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LOYOLA UNIVERSITY SCHOOL OF MEDICINE
THE EMBRYOLOGY AND FIBER TRACT CONNECTIONS OF THE
CORPUS STRIATUM IN THE ALBINO RAT.

A THESIS
SUBMITTED TO THE FACULTY
of the
GRADUATE SCHOOL
of
LOYOLA UNIVERSITY
IN
CANDIDACY FOR THE
DEGREE OF MASTER OF SCIENCE

by
James K.L. Choy, B.S.M.
1935

THE EMBRYOLOGY AND FIBER TRACT CONNECTIONS OF
THE CORPUS STRIATUM IN THE ALBINO RAT.

I. PREFACE

Before entering upon a discussion of the problem itself, I would like to take this opportunity to acknowledge the assistance and encouragement I received in the preparation of this paper. To Dr. R. M. Strong, who suggested the problem, I am deeply obligated for his encouragement, practical guidance, and helpful suggestions in the procedure of this work. Mr. Warren's advice in fixation, embedding, sectioning, and staining of the material was of inestimable value in this study. I also wish to thank Mr. Kirkland for generously allowing me the use of the slides prepared by him.

In the albino rat, the anatomy and relationship of the corpus striatum differ slightly, and perhaps significantly from the standpoint of phylogeny and function, from the conditions obtained in the human brain. These differences according to Gurdjian, E.S. are:¹

1. The so-called putamen is not connected with the caudate nucleus in the antero-inferior aspect of the latter but is connected rostrally with the caudate nucleus at the crossing of the anterior commissure.

2. The globus pallidus is not divided into two smaller parts but appears as one structure.

(1)

(1) Gurdjian, E.S. 1928. The Corpus striatum of the Albino Rat. J. Comp. Neur., Vol. 45-46: P.249-281
10. Figs.

Although Kappers, Johnston, and Winkler, have all worked on the corpus striatum of various mammals, Gurdjian is the only one to have done any work on the corpus striatum of the albino rat. He described in detail the different parts of the corpus striatum in the adult rat and emphasized especially the absence of the so-called body and tail of the caudate nucleus.

II. METHODS AND MATERIALS

The dual nature of the problem necessitated two separate and more or less correlated technical procedures. The embryological method involved the use of serial sections of albino rat brains covering a period of thirteen days prenatal to seven days postnatal. The models illustrating the embryology of the composite parts of the corpus striatum were made by the paper reconstruction method. The image of every other cross section of a complete series, starting at the cephalic end and going caudad, was projected on the cardboard from the projection lantern and set up in such a position to give a magnification of twenty-two times. The outlines of the images, including the ventricles, were drawn. The next step was to cut out the same, carefully pile and paste successive drawings on one another.

Photographs were taken of those sections which are illustrative of the significant aspects of the embryology and fiber tracts connections of the corpus striatum. These photographs are reproduced in the body of the paper to make clearer the

written exposition. The plane of section of each reproduction is described below the figure.

The study of the fiber connections entailed a specialized technique of preparation of albino rat brains covering a period from approximately at birth to two weeks postnatal. Laboratory albino rats of different litters were killed by ether and then decapitated. A small opening was made in the skull at the confluens sinus. From this point, small portions of bone were dissected away with much care. The whole brain together with a portion of the spinal cord enclosed in the skull bones was then fixed in ^{to}_{in} 10% formalin. The next day the bones of the skull were removed carefully under the dissecting microscope with a pair of small scissors and a pair of fine forceps. Finally, the dura was peeled gently off and the brain again immersed in 10% formalin for another twenty-four hours. After forty-eight hours of fixation it was washed, carried through various grades of alcohol, embedded in paraffin, and serial sections made with a thickness of twenty microns. Serial transverse sections formed the main bulk of the material studied, but this was supplemented by sections cut longitudinally in the saggittal plane.

After the material had been prepared as indicated above, the selection of specific stains became important. Although the Weigert-Kuitsinsky and the Weil stains are reputedly specific for myelinated fibers, they were found to be of

little value in this study. Their failure in this instance may be attributed, perhaps, to the fact that the material used was too young. The myelinated fibers present may not have had the chemical characteristics of adult material.

The use of the staining method of Cajal for neurofibrillae, of Weigert-Iron-Hematoxylin for myelinated fibers, and of Nissl's stain for chromodial substance completed the preparation of the material.

III. Results From the Study of the Embryology of the Corpus Striatum.

Thirteen days and seventeen hours prenatal.

In Figure #1 the corpus striatum is seen as an area of proliferation which by extensive thickening evaginates into the lateral ventricles. Figure #2 is a section made further caudally and ventrally to that of figure #1. In the second photograph the corpus striatum in gross structure is an almond shaped mass projecting into the lateral ventricle. Its length (antero-posteriorly) is 10mm. and its width (dorso-ventrally) is 9mm., A fissure, the Fissura Neo-paleostriatica, is seen as a groove only incompletely dividing the corpus striatum into two hill-like structures. This fissure is approximately one-half mm. in depth; its length is 8.12mm. In Figure #2, the fissure is shown sectioned through its deepest part. Its long dimension is perpendicular to the plane of section. The dorso-lateral hill, called the neostriatum, represents the primordia of the caudate nucleus and of the

caudate-putamen nucleus. The ventro-medial hill, the larger and more prominent of the two elevations, is called the paleostriatum. It is contiguous with the thalamic region and is the primordium of the globus pallidus.

Microscopic examination of the cells in the proliferative region (as in Figure #1) reveals them as small, round, and undifferentiated. Even in the more caudal and ventral section (as seen in Figure #2) where the Fissura Neo-palaestriatica has partly divided the primordium of the corpus striatum into two parts, we find that the cells of the paleostriatum and neostriatum are similar. The cells in both are more or less round to ovoid in outline and rather deeply stained. They cannot be distinguished. At this early stage no sharp line of demarcation between the primordia of the corpus striatum and of other regions in the cerebral cortex.

The primordium of the pia mater is rich in blood vessels. An extensive capillary plexus is seen extending into the mantle layer and is particularly abundant in the region of the two hillocks.

No fibers leading to or away from the striate body are discernible at this stage.

Fifteen Days Prenatal

The corpus striatum which at thirteen days and seventeen hours prenatal was an almond shaped mass grooved by the Fissura Neopaleostriatica has undergone two obvious gross

changes. First, the Fissura Neopaleostriatica has disappeared. Second, by cell proliferation the size of the mass of cells projecting into the lateral ventricles has increased absolutely. This growth is due to the increase in number of cells in situ, the multiplication of cells occurring in both the ependymal and periependymal or mantle zones. A lighter stained area, the primordium of the lenticular nucleus, is easily seen. (See Figure #3). The lenticular anlage is bounded laterally by a prominent white capsular band. This capsule separates the striate portion from the cortical zones of the cerebral cortex. The entire striatal body at this stage measures 13.86 mm. The anterior posterior length of the caudate material is 5.94 mm. The anterior - posterior dimension of the lenticular anlage is 12.76 mm.

Even upon microscopic examination no indication of the differentiation of lenticular anlage into the adult state of caudate - putamen and globus pallidus can be detected. Examination under high power of this area reveals the presence of numerous fibers. The comparative lightness of the region of the lenticular anlage is due to the numerous fibers present. Scattered between these fibers are a few cells having dark staining nuclei. These cells cannot be differentiated morphologically from those comprising the dark stained mass of cells protruding into the ventricle. This light area is the primordium of the lenticular nucleus which has not as

yet differentiated into the globus pallidus and caudate putamen - - the condition found in the adult.

Seventeen days sixteen hours prenatal.

At this stage, the anlage of specific structures in the lateral part of the protruded mass of densely nucleated cells is grossly visible. The lenticular portion of the striated complex has assumed the condition of the adult; i.e., the caudate-putamen and the globus pallidus are set up. The shape of the entire lenticular structure is biconvex. (See Figure #1). Note that the globus pallidus is a conspicuous feature. In the region of the diencephalon, the shape of the caudate-putamen is convex laterally and concave medially. The external capsule separates the lenticular structure laterally from the cortical substance. Medially the internal capsule, composed of fibers radiating from the thalamus and projecting into the cortex of the cerebral hemisphere, separates the lenticular structure from the caudate nucleus.

The anterior posterior extent of the globus pallidus is 8.8 mm. The anterior posterior extent of the undifferentiated caudate-putamen region is 11.64 mm. The striatal complex as a whole is 20.51 mm. in length.

Turning now from the gross evidences of embryological development to a microscopic examination of the material, we find the cells in the various regions begin to specialize.

The cells are small to ovoid. In character. In the vicinity of the internal capsule there is present a small group of cells taking a slightly deeper stain in comparison with the lenticular region in general. These cells are lighter and larger in appearance, however, than those which comprise the caudate nucleus. In the caudate and caudate-putamen regions a few large cells are intermixed with the small ovoid cells which predominate.

Throughout the corpus striatum, fibers can be distinguished lying between the cells. Some of these fibers terminate close to individual cell bodies. Near the termination of the hemisphere fibers seem to connect the thalamic region with the corpus striatum. (See Figure #5).

Nineteen Days Seventeen Hours Prenatal

While there is no significant or appreciable change in the caudal expansion of the telencephalon, the constituent parts of the corpus striatum have undergone growth and development. The overall length of the corpus striatum is 23.50 mm. More direct and evident relationships to surrounding structures than could be seen in earlier stages are now set up. In the rostral region, the corpus callosum has formed and together with the internal capsule surrounds the corpus striatum cephalically, dorsally, and laterally. The anterior commissure has become noticeable. The intertemporal portion

of the anterior commissure has appeared. This is significant for it is this portion of the anterior commissure which marks the boundary between the caudate and caudate-putamen. The caudate nucleus is 13.50 mm. long antero-posteriorly and has a maximum width of 0.75 mm. The caudate-putamen is semi-lunar in shape having a convex surface with the concavity on the medial aspect. Its antero-posterior length is 10.8 mm. The appearance of the caudate-putamen is simultaneous with that of the globus pallidus which is located on its inferior medial aspect. The globus pallidus is an ovoid or spherical body 1.50 mm. long antero-posteriorly.

The increasing specialization of the corpus striatum is evidenced also by the increase in fibers. The globus pallidus, for example, is much less nucleated and larger than in earlier stages. The cells which are present lie in between the numerous fibers bundles. The cells are smaller than they appear in the adult. Fibers now definitely connect the globus pallidus or caudate-putamen with the thalamus.

At Birth and 7 Days Postnatal.

There is no important change in the gross anatomy and structure relationships in the development of the corpus striatum at this stage other than increase in size. At birth the striate body is 27.50 in length; whereas at seven days postnatal it is 34.80 mm. long.

The component parts of the corpus striatum undergo growth in the seven days afterbirth relatively equally. The caudate nucleus is 14.40 mm. long antero-posteriorly at birth and 16.65 mm. long at seven days postnatal. The caudate-putamen is 12.60 mm. long antero-posteriorly at birth and 19.20 mm. long at seven days. The antero-posteriorly length of the globus pallidus is at birth 12.60 mm. and at seven days 19.20 mm.

The caudate nucleus extends cranially to the anterior extremity of the corpus callosum. (See Fig. 6). It does not extend dorsally into the medial and dorsolateral aspects of the internal capsule. Hence it lacks that portion usually termed the body and tail of the caudate nucleus. The caudal limit of the caudate nucleus becomes continuous with so-called caudate-putamen in the plane where the anterior commissure crosses the mid-plane. (See Fig. 7)

The gross appearance of the material at these two stages indicates a definite segregation of the composite parts of the corpus striatum. This differentiation is at most points verifiable by comparison of the histologic pictures of the composite parts. The globus pallidus is composed of many fiber bundles between which may be found medium and large sized cells with the latter predominating. These large cells are morphologically similar to the projection cells of the motor cortex. The caudate nucleus consists of

small, oval or spherical, dark-staining cells. The histological structure of the caudate is so similar to that of the caudate-putamen that the two regions can hardly be differentiated. The cranial portion of the caudate-putamen, however, is characteristically traversed by many fiber bundles.

Microscopically the pallidal region is characterized by the presence of cells which are relatively few in number but are large in comparison with those of the caudate or caudate-putamen area. (See Figs. 13 & 15). In the globus pallidus are seen multipolar cells which are large and pyramidal in shape. There is a relatively thick dendrite in the form of a narrow cone arising from the apical region of the cell body. The nucleus is eccentrically placed in the cytoplasm which is not abundant and forms a cap around the nucleus. The nucleolus is well defined and the chromidial substance appears to be distributed densely in the peripheral cytoplasm of the cell. A small portion of the basophilic granules may be seen extending into the thick apical dendrite. In addition there are small round cells relatively few in number to be seen scattered among the larger cells.

Small round cells compose the greater part of the caudate and the caudate-putamen areas. (See Figs. 13 & 15). The apical dendrites are short, in comparison to the rather long dendrites found in the pallidal region. Very thin dendrites are found protruding and extending from various

positions of the cell body.

FIBER CONNECTIONS:

We have seen in the foregoing material that fibers appear contemporaneously with the differentiation or specialization of the composite structures of the corpus striatum. These fibers have a significance in that they are an index to the embryological development of the corpus striatum. Furthermore, in previous papers on correlation of function and structure of the striate body, great emphasis has been placed on the time of myelination of fibers comprising specific tracts related to that body. Such studies necessitated the use of a specialized staining technique. Among the researches on myelination time we find the work of Donaldson, Sugita, and Watson significant. Each used a different technique. Their results are very harmonious. The method of study employed here has disclosed some new information.

Donaldson ('15) and Sugita ('17) by a technique involving the extraction by alcohol of the alcohol soluble lipoids, such as occur in myelin sheaths, found that with age there is an progressive loss of weight of the rat brain as indicated by the ratio to initial brain weight. This loss of weight is due to the increase in alcohol soluble lipoids. From this work it was inferred that myelin sheath formation is most rapid in the albino rat brain between the eleventh and thirty-third day.

In his studies on myelination in the nervous system of the rat Watson found the first evidence of myelin formation shortly after birth in the cervical region of the cord. Myelin sheaths appear next in the cerebellum and finally in the cerebrum at about eleven days. Although Watson gives the myelination time for the corpus callosum as appearing at 14 days, it was found in this study by the use of Weigert's Iron Hematoxylin stain that myelinated fibers are present in the corpus callosum even as early as one day after birth. In the case of the corpus striatum, however, the results here agree with the findings of Watson. In the corpus striatum very little myelination exists for the first 14 days. After that it progresses rapidly.

The discrepancy between the findings here and those of Watson are cited merely to indicate that differences in technique may account for many apparently inharmonious conclusions as to the structure of the striate body.

RESULTS:

2 Weeks Postnatal.

With the Cajal and the Weigert Iron Hematoxylin technique fiber relationships between the cortex and the corpus striatum, and further, between the composite parts of the corpus striatum itself were brought out.

In Figures #9 and 12 will be seen numerous fibers emanat-

ing from the cortical layers. These cross the corpus callosum and terminate in the caudate area. This region is very noticeable in the above mentioned figures. The fibers, on high power and oil immersion examination reveal relationship suggestive of synapses with the small round cells of the caudate region of the striated complex.

Similar fibers are also seen to enter the caudate and caudate-putamen regions. Fibers emerging from the cortical layers proceed through the corpus callosum and the caudate-putamen. Here again we have a spatial relationship highly suggestive of synapses with cells in the globus pallidus. Figures #10 and 12 are very good examples of the conditions of the fiber relations.

Within the caudate-putamen area, we find intrinsic fiber connections between the individual parts. The globus pallidus is definitely related structurally to the caudate-putamen and the lateral nucleus of the thalamus by very conspicuous fiber tracts. (See Figure #11). Fibers from the dorsal or anterior nucleus of the thalamus enter the caudate-putamen area. (Figure #11).

In sagittal sections, we note fiber connections taking their origin from the ^rprojections neurones of the cerebral cortex and crossing the corpus callosum to terminate in the caudate or caudate-putamen. Intrinsic fibers from the caudate-putamen proceed to the globus pallidus. From the large

cells of the globus pallidus fibers stream caudoventrally in the medial aspect as the ansa lenticularis to the hypothalamic area, red nucleus, and the substantia nigra. (See Fig. 14)

I IV. Summary:

The corpus striatum in the albino rat is composed of the caudate nucleus, caudate-putamen and the globus pallidus. The striate body arises as a proliferation of cells from the basal part of the telencephalon. By further differential growth and specialization of the primordial cells the composite parts develop. At 13 days prenatal, two hillocks have formed, separated by the Fissura Neoplaeustricatica. These hillocks will develop the composite parts of the corpus striatum. At 13 days prenatal, the stage common to all phyla in the development of the corpus striatum has ended and the lenticular anlage is definitely established. The globus pallidus makes its appearance and fiber connections between the thalamus and the striatal complex are set up by the 19th day prenatal. The 19th day prenatal finds the anterior commissure appearing as a definite structure whose fibers separate the caudate nucleus from the caudate-putamen. At this time, too, the thalamus has established fiber connections with the caudate-putamen and with the globus pallidus which has begun to differentiate. At birth and 7 days postnatal the striatal complex has assumed the adult appearance.

The 1 day and 7 days postnatal material only faintly exhibited any fiber connections. But at the 14th day postnatal (at which time myelination has progressed sufficiently to make the fiber tracts plain) certain fiber connections, intrinsic and extrinsic are established. The extrinsic connections are:

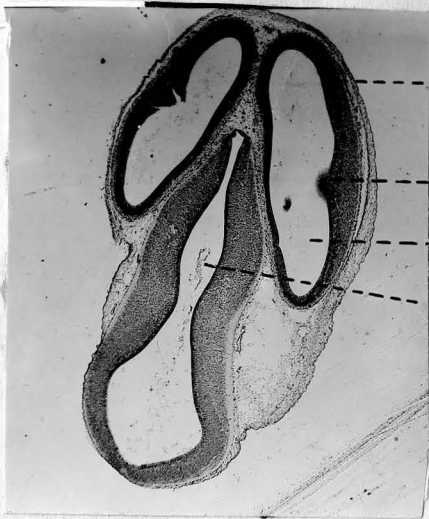
1. Cortex to caudate nucleus
2. Cortex to caudate-putamen
3. Cortex to globus pallidus
4. The thalamus to globus pallidus
5. The thalamus to caudate-putamen
6. The globus pallidus to the hypothalamic area, the red nucleus, and the substantia nigra by way of the ansa lenticularis.

The intrinsic connections are:

1. Caudate to globus pallidus
2. Caudate-putamen to globus pallidus.

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5. Watson. 1905. Animal education. Con. From the Psychol. Lab. Univ. of Chicago, Vol. 4: pp. 5-122. Plates showing medullation of the nervous system at various ages. (Studies on myelination in the Nervous System of the Rat).



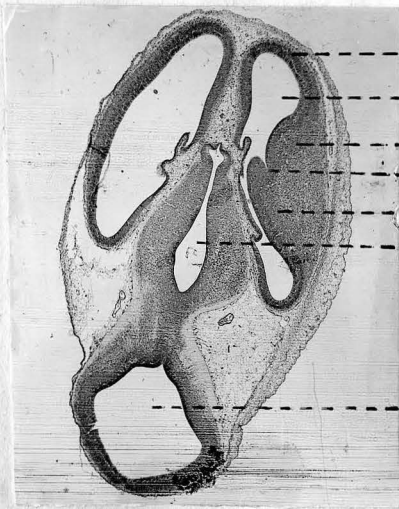
--- Cerebral hemispheres

--- Primordium of the Corpus Striatum

--- Lateral ventricle

--- Third ventricle

Fig. I. Oblique-transverse section of 13 days and 17 hours prenatal albino rat brain showing the cephalic portion of the corpus striatum. xl4.



--- Cerebral hemispheres

--- Lateral ventricle

--- Neostriatum

--- Fissure Neoplaeostriatica

--- Palaeostriatum

--- Third ventricle

--- Fourth ventricle

Fig. II. Oblique-transverse section of 13 days and 17 hours prenatal albino rat brain through corpus striatum. xl6.

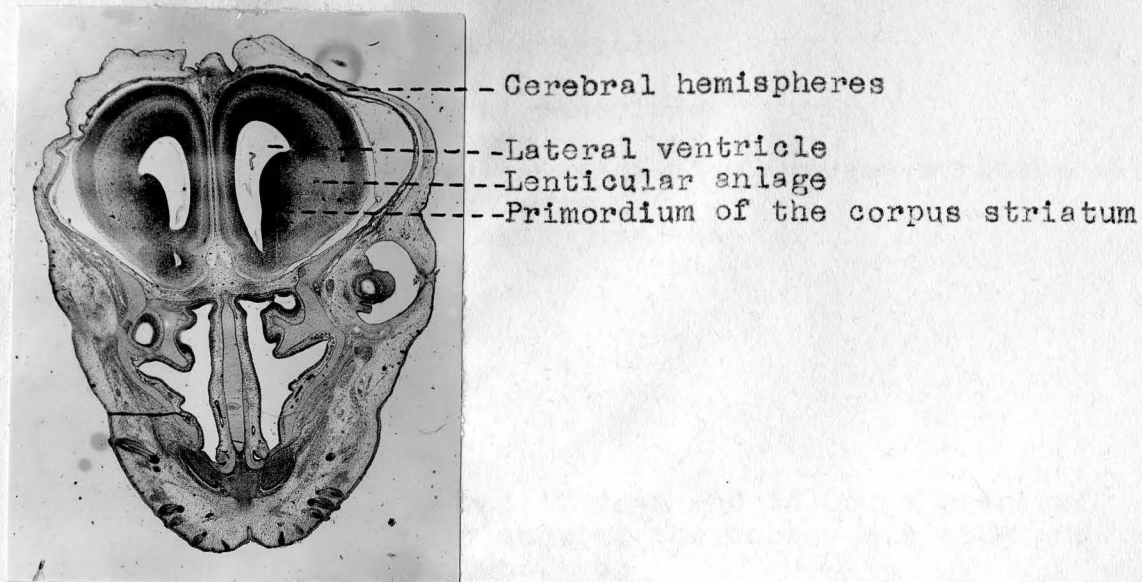


Fig. III. Transverse-section of 15 days prenatal albino rat brain through corpus striatum. $x6\frac{1}{2}$

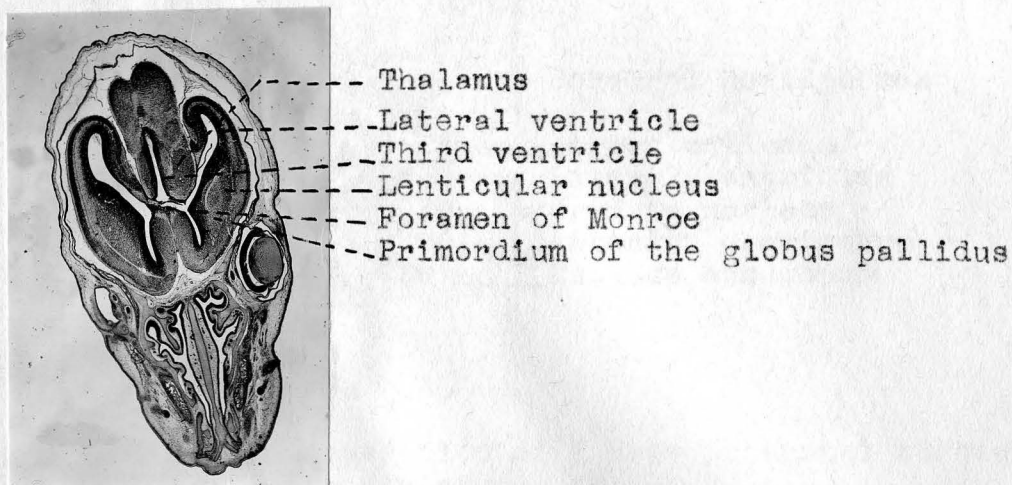
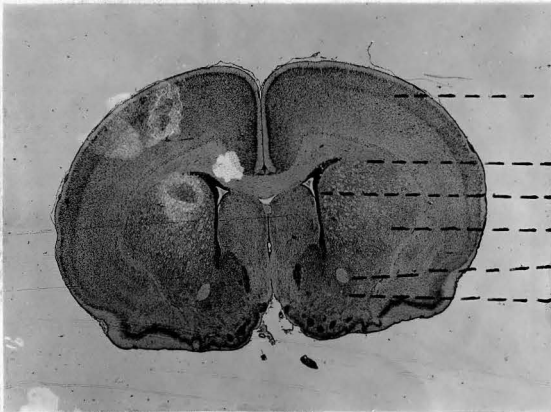


Fig. IV. Oblique-section of 17 days and 16 hours. prenatal albino rat brain to show corpus striatum. $x6\frac{1}{2}$



- Third ventricle
- Lateral ventricle
- Thalamus
- Fiber connections of corpus striatum with thalamus
- Lenticular nucleus

Fig. V. Oblique-section of 17 days and 16 hours prenatal albino rat brain showing the corpus striatum and thalamus in contact. $6\frac{1}{2}$



- Cerebral hemispheres
- Corpus callosum
- Lateral ventricles
- Caudate nucleus
- Anterior commissure
- Nucleus accumbens

Fig. VI. Transverse-section of 7 days postnatal through the corpus striatum. x8

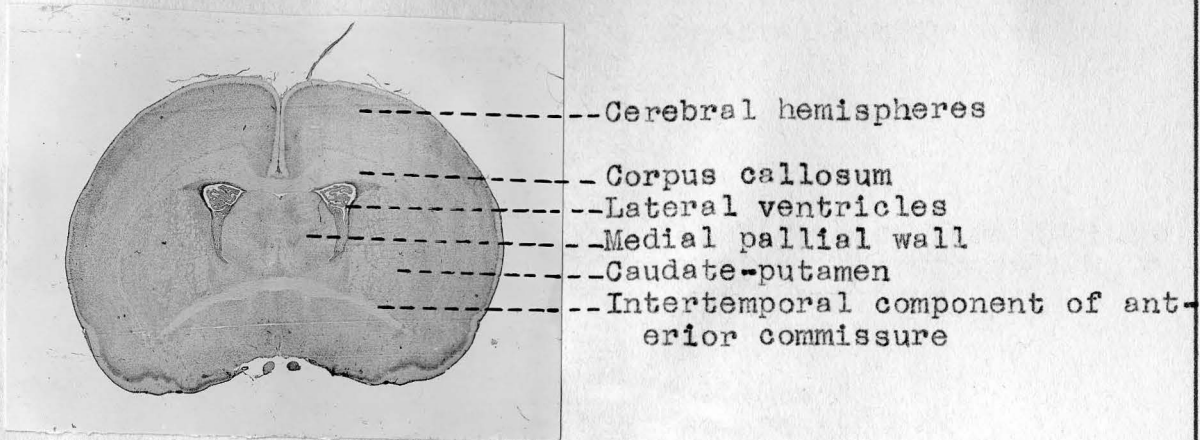


Fig. VII. Transverse-section of 7 days postnatal albino rat brain through corpus striatum. x8

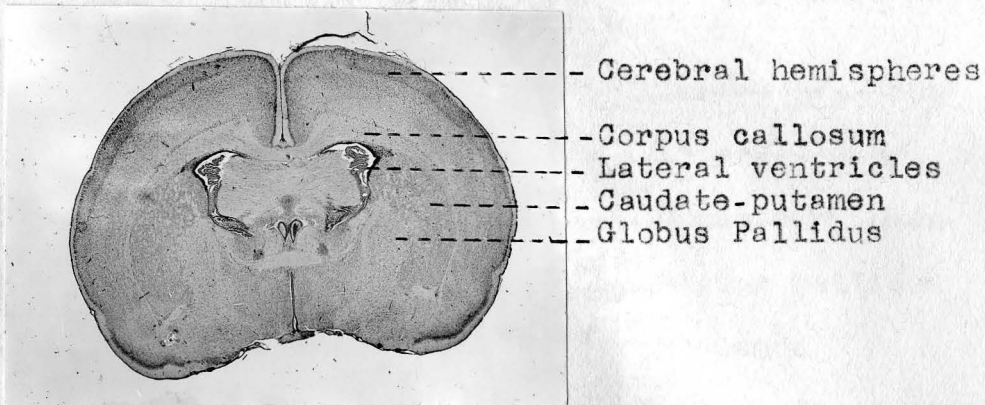


Fig. VIII. Transverse-section of 7 days postnatal albino rat brain through corpus striatum. x8



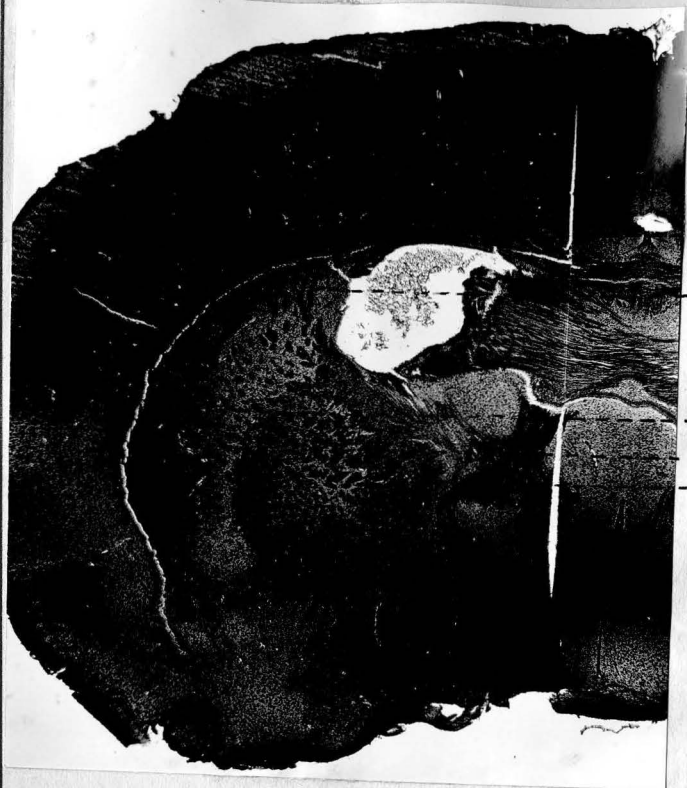
- Cerebral hemispheres
- Fiber bundles from cortical layers through corpus callosum to caudate nucleus
- Thalamus
- Caudate nucleus
- Anterior commissure

Fig. IX. Transverse-section of 14 days postnatal albino rat brain through corpus striatum. x22



- Cerebral hemispheres
- Fiber bundles from cortex to caudate putamen.
- Corpus callosum
- Lateral ventricle
- Caudate putamen
- Globus pallidus
- Thalamus

Fig. X. Transverse-section of 14 days postnatal albino rat brain through corpus striatum. x23



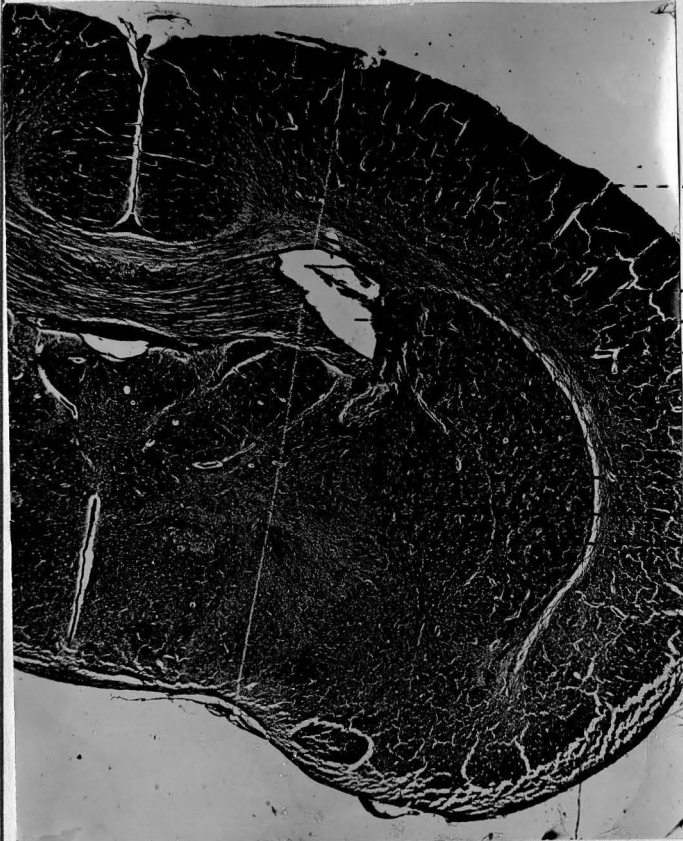
- Cerebral hemispheres
- Corpus callosum
- Fiber bundles from cortical layers to caudate-putamen and globus pallidus regions
- Caudate putamen
- Globus pallidus
- Thalamus

Fig. XI. Transverse-section of 14 days postnatal albino rat brain through the corpus striatum. x26



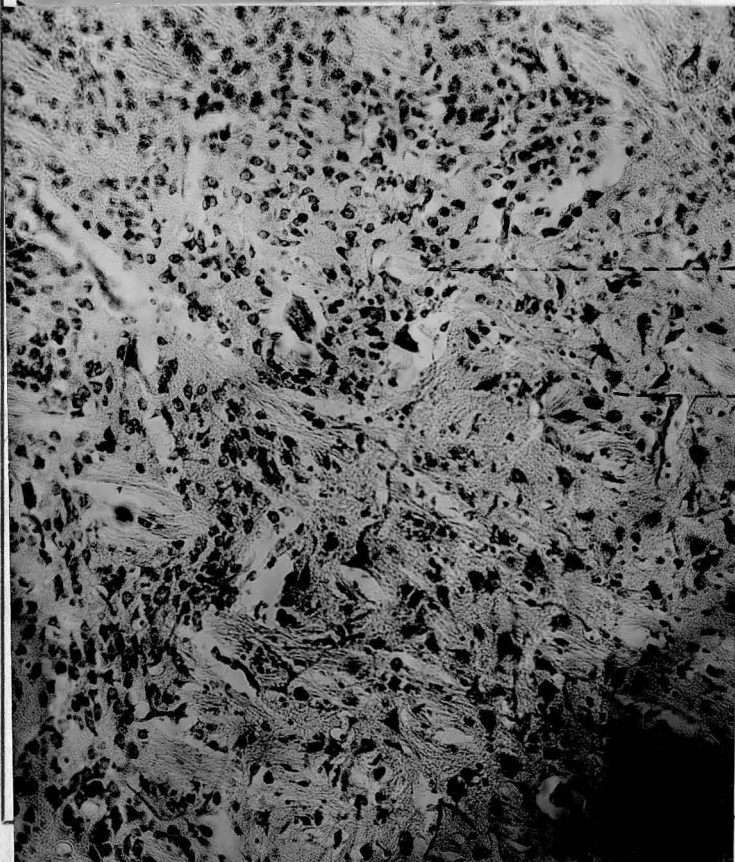
- Cerebral hemispheres
- Corpus callosum
- Hippocampus
- Fiber bundles from cortex to caudate-putamen
- Caudate putamen
- Globus pallidus

Fig. XIa. Transverse-section of 14 days postnatal albino rat brain through the corpus striatum. x23



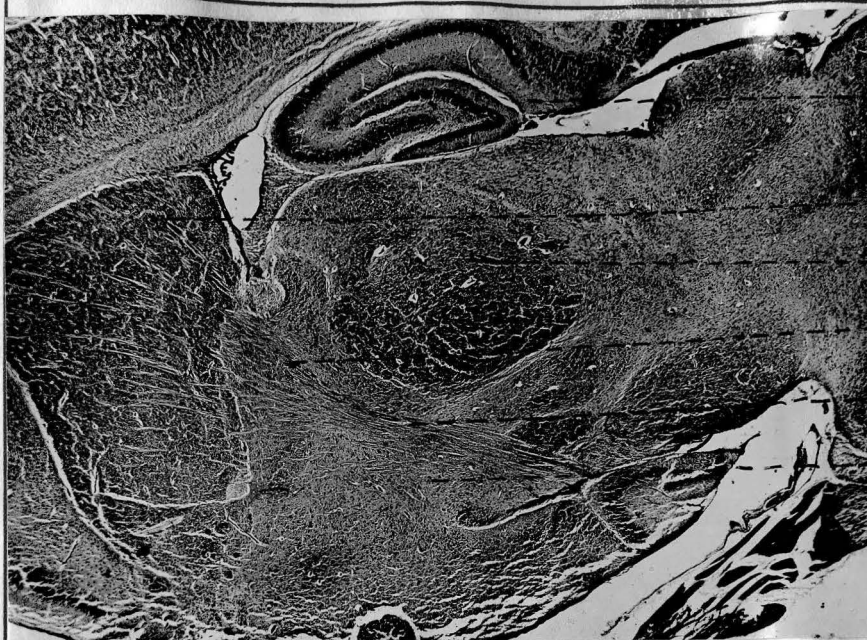
- Cerebral hemispheres
- Corpus callosum
- Lateral ventricle
- Fiber bundles from cortical layers through corpus callosum to caudate-putamen
- Caudate-putamen
- Globus pallidus
- Thalamus

Fig. XII. Transverse-section of 14 days post-natal albino rat brain through the corpus striatum. x26



- Small round cells in the caudate-putamen area
- Large cells found in the globus pallidus

Fig. XIII. Section through globus pallidus and caudate-putamen regions on high power x1900



- Hippocampus
- Caudate-putamen
- Thalamus
- Globus pallidus
- Ansa lenticularis
- Hypothalamus

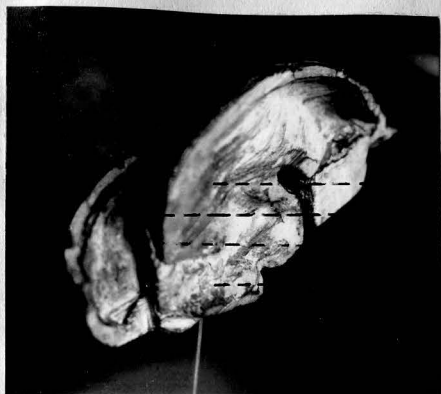
Fig. XIV. Sagittal section showing the corpus striatum. x28



Small round cells in the caudate-putamen

- Large cells in the globus pallidus region

Fig. XV. Section through globus pallidus and caudate-putamen regions on high power. x1900



-Third ventricle
 -Lateral ventricle
 -Primordium of the corpus striatum
 -Hypothalamus

Fig. XVI. Model of 13 days and 17 hours prenatal albino rat brain. Lateral view showing primordium of corpus striatum bulging into the lateral ventricle. $\times 6\frac{1}{2}$



-Primordium of the corpus striatum
 -Lateral ventricle

Fig. XVII. Model of 13 days and 17 hours prenatal albino rat brain. Top view showing primordium of corpus striatum bulging into the lateral ventricle. $\times 6\frac{1}{2}$



Fig. XVIII. Model of 19 days and 17 hours prenatal albino rat brain. Lateral view. $\times 7\frac{1}{2}$