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THE CEREBELLUM
IN THE RAT AND MOUSE.

A thesis

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by

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INTRODUCTION.

Methods.

During recent years the cerebellum has been the object of much valuable research. Stroud, Smith and others have made valuable contributions on its development in the mammal. The anatomy of its various parts has been established on a sound basis; and its nomenclature, hitherto confusing and conflicting, is gradually becoming more uniform.

Our knowledge of its lobes, nuclei and main tracts, their connections and the effect of lesion or removal of one or more of them is based largely on the valuable researches of Cajal, Thomas, Probst, Van Gehuchten, Clarke, Horsley and various other investigators who have recently studied the cerebellum. Much remains however to be done in connection with the exact relations of the different neurones of the cortex and nuclei, and the course of impulses entering and leaving the cerebellum. With this in view four methods of staining have been employed.

The greater part of the work was done on the brains of white and gray rats. For comparison with these a number of brains of the common mouse and of the rabbit were used.

Technique No.I. (Bielschowsky). In this formalin hardened brains of rats were used. On removing the brain from the formalin it should first be carefully washed and as the tissue is now fixed the membranes should be removed from the gyri, care being taken not to injure any of the delicate folia. This is necessary in order to facilitate the penetration of the stain. The brain is next placed in a 1½ % solution of silver nitrate. In this it remains for two to four days. When the tissue is of a uniform brown throughout it is removed, rinsed and placed in a solution prepared as follows: To about 40 cc. of a 1½% solution of silver nitrate add a few drops of a 40 % solution of caustic soda. To this add strong ammonia until the precipitate is dissolved, stirring constantly; then add excess of ammonia. This solution should be freshly

prepared. In this it is left for 24 hours and is then removed, washed and placed in 20% formalin for 12-36 hours. Should any of the solutions turn cloudy they should be changed. Dehydrate, imbed, section, mount.

The sections on the slide are now toned in gold chloride. This is done by placing the slide in 40 cc. of distilled water to which 1 cc. of a 1% solution of gold chloride has been added, for 10-20 minutes or until the tissue is of a slate gray color. It is then placed in a 5% solution of hypo for the same length of time. This method is invariably successful. It stains the medullated fibres, the cells of the various nuclei, the cells of Purkinje, their dendrites and ramifications and the cells of the nuclear layer of the cerebellum.

Technique No. II. (Cajal). In this we have followed the method of Cajal. Fresh brains are fixed for 24 hours in 95% alcohol and then placed in 1% or 1½ % silver nitrate and kept at 35°C for 2-4 days. They are then washed and ripened in a solution of 5%

pyrogalol. These sections may also be toned with gold chloride.

Technique No. III. Fresh material was fixed for twenty-four hours in 95% alcohol or in ammoniated alcohol. The brains were then rinsed and placed in 1½% silver nitrate at 37°C for two to four days. They were then placed in a 1½ % silver nitrate precipitated with caustic soda and redissolved in ammonia as in technique No. I. Tone in gold chloride as in Technique No. I. This method stains the cells of the nuclei better than the method in technique No. I.

Technique No. IV. (Weigert). Formalin hardened brains were used. Dehydrate, imbed, section, mount. The sections on the slide were then placed in 3 % copper bichromate for two to four hours. They were then thoroughly washed and placed for 6-12 hours in saturated solution of copper acetate, washed in running water and stained in haematoxylin for 15-30 minutes and decolorised in borax-ferrocyanide.

HISTORICAL REVIEW.

Marchi, 1891.

Marchi was the first investigator to employ a positive stain for the products of degeneration. This method has proved to be one of the most valuable methods in the technique of neurological research. As a result of his experiments he secured degeneration in the cord as a result of lesions in the cerebellum, and considered this evidence of a descending tract from the cerebellum. It has later been proved that this degeneration was probably not caused by the lesion in the cerebellum but was due to injury of the midbrain and medulla.

Russell, 1894.

Russell's researches were undertaken for the purpose of ascertaining the relations of the cerebellum to the rest of the cerebro-spinal axis. For this purpose the lesions were made so as to involve both the cortex and nuclei of the cerebellum. He employed the Marchi method and arrived at the conclusion that no

descending tract exists between the cerebellum and the cord.

Thomas, 1897.

This investigator has probably performed the most exhaustive research on the cerebellum. His conclusions may be stated as follows:

1) Lesions in the cortex of the cerebellum result in no degeneration in the spinal cord.

2) The nucleus dentatus and nucleus fastigii send fibres to the nuclei of the nervus vestibularis.

3) Descending degeneration in the cord is caused by lesions of the nuclei of Deiters and Bechterew.

4) The fibres passing from the cerebellum to the pons are fibres of cells in the lateral lobes of the cerebellum. The middle peduncle is made up largely of ponto-cerebellar fibres, relatively few are cerebello-pontile.

5) The nucleus dentatus and nucleus fastigii are directly connected with the lobes of the cortex

cerebelli.

6) Fibres pass from the cortex cerebelli through the restiform body to the nucleus cuneatus and nucleus lateralis of the medulla.

Alexander Bruce, 1898.

The purpose of Bruce's research was the determination of the termination of the fibres of the direct cerebellar and antero-lateral tracts. To this end he used the cord, medulla and cerebellum of a man in which a sarcomatons tumor had compressed the spinal cord in the cervical region and thus caused ascending degeneration. The material was hardened in Mueller's fluid and then impregnated with Marchi's solution. Dr. Bruce came to the following conclusions:

1) The direct cerebellar tract has its termination chiefly in the lobulus centralis, the lobulus monticuli, and, to some extent in the lobus lingualis of the vermis.

2) The fibres of the ventral cerebellar tract terminate in the lingual lobe of the vermis.

Cajal, 1901.

This author has arrived at the following conclusions as given in his text book:

1) Purkinje cell axones terminate in the nucleus dentatus and the nucleus fastigii.

2) The axones of the cells in the dentate nucleus bifurcate, one limb passing down to the bulb and spinal cord and the other passing through the superior peduncle.

3) Some axones of cells in the nucleus fastigii pass to the spinal cord.

Probst, 1902.

In the work of this author we find a systematic reaearch on the afferent and efferent tracts of the cerebellum. He arrived at the following conclusions in regard to the fibres of the cerebellum:

1) No fibres pass from the cortex of the cerebellum into the spinal cord or the thalamus.

2) All the centrifugal fibres of the cerebellar cortex pass to the dentate nucleus, the nucleus fastigii

and the nucleus of Deiters.

3) Fibres can be traced from the cortex cerebelli to the pontile nucleus.

4) Fibres pass from the cortex through the restiform body to the nucleus of the lateral columns.
Van Gehuchten, 1904.

The observations of this investigator on the cerebellum of rabbits has led him to the conclusion that the brachium conjunctivum is composed of efferent fibers while the afferent fibers enter by way of the corpus restiforme and brachium pontis.
Turner, 1904.

This author employed the methylene blue stain in his research on the brains of rats. He has described the nets of Golgi found in the nuclei and other parts of the brain and cord. He describes the relations of these as follows, "These are shown very distinctly closely investing the bodies and dendrites of the cells of the dentate nucleus of the cerebellum and most of the nuclei within the pons, especially

those of Deiters' nucleus, and the fore horn cells of the cord; they appear less distinctly shown around the pyramidal cells of the cerebrum, the cells of the corpus quadrigeminum and the Purkinje cells. They consist essentially of a close fitting trellis structure, something similar in appearance to a piece of perforated zinc, the apertures are usually polygonal and often contain a dark dot in the centre; the trabeculae are slender."

Clark and Horsley, 1905.

These investigators have recently published the results of an extensive series of experiments on cats and dogs. In some of these experiments the lesion was limited to a definite lobe of the cortex with the view of ascertaining the course of the fibres originating there. In other experiments the lesion involved the nuclei as well as the cortex. Their results are stated as follows:

1) "No fibres issuing from the cortex cerebelli enter any of the peduncles."

2) "All fibres leaving the cerebellum by way of the peduncles have origin in one or other of the cerebellar nuclei."

GROSS ANATOMY.

The nomenclature of the mammalian cerebellum is at the present time under revision. Any nomenclature, therefore, must be considered as temporary, and provisional until the homologies become exactly fixed. There are certain terms in common use in descriptive anatomy of the cerebellum which are convenient. Thus, the cerebellum both for developmental and anatomical reasons, has been divided into a median lobe or vermis and the two hemispheres or lateral lobes lying one on each side of the vermis. Between each lateral lobe and the vermis there is a distinct sulcus, the sulcus paramedianus.

For the further subdivision of the cerebellum the developmental history is the best guide. This has been studied by Stroug (1895), G. Elliott Smith (1902, 1903, 1903 a, 1903 b), Bolk (1905, 1905 a)

and Bradley (1903, 1904, 1904 a). These results agree with the phylogenetic history (Johnston, 1906) and have been adopted by Clarke and Horsley and others.

The vermis according to the plan of these authors is divided into three lobes, lobus anterior, lobus medius, lobus posterior. The fissure between the anterior and middle lobe is termed the fissura prima. This is a deep almost vertical fissure forming the posterior boundary of the lobus anterior and the anterior boundary of the lobus medius (Fig. 1.)

The delimiting sulcus of the lobus medius and lobus posterior is the fissura secunda. This is, next to the fissura prima, the deepest fissure of the cerebellum of the rat. It marks the anterior boundary of the lobus posticus and the posterior boundary of the lobus medius.

The lobus anterior is subdivided into the lingula, lobulus centralis, the pars praeculminata and the pars culminis. In the rat the lingula is composed of a single folium. The pars praeculminis

is made up of from one to three folia, while the pars culminis consists generally of two folia.

The lobus medius is divided into four parts lying between the fissura prima and the fissura secunda. The part lying between the fissura supra-pyramidalis and the fissura prima is composed of three lobes. The first is a V-shaped lobe situated behind the anterior lobe and forms the posterior margin of the fissura prima. It also extends lateralward forming the anterior part of the lateral lobes. In the rat it is usually a single folium while in the rabbit and cat it is composed of two folia. The second lobe is composed of one or two folia which spread out laterad into several folia which form the supero-anterior part of the lateral lobe.

The third lobule is composed of two folia. These extend laterad forming the external boundary of the paramedian fissure. The fourth lobule is the pyramid and in the rat is composed of one or two folia.

The posterior lobe is the smallest of the three

primary divisions. It is made up of two parts, namely the nodulus and the uvula. This lobe is separated from the lobus medius by the fissura secunda. The nodulus is composed of one folium and the uvula of two. The posterior of these lies in contact with the obex in the recent condition.

The lateral lobes or hemispheres are composed of several folia arranged in three tiers. But on the anterior and posterior surfaces the superior and middle tiers blend, thus forming in these parts only two tiers. The inferior tier is extended laterad to form the flocculus. The paraflocculus is continuous with the other two tiers.

These terms then may be used in mapping out the areas of the cerebellar cortex.

NUCLEI CEREBELLI.

a. Nucleus dentatus.

The nucleus dentatus is the largest of the central gray nuclei of the cerebellum. The characteristic form in man which gives it its name is not noticeable

in the mouse and rat. Taking first the main mass of gray matter, its outlines are quite irregular and ill defined. This is partly due to the fact that there is a continuity between the cells of the dentate nucleus and the nucleus cochlearis, nucleus vestibuli, nucleus fastigii and the gray matter surrounding the brachium conjunctivum.

The shape and size of the dentate nucleus can only be appreciated by a study of sections in transverse, sagittal and frontal series. Figs. 12 and 13 show the dentate nucleus in transverse, Figs. 3, 4, 6 and 7 show it in sagittal, and Figs. 8, 9, 10, and 11 in frontal sections.

The lateral cochlear nucleus (tuberculum acusticum) is in direct continuity with the dentate nucleus by a group of giant cells and middle sized cells lying in the gray matter of the corpus restiforme. Fig. 12 is a transverse section of a rat's brain and shows the group of cells connecting the dentate and cochlear nuclei. Fig. 7 shows the same relation

in sagittal sections.

Two sets of fibres connecting the vestibular area or nucleus of Deiters with the cerebellum have been described by Cajal, Koelliker and others. One of these tracts passing by way of the corpus restiforme to the nucleus fastigii and dentate nucleus is shown in Fig. 3. This is a large band of medullated fibres which are so obvious in transverse sections that it was observed and described as early as 1891 by Held. Ramon y Cajal (1904) and indeed the majority of investigators believe that these fibres have origin in the nucleus fastigii and terminate in the nucleus of Deiters of the same and of the opposite side. Von Koelliker (1896) however, has demonstrated by means of Golgi's method that some of these fibres represent axones of cells in Deiters nucleus. Other investigators have found degeneration in this tract after section of the eighth nerve. The researches thus far brought forward in regard to this tract seem to warrant the following conclusions:

1) Fibres from cells located in the nucleus fastigii pass to the nucleus of Deiters.

2) Secondary vestibular fibres pass from the nucleus of Deiters to the nucleus fastigii.

3) Primary vestibular fibres terminate in the nucleus fastigii.

Whether the nucleus of Deiters receives fibres from the cortex of the superior vermis directly is not definitely known. Clarke and Horsley (1905) found no degeneration to Deiters nucleus when the lesion was restricted to the cortex. This point, however, must be settled by further research with Marchi's method.

The second tract from the nucleus of Deiters passes by way of the brachium conjunctivum to the cerebellum. In Fig. 7 the superior vestibular nucleus lies adjacent to the distal part of the superior peduncle. Its relation is shown clearly. Here also there is continuity of the cells of the two nuclei. Fibres can be traced from one nucleus to the other.

Another bundle of fibres passes round the ventral margin of the dentate nucleus to the superior vermis. Whether these terminate in the nucleus fastigii or in the cortex is not definitely known. The difficulty in ascertaining the exact termination of these fibres lies in the fact that Marchi's method can be applied only with great difficulty since a lesion in the vestibular area is likely to involve other fibres than vestibular.

The types of cells found in the dentate nucleus conform with those already described by Cajal (1901). There is a striking resemblance between the type of cells in the dentate nucleus and the cells of Purkinje of the cortex. Their size, shape and staining properties are the same, and it would seem reasonable to suppose that they are alike also in function and origin. This however further research must establish.

It is interesting to note that in the lower mammals the dentate nucleus is not so completely enclosed in a capsule of fibres as it is in man.

Instead, fibres enter and leave the nucleus on any of its surfaces. Indeed in the mouse and rat scattered cells may be found in all the tracts which leave the nucleus. These scattered neurones may sometimes be found in the white layer of the folia of the cortex. Scattered neurones also connect the dentate nucleus with the other nuclei of the cerebellum and the cochlear and vestibular nuclei. (Figs. 6, 7, 9, 10, 11 and 13.)

In Fig. 13 a group of cells is shown lying in the lateral apex of the dentate nucleus nearest the flocculus. This group of cells constitutes a characteristic feature of that part of the dentate nucleus. The cells are crowded together in a dense mass, both the pyramidal and giant cells taking part in its formation. The axones of these cells can be traced into the flocculus and paraflocculus. This establishes a tract from the dentate nucleus to the flocculus. This tract is distinct from the tract

between the flocculus and the nucleus fastigii. This tract is made up of both corticipital and corticifugal fibres. The connections of the dentate nucleus with other parts of the cortex will be explained in connection with the cortex.

b. Nucleus fastigii.

In the rat this nucleus lies at a higher level and closer to the median plane than the dentate nucleus. In transverse sections it may vary in size and form, but in most cases examined, it is somewhat triangular. Like the other nuclei of the cerebellum it contains giant cells. The axones of these may be traced into the nucleus dentatus and into the gray matter between the nucleus fastigii and the nucleus dentatus.

The connections of this nucleus are more extensive than those of the other cerebellar nuclei. The axones of the cells of Purkinje can be traced into it from all lobes of the vermis, and nearly all folia of the lateral lobes. One of the most conspicuous tracts in oblique transverse sections is that connecting it with the flocculus. This tract may appropriately be

called the flocculo-fastigial tract. The fibres of this tract pass from the flocculus along the ventral border of the dentate nucleus and curving around its medial end pass backward into the nucleus fastigii. (c. Fig. 13).

Some of the fibres instead of passing along the ventral margin may turn backward along the convex posterior surface of the nucleus dentatus and thus reach the nucleus fastigii (Fig. 13). This connection between the roof nuclei and the flocculus and paraflocculus agrees with the findings of Stroud and G. Elliott Smith as to the development of the flocculus and paraflocculus. "The flocculus arises from the caudo-lateral part of the roof, between the paraflocculus and kilos." "The supra flocculus is connected with the post pileum by substantial nervous tissue."--(Stroud, 1895).

"At an early stage in its developmental history two fissures (floccular and paraflocculer) cut into the lateral margin of the cerebellum and mark off a

small caudal (ventral) appendage, which Stroud has called paraflocculus."--(G. Elliott Smith, 1903).

Another important connection of the nucleus fastigii is with the nuclei pontis. The fibres originating in the nucleus fastigii pass by way of the brachium pontis to the nucleus pontis of the same and opposite side. Those originating in the nuclei pontis across the median plane and taking the same course as the fastigio-pontile fibres terminate in the nucleus fastigii. Other fibres originating in the nuclei pontis terminate in the cortex of the lateral hemispheres. That these connections exist is established by the researches of Ramon y Cajal (1901), Thomas (1897) and Clarke and Horsley (1905).

The connection of the nuclei fastigii with the vestibular nuclei has been clearly established by the investigations of Held (1891), Russell (1897) and Ramon y Cajal (1901).

c. Nuclei emboliformis and globosus.

I have thus far been unable to identify these as independent nuclei in the brains studied.

CORTEX CEREBELLI.

The structure of the cerebellar cortex has been worked out by Cajal (1901), Koelliker (1896), and others. "Throughout the whole cerebellum except the anterior lobe it consists of the following layers from without inward. 1. Molecular layer, consisting of (a) cells, (b) non-myelinated fibres derived from the granule cells, and (c) the dendrites of Purkinje cells. 2. Layer of Purkinje cell-bodies. 3. Granular layer consisting chiefly of granule cells. 4. Layer of myelinated fibres. This layer is very voluminous and its subdivisions to the various lobes gives rise to the well known arbor vitae. In the region of the anterior lobe the structure is the same as elsewhere except that the fourth or fibre layer is largely occupied by a number of gray masses or nuclei." (Johnston, 1906).

The details of structure in the cortex of the rat are will brought out by the Cajal and Bielschowsky methods. A full study of the minute structure has

not been attempted but the Purkinje cells, the baskets of fibres around their cell bodies and the blimbing fibers related to their dendrites are represented in Figs. 7 and 14.

The Arcuate System in the Cerebellum.

When we bear in mind that the structure of the cerebellar cortex is uniform throughout, the importance of the arcuate system in the cerebellum is obvious. It is composed largely of fine fibres which stain best in a weak solution of silver nitrate. These fibres can be best seen in transverse and sagittal sections. Compare Figs. 7 and 13.

In the vermis the system is the most elaborate, and in this the pars suprapyr amidalis, pars culminis and pars praeculminata are brought into an intimate relation with each other and with other parts of the cerebellum. Here large bundles of arcuate fibres pass in an antero-posterior direction. Fibres originating in the pars suprapyramidalis pass backward to the pyramid and uvula and possibly a few fibres pass to

the nodulus. In a forward direction they pass to the pars culminis and pars praeculminis. Comparatively few fibres seem to pass to the lateral lobes. In general it may be stated that for any one lobe or folium of the cerebellum the number of arcuate fibres pass lateralward to the folia in the following order: most of the fibers terminate in the adjacent folium; the remainder terminate in the second and third folia, relatively few extending as far as the third.

The connections and relations of the cortex to the nuclei of the cerebellum is probably not as complicated as has generally been thought. Two main methods have been used in determining this connection. By the first method the tissue is stained directly as by Golgi's or Weigert's method. The fibre bundles are then traced and their course ascertained. By the second method a lesion is made in the region to be investigated and if the animal lives for two or three weeks degeneration has occured in the fibres severed from their cell bodies. This tissue may then be stained

with Busch's osmic acid and iodate of sodium mixture after previous hardening in formalin. By these methods definite tracts of fibres can be mapped out between the folia and the dentate and fastigial nuclei.

These tracts are fairly constant in the rat and mouse. So far as the folia in the rat and mouse can be compared, the connections of a given folium with one or both of the deep nuclei are the same in the two species. Further, in the case of the dentate nucleus the fibers of certain folia are found to be connected with definite groups of cells.

In general it may be stated that any one folium is in relation with one or both of the nuclei on the same side. In the vermis, however, some fibres may cross through the superior commissure of the cerebellum and enter a nucleus of the opposite side. The fibres on reaching the nucleus may enter it directly, or curving around it may enter on any of its surfaces.

Our conclusions in regard to the details of the

connections of the folia and lobes can probably be best given in the form of a table.

Cortico-fastigial fibers:

- flocculus
- pyramid
- uvula
- pars suprapyramidalis
- pars culminis
- area lunata
- area postpteroidea

Cortico-dentate fibers:

- pars suprapyramidalis
- pars culminis
- pars praeculminata
- pars parapyramidalis

Nucleo-cortical fibres from Nucleus dentatus to

- pyramis
- pars suprapyramidalis
- pars culminis
- pars praeculminata

pars parapyramidalis

flocculus

parafloccculus

CORPUS RESTIFORME.

The restiform bodies occupy the same position and bear the same relations to the medulla and cerebellum that has been assigned to them in other mammals. The restiform bodies enter the cerebellum between the middle peduncle externally and the superior peduncle internally. Compare Figs. 3, 4 and 7.

A large portion of the fibres of the restiform body, upon entering the cerebellum, curve around the anterior border of the dentate nucleus and thus reach their ultimate destination. Fig. 3.

The fibres of the dorsal cerebellar tract constitute a conspicuous bundle in the restiform body. In the medulla this tract occupies the position usually assigned to it. Upon entering the restiform body it occupies its central core. After it has entered the cerebellum, it ascends close to the

external convex margin of the superior cerebellar peduncle close to the plane where it emerges from the hilus of the dentate nucleus. Externally it lies in close relation to the middle peduncle. When it again turns backward around the anterior margin of the dentate nucleus some of its fibres become associated with fibres of the lower part of the middle peduncle. Here the fibres begin to separate and turning inward toward the vermis reach their final destination. From behind forwards the fibres end in the following lobes of the vermis, lobus centralis (pars suprapyramidalis) pars culminis, and pars praeculminis and to a slight extent in the lingula (Fig. 3 and 4). According to Bruce (1898) the majority of the fibres end on the same side, but some can be traced through the commissure of Stilling to end in the cortex of the corresponding lobes of the opposite side. Other fibers of this tract terminate in the nucleus fastigii.

Fibres from the nucleus cochlearis and nucleus vestibuli and superior olive join this bundle of

fibres, and taking the same course terminate in the nuclei of the cerebellum.

In transverse and sagittal sections it appears as though fibers emanated from the nucleus of the fifth and joining this bundle pass to the cerebellum. But on this various observers do not agree. The majority of neurologists believe that this bundle originates from the nucleus of the fifth nerve. Those opposed to this view have the authoritative support of Bechterew (1887) and Turner (1895). These authors believe that this bundle comes from Deiter's and Bechterew's nuclei. Obersteiner (1896) believes that there is a direct relation of the nervus trigeminus with the cerebellum.

The remaining systems of fibres composing the corpus restiforme are:

1) Fibres from the nucleus funiculi cuneatus which terminate in the nucleus fastigii of both sides and in the inferior vermis.

2) Fibres from the nucleus gracilis occupying the medio-ventral part of the corpus restiforme and following the same course as the dorsal cerebellar

tract finally terminate in the nucleus dentatus and the superior vermis.

3) Fibres from the nucleus olivaris inferior pass to the cerebellum.

BRACHIUM PONTIS.

The extensive researches of Thomas (1897) on the present subject seem to indicate that fibres pass from the lateral hemisphere to the pons. He considers the fibres composing the brachium pontis to be mainly ponto-cerebellar and that relatively few are cerebello-pontile. Clarke and Horsley (1905) did not secure degeneration in the brachium pontis from lesions in the cerebellar cortex. But when the nucleus fastigii was involved in the lesion degeneration occured.

These authors conclude that no fibers pass from the cortex cerebelli into the brachium pontis, but that fibers of the nuclei fastigii pass to the pons.

Our present knowledge of this subject does not warrant a definite conclusion in regard to the course of all these fibres. It seems probable, however,

that both efferent and afferent fibres connect the nucleus fastigii with the pons, and that incoming fibres terminate in the lateral hemispheres of the cerebellum.

BRACHIUM CONJUNCTIVUM.

The fibres composing the brachium conjunctivum have for some time been an object of dispute among neurologists. Ramon y Cajal (1901) by the application of Golgi's method, finds that certain fibres of the brachium conjunctivum in the mouse arise in the dentate nucleus. He has suggested also that fibres of Purkinje cells may pass directly into the brachium conjunctivum. Clarke and Horsley (1905) find no degeneration in the brachium conjunctivum when the lesion is restricted to the cortex and from this conclude that no fibres pass from the cerebellar cortex to the brachium conjunctivum. Van Gehuchten's recent researches on the cerebellum have led to the conclusion that the brachium conjunctivum is made up largely if not entirely of out-going fibres arising in the dentate nucleus.

Most investigators have found many fibres ending

in the nucleus ruber while others bend around the nucleus thus forming a capsule for it and ultimately reach the optic thalamus into which they enter. Some of these fibres end in the thalamus while others pass through it and entering the posterior limb of the internal capsule pass to the Rolandic area (Ferier and Turner). Some authors state that the brachium conjunctivum also contains afferent fibres.

From our studies of the cerebellum of the mouse and rat we believe the following fibres can be demonstrated:

1) Fibres from the vestibular nucleus terminating in the nucleus fastigii. These arise from the most anterior portion of the vestibular center and pass upward and backward along the inner surface of the brachium conjunctivum.

2) Efferent fibres arising in the nucleus dentatus. These constitute the bulk of the brachium conjunctivum proper.

3) Fibres from the nucleus fastigii to the gray matter surrounding the superior cerebellar peduncles.

This tract may appropriately be called the fastigio-brachial tract (Clarke and Horsley, 1905)

4) Fibres from the cortex of the cerebellum to the gray matter around the peduncles. This tract may be called the cortico-brachial tract (Fig. 5).

Lying on the outer side of the superior cerebellar peduncle is the ventral spino-cerebellar tract. This turns inwards round its dorsal surface and entering the anterior medullary velum passes to the lingula of the vermis.

Course of Impulses to and from the Cerebellum.

1. The course of impulses to and from the cerebellum may be grouped into five systems, (1) the spino-cerebellar and cerebello-spinal system, (2) the arcuate system, (3) the olivo-cerebellar system, (4) the vestibulo-cerebellar system, and (5) the cerebro-cerebellar and cerebello-cerebral system.

The spino-cerebellar fibres originate in the gray matter of the cord, and, passing by way of the corpus restiforme, terminate in the cortex of the vermis.

An impulse ascending to the cerebellar cortex in this tract can now pass by way of axones of Purkinje cells either to the nucleus fastigii or nucleus dentatus. If it pass to the nucleus fastigii it would here make its second relay with the cells giving rise to the fastigio-vestibular tract (direct sensory tract of Edinger.) Through this it would pass to the nucleus of Deiters and thence descend to the spinal cord by way of the vestibulo-spinal tract (anterior marginal tract of Lowenthal). If the impulse pass from the cortex cerebelli to the nucleus dentatus instead of the nucleus fastigii, it might pass by way of the brachium conjunctivum to the nucleus ruber, thalamus and cortex cerebri.

2. Arcuate system. An impulse originating in the periphery or cord may ascend in the fibres of the fasculus gracilis or fasciculus cuneatus. This would first be interrupted by nerve cells in the gracile and cuneate nuclei. Thence it may pass through the corpus restiforme of the same or opposite side and finally arrive

in the cortex of the vermis or directly in the dentate nucleus by means of collaterals. From the cortex the impulse would pass through cortico-nuclear fibres to the nucleus fastigii or nucleus dentatus. From the nucleus fastigii the course would be through the fastigio-vestibular tract to the nucleus of Deiters and thence by the vestibulo-spinal tract to the cord.

If the impulse pass to the nucleus dentatus it would pass through the brachium conjunctivum to the nucleus ruber, thalamus, and cortex cerebri.

3. Olivo-Cerebellar System. The fibres leaving the inferior olivary body run to the cortex cerebelli forming the olivo-cerebellar tract. From the cortex the impulse may pass to the nucleus dentatus and then to the cortex cerebri by way of the brachium conjunctivum, or instead of passing to the nucleus dentatus it may pass to the nucleus fastigii and thence by the fastigio-vestibular tract to the nucleus fastigii and thence to the cord.

4. Vestibulo-Cerebellar System. An impulse from

the vestibular nerve would be first interrupted in the nucleus vestibuli or nucleus fastigii. From the nucleus vestibuli it may pass to the nucleus fastigii and thence to cortex cerebelli, nucleus dentatus, and through the brachium conjunctivum to the cortex cerebri; or it may descend directly into the cord from the nucleus fastigii.

5. The cerebro-cerebellar and cerebello-cerebral system may begin in the cerebral pallium. An impulse originating here may pass by way of the crus cerebri to the nuclei pontis and thence through the brachium pontis to the lateral lobes of the cerebellum, chiefly to those of the opposite side. Thence to the dentate nucleus and by way of the brachium conjunctivum to the cerebral pallium.

In the foregoing outline I have purposely omitted the extensive system of collaterals which doubtless have an important place in elaborating the connections of the various nuclei and several of the cranial nerves.

The exact seat of vestibular sensations in the cerebrum is not definitely known. In the past much

emphasis has been laid on the fact that the somaesthetic area is directly connected with the nuclei pontis and consequently with the cerebellum. There is now no question but that such an association exists by means of pyramidal collaterals (Cajal and others).

More recently the temporal lobe has been considered as the more probable seat of vestibular sensations and equilibration. Dejerine has now the support of most neurologists in his view that the temporo-pontile bundle originates in the middle third of the temporal lobe and terminates in the pons. If we add to this the opinion of Mills who locates "equilibration" and "orientation" in the second and third gyri of the temporal lobe, it seems probable that this may also be the seat of vestibulo-cerebellar sensations, since it is adjacent to the seat of auditory sensations.

FUNCTIONS OF THE CEREBELLUM.

It is generally agreed that the cerebellum has for its main function some form of control over muscular action. Whether this is the nature of co-ordination

of the action of muscles and groups of muscles or takes the form of sustaining the tone and controlling the rythm and strength of contraction of muscles (Luciani, 1903) is at present in dispute. The anatomical findings, however, make two things clear: (1) that the cerebellum receives sensory impulses chiefly from the organs of touch (skin) and equilibration (vestibular apparatus); and (2) that the cerebellum has connections with the motor centers of nearly the whole extent of the cerebrospinal axis. These facts point to the conclusion that the cerebellum not only is in position to exercise control over the muscles, but that such control is determined chiefly by tactile and equilibrative (vestibular) impulses. To these are added voluntary impulses from the cerebral cortex.

NEW RESULTS.

The following points brought out in the present paper I believe are new or heretofore not well understood:

1) The existence of the cortico-brachial and

fastigio-brachial tracts.

2) The analysis of the fibers connecting the cortex and the deep nuclei into bundles connecting individual folia of the cortex with certain nuclei.

3) The recognition of a continuity of gray matter between the nucleus fastigii and the nucleus dentatus and nucleus vestibuli; and between the nucleus dentatus and the nucleus vestibuli and nucleus cochleae.

Description of Figures.

List of abbreviations used:

A. Fi. -- arcuate fibres.

B. C. -- brachium conjunctivum.

B. P. -- brachium pontis.

C. R. -- corpus restiforme.

C-B.T. -- cortico-brachial tract.

C.D.T. -- cortico dentate tract.

Fl. -- flocculus.

F. P. -- fissura prima.

F. S. -- fissura secunda.

F.Su. -- fissura suprapyramidalis.

L. A. -- lobus anticus.

Li. -- lingula.

L. M. -- lobus medius.

L. P. -- lobus posticus.

N.C., Nu.C. -- nervus cochlearis.

N.V. -- nervus vestibuli.

Nod. -- nodulus.

Nu.D. -- nucleus dentatus.

Nu.F. -- nucleus fastigii.

Nu.N.V.-- nucleus nervi vestibuli.

Pa.S. -- pars suprapyramidalis.

Pa.Cu. -- pars culminis.

Pa.Pra.-- pars praeculminis.

Py. -- pyramid.

R.N.O. -- rodix N.C.

T.S.N.Tr. -- tractus spinalis nervi trigemini.

T.S.V. -- tractus spino-cerebellaris ventralis.

U. -- uvula.

V-F.T. -- vestibulo-flocculor tract.

Fig. 1. Sagittal section through the median part of the cerebellum of a rat. The fissures and lobes are obvious. (X 25).

Fig. 2. A drawing of the dorsal surface of the cerebellum of a rat showing the lobes and fissures.

Fig. 3. Sagittal section of the cerebellum of a mouse showing the corpus restiforme and dentate nucleus. Gower's tract is also seen in this section.

Fig. 4. Sagittal section through the cerebellum of a mouse passing through the brachium pontis in the plane of the root of the nervus octavus. (x 25).

Fig. 5. Sagittal section through the brachium conjunctivum of the brain of a mouse. It shows fibres passing into the dentate nucleus from lobus medius of the cerebellum. The cortico-brachial tract is also shown. The gray matter of the brachium conjunctivum (nucleus pedunculi of some authors) establishes continuity between the dentate nucleus and the vestibular nucleus. (x 25).

Fig. 6. Sagittal section of the cerebellum of a mouse passing through the brachium conjunctivum. (x 25).

Fig. 7. Sagittal section of the cerebellum of a rat. It shows the dentate nucleus and the scattered cells connecting it with the nucleus cochlearis. Fibres can be seen passing from the middle lobe of the cerebellum into the dentate nucleus. The arcuate fibers are also seen. (x 25).

Fig. 8. Frontal section of the cerebellum of a rat passing through the dorsal part of the dentate nucleus.

Fig. 9. Frontal section slightly ventral to that shown in Fig. 8. Nucleus fastigii and nucleus dentatus.

Fig. 10. Frontal section of the cerebellum at the level of the nucleus cochlearis.

Fig. 11. Shows the nucleus fastigii and nucleus dentatus in frontal section.

Fig. 12. Transverse section of the cerebellum of a rat at the level of the seventh nerve. It shows the dentate nucleus and fastigial nucleus. The vestibulo-fastigial tract is also shown.

Fig. 13. This section passes through the flocculus of the cerebellum of a rat. It shows the dentate nucleus and its connection with the flocculus; also the fastigial nucleus and the fastigio-flocculor tract.

Fig. 14. Sagittal section through folium of the cerebellum of a rat. The drawing is slightly diagrammatic. A. is a Purkinje cell surrounded by fibres from a basket cell as well as by climbing fibres. B. is a glia cell. C. is a basket cell. D. is the granular layer. E. is the molecular layer.

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Vita.

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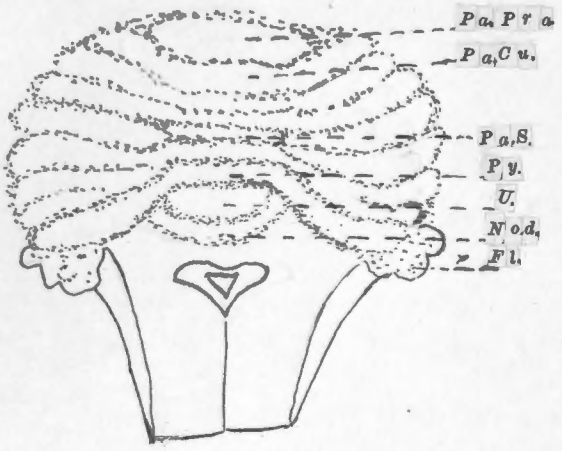
Fig. 1



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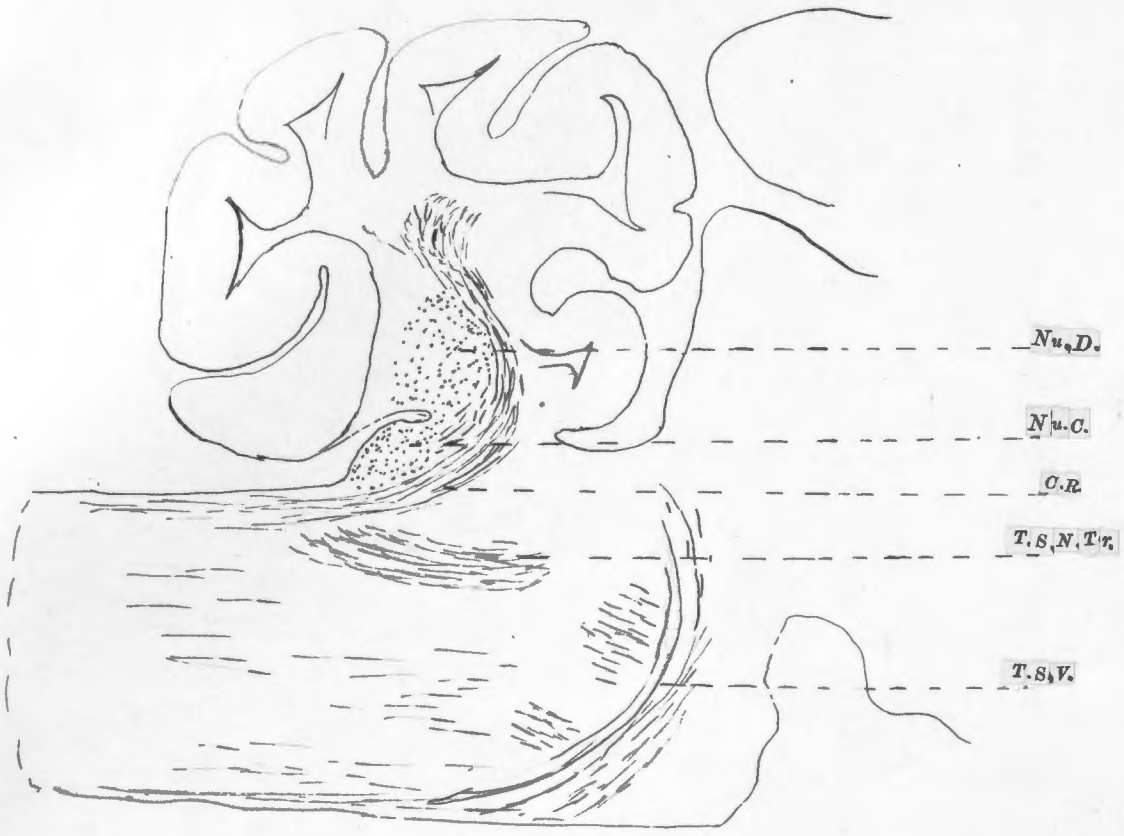

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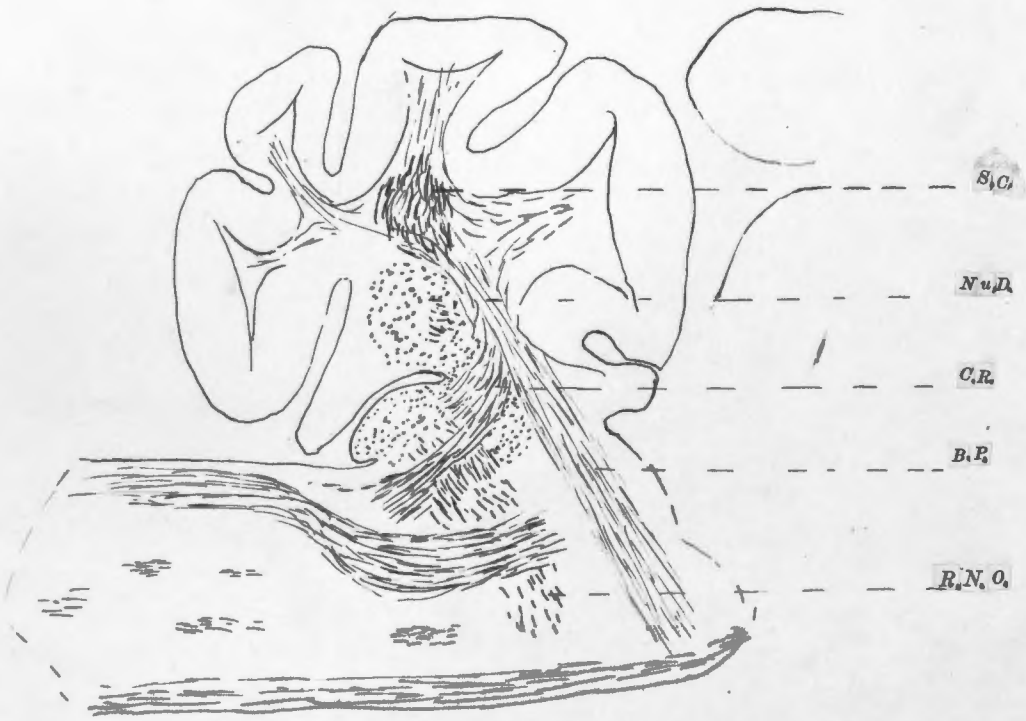

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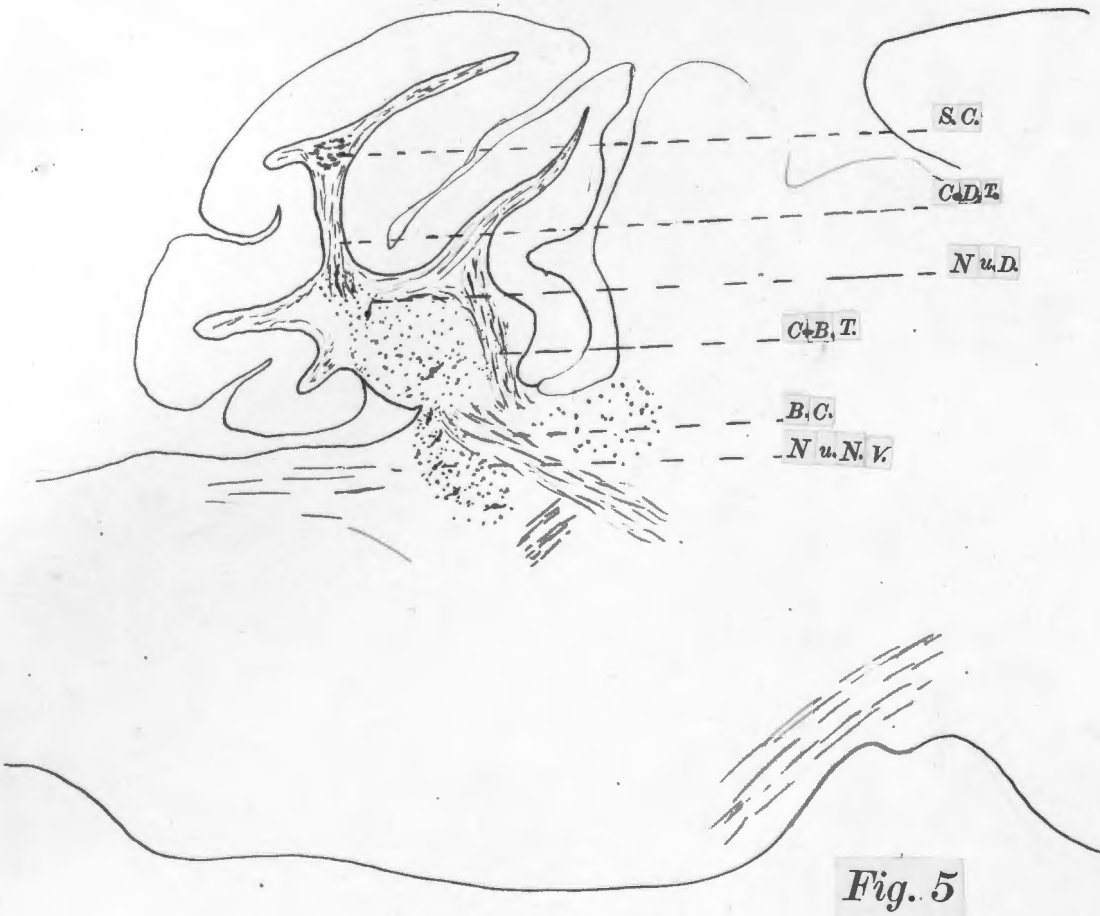

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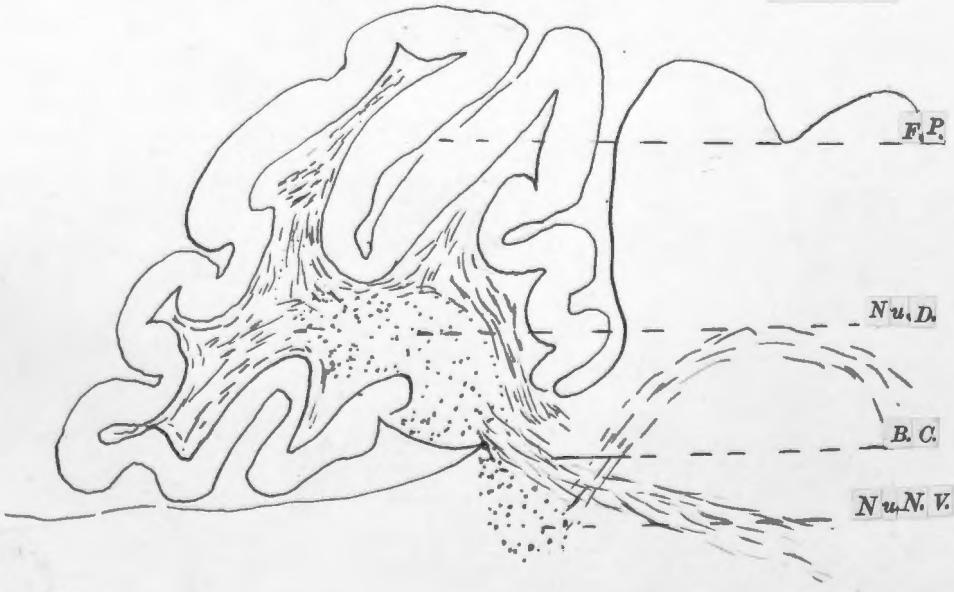

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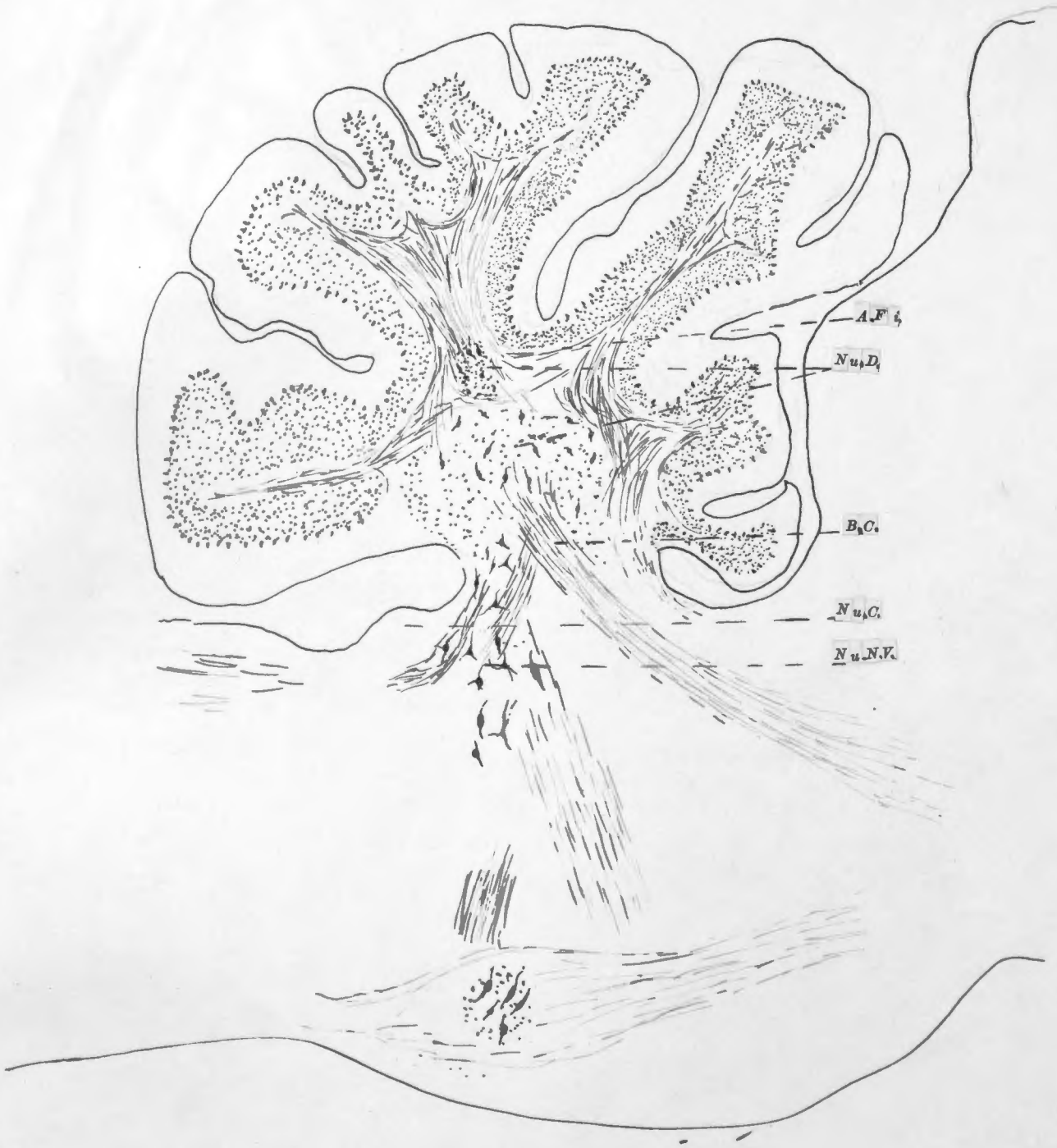

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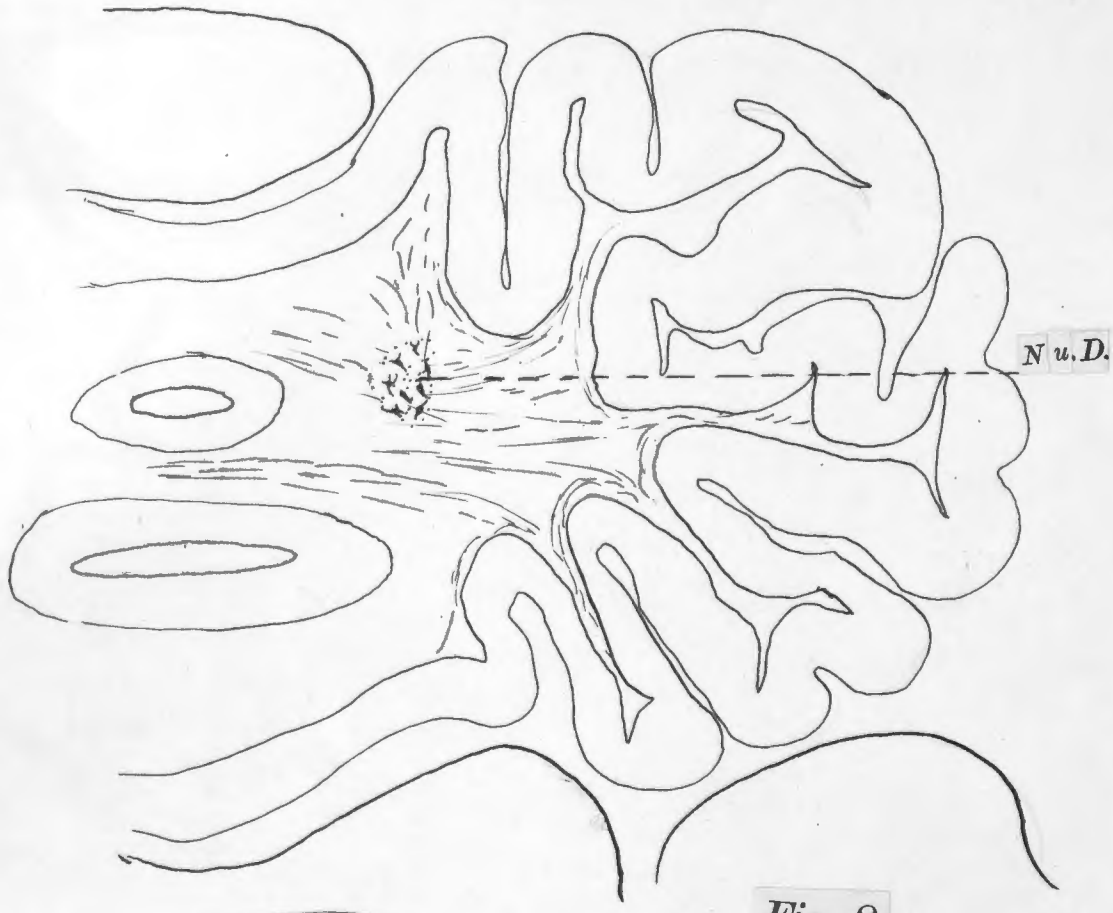

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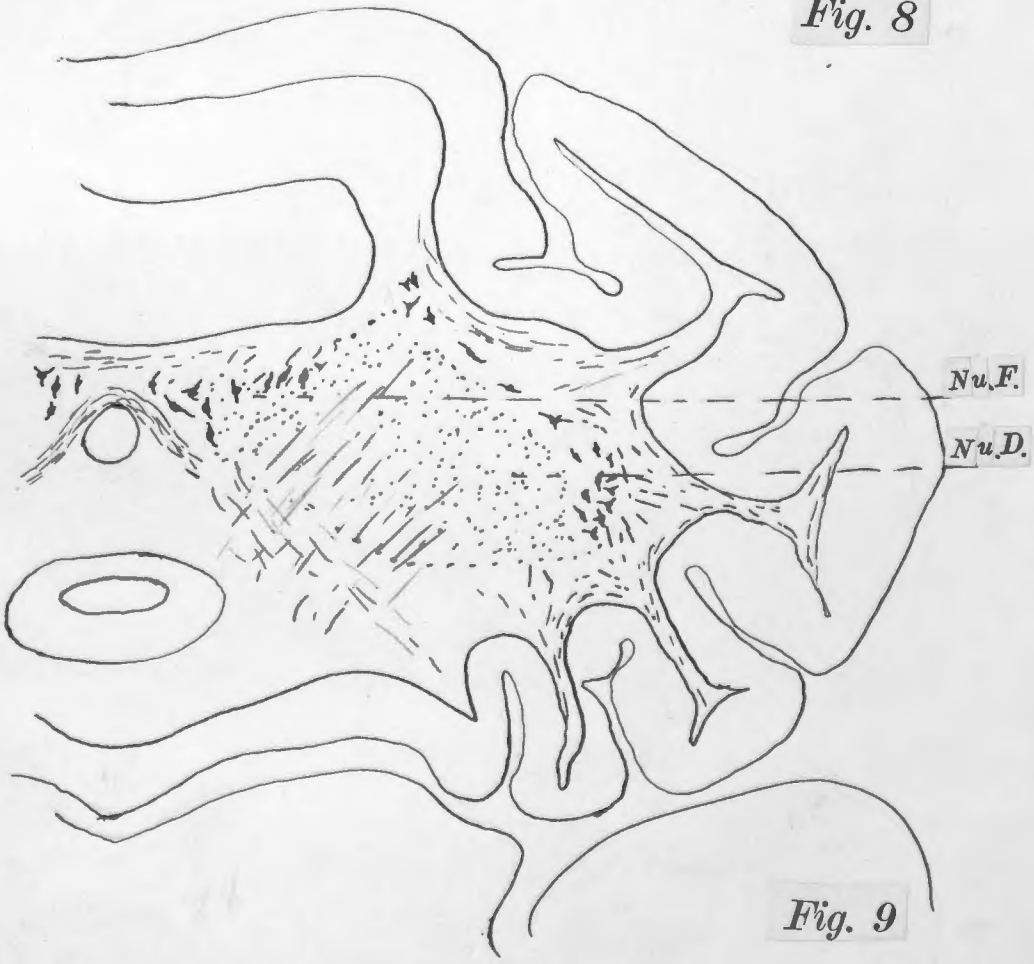

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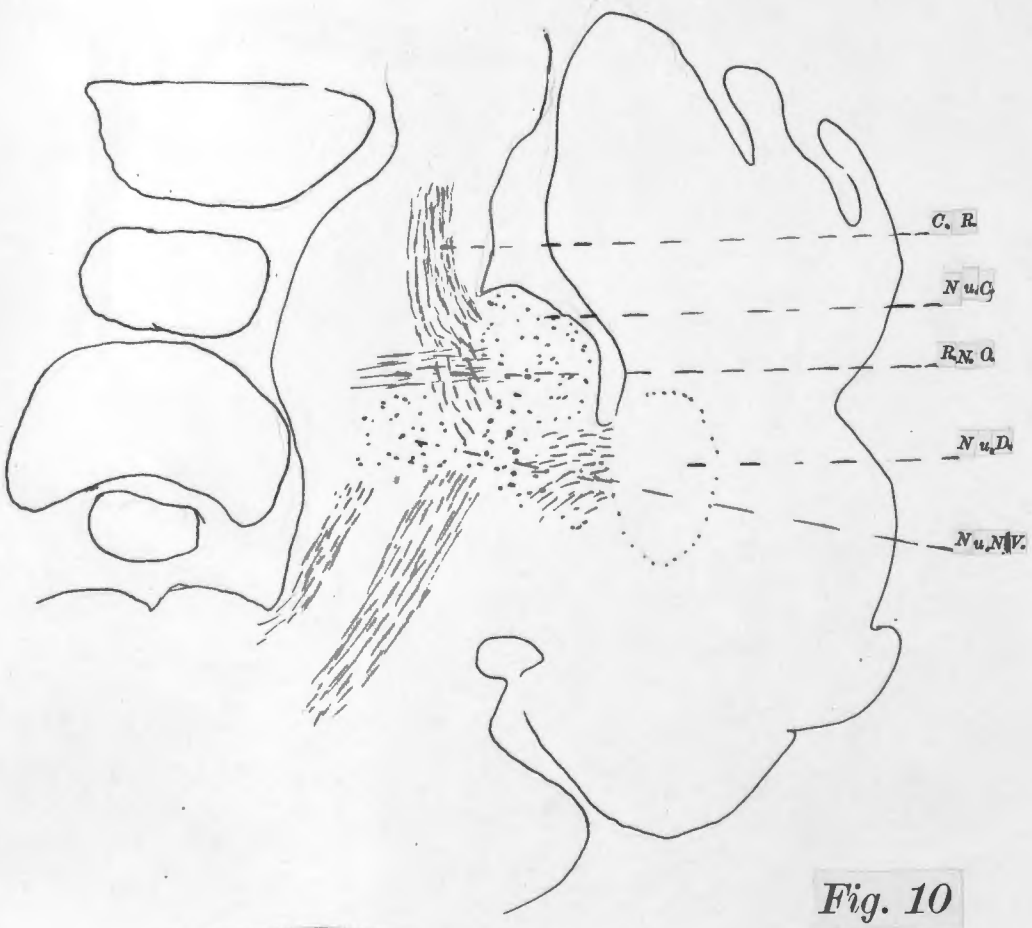

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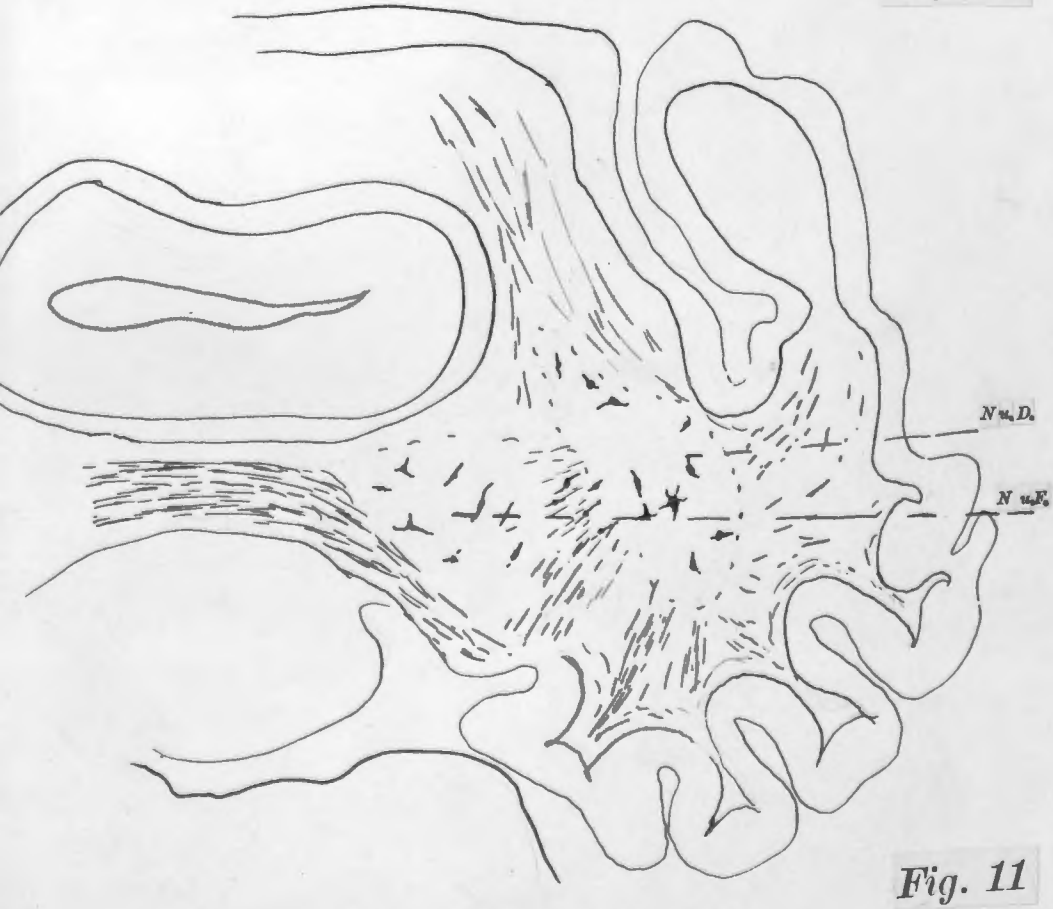

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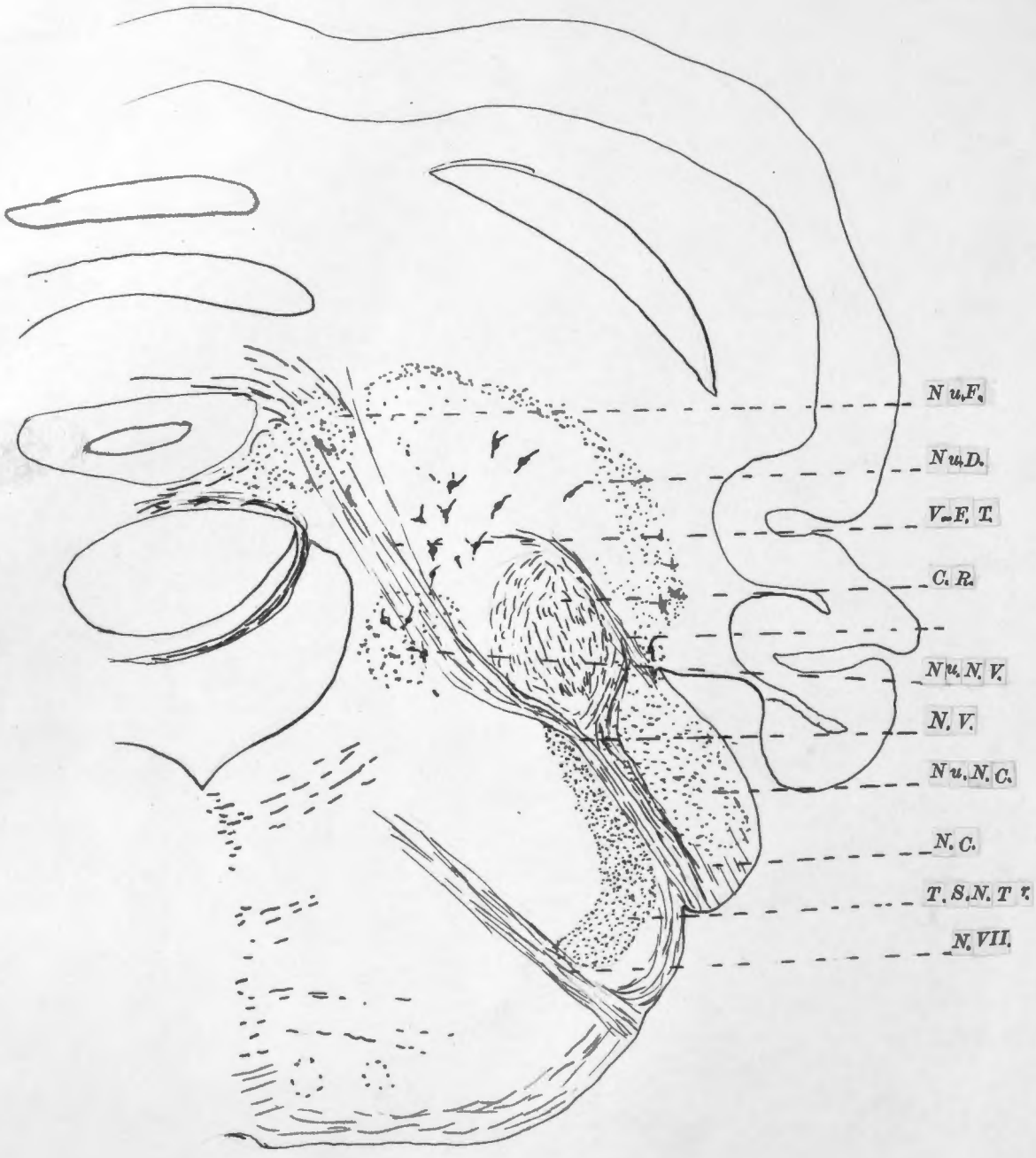

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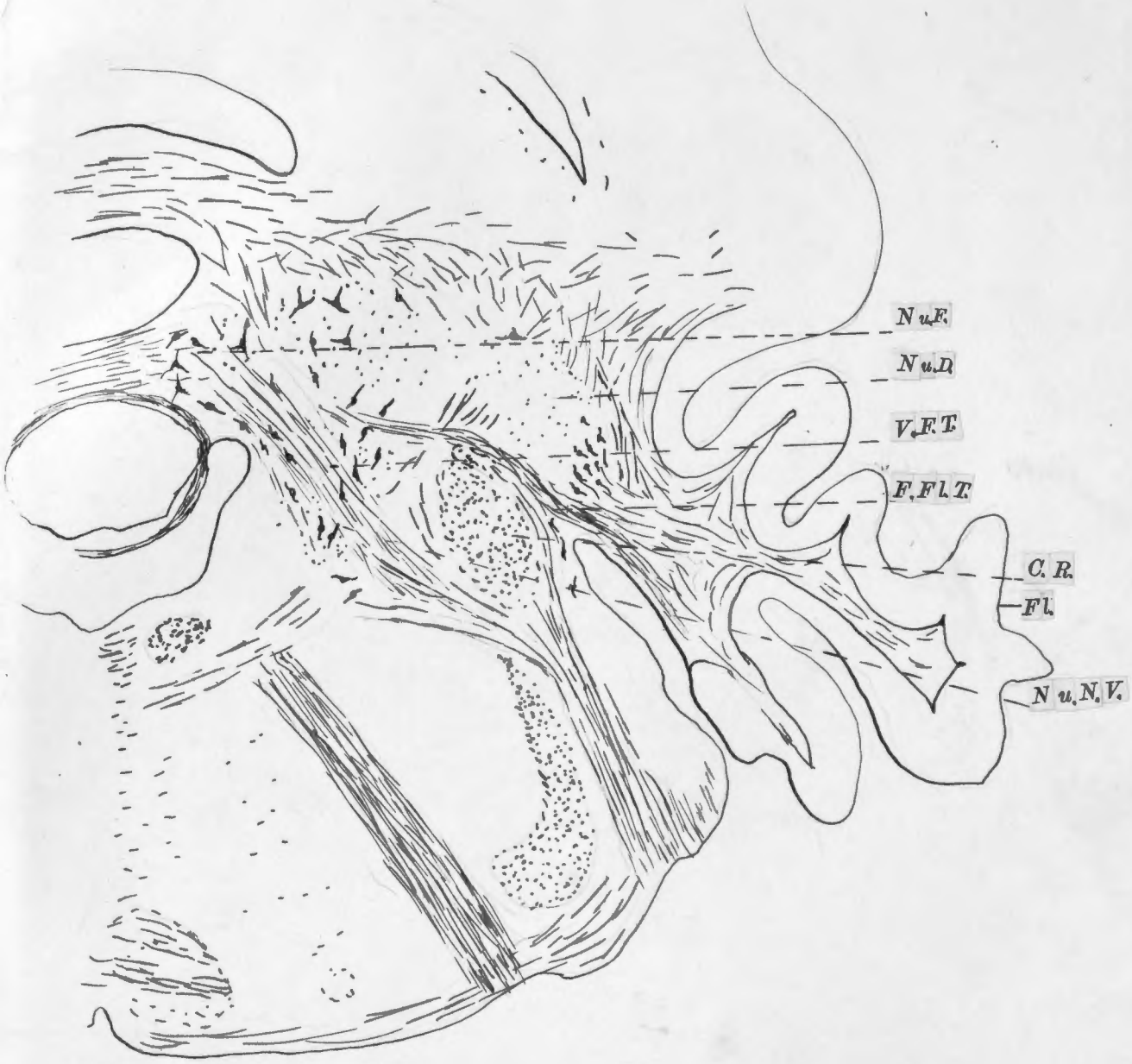

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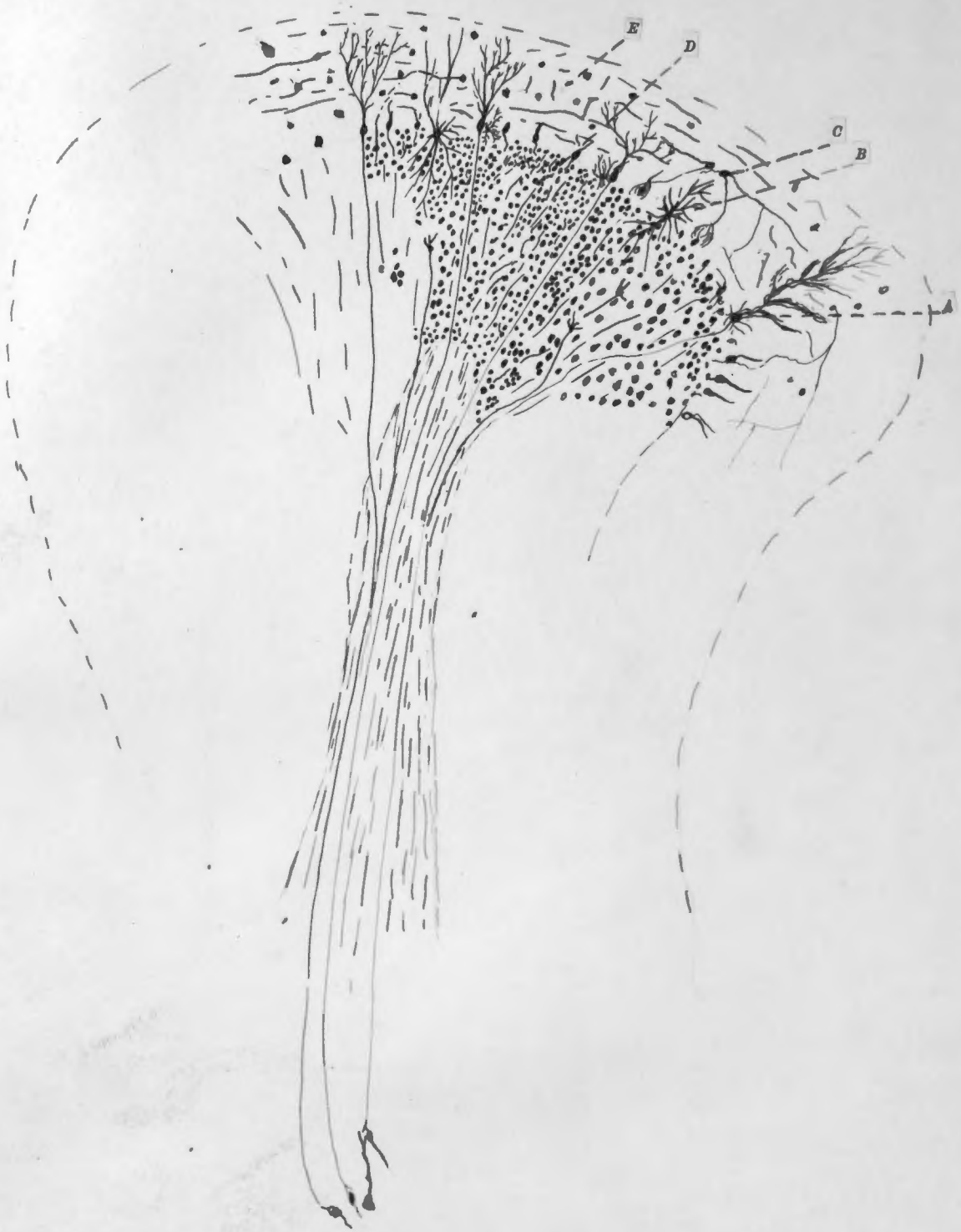

Fig. 14