THE DIENCEPHALON OF THE ALBINO RAT[1]

STUDIES ON THE BRAIN OF THE RAT. NO. 2

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THIRTY FIGURES

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[1] A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

INTRODUCTION

The present paper is the second of a series of contemplated contributions on the brain of the albino rat and forms a part of a comprehensive investigation of the diencephalon in a series of vertebrate brains which this laboratory of anatomy has undertaken.

In this investigation use has been made of Cajal, Weigert, Nissl, and Golgi-Cox preparations. It is fortunate that there is at hand more than one series of sections prepared according to any one of the above-mentioned methods. It is felt the results are more accurate and the work more satisfying if the investigator is able to study a given tract or nucleus in more than one series and in sections cut in several planes. Series of Golgi-Cox preparations have made it possible to determine in part at least the direction of conduction in certain paths.

The present work deals essentially with the diencephalon of the albino rat. Detailed consideration is given of the hypothalamus (including the mammillary bodies), the metathalamus, optic and postoptic systems, the subthalamus (excepting the substantia nigra), and the thalamus proper. The epithalamus was quite fully described in our first paper (Gurdjian, '25). We shall consider the epithalamus here for the sake of completeness and for the purpose of presenting further additions to our knowledge of this region in the rat. In the presentation of our observations on the hypothalamus and tracts contained therein (for example, medial forebrain bundle), it became imperative that consideration be given the preoptic area (see discussion of the hypothalamus, pp. 78–80). Throughout this contribution it has been the aim to record observed facts rather than indulge in theoretical discussions. Well-known paths and nuclear centers have been given only sufficient consideration to maintain continuity and bring out the differences which we thought were worthy of note as shown in our preparations of the albino rat.

I should like here to express my gratitude and indebtedness to Professor Huber for the supervision of this work and the placing at my disposal the facilities and the collections of the anatomical laboratory, and to Dr. Elizabeth Crosby for her untiring energy in helping in every particular of the present paper.

MATERIAL AND METHODS

The preparations used in the prosecution of this study consist of thirty-six complete series of normal albino rat brains. Of this number, nineteen complete series were prepared according to the Cajal methods; four after Weigert's myelin-sheath methods; ten according to Nissl method, and three after the Golgi-Cox methods.

The silver material was prepared according to certain modifications of Cajal's original 'nitrate d'argent réduit' method. Emphasis may be given to the fact that Cajal's methods and its modifications are applicable to relatively large pieces of nervous tissue. Thus, with the use of the method IV of this description, it was found possible to impregnate successfully a whole brain stem of a seventeen-year-old boy, a brain stem of a large adult dog, adult rat brains, adult pigeon brains, etc. To insure more uniform and rapid fixation, if possible, the animal may be injected with the fixing fluid.[2] However, this has not been necessary with the rat-brain material. The modifications as used in the preparations of series stained after the Cajal methods are as follows:

Method I. Fix in 1 per cent solution of concentrated ammonia in 95 per cent alcohol for three to five days (four changes).

Transfer into a solution of 2 to 5 per cent chloral hydrate in 95 per cent alcohol for three to five days (four changes).

Transfer to 1 per cent solution of concentrated ammonia in 95 per cent alcohol for two to three days (two or three changes).

Place in 1 to 1½ per cent aqueous solution of silver nitrate for seven to ten days (in the dark, at about 30°C., three changes).

Reduce in—

Pyrogallic acid,	5
Formalin,	5
Water,	100

(three changes).

The material is now ready for dehydration and embedding. The latter is done in paraffin. The material is left in xylol for not more than two days and not less than thirty-six hours (four or five changes). This method has been successfully used on the brains of bats, rats, dogs, and pigeons.

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[2] In this laboratory the following method of injection is used: The animal is etherized; the thorax opened before the heart action stops; a cut is made into the left ventricle, and the animal allowed to bleed. In opening the thorax one should be careful not to injure blood vessels, especially the internal mammary arteries. The clots, etc., in the thoracic cavity are washed out. A cannula is inserted into the aorta (in case of rats, turtles, small alligators, pigeons, etc.). The cannula is filled with physiologic salt solution. Hemostatic forceps are placed on the axillary vessels and the thoracic aorta. The fixing fluid is then injected under 5 to 10 pounds pressure. For such animals as enumerated above we use about 300 to 600 cc. of the fixing fluid.

Method II. Whole heads of small animals, such as rats, can be stained according to this method. Such preparations would enable one to follow peripheral nerves into the central nervous system or would permit the study of the central nervous system in relation with the peripheral nervous system in embryos.

Fix in 1 per cent ammoniated alcohol solution for three to five days (three changes).

Transfer into a 7 per cent nitric-acid solution in water for seven to fourteen days (three or four changes). Large amounts of the solution should be used.

Transfer into a 1 per cent ammoniated alcohol solution for five days (four changes).

Place in a solution of 3 to 5 per cent chloral hydrate in 95 per cent alcohol for five days (three changes).

Treat with silver nitrate the same as in method I.

Reduce either in the above-mentioned reducing mixture or—

Pyrogallic acid,	3
Hydroquinone,	2
Formalin,	5
Water,	100

for three to five days (three changes).

Dehydrate and embed as in method I.

Method III. This method has given us quite constantly certain differential staining changes which are very helpful if conservatively used (in the present paper the proper course of the medial amygdalo-hypothalamic tract was worked out in material prepared according to this method).

Fix in—

Concentrated ammonia,	1 cc.
Chloral hydrate,	3 grams
95 per cent alcohol,	100 cc.

for five days (three changes).

Place in 1 to 1½ per cent silver-nitrate solution for seven to ten days as in method I.

Reduce in the reducing mixture mentioned under method II. This is very important.

Method IV. This method is employed where it is desired to impregnate large pieces. If possible to inject the material, this is done. This method is essentially the same as the method I, except that the material is left in the fixing fluid for ten to twenty days, in the silver solution (0.75 per cent) for two to four weeks, if necessary. For the silver reduction the material is left in the reducing fluid for a week to ten days and longer, if necessary.

LITERATURE

The mammalian diencephalon has been the subject of exhaustive study by a goodly number of contributors. To deal fully with this extensive literature would lead, on the one hand, to excessive length of this article and, on the other hand, to frequent repetition in the subsequent pages. It is felt that, since the diencephalon has been quite comprehensively considered as to related literature in a number of relatively recent standard texts on the anatomy of the nervous system (Déjerine, '01; Barker, '02; Cajal, '11; Edinger, '11, and others), an introductory discussion of this literature is not necessary. In our review of the literature we have observed that the majority of the contributions on the diencephalon are concerned mainly with certain portions of the center and are the outcome of studies made either with myelotectonic methods or are nuclear studies. Few authors have endeavored to discuss this center as a whole and given consideration both to nuclear pattern and fiber connections. For this reason, the literature consulted has been considered under the respective divisions of the work, due consideration being given to the contributions of other authors in so far as we were familiar with their work and in so far as it was pertinent to the description and interpretation of the material at hand.

Most of the work on the mammalian diencephalon has been accomplished in the last thirty-five years. The pioneer work of Cajal ('11) stands out as probably the most important contribution to our present knowledge of this center. Cajal is one of the few authors who take up systematically both the nuclear configurations and fiber connections of the different divisions of the diencephalon. The nuclear configuration of the thalamus proper has been considered in detail in the works of Munzer and Wiener ('02) and Hollander ('13) for the rabbit. Hollander also makes an attempt at describing the connections of the nuclear centers concerned. Winkler and Potter's ('14) atlas on the cat's brain is also very valuable. These works have been of great help to us in so far as these forms are not too far removed from the rat in the phylogenetic scale of the animal kingdom. The works of Vogt ('09) and Friedman ('13) on the diencephalon of the monkey are worthy of special mention.

The study of the epithalamus is relatively recent, and the names of Cajal ('11), Herrick ('13), Johnston ('23), Gurdjian ('25), and others should be mentioned as having contributed to our knowledge of this region in lower mammals.

In general, we have discovered that the subthalamus and the hypothalamus are the least known of the divisions of the diencephalon in mammalia. In this connection the works of Cajal ('11), Probst ('05), Bernheimer ('07), Kosaka and Hiraiwa ('15), and others are worthy of special mention.

Excellent work has been done on the diencephalon of lower vertebrates (Herrick, '10 and '17; Huber and Crosby, '26). These contributions have been very helpful in elucidating the mammalian diencephalon, and frequent reference is made to them in subsequent pages, especially to the latter.

NUCLEAR MASSES AND FIBER PATHS

EPITHALAMUS

The nuclear pattern of the habenular complex was considered in a former communication (Gurdjian, '25). New material reconfirms our previous findings. We are glad to note that Craigie ('25) also finds the same nuclear configuration in his rat material. Tsai ('25), working on the opossum, has arrived at similar conclusions, i.e., he has divided the medial habenular nucleus into two parts rostrally. Huber and Crosby ('26) have discovered essentially similar conditions in the alligator brain, except for differences in dimensions of respective nuclei.

The connections of the habenular complex were also taken up in detail (Gurdjian, '25). Better preparations and differential staining have brought out certain facts worthy of mention. We now think that the major portion of what used to be taken for a connection between the stria terminalis and the stria medullaris (of an amygdalo-habenular significance; Johnston, '23) is of a different nature altogether. It is granted that our preparations show a connection between the stria terminalis and the stria medullaris in the plane of the caudal aspect of the anterior commissure. But this is relatively small. In this plane bundles leave the stria terminalis, course medially toward the forming stria medullaris, pass ventral to the latter, between it and the fornix bundle in company with the medial amygdalo-hypothalamic tract (see discussion of the medial cortico-hypothalamic tract, p. 102). They then reach the dorsomedial aspect of the fornix bundle and run posteriorly with the latter for a very short distance (about fifteen sections of 25 μ each). A little farther caudad, in company with the medial cortico-hypothalamic tract, they enter the most medial portions of the preoptic and the hypothalamic areas (figs. 1, 11, 12, 26). We have described this tract as the medial amygdalo-hypothalamic path (see discussion of the same, p. 103). We do not know whether this is a condition peculiar to the brain of the rat or whether it is found in all associated forms. The latter assumption seems to us more plausible.

OPTIC AND POSTOPTIC SYSTEMS, METATHALAMUS, AND SUBTHALAMUS

The optic system and the associated optic centers have been extensively studied, so that we will not take up much space by discussing the literature on the subject. Some of the larger texts in nervous anatomy (Déjerine, '01; Barker, '02; Edinger, '11; Cajal, '11) as well as some of the older papers on the subject (Singer and Munzer, '89; Dexler, '97; Probst, '00; Berl, '02; Myers, '02; Tello, '04; Brouwer, '17, and others) will enable one to get a sufficient background on the literature concerning this topic.

This is not the case with the supraoptic system of fibers. We are alluding to the commissures associated with the names of Ganser, Meynert, and Gudden. In reviewing the literature on the subject, we have been struck by the existing confusion pertaining to these terms; in more than one instance were these names used synonymously, so that one was unable to determine whether the author was thinking of one system or another. It is our endeavor in this communication to clarify some of the facts concerning this system. In this connection, the works of Probst ('05), Bernheimer ('07), Ziehen ('08), Cajal ('11), and others on mammalia as well as those of Herrick ('10), Huber and Crosby ('26), and others on the structure of the lower vertebrate brain are worthy of mention.

The subthalamus constitutes a comparatively unknown field in neurology. A very distinct controversy exists in the minds of most workers as to the connections in this region. The zona incerta, as the name implies, is a truly uncertain zone as far as we have been able to find out in the literature consulted. The connections of the body of Luys are not clear in the minds of most authors. The radiations of Forel and the fields of Forel do not seem to have been clearly defined. The only author who has endeavored to answer all of these questions systematically is Ramón y Cajal. Bits of information are found here and there in the literature (Déjerine, '01; Probst, '05; Ziehen, '08; Sano, '10; Bernheimer, '07; Kosaka and Hiraiwa, '15; Kappers, '21).

The supraoptic system of commissures

In the rat we have been able to divide the supraoptic system of commissures (Ganser's, Meynert's, Gudden's commissures) into ventral and dorsal portions. The dorsal portion is divisible into a dorsal and a ventral part. Thus we have the following: Commissura supraoptica dorsalis, pars dorsalis (Ganser's commissure); commissura supraoptica dorsalis, pars ventralis (Meynert's commissure); commissura supraoptica ventralis (Gudden's commissure).

The division of the commissura supraoptica dorsalis into dorsal and ventral portions is dependent upon a different distribution of the two systems as well as on morphologic characteristics. The commissura supraoptica dorsalis pars dorsalis is made up of thicker fibers, well myelinated, and the component parts do not form compact bundles. From a review of literature, we have come to the conclusion that this corresponds to the commissure of Ganser. The commissura supraoptica dorsalis pars ventralis is ventral to the abovementioned pars dorsalis and is made up of finer fibers in close juxtaposition, the mass as a whole being many times richer in number of fibers than the pars dorsalis. This undoubtedly represents the commissure of Meynert. The ventral portion of the supraoptic commissural system is the commissura supraoptica ventralis. In our preparations the commissura supraoptica ventralis is stained exactly the same as the optic fibers, so that it is not differentiable from the latter except through its connection with the medial geniculate body. The commissura supraoptica ventralis represents the commissure of Gudden.

Commissura supraoptica dorsalis, pars dorsalis (figs. 13, 27). This is the same as the commissure of Ganser. It is a highly rarified component on the most dorsal aspect of the chiasma region. In silver preparations the fibers are thick, and Weigert material shows that they are well myelinated. They do not form compact bundles, and in their course on the ventral aspect of the hypothalamus they pass through a scattered group of nerve cells. These are mostly small, with here and there large cells.

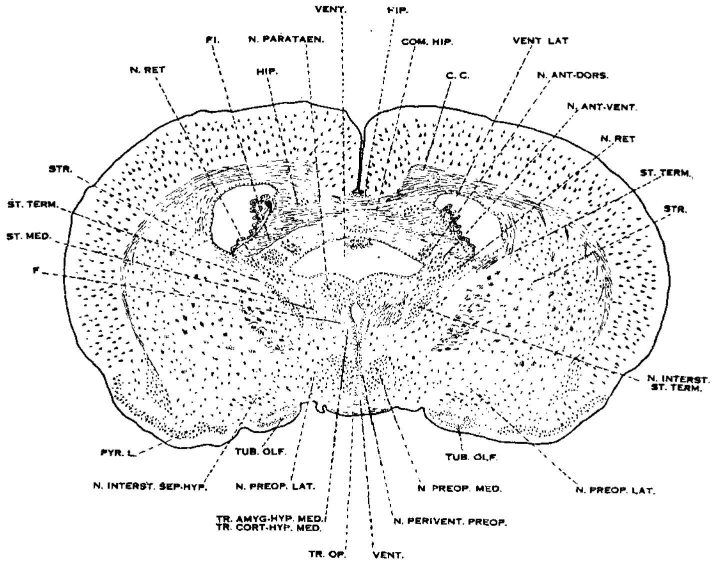
Cox preparations show characteristic pictures (fig. 20, nucleus supraopticus diffusus). In such preparations one is at times able to trace axons from these cells into the commissural system. We think that they form a bed nucleus for the commissure of Ganser, to the fibers of which they contribute. The fibers of the commissura supraoptica dorsalis pars dorsalis can be followed in our preparations laterally and dorsally. They pass through the medial forebrain bundle and are traceable to the subthalamic area, especially the medial third of the latter. Some of them (very few in number) course along the medial aspect of the Meynert's commissure and still others are seen to course through the interstices of the medial forebrain bundle. We are convinced, however, that the majority of these fibers are concerned with the subthalamus and the hypothalamus. Probst ('05) thinks that the Ganser's commissure is associated with the tectum and the tegmentum. Cajal ('11) does not speak of a Ganser's commissure in the mouse. From a study of his drawings, we have come to the conclusion that he includes the Ganser's in the Meynert's commissure. Tsai ('25), speaking of the Ganser's commissure in the opossum, concludes that it probably is a commissural system between the subthalami of the opposite sides.

Commissura supraoptica dorsalis, pars ventralis (figs. 8, 13 to 17, 27, 28). This corresponds to the commissure of Meynert. It is a large commissural band on the caudo-dorsal aspect of the optic chiasm. It runs laterally and dorsally on

Fig. 1 Toluidine-blue preparation. Transverse section passing through the plane of the anterior extreme of the diencephalon. × 8. *C.c.*, corpus callosum; *Com.hip.*, commissura hippocampi; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *N.ant.-dors.*, nucleus anterior dorsalis; *N.ant.-vent.*, nucleus anterior ventralis; *N.interst.sep.-hyp.*, nucleus interstitialis septo-hypothalamicus; *N.interst. st.term.*, nucleus interstitialis stria terminalis; *N.parataen.*, nucleus parataenialis; *N.perivent.preoptic.*, nucleus periventricularis preopticus; *N.preop.lat.*, nucleus preopticus lateralis; *N.preop.med.*, nucleus preopticus medialis; *N.ret.*, nucleus reticularis thalami; *Pyr.l.*, pyriform lobe area; *St.med.*, stria medullaris; *Str.*, striatum; *St.term.*, stria terminalis; *Tr.amyg.-hyp.med.*, tractus amygdalo-hypothalamicus medialis; *Tr.cort.-hyp.med.*, tractus cortico-hypothalamicus medialis; *Tr.op.*, tractus opticus; *Tub.olf.*, tuberculum olfactorium; *Vent.*, ventricle; *Vent. lat.*, ventriculus lateralis.

Fig. 2 Toluidine-blue preparation. Transverse section passing through the plane of the middle third of the anterior group of thalamic nuclei. × 8. *C.c.*, corpus callosum; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lat.forb.*, lateral forebrain bundle (capsula interna); *N.ant.-dors.*, nucleus antero-dorsalis; *N.ant.-med.*, nucleus antero-medialis; *N.ant.-vent.*, nucleus antero-ventralis; *N.hyp.ant.*, nucleus hypothalamicus anterior; *N.hyp.lat.*, nucleus hypothalamicus lateralis; *N.interst.sep.-hyp.*, nucleus interstitialis septo-hypothalamicus; *N.lat.*, nucleus lateralis thalami; *N.ovoid.*, nucleus ovoidus; *N.parataen.*, nucleus parataenialis; *N.paravent.ant.*, nucleus paraventricularis anterior; *N.perivent.hyp.ant.*, nucleus periventricularis hypothalamicus anterior; *N.ret.*, nucleus reticularis thalami; *N.reuniens*, nucleus reuniens; *N.tr.olf.lat.*, nucleus tractus olfactorius lateralis; *Pyr.l.*, pyriform-lobe area; *Rad.thal.inf.*, radiatio thalamica inferior; *Rad.thal.int.*, radiatio thalamica intermedius; *Rad.thal.sup.*, radiatio thalamica superior; *St.med.*, stria medullaris; *Str.*, striatum; *St.term.*, stria terminalis; *Tr.forb.-n.ant.dors.*, internal capsule fibers going to the nucleus antero-dorsalis; *Tr.forb.-n.ant.vent.*, internal capsule fibers going to the nucleus antero-ventralis; *Tr.op.*, tractus opticus; *Vent.*, ventriculus; *Vent.lat.*, ventriculus lateralis.

the medial aspect of the optic tract. It is essentially made up of finely myelinated fibers. In our silver preparations the differentiation of this tract is rather difficult; however,



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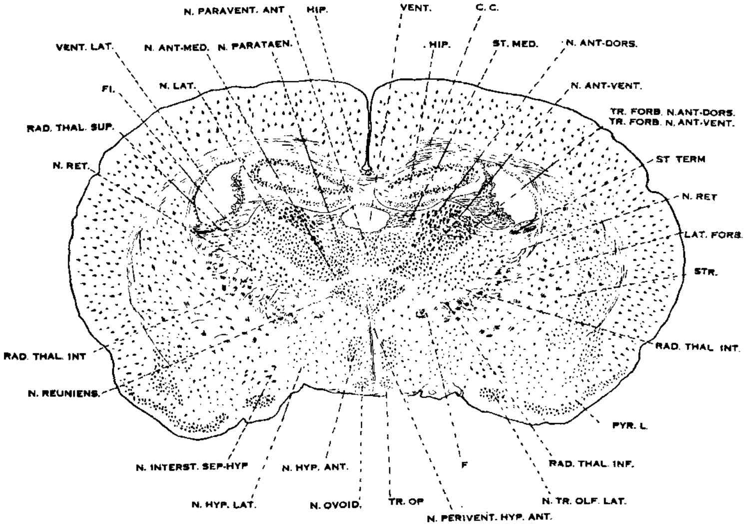

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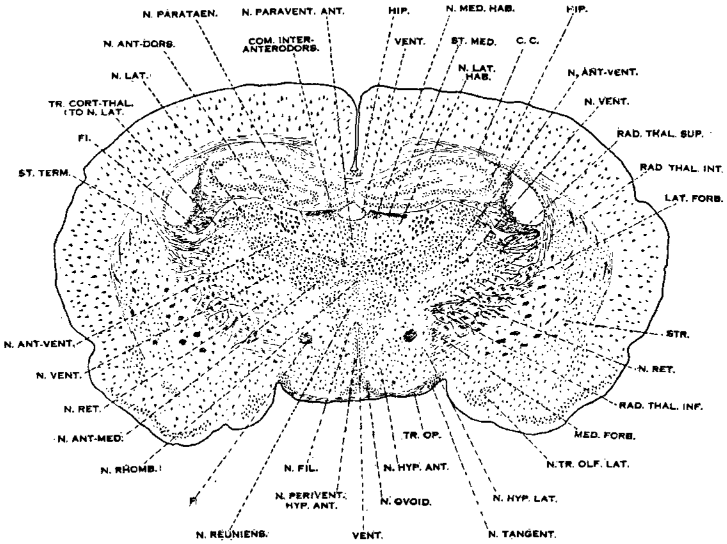
Weigert preparations show the difference between this component and the optic system very vividly. As the tract courses on the lateral aspect of the cerebral peduncle it gives off branches which enter the interstices of the lateral forebrain bundle and which traverse the same in order to enter the subthalamic areas. Some of the bundles of the latter group can be followed through the substance of the zona incerta up to about the plane of the rostral extreme of the medial geniculate bodies where they turn dorsally and me-

Fig. 3 Toluidine-blue preparation. Transverse section passing through the rostral extreme of the ventral thalamic nucleus. × 8. Note in particular the thalamic nuclei of the midline. *C.c.*, corpus callosum; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lat.forb.* lateral forebrain bundle (capsula interna); *Med.forb.*, medial forebrain bundle; *N.ant.-dors.*, nucleus antero-dorsalis; *N.ant.-med.*, nucleus antero-medialis; *N.ant.-vent.*, nucleus antero-ventralis; *N.fil.*, nucleus filiformis; *N.hyp.ant.*, nucleus hypothalamicus anterior; *N.hyp.lat.*, nucleus hypothalamicus lateralis; *N.lat.*, nucleus lateralis thalami; *N.lat.hab.*, nucleus lateralis habenulae; *N.med.hab.*, nucleus medialis habenulae; *N.ovoid.*, nucleus ovoidus; *N.parataen.*, nucleus parataenialis; *N.paravent.ant.*, nucleus paraventricularis anterior; *N.perivent.hyp.ant.*, nucleus periventricularis hypothalamicus anterior; *N.ret.*, nucleus reticularis thalami; *N.reuniens*, nucleus reuniens; *N.rhomb.*, nucleus rhomboidalis; *N.tangent.*, nucleus tangentialis; *N.tr.olf.lat.*, nucleus tractus olfactorius lateralis; *N.vent.*, nucleus ventralis thalami; *Rad.thal.inf.*, radiatio thalamica inferior; *Rad.thal.int.*, radiatio thalamica intermedius; *Rad.thal.sup.*, radiatio thalamica superior; *St.med.*, stria medullaris; *St.term.*, stria terminalis; *Tr.cort.-thal.*, tractus cortico-thalamicus (to nucleus lateralis thalami); *Tr.op.*, tractus opticus; *Vent.*, ventriculus.

Fig. 4 Toluidine-blue preparations. Transverse section passing through the middle third of the nucleus filiformis. × 8. Note the nuclei of the midline. *C.c.*, corpus callosum; *Com.inter-anterodors.*, nucleus commissura inter-anterodorsalis; *Com.inter-anteromed.*, nucleus commissura inter-anteromedialis; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lat.forb.*, lateral forebrain bundle (capsula interna); *Med.forb.*, medial forebrain bundle; *N.ant.-dors.*, nucleus antero-dorsalis; *N.ant.-vent.*, nucleus antero-ventralis; *N.fil.*, nucleus filiformis; *N.hyp.ant.*, nucleus hypothalamicus anterior; *N.hyp.lat.*, nucleus hypothalamicus lateralis; *N.lat.*, nucleus lateralis thalami; *N.lat.hab.*, nucleus lateralis habenulae; *N.med.-dors.*, nucleus medialis dorsalis; *N.med.hab.*, nucleus medialis habenulae; *N.ovoid.*, nucleus ovoidus; *N.paravent.ant.*, nucleus paraventricularis anterior; *N.perivent.hyp.ant.*, nucleus periventricularis hypothalamicus anterior; *N.ret.*, nucleus reticularis thalami; *N.reuniens*, nucleus reuniens; *N.rhomb.*, nucleus rhomboidalis; *N.tangent.*, nucleus tangentialis; *N.vent.*, nucleus ventralis thalami; *Pyr.l.*, pyriform lobe area; *Rad.thal.sup.*, radiatio thalamica superior; *St.med.*, stria medullaris; *Str.*, striatum; *St.term.*, stria terminalis; *Tr.cort.-thal.*, tractus cortico-thalamicus; *Tr.op.*, tractus opticus; *Vent.III.*, third ventricle; *Vent.lat.*, ventriculus lateralis.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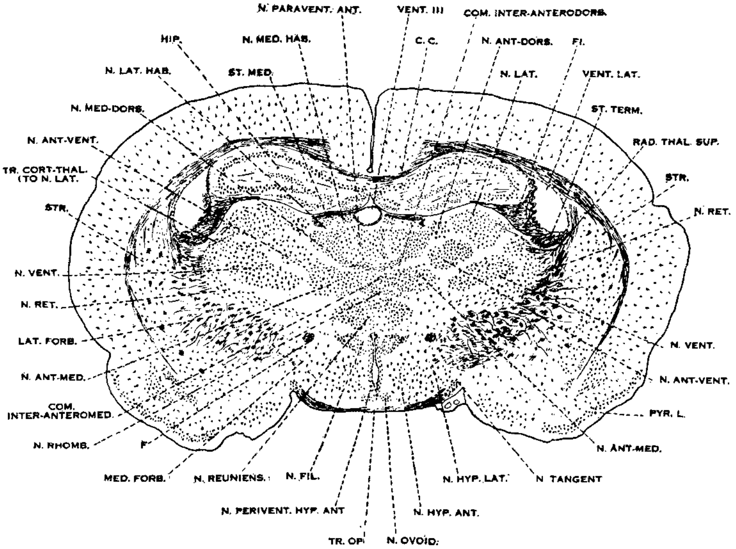
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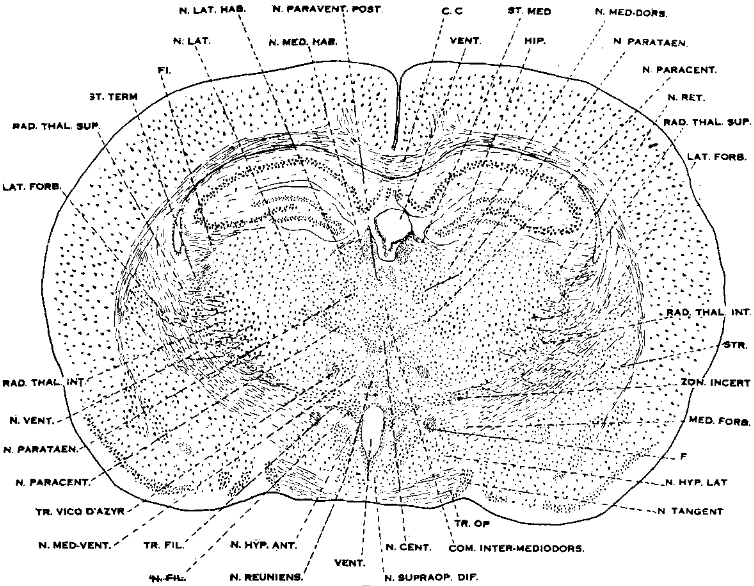
dially in order to go to the tectum in company with the cortico-tectal fibers. The group of fibers going to the tectum is very small, and were it not for a differential staining in some of our silver series it would have been impossible for us to follow them so far back. In our preparations the Meynert's commissure is also intimately associated with the ventral portion of the lateral geniculate bodies.

Fig. 5 Toluidine-blue preparation. Transverse section passing through the middle third of the habenular complex. Note in particular the nuclei of the midline and the nucleus filiformis, with the tractus filiformis extending from its lateral aspect. × 8. *C.c.*, corpus callosum; *Com.inter-mediodors.*, nucleus commissura inter-medialis dorsalis; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lat.forb.*, lateral forebrain bundle (capsula interna); *Med.forb.*, medial forebrain bundle; *N.cent.*, nucleus centralis; *N.fil.*, nucleus filiformis; *N.hyp.ant.*, nucleus hypothalamicus anterior; *N.hyp.lat.*, nucleus hypothalamicus lateralis; *N.lat.thal.*, nucleus lateralis thalami; *N.lat.hab.*, nucleus lateralis habenulae; *N.med.-dors.*, nucleus medialis dorsalis; *N.med.hab.*, nucleus medialis habenulae; *N.med.vent.*, nucleus medialis ventralis; *N.paracent.*, nucleus paracentralis; *N.parataen.*, nucleus parataenialis; *N.paravent.post.*, nucleus paraventricularis posterior; *N.ret.*, nucleus reticularis thalami; *N.reuniens*, nucleus reuniens; *N.supraop.dif.*, nucleus supraopticus diffusus; *N.tangent.*, nucleus tangentialis; *N.vent.*, nucleus ventralis thalami; *Rad.thal.int.*, radiatio thalamica intermedius; *Rad.thal.sup.*, radiatio thalamica superior; *St.med.*, stria medullaris; *Str.*, striatum; *St.term.*, stria terminalis; *Tr.fil.*, tractus filiformis; *Tr.op.*, tractus opticus; *Tr.Vicq d'Azyr*, tractus Vicq d'Azyr; *Vent.*, ventriculus; *Zon.incert.*, zona incerta.

Fig. 6 Toluidine-blue preparations. Note in particular the nucleus ventralis thalami. The linearly arranged group of cells stand out plainly in all of our series. × 8. *C.c.*, corpus callosum; *Com.inter-medio-dors.*, nucleus commissura inter-medialis dorsalis; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lat.forb.*, lateral forebrain bundle (pedunculus cerebri); *Lem.med.*, lemniscus medialis; *Med.forb.*, medial forebrain bundle; *N.ent.-ped.*, nucleus entopeduncularis; *N.gen.lat.p.dors.*, nucleus geniculatus lateralis pars dorsalis; *N.gen.lat.p.vent.*, nucleus geniculatus lateralis pars ventralis; *N.hyp.lat.*, nucleus hypothalamicus lateralis; *N.hyp.vent.-med.*, nucleus hypothalamicus ventromedialis; *N.lat.hab.*, nucleus lateralis habenulae; *N.lat.p.post.*, nucleus lateralis pars posterior; *N.med.-dors.*, nucleus medialis dorsalis; *N.med.hab.*, nucleus medialis habenulae; *N.med.-vent.*, nucleus medialis ventralis; *N.paravent.post.*, nucleus paraventricularis posterior; *N.perivent.hyp.post.*, nucleus periventricularis hypothalamicus posterior; *N.pretect.*, nucleus pretectalis; *N.ret.*, nucleus reticularis thalami; *N.reuniens*, nucleus reuniens; *N.vent.*, nucleus ventralis thalami; *N.vent.p.dors.-med.*, nucleus ventralis pars dorsomedialis; *Rad.thal.sup.*, radiatio thalamica superior; *St.med.*, stria medullaris; *Str.*, striatum; *St.term.*, stria terminalis; *Tr.cort.-tect.*, tractus cortico-tectalis; *Tr.op.*, tractus opticus; *Tr.Vicq d'Azyr*, tractus Vicq d'Azyr; *Vent.*, ventriculus; *Zon.incert.*, zona incerta.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ST. TERM
N. RET.
RAD. THAL. SUP.
RAD. THAL. SUP.
LAT. FORB.
LAT. FORB.
RAD. THAL. INT.
STR.
RAD. THAL. INT.
ZON. INCERT
N. VENT.
MED. FORB.
N. PARATAEN.
F
N. PARACENT.
N. HYP. LAT
TR. VICQ D'AZYR
N TANGENT
TR. OP
N. MED-VENT.
TR. FIL.
N. HYP. ANT.
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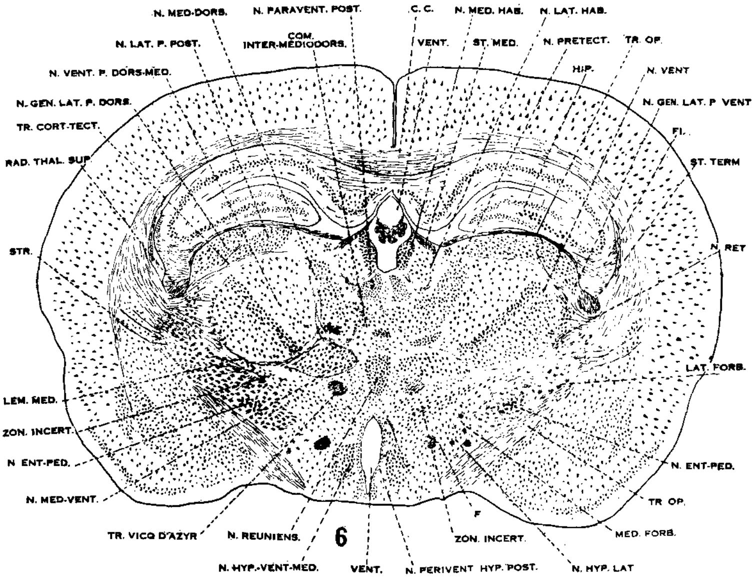
COM. INTER-MEDIODORS.
VENT.
~~N. FIL.~~
N. REUNIENS.
N. SUPRAOP. DIF.

5


N. MED-DORS.
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C. C.
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ST. MED.
N. PRETECT.
TR. OP.
N. VENT. P. DORS-MED.
HIP.
N. VENT
N. GEN. LAT. P. DORS.
N. GEN. LAT. P VENT
TR. CORT-TECT.
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RAD. THAL. SUP.
ST. TERM
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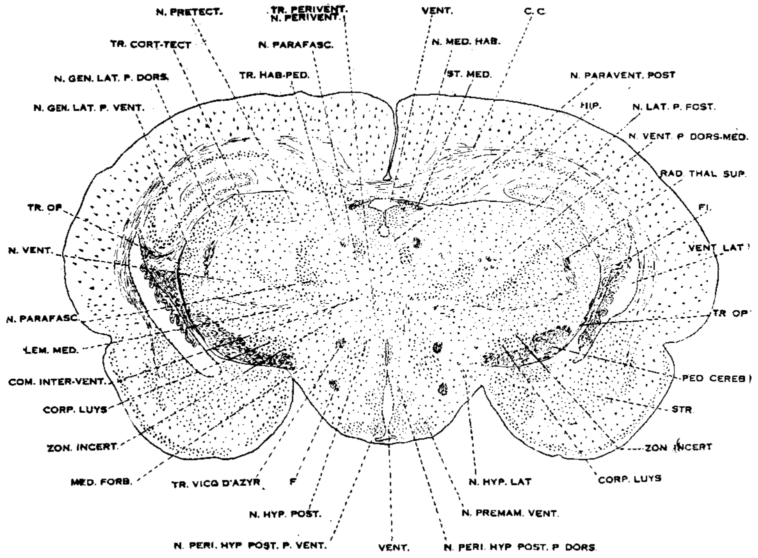
N RET
LAT. FORB.
LEM. MED.
ZON. INCERT.
N ENT-PED.
N. ENT-PED.
N. MED-VENT.
TR OP.
F
MED. FORB.
TR. VICQ D'AZYR
N. REUNIENS.
ZON. INCERT.
N. HYP.-VENT-MED.
VENT.
N. PERIVENT HYP. POST.
N. HYP. LAT

6

From the above description it can be noted that this commissure is intimately associated with the subthalamus, the tectum, and the ventral portions of the lateral geniculate

Fig. 7 Toluidine-blue preparation. Transverse section passing through the plane of the posterior third of the diencephalon. Note in particular the hypothalamus and the periventricular group of nuclei in the same. × 8. *C.c.*, corpus callosum; *Com.inter-vent.*, nucleus commissura interventralis; *Corp.Luys.*, corpus Luysii; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lem.med.*, lemniscus medialis; *Med.forb.*, medial forebrain bundle (pedunculus cerebri); *N.gen.lat.p.dors.*, nucleus geniculatus lateralis pars dorsalis; *N.gen.lat.p.vent.*, nucleus geniculatus lateralis pars ventralis; *N.hyp.lat.*, nucleus hypothalamicus lateralis; *N.hyp.post.*, nucleus hypothalamicus posterior; *N.lat.p.post.*, nucleus lateralis pars posterior; *N.med.hab.*, nucleus medialis habenulae; *N.parafasc.*, nucleus parafascicularis; *N.paravent.post.*, nucleus paraventricularis posterior; *N.perivent.hyp.post.p.dors.*, nucleus periventricularis hypothalamicus posterior pars dorsalis; *N.peri.hyp.post.p.vent.*, nucleus periventricularis hypothalamicus posterior pars ventralis; *N.perivent.*, nucleus periventricularis; *N.premam.vent.*, nucleus premammillaris ventralis; *N.pretect.*, nucleus pretectalis; *N.vent.* nucleus ventralis thalami; *N.vent.p.dors.-med.*, nucleus ventralis pars dorsomedialis; *Ped.cereb.*, pedunculus cerebri; *Rad.thal.sup.*, radiatio thalamica superior; *St.med.*, stria medullaris; *Str.*, striatum; *Tr.cort.-tect.*, tractus cortico-tectalis; *Tr.hab.-ped.*, tractus habenulo-peduncularis; *Tr.op.*, tractus opticus; *Tr.perivent.*, periventricular system of fibers; *Tr.Vicq d'Azyr*, tractus Vicq d'Azyr; *Vent.*, ventriculus; *Vent.lat.*, ventriculus lateralis; *Zon.incert.*, zona incerta.

Fig. 8 Toluidine-blue preparation. Transverse section passing through the plane of the anterior third of the posterior commissure. Note the commissural nuclear masses between the ventral thalamic nuclei. × 8. *C.c.*, corpus callosum; *Com.inter-vent.*, nucleus commissura interventralis; *Com.Meynert*, Meynert's commissure; *Com.post.*, commissura posterior; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lem.med.*, lemniscus medialis; *Med.forb.*, medial forebrain bundle; *N.gen.lat.p.dors.*, nucleus geniculatus lateralis pars dorsalis; *N.gen.lat.p.vent.*, nucleus geniculatus lateralis pars ventralis; *N.hyp.dors.-med.*, nucleus hypothalamicus dorsomedialis; *N.hyp.lat.*, nucleus hypothalamicus lateralis; *N.hyp.vent.-med.*, nucleus hypothalamicus ventromedialis; *N.lat.p.post.*, nucleus lateralis pars posterior; *N.parafasc.*, nucleus parafascicularis; *N.paravent.post.*, nucleus paraventricularis posterior; *N.peri.hyp.post.p.vent.*, nucleus periventricularis hypothalamicus posterior pars ventralis; *N.perivent.*, nucleus periventricularis; *N.perivent.hyp.post.*, nucleus periventricularis hypothalamicus posterior; *N.post.thal.*, nucleus posterior thalami; *N.ret.*, nucleus reticularis thalami; *N.vent.*, nucleus ventralis thalami; *N.vent.p.dors.-med.*, nucleus ventralis pars dorsomedialis; *Ped.cereb.*, pedunculus cerebri; *Rad.thal.sup.*, radiatio thalamica superior; *St.med.*, stria medullaris; *Str.*, striatum; *Tr.cort.-incert.*, tractus cortico-incertalis; *Tr.cort.-thal.*, tractus cortico thalamicus to nucleus lateralis pars posterior; *Tr.incert.-tect.*, tractus incerto-tectalis; *Tr.incert.-teg.*, tractus incerto-tegmentalis; *Tr.op.*, tractus opticus; *Tr.perivent.*, periventricular system of fibers; *Tr.Vicq d'Azyr*, tractus Vicq d'Azyr; *Vent.III.*, ventriculus III; *Vent.lat.*, ventriculus lateralis; *Zon.incert.*, zona incerta.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VENT.
C. C.
TR. CORT-TECT
N. PARAFASC.
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TR. HAB-PED.
ST. MED.
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N. GEN. LAT. P. VENT.
HIP.
N. LAT. P. POST.
N. VENT. P. DORS-MED.
RAD. THAL. SUP.
TR. OP
FI.
N. VENT.
VENT. LAT.
N. PARAFASC.
TR. OP.
LEM. MED.
COM. INTER-VENT.
PED. CEREB.
CORP. LUYS
STR.
ZON. INCERT.
ZON. INCERT.
MED. FORB.
TR. VICQ D'AZYR
F
N. HYP. LAT.
CORP. LUYS
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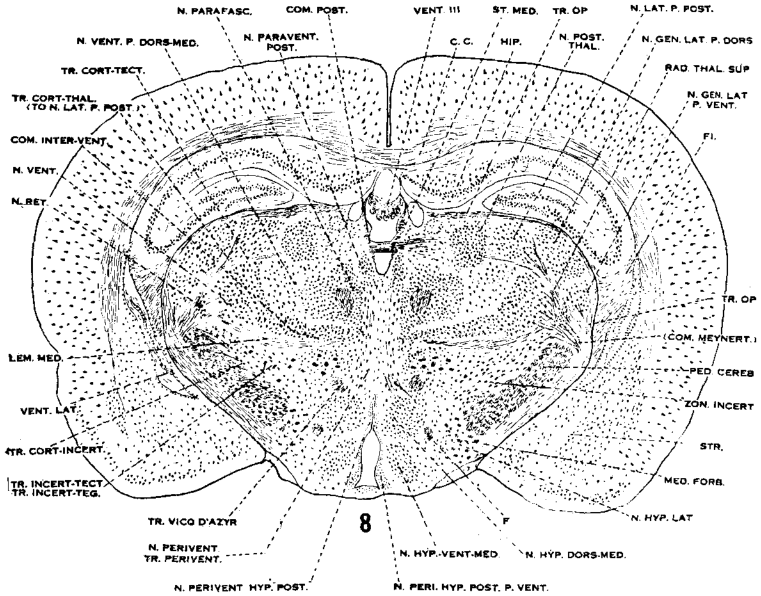
7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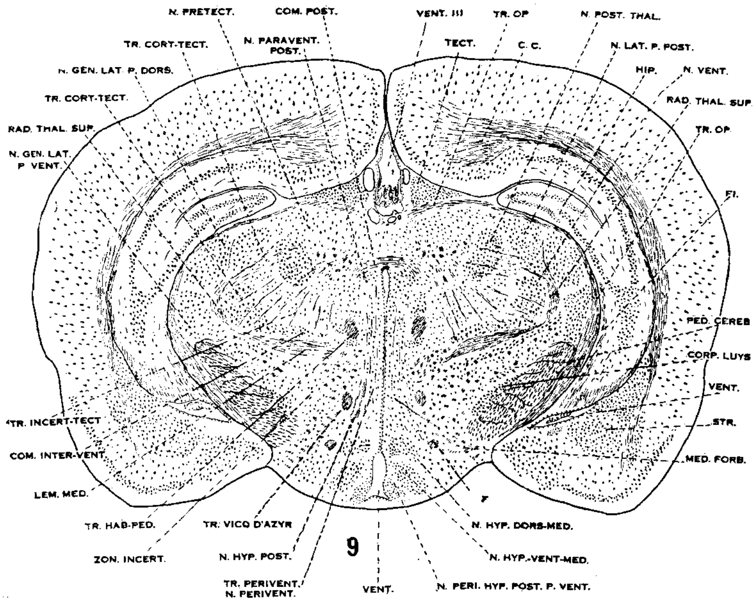
C. C.
HIP.
N. POST. THAL.
N. GEN. LAT. P. DORS
TR. CORT-TECT.
RAD. THAL. SUP
TR. CORT-THAL. (TO N. LAT. P. POST.)
N. GEN. LAT P. VENT.
COM. INTER-VENT.
FI.
N. VENT.
N. RET.
TR. OP
(COM. MEYNERT.)
LEM. MED.
PED. CEREB
VENT. LAT.
ZON. INCERT
TR. CORT-INCERT.
STR.
TR. INCERT-TECT.
TR. INCERT-TEG.
MED. FORB.
TR. VICQ D'AZYR
F
N. HYP. LAT.
N. PERIVENT.
TR. PERIVENT.
N. HYP.-VENT-MED.
N. HYP. DORS-MED.
N. PERIVENT. HYP. POST.
N. PERI. HYP. POST. P. VENT.

8

bodies—a condition which is comparable to findings in lower forms (Huber and Crosby, '26). We will take up some of these homologies in our discussion (discussion, pp. 107, 108). Probst ('05) speaks of a lenticular connection, and his figures are very characteristic of such a relation. We have not been able to observe a striatal connection in our preparations. The only possible alternative for a homologue of this path in the human (Probst, '05) and the avian (Edinger, '11) brains would be the following: that some of the fibers of the commissura supraoptica dorsalis pars ventralis which enter the interstices of the cerebral peduncle run cephalad along with the fibers of the internal capsule and become distributed to the striatum. With our present preparations we cannot answer the question, and this possibility seems to us a very improbable one.

Fig. 9 Toluidine-blue preparation. Transverse section passing through the anterior extreme of the tectum. Note in particular the hypothalamus. × 8. *C.c.*, corpus callosum; *Com.inter-vent.*, nucleus commissura interventralis; *Com. post.*, commissura posterior; *Corp.Luys.*, corpus Luysi; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lem.med.*, lemniscus medialis; *Med.forb.*, medial forebrain bundle; *N.gen.lat.p.dors.*, nucleus geniculatus lateralis pars dorsalis; *N.gen.lat.p.vent.*, nucleus geniculatus lateralis pars ventralis; *N.hyp.dors.-med.*, nucleus hypothalamicus dorsomedialis; *N.hyp.post.*, nucleus hypothalamicus posterior; *N.hyp.vent.-med.*, nucleus hypothalamicus ventromedialis; *N.lat. p.post.*, nucleus lateralis pars posterior; *N.paravent.post.*, nucleus paraventricularis posterior; *N.peri.hyp.post.p.vent.*, nucleus periventricularis hypothalamicus posterior pars ventralis; *N.perivent.*, nucleus periventricularis; *N.post.thal.*, nucleus posterior thalami; *N.pretect.*, nucleus pretectalis; *N.vent.*, nucleus ventralis thalami; *Ped.cereb.*, pedunculus cerebri; *Rad.thal.sup.*, radiation thalamica superior; *Str.*, striatum; *Tect.*, tectum; *Tr.cort.-tect.*, tractus cortico-tectalis; *Tr.hab.-ped.*, tractus habenula-peduncularis; *Tr.incert.-tect.*, tractus incerto-tectalis; *Tr.op.*, tractus opticus; *Tr.perivent.*, periventricular system of fibers; *Tr.Vicq d'Azyr*, tractus Vicq d'Azyr; *Vent.*, ventriculus; *Vent.III.*, ventriculus III; *Zon.incert.*, zona incerta.

Fig. 10 Toluidine-blue preparation. Transverse sections passing through the different levels of the mammillary body. Note the complexity of structure of this center in the rat. × 12. *Cap.mam.*, capsula mammillaris; *F.*, fornix; *Inf.*, infundibulum; *N.lat.*, nucleus lateralis mammillaris; *N.mam.med.p.com.vent.*, nucleus mammillaris medialis pars commissuralis ventralis; *N.mam.med.p.lat.*, nucleus mammillaris medialis pars lateralis; *N.mam.med.p.med.*, nucleus mammillaris medialis pars medialis; *N.mam.med.p.medianus*, nucleus mammillaris medialis pars medianus; *N.mam.med.p.post.*, nucleus mammillaris medialis pars posterior; *N.premam.dors.*, nucleus premammillaris dorsalis; *N.premam.vent.*, nucleus premammillaris ventralis; *Tr.Vicq d'Azyr*, tractus Vicq d'Azyr.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TECT.
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N. LAT. P. POST.
N. GEN. LAT. P. DORS.
HIP.
N. VENT.
TR. CORT-TECT.
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RAD. THAL. SUP.
TR. OP.
N. GEN. LAT. P. VENT.
FI.
PED. CEREB
CORP. LUYS
VENT.
TR. INCERT-TECT
STR.
COM. INTER-VENT.
MED. FORB.
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F
TR. HAB-PED.
TR. VICQ D'AZYR
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VENT.
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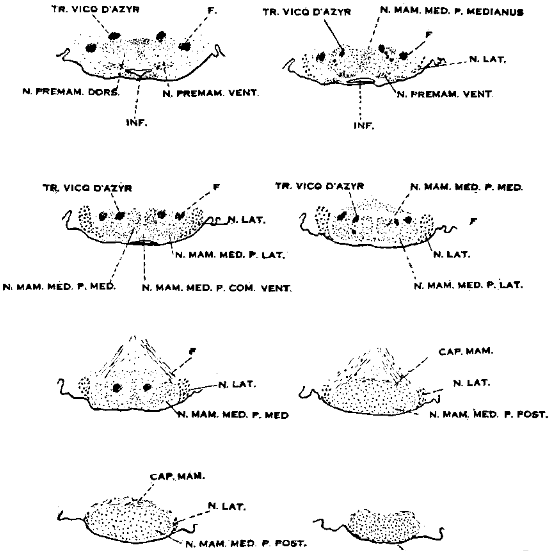
9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F.
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N. PREMAM. VENT.
INF.
TR. VICQ D'AZYR
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F
N. LAT.
N. PREMAM. VENT.
INF.
TR. VICQ D'AZYR
F
N. LAT.
N. MAM. MED. P. LAT.
N. MAM. MED. P. MED.
N. MAM. MED. P. COM. VENT.
TR. VICQ D'AZYR
N. MAM. MED. P. MED.
F
N. LAT.
N. MAM. MED. P. LAT.
F
N. LAT.
N. MAM. MED. P. MED
CAP. MAM.
N. LAT.
N. MAM. MED. P. POST.
CAP. MAM.
N. LAT.
N. MAM. MED. P. POST.
N. MAM. MED. P. POST.

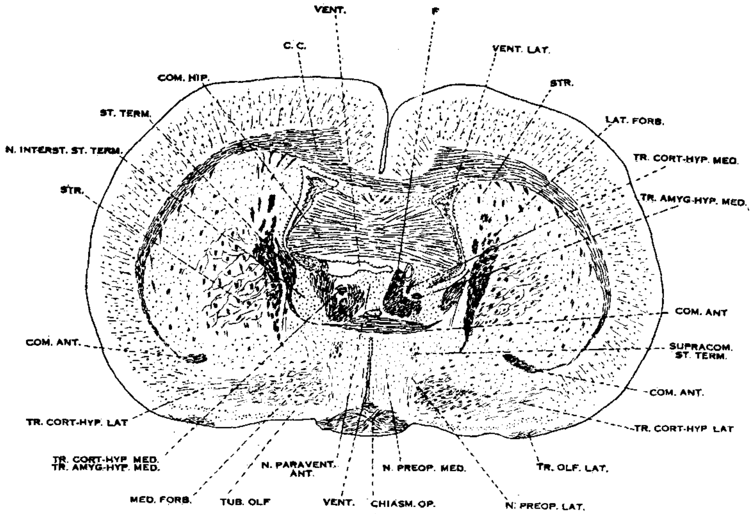
10

Commissura supraoptica ventralis (figs. 13, 27). This corresponds to the commissure of Gudden. In our material it cannot be differentiated from the optic fibers. We have been able to note its presence in the rat by tracing it from the medial geniculate body forward. It is well defined. Some of our series are indicative of the fact that it is also connected with the tectum. We think the question can be very well answered by destroying both eyes and studying the commissure of Gudden in preparations where both optic tracts are degenerated. We reserve this for future work. Bernheimer ('07) has described this tract in the white rat,

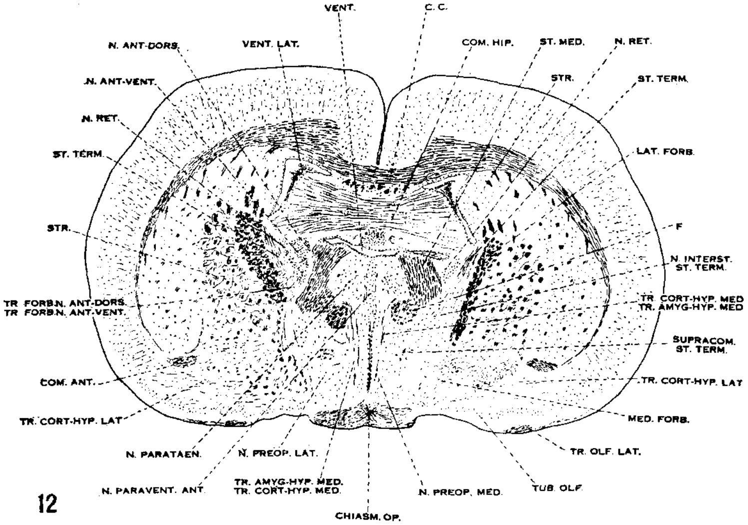
Fig. 11 Silver material prepared according to method III of our description under Methods and Material. Transverse section passing through the anterior extreme of the diencephalon. Note in particular the medial cortico-hypothalamic and the medial amygdalo-hypothalamic tracts. × 8. *C.c.*, corpus callosum; *chiasm.op.*, chiasma optici; *Com.ant.*, commissura anterior; *Com.hip.*, commissura hippocampi; *F.*, fornix; *Lat.forb.*, lateral forebrain bundle; *Med.forb.*, medial forebrain bundle; *N.interst.st.term.*, nucleus interstitialis stria terminalis; *N.paravent. ant.*, nucleus paraventricularis anterior; *N.preop.lat.*, nucleus preopticus lateralis; *Str.*, striatum; *St.term.*, stria terminalis; *Supracom.st.term.*, supracommissural portion of stria terminalis; *Tr.amyg.-hyp.med.*, tractus amygdalo-hypothalamicus medialis; *Tr.cort.-hyp.lat.*, tractus cortico-hypothalamicus lateralis; *Tr.cort.-hyp.med.*, tractus cortico-hypothalamicus medialis; *Tr.olf.lat.*, tractus olfactorius lateralis; *Tub.olf.*, tuberculum olfactorium; *Vent.*, ventriculus; *Vent. lat.*, ventriculus lateralis.

Fig. 12 Silver preparation prepared according to method III of our description under Methods and Material. Transverse section passing through where the medial cortico-hypothalamic and the medial amygdalo-hypothalamic tracts are seen coursing down toward the hypothalamus. Note also the fibers from the lateral forebrain bundle entering the anterior group of thalamic nuclei. × 8. *C.c.*, corpus callosum; *Chiasm.op.*, chiasma optici; *Com.ant.*, commissura anterior; *Com.hip.*, commissura hippocampi; *F.*, fornix; *Lat.forb.*, lateral forebrain bundle; *Med.forb.*, medial forebrain bundle; *N.ant.dors.*, nucleus anterior dorsalis; *N.ant.vent.*, nucleus anterior ventralis; *N.interst.st.term.*, nucleus interstitialis stria terminalis; *N.parataen.*, nucleus parataenialis; *N.paravent.ant.*, nucleus paraventricularis anterior; *N.preop.lat.*, nucleus preopticus lateralis; *N.preop. med.*, nucleus preopticus medialis; *N.ret.thal.*, nucleus reticularis thalami; *St. med.*, stria medullaris; *Str.*, striatum; *St.term.*, stria terminalis; *Supracom.st. term.*, supracommissural portion of the stria terminalis; *Tr.amyg.-hyp.med.*, tractus amygdalo-hypothalamicus medialis; *Tr.cort.-hyp.lat.*, tractus cortico-hypothalamicus lateralis; *Tr.cort.-hyp.med.*, tractus cortico-hypothalamicus medialis; *Tr.forb.n.ant.-dors.*, fibers from the lateral forebrain to nucleus anterior dorsalis; *Tr.forb.n.ant.-vent.*, fibers from the lateral forebrain to the nucleus anterior ventralis; *Tr.olf.lat.*, tractus olfactorius lateralis; *Tub.olf.*, tuberculum olfactorium; *Vent.*, ventriculus; *Vent.lat.*, ventriculus lateralis.

but we are not certain whether he does not confuse this tract with the commissure of Meynert. In lower vertebrate forms the commissure of Gudden is very much better developed (Kappers, '21; Huber and Crosby, '26).



11



12

Optic tract

The optic tract in the rat is made up of crossed and uncrossed fibers. The crossed variety form by far the major portion of the structure. The whole complex courses on the lateral aspect of the diencephalon to come in relation with the lateral geniculate bodies and the tectum. In its relations and constitution it is essentially the same as the one described for other forms (figs. 2 to 9, 15 to 18, 23 to 30).

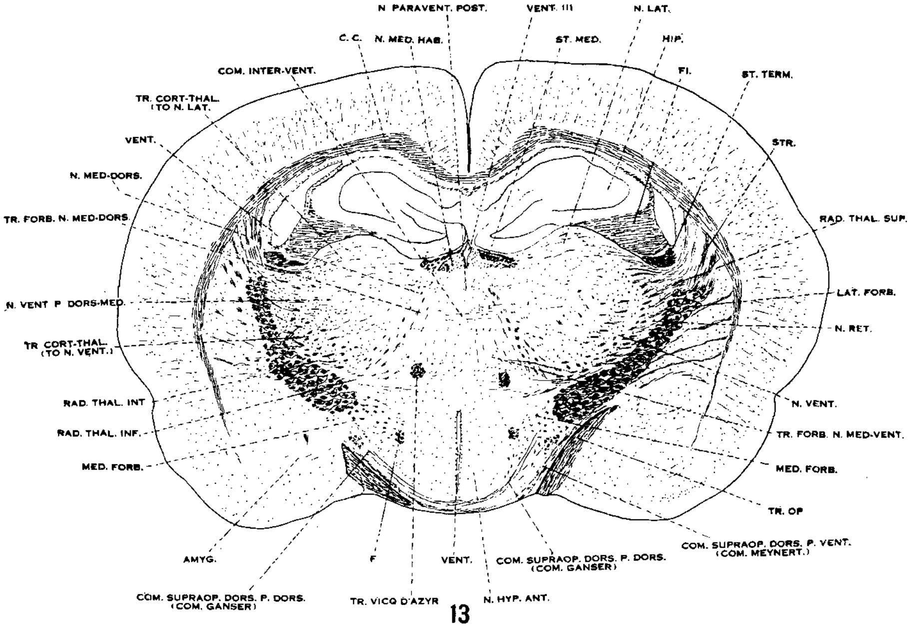
We would here like to mention the tractus pedunculus transversus (figs. 17, 18) which has been studied in the rat by Kosaka and Hiraiwa ('15). These investigators have come to the conclusion that the tract is of optic-nerve origin, as shown in their experimental researches. We have identified the tract in our preparations (figs. 17, 18) as well as the nucleus ectomammillaris with which it comes in synaptic relations. Our preparations are not favorable to confirm the findings of the above-mentioned investigators; that is, in our normal material we have not been able to trace the tractus pedunculus transversus into the optic nerve.

We have not been able to definitely identify the anterior accessory optic tract of Bochenek. Kosaka and Hiraiwa do not think it is well developed in the rat, and they were not able to follow its fibers into the peduncular bundles (cerebral peduncle) in this form.

In our material the optic tract is essentially concerned with the dorsal portion of the lateral geniculate body. It is also in synaptic relations with the nucleus posterior as well as the nucleus lateralis pars posterior. The latter-mentioned nucleus through such an association becomes the homologue of the pulvinar in the higher forms. In the tectum the optic fibers help to form the most dorsal fibrous layer. The pretectal area which we will describe next receives optic fibers also.

Pretectal area

The pretectal area has been described for the opossum by Tsai ('25). In the rat (figs. 6, 7, 9, 16, 17) it is an undifferentiated mass of gray matter which is found rostral to the tectum and in front becomes continuous with the lateral nu-



13

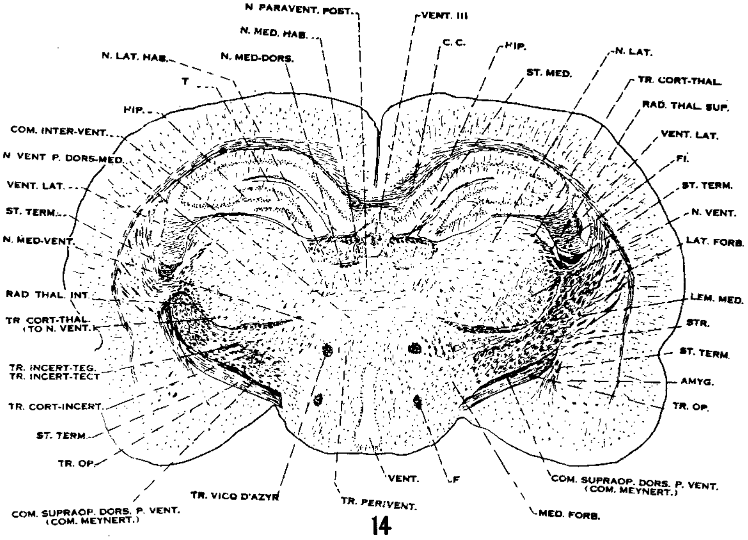
Fig. 13 Weigert preparation. Transverse section passing through the supraoptic commissures. Note in particular the hypothalamic region. × 8. *Amyg.*, amygdala; *C.c.*, corpus callosum; *Com.inter-vent.*, commissura interventralis; *Com.supraop.dors.p.dors.*, commissura supraoptica dorsalis pars dorsalis; *Com. supraop.dors.p.vent.*, commissura supraoptica dorsalis pars ventralis; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lat.forb.*, lateral forebrain bundle; *Med. forb.*, medial forebrain bundle; *N.lat.*, nucleus lateralis thalami; *N.hyp.ant.*, nucleus hypothalamicus anterior; *N.med.dors.*, nucleus medialis dorsalis; *N.med.hab.*, nucleus medialis habenulae; *N.paravent.post.*, nucleus paraventricularis posterior; *N.ret.*, nucleus reticularis thalami; *N.vent.*, nucleus ventralis thalami; *N.vent.p. dors.-med.*, nucleus ventralis pars dorso-medialis; *Rad.thal.inf.*, radiatio thalamica inferior; *Rad.thal.int.*, radiatio thalamica intermedius; *Rad.thal.sup.*, radiatio thalamica superior; *St.med.*, stria medullaris; *Str.*, striatum; *St.term.*, stria terminalis; *Tr.cort.-thal.*, tractus cortico-thalamicus to nucleus lateralis thalami; *Tr. cort.-thal.*, tractus cortico-thalamicus to nucleus ventralis thalami; *Tr.forb.n.med.-dors.*, fibers from the lateral forebrain bundle to the nucleus medialis dorsalis; *Tr.forb.n.med.-vent.*, fibers from the lateral forebrain bundle to the nucleus medialis ventralis; *Tr.op.*, tractus opticus; *Tr.Vicq d'Azyr*, tractus Vicq d'Azyr; *Vent.*, ventriculus; *Vent.III.*, ventriculus tertius.

cleus, the zone of transition being a very gradual one. It is connected with the lateral forebrain bundle through cortico-pretectal fibers. It is also connected with the dorsal portions of the lateral geniculate bodies as well as the tectum

Fig. 14 Silver material prepared according to method I of our description under Methods and Material. Transverse section passing through the plane of the middle third of the habenular complex. Note in particular the commissural fibers of the thalamus. × 8. *Amyg.*, amygdala; *C.c.*, corpus callosum; *Com. inter-vent.*, commissura interventralis; *Com.supraop.dors.p.vent.*, commissura supraoptica dorsalis pars ventralis; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lat.forb.*, lateral forebrain bundle; *Lem.med.*, lemniscus medialis; *Med. forb.*, medial forebrain bundle; *N.lat.*, nucleus lateralis; *N.lat.hab.*, nucleus lateralis habenulae; *N.med.dors.*, nucleus medialis dorsalis; *N.med.hab.*, nucleus medialis habenulae; *N.med.vent.*, nucleus medialis ventralis; *N.paravent.post.*, nucleus paraventricularis posterior; *N.vent.*, nucleus ventralis thalami; *N.vent.p. dors.-med.*, nucleus ventralis pars dorsomedialis; *Rad.thal.int.*, radiatio thalamica intermedius; *Rad.thal.sup.*, radiatio thalamica superior; *St.med.*, stria medullaris; *Str.*, striatum; *St.term.*, stria terminalis; *Tr.cort.-incert.*, tractus cortico-incertalis; *Tr.incert.-tect.*, tractus incerto-tectalis; *Tr.incert.-teg.*, tractus incerto-tegmentalis; *Tr.cort.thal.*, tractus cortico-thalamicus; *Tr.cort.-thal.*, tractus cortico-thalamicus to nucleus ventralis; *Tr.op.*, tractus opticus; *Tr.perivent.*, periventricular system of fibers; *Tr.Vicq d'Azyr*, tractus Vicq d'Azyr; *Vent.*, ventriculus; *Vent.III*, ventriculus tertius; *Vent.lat.*, ventriculus lateralis.

Fig. 15 Silver material prepared according to method I of our description under Methods and Material. Transverse section passing through the plane of the posterior third of the habenula. Note in particular the periventricular system of fibers; note the zona incerta and its connections. × 8. *C.c.*, corpus callosum; *Com.inter-vent.*, commissura inter-ventralis; *Com.supraop.dors.p.vent.*, commissura supraoptica dorsalis pars ventralis; *Corp.Luys.*, corpus Luysii; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lat.forb.*, lateral forebrain bundle; *Med.forb.*, medial forebrain bundle; *N.gen.lat.p.dors.*, nucleus geniculatus lateralis pars dorsalis; *N.hyp.lat.*, nucleus hypothalamicus lateralis; *N.lat.hab.*, nucleus lateralis habenulae; *N.lat.p.post.*, nucleus lateralis pars posterior; *N.med. hab.*, nucleus medialis habenulae; *N.med.vent.*, nucleus medialis ventralis; *N.parafasc.*, nucleus parafascicularis; *N.paravent.post.*, nucleus paraventricularis posterior; *N.perivent.*, nucleus periventricularis; *N.perivent.hyp.post.*, nucleus periventricularis hypothalamicus posterior; *N.vent.*, nucleus ventralis thalami; *N.vent. p.dors.-med.*, nucleus ventralis pars dorso-medialis; *Rad.thal.sup.*, radiatio thalamica superior; *St.med.*, stria medullaris; *Str.*, striatum; *St.term.*, stria terminalis; *Tr.cort.-tect.*, tractus cortico-tectalis; *Tr.cort.-thal.*, tractus cortico-thalamicus to nucleus lateralis pars posterior; *Tr.hab.-ped.*, tractus habenulo-peduncularis; *Tr. incert.-tect.*, tractus incerto-tectalis; *Tr.incert.-teg.*, tractus incerto-tegmentalis; *Tr.op.*, tractus opticus; *Tr.op.-gen.*, tractus optico-geniculatus; *Tr.perivent.*, periventricular system of fibers; *Tr.Vicq d'Azyr*, tractus Vicq d'Azyr; *Vent.*, ventriculus; *Vent.III.*, ventriculus tertius; *Vent.lat.*, ventriculus lateralis; *Zon.incert.*, zona incerta.

and with the optic tract. In its more caudal portions it presents here and there small collections of cells which stand out characteristically in our preparations. It is traversed by optic and lateral forebrain bundles which course toward



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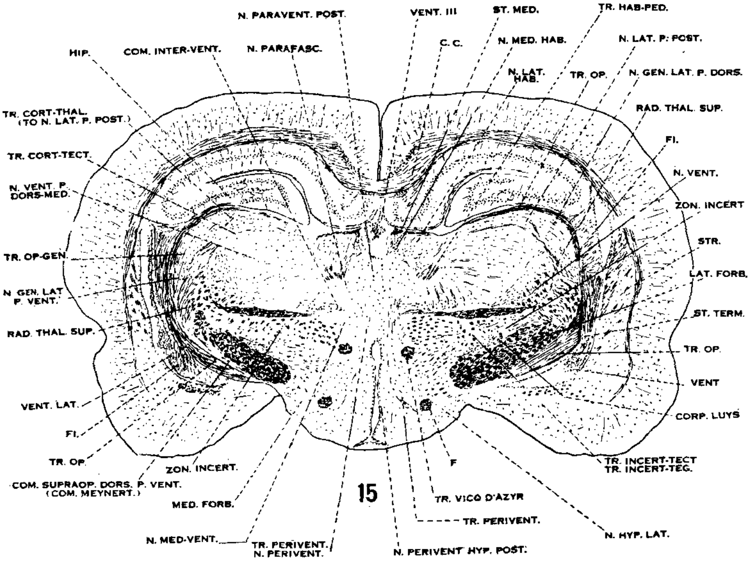

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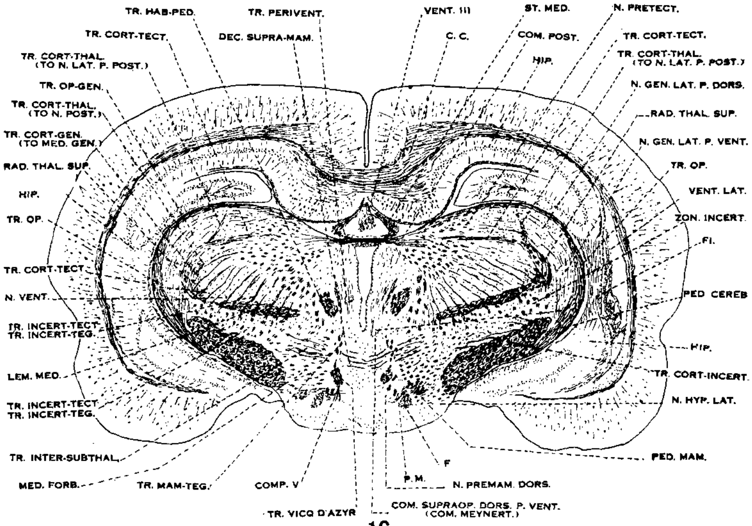
the tectum. The latter circumstance gives the area a certain striated appearance. Through its connections one may be

Fig. 16 Silver preparation prepared according to method I of our description under Methods and Material. Transverse section passing through the anterior third of the posterior commissure. Note in particular the subthalamus, the inter-subthalamic commissure, the zona incertal connections. × 8. *C.c.*, corpus callosum; *Com.post.*, commissura posterior; *Comp.V.*, component V of the combined mammillo-thalamic and the mammillo-tegmental tracts; *Com.supraop.dors.p.vent.*, commissura supraoptica dorsalis pars ventralis; *Dec.supramam.*, decussatio supramammillaria; *F.*, fornix; *Fi.*, fimbria fornicis; Hip., hippocampus; *Lem.med.*, lemniscus medialis; *Med.forb.*, medial forebrain bundle; *N.gen.lat.p.dors.*, nucleus geniculatus lateralis pars dorsalis; *N.gen.lat.p.vent.*, nucleus geniculatus lateralis pars ventralis; *N.hyp.lat.*, nucleus hypothalamicus lateralis; *N.premam.dors.*, nucleus premammillaris dorsalis; *N.pretect.*, nucleus pretectalis; *N.vent.*, nucleus ventralis thalami; *Ped.cereb.*, pedunculus cerebri; *Ped.mam.*, mammillary peduncle; *P.M.*, mammillary peduncular fibers to the mammillary nuclei; *Rad.thal.sup.*, radiatio thalamica superior; *St.med.*, stria medullaris; *Tr.cort.-gen.*, tractus cortico-geniculatus to medial geniculate body; *Tr.cort.-incert.*, tractus cortico-incertalis; *Tr.cort.-tect.*, tractus cortico-tectalis; *Tr.cort.-thal.*, tractus cortico-thalamicus to nucleus posterior; *Tr.hab.-ped.*, tractus habenulo-peduncularis; *Tr. incert.-tect.*, tractus incerto-tectalis; *Tr.incert.-teg.*, tractus incerto-tegmentalis; *Tr.inter-subthal.*, tractus inter-subthalamicus; *Tr.mammillo-teg.*, tractus mammillo-tegmentalis; *Tr.op.*, tractus opticus; *Tr.perivent.*, periventricular system of fibers; *Tr.Vicq d'Azyr*, tractus Vicq d'Azyr; *Vent.III.*, third ventricle; *Vent.lat.*, lateral ventricle; *Zon.incert.*, zona incerta.

Fig. 17 This is from a series prepared according to method I of our description under Methods and Material. Transverse section through the plane of the middle third of the posterior commissure. Note the mammillary body. × 8. *C.c.*, corpus callosum; *Com.hab.*, commissura habenulae; *Com.Meynert.*, commissura Meynerti; *Comp.IV.*, component IV of the combined mammillo-tegmental and the mammillo-thalamic tracts; *Com.post.*, commissura posterior; *Dec.supramam.*, Decussatio supramammillaria; *F.*, fornix; *Hip.*, hippocampus; *Lem.med.*, lemniscus medialis; *N.gen.lat.p.dors.*, nucleus geniculatus lateralis pars dorsalis; *N.gen.lat.p.vent.*, nucleus geniculatus lateralis pars ventralis; *N.III.*, nucleus of the third nerve; *N.lat.p.post.*, nucleus lateralis pars posterior; *N.mam.lat.*, nucleus mammillaris lateralis; *N.perivent.*, nucleus periventricularis; *N.post.thal.*, nucleus posterior thalami; *N.pretect.*, nucleus pretectalis; *Ped.cereb.*, pedunculus cerebri; *Ped.mam.*, mammillary peduncle; *Rad.Forel*, radiations of Forel; *Subst.nig.*, substantia nigra; *Tr.cort.-gen.*, tractus cortico-geniculatus to medial geniculate body; *Tr.cort.-tect.*, tractus cortico-tectalis; *Tr.cort.-thal.*, tractus cortico-thalamicus to nucleus lateralis pars posterior; *Tr.cort.-thal.*, tractus cortico-thalamicus to nucleus posterior; *Tr.gen.-tect.*, tractus geniculato-tectalis; *Tr.hab.-ped.*, tractus habenulo-peduncularis; *Tr.incert.-tect.*, tractus incerto-tectalis; *Tr.incert.-teg.*, tractus incerto-tegmentalis; *Tr.mam.-teg.*, tractus mammillo-tegmentalis; *Tr.op.*, tractus opticus; *Tr.op.-gen.*, tractus optico-geniculatus; *Tr.ped.tr.*, tractus pedunculus transversus; *Tr.perivent.*, periventricular system of fibers; *Tr.Vicq d'Azyr*, tractus Vicq d'Azyr; *Vent.III.*, third ventricle; *Zon.incert.*, zona incerta.

led to think of a possible homology between this nucleus and the pulvinar of higher forms.



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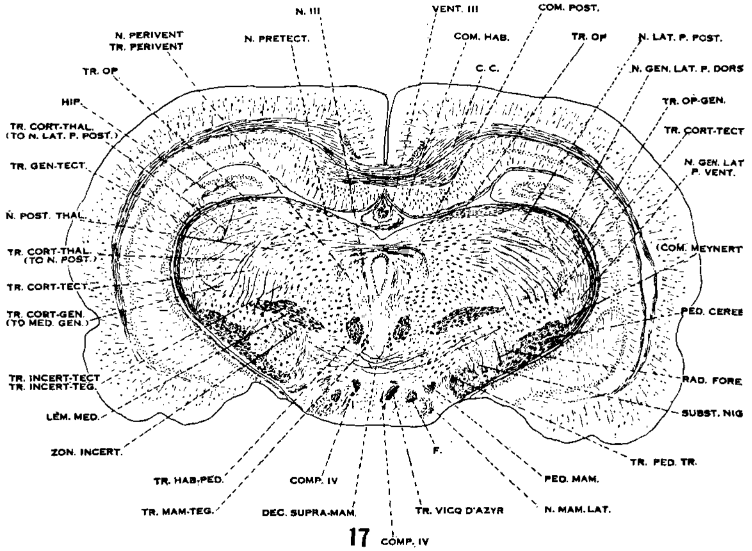

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Lateral geniculate body

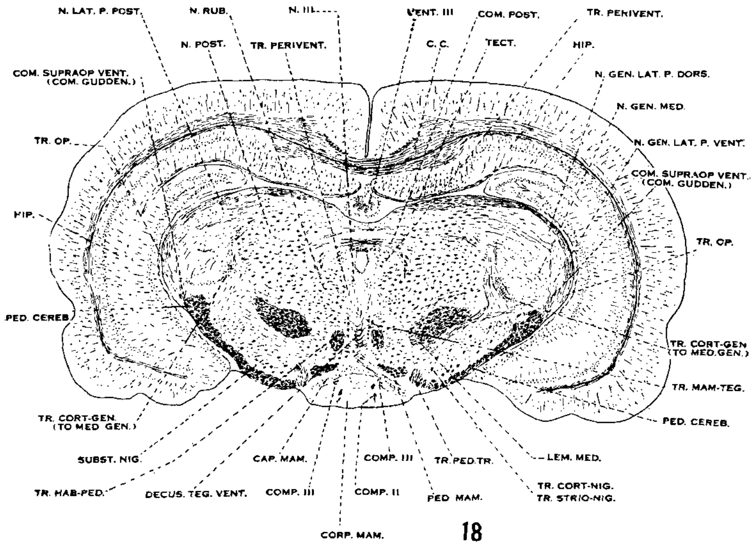
The lateral geniculate body in the rat is made up of two portions: the nucleus geniculatus lateralis pars dorsalis and the nucleus geniculatus lateralis pars ventralis. These have been described in the rabbit by Munzer and Wiener ('02), Winkler and Potter ('11), and others. Malone ('10) describes it in the human, while Vogt ('09) and Friedman ('13) do the same for the monkey. In the rat our findings are as follows:

Nucleus geniculatus lateralis, pars ventralis (figs. 6 to 9, 16 to 18). This nucleus is composed of small and medium-sized cells and its rostral extreme may be seen in the plane where the stria terminalis dips into the amygdaloid complex. It is at first triangular in outline and is bounded by the stria terminalis laterally, and nucleus reticularis thalami medially, the nucleus geniculatus lateralis pars dorsalis dorsally. More caudad it enlarges rapidly in size and assumes a somewhat more nearly round shape and expands medially at the ex-

Fig. 18 Silver preparation prepared according to the method III of our description under Methods and Material. A transverse section through the plane of the middle third of the medial geniculate bodies. Note in particular the connections of the medial geniculate bodies. × 8. *C.c.*, corpus callosum; *Cap.mam.*, mammillary capsule; *Comp.II.*, component II of the combined mammillo-thalamic and the mammillo-tegmental tracts; *Comp.III.*, component III of the combined mammillo-thalamic and the mammillo-tegmental tracts; *Com.post.*, commissura posterior; *Com.supraop.vent.*, commissura supraoptica ventralis; *Corp.mam.*, mammillary body; *Decus.teg.vent.*, decussatio tegmentalis ventralis; *Hip.*, hippocampus; *Lem.med.*, lemniscus medialis; *N.gen.lat.p.dors.*, nucleus geniculatus lateralis pars dorsalis; *N.gen.lat.p.vent.*, nucleus geniculatus lateralis pars ventralis; *N.gen.med.*, nucleus geniculatus medialis; *N.III.*, Oculomotor nucleus; *N.lat.p.post.*, nucleus lateralis pars posterior; *N.post.*, nucleus posterior; *N.rub.*, nucleus ruber; *Ped.cereb.*, pedunculus cerebri; *Mam.ped.*, mammillary peduncle; *Subst.nig.*, substantia nigra; *Tect.*, tectum; *Tr.cort.-gen.*, tractus cortico-geniculatus to medial geniculate body; *Tr.cort.-nig.*, tractus cortico-nigralis; *Tr.hab.-ped.*, tractus habenulo-peduncularis; *Tr.mam.teg.*, tractus mammillo-tegmentalis; *Tr.op.*, tractus opticus; *Tr.ped.tr.*, tractus pedunculus transversus; *Tr.perivent.*, periventricular system of fibers; *Tr.strio-nig.*, tractus strio-nigralis; *Vent.III.*, third ventricle.

Fig. 19 Neurones drawn from Cox-Golgi preparations. These are to illustrate the neurone types in the various nuclei enumerated. × 115. *A*, tuberculum olfactorium; *B*, islands of Calleja; *C*, cells from the nucleus interstitialis septo-hypothalamicus; *D*, cells from the nucleus accumbens.

pense of the reticular nucleus. After the disappearance of the latter, it comes in relation with the zona incerta, and in more than one place the two masses seem to be continuous with each other. In the plane of the middle third of the medial geniculate body this nucleus disappears entirely. It



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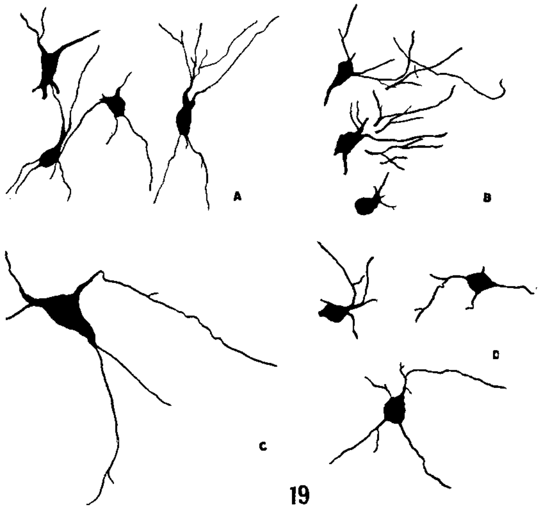

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has a certain striated appearance in our preparations due to the passage of optic bundles through its substance. On its medial aspect one notes the presence of cortical bundles connecting the cortex with the tectum and the postero-dorsal thalamus. This nucleus is intimately related to the Meynert's commissure. We have not been able to note any connections between the cortex and this portion of the lateral geniculate body. Cajal ('11) describes a few collaterals to this nucleus from the cortico-geniculate fibers to the nucleus geniculatus lateralis pars dorsalis. The ventral portion of the lateral geniculate body is undoubtedly in intimate synaptic relations with the zona incerta, as shown in our preparations.

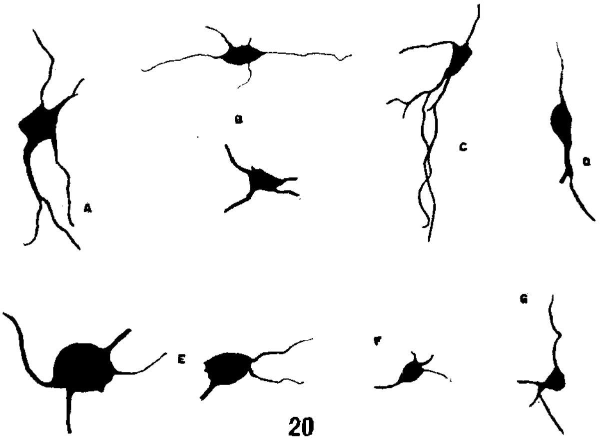

Fig. 20 Neurones drawn from Cox-Golgi preparations. These are to illustrate the neurone types in the various nuclei enumerated. × 115. *A*, a cell from the ventral premammillary nucleus; *B*, a cell from the nucleus supraopticus diffusus; *C*, a cell from the nucleus hypothalamicus lateralis; *D*, a cell from the nucleus hypothalamicus posterior; *E*, cells from the nucleus tangentialis; *F*, a cell from the dorsal premammillary nucleus; *G*, a cell from the medial mammillary nucleus.

Nucleus geniculatus lateralis, pars dorsalis (figs. 6 to 9, 15 to 18, 23, 24, 29, 30). The rostral extreme of this nucleus extends farther cephalad than that of the pars ventralis. The cells look somewhat larger and are not as closely packed together. More caudad, it assumes an elongated oval shape.

The structure as a whole is more dorsally placed than in the rabbit or cat (Winkler and Potter, '11, '14). It is bounded by the optic tract laterally and dorsally, nucleus geniculatus lateralis pars ventralis and nucleus ventralis thalami ventrally, nucleus lateralis pars posterior medially. It is largest in the rostral extreme of the posterior commissure. Farther caudad, it is more distinct in outline and recedes somewhat ventrally, so that it forms one of the ventrolateral masses of the diencephalon. It disappears in the plane of the middle third of the medial geniculate body. It is traversed by optic fibers which tend to give it a striated appearance. On its medial aspect one notes the cortico-tectal group of fibers which separate it from the ventral thalamic nucleus as far back as the caudal aspect of the latter.

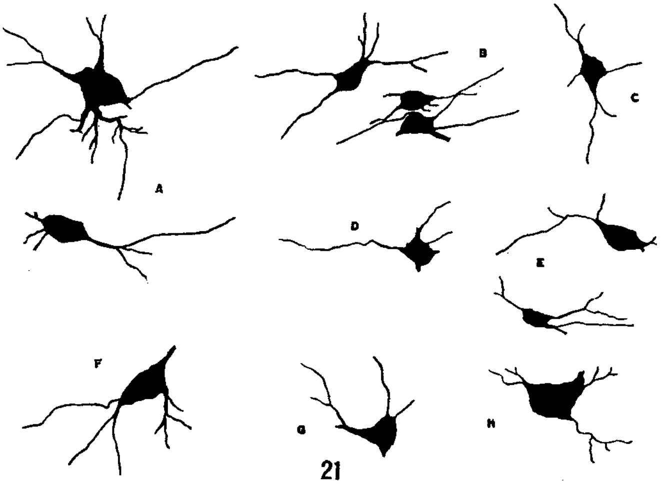

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Fig. 21 Neurones drawn from Cox-Golgi preparations. These are to illustrate the neurone types in the various nuclei mentioned. × 115. *A*, nucleus ventralis thalami; *B*, nucleus reuniens; *C*, nucleus parafascicularis; *D*, nucleus medialis ventralis; *E*, nucleus parataenialis; *F*, nucleus lateralis thalami; *G*, nucleus parataenialis (specialized portion); *H*, nucleus anterior ventralis.

The connections of the nucleus geniculatus lateralis pars dorsalis are numerous:

a. Optic connections. The most medial fibers break away from the main optic tract and enter this nucleus at different levels. Some of these fibers run through the whole length of the nucleus and evidently have a different distribution.

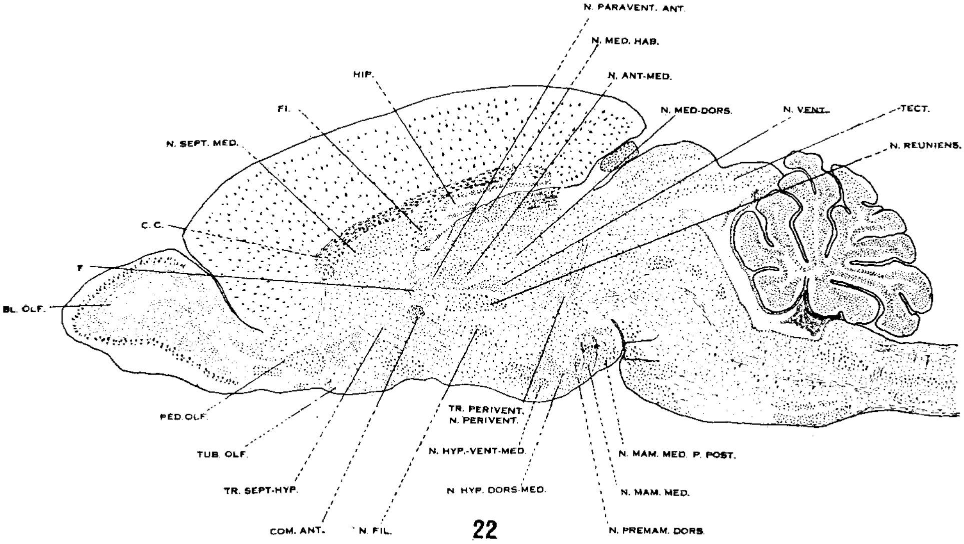

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Fig. 22 Toluidine-blue preparation. A sagittal section passing through the plane of the medial habenular nucleus. Note in particular the hypothalamic nuclei; also all those which are associated with the medial forebrain bundle. × 8. *Bl.olf.*, bulbus olfactorius; *C.c.*, corpus callosum; *Com.ant.*, commissura anterior; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *N.ant.-med.*, nucleus anterior medialis; *N.fil.*, nucleus filiformis; *N.hyp.dors.-med.*, nucleus hypothalamicus dorsomedialis; *N.hyp.vent.-med.*, nucleus hypothalamicus ventromedialis; *N.mam.med.*, nucleus mammillaris medialis; *N.mam.med.p.post.*, nucleus mammillaris medialis pars posterior; *N.med.dors.*, nucleus medialis dorsalis; *N. med.hab.*, nucleus medialis habenulae; *N.paravent.ant.*, nucleus paraventricularis anterior; *N.perivent.*, nucleus periventricularis; *N.premam.dors.*, nucleus premammillaris dorsalis; *N.reuniens*, nucleus reuniens; *N.sept.med.*, medial septal nucleus; *N.vent.*, nucleus ventralis thalami; *Ped.olf.*, olfactory peduncle; *Tect.*, tectum; *Tr.perivent.*, periventricular system of fibers; *Tr.sept.-hyp.*, tractus septo-hypothalamicus; *Tub.olf.*, tuberculum olfactorium.

There are, however, others which end in the nucleus geniculatus lateralis pars dorsalis.

b. Internuclear connections. The two divisions of the lateral geniculate body are interrelated by a fine plexus of fibers, as seen in our silver preparations.

c. Connections between this nucleus and the pretectal, posterior thalamic and the posterior part of the lateral nuclei. There are many more fibers in the dorsal portion of the lateral geniculate body than the optic fibers could account for. Of the latter category of fibers there are those which are traceable to the above-mentioned nuclei, namely, the pretectal nucleus, the nucleus posterior thalami, and the nucleus lateralis pars posterior.

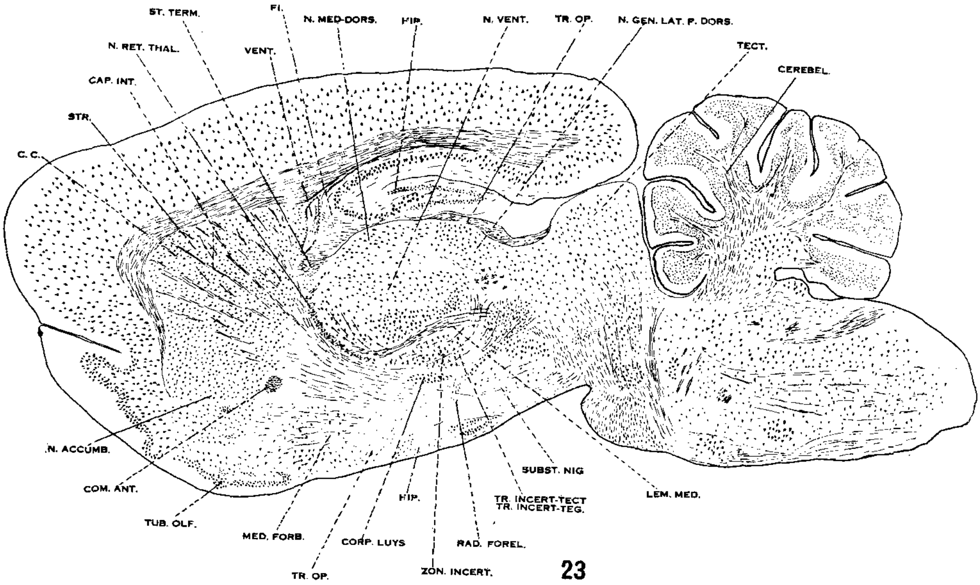

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Fig. 23 Toluidine-blue preparation. A parasagittal section passing through the plane of the middle third of the hippocampus. Note in particular the body of Luys and the zona incerta with their connections. × 8. *Cap.int.*, capsula interna; *C.c.*, corpus callosum; *Cerebel.*, cerebellum; *Com.ant.*, commissura anterior; *Corp.Luys.*, corpus Luysii; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lem.med.*, lemniscus medialis; *Med.forb.*, medial forebrain bundle; *N.accumb.*, nucleus accumbens; *N.gen.lat.p.dors.*, nucleus geniculatus lateralis pars dorsalis; *N.med.dors.*, nucleus medialis dorsalis; *N.ret.thal.*, nucleus reticularis thalami; *N.vent.*, nucleus ventralis; *Rad.Forel*, radiations of Forel; *St.term.*, stria terminalis; *Str.*, striatum; *Subst.nig.*, substantia nigra; *Tect.*, tectum; *Tr.incert.-tect.*, tractus incerto-tectalis; *Tr.incert.-teg.*, tractus incerto-tegmentalis; *Tr.op.*, tractus opticus; *Tub.olf.*, tuberculum olfactorium; *Zon.incert.*, zona incerta; *Vent.*, ventricle.

d. Connections between this nucleus and the tectum. These fibers belong to the same group as the preceding ones. They are seen coursing through the nucleus posterior thalami and the nucleus pretectalis in order to enter the tectal region, where they turn caudad.

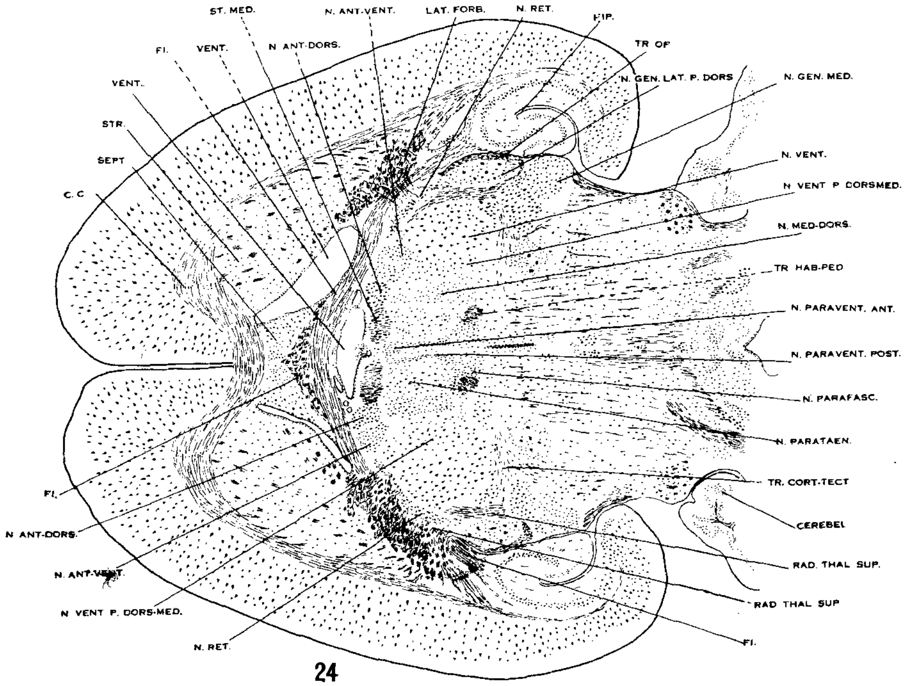

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Fig. 24 Toluidine-blue preparation. A coronal section passing through the plane of the upper third of the diencephalon. Note in particular the nuclei of the midline. × 8. *C.c.*, corpus callosum; *Cerebel.*, cerebellum; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lat.forb.*, lateral forebrain bundle; *N.ant. dors.*, nucleus anterior dorsalis; *N.ant.vent.*, nucleus anterior ventralis; *N.gen. lat.p.dors.*, nucleus geniculatus lateralis pars dorsalis; *N.gen.med.*, nucleus geniculatus medialis; *N.med.dors.*, nucleus medialis dorsalis; *N.parafasc.*, nucleus parafascicularis; *N.parataen.*, nucleus parataenialis; *N.paravent.ant.*, nucleus paraventricularis anterior; *N.ret.*, nucleus reticularis thalami; *N.vent.*, nucleus ventralis thalami; *N.vent.p.dors.-med.*, nucleus ventralis pars dorsomedialis; *Rad.thal.sup.*, radiatio thalamica superior; *Sept.*, septum; *St.med.*, stria medullaris; *Str.*, striatum; *Tr.cort.-tect.*, tractus cortico-tectalis; *Tr.hab.-ped.*, tractus habenulo-peduncularis; *Tr.op.*, tractus opticus; *Vent.*, ventricle.

e. Connections between the cortex and the nucleus geniculatus lateralis, pars dorsalis. These are included among the fibers of the dorsal thalamic radiation (see discussion of the same, p. 53). They are especially well seen in our horizontal preparations (fig. 29). This connection, however, is not a very rich one.

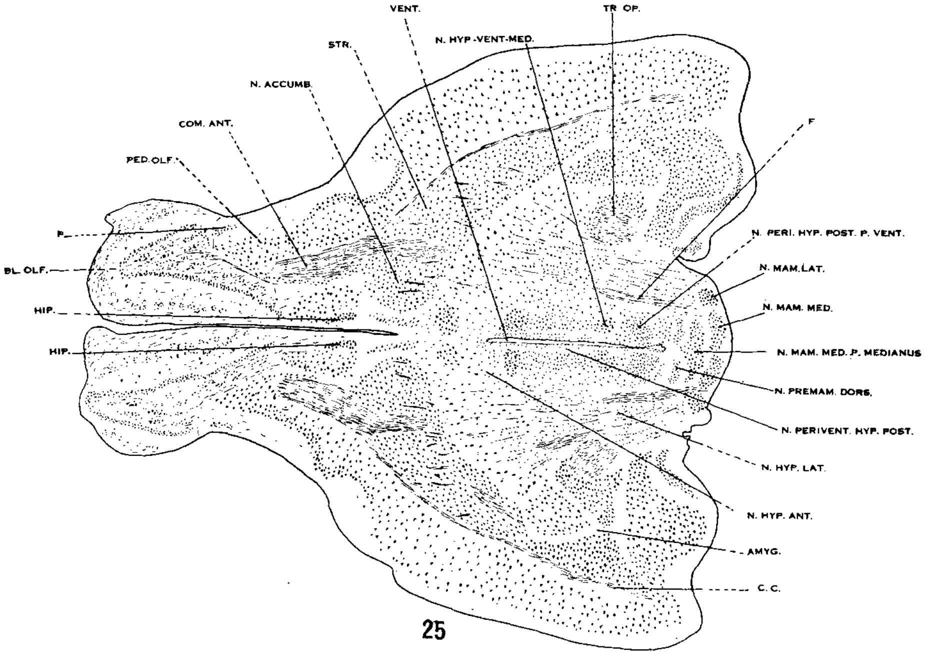

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Fig. 25 Toluidine-blue preparation. A coronal section passing through the middle third of the hypothalamus. Note in particular the nuclei about the ventricle. × 8. *Amyg.*, amygdala; *Bl.olf.*, bulbus olfactorius; *C.c.*, corpus callosum; *Com.ant.*, commissura anterior; *F.*, fornix; *Hip.*, hippocampus; *N.accumb.*, nucleus accumbens; *N.hyp.ant.*, nucleus hypothalamicus anterior; *N.hyp.lat.*, nucleus hypothalamicus lateralis; *N.hyp.vent.-med.*, nucleus hypothalamicus ventromedialis; *N.mam.lat.*, nucleus mammillaris lateralis; *N.mam.med.*, nucleus mammillaris medialis; *N.mam.med.p.medianus*, nucleus mammillaris medialis pars medianus; *N.peri.hyp.post.p.vent.*, nucleus periventricularis hypothalamicus posterior pars ventralis; *N.peri.hyp.post.*, nucleus periventricularis hypothalamicus posterior; *N.premam.dors.*, nucleus premammillaris dorsalis; *P.*, nucleus olfactorius anterior pars externa; *Ped.olf.*, olfactory peduncle; *Str.*, striatum; *tr.op.*, tractus opticus; *Vent.*, ventricle.

The medial geniculate body

The medial geniculate body has been described in the rabbit (Munzer and Wiener, '02; Winkler and Potter, '11), in the cat (Winkler and Potter, '14), in the monkey (Vogt, '09; Friedman, '13), in the human (Malone, '10). By comparing the position of this nucleus in the rat with that of forms mentioned above, we note the interesting fact that the medial geniculate body in the rat is farther posterior than in forms higher up. When a comparison is made of the position of this nucleus in the rat with that in lower forms, such as reptiles, one notes that the reptilian geniculate body is farther posterior than the one in the rat. This migration, so to speak, of the medial geniculate body forward in the evolutionary scale is probably indicative of the increasing importance of cortex running parallel with the increasing subsidiary nature of the tectum (discussion, p. 108).

Cephalad the medial geniculate body abuts against the posterior aspect of the nucleus ventralis thalami, the transition between the two structures being a very gradual one. The nucleus is made up of large and medium-sized cells. In the more rostral portions the nuclear mass is divided into smaller linear groups caused by the passage of the corticotectal fibers. The dorsal portion of the lateral geniculate body forms its lateral boundary for the rostral third. After the disappearance of the lateral geniculate body, the medial geniculate becomes the most peripheral diencephalic nuclear mass in this region. In its rostral third it presents a lateral portion with cells thickly placed together and a medial portion, somewhat dorsally inclined, with scattered cells. These two masses join posteriorly with the consequent formation of one oval mass with characteristic and classical evagination of the same after the disappearance of the stratum zonale belonging to the optic system (figs. 18, 24, 29, 30). In the plane of the caudal extreme of the nucleus posterior thalami one notes the appearance of two other nuclear masses which, farther caudad, become continuous with the medial geniculate body. A detailed consideration of the nuclear configuration of these masses will be taken up in future work.

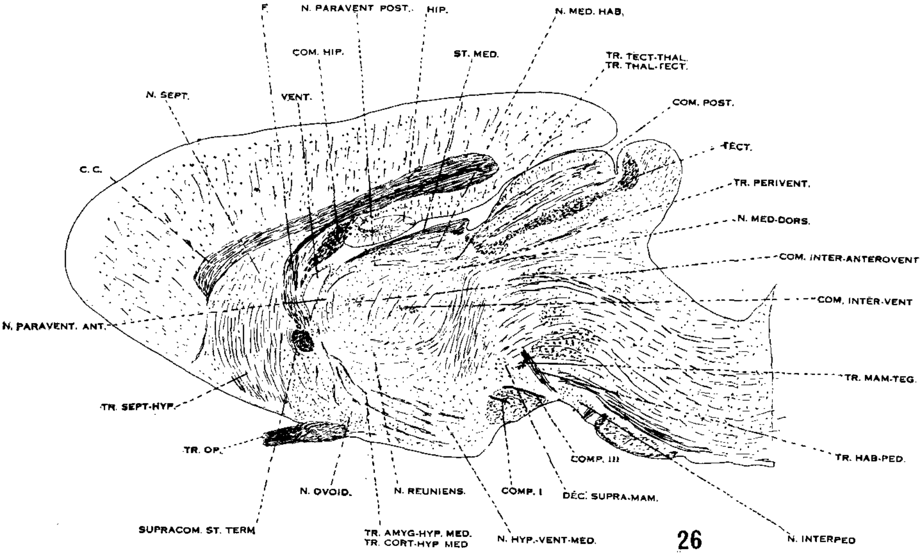

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Fig. 26 Silver preparation prepared according to method III of our description under Methods and Material. A parasagittal section passing through the medial third of the diencephalon. Note in particular the periventricular system of fibers and the medial amygdalo-hypothalamic and the medial cortico-hypothalamic tracts. × 8. *C.c.*, corpus callosum; *Com.hip.*, commissura hippocampi; *Com.inter-anterovent.*, commissura inter-anteroventralis; *Com.inter-vent.*, commissura inter-ventralis; *Com.post.*, commissura posterior; *Comp.I.*, *Comp.III.*, components I and III of the combined mammillo-thalamic and the mammillo-tegmental tracts; *Dec.supra-mam.*, decussatio supra-mammillaris; *F.*, fornix; *Hip.*, hippocampus; *N.hyp.vent.-med.*, nucleus hypothalamicus ventromedialis; *N.interped.*, nucleus interpeduncularis; *N.med.dors.*, nucleus medialis dorsalis; *N.med.hab.*, nucleus medialis habenulae; *N.ovoid.*, nucleus ovoidus; *N.paravent.ant.*, nucleus paraventricularis anterior; *N.paravent.post.*, nucleus paraventricularis posterior; *N.reuniens*, nucleus reuniens; *N.sept.*, septal nucleus; *St.med.*, stria medullaris; *Supracom.st.term.*, supracommissural portion of the stria terminalis; *Tect.*, tectum; *Tr.amyg.-hyp.med.*, tractus amygdalo-hypothalamicus medialis; *Tr.cort.-hyp. med.*, tractus cortico-hypothalamicus medialis; *Tr.hab.-ped.*, tractus habenulo-peduncularis; *Tr.mam.-teg.*, tractus mammillo-tegmentalis; *Tr.op.*, tractus opticus; *Tr.perivent.*, periventricular system of fibers; *Tr.sept.-hyp.*, tractus septo-hypothalamicus; *Tr.tect.-thal.*, tractus tecto-thalamicus; *Tr.thal.-tect.*, tractus thalamo-tectalis; *Vent.*, ventricle.

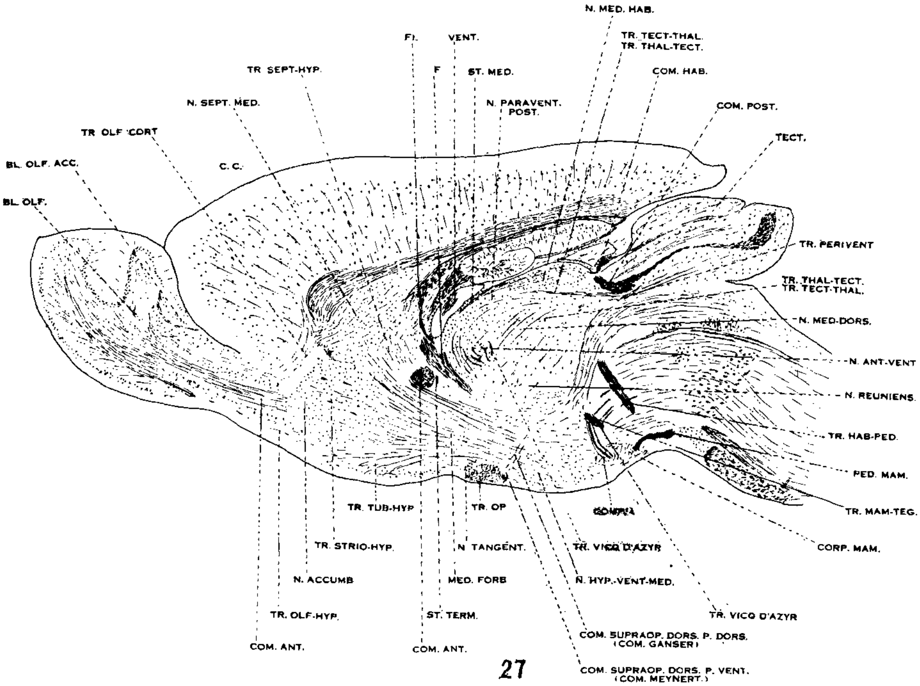
We have limited ourselves in this work to a few of the various connections of the medial geniculate body. In our silver preparations the anterior half of the nucleus is very rich in cross-cut fibers which impart to the nucleus in this situation a granular appearance (a condition also noted by Vogt, '09, in the monkey). Most of these fibers are cortical in nature (figs. 16, 17, 18, 30). They accompany the dorsal thalamic radiation to cortex. The medial geniculate bodies of the opposite sides are interconnected through the commissure of Gudden. The lateral fillet and the tectal connections will not be discussed at this time.

The following centers in the subthalamus will be taken up in the present paper: entopeduncular nucleus, corpus Luysii, zona incerta, and field of Forel.

Fig. 27 Silver preparation prepared according to method I of our description under Methods and Material. Parasagittal section passing through the middle third of the diencephalon, somewhat lateral to the preceding one. Note in particular the constitution of the medial forebrain bundle and the periventricular system of fibers. × 8. *Bl.olf.*, bulbus olfactorius; *Bl.olf.acc.*, bulbus olfactorius accessorius; *C.c.*, corpus callosum; *Com.ant.*, commissura anterior; *Com.hab.*, commissura habenulae; *Com.post.*, commissura posterior; *Comp.I.*, component I of the combined mammillo-thalamic and the mammillo-tegmental tracts; *Com.supraop.dors.p.dors.*, commissura supraoptica dorsalis pars dorsalis; *Com. supraop.dors.p.vent.*, commissura supraoptica dorsalis pars ventralis; *Corp.mam.*, corpus mammillaris; *F.*, fornix; *Fi.*, fimbria fornicis; *Med.forb.*, medial forebrain bundle; *N.accumb.*, nucleus accumbens; *N.ant.vent.*, nucleus anterior ventralis; *N.hyp.vent.-med.*, nucleus hypothalamicus ventromedialis; *N.med.dors.*, nucleus medialis dorsalis; *N.med.hab.*, nucleus medialis habenulae; *N.paravent. post.*, nucleus paraventricularis posterior; *N.reuniens*, nucleus reuniens; *N.sept. med.*, nucleus septi medialis; *N.tangent.*, nucleus tangentialis; *Ped.mam.*, mammillary peduncle; *St.med.*, stria medullaris; *St.term.*, stria terminalis; *Tect.*, tectum; *Tr.hab.-ped.*, tractus habenulo-peduncularis; *Tr.mam.-teg.*, tractus mammillo-tegmentalis; *Tr.olf.-cort.*, tractus olfacto-corticalis; *Tr.olf.-hyp.*, tractus olfacto-hypothalamicus; *Tr.op.*, tractus opticus; *Tr.perivent.*, periventricular system of fibers; *Tr.sept.-hyp.*, tractus septo-hypothalamicus; *Tr.strio-hyp.*, tractus strio-hypothalamicus; *Tr.tect.-thal.*, tractus tecto-thalamicus; *Tr.thal.-tect.*, tractus thalamo-tectalis; *Tr.tub.-hyp.*, tractus tuberculo-hypothalamicus; *Tr.Vicq d'Azyr*, tractus Vicq d'Azyr; *Vent.*, ventricle.

Entopeduncular nucleus

In the plane of the posterior third of the habenula one notes the appearance in the substance of the lateral forebrain bundle of a group of medium-sized and large cells. It is absolutely enclosed in the bundles of the internal capsule and is found in the medial third of the latter (in cross-sectional series). This nucleus has been described in lower forms (Edinger, '11; Huber and Crosby, '26). It is not the same as Cajal's nucleus of the internal capsule which we have been able to identify as the most rostral portion of the zona incerta. Undoubtedly, this nucleus represents a substation for descending impulses through a group of peduncular fibers (fig. 6).



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Corpus Luysii

The body of Luys in the rat is essentially the same as the one described for other forms (Cajal, '11; Friedman, '13;

Winkler and Potter, '11, '14). It appears in the plane of the middle third of the ventromedial hypothalamic nucleus (figs. 7, 9, 15, 23, 28). Found on the dorsal aspect of the cerebral peduncle, it assumes in our cross-sectional series the shape of a lens. In places it becomes intimately associated with the lateral hypothalamic gray. It disappears entirely just before the appearance of the substantia nigra.

Connections of the corpus Luysii. Sano ('10), Kosaka and Hiraiwa ('15), and others think that optic fibers enter the body of Luys. Probst ('00, '05), Cajal ('11), and others deny this fact. From a study of our normal preparations, we have come to the following conclusions:

a. Connections with the internal capsule. In our cross-cut and sagittal preparations fibers are seen to be given off from the cerebral peduncle and enter the corpus Luysii. Cox preparations show that most of these fibers are terminal in type. A smaller number of finer fibers which we think are collaterals from the peduncular system are also seen entering this nucleus (this connection was seen by Cajal years ago).

b. Connections with the zona incerta. In our silver preparations we have noted the presence of fine fibers connecting these associated centers of the subthalamus.

c. Connections with lower centers. In our sagittal preparations we see arising from the caudal aspect of the body of Luys fibers which run caudad along with the bundles from the zona incerta. These can certainly be followed to the tegmentum. The special distribution of these fibers is still unknown to us.

We have not been able to identify any optic fibers entering this nucleus. This would seem to us mechanically impossible, unless we are mistaken in the proper identification of the commissure of Meynert. The latter comes to lie in our preparations between the optic tract and the cerebral peduncle. No optic fibers cross the Meynert's commissure in our series of sections of the rat's brain.

Zona incerta

In the rat the zona incerta is a very large nuclear mass and extends from the plane of the nucleus filiformis an-

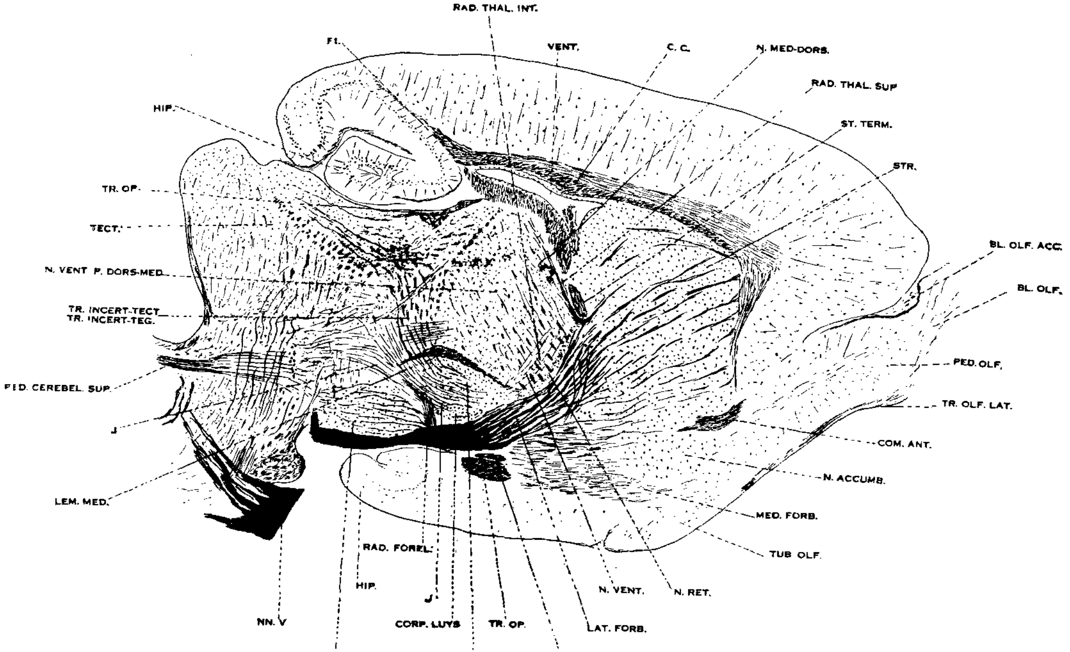

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Fig. 28 Weigert preparation. A sagittal section passing through the plane of the lateral third of the diencephalon. Note in particular the connections of the zona incerta and the body of Luys. × 8. *Bl.olf.*, bulbus olfactorius; *Bl.olf. acc.*, accessory olfactory bulb; *C.c.*, corpus callosum; *com.ant.*, commissura anterior; *Com.supraop.dors.p.vent.*, commissura supraoptica dorsalis pars ventralis; *Corp.Luys.*, corpus Luysii; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *J*, fibers from the body of Luys to tegmentum and possibly also to tectum; *Lat.forb.*, lateral forebrain bundle; *Lem.med.*, lemniscus medialis; *Med.forb.*, medial forebrain bundle; *N.accumb.*, nucleus accumbens; *N.med.dors.*, nucleus medialis dorsalis; *Nn.V.*, nervus trigeminus; *N.ret.*, nucleus reticularis; *N.vent.*, nucleus ventralis; *N.vent.p.dors.-med.*, nucleus ventralis pars dorsomedialis; *Ped.cerebel.sup.*, superior cerebellar peduncle; *Ped.olf.*, olfactory peduncle; *Rad.Forel*, radiations of Forel; *Rad.thal.int.*, radiatio thalamica intermedius; *Rad.thal.sup.*, radiatio thalamica superior; *Str.*, striatum; *St.term.*, stria terminalis; *Subst.nig.*, substantia nigra; *Tect.*, tectum; *Tr.incert.-tect.*, tractus incerto-tectalis; *Tr.incert.-teg.*, tractus incerto-tegmentalis; *Tr.olf.lat.*, tractus olfactorius lateralis; *Tr.op.*, tractus opticus; *Tub.olf.*, tuberculum olfactorium; *Vent.*, ventriculus; *Zon.incert.*, zona incerta.

teriorly to that of the substantia nigra posteriorly (figs. 5 to 9, 15 to 17, 23, 28). Dorsally, it is bounded by the lemnisci system of fibers throughout most of its extent, except most anteriorly where the thalamic reticular nucleus becomes its most dorsal boundary. Ventrally, it is seen resting on the cerebral peduncle and its cephalic continuation, the internal

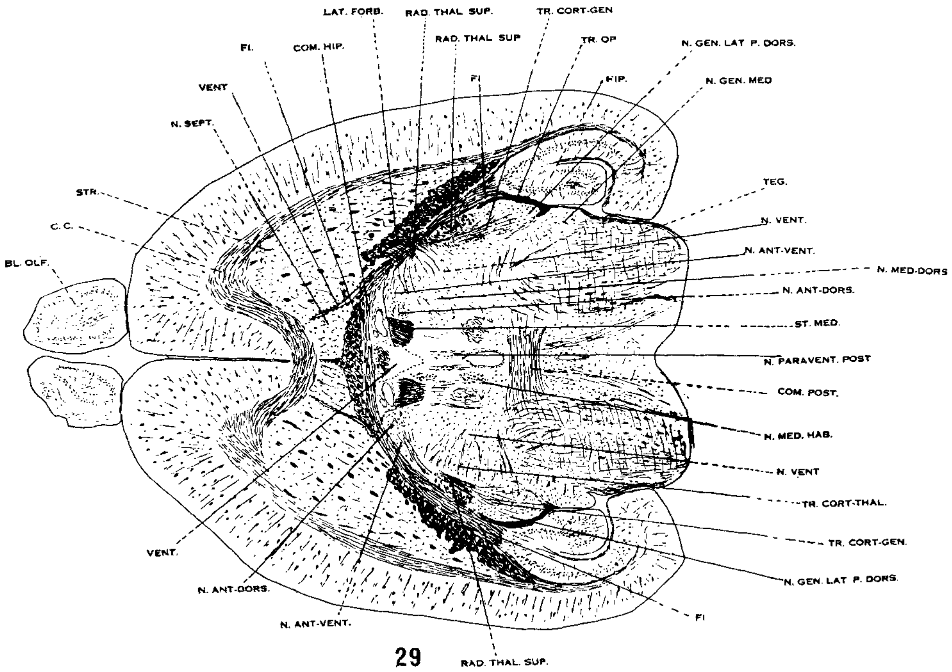

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Fig. 29 Silver material prepared according to method I of our description under Methods and Material. A coronal section passing through the plane of the posterior commissure. Note in particular the cortico-geniculate fibers to the lateral geniculate body. × 8. *Bl.olf.*, bulbus olfactorius; *C.c.*, corpus callosum; *Com.hip.*, commissura hippocampi; *Com.post.*, commissura posterior; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lat.forb.*, lateral forebrain bundle; *N.ant.dors.*, nucleus anterior dorsalis; *N.ant.vent.*, nucleus anterior ventralis; *N.gen.lat.p.dors.*, nucleus geniculatus lateralis pars dorsalis; *N.gen.med.*, nucleus geniculatus medialis; *N.med.dors.*, nucleus medialis dorsalis; *N.med.hab.*, nucleus medialis habenulae; *N.paravent.post.*, nucleus paraventricularis posterior; *N.sept.*, nucleus septi; *N.vent.*, nucleus ventralis; *Rad.thal.sup.*, radiatio thalamica superior; *St.med.*, stria medullaris; *Str.*, striatum; *Teg.*, tegmentum; *Tr.cort.-gen.*, tractus cortico-geniculatus to lateral geniculate body; *Tr.cort.-thal.*, tractus cortico-thalamicus; *Tr.op.*, tractus opticus; *Vent.*, ventriculus.

capsule. It is intimately associated with the latter system, this being evident even in cell preparations. In its most rostral extreme it is continuous with the lateral aspect of the nucleus filiformis and farther caudad with the nucleus hypothalamicus dorsomedialis (see discussion of hypothalamus,

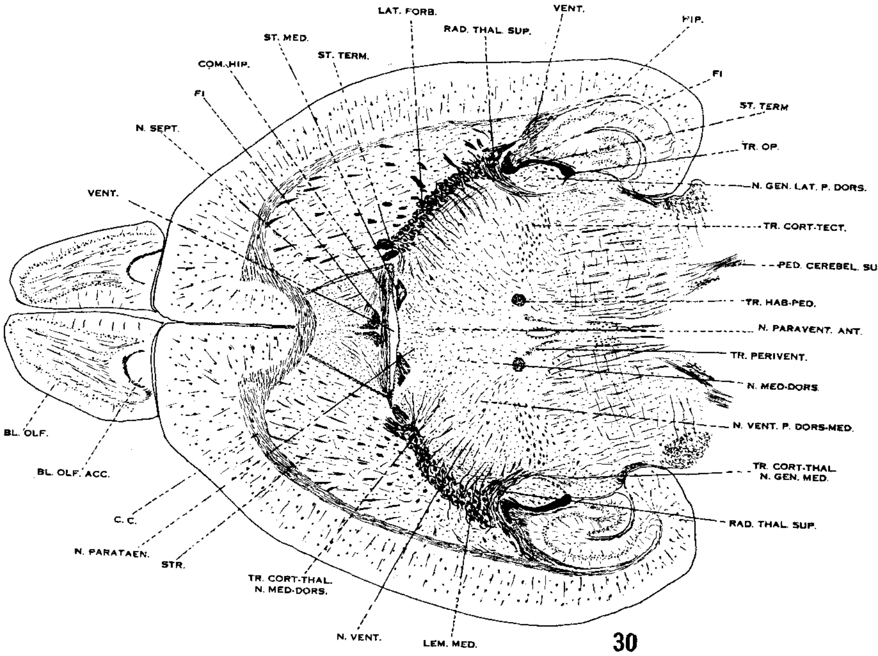

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Fig. 30 Prepared according to method I of our description under Material and Methods. A coronal section passing through the plane of the middle third of the diencephalon. Note in particular the cortico-geniculate fibers to the medial geniculate body. × 8. *Bl.olf.*, bulbus olfactorius; *Bl.olf.acc.*, bulbus olfactorius accessorius; *C.c.*, corpus callosum; *Com.hip.*, commissura hippocampi; *F.*, fornix; *Fi.*, fimbria fornicis; *Hip.*, hippocampus; *Lat.forb.*, lateral forebrain bundle; *Lem.med.*, lemniscus medialis; *N.gen.lat.p.dors.*, nucleus geniculatus lateralis pars dorsalis; *N.med.dors.*, nucleus medialis dorsalis; *N.parataen.*, nucleus parataenialis; *N.paravent.ant.*, nucleus paraventricularis anterior; *N.sept.*, nucleus septi; *N.vent.*, nucleus ventralis thalami; *N.vent.p.dors.-med.*, nucleus ventralis pars dorsomedialis; *Ped.cerebel.sup.*, pedunculus cerebellaris superior; *Rad.thal.sup.*, radiatio thalamica superior; *St.med.*, stria medullaris; *Str.*, striatum; *St.term.*, stria terminalis; *Tr.cort.-tect.*, tractus cortico-tectalis; *Tr.cort.-thal.*, tractus cortico-thalamicus to the medial geniculate body; *Tr.cort.-thal.*, tractus cortico-thalamicus to nucleus medialis dorsalis; *Tr.hab.-ped.*, tractus habenulo-peduncularis; *Tr.op.*, tractus opticus; *Tr.perivent.*, periventricular system of fibers; *Vent.*, ventriculus.

p. 83). Dorsally, in its middle third the uncertain zone becomes intimately associated with the nucleus medialis ventralis thalami. A very close continuity exists between the nucleus geniculatus lateralis pars ventralis and the zona incerta. In its posterior third the uncertain zone is traversed by a multitude of bundles which are very evident even in cell preparations.

Most authors have not contributed to our meager knowledge of the connections of this center. Cajal ('11) speaks of internal capsule and lemniscus fibers as the possible paths associated with this region. Déjerine ('01), Munzer and Wiener ('02), Sano ('10), and Kappers ('21) either do not discuss its connections or they speak of them with great hesitancy. The conclusions that we have arrived at from a study of our material are as follows:

a. Connections with the internal capsule. Fibers are given off at intervals as the cerebral peduncle passes caudad through the subthalamic region. These are most probably cortical in nature, although a few may be striatal in nature.

b. Incerto-tectal connections (figs. 8, 9, 14 to 17, 23, 28). Fibers especially from the medial two-thirds of the zona incerta are seen coming together and forming small bundles which course caudad, and in the plane of the rostral extreme of the medial geniculate body turn dorsad to enter the tectum. Not all of the bundles seen in this plane are from the zona incerta. Especially the more laterally placed bundles are cortical in nature (cortical-tectal paths, see discussion of the lateral forebrain bundle, p. 53).

c. Incerto-tegmental connections (figs. 8, 9, 14 to 17, 23, 28). These bundles are especially evident in the medial third of the zona incerta. They extend a little distance dorsad and course caudad in the substance of the nucleus medialis ventralis thalami. The conduction in this path is probably in both directions.

d. The commissure of Meynert connects the more rostral portions of the uncertain zones of the two sides.

e. Hypothalamico-incertal connections. In the plane where the zona incerta is intimately associated with the hypothalamus, fine fibers are seen interconnecting the two areas. It is possible that a few fibers from the medial forebrain bundle also reach the zona incerta in this situation.

f. The supramammillary decussation interconnects the more posterior portions of the zona incerta (figs. 17, 26).

From the above connections it can be seen that the zona incerta is probably a very important correlation center. Future careful physiologic work should enable us to know more about the true nature of this region. It is probably true that it is concerned with subconscious mechanisms of a vegetative nature.

Field of Forel

In our preparations the field of Forel constitutes one of the more caudal subthalamic formations. It is made up of small and medium-sized cells and is not easily differentiable from the surrounding gray, especially is this true laterally, where it becomes continuous with the zona incerta. It receives fibers from the lateral forebrain bundle. These were described by Forel, and later they were named after him as the radiations of Forel (figs. 17, 23, 28). It is the radiations of Forel that enable us to pick out the so-called field of Forel in our preparations.

Supramammillary decussation

The supramammillary decussation in our preparations can be divided into three parts: an anterior middle portion, essentially intersubthalamic in nature; a posterior ventral portion made up of the decussation of the fornix bundles; a posterior dorsal portion, which is essentially rubro-commissural in nature.

The intersubthalamic component (figs. 17, 26) brings about an association between the subthalami of the two sides, particularly their more medial portions. In this group there are seen some fibers which course dorsally along the ventricle after decussation, the exact nature of which we have not as yet been able to work out. The more posterior part of this component interconnects the field of Forel regions. The ventral tegmental nuclei are also interrelated through this system.

Decussation of the fornix bundles has been taken up in the discussion of the hypothalamus (p. 98).

Rubro-commissural fibers. These are found crossing in the most dorsal position and are practically the most caudal component of the group. They come down in gentle curves from the region of the red nucleus. Whether some of these fibers are tectal in nature it is hard to tell from the preparations at hand. More caudad, this component becomes contiguous with the ventral tegmental decussation.

LATERAL FOREBRAIN BUNDLE (INTERNAL CAPSULE AND CEREBRAL PEDUNCLE)

Under the heading lateral forebrain bundle we will summarize our findings in the rat as concerns this path. We will try to discuss it completely (so far as possible) from its beginning and formation to its termination and distribution. Naturally, only the diencephalic portion of its distribution will be taken up in detail. The lateral forebrain bundle has been described in lower forms (Herrick, '10; Huber and Crosby, '26) and in Mammalia (Déjerine, '01; Cajal, '11; Hollander, '13; Kappers, '21, and others). Our findings in the rat are quite characteristic and somewhat more complete than any account of this structure as found in the mammalian literature we have consulted. We should like to emphasize especially the connections between thalamus and forebrain and those between forebrain and tectum.

After coursing through the striatum, the portion of the internal capsule from the frontal end of the hemisphere collects on the medial aspect of the striatum in the form of compact bundles. The further contributions from the cortex, both dorsally and laterally, push this frontal component ventrally and medially. Undoubtedly, some of the fibers of the internal capsule are of striatal origin, but in our normal preparations we are not able to distinguish the cortical from the striatal fibers. Future experimental research will most probably answer this question. In our present paper we will not try to distinguish the striatal from the cortical fibers, but will group the whole under the term of lateral forebrain bundle or internal capsule. In the transverse plane of the rostral end of the diencephalon, the nucleus reticularis thalami appears just medial to the forming internal capsule. Both become very intimately associated, and bundles are seen passing from one to the other. Most of these bundles cross the reticular nucleus and enter the diencephalon. A little farther caudad there are seen bundles which cross the fibers of the internal capsule in the ventromedial third of the latter. After the appearance of the mammillo-thalamic tract in the field, some of the last-mentioned group of fibers pass medial to the Vicq d'Azyr bundle and then course dorsally to be distributed in the more medial portions of the diencephalon. We have taken this group of fibers and named it the inferior thalamic radiation (figs. 2, 3, 13). In the plane of the anterior thalamic nuclei and all along the lateral aspect of the thalamus to about the plane of the stria terminalis dipping into the amygdaloid complex, one can note groups of bundles which cross the most dorsal portion of the reticular nucleus in order to enter the dorsolateral aspect of the diencephalon. We will discuss this group of fibers under the name of superior thalamic radiation (figs. 2 to 9, 13 to 16, 24, 28 to 30). In between the superior and the inferior thalamic radiations and all along the rostrolateral aspect of the diencephalon we see groups of fibers entering the latter which we have termed the intermediate thalamic radiation.

The internal capsule all along the anterior two-thirds of the diencephalon receives contributions from the lateral and dorsal hemispheric walls. Those from the lateral wall of the hemisphere cross the striatum and join the external aspect of the lateral forebrain bundle. Those from the dorsal wall of the hemisphere extend ventrally in huge formations and then laterally applying themselves to the dorsal aspect of the internal capsule. The more frontal portions of the contributions from the dorsolateral wall are probably of motor significance. The more caudal portions represent fibers from the temporal and the occipital areas of the hemisphere. It is important to note here that the posterior third of the superior thalamic radiation is a part of this group of fibers; that is, it connects the posterior portion of the diencephalon and the tectum with the more posterior portions of the hemisphere—the occipital and temporal regions.

As one follows the lateral forebrain bundle caudad in serial sections, one observes that it recedes somewhat ventrally and medially and thus approaches the medial forebrain bundle. In the region of the rostral end of the medial habenular nucleus the whole mass is surrounded by the striatum laterally, the reticular nucleus medially, the medial forebrain bundle ventrally, the fimbria fornicis and huge contributions from the dorsal cortex dorsally. In the middle third of the habenular complex the ventromedial portion of the internal capsule is free from fibers that cross it in order to enter the thalamus (that is, the inferior thalamic radiation). At about this plane the entopeduncular nucleus appears which is in synaptic relations with fibers in the middle third of the lateral forebrain bundle. In the plane where the stria terminalis dips into the amygdaloid complex, the internal capsule rounds off and does not receive any more contributions from cortex or striatum. From this plane caudalward it can in justice be spoken of as the cerebral peduncle.

From the above description one may, in general terms, consider the cerebral peduncle in the rat as having essentially the same topographic relations as to the origin of component fibers as the cerebral peduncle in higher forms; that is, the frontal component is the most ventromedial, the motor component is the central, and the temporal and the occipital components are the most lateral in the constitution of the peduncle.

In its course through the diencephalon in the ventral aspect of the subthalamus the cerebral peduncle contributes fibers to the zona incerta, the corpus Luysii, it gives rise to the radiations of Forel, and supplies the substantia nigra.

Superior thalamic radiation

It is in general true that the superior thalamic radiation is associated with the more dorsolateral portions of the thalamus, the metathalamus, and the tectum. It is first seen at the rostral end of the diencephalon and extends as far back as the plane where the stria terminalis enters the amygdaloid complex. In the most rostral portion the fibers of this radiation seem to reach the anterior thalamic nuclei and, somewhat more caudad, the nucleus lateralis thalami. More caudad, there are seen fibers which enter the dorsomedial portion of the nucleus ventralis thalami. In the plane of the caudal third of the habenula the bundles forming this radiation become more numerous; they are mostly obliquely cut and run caudad. After the termination of the stria terminalis in the amygdaloid complex these bundles are seen at the most dorsal aspect of the internal capsule in the form of a triangular mass with the concavity medially, the latter forming the external boundary of the nucleus ventralis thalami in that region. This triangular mass at first forms a cap over the rest of the internal capsule, which in this plane should be called the cerebral peduncle. From the dorsal end of this triangular mass fibers turn in toward the lateral nucleus (connection between the cortex and the nucleus lateralis pars posterior). More caudad, isolated bundles are given off which cross the nucleus ventralis thalami and, reaching the lateral aspect of Meynert's bundle, turn caudad to go to the tectal and the pretectal regions (connections between the cortex and the pretectal area, cortex and tectum). Others belonging to the last group are more ventrally placed and go to the medial group of nuclei in that region and the tegmentum lower down (connections between the cortex and the nucleus posterior thalami, cortex and nucleus parafascicularis, cortex and tegmentum). Others enter the lateral geniculate body, and still others remain in their original position and are seen to enter the medial geniculate body (cortico-geniculate fibers to the medial and the lateral geniculate bodies). We will next take up these connections more in detail.

a. Connections between forebrain and anterior group of nuclei (fig. 12). These fibers are seen in the most rostral portion of the diencephalon. In our normal preparations we are not able to state definitely as to whether these fibers are of cortical or striatal origin. Previous work especially on lower forms (Huber and Crosby, '26) indicates that they may be striatal. At any rate, these fibers mostly end in the anterodorsal and the anteroventral thalamic nuclei, the former receiving more fibers than the latter. In our series the anteromedial thalamic nucleus receives but very few fibers (if any at all) from this system. This particular portion of the superior thalamic radiation is as much a part of the superior as of the intermediate and inferior. At the rostral end of the diencephalon the three are absolutely continuous with each other, as we will bring out a little later.

b. Cortico-thalamic fibers to the nucleus lateralis thalami and the nucleus lateralis pars posterior (figs. 3, 4, 8, 15–18). These connections are very evident in our preparations. They enter these nuclei all along the lateral aspect of the diencephalon. The direction of conduction is probably both ways.

c. Cortico-thalamic connections with the nucleus ventralis thalami, nucleus ventralis pars dorsomedialis (figs. 13, 14). This group is also very evident. It should here be stated, however, that the dorsomedial portion of the ventral nucleus also receives fibers from the intermediate thalamic radiation.

d. Cortico-thalamic connections with the nucleus posterior thalami, nucleus parafascicularis (figs. 16, 17). In the plane where the Meynert's bundle is given off from the habenular complex, a few of the fibers belonging to the cortical system in question enter the nuclei above mentioned. We think that they most probably come in synaptic relations with these nuclei.

e. Cortico-geniculate connections with the nucleus geniculatus lateralis, pars dorsalis. These are especially well seen in our horizontal preparations (fig. 29). They are not many in number. It is only the dorsal portion of the lateral geniculate body that is related to the cortex, so far as we can determine.

f. Cortico-geniculate connections with the nucleus geniculatus medialis (fig. 30). Our horizontal preparations are especially favorable for a study of this complex. In cross-sectional series they are seen cross cut and give the cephalic end of the medial geniculate body a granular appearance. Apparently this connection is very much better developed in the rat than in lower forms (see discussion of medial geniculate body, p. 38).

g. Cortico-tectal connections are very well shown in our series (figs. 6 to 9, 15 to 17, 24, 30). The majority of them are seen leaving the main complex from its dorsomedial portion, forming a structure of a capsular nature over the nucleus ventralis thalami and then running horizontally across the field in our cross-sectional preparations to the lateral aspect of the habenular complex. At this point in sections farther caudad the same bundles are seen as cross-cut, indicative of their having a caudal direction. This particular group of fibers enters the most dorsal fibrous layer in the tectum. Aside from this first group, one sees a great many other fibers more caudally placed which also enter the tectum. The latter group of cortico-tectal fibers accompany the cortico-thalamic and the cortico-tegmental tracts in the same situation, so that their course is somewhat different than the one given above. These fibers enter the more ventral fibrous layers in the tectum.

h. Our preparations are very suggestive of the presence of fibers forming connections with the pretectal area (cortico-pretectal fibers).

i. Cortico-tegmental connections. The cortico-tegmental fibers leave the lateral forebrain bundle in the plane of the rostral third of the medial geniculate body in company with cortico-thalamic and cortico-tectal fibers. They run dorsally and medially, and after reaching the lateral aspect of the habenular complex they turn caudad and extend down toward the tegmentum. In the tegmentum they are found running most dorsally near the midline. We have not worked out their further distribution in the latter region.

Inferior thalamic radiation

The inferior thalamic radiation constitutes a group of fibers which pass through the ventral third of the internal capsule. No definite line of demarcation can be drawn between the inferior and the intermediate thalamic radiations, as mentioned above.

The fibers are seen as far rostral as the cephalic end of the diencephalon and as far back as practically the plane of the middle third of the habenular complex. The ones most rostrally placed are seen running medially and dorsally into the diencephalon. In their course through the diencephalon they pass through the anterior ventral nucleus, and some of them seem to end therein. Others evidently cross that nuclear mass in order to get access to nuclei farther caudad and dorsad. With the appearance of the mammillo-thalamic tract, the inferior thalamic radiation becomes pushed more medially, and now it is seen to course as follows: Fibers from the interstices of the internal capsule pass medially, and after reaching the medial aspect of the Vicq d'Azyr bundles, they course dorsally toward the dorsal aspect of the nucleus paraventricularis anterior as a limit. These bundles are thicker in the more ventral portion of their course than in the more dorsal, which is indicative of the fact that they come to be associated with the medial group of nuclei on their way. It is the more medial portions of these nuclei as well as those of the midline which are supplied by these fibers. The more lateral portions of the medial group of nuclei also receive fibers from the intermediate thalamic radiation. We are not prepared to say as to what percentage of the inferior thalamic radiation fibers are of cortical or striatal origin. They should not be confused with the medial olfacto-habenular fibers which are found more medially (next to the midline) and arise from the hypothalamic and the preoptic areas. The observations of Probst ('98), Sachs ('09), and others give us suggestive data as to the direction of conduction of these paths, but since the forms they have worked upon are quite different when compared with the rat made use of by us, it is the part of wisdom to be conservative as to homologies to be drawn. The connections we have been able to establish are as follows:

a. Fibers to the nucleus reuniens (figs. 2, 3, 13). These are very evident in our preparations. Most of the fibers connected with centers higher up pass through this nucleus, and in their course through the same they lose a few of their fibers, which accordingly end in the nucleus reuniens.

b. Fibers to the nucleus parataenialis. These are given off in the more rostral portion of the diencephalon. The fibers form a capsular structure about the ventral aspect of the nucleus. Others enter the nucleus and come in synaptic relation with the more ventral portion of the nucleus with the consequent appearance of a characteristic round plexus of fibers about the cells in the region, this being evident even in cell preparations.

c. Fibers to the anterior paraventricular nucleus. These are the most medial fibers of the system as the latter courses dorsally.

d. Fibers to the nucleus medialis ventralis (figs. 2, 13). They enter the nucleus on its medial aspect. In our fiber preparations the nucleus medialis ventralis shows a medial portion (medial to the Vicq d'Azyr bundle), which is relatively free from fibers, and a lateral portion (nucleus triangularis of Cajal), through which the bundles of the intermediate radiation pass. It is the more medial portion of the nucleus which receives fibers from the inferior thalamic radiation.

e. Fibers also reach the nucleus medialis dorsalis both from the inferior and the intermediate thalamic radiations (figs. 2, 13, 30).

Intermediate thalamic radiation

The intermediate thalamic radiation (figs. 2 to 5, 13, 14, 28) is that portion which is given off in the middle third of the internal capsule (speaking from the standpoint of cross-sectional series, of course). Here, again, we will emphasize the fact that all three systems are contiguous with each other, and our analysis is dependent upon a regional topography rather than other important anatomical data. In general, this portion of the thalamic radiation is essentially concerned with the more lateral aspects of the thalamus as well as the medial group of nuclei. Rostral to the Vicq d'Azyr bundle, the inferior and the intermediate groups are contiguous with each other. More posteriorly, the mammillo-thalamic bundle is taken as the boundary between these two systems. In the more rostral portions of the diencephalon the fibers of the intermediate thalamic radiation are seen passing caudad in the substance of the anterior ventral and the anterior medial thalamic nuclei. Most of them cross these nuclei without ending in the same. Some of them pass dorsally and reach the ventral border of the parataenial nucleus. More caudad with the appearance of the ventral nucleus we note that most of the bundles of this group pass through the substance of the latter and are undoubtedly in synaptic relations with the same. Another group of fibers belonging to this system are seen to course through the more lateral portion of the nucleus medialis ventralis (triangular nucleus of Cajal). These fibers would correspond to the lamina medullaris interna of higher forms (Hollander, '13). The latter group of fibers course caudodorsad and come in relation with the nucleus medialis dorsalis and the nucleus ventralis pars dorso-medialis. The connections, as we have been able to note, are as follows:

a. Cortico-thalamic connections with the nucleus ventralis thalami. These are very evident in our preparations. Large bundles are seen traversing the substance of the nucleus ventralis and ending in the same. Others pass dorsally and enter the dorsomedial portion of the ventral nucleus.

b. Cortico-thalamic connections with the nucleus ventralis pars dorsomedialis. Bundles are seen traversing the ventral nucleus and entering the dorsomedial portion of the same. The more medial portion of this nucleus also receives fibers from the inferior thalamic radiation.

c. Connections with the nucleus medialis dorsalis. These reach the nuclear mass from the more medial portions of the intermediate thalamic radiations. They are many in number and very evident in our preparations. The posterior continuation of this nucleus also receives fibers from this system (nucleus parafascicularis).

Aside from the thalamic radiations, the following are also given off from the internal capsule or its caudal continuation, the cerebral peduncle:

a. The lateral cortico-hypothalamic tract. The lateral cortico-hypothalamic tract is described in our consideration of the hypothalamus (p. 100).

b. Fibers to the nucleus entopeduncularis. These fibers have been sufficiently considered under the general discussion of the internal capsule and that of the entopeduncular nucleus.

c. Fibers to the zona incerta. These fibers are very evident and have been considered under our discussion of the zona incerta.

d. Fibers to the corpus Luysii. These fibers have been taken up under the discussion of that body. Cox preparations show that they are mostly stem fibers.

e. Radiations of Forel (figs. 17, 23, 28). Our results agree with those of Cajal ('11) as to the origin of these fibers in that he considers them as mostly collaterals from the peduncular system. Our sagittal series are especially favorable for a study of this path. They show that some of the fibers of the tract can be followed caudal to the region of the field of Forel and are seen entering the tegmentum.

THALAMUS

The literature on the mammalian thalamus is very extensive. From a study of the works of different authors, we have come to the conclusion that there exists a confusion in so far as nomenclature of the region is concerned. Probably this is due to an effort on the part of different investigators to homologize distantly related forms. Especially is this true when one tries to homologize the nuclear pattern of a higher form, such as the monkey, with that found in a lower form, such as the rat. Such attempts at homologies will be successful only when we know given nuclear patterns along with their connections. Just a superposition of nuclear pictures in different forms is not a safe method of assuming certain homologies and analogies. We will therefore refrain from making homologies unless these can be well established.

In the excellent work of Hollander ('13) on the rabbit we find a form which is not very far from the rat in the evolutionary scale and which presents many instructive relations and similarities. Further, Hollander makes an attempt to give the fiber connections of the nuclei. The atlas of the cat's brain by Winkler and Potter ('14) is another work deserving special consideration, and we have made use of it in the preparations of the present contribution. However, the thalamic differentiation in the cat has gone far enough to make it rather difficult to homologize every detail with our findings in the rat. We have consulted with great interest the works of Forel ('72), Monakow ('95), Probst ('98, '00), Déjerine ('01), Munzer and Wiener ('02), Bianchi ('09), Sachs ('09 a, b), Vogt ('09), Malone ('10), Fortuyn ('12), Nissl ('13), Friedman ('13), Cajal ('11), Kappers ('21), and others. Special mention should here be made of the atlas on the rat's brain by Craigie ('25). This author describes the thalamus of the rat very briefly. He speaks of an anterior, a medial, and a ventro-lateral division. He mentions the lateral nucleus, the ventral nucleus, the anterior dorsal and the anterior ventral nuclei, a nucleus reuniens (this is not the same as the nucleus reuniens described by us under the same name), and nucleus posterior. A detailed description of these nuclei and their connections are not given.

Thalamic nuclei and their connections

In order to facilitate the comprehension of the thalamic nuclear pattern in the rat (for it is quite complicated), we will divide the nuclear masses into groups. We would like to emphasize the fact that these groupings are not dependent upon any functional or important anatomic data. They are essentially regional in character. Our division of the thalamus proper is as follows: anterior group of nuclei, lateral group of nuclei, medial group of nuclei, the nuclei of the midline.

The anterior group of nuclei

There are three nuclei in the anterior thalamic group: nucleus anterior dorsalis, nucleus anterior ventralis, nucleus anterior medialis.

Nucleus anterior dorsalis. In the rat the rostral extreme of this nucleus is found to be as far forward as the caudal plane of the anterior commissure. In this situation the nucleus anterior ventralis is lateral and somewhat ventral to it and separates it from the reticular nucleus. As one follows the nucleus anterior dorsalis caudad, one notes that it becomes larger and larger and assumes the position of a pear-shaped structure with the thin wedge ventromedially placed between the nucleus anterior ventralis and the ascending fibers of the stria medullaris. In the plane of the rostral extreme of the medial habenular nucleus the boundaries of the nucleus anterior dorsalis are as follows: Dorsally, the transverse fissure separating from the hippocampus; medially and dorsally, the stria medullaris; medially and ventrally, the parataenial nucleus; ventrally and somewhat laterally, the nucleus ventralis (figs. 3, 4). In this particular plane the dimensions of the nucleus are the largest. Even in toluidine-blue preparations one notes the presence of a tract leaving the ventromedial portion of the nucleus in this plane.

By following this out one comes to the conclusion that it is a bed nucleus for the commissure connecting the two anterodorsal nuclei (nucleus commissuralis inter-anterodorsalis).

This nucleus throughout its extent is very sharply demarcated with many large multangular cells which have many processes and take a very deep blue color with toluidine blue. Cox preparations are characteristic (fig. 22). This nucleus has been described in the rabbit by Munzer and Wiener ('02), Winkler and Potter ('11), and Hollander ('13); in the mouse by Cajal ('11). In our preparations it is not in relation with the Vicq d'Azyr bundle. Cajal ('11) believes that synaptic relations exist between the mammillo-thalamic tract and the nucleus anterior dorsalis. The nucleus is connected with fibers from the internal capsule (superior thalamic radiation). These fibers are either cortical or striatal in nature (fig. 12). It is very distinctly related to its fellow of the opposite side through a band of commissural bundles, the latter being associated with an interstitial nucleus. This commissural band is pictured in Cajal's text (Histologie du système nerveux, p. 429).

Nucleus anterior ventralis. The cephalic end of the nucleus anterior ventralis is seen in the same plane as that of the anterodorsal nucleus. Here it is found just lateral and somewhat dorsal to the ventricle and between the nuclei anterodorsalis and reticularis. More caudad, it is very much larger in the cross-sectional view and assumes an elongated oval shape obliquely placed with the obliquity directed medially and ventrally. In the sagittal series it is seen to have an irregularly round shape. In the plane of the rostral extreme of the habenula it is surrounded by the nucleus anterior dorsalis dorsally and medially, fimbria fornicis dorsolaterally, nucleus reticularis ventrally and ventrolaterally, nucleus anterior medialis medially. The nucleus anterior medialis seems to be continuous with the nucleus anterior ventralis in more than one plane. However, in some areas it is possible for one to note a demarcating boundary between the two nuclear masses. With the appearance of the nucleus lateralis thalami the nucleus anterior ventralis is pushed medially and ventrally. In the plane where the nucleus anterior dorsalis has just disappeared, the nucleus anterior ventralis is very small and presents an oval shape in our cross-sectional series. It is here surrounded by the nucleus lateralis dorsally and laterally, the rostral extreme of the nucleus ventralis, and the nucleus paraventricularis anterior medially. A little more caudad, the nuclear mass disappears entirely in our cross-sectional preparations. The cells in this nucleus are smaller than those in the nucleus anterior dorsalis and stain faintly. Cox preparations show them to be multipolar cells with relatively few processes. This nucleus has been described in the rabbit (Munzer and Wiener, '02; Winkler and Potter, '11; Hollander, '13); in the mouse (Cajal, '11); in the monkey (Vogt, '09). It comes into synaptic relations with the Vicq d'Azyr bundle, to a lesser extent, however, than the nucleus anterior medialis. It is traversed by lateral forebrain bundles which course toward the nucleus anterior dorsalis. Some of these end in the nucleus anterior ventralis as shown by characteristic preparations. It is related to its fellow of the opposite side by a strong commissural band which passes through the nucleus anterior medialis. There are undoubtedly internuclear fibers interrelating the three anterior nuclei (figs. 1 to 4, 12, 21, 24, 27, 29).

Nucleus anterior medialis. The rostral extreme of the nucleus anterior medialis (figs. 2 to 4) comes in very close relation to the nucleus anterior ventralis, as mentioned above. In fact, one may say that rostrally the two nuclear masses are continuous with one another. It is at first found on the medial aspect of the nucleus anterior ventralis. In its more caudal relations the nucleus has extended ventrally and at the same time medially approaching the midline as a limit. In its more caudal portions it is absolutely distinct and separate from the nucleus anterior ventralis. In the plane of the cephalic third of the medial habenular nucleus the mass has practically reached the midline and is surrounded by the nucleus reuniens medially and ventrally, the nucleus anterior ventralis laterally, the nucleus parataenialis and the nucleus paraventricularis anterior dorsally. However, the nucleus commissuralis inter-anterodorsalis comes to lie between it and its dorsal neighbors a little farther caudad. After the disappearance of the nucleus anterior ventralis, the nucleus anterior medialis is seen to gradually approach the midline and become continuous with an analogous process from the opposite side (nucleus commissuralis inter-anteromedialis). At the same time, the more lateral portions of the nucleus disappear, while the commissural portion is still present more caudad. In other words, the two anterior medial nuclei with their commissural portion form a horseshoe effect with the concavity anteriorly. Its most caudal relations in our cross-sectional series are as follows: the nucleus ventralis laterally, the nucleus rhomboidalis ventrally, the nucleus commissuralis inter-anterodorsalis dorsally. The cell type in this nucleus is essentially the same as in the anteroventral nucleus. This nucleus has been described in the rabbit (Hollander, '13), and in the monkey (Vogt, '09). In our preparations it is this portion of the anterior group of nuclei which is especially related to the mammillo-thalamic bundle. In our preparations most of the fibers of the Vicq d'Azyr bundle end here, while a minority go to the nucleus anterior ventralis. It is related to its fellow of the opposite side by a commissural system of fibers intermingled with that interconnecting the anterior ventral nuclei. The commissural portion between the two anterior medial nuclei has been described by Cajal ('11) under the name of interdorsal nucleus.

A comparison of the above description of the anterior group of nuclei with that of higher mammalian forms is indicative of the fact that this region in the thalamus is an area which we can homologize with such higher forms. It is of special interest to note that Vogt's description of the anterior group of nuclei in the monkey is practically the same as the above description. Hollander ('13) finds analogous results for the rabbit.

Lateral group of nuclei

The lateral group of nuclei are six in number and are here named as follows: nucleus reticularis, nucleus ventralis, nucleus ventralis pars dorsomedialis, nucleus lateralis, nucleus lateralis pars posterior, nucleus posterior thalami.

Nucleus reticularis. The rostral extreme of the nucleus reticularis (figs. 1 to 6, 8, 12, 13, 23, 24, 28) is in the same plane as that of the nucleus anterior dorsalis. In this situation it is distinctly associated with fiber tracts which are part of the thalamic radiation. Here it is in relation with the nucleus anterior ventralis dorsally, fimbria fornicis dorsolaterally, stria terminalis laterally, and the nucleus reuniens medially. More caudad, the mass is seen enlarging rapidly and assuming an elongated oval shape. We think that this portion of the reticular nucleus is the same as the nucleus semilunaris anterior of Cajal's description. In the plane of the rostral extreme of the medial habenular nucleus the relations are as follows: nucleus anterior ventralis and nucleus lateralis, dorsally and medially; nucleus lateralis, dorsally; nucleus reuniens, medially, and internal capsule, laterally. With the appearance of the nucleus ventralis thalami, the reticular nucleus is seen to become comma-shaped and surrounds the nucleus ventralis laterally and ventrally. The more caudad relations show that the nucleus becomes very much thinner, but preserves its characteristic comma shape around the ventral nucleus. It is distinctly associated with the thalamic radiations, and as the latter disappear from the field the same becomes true of the nucleus reticularis. Thus, in the plane of the posterior third of the habenula, where most of the inferior and the intermediate thalamis radiations have disappeared, the reticular nucleus becomes reduced in its ventral and ventromedial portions. In the region of the habenular commissure the nucleus is essentially associated with the superior thalamic radiation and is surrounded by the nucleus ventralis medially, the nucleus lateralis dorsally and medially, the internal capsule laterally and ventrally. With the disappearance of the superior thalamic radiation the nucleus reticularis also disappears. The nucleus as a whole could at least be divided into two parts, ventral and dorsal. We prefer describing it as a whole in order to bring out its interstitial nature for the fibers of the thalamic radiations. The majority of its cells are medium-sized or slightly larger. This nucleus has been noted in the mouse by Cajal ('11); in the rabbit by Winkler and Potter ('11) and Hollander ('13); in the cat by Winkler and Potter ('14). These different authors divide the nucleus into different parts, but on the whole the formation is very analogous to the one here described for the rat. The nucleus is undoubtedly in synaptic relations with some of the fibers of the thalamic radiations. Cajal ('11) thinks that these may be striatal in nature (in the mouse and the rabbit).

Nucleus ventralis thalami. The cephalic border of this nucleus is seen in the plane of the anterior third of the habenular complex. It begins as an irregularly oval mass of cells surrounded on all sides by the reticular nucleus except medially and dorsally (figs. 3 to 9, 13 to 16, 21 to 24, 28, 30). More caudad, it is seen enlarging enormously and it assumes a more or less globular shape. In the plane of the middle third of the habenula it is surrounded by the nucleus reticularis ventrally and laterally, the nucleus lateralis dorsally, the nucleus medialis dorsalis and the nucleus medialis ventralis medially. Farther caudad, the nucleus as a whole looks rounder, but on close examination one notes that its ventrolateral half is sharply demarcated from its dorsomedial portion, this on the basis of nuclear staining rather than cell arrangement, although at the line of demarcation there is a linear arrangement of cells in small groups. Just in front of the habenular commissure the ventrolateral portion of the nucleus ventralis thalami is seen sending a prolongation medially which comes in relation with a similar prolongation from the opposite side. This constitutes the nucleus commissuralis inter-ventralis. In our silver preparations it is associated with commissural fibers. Just cephalad to the commissural band the relations of the nucleus ventralis thalami are as follows: lateral geniculate body laterally, nucleus parafascicularis medially, nucleus lateralis pars posterior dorsally, zona incerta ventrally. It extends as far back as the cephalic border of the medial geniculate body where the two nuclei become contiguous with each other. This nucleus has been described in the mouse by Cajal ('11); in the rabbit by Winkler and Potter ('11), Hollander ('13), and others. In our preparations it is the ventrolateral portion of the globular formation that comes in relation with the lemnisci system of fibers. In fiber preparations the same semilunar effect is noted as described for Nissl preparations; this time on the basis of a rich plexus of fibers which fill the ventrolateral portion of the complex and leave the dorsomedial part relatively free. From a study of our preparations, we are led to believe that this dorsomedial part is functionally and structurally different, and we will give it, therefore, a separate description. The ventral nucleus is connected to the tectum, especially in its posterior third. This connection is made up of slender bundles, which can be differentiated from the other tectal connections in that region. The connections of the ventral nucleus with the cortex are very evident in our preparations and constitute a portion of the intermediate and the superior thalamic radiations.

Nucleus ventralis, pars dorsomedialis. The nucleus ventralis, pars dorsomedialis (figs. 6 to 8, 13 to 15, 24, 28 to 30) is intimately associated with the ventral nucleus. Dorsally, it is in relation with the nucleus lateralis, with which it becomes continuous in places. Medially, it is in relation with the medial group of nuclei. Laterally and ventrally, it is continuous with the ventral nucleus proper (see discussion of the ventral nucleus in the preceding paragraph). It is connected to its fellow of the opposite side by commissural fibers associated with the nucleus commissuralis inter-ventralis pars dorsomedialis. It receives fibers mainly from the intermediate thalamic radiation. Most posteriorly, this nucleus is in relation with the pretectal nucleus dorsally, nucleus lateralis pars posterior dorsolaterally, nucleus ventralis laterally and ventrally, nucleus parafascicularis medially. We think that at least a part of this nucleus constitutes the 'nucleus x' of Hollander's description ('13). We are not prepared to discuss the ascending connections of this nucleus.

Nucleus lateralis thalami. The nucleus lateralis thalami (figs. 2 to 5, 13, 14, 21) extends as far forward as the cephalic extreme of the medial habenular nucleus. It begins as a small mass of scattered cells. Golgi pictures are characteristic (fig. 21). Its most rostral relations are as follows: fimbria fornicis, laterally and dorsally; nuclei anteriores dorsales et ventrales, ventrally and medially. Farther caudad, it is seen enlarging rapidly, and in the plane where the nucleus anterior dorsalis has just disappeared this mass forms the whole of the dorsolateral wall of the thalamus. In the plane of the middle third of the habenula it is in relation with the nucleus ventralis pars dorsomedialis, ventrally; the nucleus reticularis, dorsolaterally; the transverse fissure, dorsally and dorsolaterally; the nucleus medialis dorsalis, medially. The lateral geniculate body appears on its lateral aspect a little farther caudad. In the region of the posterior commissure it becomes continuous with the nucleus lateralis pars posterior. This nucleus has been described in the rabbit (Hollander, '13), in the cat (Winkler and Potter, '14), and recently in the rat (Craigie, '25). It receives fibers from the superior thalamic radiation. It probably has connections by way of commissural fibers with its fellow of the opposite side. More particularly, its posterior portion is connected with the tectum. There are undoubtedly internuclear fibers between this nucleus and the dorsomedial portion of the ventral nucleus. The ascending paths associated with this nucleus will receive consideration at another time.

Nucleus lateralis, pars posterior. In the plane where the nucleus geniculatus lateralis is best seen (about its middle third) the nucleus lateralis pars posterior also becomes very well defined. The nucleus lateralis pars posterior (figs. 6 to 9, 15, 17, 18) is continuous in front with the nucleus lateralis. The cell type is essentially the same as that found in the nucleus lateralis. The pars posterior is irregularly pear-shaped in outline, the convex border being dorsomedially directed, while the acute end is found ventrolaterally. It is surrounded dorsally and laterally by the optic tract, laterally by the dorsal part of the lateral geniculate body, ventrally by the nucleus ventralis, and medially by the pretectal area and the nucleus posterior thalami. Posteriorly, it disappears in the same plane as do the lateral geniculate bodies. Although essentially of the same structure as the nucleus lateralis, it differs from the same in that it receives optic fibers and has a special cortical connection through the superior thalamic radiation. It is probably the homologue of the pulvinar in the higher mammalian forms. It is also connected with the tectum by distinct bands of fibers. In our preparations internuclear fibers between this mass and the dorsal portion of the lateral geniculate body are very evident.

Nucleus posterior thalami. The rostral extreme of the nucleus posterior thalami (figs. 8, 9, 17, 18) is in the plane of the posterior third of the habenular complex and extends caudad to the middle third of the medial geniculate body. It is made up of medium-sized and small cells. In silver preparations it is exceedingly difficult to distinguish this nuclear mass. Rostrally, it appears on the most dorsal aspect of the diencephalon, just medial to the nucleus lateralis pars posterior and lateral and ventral to the pretectal area. Farther caudad, it is seen to increase in size rapidly. In its more cephalic portion it is traversed by numerous fibers, namely, of optic-tract origin. With the appearance of the tectum the nucleus is pushed ventrally. In its middle third it is in relation with the nucleus lateralis pars posterior and with the medial geniculate body, laterally; the tectum, dorsally; the posterior commissure, medially. In about this plane it is traversed by the cortico-tectal system of fibers. Farther caudad, it is pushed more ventrally so that it comes to lie just medial to the medial geniculate body. This nucleus has been noted by Hollander ('13) in the rabbit, in which form the nucleus evidently extends more cephalad than in the rat.

It receives fibers from the superior thalamic radiation and the optic tract. It is also connected with the tectum. Our preparations are suggestive of the fact that the nuclei of opposing sides are interrelated through the posterior commissure.

Medial group of nuclei

In our preparations the medial group of nuclei are made up of the following: nucleus parataenialis, nucleus medialis dorsalis, nucleus medialis ventralis, nucleus parafascicularis, nucleus paracentralis.

Nucleus parataenialis. The nucleus parataenialis extends as far forward as the rostral end of the diencephalon. It is separated from its fellow of the opposite side by the nucleus paraventricularis anterior. Its cells are small and medium-sized, and in Cox preparations they are characteristic (fig. 21). The nucleus parataenialis is in relation dorsally with the stria medullaris, but is not in any way connected with the same. In the plane of the rostral end of the medial habenular nucleus it is bounded by the taenia thalami, dorsally; the nucleus anterior dorsalis, laterally; the nucleus anterior medialis and its commissural portion, ventrally; the nucleus paraventricularis anterior, medially. It is of interest to note that at about this plane one observes the appearance in the ventral aspect of this nucleus of a rounded mass of cells circumscribed to a certain extent and very characteristic in our silver preparations by reason of the presence of a fine plexus of nerve fibers which is found therein. This mass both in front and behind becomes continuous with the nucleus parataenialis. We consider it, therefore, a part of the nucleus parataenialis. Farther caudad, there appears, on the lateral aspect of the nucleus parataenialis, the rostral end of the nucleus medialis dorsalis. With the increase in size of the latter the parataenial nucleus becomes replaced by the nucleus medialis dorsalis, so that in the plane of the rostral end of the nucleus paraventricularis posterior a differentiation between the two nuclear masses is very difficult.

This nucleus has been described by Hollander ('13) for the rabbit. In our preparations this nucleus receives fibers from the intermediate and the inferior thalamic radiations. It is intimately associated with the nucleus medialis dorsalis. It is connected to its fellow of the opposite side by commissural fibers (figs. 1, 2 to 5, 12, 21, 24, 30).

Nucleus medialis dorsalis. In the plane where the nucleus anterior dorsalis disappears there appears, on the lateral aspect of the parataenial nucleus, a medium-sized group of cells somewhat oval in outline and connected to its fellow of the opposite side by a commissural band of cells. This constitutes the nucleus medialis dorsalis and is very distinct in our preparations (figs. 4 to 6, 13 to 14, 22 to 24, 26 to 30). Farther caudad, the oval mass increases in size. Just before the disappearance of the nucleus anterior ventralis, it is seen to be surrounded by the habenular complex, dorsally; the nuclei lateralis and anterior ventralis, laterally; the nuclei anteroventralis and anteromedialis, ventrally; the nucleus parataenialis, medially. After the disappearance of the parataenial nucleus it replaces the same and becomes somewhat irregular in outline; for this reason, its lateral and ventral relations are somewhat vague in our preparations. It extends as far back to the plane where the Meynert's bundle is given off from the habenular complex. Its posterior third is seen to be continuous with its fellow of the opposite side by a mass of cells which appear undifferentiated. Farther back, it becomes continuous with the nucleus parafascicularis. It receives fibers from the intermediate thalamic radiation. It is connected to its fellow of the opposite side by commissural fibers, evident in our silver preparations. We will not take up at this time its relation to ascending paths. This nucleus has been described in the rabbit by Winkler and Potter ('11) and Hollander ('13); in the cat by Winkler and Potter ('14).

Nucleus medialis ventralis. The nucleus medialis ventralis (figs. 5, 6, 14, 15, 21) extends as far forward as the plane of the posterior aspect of the nucleus anterior ventralis. In the planes farther posterior where the mammillo-thalamic bundle is distinct and well formed, one observes that the latter is enclosed in this nucleus, dividing it roughly into two portions: a medial and a lateral (the latter is the same as Cajal's nucleus triangularis). The nucleus medialis ventralis throughout most of its extent is triangular in outline. In the plane of the middle third of the habenular complex it is surrounded by the nucleus reuniens, medially; the nucleus ventralis, laterally; the nucleus reticularis and the hypothalamus, ventrally; the nucleus paracentralis, dorsally. It is to be noted that the portion of the nucleus medial to the mammillo-thalamic tract stains less intensely and is made up of smaller cells than the portion lateral to the bundle. As mentioned under the discussion of the lateral forebrain bundle, a portion of the intermediate thalamic radiation comparable to the lamina medullaris interna of higher forms passes through the lateral portion of the nucleus and gives it a different appearance even in cell preparations. One might even divide the nucleus into two parts from the myeloarchitectonic standpoint. In the plane of the posterior third of the habenular complex the nucleus is surrounded by the nucleus commissuralis inter-ventralis, dorsally; the nucleus ventralis, laterally; zona incerta and the Vicq d'Azyr bundle, ventrally; the nucleus reuniens, medially. In the plane of the rostral aspect of the posterior commissure it disappears entirely. In its posterior third this nucleus is traversed by ascending tracts from lower centers. These will be taken up later. This nucleus receives fibers from the inferior and the intermediate thalamic radiations. It also receives ascending fibers from lower centers. It is connected to its fellow of the opposite side by commissural fibers associated with a bed nucleus. This nucleus has been described in the rabbit by Hollander ('13). In the cat it is taken as a part of the medial nucleus by Winkler and Potter ('14).

Nucleus parafascicularis. The nucleus parafascicularis (figs. 7, 8, 15, 24) is a differentiation of the nucleus medialis dorsalis in its most posterior portion, brought about by the passage of the Meynert's bundle through the mass. The cells here are closely packed together and assume as a whole the shape of a quadrangle with a dorsal concavity for the Meynert's bundle. In its middle third the nucleus is bounded dorsally by the pretectal area, laterally by the ventral nucleus, medially by the periventricular gray, and ventrally by the commissural portion of the ventral nucleus. In the plane of the middle third of the posterior commissure it disappears entirely. It has been described in the rabbit by Hollander ('13), who considers it to be the posterior differentiated portion of the medial thalamic nucleus. It receives fibers from the intermediate thalamic radiation and is seen to be connected with the tectum. In our silver preparations the nucleus is covered with a fine plexus of nerve fibers.

Nucleus paracentralis. The nucleus paracentralis (fig. 5) is a mass situated just lateral to the nucleus centralis and is essentially made up of small and medium-sized cells. In certain planes it is linear in arrangement, indicative of the passage of fiber tracts which are found to be commissural in nature. Nucleus paracentralis extends from the plane of the posterior aspect of the nucleus rhomboidalis to the plane of the posterior third of the habenular complex. Dorsally, it is in relation with the nucleus medialis dorsalis, medially with the nucleus centralis, ventrally with the nucleus medialis ventralis, laterally with the nuclei ventralis and lateralis. This nucleus could undoubtedly be divided into several different masses which may receive passing mention: *a*) a division which is associated with the commissural fibers interconnecting the dorsomedial parts of the ventral nuclei. This is found in the more rostral portion of the whole complex and is probably the homologue of the nucleus lamellaris of Hollander's description; *b*) a division which is essentially associated with the medial dorsal nuclei and helps interconnect the opposing sides; *c*) a part which is associated with the medial ventral nuclei. All of these converge medially toward the nucleus centralis. We think that this nuclear complex is essentially commissural in nature.

Nuclei of the midline

The nuclei of the midline may be enumerated as follows: nucleus reuniens, nucleus rhomboidalis, nucleus paraventricularis anterior, nucleus paraventricularis posterior, nucleus commissuralis inter-anterodorsalis, nucleus commissuralis inter-anteromedialis, nucleus commissuralis inter-ventralis, nucleus commissuralis inter-mediodorsalis, nucleus commissuralis inter-medioventralis, nucleus centralis.

Nucleus reuniens. In the plane of the extreme rostral end of the diencephalon, just dorsal and medial to the fornix bundle, continuous dorsally with the nucleus paraventricularis anterior and capping over the dorsal aspect of the ventricular cavity, one notes a group of medium-sized cells, divided into two lateral halves by a median rarifaction. Farther caudad, the continuity with the anterior paraventricular nucleus disappears and the two masses become larger, being separated from each other by a median group of cells. The mass as a whole is now oval in outline and slightly caps over the dorsal aspect of the ventricle. This picture constitutes the rostral portion of the nucleus reuniens (figs. 3, 4). The median ridge of cells is very distinct for a certain distance, but about the plane of the middle third of the habenula it is not as conspicuous; in fact, a little farther caudad it disappears entirely with the consequent amalgamation of the two lateral masses into a single group of cells (figs. 2 to 6, 21, 22, 26, 27). This takes place at about the plane of disappearance of the nucleus anterior ventralis. In this situation the nucleus reuniens is surrounded by the nucleus rhomboidalis dorsally and dorsolaterally, the third ventricle and the nucleus filiformis ventrally and ventrolaterally. From this plane on to its termination caudad the nucleus is a single oval mass, with here and there groupings of cells in linear arrangements, but with no distinct morphologic differentiation to enable us to further subdivide the nuclear mass. In the plane of the caudal aspect of the habenula it disappears entirely. This is the same as the nuclei (3) and (4) in the Hollander figures of the topography of the thalamus in the midline. In some of the figures of the cat's brain by Winkler and Potter ('14), our nucleus reuniens has been given the name of 'nucleus centralis a.' Their nucleus reuniens is certainly not the same as the one described above. The nucleus reuniens receives fibers from the inferior thalamic radiation. Posteriorly, it helps in the formation of the periventricular system of fibers (see discussion of the same, p. 103). This is especially evident in our sagittal preparations.

Nucleus rhomboidalis. The nucleus rhomboidalis (figs. 3, 4) extends as far forward as the anterior extreme of the medial habenular nucleus. It is made up of small cells. Its most rostral relations are as follows: dorsally, the nucleus commissuralis inter-anteromedialis; laterally and ventrally, the nuclei anteromedialis and reticularis. The whole mass presents a concavity which caps over the nucleus reuniens. More caudad, this nucleus changes its characteristics quite markedly: as concerns its shape, it loses its concavity and becomes linearly placed at right angles to the midline; as concerns structure, it may be noted that the cells are larger and more closely packed together. Still farther caudad, it is replaced by the nucleus centralis. Cajal ('11) has described such a nuclear mass in the guinea-pig. The nucleus under discussion probably corresponds to the nucleus number (2) of Hollander nuclei of the midline in the rabbit. In the cat it is probably the same as the nucleus reuniens of Winkler and Potter's description ('14). In our silver preparations the nucleus is richly supplied with a fine plexus of fibers, especially in the plane of the nucleus commissuralis inter-anteromedialis. This nucleus probably receives fibers from the inferior thalamic radiation.

Nucleus paraventricularis anterior. The nucleus paraventricularis anterior (figs. 2, 3, 9, 11, 13, 22, 24, 26, 30) is continuous with the periventricular gray in front and is made up essentially of the same type of cells. It is found to be the most dorsal of the nuclei of the midline. In its anterior third it is in relation with the third ventricle dorsally, the parataenial nuclei laterally, the nucleus commissuralis inter-anteromedialis ventrally. Farther caudad, it becomes more distinct and elongated in the dorsoventral direction. Still farther back, in the plane of the disappearance of the nucleus rhomboidalis, it becomes continuous with the nucleus paraventricularis posterior. This nucleus has been described in the rabbit by Hollander ('14). He labels it (1) in his pictures of the nuclei of the midline. In the cat, Winkler and Potter ('14) name it the nucleus parependymalis. Both authors do not distinguish between the anterior and the posterior paraventricular nuclei. This nucleus probably receives fibers from the inferior thalamic radiation. At its most dorsal portion one sees in the cross-sectional series a mass of cross-cut bundles which in part at least belong to the medial olfacto-habenular group. The fact that this whole mass of cross-cut bundles is not solely habenular in nature will be brought out in later work.

Nucleus paraventricularis posterior. Anteriorly it is continuous with the nucleus paraventricularis anterior and posteriorly it extends as far back as the anterior third of the posterior commissure to become continuous with the periventricular gray in that situation (figs. 5 to 9, 13 to 15, 24, 26, 27, 29). Unlike the anterior paraventricular nucleus, it is a bilateral formation and not a median one. Each nucleus is triangular in form in the cross-sectional series, with the base directed medially so that the opposite masses taken together form a rough quadrangle. It increases in size farther caudad and is largest in the plane where the Meynert's bundle is given off. With the appearance of the Meynert's bundle the nucleus loses its triangular shape and becomes divisible into two portions: 1) a portion closely applied to the medial aspect of the Meynert's bundle and, 2) a more medial portion which is next to the midline and roundish in appearance. Farther caudad, the mass is seen to be continuous with the periventricular gray forming the most dorsal portion of the same in that situation. Throughout most of its extent the nucleus is surrounded by the nucleus medialis dorsalis. Hollander ('13) and Winkler and Potter ('14) describe this nucleus as a part of the preceding one. In our preparations it is distinct from the nucleus paraventricularis anterior, which is a median nucleus in the true sense of the word. There are two posterior paraventricular nuclei, one on each side of the midline. The two masses, however, are intimately interconnected. This nucleus receives fibers from the inferior thalamic radiation. It contributes to the formation of the periventricular group of fibers and is also in intimate association with the nucleus paraventricularis anterior.

Nucleus commissuralis inter-anterodorsalis. This is the bed nucleus of the commissure that interconnects the opposite anterodorsal thalamic nuclei. It is made up of small and medium-sized cells (figs. 2 to 4, 6).

Nucleus commissuralis inter-anteromedialis. We have already discussed this nucleus under the heading of the nucleus anterior medialis. It is posterior to the plane of the latter nuclei and not only connects the anteromedial nuclei of the opposite sides, but through the latter the anteroventral masses also. It was described by Cajal ('11) in the mouse as the interdorsal nucleus. It is traversed by distinct commissural fibers which are even evident in myelin preparations. In the monkey, Vogt ('09) has described its presence and its relation to the anteromedial and the anteroventral nuclei.

Nucleus commissuralis inter-ventralis. This nucleus (figs. 7, 9, 13 to 15, 26) is found in the plane of the posterior third of the ventral nuclei. It is very well shown in our preparations and is associated with distinct commissural fibers. Hollander ('13) intimates the presence of such a connecting band in his rabbit material.

Nucleus commissuralis inter-mediodorsalis. In our preparations the most rostral portion of the mediodorsal nuclei is interconnected to the one of the opposite side by a band of flattened cells (figs. 5, 6). In the more caudal portion the opposite nuclei run into each other in the midline. Both of these commissural portions are associated with distinct fibers.

Nucleus commissuralis inter-medioventralis. The most ventral portion of the nucleus centralis is seen to be associated with the medial ventral nuclei, interconnecting the same. We will take this up again under the discussion of the central nucleus.

Nucleus centralis. The nucleus centralis replaces the nucleus commissuralis inter-anteromedialis and the nucleus rhomboidalis after the disappearance of the same. Throughout its extent it is closely associated with the paracentral group of nuclei. In places it presents linear groupings of cells parallel to and on the midline. It extends as far caudal as the posterior third of the habenular complex where it becomes undifferentiable from the nucleus commissuralis inter-mediodorsalis. In its middle third it is seen to be in relation with the nucleus reuniens and the two medial ventral nuclei ventrally, the two mediodorsal nuclei dorsally, the paracentral nuclei laterally. We think that it is primarily a commissural nucleus through which the medioventral nuclei, the dorsomedial portions of the ventral nuclei, and possibly also the lateral nuclei are interconnected. It is probably homologous with the nucleus reuniens of Winkler and Potter's description in the cat (fig. 5).

HYPOTHALAMUS[3]

The hypothalamus in the rat is so intimately related to the preoptic area, its rostral continuation, that it seemed im-

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[3] A portion of this work was reported at the New Haven meeting of the American Association of Anatomists (April, 1926). At that time the following résumé was published (Anat. Rec., vol. 32):

"The hypothalamus in the rat has at least twelve nuclei. It is imperceptibly continuous with the preoptic area in front and the subthalamus dorsally. The medial forebrain bundle relates it to the olfactory centers anteriorly. Cortico-hypothalamic and strio-hypothalamic tracts are present. Ascending fibers from the region of the median fillet reach it through the mammillary peduncle. It is intimately connected with the mammillary bodies. The periventricular system of fibers connects the hypothalamus with lower centers and possibly also with the tectum. There are three distinct paths connecting the amygdaloid. complex and the hypothalamus.

"The mammillary bodies in the rat are highly differentiated, having a nuclear pattern which has distinct relations to the origin of the combined mammilloperative to consider the preoptic field also in order to admit of analyzing somewhat more fully the hypothalamus. No definite line of demarcation can be drawn between the two regions in so far as the nervous system of the rat is concerned. The delimitation is a conventional one rather than a division based on differential morphologic findings. In our description of facts we have considered the hypothalamus as extending from the plane of the optic chiasm and tract to the caudal end of the mammillary body. By preoptic area we meant a field in front of the optic chiasm and extending as far forward as the caudal end of the septal and the tubercular areas. The cephalic boundary of the preoptic area is not any clearer than its caudal one. Here, also, the nuclear masses merge into each other and become inseparably continuous.

Literature

The study of the literature reveals the fact that the hypothalamic region is deserving of extensive investigation. Except for the pioneer work of Cajal ('11), most of the works of different authors may be summarized in a few words. We will not take up space at this time by a detailed account of the literature on this field. Suffice it to say that such literature may be procured from standard texts on nervous anatomy (Déjerine, '01; Barker, '02; Edinger, '11; Cajal, '11).

Quite a complete configuration of the nuclear pattern of the hypothalamus is found in the work of Nissl ('13) and in the atlas of the cat's brain by Winkler and Potter ('14). However, from a study of both of these contributions, we have come to the conclusion that the nuclear masses have

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thalamic and the mammillo-tegmental tracts. We were able to divide the latter into its component portions on the basis of their origin from the different parts of the medial group of nuclei. The mammillo-tegmental tract arises from the more anterior portions of the mammillary complex. It is in part at least a bifurcation product of fibers, the cell bodies of which are located in the medial group of mammillary nuclei. The other product of bifurcation forms the mammillo-thalamic tract. The mammillary peduncle in the rat consists of both ascending and descending fibers; by far the majority, however, are ascending in nature.''

been identified without an accompanying description of their topographic distribution. Furthermore, these authors do not take up any of the fiber connections of these areas.

The posterior portion of the hypothalamus as represented by the mammillary bodies has been investigated more exhaustively. Thus, in the works of Gudden ('89), Hatschek ('03), Cajal ('11), Wallenberg ('99), Edinger and Wallenberg ('02), Déjerine ('01), Spitzer and Karplus ('07), Valkenberg ('12), Nissl ('13), Winkler and Potter ('14), and others we find contributions on the whole mammillary body and its related connections or parts of the same. The nuclear pattern in the forms studied by these different authors is apparently very simple as compared with those found by us in the rat, and there appears to be no unanimity among these authors as to the connections of the mammillary bodies in the forms described.

Preoptic area

This area extends as far forward as the caudal extreme of the septum and the tuberculum olfactorium. Behind it merges insensibly into the hypothalamus, the conventional line of demarcation in this paper being the plane of the nucleus ovoidus. In this area are included the following nuclear masses or groups: interstitial nucleus of the septal portion of the medial forebrain bundle, continuation of the bed nucleus of the stria terminalis, lateral preoptic area, medial preoptic area, and preoptic periventricular nucleus.

Interstitial nucleus of the septal portion of the medial forebrain bundle. This mass is made up of large cells and accompanies the septal portion of the medial forebrain bundle (figs. 1, 2, 19). In front it is continuous with the large-celled medial septal nucleus. It thus accompanies the septal component ventrally (in front of the anterior commissure), laterally (in the plane of the anterior commissure and farther back), and then caudad toward the hypothalamus. It is a well-defined and easily recognizable structure in our preparations and disappears from view in the plane of the nucleus of the lateral olfactory tract. It undoubtedly gives rise to a number of septo-hypothalamic fibers. Cox pictures of this nuclear mass are characteristic (fig. 19).

Continuation of the bed nucleus of the stria terminalis. The continuation of the bed nucleus of the stria terminalis, accompanying its preoptic component, is a well-defined nuclear mass (figs. 1, 12, 13). It is made up of thickly placed small cells staining very deeply in our preparations. It extends downward and medially from the bed nucleus of the stria terminalis and somewhat lateral to the midline turns caudad and becomes lost in the undifferentiated gray mass in that region. It undoubtedly receives fibers from the stria terminalis and sends its axons farther caudad toward the hypothalamic complex, particularly the medial group of nuclei therein.

Lateral preoptic area. The lateral preoptic area or the bed nucleus of the medial forebrain bundle in the preoptic region is found in the more lateral portions of the latter, and cephalad it extends as far forward as the caudal prolongation of the interstitial nucleus of the septal portion of the medial forebrain bundle. It is found lateral to the medial preoptic area and the preoptic portion of the bed nucleus of the stria terminalis (figs. 1, 11, 12).

Medial preoptic area. The medial preoptic area extends between the periventricular gray of the preoptic region and the lateral preoptic area. In it one can differentiate at least two nuclear masses: a well-defined nucleus (*a*), which is placed laterally and comes in close relation with the preoptic prolongation of the bed nucleus of the stria terminalis, and a nucleus (*b*) which is more medially placed and is right next to the periventricular gray. The former is a round collection of small and medium-sized cells and extends from the plane of the rostral extreme of the diencephalon to the plane of the caudal extreme of the preoptic area. Its cells are closely packed and stain very deeply, forming a characteristic picture in the field. The nucleus (*b*) is made up of cells which are paler in their staining characteristics. It is more of an undifferentiated gray and posteriorly becomes continuous with the anterior hypothalamic gray. The medial preoptic area receives fibers from the preoptic component of the stria terminalis, fibers from the medial cortico-hypothalamic tract, and its more dorsal portion receives a few fibers from the supracommissural component of the stria terminalis. It must be intimately associated with the medial group of nuclei in the hypothalamus, because it is continuous with the same over the optic chiasm (figs. 1, 11, 13).

Preoptic periventricular nucleus. The preoptic periventricular nucleus is a gray mass surrounding the third ventricle in the preoptic region (fig. 1). It is made up of small cells, and in more than one plane presents a characteristic stratification made up of three to five layers of cells. It receives fibers from the medial cortico-hypothalamic tract and from the preoptic component of the stria terminalis.

Hypothalamic nuclei and their connections

A study of the hypothalamus in Nissl preparations reveals the fact that it is made up essentially of small and medium-sized cells. In more than one plane the whole mass looks like a homogeneous collection of cells. In the intervening area between the nuclear masses one may readily determine undifferentiated gray. In more than one plane a close continuity exists between the more dorsal portions of the hypothalamus and the subthalamus. With some such picture in mind, we will describe the nuclear masses seen in this hypothalamic gray.

Nucleus ovoidus. The cephalic extreme of the nucleus ovoidus is found in the rostral extreme of the hypothalamus. It extends as far back as the plane where the anterior ventral nucleus of the thalamus disappears. So far as we have been able to determine, no mention of this nucleus is made in the description of the mammalian hypothalamus by different authors. It is intimately related to the supraoptic complex of fibers. It also receives fibers from the stria terminalis through the supracommissural and the preoptic components of the latter. The nucleus is lateral to the nucleus hypothalamicus periventricularis anterior. It is round in outline and keeps this shape throughout its course in our cross-sectional series (figs. 2, 3, 4, 26).

Nucleus filiformis. In the plane where the nucleus ovoidus has just disappeared the nucleus filiformis makes its appearance (figs. 2 to 5, 22). It is triangular in outline with one side parallel to the wall of the third ventricle. Nissl preparations show that it is essentially made up of a medial small-celled portion which is intimately associated with the hypothalamic periventricular gray and, in certain planes, is shown to be continuous with the same; a lateral medium-sized group of cells which are closely packed, this group as a whole extends laterally; and a dorsal portion which stands out in our preparations, due to its different staining characteristics, namely, the fact that the nuclei of its cells contain more chromatin material. In the plane of the anterior third of the medial habenular nucleus, this mass is bounded by the ventricle medially, the nucleus reuniens dorsally, the undifferentiated hypothalamic gray ventrally, and the lateral hypothalamic nucleus laterally. It extends as far back as the junction of the middle and the posterior thirds of the habenula. This nuclear mass comes in relation with a very fine fiber tract which extends toward its lateral angle from the region of the medial forebrain bundle. In their course toward the nuclear mass the fibers sweep across in gentle curves over the fornix column. A few of the bundles of the supracommissural portion of the stria terminalis do pass through the nuclear mass and seem to be lost in the same. This nucleus was first described by Fortuyn ('12), who gave it its present name (quoted by Nissl, '13). Nissl describes it in the rabbit from the standpoint of cell preparations.

Anterior hypothalamic area. The anterior hypothalamic area (figs. 2 to 5, 13, 25) is bounded by the nucleus ovoidus in front and the nucleus filiformis behind. Medially, it is in relation with the anterior hypothalamic periventricular nucleus and laterally with the lateral hypothalamic area or the bed nucleus of the medial forebrain bundle. In this area one can differentiate at least three nuclear masses which are very small in size. In this paper we have taken the whole group and included the same under one heading, for, as far as our present preparations show, they have the same relation to fiber tracts. This area receives fibers from the most caudal portion of the preoptic component of the stria terminalis, also fibers from its supracommissural portion, also fibers from the medial cortico-hypothalamic tract.

Nucleus hypothalamicus ventromedialis. The nucleus hypothalamicus ventromedialis (figs. 6, 8, 9, 22, 25, 27) is first seen as a group of cells in the plane of the posterior boundary of the tangential nucleus, just above the ventral extreme of the hypothalamus, lateral to the ventricle and in the plane of the ventral third of the same. This mass is round in outline and is made up of medium-sized and small cells not closely packed together. It enlarges rapidly in size and extends both dorsomedially and ventrolaterally. A little farther caudad, the dorsomedial prolongation becomes distinct in itself, due to the fact that the cells are more closely applied together. In the farther caudal sections this portion may be called a distinct nuclear mass, for such are its characteristics. The more ventrolateral portion stands out very distinctly also. For a certain distance caudad the whole mass enlarges. At the level of the posterior third of the habenula the two masses gradually approach each other with the consequent formation of an oval mass. In this plane the nucleus is surrounded by the periventricular hypothalamic nucleus medially, the lateral hypothalamic nucleus laterally, the undifferentiated hypothalamic gray dorsally. In this oval mass the differentiation between the two components taking parts in its formation is not possible. Up to the plane of the posterior third of the habenular complex, this nucleus is a prominent feature of the hypothalamus. It occupies the larger portion of the ventral aspect of the hypothalamus on each side. It disappears from view in the region of the anterior third of the posterior commissure.

The nucleus hypothalamicus ventromedialis we regard as the same as Cajal's principal nucleus of the hypothalamus. In this connection it is interesting to note that our one-day-old rat series show this nucleus as constituting the major portion of the hypothalamus, as Cajal states to be the fact in the case of newborn mice. In the adult material, however, this is not true, and this nucleus is one of the many hypothalamic nuclei seen in the latter region. We will not try to homologize this mass with the nucleus infundibularis medialis of Nissl's description ('13). The designation he uses, together with a lack of further description of the mass in relation to other structures, make us hesitate as to possible homologies. Presumably, following his terminology, Winkler and Potter ('14) label a nuclear mass in the cat resembling ours by the same name.

The fiber connections of this nuclear mass are numerous. It comes in relation with the medial cortico-hypothalamic bundle, with the stria terminalis through its supracommissural component, with fibers from the medial forebrain bundle, especially the latter's septal component. Our sagittal series are particularly instructive in this respect, and in some planes one is able to note all these different components entering the nucleus (fig. 27). It is of interest to note that the fibers entering the nucleus form a capsule. Cox preparations show characteristic pictures.

Nucleus hypothalamicus dorsomedialis. In the plane where the amalgamation of the two nuclear masses takes place with the consequent formation of one oval mass (nucleus hypothalamicus ventromedialis) one sees the beginning of the differentiation of a nuclear mass just dorsal to it and found on the lateral aspect of the third ventricle (figs. 8, 9, 22). This constitutes the rostral extreme of the nucleus hypothalamicus dorsomedialis. In the sections farther caudad the nucleus enlarges in size considerably and extends dorsolaterally, in some planes becoming continuous with the subthalamic gray. In the middle third of the nuclear mass one observes the differentiation of a distinct, elongated, oval group of cells, obliquely placed in the nucleus as a whole and at an angle with the ventricle (the acute angle being dorsally directed). In certain planes this portion of the nucleus is intimately associated with the posterior hypothalamic periventricular nucleus, and in places it is inseparably continuous with the same.

It receives fibers from the supracommissural portion of the stria terminalis, also fibers from the medial forebrain bundle. It gives rise to at least a small group of fibers belonging to the periventricular system. The cells are small and medium-sized in Nissl preparations. The elongated oval mass is essentially made up of small cells.

Nucleus hypothalamicus posterior. Even before the disappearance of the nucleus hypothalamicus dorsomedialis one notes on the dorsal aspect of the latter the appearance of a nuclear mass which we have distinguished as nucleus hypothalamicus posterior. Its cells are arranged in gentle curves characterizing the presence of a relatively prominent fiber tract associated with it. Dorsally, this nuclear mass is continuous with the periventricular gray in the tegmentum. Laterally, it is in relation with the lateral hypothalamic nucleus, the mammillo-thalamic bundle intervening between the two structures. Ventrally, it is in relation with the hypothalamic periventricular gray. It disappears entirely from view in the region of the dorsal premammillary nucleus. This nuclear mass is intimately associated with the periventricular system of fibers giving rise to a majority of the same. Our Cox preparations have enabled us to follow axons into the periventricular system of fibers from cells which are located in this nucleus. It also receives fibers from the medial forebrain bundle (figs. 7, 9, 20).

Nucleus tangentialis (Cajal). The tangential nucleus of Cajal is made up of medium-sized and large cells and is found as far rostral as the plane where the optic tract begins to turn toward the diencephalon. It is found on the most ventrolateral aspect of the hypothalamus and surrounds the optic tract rostrad, ventrally, and ventrocaudad. The main mass of the nucleus, however, is cephalad to the optic tract. Cox preparations show very characteristic cells with few processes (fig. 20). Cajal ('11) thinks that it is intimately associated with the Meynert's bundle. In our preparation it is more ventrally placed than the Meynert's bundle and we have not been able to note any relation between the two structures (figs. 3 to 5, 27).

Nucleus hypothalamicus lateralis. What we have designated as the lateral hypothalamic nucleus is a group of medium-sized and large cells which are found in the course of the medial forebrain bundle. It is a nucleus of an interstitial nature and extends from the anterior boundary of the hypothalamus to the cephalic extreme of the mammillary complex (figs. 2 to 8, 15, 16, 20, 25). It does not present any peculiar arrangement of cells and is found forming the lateral portion of the hypothalamus. Cox preparations show characteristic cells (fig. 20). It receives fibers from the medial forebrain bundle and is intimately associated with the medial group of hypothalamic nuclei. In its most caudal portion it is also in intimate relation with the periventricular system of fibers, to a minority of which it probably gives rise. In certain planes the nuclear mass becomes continuous with the subthalamic masses dorsally. Anteriorly, it is continuous with the lateral preoptic area which is of a similar significance as regards the medial forebrain bundle. This gray mass corresponds, in part at least, to the lateral hypothalamic nucleus as described by Nissl ('13) and Winkler and Potter ('14).

Dorsal premammillary nucleus. In the plane of the middle third of the posterior commissure where the periventricular systems of fibers are the richest one notes on the medial aspect of the fornix bundle at a level dorsal to the infundibulum a group of medium-sized cells which represent the most rostral extreme of the nucleus premammillaris dorsalis. More caudad, it has larger dimensions and approaches the midline as a limit. Where it is the largest it assumes an oval shape, and in this situation it is surrounded by the fornix laterally, the ventral premammillary nucleus and the posterior hypothalamic periventricular nucleus ventrally, tegmental gray associated with the ventral tegmental decussation dorsally. With the appearance of the pars medianus, nucleus medialis of the mammillary body, our nucleus becomes smaller, its dorsal portion disappearing first, while a portion of its ventral part continues caudad into the mammillary body. The latter portion recedes ventrally with the increase in size of the medial mammillary nuclear complex and becomes reduced to a linearly arranged group of cells. More caudad in the plane of the anterior third of the mammillary body, it disappears entirely. It is intimately associated with the medial mammillary nuclear complex, and it is also connected to its fellow of the opposite side by commissural fibers (figs. 7, 10, 16, 20, 22, 25).

Ventral premammillary nucleus. The ventral premammillary nucleus extends more rostrad than the dorsal, and in its cephalic portion it is intimately related to the periventricular system of fibers, giving rise to a distinct group of the same. Our Cox preparations enable us to note the presence of axons extending toward the periventricular system, the cells of which are located in this nucleus (fig. 20). The cells are essentially medium-sized and Cox preparations are characteristic. In our Nissl preparations in the plane where the periventricular system of fibers is well shown, linearly arranged groups of cells extend from the dorsomedial aspect of the ventral premammillary nucleus dorsally and medially in gentle curves, thus assuming the characteristics of an interstitial nucleus for these fibers. The latter are intimately associated with the ventral portion of the nucleus hypothalamicus posterior. In a plane farther caudad, the nucleus rounds off, becomes smaller, and occupies a position between the rostral extreme of the lateral mammillary nucleus and the hypothalamic periventricular nucleus. In the plane of the middle third of the mammillary body this nucleus disappears (fig. 10).

Nucleus hypothalamicus periventricularis anterior. The nucleus hypothalamicus periventricularis anterior is the continuation of the periventricular gray in the preoptic region into the hypothalamus. It has essentially the same characteristics, being made up of small cells, which tend to arrange themselves in layers of four or five, more marked in certain places than in others. It extends as far back as the plane of the posterior third of the habenular complex, at which level it becomes continuous with what we have termed as the posterior hypothalamic periventricular nucleus. It receives fibers from the medial cortico-hypothalamic tract and a few from the supracommissural portion of the stria terminalis (figs. 3, 4).

Nucleus hypothalamicus periventricularis posterior. The rostral extreme of this nucleus hypothalamicus periventricularis posterior is characterized by a thickening of its wall. This takes place ventrally first, and farther back the thickening involves the more dorsal portion of the periventricular gray. It is not uniform throughout and there is an intervening area between the dorsal and the ventral thickenings which is not enlarged. At the most caudal extreme of the hypothalamus the two masses come together and form one uniform mass which extends back toward the infundibulum of the hypophysis and becomes continuous with the cellular structure surrounding the same. These two portions will be described separately (figs. 2, 6, 15, 25).

Nucleus hypothalamicus periventricularis posterior, pars dorsalis. In the plane of the rostral extreme of the dorsomedial hypothalamic nucleus one notes an increase in thickening of the periventricular gray dorsally, and as one follows the sections more caudad this becomes more apparent until in the plane of the middle third of the dorsomedial hypothalamic nucleus a continuity is noted between the latter and this nucleus (see account of the nucleus hypothalamicus dorsomedialis, p. 83). Just in front of the mammillary body it unites with the ventral portion of the posterior hypothalamic periventricular nucleus. From a study of our preparations it is apparent that it is intimately associated with the periventricular system of fibers (figs. 7, 8).

Nucleus hypothalamicus periventricularis posterior, pars ventralis. This is a thickening in the ventral portion of the periventricular gray in this region. This thickening is visible farther anteriorly than that of the pars dorsalis. In the more caudal areas it unites with the pars dorsalis, with the consequent formation of one mass which surrounds the ventricular projection toward the hypophysis. Our preparations are suggestive of the fact that these cells also contribute fibers to the periventricular system of fibers (figs. 7, 8, 9, 25).

Nucleus supraopticus diffusus. The nucleus supraopticus diffusus constitutes a nuclear mass found above the level of the optic chiasm and below that of the ventricle (figs. 5, 20). The commissura supraoptica dorsalis pars dorsalis passes through this nuclear mass as it crosses to the opposite side. Some sections are very suggestive of the fact that this nucleus acts as a bed nucleus for the fibers of the Ganser's commissure, and therefore contributes to the same.

Mammillary bodies and their connections

The literature relating to the mammillary bodies and their connections is very extensive and cannot be regarded as a record of unanimity of views. We will not endeavor to cover it completely, for the same has been done in more or less detail in the different texts on nervous anatomy and in most of the papers consulted for this work.

The consensus of opinion as to the nuclear configuration in the mammillary bodies is practically uniform. A medial and a lateral nucleus have been universally observed. Cajal ('11) describes also a limiting nucleus on the anterosuperior aspect of the medial nucleus. Nissl ('13), in his preparations of the rabbit material, notes a further division of the medial mammillary nucleus into an anterodorsal and a posteroventral part. Tsai ('25) finds in the mammillary bodies of the opossum a medial, a lateral, and a ventral nucleus.

The determination of the connections of the mammillary bodies with other centers presents many difficulties. The peduncle of the mammillary bodies has been considered as an afferent path by some (Cajal, '11; Spitzer and Karplus, '07; Papez, '23, and others), as an efferent path by others (Déjerine, '01; Edinger and Wallenberg, '02; Hatschek, '03, and others), as an afferent and an efferent path both by still others (Kappers, '21, and others). Those considering it afferent or partly so note its intimate relation to the medial lemniscus and the fact that some fibers come from the vicinity of the superior cerebellar decussation (Cajal, '11). Those who consider it efferent trace the fibers to a nuclear mass in the tegmentum: nucleus tegmenti profundum (Hatschek, '03); nucleus tegmenti dorsalis (Déjerine, '01). The third group of investigators describes an intimate connection with the medial lemniscus constituting the afferent portion of the tract and a smaller tegmental portion, the fibers of which arise in the lateral mammillary nucleus and course toward the tegmentum. Kappers ('21) even thinks, on the basis of comparative work on lower forms, that the latter portion is probably related to the motor trigeminus and the facial nuclei.

The consensus of opinion on the connections between the mammillary bodies and the thalamus is at present practically uniform except for certain details. For instance, Edinger ('11) theorizes on the possibility of a thalamo-mammillary path contained in the Vicq d'Azyr bundle. Cajal ('11) has noted that the mammillo-thalamic and the mammillo-tegmental tracts are products of bifurcation of axons, the cell bodies of which are located in the mammillary nuclei. Valkenberg ('12) denies this possibility. The mammillo-tegmental tract carries impulses to the Gudden's nucleus or nucleus tegmenti profundum (Déjerine, '01; Kappers, '21).

The fornix bundle in relation to the mammillary body has been very carefully studied by Cajal ('11), Edinger and Wallenberg ('02), and others. Cajal's opinion is that most of the fibers ending in the mammillary nuclei are collaterals of the fornix system. The chief part of the bundle accordingly passes through the mammillary body, crosses to the opposite side in the supramammillary decussation, then turns caudad toward the tegmentum. Edinger and Wallenberg, on the basis of degeneration work, have come to the conclusion that a part of the fornix ends in the lateral and the dorsal sections of the medial mammillary nucleus. Farther caudad, the tract divides into smaller bundles which in part cross to the opposite side and pass down to the nucleus tegmenti profundum, others end in the nuclei adjacent to the ventricle in the plane of the oculomotor nucleus, still others remain uncrossed and help to form the mammillary capsule.

Recently connections between the medial forebrain bundle, tuber cinereum, and the mammillary bodies have been described.

It should be mentioned here that the mammillary bodies in the rat resemble those of many of the lower mammals in that the two masses are fused into a single mass. Although the mammillary bodies in the rat are not prominent structures grossly, the nuclear configuration in the same is very complex, as will be seen in the following paragraphs. The nuclei, as we have been able to observe, are as follows:

Nucleus mammillaris lateralis. The nucleus mammillaris lateralis (figs. 10, 17, 25) begins at the level of the rostral extreme of the posterior commissure, and shows itself as a small group of cells linearly arranged at the ventrolateral border of the hypothalamus. Rostrally, the number of cells is small, but they stain very deeply in counterdistinction to the other hypothalamic masses. Farther caudad, it enlarges in size and assumes the shape of a comma with the concavity placed medially and the sharp edge ventrally. In this position it forms the most lateral mass of the mammillary bodies. Its cells are distinctly larger and richer in granules than those of the more medial masses. It disappears entirely in the extreme caudal aspect of the mammillary bodies. Its most caudal portion is also stretched out and is made up of few deeply staining cells linearly arranged at the lateral periphery of the mammillary bodies. It is interesting to note that the nucleus is so prolonged in its rostral and caudal relations. With the preparations at hand, we are not able to observe any fibers arising from this nucleus which take part in the formation of the Vicq d'Azyr bundle. This nucleus comes in very intimate relation with the mammillary peduncle, and fibers from the latter course through the nuclear mass in gentle curves and are traced to the medial nuclear complex (fig. 16). We are of the opinion that the axons arising from the lateral mammillary nucleus course toward the tegmentum and thus form a part of the mammillary peduncle. Fibers from the medial forebrain bundle reach the lateral mammillary nucleus.

Medial group of mammillary nuclei. Just above the infundibular process of the ventricular system in the plane of the rostral third of the posterior commissure, one notes between the dorsal premammillary nuclei a median thickening made up of medium-sized cells. With the decrease in the size of the dorsal premammillary nuclei, this median thickening extends laterally, with the consequent formation of a roughly quadrangular structure. The median group of cells still preserves its entity as such in more caudal sections and divides the whole mass into lateral halves. Farther caudad, the division becomes more marked. On the lateral aspect of the whole mass one sees the fornix bundle, while dorsally and mixed in with the cells are the bundles of the combined mammillo-thalamic and the mammillo-tegmental tracts. A little farther caudad there is a further division of the masses into two distinct parts caused by the presence of the mammillo-thalamic and the mammillo-tegmental tracts. Thus, in the plane of the middle third of the mammillary bodies one notes a median group of cells about the midline, separating two oval masses, the latter being bounded laterally with wedge-shaped nuclear masses, the whole complex constituting the medial group of nuclei. In our preparations it is the medial group of nuclei that give rise to the mammillo-thalamic and the mammillo-tegmental tracts. Our preparations are indicative of the fact that the mammillo-tegmental tract arises from the more anterior portion of the medial group of nuclei in the mammillary body. We have divided this nuclear complex into the following components: nucleus medialis, pars medianus; nucleus medialis, pars medialis; nucleus medialis, pars lateralis; nucleus medialis, pars posterior; nucleus medialis, pars commissuralis ventralis; nucleus medialis, pars commissuralis dorsalis.

Nucleus medialis, pars medianus (figs. 10, 25). This nucleus medialis pars medianus represents the most rostral prolongation of this group. It is found lining the midline and appears soon after the disappearance of the premammillary nuclei. It is made up of medium-sized cells which are characteristic in Cox preparations (fig. 20). Farther caudad, it becomes a dividing line between the two partes mediales. In the posterior third of the mammillary body it becomes continuous with the nuclei mediales, partes mediales, with the consequent formation of a round nuclear mass. After the disappearance of the partes mediales, it continues caudad as a dividing line between the two partes laterales. It eventually becomes continuous with the latter at the extreme caudal aspect of the mammillary bodies. Nucleus medialis pars medianus is essentially of a commissural nature, and fibers are seen crossing from one side to the other through the nuclear mass. It helps to form a very small portion of the mammillo-thalamic and the mammillo-tegmental tracts. The latter constitutes a part of the component V taking part in the formation of the combined mammillo-thalamic and mammillo-tegmental tracts, and which will be described later (p. 96).

Nucleus medialis, pars medialis (fig. 10). With the disappearance of the premammillary nuclei there appears on the lateral aspect of the pars medianus a roundish mass of cells, at the extreme lateral aspect of which one notes a greater degree of thickening of a somewhat crescentic nature. The latter is the most rostral extreme of the nucleus medialis pars lateralis. With the coming in of the mammillo-thalamic and the mammillo-tegmental tracts, the two masses become more separable. The pars medialis is somewhat oval at first, with the long axis placed ventrodorsally. Dorsally, it is separated off from the pars lateralis by the combined mammillo-thalamic and the mammillo-tegmental bundles, while ventrally it is continuous with the pars lateralis through a thick band of cells. Farther caudad, the ventral connection between the two masses disappears, and now the pars medialis assumes a more or less roundish appearance. At this plane one notes ventral to the partes mediales a commissural band of cells evidently connecting the two partes laterales. In Nissl preparations the pars medialis stains more deeply than the pars lateralis, and in places the cells are more thickly placed. In the posterior third of the mammillary bodies the partes mediales fuse with the pars medianus with the consequent formation of a round nuclear mass above mentioned. A little farther caudad, it disappears entirely, the region left behind becoming occupied by the extensions of the partes laterales. Pars medialis, nucleus medialis, is responsible for the component III and a portion of the components IV and V in the production of the combined mammillo-thalamic and the mammillo-tegmental tracts.

Nucleus medialis, pars lateralis (fig. 10). The nucleus medialis pars lateralis begins as a crescentic mass capping over the lateral aspect of the pars medialis, and is found enlarging as one follows it caudad. It is at first intimately related to the medial part (pars medialis), being continuous with it ventrally (see above). More caudad with the disappearance of this ventral connection, the pars lateralis assumes the shape of a wedge with the sharp end ventromedially. From this sharp end a medial extension crosses over the midline to meet an extension of the same nature from the opposite side. This constitutes the nucleus medialis pars commissuralis ventralis. A concavity at the dorsal border of the nuclear mass is brought about by the presence of the fornix bundle at this point. Farther caudad, with the disappearance of the fornix from the field, this gap is filled in. At the caudal extreme of the pars medialis there is seen an extension from the dorsomedial aspect of the pars lateralis which crosses over the midline to meet an extension of the same type from the opposite side. This constitutes the nucleus medialis, pars commissuralis dorsalis. In the posterior third of the mammillary body the pars medialis after fusion with the pars medianus becomes surrounded on all sides by the partes laterales and their commissural extensions. After the disappearance of the last-mentioned group, the two partes laterales come together and form an undifferentiated mass—the nucleus medialis pars posterior or caudalis.

Nucleus medialis, pars posterior (fig. 10). The nucleus medialis pars posterior is an undifferentiated nuclear mass of cells at the caudal extreme of the mammillary bodies and is continuous in front with the partes laterales of the two sides. It is an oval mass with the long axis placed transversely and gives rise to the component I of the combined mammillo-thalamic and the mammillo-tegmental tracts. Its more dorsal portions are also related to the component III, to the fibers of which it contributes. The cells here are small and medium-sized and do not differ from those in the pars lateralis.

Nucleus medialis, pars commissuralis dorsalis. This nucleus has already been mentioned above. It helps to connect the two partes laterales on their dorsal aspect. It is associated with fibers which interconnect the two masses of the opposite sides. The cells are essentially of the same type as those in the partes laterales.

Nucleus medialis, pars commissuralis ventralis. This nucleus has already received mention, and is found extending more rostrad than the dorsal commissural component. It interconnects the ventral portions of the partes laterales and is traversed by commissural fibers. The cells are essentially of the same type as in the pars lateralis.

From the above description of nuclei in the mammillary bodies, it can be seen that in the rat we are dealing with a highly specialized center. In our preparations the combined mammillo-thalamic and the mammillo-tegmental tracts arise from the medial group of nuclei. Most of the differentiation of the medial group is caused, we believe, by an orderly grouping of cells which give rise to the different components making up these tracts. These components will be described under the connections of the mammillary bodies. It is also to be emphasized that the medial group of nuclei of the two sides are very intimately interconnected. The medial group of nuclei receive impulses from the fornix bundles, and the mammillary peduncle thus being related to higher and lower centers, respectively, through those paths. The lateral nucleus, although very small compared with the medial group of nuclei, is very characteristic in our preparations. It comes in relation with the mammillary peduncle and the fornix bundle. It is also in intimate relation with the medial group of nuclei. As far as we are able to determine, it does not take part in the formation of the combined mammillo-thalamic and the mammillo-tegmental tracts. It gives rise to fibers which descend toward the tegmentum in the mammillary peduncle. It receives fibers from the tuber cinereum region.

Mammillary peduncle

A study of the mammillary peduncle in the preparations at hand reveals that the majority of its fibers join the medial lemniscus system. Leaving the ventral aspect of the medial lemniscus, these fibers are collected into a compact tract, just ventral to the ventral tegmental nucleus and lateral to the interpeduncular nucleus. In this position the path courses cephalad toward the mammillary bodies and enters the same on their dorsolateral aspect. It can be identified as such in the mammillary bodies for a certain distance, but in the more cephalic portions it becomes intimately associated with the lateral mammillary nucleus. In its course through the mammillary bodies it gives off side branches which traverse the lateral nucleus and enter the medial group of nuclei (fig. 16). According to Cajal ('11), the fibers forming the side branches are products of bifurcation of the main peduncular fibers. Our Cox preparations are not adequate for the confirmation of this observation.

A study of the series of cross-sections reveals the fact that the mammillary peduncle is noticeably larger in a plane just caudal to the mammillary bodies, as compared with its size before it joins the lemniscus system of fibers. It is apparent, therefore, that in its course through the tegmentum some fibers must be added to it as it is traced cephalad or subtracted from the same as one traces it caudad. It is our belief, consequently, that it contains not only fibers coming from the region of the medial lemniscus, but also fibers that arise in the lateral nucleus of the mammillary body and course down toward the tegmentum. These fibers forming a small minority of the peduncular system come in intimate relation with the ventral tegmental nucleus.

We have been able to follow the peduncular fibers forward into an area of the hypothalamus in front of the mammillary bodies. Here they are lost in and among the fibers of the medial forebrain bundle. The further distribution of these fibers is not determinable from our preparations.

Mammillo-thalamic and mammillo-tegmental tracts

Our preparations show that both the mammillo-thalamic and the mammillo-tegmental tracts arise from the medial group of mammillary nuclei. The whole length of this portion of the mammillary bodies does contribute fibers to these tracts, as shown by the fact that cross-cut bundles representing component portions of these tracts are seen throughout the medial group of nuclei including the most caudal portions. The respective sides are responsible for the respective tracts; however, it should be kept in mind that both sides are richly interrelated by commissural fibers.

Our preparations are favorable for an analysis of the combined mammillo-thalamic and the mammillo-tegmental tracts into several components based upon the origin of these various components from the nuclear masses in the mammillary bodies. We will designate them in the present paper numerically:

Component I. This arises from the pars posterior, nucleus medialis (figs. 26, 27).

Component II. The component II arises essentially from the pars medialis, nucleus medialis. It is the more caudal portions of this nucleus that give origin to these fibers (fig. 18).

Component III. Component III is made up of a few fascicles which arise from the dorsal aspect of the partes lateralis and medialis, nucleus medialis. These fascicles course anteriorly on the dorsal aspect of the mammillary bodies, between the latter and the capsule, then farther forward unite with the rest of the tracts (figs. 18, 26).

Component IV. This component arises from the more anterior portions of the pars lateralis, nucleus medialis. Some of it can be seen on the medial aspect of the fornix bundle (fig. 17).

Component V. This portion arises from the most anterior part of the pars medialis, nucleus medialis (fig. 16).

At the extreme cephalic end of the mammillary body these different components are contained in a compact bundle which courses dorsally. Just above the level of the hypothalamus and in the plane of the posterior commissure, the mammillo-tegmental tract separates off from the mammillo-thalamic.

Are the mammillo-thalamic and the mammillo-tegmental tracts bifurcation products of axons, the cell bodies of which are located in the mammillary nuclei? Our Cox preparations do answer the question to a certain extent. We have been able to note very few bifurcations either due to a lack of complete impregnation or a lack of proper orientation. We have been able to trace fibers into both tracts without a visible bifurcation at the junction of the two. But we have also been able to note fibers of different caliber in both tracts: those that are quite thin and those that are moderately thick. The very few products of bifurcation that we have been able to observe essentially belong to the thin group. The assumption seems justified that the thinner fibers represent products of bifurcation and the thicker ones stem fibers.

The further course of the mammillo-thalamic tract is essentially the same as the one described for other mammals. It comes in relation with the anteromedial and the anteroventral thalamic nuclei.

The mammillo-tegmental tract in our preparations is first closely applied to the medial aspect of the Meynert's bundle. It accompanies it for a certain distance caudad, then leaves the same and becomes more and more scattered as one follows it farther back. In the region of the third nucleus and ventral to the same, the bundles are lost track of, probably ending in the central tegmental nucleus.

Mammillary capsule

Our findings on the mammillary capsule in the rat are essentially the same as those described by Cajal ('11) for his mouse material. The capsule is best defined on the posterosuperior aspect of the mammillary bodies. In this situation it is made up of a bed nucleus of small cells, in the meshes of which one notes the fornix extending dorsally and medially to cross to the opposite side; a few fibers arising from the mammillary nuclei; fibers that are products of the capsular bed nucleus itself; in the posterior aspect of the mammillary bodies the component three (III) of the mammillo-thalamic and the mammillo-tegmental tracts at the junction of the capsule with the mammillary nuclei.

The fornix bundle

We have nothing essential to contribute to the findings on the fornix bundle as given by previous investigators. Our preparations show that it comes in relation with the lateral aspect of the medial group of nuclei and with the lateral nucleus in the mammillary bodies. Our preparations are not favorable to determine the nature of the fornix fibers ending in the mammillary nuclei (as to whether or not they are bifurcation products of fornix stem fibers). The close relation of the medial cortico-hypothalamic tract and the fornix bundles will be taken up under another heading. Suffice it to say that they both come down from the hippocampus together, the fornix being on the lateral aspect of the medial cortico-hypothalamic tracts (figs. 1 to 9, 10 to 17, 22, 25, 26, 27).

Medial forebrain bundle

In our previous paper we gave a brief résumé of the medial forebrain bundle as found in the rat (Gurdjian, '25). Since then the same has been described in the opossum (Tsai, '25). Tsai also considers the literature on the subject in detail. In the present paper we will take up the components making up the medial forebrain bundle, for these are characteristically represented in our preparations. Nuclear description will be taken up along with fiber-tract presentation in so far as it may be necessary for a better understanding of the composition of the medial forebrain bundle. Some paths which are regarded usually as helping to form the medial forebrain bundle (supracommissural portion of the stria terminalis, the preoptic portion of the stria terminalis, etc.) will not be described as such in our description, for the same can be followed from their origin to their termination. Such tracts may better be described by themselves and be given names which are more descriptive and true to facts.

Septo-hypothalamic component (figs. 22, 26, 27). The septo-hypothalamic component of the medial forebrain bundle is by far the largest component. The fibers descend from the septal regions ventrally and enter into the formation of the bundle. In their course ventrally they are accompanied by an interstitial nucleus made up of large cells. This nuclear mass is continuous in front with the large-celled medial septal nucleus. The bundle then moves laterally along with the rest of the formation, so that in our sagittal preparations only their course toward the preoptic region is seen, while their course toward the hypothalamus is noted in more lateral sections. Our preparations suggest in certain planes that this component also contains some fibers from the fimbria fornicis and the bed nucleus of the commissura fornicis. The septo-hypothalamic component is undoubtedly in synaptic relations also with the preoptic area and the caudal end of the tuberculum olfactorium. It is related to the lateral hypothalamic nucleus. Our sagittal preparations show very distinctly fibers going to the ventromedial and the dorsomedial hypothalamic nuclei. It is mainly concerned, however, with the more lateral portions of the hypothalamus.

Lateral cortico-hypothalamic component (figs. 11, 12). We have designated this component of the medial forebrain bundle the lateral cortico-hypothalamic, in counterdistinction to the medial cortico-hypothalamic tract which comes from the region of the hippocampus. The lateral cortico-hypothalamic component comes from the region of the pyriform lobe. It is probably homologous to the ventral olfactory projection tract of lower forms (Crosby, '17). It forms the most lateral component of the medial forebrain bundle and is primarily concerned with the lateral hypothalamic area. In planes where the medial and the lateral forebrain bundles are contiguous, this component forms the dividing line between the two.

Strio-hypothalamic component (fig. 27). The strio-hypothalamic component of the medial forebrain bundle is composed of fibers which arise from the nucleus accumbens and the head of the caudate nucleus. They are very evident in our preparations. The cells that give rise to these fibers are characteristic and are shown in figure 19. One has to be very careful in sagittal preparations not to mistake the lateral forebrain (internal capsule) bundles for strio-hypothalamic ones. The strio-hypothalamic bundles are medial to the cortico-hypothalamic and lateral to the septo-hypothalamic in the medial forebrain bundle. Our preparations are indicative of the fact that they are essentially concerned with the lateral hypothalamic area.

Tuberculo-hypothalamic component (figs. 19, 27). In our sagittal preparations it is very evident that fibers arising from the tuberculum olfactorium accompany the medial forebrain bundle to the hypothalamus. Some fibers arising from the islands of Calleja may also be followed into the medial forebrain bundle. The tuberculum olfactorium has been described in our previous paper. With our present preparations we are able to note the cells that give rise to the axons forming this component. Cox preparations of the tuberculum olfactorium and the island of Calleja are very characteristic.

Parolfacto-hypothalamic component. Fibers arising from the region in front of the septal areas are also seen taking part in the formation of the medial forebrain bundle. The parolfactory areas have been defined and described in our previous communication (Gurdjian, '25).

Olfacto-hypothalamic component. These are fibers that arise from the rostral prolongation of the medial olfactory areas of the hemisphere. They are few in number and well shown in figure 27. They are essentially concerned with the more medial portions of the hypothalamus.

Olfacto-mammillary tract. The olfacto-mammillary tract is given off from the medial forebrain bundle and enters the mammillary bodies supplying essentially the lateral group of nuclei. It has been described in the opossum (Tsai, '25). We are not sure from our preparations which component of the medial forebrain bundle gives rise to this tract. Certain fields are very suggestive of its being septal in nature.

From the above discussion of the components of the medial forebrain bundle it should be noted that this bundle is a complex system of fibers and therefore connects not only any two given areas, but a whole group of areas adjacent to each other. Thus a fiber arising in the septal area and taking part in the formation of the bundle is not necessarily hypothalamic bound, it may very well stop in the preoptic area. This is the reason why we term this whole group by the general name of medial forebrain bundle rather than follow the system of B.N.A. nomenclature. In order to follow the latter and do justice we would have to analyze the complex more completely than our present preparations permit and note exactly the position of each component and describe the same as an independent fiber tract. It is hoped that future work will enable us to do this.

In the caudal end of the hypothalamus the medial forebrain bundle becomes very small. This proves that in the rat the bundle is essentially concerned with the hypothalamus. In some planes there is a suggestion of the possibility of some fibers turning into the subthalamic areas. At least, they certainly do get there, but whether they end there or are going somewhere else we are not prepared to state. A little farther caudad some of the fibers are seen to turn up and enter the most rostral portion of the tegmentum. Do they turn caudad and course toward the tegmentum? This cannot be answered with the preparations at hand. From a study of lower forms we are convinced that they do. In this connection it is interesting to note the close proximity of these fibers to the fibers taking part in the supramammillary decussation. In sagittal preparations a deceptive picture is often brought about by the conglomeration of the two systems of fibers which in places look as if they were continuous.

The medial cortico-hypothalamic tract

The medial cortico-hypothalamic bundle is first seen on the lateral aspect of the stria medullaris in the plane of the posterior third of the anterior commissure. In this situation it comes to lie in close proximity to the medial amygdalo-hypothalamic tract. It courses along with the latter toward the medial aspect of the fornix bundle passing between the stria medullaris and the fornix. We have been able to identify the tract in one of our series where the same is differentially stained (figs. 1, 11, 12, 26). After coursing posteriorly along with the fornix bundle, the combined medial cortico-hypothalamic and the medial amygdalo-hypothalamic tracts run ventrally for a certain distance and then caudad. These relations are well shown in the sagittal preparations (fig. 26). As they course down they break down into small bundles characteristic of their supplying the whole area which they traverse. They are distinct from the medial forebrain bundle and can be recognized as such in all of our series. They supply the periventricular gray in the preoptic and the hypothalamic regions, as well as the medial group of nuclei in the hypothalamus, especially, the nucleus dorsomedialis, and the nucleus ventromedialis.

The medial amygdalo-hypothalamic tract

The medial amygdalo-hypothalamic tract arises from the stria terminalis in the plane of the middle third of the anterior commissure. It extends medially toward the forming stria medullaris, passes ventral to the latter, between it and the fornix bundle, in company with the medial cortico-hypothalamic tract. The further course of the tract is essentially the same as the one described under the discussion of the medial cortico-hypothalamic tract (see above). It essentially supplies the same regions as the latter—the medial wall of the preoptic and the hypothalamic areas (figs. 1, 11, 12, 26).

The supracommissural portion of the stria terminalis

The supracommissural portion of the stria terminalis was described in a previous paper (Gurdjian, '25). It essentially supplies the medial group of nuclei in the hypothalamus.

Periventricular system of fibers

We have grouped these fibers under the above-mentioned name not because they are essentially periventricular in origin and termination, but because of their close proximity to the ventricular cavity. Cephalad, the system can be divided into two portions: a larger hypothalamic and a smaller thalamic division.

The hypothalamic division arises from the ventral premammillary nucleus, the posterior hypothalamic nucleus, the posterior hypothalamic periventricular nucleus, the dorsomedial hypothalamic nucleus. Most of the cell bodies of this portion of the system are found in the above-mentioned nuclei, for we have been able to trace the axons of the cells located in a number of the above-mentioned nuclei into the periventricular system of fibers.

The thalamic division of the system is essentially connected to the nucleus reuniens region. We are still ignorant of the direction of conduction in this portion.

The two divisions unite in the plane of the caudal third of the habenula and, extending dorsally on the medial aspect of Meynert's bundle, they reach the ventral aspect of the posterior commissure (figs. 7 to 9, 14 to 18, 22, 26, 27, 29). They then turn caudad and run toward the lower centers of the brain, being always found in the periventricular gray. They can be followed as far down as the medulla. Our preparations are indicative of the fact that they supply certain centers in the whole region lower down. A well-defined portion of the system enters the tectum, as shown in our sagittal preparations. Here they are seen to enter the most ventral fibrous layer in the tectum. In their course toward the latter they pass ventral to the posterior commissure.

Through the periventricular system the hypothalamus is put into relation with the lower centers of the brain and the tectum. It is interesting to note that analogous conditions exist in lower forms, such as Reptilia (Huber and Crosby, '26). As far as we know, this system has not been taken up systematically in any mammal.

SUMMARY AND CONCLUSIONS

In our consideration of the epithalamus we tried to bring out the fact that the connection between the stria terminalis and the stria medullaris, of a supposed amygdalo-habenular significance, is in great part a connection between the stria terminalis and the hypothalamus. It is essentially concerned with the more medial portions of the hypothalamic and the preoptic areas.

We have emphasized the fact that, at least in our rat material, a continuity is noted between the preoptic and the hypothalamic areas. The line of division between these two areas is a conventional one rather than based upon morphologic data. The preoptic area presents for examination at least five nuclear masses. The connections in the preoptic area are comparable to those of the hypothalamus. Olfactory centers farther forward, the olfactory cortex, the hippocampus, the amygdala, the habenula, etc., are related to the preoptic area.

The hypothalamus presents many interesting features. The nuclear configuration is complex. We have differentiated and described at least twelve such nuclear masses. It would be possible to carry the classification even further, but we do not see the necessity for such detail with our present knowledge of the fiber connections of the area.

The connections of the hypothalamus are very numerous. The medial forebrain bundle relates it to the olfactory regions of the medial hemispheric wall farther forward. It is connected to the cortex through two distinct paths: the medial cortico-hypothalamic tract, a connection between the hippocampus and the hypothalamus; the lateral cortico-hypothalamic tract, a connection between the pyriform lobe area and the hypothalamus. Strio-hypothalamic connections from the region of the nucleus accumbens are also present. Ascending fibers of a sensory significance reach the posterior portions of the hypothalamus through the mammillary peduncle. It is intimately connected with the mammillary body. The periventricular system of fibers connects the posterior portion of the hypothalamus with lower centers and possibly also with the tectum. It is very probable that some of these fibers are media of interrelation between the ventral and the dorsal portions of the diencephalon, segmental in nature. Such fibers are also seen in the most rostral portions of the diencephalon, where connections exist between the hypothalamus and the preoptic areas, on the one hand, and the more dorsal portions of the thalamus about the midline, on the other.

In our text emphasis has been given to the close continuity between the hypothalamic and the subthalamic areas. This is probably of important physiologic significance, giving these areas some related groups of function.

The connections of the preoptic and the hypothalamic areas with the amygdaloid complex are overwhelmingly numerous. These centers are interrelated by means of three different paths. The supracommissural portion of the stria terminalis, the preoptic component, and the medial amygdalo-hypothalamic tract connect all the different planes and levels of the preoptic and the hypothalamic areas with the amygdala. The direction of conduction is not known. Conduction probably takes place in both directions. As to the significance of this extensive interrelation, we do not as yet have an opinion to offer.

The experiments of Smith ('26) add to our knowledge of the various functions of the hypothalamus. This observer notes that general adiposity ensues if the perihypophysial hypothalamic gray is injured without injury to the hypophysis. The reported observations of this author suggest another evidence of the vegetative nature of this region. The fact that the periventricular system of fibers connects the posterior portion of the hypothalamus with lower centers would suggest the possibility that these fibers influence sympathetic centers lower down. And the action of the latter centers on the endocrine system of the body with derangement of function of the same would be a possible explanation of such changes as adiposity, etc., as this author notes in his experimental animals.

The mammillary bodies in the rat are very interesting. The complex is made up of more than a medial and a lateral nucleus. It consists of a highly differentiated nuclear pattern which has distinct and definite relations to the origin of the combined mammillo-thalamic and the mammillo-tegmental tracts. It has been possible to subdivide the latter into its component portions as to their origin from the different parts of the medial group of nuclei in the mammillary bodies. The opposite sides are intimately interrelated. We think that the mammillo-tegmental tract arises from the more anterior portions of the medial group of nuclei. It is, in part at least, a bifurcation product of fibers, the cell bodies of which are located in the medial group of mammillary nuclei. The other product of bifurcation forms a portion of the Vicq d'Azyr bundle (p. 96). We think that the mammillary peduncle in the rat is made up of both ascending and descending fibers. By far the majority of the group, however, are ascending in nature.

We have described the medial forebrain bundle and analyzed its component portions. It is essentially a medium of connection between the anterior olfactory centers and the hypothalamus. The more medial portions of the subthalamus may also receive fibers from this system.

Detailed consideration has been given to the supraoptic system of commissures. The commissura supraoptica dorsalis, pars ventralis (Meynert's commissure) is essentially associated with the subthalamus, the tectum and the ventral portions of the lateral geniculate bodies. The tectal connection in the rat is very small compared with that found in the alligator (tractus tecto-thalamicus cruciatus, Huber and Crosby, '26). We have not been able to note a striatal connection in our preparations. The latter has been noted in the human (Probst, '05) and in birds (Edinger, '11). The commissura supraoptica dorsalis pars dorsalis (Ganser's commissure) is essentially a connection between the subthalami and the hypothalami of the two sides. In their course on the dorsal aspect of the optic chiasm, the fibers of the commissure of Ganser come into an intimate relation with a nuclear mass in the ventral portion of the hypothalamus. We think this nuclear mass is of an interstitial significance as concerns the commissura supraoptica dorsalis, pars dorsalis. The commissura supraoptica ventralis is recognizable in our preparations only on the basis of its connection with the medial geniculate bodies. The supraoptic system of commissures is, then, concerned primarily with the metathalamus, subthalamus, tectum, and a portion of the hypothalamus. With the increase in the functional significance of the forebrain in the animal scale, it seems, that the tectal relations of the supraoptic system become progressively less important. Probably this connection is still smaller in forms higher than the rat (compare alligator, rat, and higher forms).

The subthalamus is a highly organized center in the rat. The zona incerta through its connections with the internal capsule, the tectum, the tegmentum, the hypothalamus, takes on the function of a correlation center, the importance of which has hitherto been overlooked. It is probably concerned with vegetative functions which we cannot specify at this time. The corpus Luysii and its connections present many interesting features; further research is necessary to elucidate their significance. The radiations of Forel and the field of Forel have been considered. In the rat the field of Forel is not an entity in itself. The recognition of the mass is dependent on its relations with the radiation of axones first described by Forel. The supramammillary decussation is partly a commissural system for the caudal end of the subthalamus.

The optic tract and the metathalamus have been considered. Definite cortico-geniculate fibers are present in the rat. This represents another step in the phylogenetic development of the brain in the rat when we compare it with a form like the alligator, where investigators have not been able to locate cortico-geniculate fibers (Huber and Crosby, '26). The presence of such a tract in the rat demonstrates beyond doubt the increasing importance of the cortex and the ability of the latter to subjugate a center like the metathalamus which was predominated by the tectum in the lower forms. A further expression of the same mechanism is represented by the topographic relations of the lateral geniculate body. In the phylogenetic development of the lateral geniculate body we note that under the influence of tectum this center moves posteriorly as one examines graded forms. With the coming in of the cortical influence there is produced an added mechanism whereby a part of the center (the part which is connected to the cortex) moves farther forward in the further phylogenetic development of the same. Thus a comparison of the rat and higher forms is very suggestive of such a possibility. Furthermore, in the rat, for example, the portion of the lateral geniculate body which is related to the cortex (nucleus geniculatus lateralis, pars dorsalis) is more cephalad (closer to the area of emergence of the cortico-geniculate fibers) than the portion (nucleus geniculatus lateralis, pars ventralis), which, as far as we know, does not possess cortical connections.

In our consideration of the lateral forebrain bundle we have taken up in detail its connections with the thalamus and tectum. Of special significance is the relation of the forebrain to tectum which has not been emphasized by previous investigators. Such a connection has been shown to exist in lower forms (Huber and Crosby, '26). We have divided the cortico-thalamic connection into three parts: the superior, middle, and inferior thalamic radiations. The tectal connection accompanies the superior thalamic radiation. In general, the superior thalamic radiation is related to the dorsolateral thalamus and tectum. The middle thalamic radiation is related to the ventral and lateral thalamus, while the inferior is associated with the medial and the median group of thalamic nuclei. The inferior thalamic radiation is probably the homologue of the lamina medullaris interna of higher forms. The posterior portion of the superior thalamic radiation is undoubtedly the lamina medullaris externa of higher forms.

The thalamus proper in the rat is comparable to that found in related forms, such as the mouse, the rabbit, cat, etc. We have divided it for descriptive purposes into groups dependent on their topographic distribution. The anterior group of nuclei made up of the nucleus anterior dorsalis, the nucleus anterior ventralis, and the nucleus anterior medialis is essentially the same as was found in practically all Mammalia, including the monkey (Vogt, '09). The lateral group of nuclei in the rat present certain peculiarities. The nucleus magnocellularis described in the rabbit by Hollander ('13) is not determinable as such in our preparations. By comparing topographical relations in the two forms, we have come to the conclusion that this nucleus is included in the nucleus ventralis pars dorsomedialis of our description. The ventromedial nucleus of Hollander's description is our nucleus medialis ventralis. We think that this essentially belongs to the medial group of nuclei, and is not a part of the ventral nucleus; certainly not the portion with the following characteristics: "La limite interne du ventromédial (V.M.) est formée par les fibrilles thalamiques médiales; la limite externe par le faisceau de Vicq d'Azyr." In the posterior plane of the ventral nucleus we see a medial prolongation, the nucleus commissuralis interventralis, which is comparable to Hollander's ventromedial nucleus, but ours is too far back, and we are skeptical of homologies here. The nucleus X of Hollander's description is enclosed in the dorsomedial portion of the ventral nucleus in our material.

The nucleus lateralis pars posterior in the rat receives optic fibers, and in this respect simulates the pulvinar of higher forms. The nucleus posterior thalami in our preparations is connected with cortex and tectum. It may be related to its fellow of the opposite side through the posterior commissure.

The medial group of nuclei are in general connected with the forebrain through the inferior thalamic radiation. Posteriorly, they are connected with the tectum. They are richly related to their fellows of the opposite side through commissural bands.

We have named all the nuclei of the midline instead of numbering them. It is thought that the nucleus paramedianus of Hollander's description is the lateral portion of our nucleus reuniens. We have noted the presence of an anterior and a posterior paraventricular nuclei. They are comparable to number '1' of Hollander's topography of the nuclei of the midline. We desire to emphasize the commissural bands of nuclear material existing between the anterodorsal, the anteromedial, the ventral, the mediodorsal, and the medioventral nuclei. The nuclei of the midline are connected with the tectum.

The commissures connecting symmetrical portions of the thalamus are well shown in our preparations. In our silver material there are two distinct masses of fibers crossing the midline. The more rostral thalamic commissure is a thick band of fibers intercommunicating the anterior thalamic nuclei primarily. This can be divided into a dorsal and a ventral portion. The dorsal commissural band interconnects the anterodorsal nuclei, while the ventral commissural band is concerned with the anteromedial and the anteroventral nuclei. In the plane of the middle third of the thalamus the rostral thalamic commissural band has practically disappeared. Its place is now taken by the caudal thalamic commissure which interconnects the ventral, the medial, and the lateral nuclei. The rôle of these commissural bands must be quite an important one in the thalamus of the rat, for they are so well differentiated.

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