLATE 4

EXPLANATION OF FIGURES

7 Transverse section passing through the red nucleus behind the level of the exit of the oculomotor nerve. Three-day-old puppy. Pyridine-silver preparation (1929.87: 5). $\times 5\frac{1}{2}$. *acq.*, aqueductus; *col.sup.*, colliculus superior; *n.E.-W.*, nucleus of Edinger-Westphal; *n.interped.*, nucleus interpeduncularis; *n.N.III.*, nucleus nervi oculomotorii; *n.N.V.mes.*, nucleus nervi trigemini mesencephalici; *n.rub.*, nucleus ruber; *ped.cer.*, pedunculus cerebri; *s.n.comp.*, substantia nigra compacta; *s.n.ret.*, substantia nigra reticularis; *str.alb.pro.*, stratum album profundum; *tr.nigro-tect.lat.*, tractus nigro-tectalis lateralis; *tr.nigro-tect.med.*, tractus nigro-tectalis medialis; *tr.nigro-teg.*, tractus nigro-tegmentalis; *tr.str.nigr.*, tractus strio-nigralis; *tr.tect.nigr.*, tractus tecto-nigralis; *tr.tect.rub.lat.*, tractus tecto-rubralis lateralis; *tr.tect.rub.med.*, tractus tecto-rubralis medialis.

8 Transverse section through the level of the rostral pole of the nucleus geniculatus lateralis dorsalis. Adult dog. Toluidin-blue preparation (1928. 258: 1). $\times 5\frac{1}{2}$. *a.pretect.*, area pretektalis; *f.*, fornix; *H₁*, field H₁ of Forel; *H₂*, field H₂ of Forel; *lat.hyp.*, lateral hypothalamic area; *n.cent.lat.*, nucleus centralis lateralis; *n.cent.med.*, nucleus centralis medialis; *n.entoped.*, nucleus entopeduncularis; *n.g.l.d.parr.*, nucleus geniculatus lateralis dorsalis, lamina parvocellularis; *n.g.l.d.pra.*, nucleus geniculatus lateralis dorsalis, lamina principalis anterior; *n.g.l.d.prp.*, nucleus geniculatus lateralis dorsalis, lamina principalis posterior; *n.g.m.m.*, nucleus geniculatus medialis, pars magnocellularis; *n.g.m.pr.*, nucleus geniculatus medialis, pars principalis; *n.hab.lat.*, nucleus habenularis lateralis; *n.hab.med.*, nucleus habenularis medialis; *n.hyp.post.*, nucleus hypothalamicus posterior; *n.inter-vent.*, nucleus commissuralis interven-tralis; *n.lat.post.d.*, nucleus lateralis pars posterior, portio dorsalis; *n.lat.post.m.*, nucleus lateralis pars posterior, portio medialis; *n.lat.post.v.*, nucleus lateralis pars posterior, portio ventralis; *n.mam.lat.*, nucleus mamillaris lateralis; *n.mam.med.*, nucleus mamillaris medialis; *n.med.dor.*, nucleus medialis dorsalis; *n.paraf.*, nucleus parafascicularis; *n.paravent.post.*, nucleus paraventricularis posterior; *n.ret.*, nucleus reticularis; *n.sub-paraf.*, nucleus subparafascicularis; *n.subthal.*, nucleus subthalamicus; *n.supra-mam.*, nucleus supramamillaris; *n.tr.h.-p.l.*, nucleus tractus habenulo-peduncularis lateralis; *n.tr.h.-p.m.*, nucleus tractus habenulo-peduncularis medialis; *n.vent.arc.*, nucleus ventralis, pars arcuata; *n.vent.ext.*, nucleus ventralis, pars externus; *ped.cer.*, pedunculus cerebri; *periv.gr.*, periventricular gray; *pul.*, pulvinar; *str.med.*, stria medullaris; *subs.gr.pre-gen.*, substantia grisea pregeniculata; *tr.mam.thal.*, tractus mamillo-thalamicus; *tr.opt.*, tractus opticus; *zinc.pr.*, zona incerta proper.

9 Neurones of the nucleus ruber, showing axones passing dorsolaterally into the tegmentum and ventrolaterally toward the substantia nigra. The relative sizes of the types of cells are also shown. Three-day-old puppy. Pyridine-silver preparation (transverse series 1929.81: 6). $\times 167$.

