PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

An Experimental Study of Thalamic Connections in the Rat

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PHILOSOPHICAL TRANSACTIONS.

I. *An Experimental Study of Thalamic Connections in the Rat.*

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[Plates 1–5.]

With the exception of the work of von Monakow (1895), Probst (1900), Wallenberg (1900), Sachs (1909) and Glorieux (1929), experimental observations on the connections of thalamic nuclei are isolated and scattered in the literature of neurology. Recent studies of the structure of the mammalian thalamus, based on the examination of normal material, have led to a much more complete definition of the nuclear components of the thalamus. Hence the time is ripe for a renewed investigation by experimental methods of this important part of the brain. The difficulties of applying to the thalamus the method of study by Marchi degeneration are, obviously, great, because it is not easy to produce isolated lesions of the thalamus without serious injury to adjacent parts of the brain. It is desirable that the experimental material should be examined as extensively as possible in serial sections so that the precise limit of the lesion may be ascertained. From this point of view it is of advantage to use the brain of a small mammal. In selecting the albino rat for experiments, it has been borne in mind that the diencephalon of this laboratory animal has been studied anatomically in considerable detail by Gurdjian (1927), while the cerebral cortex has been submitted to a very complete survey histologically by Fortuyn (1914). The publications of these authors provide a fairly comprehensive anatomical basis for the interpretation of Marchi sections.

Method

Under ether anæsthesia, the skull was opened immediately above the required point on the surface of the brain by a small dental burr. In the case of cortical lesions, a cystotome was introduced through the trephine opening and a small superficial injury produced in the cortex. The positions of the cortical lesions produced in different experiments are shown in fig. 1. Most of the lesions were examined histologically. For purposes of reference, Fortuyn's diagrams have been reproduced alongside my own diagrams in fig. 1 to display the distribution of the areas which can be histologically differentiated in the rat's brain.

In the series of rats designated *Th.* in this record, attempts were made to produce lesions limited to the thalamus of one side without injury to other parts of the

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hemisphere of this side. A fine discission needle was introduced through the cerebral hemisphere of one side at particular points, and carried more or less transversely across the mid-line into the thalamus of the opposite side. In order to produce a lesion in any specific part of the opposite thalamus, reference was made to serial sections through the rat's brain and the point of entry of the needle, the direction of the puncture wound, and the distance through which it was necessary to introduce the needle, were judged accordingly. Obviously, this method admits of no certainty in the production of local intra-thalamic lesions, and the precise site of the latter can only be determined after death by the examination of serial sections.

The animals were killed fourteen to eighteen days after the operation by opening the thorax under ether anæsthesia, inserting a cannula into the aorta, washing through with saline and injecting with formalin solution. The brain was removed after an hour or two, washed over-night in running water, and cut into transverse sections one to two millimetres in thickness. These were transferred to 2 per cent. bichromate and stained by the usual Marchi technique. Paraffin embedding was at first tried, the sections being infiltrated with 40° paraffin wax and embedded in 55° wax. These sections showed a good contrast in the osmic staining, but the difficulties in the way of securing a set of serial sections of uniform excellence were so great that ultimately celloidin embedding was used in every case.

As regards the nomenclature of the thalamic nuclei used here reference should be made to the paper published in 'Brain,' Clark (1932).

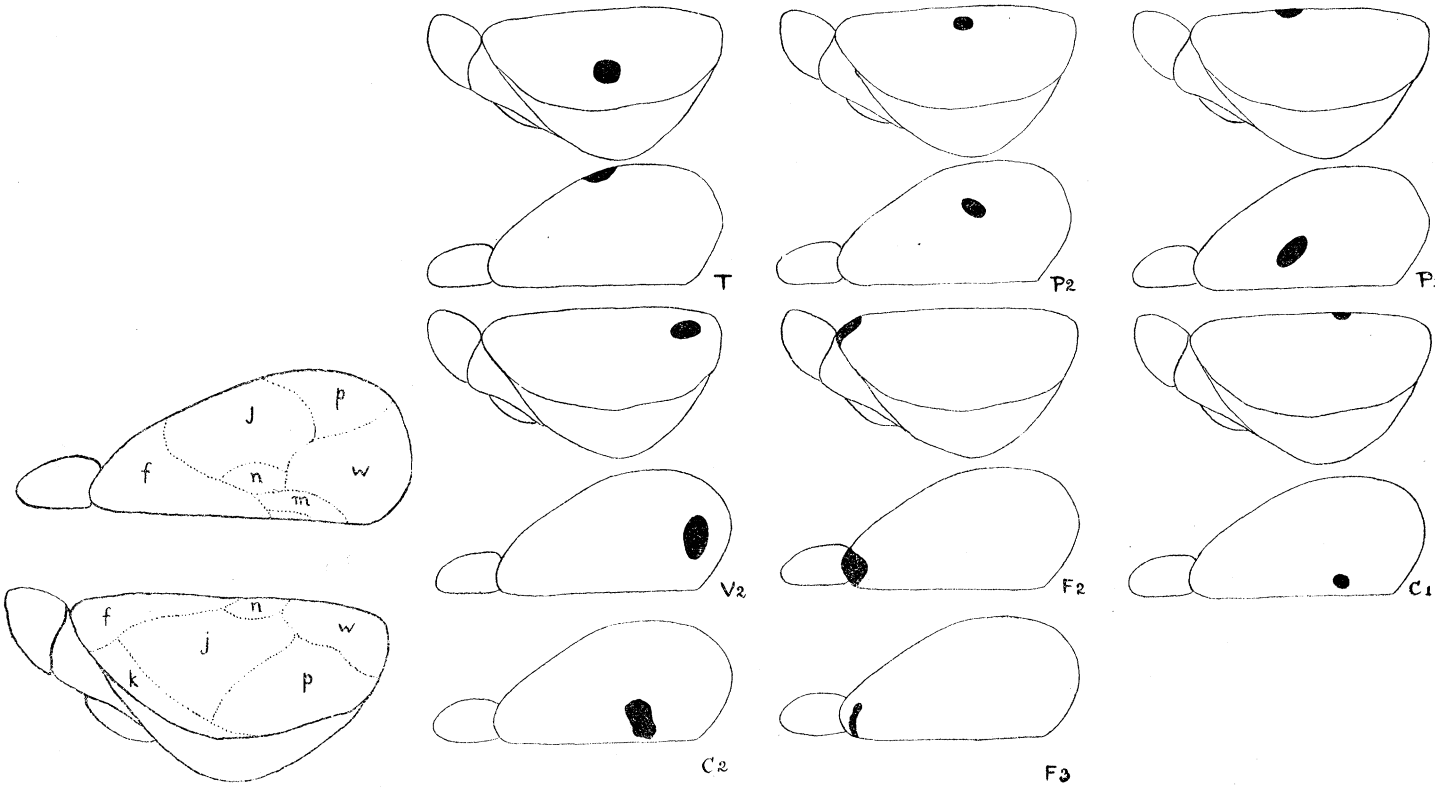

Fig. 1.—Diagrams showing the position of the cortical lesions in the rat's brain × 2.

Details of Experiments

Rat P 1, figs. 1, *P* 1 and 2.—A lesion was made on the dorsal surface of the cortex about mid-way between the frontal and occipital poles. After death the lesion was seen macroscopically to be oval with a long axis of 3 mm., and extending medially to a point a little more than a millimetre from the mid-line, fig. 2, *a*. Here the lesion extends into the corpus callosum and the septum of the same side, involving also the lateral edge of the fornix. At the level of the anterior nucleus, the lesion is 2·3 mm. from the mid-line and just involves the width of the cortex. Thus the anterior part of the lesion involves the fibres running laterally from the anterior cingular areas. Immediately behind the rostral extremity of the lesion there is degeneration in the cingulum. Coarse degeneration is also present in the fasciculi which run down from the cortical lesion and penetrate the dorsal part of the lenticular nucleus to extend into the internal capsule. Slight degeneration is present in the lateral margin of the fornix but none was noted in the stria terminalis, habenular nuclei, or anterior commissure.

More caudally abundant degenerated fibres pass through the putamen into the internal capsule where they divide into two main groups. Fine degenerated fibres run in the superior thalamic radiations by the stratum subcaudatum and extend in a dorso-medial direction to penetrate the antero-ventral nucleus of the thalamus, as is also the case in rats *C* 1 and *C* 2 (*vide infra*). No degenerated fibres could be traced beyond this nucleus in the dorsal part of the thalamus. The main group of degenerated fibres passes further ventrally and caudally, and, in sections immediately caudal to the anterior nuclei, some of them leave the internal capsule and disappear in the lateral portion of the anterior part of the ventral nucleus, fig. 2, *b*. No degeneration was observed in the other thalamic nuclei, nor in the ventral nucleus at or behind the level of the rostral margin of the corpus mammillare.

Degenerated fibres run caudally in the cingulum to the posterior part of the hemisphere where they are last to be seen behind the corpus callosum and alongside the subiculum. In the pes pedunculi degenerated fibres can be followed as far as the pons, occupying its second fifth (from the medial side).

In this experiment the cortical lesion involves the most anterodorsal part of FORTUYN's area *j*, the parietal area. It will be observed that it also involves the fibres running down from the cingular areas. This sub-cortical lesion accounts for the presence of Marchi degeneration in the cortico-thalamic fibres which penetrate into the antero-ventral nucleus and provides evidence confirmatory of the results obtained in the case of rats *C* 1 and *C* 2.

Rat P 2, figs. 1, *P* 2, and 3.—A lesion was made in the parietal region of the cortex just behind the mid-point between frontal and occipital poles. The lesion was 2 mm. in length, its anterior extremity 5·5 mm. from the mid-line, and the posterior extremity 4·5 mm., fig. 1, *P* 1. Histological examination showed that the lesion was confined to the cortex.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Coarsely degenerated fibres run ventrally from the lesion into the internal capsule, many also passing for a short distance in the external capsule before penetrating the dorsal part of the rostral end of the putamen.

At the level of the rostral extremity of the lateral geniculate body and a little caudal to the optic chiasma, many degenerated fibres have penetrated the lateral aspect of the ventral nucleus of the thalamus, fig. 3, *a*. These fasciculi break up in the ventral nucleus and the area of their termination is indicated by the rich deposit of fine osmic granules among the cells of the nucleus. Serial sections show that these cortico-thalamic fibres end in a region corresponding to rather more than the middle-third of the dorso-lateral part of the ventral nucleus. At the level of the caudal end of the ventral nucleus, bundles of fibres with osmic staining leave the posterior part of the internal capsule and skirt the ventral margin of the ventral nucleus, passing in a caudal direction in the ventral medullary lamina. These fasciculi can be traced in continuity round the posterior convex surface of the ventral nucleus and course dorso-medially to terminate in the region of the ventral and caudal part of the pretectal nucleus, fig. 3, *b*.

In the cerebral peduncle the fibres originating from the site of the cortical lesion are spread over approximately the outer half of this structure, except for its most lateral portion. They were traced down as far as the pons.

A comparison with Fortuyn's charts shows that the lesion in this experiment is situated in the posterior part of his area *j*, the parietal area. This region of the cortex appears thus to be connected with ventral nucleus and the pretectal nucleus.

Rat T, figs. 1, *T* and 4.—The lesion, which was made in the temporal region of the brain, was found to extend forward to the level of the anterior commissure and to measure 1·5 mm. in diameter. It was situated 6·3 mm. from the dorsal border of the hemisphere and 2·9 mm. from the rhinal fissure, fig. 4, *a*. At the level of the caudal margin of the optic chiasma it encroaches on the lateral margin of the putamen involving the external capsule at this point. At the level of the anterior part of the lesion degenerated fibres run through the putamen, and osmic granules are present in the globus pallidus. At the level of the anterior thalamic nucleus degeneration is limited to the external capsule, the corpus callosum, and fibres penetrating the lenticular nucleus and the rostral part of the zona incerta. A little more caudally many of the degenerated fibres have passed through the putamen to reach the caudal and lateral part of the internal capsule. More caudally still some of these leave the internal capsule, extending through the reticular nucleus to reach the ventral thalamic nucleus. At the level of the fasciculus retroflexus, the ventral third of the ventral nucleus is rich in black granules marking the termination here of the degenerated cortico-thalamic fibres, fig. 4, *b*. There is no Marchi degeneration elsewhere in the thalamus, in the geniculate bodies, pretectal nucleus or colliculi. Degenerated fibres occupy the second fifth of the pes pedunculi (from the lateral side) and pass down into the pons.

In this experiment, the lesion involves the most caudo-ventral part of Fortuyn's area *j*, which is thus connected with the ventral region of the most caudal part of the ventral nucleus.

Rat V 2, fig. 1, *V* 2.—A lesion was made in the occipital region extending forward 3 mm. from the occipital pole, fig. 1, *V* 2. Serial sections showed that the lesion had extended much deeper than had been intended, so that the injury had also affected the posterior part of the ventral and the lateral thalamic nuclei, the pretectal nucleus, the lateral part of the anterior colliculus, the medial geniculate body and the medial part of the subthalamus and pes pedunculi. The resulting degeneration was too widespread to allow of much differentiation of the individual fibre connections of the injured parts of the brain. It was possible, however, to trace in continuity degenerated fibres from the cortical lesion into the dorsal nucleus of the lateral geniculate body. The cortico-tectal connections were involved by the lesion and were seen extending into the deeper layers of the anterior colliculus. No degeneration was present in the thalamic radiations entering the anterior nucleus nor in the anterior commissure. The mammillo-thalamic tract had been injured slightly on the side of the lesion close to its emergence from the mammillary body. A deposit of osmic granules could be followed up among the fibres of the tract, and some of these degenerated fibres cross over in the commissure which GURDJIAN has called the commissura interantero-dorsalis towards the antero-dorsal nucleus of the opposite side.

Rat C 1, figs. 1, *C* 1, and 5.—A lesion was made close to the caudal extremity of the superior border of the hemisphere and macroscopically was approximately circular, with a diameter of 1 mm., being situated 1 mm. from the superior border and 3 mm. from the caudal extremity of this border, fig. 1, *C* 1. Serial sections showed the centre of the lesion to be 1 mm. from the mid-line at the level of the splenium, fig. 5, *a*. At its maximum extent the lesion encroaches on the subjacent white matter as far as the dorsal surface of the corpus callosum, involving also the lateral border of the cingulum. A comparison with methylene blue sections of the rat's brain at the same level shows that the lesion has involved the lateral part of the cortical area 29 of Brodmann.

At the site of the lesion degenerated fibres are present in the most dorsal part of the corpus callosum and in the lateral part of the middle-third of the pes pedunculi. The latter fibres have passed down through the internal capsule at a more anterior level. At a more rostral level bundles of degenerated fibres run from the position of the cortical lesion through the most dorsal part of the putamen into the anterior part of the interior capsule. From here finely degenerated fibres pass medially below the stria terminalis and then stream dorso-medially towards and into the antero-ventral nucleus. The whole of this nucleus is filled with a fine deposit of osmic granules. No Marchi degeneration can be traced into the antero-dorsal or antero-medial nucleus, fig. 5, *b*. Degeneration was also absent in the other thalamic nuclei.

Well-marked degeneration was present in the cingulum caudal (but not rostral) to the lesion, which could be traced to the caudal pole of the hemisphere alongside the subicular cortex and as far as the caudal extremity of the piriform lobe.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Rat C 2, figs. 1, *C* 2, and 6.—A small superficial lesion was made in the dorsal surface of the cortex close to the mid-line. Macroscopically, it was seen to extend laterally for 3 mm. and to lie about two-thirds of the way back along the dorsal border of the hemisphere, fig. 1, *C* 2. Microscopically the lesion was found to be confined to the cortex, involving the lateral border of the area cingularis and the medial part of the superior parietal cortex. From the lesion, bundles of degenerated fibres run down through the head of the caudate nucleus and the dorsal part of the putamen to reach the stratum subcaudatum, through which a fine Marchi degeneration extends medially up to the antero-ventral nucleus. In the substance of this nucleus, but confined to its caudo-ventral part, there is a fine scattering of osmic granules, which, however, is not so plentiful as in the case of rat *C* 1 (*vide supra*).

Further, caudally, many fasciculi of finely degenerated fibres can be followed into the main part of the lateral nucleus (nucleus lateralis *a*). The anterior end of this nucleus is free of Marchi degeneration but the greater part is filled with a fine deposit which can be traced in continuity with degenerated fibres of the stratum subcaudatum, fig. 6. Coarsely degenerated fibres extend from the site of the injury into the internal capsule to reach the pes pedunculi and pass down into the brain stem.

The cortical lesion in this experiment occupies the position of an area designated by Fortuyn as *m'*. It is not clear from Fortuyn's paper what this area corresponds to in the terminology of other authors. It is situated between the postero-superior part of the general sensory area and the anterior part of the area striata, and thus is topographically equivalent to the parietal association areas which attain to much greater dimensions in higher mammals. This was the only cortical area found in these experiments to be connected with the lateral nucleus (pars principalis) of the thalamus by corticifugal fibres, and the results of intra-thalamic lesions indicate such a fibre connection in the reverse direction (*vide infra*).

Rat F 2, fig. 1, *F* 2.—A cortical lesion was made at the extreme tip of the left frontal pole extending back for a little under 2 mm. The site of this lesion was not examined microscopically.

The most rostral section examined is at the level of the anterior border of the fornix commissure and here there is a rich deposit of osmic granules among the most medially situated fibres of the internal capsule extending as far dorsally as the floor of the lateral ventricle, and ventrally as far as the medial forebrain bundle. Degeneration is also present in the cingulum of the left side. At the level of the rostral part of the anterior nucleus, the degenerated fibres separate into two contiguous bundles. The medial smaller fasciculi are filled with fine Marchi granules and penetrate the thalamus from its antero-lateral aspect, while the lateral bundles, filled with coarse granules, pass into the medial extremity of the cerebral peduncle. There is no degeneration in the anterior nucleus. The course of the degenerated cortico-thalamic fibres was not followed in continuity. At the caudal sections of the first block, they are seen proceeding medially towards the rostral end of the dorso-medial nucleus. The first sections of the next

succeeding block pass through the middle of this nucleus. Here, on the side of the lesion, a deposit of fine granules is present in the lateral part of the " capsule " of the dorso-medial nucleus and of the nucleus itself.

Although these particular sections were not complete, they certainly indicate a cortico-thalamic connection between the frontal pole and the dorso-medial nucleus, and this is corroborated by the much more definite evidence supplied by rat *F* 3 (*vide infra*) as well as by the evidence derived from a study of normal sections.

Rat F 3, figs. 1, *F* 3, and 7.—A superficial lesion was made in the left frontal pole which macroscopical examination showed to extend 2·5 mm. laterally from the mid-line, fig. 1, *F* 3. The lesion was not examined histologically. At the level of the anterior commissure, fig. 7, *a*, the fasciculi of the internal capsule which lie most medially and ventrally alongside the septal region are filled with Marchi granules. The deposit is confined to fibre bundles and is not present in the substance of the striatum through which these are running. A few degenerated fibres are present in the cingulum but none in the anterior commissure, corpus callosum, or cortex at this level. At the level of the anterior nucleus (which is quite clear of Marchi deposit) the degenerated fibres become more compactly collected at the medio-ventral extremity of the internal capsule. In sections passing through the middle of the thalamus, slender fasciculi of degenerated fibres course upwards and inwards from the medial end of the pes pedunculi through the ventral nucleus to reach the medial medullary lamina and can be traced thence into the lateral part of the dorso-medial nucleus, fig. 7, *b*. No degeneration is present in the lateral, ventral, or habenular nuclei.

At the level of the mammillary body, a diffuse bundle of finely degenerated fibres leaves the medial end of the crus cerebri and passes up into the zona incerta which at this level is sprinkled with fine Marchi granules, fig. 7, *c*. No degenerated fibres were traced to the red nucleus.

This experiment demonstrates clearly the corticifugal connection between the frontal pole and the dorso-medial nucleus. Equally distinct are the fibres from the frontal cortex which terminate in the zona incerta of the subthalamus.

Rat Th. 1, fig. 8.—In this experiment the needle was entered behind on the left side through the tectal region towards the caudal part of the thalamus, passing somewhat downwards and to the right and involving the subthalamus and the pes pedunculi of the opposite side. The lesion is thus somewhat extensive, but the results nevertheless yield some useful information. The most caudal section passes through the mid-brain at the level of the superficial origin of the third nerve. Here a minute lesion appears in the ventricular surface of the left hippocampus and degeneration is present in the cingulum ammonale. The neopallium, however, has nowhere been injured by the lesion. A round clot occupies the caudal pole of the left medial geniculate body and from here fasciculi of degenerated fibres run as far as the stratum profundum of the anterior colliculus. Many degenerated fibres are present in the posterior longitudinal bundles, and also in the tecto-spinal tract crossing over the mid-line from the left side. No

degeneration is present in the pes pedunculi of the left side, but it is extensive on the right as the result of the lesion involving the pes at a more rostral level. Degeneration is present in the stratum album medium of both anterior colliculi and to a slight extent in the stratum opticum of the right. A little in front of this level, the lesion extends across from the medial margin of the posterior part of the left medial geniculate body up to the floor of the aqueduct, cutting across the tecto-spinal tracts and tegmental fasciculi, and, at the level of the front part of the anterior colliculus, it extends across the mid-line to the right, reaching the lateral margin of the right pes pedunculi and the caudal margin of the optic tract. The track of the needle passes immediately ventral to the right medial geniculate body and cuts right into the medial lemniscus of this side which is completely severed at the level of the posterior boundary of the thalamus, fig. 8, *a*.

The left medial lemniscus is intact. Degeneration is marked in the right fasciculus retroflexus and the fibres of the posterior commissure. At the level of the caudal end of the lateral geniculate body the lesion on the left side is confined to the left margin of the aqueduct, and on this side scattered degeneration is present in the formatio reticularis, the posterior end of the ventral nucleus, and the medial geniculate body. On the right side the lesion involves the whole of the nucleus parafascicularis and the fasciculus retroflexus, and, passing ventro-laterally below the level of the ventral nucleus, crosses the subthalamic region to reach the pes pedunculi. In sections passing through the middle of the thalamus, there is degeneration in the upper end of the fasciculus retroflexus and in the substance of the habenular ganglion of the right side, which is not present on the left. Fine granules are scattered throughout the medial medullary lamina of both sides (more numerous on the right) and otherwise there is no definite degeneration on the left side of the thalamus at this level. On the right side, the rostral extremity of the lesion is seen, confined here to the zona incerta and the middle-third of the pes pedunculi. The degenerated fillet fibres in the ventral medullary lamina can be traced up into the ventral thalamic nucleus, the whole of which is strewn with osmic granules, fig. 8, *b*. The nucleus medialis ventralis of both sides, as well as the lateral nucleus (main part and pars posterior), is free of degenerated fibres. The degenerated fibres running through the right medial medullary lamina (in the substance of the nucleus paracentralis and nucleus centralis lateralis) appear to distribute ultimately to the dorso-medial part of the ventral nucleus. In the lateral margin of the caudal extremity of the dorso-medial nucleus, close to the upper end of the fasciculus retroflexus, some osmic granules are to be found, but the main part of the dorso-medial nucleus contains no degenerated fibres. It is to be noted that the parafascicular nucleus (which is in fibre relation with the caudal end of the dorso-medial nucleus) has been involved by the lesion on this side, and this is probably the origin of the degenerated fibres found in the margin of the caudal end of the dorso-medial nucleus. The evidence of this experiment suggests that the latter nucleus is not concerned with the reception of any fillet fibres.

Summarising, Marchi degeneration in the thalamus is confined on the left side to the medial medullary lamina and the posterior extremity of the ventral nucleus (probably fibres of tectal origin), and on the right side to the medial medullary lamina, caudal extremity of the dorso-medial nucleus, ventral nucleus, and habenular nucleus. No evidence of degeneration extending into the neopallium was anywhere to be found, in spite of the fact that the caudal pole of the medial geniculate body and the pretectal nucleus of the left side were injured. All the degenerated fibres which result from the lesion involving the whole of the medial lemniscus at the caudo-ventral margin of the thalamus appear to terminate in the ventral nucleus.

Rat Th. 2, fig. 9.—In this experiment, the needle was passed through the left frontal cortex in a direction passing caudally and to the right, and with a slight ventral inclination. The lesion passed through the anterior nucleus of the left side and across the mid-line into the anterior part of the right ventral nucleus, extending as far as the internal capsule which it partially involves. In the anterior part of the thalamus the lesion extends linearly through the ventral margin of the left fimbria, the centre of the antero-ventral nucleus and the stria medullaris of the left side and obliquely downwards into the right habenular nucleus, fig. 9, *a*. A few sections more caudally the lesion passes ventro-laterally on the right side immediately below the anterior nucleus which, on this side, has not been injured. It injures the upper part of the right mammillo-thalamic tract, extends through the dorsal region (but missing the most dorso-lateral part) of the ventral nucleus into the internal capsule, and involves also the most medial margin of the globus pallidus. At this level, on the left side, Marchi degeneration is present in the centrum ovale throughout the dorsal third of the lateral aspect of the hemisphere, and there is conspicuous degeneration among fibres extending down into the internal capsule from the site of the lesion. On the right side, degenerated fibres course through the putamen to the cortex from the lesion involving the ventral nucleus and the internal capsule, but there is no evidence that any of these fibres terminate in the putamen. In the cortex on this side, degeneration is confined to the ventral half of the lateral surface of the hemisphere.

More caudally, the right mammillo-thalamic tract is seen below the point where it has been injured by the lesion, and here contains a deposit of osmic granules. The left tract is free of deposit. On the left side, a fine Marchi deposit is present in the rostral portion of the main part of the lateral nucleus and also throughout the dorso-lateral region of the ventral nucleus—the result of the involvement by the lesion of the corresponding cortico-thalamic fibres in the internal capsule. On the right side, strands of degenerated fibres run from the ventral nucleus (in which, at this plane, the lesion has produced a small cavitation at its lateral border) through the fibres of the internal capsule into the globus pallidus.

At the levels of all the sections which have been followed caudally thus far, the fibres running into the cingular area of the cortex on the left side are filled with osmic granules while, on the right side, there is no degeneration in this area. The degeneration

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

of the left cingular cortex extends back to the caudal part of the cerebral hemisphere, becoming, indeed, rather more conspicuous posteriorly. Thus the whole length of the strip of cortex which abuts on the corpus callosum—the area cingularis—is the recipient of degenerated fibres, fig. 9, *b*. This degeneration cannot be secondary to the small lesion in the left frontal cortex, nor is it likely that it is secondary to the involvement by the lesion of the anterior part of the internal capsule. The presumption is that the fibres originate from the antero-ventral nucleus, which is the only part of the thalamus proper which has been injured by the lesion on the left side.

The lesion does not extend so far caudally as the posterior part of the thalamus. Scattered osmic granules are present in the stratum album medium of the anterior colliculus (due to the injury of cortico-tectal fibres by the caudal extremity of the lesion), and at this level there is a slight degeneration in both tracts of Meynert, and a definite osmic deposit in the right mammillo-thalamic tract. Degenerated fibres are present in the medial half of the right pes pedunculi (but not involving the most medially situated fasciculi), and also in the second fifth (from the lateral border) of the left pes pedunculi. At this caudal level, degenerated fibres in the left cingular area are very distinct, extending medio-ventrally in their distribution as far as the margin of the retrosplenial granular cortex.

Rat Th. 3, fig. 10.—In this case, a needle was passed through the temporal cortex of the left side and horizontally, with a slight forward inclination, through the internal capsule and thalamus of the left side, across the mid-line, and through the dorsal limit of the right ventral nucleus up to, but not involving, the internal capsule this side. The experiment proved a favourable one for the study of the thalamo-cortical connections of the dorso-lateral extremity of the ventral nucleus on the right side.

At the level of the anterior nucleus (in front of the anterior extremity of the lesion), the upper end of the left mammillo-thalamic tract contains degenerated fibres which pass up in a dorso-lateral direction into the anterior nucleus, fig. 10, *a*. All three elements of this nucleus contain a rich deposit of osmic granules, marking the termination of mammillo-thalamic fibres. Many degenerated fibres also extend along the interantero-dorsal commissure up to and into the antero-dorsal nucleus of the right side. These fibres are apparently derived from the left mammillo-thalamic tract. The right tract contains no degenerated fibres. On the left side in these rostral sections, strands of degenerated fibres run from the ventral medullary lamina across the zona incerta, in among the fasciculi of the internal capsule, and into the globus pallidus. Coarse degeneration is also present in the fibres of the internal capsule which are here penetrating the putamen, and in the deeper layers of the cortex over the lower two-thirds of its lateral surface.

All the ventral nucleus of this side (the side from which the lesion was produced) is extensively strewn with osmic deposit as the result of the involvement by the lesion

of the internal capsule and the posterior part of the ventral nucleus itself. The anterior end of the main part of the lateral nucleus is, however, free of degeneration. On the right side, the dorsal third of the rostral part of the ventral nucleus contains degenerated fibres which can be traced in continuity through the internal capsule into the parietal cortex extending over about the middle-third (in cross-section) of the lateral surface of the neopallium. More caudally, the anterior end of the lesion is seen on the left side, involving here the medial part of the ventral nucleus and the nucleus medialis ventralis, and cutting into the mammillo-thalamic tract. On both sides the fasciculi of the thalamic radiations, extending up towards the dorso-medial nucleus, contain degenerated fibres, due to their involvement at a more caudal level.

At the level of the anterior end of the lateral geniculate body the lesion extends across the mid-line, cutting right across the thalamus of the right side just below the nucleus habenulae, and through the most dorsal part of the ventral nucleus as far as the internal capsule, fig. 10, *b*. On this side the ventral two-thirds of the ventral nucleus and the nucleus medialis ventralis are free of degeneration. At a more caudal level, the lesion on the left side extends into the nucleus reuniens, but no degenerated fibres pass from this median nucleus into the hypothalamus or into the internal capsule of the right side. No degeneration is present in the thalamic radiations emerging from the right anterior and lateral nuclei. On the left side, degeneration is present in the fibres entering the posterior region of the main part of the lateral nucleus as the result of their involvement by the lesion in the internal capsule. These degenerated fibres reach up into the most dorsal parietal region of the cortex. No degenerated fibres pass from the injured portion of the right ventral nucleus into the globus pallidus.

At the level of the upper extremity of the fasciculus retroflexus, the lesion does not extend to the right side of the mid-line. Here Marchi degeneration in the thalamus is confined to the extreme dorso-lateral region of the ventral nucleus and to the fasciculus retroflexus. Degenerated fibres in the right cortex have practically disappeared in this caudal plane, except for a small patch about midway between the rhinal fissure and the dorsal border of the hemisphere. There is no degeneration in the lateral geniculate body, the pars posterior of the lateral nucleus, or the pes pedunculi of the right side. The degeneration in the right cortex is thus entirely due to the injury of the dorsal border of the ventral nucleus and especially of its dorso-lateral extremity. On the left side the lesion has at this level interrupted the fibres of the optic radiations, and the lateral geniculate body and the area striata show a rich osmic deposit.

In the most caudal part of the thalamus, descending degeneration in the left mammillo-thalamic tract is very evident, and the degenerated fibres end in the medial nucleus of the mammillary bodies. At this level degeneration on the right side is limited to the fasciculus retroflexus. On the left side, the degenerated fibres in the pes pedunculi are confined to its lateral third.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Rat Th. 4, fig. 11.—The needle was entered at a level of the caudal pole of the left hemisphere. The track of the needle made a linear lesion extending forwards, medially, and a little ventrally, so that it involved the deeper part of the left anterior colliculus and the tegmental region of the mid-brain at this level, entering the thalamus from behind, reaching the medial part of the left ventral nucleus, and extending across the mid-line to involve the dorso-medial nucleus and the nucleus medialis ventralis of the right side. The lesion did not extend laterally beyond the level of the right medial medullary lamina. No part of the neopallium was injured. This specimen is thus especially favourable for the study of the fibre connections of the more medially situated nuclei.

At the level of the anterior border of the pons degeneration is present in the tecto-spinal tract, but there is none in the posterior longitudinal bundles or the crura cerebri. The caudal margin of the left hemisphere shows a small lesion at the dorsal border involving the subicular cortex and the immediately subjacent white matter, and the caudal extremity of the cingulum. Further forwards, the degenerated tecto-spinal fibres are seen forming the dorsal tegmental decussation. There is a fine degeneration in the most caudal fibres of the optic tract entering the anterior colliculus, but sections further forward show that the great bulk of the optic tract has not been involved by the lesion, and the lateral geniculate body is free of degeneration. Degeneration is present in the stratum album medium of the left anterior colliculus, due to the involvement on a more rostral plane of cortico-tectal fibres. There is no Marchi degeneration in the caudal part of the cerebral cortex, except in the white matter immediately adjacent to the lesion in the subiculum, and there are no degenerated fibres in the cingulum rostral to the site of the lesion.

At the level of the anterior part of the anterior colliculus is seen the caudal end of that part of the lesion which involves the mid-brain, extending from the left extremity of the main part of the commissure of the anterior colliculus in a ventro-lateral direction almost as far ventrally as the medial fillet. Just in front of this level, the lesion cuts through the posterior commissure to the left of the mid-line and degenerated fibres pass across the mid-line in this commissure, and run caudally for a short distance on the right side to the region of the nucleus of the posterior commissure and into the formatio reticularis, but not as far as the oculomotor nucleus, nor into the posterior longitudinal bundle. Degeneration is present in both Meynert's tracts and in the left mammillo-thalamic tract at this level, as the result of the involvement of these tracts by the lesion more anteriorly. The zona incerta of the left side is filled with black granules, associated with a lesion of this part of the subthalamus further forwards.

Sections through the most caudal part of the thalamus show that the lesion extends here into the mid-line immediately below the aqueduct, and involves the greater part of the left pretectal nucleus. There is no evidence of thalamo-cortical fibres originating in the pretectal nucleus. Further forwards the lesion cuts into the upper end of the right fasciculus retroflexus, and involves also the caudal part of the right dorso-medial nucleus, fig. 11, *a*. At this level degeneration on the right side is confined to fibres in

the immediate neighbourhood of the lesion. On the left side the lesion cuts into the left mammillo-thalamic tract, the nucleus medialis ventralis, and the most medial part of the ventral thalamic nucleus.

In the middle of the thalamus, the lesion on the left side involves the medial portion of the zona incerta as well as the nucleus medialis ventralis and the medial extremity of the ventral nucleus, cutting across the thalamic radiations passing up to the dorso-medial nucleus. It extends across the mid-line in the region of the nucleus reuniens and reaches the right nucleus medialis ventralis, but not further laterally, fig. 11, *b*. At this level degenerated fibres run transversely in the commissura mollis (in the position of the nucleus centralis medius), and are present in the left mammillo-thalamic tract which is here passing up from the site of the lesion which involves it. On the right side the mammillo-thalamic tract is intact. On the left side, osmic granules are scattered throughout the ventral nucleus and the caudal region of the main part of the lateral nucleus, and many well-defined fascicles of degenerated fibres pass from the zona incerta through the internal capsule and into the globus pallidus. On the right side degenerated fibres course ventro-laterally from the dorso-medial nucleus (which is involved by the lesion in its caudal part) and others run from the injured nucleus medialis ventralis into the ventral medullary lamina. No degenerated fibres can be traced passing from the site of the lesion in the mid-line down into the hypothalamus.

More rostrally, the degenerated left mammillo-thalamic tract can be readily followed up into the anterior nucleus, all the elements of which are bestrewn with a fine deposit of osmic granules. Moreover, degenerated fibres can be traced in continuity from the upper end of the left mammillo-thalamic tract through the commissura interantero-dorsalis and into the antero-dorsal nucleus of the right side. Still further anteriorly on the right side, the degenerated fibres which arise from the nucleus medialis ventralis and the dorso-medial nucleus collect at the medial part of the internal capsule, and many penetrate the capsule to terminate in the globus pallidus, fig. 11, *c*. These latter fibres are judged by their position to be those which come from the nucleus medialis ventralis, and they were not observed in Rat Th. 6 in which the dorso-medial nucleus alone was injured on one side. The fibres from the dorso-medial nucleus pass forwards in the medial part of the internal capsule into the frontal lobes of the brain.

At the level of the anterior commissure, degenerated fibres on the left side (originating from the lesion in the medial part of the ventral nucleus) pass through the putamen to reach the external capsule, and distribute to a small area of cortex corresponding topographically to the insular area. There is no evidence that any of the degenerated fibres which penetrate the internal capsule on the right side to reach the globus pallidus extend further laterally to the cortex. The degenerated fibres which originate in the dorso-medial nucleus of the right side occupy at this level the most medial small fasciculi of the internal capsule, in close apposition to the septal region. Horizontal sections through the frontal poles of the hemisphere show that these degenerated fibres extend right into the cortex of the frontal pole.

Rat Th. 5.—The puncture wound entered the left hemisphere 2·6 mm. from the mid-line and at the level of a transverse plane passing through the anterior colliculus, the lower end of the fasciculus retroflexus, and caudal to the posterior end of the corpus callosum. The lesion passed obliquely forwards and medially, through the upper border of the occipital cortex, the subsplenial portion of the hippocampus, the rostral margin of the anterior colliculus, the pars posterior of the lateral nucleus and the habenular nucleus, all on the left side. The lateral nucleus and the anterior nucleus of the left side are also extensively damaged. At the level of the main part of the lateral nucleus the lesion extends across the third ventricle into the habenular nucleus and stria medullaris of the right side, passing laterally between these structures and the dorso-medial nucleus. Further, laterally on this side it extends ventral to the main part of the lateral nucleus and through the dorsal margin of the ventral nucleus, reaching as far laterally as the most medial fasciculi of the internal capsule. The right anterior and lateral nuclei and the thalamic radiations associated with them are undamaged.

On the right side of the brain degenerated fibres run from the dorsal half of the ventral nucleus into the dorsal half of the internal capsule and, passing rostrally and dorsally through the dorsal half of the putamen and the head of the caudate nucleus, finally to terminate in the dorsal half of the parietal cortex with the exception of the cingular area and the most dorsal margin of the parietal area. At the level of the main part of the lateral nucleus this cortical degeneration extends up to a level 2·5 mm. from the mid-line. There is no degeneration in the stratum subcaudatum or among the fasciculi which run into the lateral nucleus, and there is complete absence of Marchi granules in the ground substance of the lenticular nucleus and the head of the caudate nucleus. Degeneration is present in the anterior pillar of the fornix, stria medullaris, olfacto-habenular tract, the interantero-dorsal commissure and the paratænial nucleus. No degeneration is present in the mammillo-thalamic tract or the pretectal nucleus of this side.

On the left side the degeneration is more extensive. Many degenerated fibres are present in the anterior pillar of the fornix, the mammillo-thalamic tract, the fasciculus retroflexus, and the dorsal half of the thalamic radiations. The latter terminate in the dorsal half of the neopallium, including the cingular areas. It is to be noted that the lesion involved only the caudal part of the internal capsule and that to a slight extent; it is certain, therefore, that the degeneration in the anterior thalamic radiations is due to the injury of the thalamic nuclei of origin of the thalamo-cortical fibres.

The main difference in the degeneration of the two sides is associated with the involvement by the lesion of the anterior nucleus and the main part of the lateral nucleus on the left side, and by the presence on this side of terminal degenerated fibres in the cingular area and the uppermost part of the parietal area of the cortex. This suggests that these regions of the cortex receive projection fibres from the anterior nucleus or the lateral nucleus or both. In view of the presence of cortico-thalamic connections between the antero-ventral nucleus and the cingular cortex (*vide supra*, rats *P* 1, *C* 1, and *C* 2),

the explanation is probably that the anterior nucleus sends corticipetal fibres to the cingular area, while the lateral nucleus (main part) is similarly related to the most dorsal part of the parietal area.

The following points may also be noted in this experiment. The lesion involved the mammillo-thalamic tract in which distinct descending degeneration can be traced down into the medial mammillary nucleus. Degenerated fibres in the fornix extend down into the lateral mammillary nucleus and into the lateral part of the medial mammillary nucleus, very few crossing over in the supramammillary decussation to the opposite hypothalamus. No evidence was found that fornix fibres terminate in other regions (such as the pre-optic region, tuber cinereum, or mid-brain).

Rat Th. 6, fig. 12.—The puncture wound entered the left temporal cortex 2·8 mm. above the rhinal fissure at the level of the rostral extremity of the lateral geniculate body and the anterior part of the mammillary body. The track of the needle passes through the upper end of the descending horn of the lateral ventricle, the ventral margin of the fimbria, the rostral and dorsal pole of the lateral geniculate body. Further medially, it makes a horizontal slit passing across between the main part of the lateral nucleus and the ventral nucleus, and then obliquely medio-ventrally into the rostral part of the left dorso-medial nucleus. More anteriorly, the lesion extends across into the anterior extremity of the right dorso-medial nucleus, but not reaching further laterally on this side than the medial margin of the antero-ventral nucleus.

At the level of the lesion in the right side of the thalamus, numerous degenerated fibres extend up in the interantero-dorsal commissure as far as the antero-dorsal nucleus, fig. 12, *a*. Others pass in small bundles dorso-medially into the paratænial nucleus and towards the rostral part of the dorso-medial nucleus, and ventro-laterally from the lesion in fine bundles towards the most medial part of the internal capsule. The latter run rostrally alongside the caudal part of the septum and adjacent to the floor of the anterior horn of the lateral ventricle, fig. 12, *b*, occupying the same position as the degenerated cortico-thalamic fibres traced back to the dorso-medial nucleus from a lesion in the frontal pole of the hemisphere (*vide supra*, rats *F* 2 and *F* 3). Serial sections of this brain were not taken as far rostrally as the cortex of the frontal pole and so it is not possible to affirm from this case that the degenerated fibres from the dorso-medial nucleus actually terminated in the cortex. There is no evidence that they end in the corpus striatum. The only other Marchi degeneration to be noted on the right side is in the fibres of the inferior peduncle of the thalamus disappearing in the caudal region of the olfactory tubercle, and in fibres running vertically down alongside the ventricle in the periventricular system from the site of the lesion as far as a level just ventral to the interantero-ventral commissure.

On the left side, in addition to the ventral margin of the lateral nucleus, the dorsal margin of the ventral nucleus, the ventral part of the dorso-medial nucleus and the rostral margin of the lateral geniculate body, the lesion involves the lateral margin of the caudal part of the antero-ventral nucleus. Rostrally the dorsal half of the pallium,

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

including the cingular areas, is filled with Marchi deposit, and at its caudal extremity the cortex contains degenerated fibres throughout most of its lateral surface, and also in the retrosplenial granular area. Degeneration is present in the antero-ventral nucleus, the main part of the lateral nucleus, the dorso-medial nucleus, and the lateral quarter of the cerebral peduncle. A fine deposit is also scattered through the caudal half of the ventral nucleus, the pretectal nucleus, the pars posterior of the lateral nucleus, and lateral geniculate body (especially the dorsal nucleus). Marchi granules in the medial geniculate body are the result of degeneration of fibres originating in the temporal cortex at the site of the puncture wound. There is no degeneration in the nucleus medialis ventralis.

This experiment is of interest because on one side the lesion is limited to the dorso-medial nucleus. That the degenerated fibres arising in this nucleus are corticipetal with reference to the frontal pole is rendered practically certain by comparison with the results of the experiment, rat *Th.* 4. The cortical Marchi degeneration on the left side (involving the whole of the dorsal half of the pallium) is evidently secondary to the injury of the lateral nucleus, antero-ventral nucleus, and the dorsal margin of the ventral nucleus.

Rat Th. 7, fig. 13.—The needle was entered through the posterior parietal region of the left side and directed transversely with a slight caudal inclination. It passed through the left lateral ventricle, the fimbria (involving the hippocampus slightly), and injured to a small extent the rostral end of the pars posterior of the lateral nucleus. On the right side the lesion entered the ventral nucleus and the medial geniculate body, reaching also the internal capsule. The series of sections of this specimen is not entirely satisfactory, as a part of the lesion on the left side lies in the junction of two of the separate blocks which were stained and cut. A gap thus exists in the sections where the precise extent of the lesion must be inferred indirectly.

At the level of the anterior colliculus and the interpeduncular ganglion, degeneration is present on the left side in the most lateral fasciculi of the pes pedunculi, in the stratum opticum of the anterior colliculus, and in a clearly limited patch of cortex corresponding to the area striata. On the right side degenerated fibres are present in the lateral two-thirds of the pes pedunculi, in the stratum medium of the anterior colliculus, the lateral part of the substantia nigra, and the tegmental area between this and the medial geniculate body. All the neopallium at this level on the right side contains degenerated fibres as far up as the dorsal border of the area striata.

At the level of the corpus mammillare, degeneration is present in both Meynert's tracts. The degeneration in the lateral edge of the left pes pedunculi is very sparse, from which it may be inferred that the track of the needle on this side produced comparatively slight injury of the cortex and the internal capsule. At this level, the left cortical Marchi degeneration is confined to the area striata and the upper margin of the cortical area immediately below. On the right side, coarse degeneration is present throughout the lateral half of the pes pedunculi and in the medial part of the

medial geniculate body, as well as in the lateral region of the zona incerta and the deeper layers of the anterior colliculus. Degenerated fibres are present in the cortex of this side from the dorsal margin of the striate area down to the rhinal fissure.

More anteriorly, the caudal end of the lesion on the right side is seen, cutting obliquely in a ventro-lateral direction across the medial geniculate body and just reaching the medial margin of the optic tract. At this level on the right side there is extensive degeneration among the cortico-tectal fibres passing to the stratum medium of the anterior colliculus and in the neopallium up to the dorsal border of the area striata, while on the left side cortical degeneration only reaches up into the lateral border of the striate area and below extends over the upper part of the immediately adjacent cortical area. No degeneration is present in the caudal end of the lateral geniculate body or the caudal end of the pars posterior of the lateral nucleus of either side.

In the next block of tissue the caudal section passes through the middle of the thalamus, and here the lesion on the right extends laterally and slightly ventrally through the stria medullaris, below the pars posterior of the lateral nucleus and the lateral geniculate body, and through the dorsal part of the ventral nucleus. The habenular ganglion and the whole of the ventral nucleus and the lateral geniculate body on the right side are at this level strewn with Marchi granules, while the nucleus medialis ventralis is free of deposit. On the left side, the left extremity of the lesion just reaches the centrum ovale of the hemisphere, and the upper part of the internal capsule (just ventral to this point) contains degenerated fibres derived from this lesion. There is plentiful degeneration on this side in the anterior end of the pars posterior of the lateral nucleus, and in the fasciculi which run from this nucleus through the lateral geniculate body to the internal capsule. No degenerated fibres are observed to terminate in the rostral part of the lateral geniculate body which is to be seen at this level.

At the level of sections passing through the anterior extremity of the lateral geniculate body, degenerated fibres have practically disappeared from the left cortex. In the anterior part of the thalamus no Marchi degeneration is present on the left side of the brain except in the fimbria and the stria medullaris (the anterior nucleus and the main part of the lateral nucleus of both sides being clear of osmic deposit). On the right side the lesion of the ventral nucleus and the internal capsule is rather extensive, and there is a wide distribution of degenerated fibres in the cortex which, however, does not include the cingular areas or the most dorsal part of the parietal area.

Summarising the results of this experiment, the thalamic lesion on the right side is limited to the ventral nucleus, the medial geniculate body, and some of the fibres of the optic radiations. The distribution of Marchi degeneration in the cortex of this side extends over all the lower part of the neopallium in the occipital and parietal regions, reaching from the rhinal fissure below to the dorsal margin of the area striata and up to the dorsal region of the parietal area above. The absence of Marchi degeneration in the cingular area and in the most dorsal part of the parietal area is related to the fact that

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

the anterior nucleus and the lateral nucleus (main part) of this side were uninjured. On the left side degenerated fibres are present in the area striata and in a zone of cortex bounding this area ventrally and anteriorly. This is apparently associated—at least in part—with the involvement by the lesion on this side of the anterior part of the pars posterior of the lateral nucleus. As the serial sections at the site of the lesion were not complete, it is not possible positively to exclude injury to the middle part of the left lateral geniculate body.

Rat BS 1, fig. 14.—A lesion was made in the brain stem involving the main sensory nucleus of the trigeminal nerve in the rostral part of the hind-brain. In addition, a portion of the superior and middle peduncles of the cerebellum were injured, as well as the cochlear nuclei, trapezoid fibres, and secondary auditory nuclei of the same side. The fibres of the medial and spinal lemnisci were uninjured and show no degeneration.

Tracing the sections rostrally from the site of the lesion, degenerated fibres are noted in the trapezoid body, in the position of the sensory nucleus of the fifth nerve, and in the brachium conjunctivum. The latter cross over in the decussation of Wernicke and course up to the opposite red nucleus. The degenerated fibres of the trapezoid body, after crossing the mid-line, appear to terminate mostly in the nucleus of the lateral lemniscus which is filled with a deposit of fine Marchi granules. Some, however, can be traced into the deeper strata of the posterior colliculus but not as far as the medial geniculate body.

From the site of the lesion of the sensory trigeminal nucleus slender fasciculi of the degenerated fibres course medio-ventrally to form the decussation of the trigeminal lemniscus at the level of the pons, fig. 14, *a*. This decussation is completed when the level of the decussation of the main part of the fibres of the brachium conjunctivum is reached. After crossing, the trigeminal fillet fibres come to occupy the most medial fasciculi of the medial or main fillet of the opposite side, fig. 14, *b*. At the level of the interpeduncular ganglion, the degenerated fibres are confined entirely to the side opposite to that of the lesion. Most of the degenerated fibres of the brachium conjunctivum apparently end in the red nucleus, but a proportion of them pass up medial to this to the thalamic region. Their precise termination in the thalamus cannot be determined, as they intermingle with the fibres of the fillet.

From the main fillet, a few degenerated fibres course dorsally towards the anterior colliculus to end in the deeper layers of this structure. A little further rostrally, a few fasciculi containing degenerated fibres pass dorso-medially into the substance of the pretectal nucleus. No degeneration extends into the mammillary body, but scattered Marchi granules are present in the medial part of the zona incerta.

At the level of the anterior part of the lateral geniculate body, the whole of the main ventral nucleus of the thalamus is sprinkled with a fine osmic deposit which is rather more dense in the medial part of the nucleus. There is no degeneration in the dorso-medial nucleus, the lateral nucleus, in the paracentral and lateral central nuclei, or in

the nucleus medialis ventralis. In more rostral sections the degenerated fillet fibres extend dorso-laterally into the rostral part of the main ventral nucleus, fig. 14, *c*.

Although degenerated fibres of the brachium conjunctivum extend into the thalamus, they are few in relation to the degenerated fibres of the trigeminal fillet, and it may be assumed that the greater part of the osmic deposit in the ventral nucleus of the thalamus is secondary to the fillet lesion. These sections indicate, then, that the trigeminal fillet fibres arising from the main sensory nucleus terminate in the ventral nucleus of the thalamus reaching up to its antero-lateral extremity, and that none reach the nucleus medialis ventralis, the dorso-medial nucleus, or the lateral nucleus. Further, no degeneration could be traced up beyond the level of the thalamus.

Rat BS 2, fig. 15.—A partial hemisection of the left side of the lower end of the medulla (at the level of the rostral part of the hypoglossal nucleus) was made by inserting a fine discission needle through the atlanto-occipital membrane. Histologically, the lesion cuts through the medial half of the left side of the medulla, involving here the medial fillet and the formatio reticularis. Numerous degenerated fibræ arcuatæ cross over to the opposite side from the site of the injury, partly taking up a position in the right medial fillet, and partly running into the dorsal part of the formatio reticularis.

At the anterior border of the pons, the medial fillet on both sides (but more so on the left) is filled with Marchi granules. On the right side there is a diffuse deposit in the tegmentum more dorsally. Degenerated fibres run dorso-laterally from the fillet into the tectum, reaching the deeper layers of the anterior colliculi, fig. 15, *a*. There is no degeneration in the posterior commissure.

At the level of the caudal extremity of the thalamus, some fine fasciculi containing degenerated fibres course dorso-medially over the posterior aspect of the ventral thalamic nucleus to reach the position of the pretectal nucleus where they terminate, fig. 15, *b*. At this level, also, there is a fine osmic deposit in the zona incerta immediately ventral to the medial fillet, quite well marked on the left side, but no degenerated fibres can be detected in the mammillary peduncle or the mammillary body. On both sides a few osmic granules are to be seen in the medial fore-brain bundle, but the significance of these is indeterminate.

At the level of the middle of the thalamus, the compact bundle of the medial fillet breaks up into numerous fibres which can be traced by their osmic staining into the ventral nucleus of the thalamus, entering it mainly from the ventral and lateral aspects. On the right side, a few degenerated fibres run forwards through the lateral part of the medial medullary lamina (in the region of the nucleus centralis lateralis) in order, it appears, to enter the ventral nucleus from the dorso-medial aspect. No degeneration is present in the dorso-medial nucleus, the lateral nucleus, or the nucleus medialis ventralis, and no evidence was found that any of the degenerated fibres pass up beyond the level of the ventral nucleus of the thalamus.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Discussion

The results of these experiments may best be summarised and discussed by considering separately the various thalamic elements which were involved.

Nucleus ventralis.—It is a well-established fact that the ventral nucleus of the thalamus is the main terminal nucleus of the fillet system. In three of the experiments the fillet was directly involved by the lesion. In rat *BS* 1, fig. 14, the lesion was confined to the upper part of the trigeminal fillet, and the medial and spinal fillets escaped injury. Degenerated fibres were traced up from the site of the lesion to the most medial part of the fillet of the opposite side into the anterior colliculus, the region of the pretectal nucleus and the ventral thalamic nucleus. In the latter, Marchi granules extended up to its antero-lateral portion. In rat *BS* 2, fig. 15, the fillet system was injured in the medulla. Here, again, degenerated fibres were traced to the anterior colliculus, the pretectal nucleus, and the ventral nucleus. On one side there was a fine deposit of Marchi granules in the medial medullary lamina (in the substance of the intralaminar nuclei—nucleus paracentralis and nucleus centralis lateralis). This deposit is apparently associated with fillet fibres which course through the medial medullary lamina in order finally to reach the dorso-medial part of the ventral nucleus. They may partly terminate in the paracentral and the lateral central nuclei, but these intralaminar nuclei (in the rat) are rather to be regarded as peripheral zones of the main ventral nucleus the cytoarchitecture of which has been modified by the fibres of passage which run through them. They probably correspond to Cajal's (1911) posterior semilunar nucleus which this author describes as having a terminal relation to fibres of the trigeminal fillet. In rat *Th.* 1, fig. 8, the fillet was cut across at the level at which it enters the thalamus. Here Marchi degeneration was found throughout the ventral nucleus and in the fibres of the medial medullary lamina. In none of these cases was there any evidence that fillet fibres reached the lateral nucleus or into the substance of the dorso-medial nucleus. Moreover, no Marchi degeneration was traced above the level of the thalamus.

In most of the intra-thalamic lesions, the ventral nucleus of the thalamus was involved on one or both sides, and in these cases Marchi degeneration was followed in the fibres of the thalamic radiations to an extent directly dependent upon the severity of the injury. In rat *Th.* 2, fig. 9, the lesion involved most of the ventral nucleus on one side, except its most dorso-lateral part, and on the same side cortical fibres, reaching to approximately the ventral half of the lateral surface of the neopallium in the region of the parietal area, showed Marchi staining. In rat *Th.* 3, fig. 10, the dorsal part of the ventral nucleus was injured on one side, with resulting Marchi degeneration extending over about the middle-third (in a dorso-ventral direction) of the parietal area, while on the opposite side, where the whole ventral nucleus was involved, the cortical degeneration extended down to the rhinal fissure in the parietal region. In rat *Th.* 4, fig. 11, a lesion of the most medial part of the ventral nucleus led to a Marchi deposit in fibres distributed to the "insular" region of the cortex, abutting on the more anterior part of the rhinal

fissure. In rats *Th.* 5 and *Th.* 6, again, evidence was provided to show that the dorsal part of the ventral nucleus is connected by thalamo-cortical fibres with the dorsal part of the parietal cortex. These experiments, together with those in which the parietal cortex was injured, indicate that the ventral nucleus is related by fibre connections with the cortical areas which FORTUYN has indicated by the letters *j* and *k*, and which appear to correspond to the general sensory cortex and the "insular" area, the most lateral and dorsal parts of the nucleus being related to the dorsal region of the parietal area, and the more ventral and medial parts to the ventral region of the parietal area and the "insular" area. Thus the fibres from different parts of the ventral nucleus take the most direct route to the cortex and their topographical distribution in the cortex is directly dependent upon their topographical position of origin in the thalamus. This is in accord with a principle which was enunciated by ELLIOT SMITH (1910) in his lectures on the evolution of the cerebral hemispheres.

Nucleus medialis ventralis.—This nucleus (which may be included for descriptive convenience in the ventral group of nuclei) is quite well-defined in the rat's brain. It corresponds to CAJAL'S "ovoid mesial nucleus." By some authors (*e.g.*, RIOCH (1929)) it is called the nucleus submedius, but this term has also been used to include other elements which do not appear to be homologous with the nucleus medialis ventralis. In none of the experiments was it possible to trace by Marchi degeneration any afferent fibres to this nucleus. After lesions involving the ventral and other thalamic nuclei, the tectum, the fillet system and most parts of the cortex, the nucleus medialis ventralis remained quite clear of osmic deposit. The conclusion is reached that its afferent connections consist entirely of short fibres from immediately adjacent nuclear structures. Normal Weigert sections indicate that it is connected in this way with the medial part of the ventral nucleus, the antero-medial nucleus, and the periventricular system. In two cases, rats *Th.* 3 and *Th.* 4, the nucleus was involved on one side by an intra-thalamic lesion, and in the latter case, the lesion on this side did not extend further laterally. No thalamo-cortical fibres from this nucleus were detected in the Marchi material. On the other hand, degenerated fibres were traced from the site of the lesion to the medial end of the ventral medullary lamina, and through the fasciculi of the pes pedunculi into the globus pallidus, fig. 11, *c*. These degenerated fibres were absent in cases in which the ventral nucleus of the thalamus was injured while the nucleus medialis ventralis was left intact. It therefore appears that the medio-ventral nucleus sends off thalamo-striate fibres, but is unrelated to the cortex. It has been suggested elsewhere (CLARK, 1932) that if there is any one element in the mammalian thalamus which can be regarded as strictly homologous with the nucleus rotundus of the reptilian diencephalon, it is the nucleus medialis ventralis. This nucleus satisfies topographical criteria of homology, and its fibre connections with the corpus striatum recall the striate connections which are so characteristic of the nucleus rotundus. It is also worthy of note that the nucleus medialis ventralis is well-defined in the thalamus of primitive mammals, but in higher types it becomes less distinct until it loses its individuality altogether in the Primates.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Anterior Nuclei.—It is well known that the anterior group of thalamic nuclei is related to the termination of the fibres of the bundle of Vicq D'Azyr. There has, however, been some dispute as to whether these fibres end in all the three elements of this group, the antero-dorsal, antero-ventral, and antero-medial nuclei, and especially in regard to the first of these. I have shown previously (Clark, 1929) that where the antero-dorsal nucleus is developed in an exaggerated fashion (*e.g.*, in *Macroscelides*), it is possible to trace mammillo-thalamic fibres into it by a study of normal Weigert preparations. This connection has more recently been confirmed by Glorieux, 1929, who demonstrated experimentally in the dog's thalamus by the Marchi method that the mammillo-thalamic tract does reach up into the antero-dorsal nucleus. In the series of experiments described here, the mammillo-thalamic tract was injured unilaterally in several cases, and in rats *Th.* 3, *Th.* 4, and *V* 2, the Marchi degeneration was traced up to all the elements of the anterior group of nuclei on the affected side. In addition to this, some degenerated fibres were followed into the commissure linking up the antero-dorsal nuclei (commissura interantero-dorsalis) across the mid-line and into the substance of the antero-dorsal nucleus of the opposite side. This latter observation confirms what I described to be the case in the thalamus of *Macroscelides*. Further, in cases in which the bundle of Vicq D'Azyr had been injured at the upper part of its course, a distinct descending Marchi degeneration was found, although the osmic deposit was less heavy than in the ascending degeneration. In these cases (rats *Th.* 2, *Th.* 4, and *Th.* 5), the tract could be followed down into the medial mammillary nucleus of the same side, the osmic deposit being limited to this nucleus. This evidence is in harmony with Edinger's contention that there is a thalamo-mammillary component of the bundle of Vicq D'Azyr.

As regards the cortical connections of the anterior nuclei, in three experiments in which localised cortical lesions were produced (rats *C* 1, *C* 2, and *P* 1), a fine Marchi degeneration was followed along the fibres of the stratum subcaudatum into the substance of the antero-ventral nucleus. In these cases the lesion involved the cingular cortex (at either its anterior or posterior part) or the corticifugal fibres running laterally from this cortical area to reach the upper end of the internal capsule. Lesions in other parts of the cortex, including the frontal pole, produced no such degeneration in the anterior nuclei. It is interesting to note that the cortico-thalamic fibres terminating in the antero-ventral nucleus were described by Villaverde (1923) in Marchi preparations of the rabbit's brain after a lesion which he stated to involve the " motor " area (Brodmann's area 4). This was subsequently denied by Riese (1924), who repeated the experiment. On consulting Villaverde's original paper, it may be seen from his text figures that his lesion extended subcortically so as to involve the fibres running between the area cingularis and the upper end of the internal capsule, while it seems doubtful whether the so-called motor area was damaged to any extent. Thus Villaverde's results appear to harmonize completely with my own. In three of the intra-thalamic lesions produced in the rat's brain, the antero-ventral nucleus was involved. In one case

(rat *Th.* 2), the lesion was practically confined on one side to this element, and, in the cerebral hemisphere of this side, Marchi degeneration was limited to the fibres ending in the whole length of the cingular area of the cortex except anteriorly where some of the thalamic radiations from the dorsal part of the ventral nucleus were involved. In another case (rat *Th.* 5), the lesion involved on one side the antero-ventral nucleus and the main part of the lateral nucleus. On this side, again, Marchi degeneration was found throughout the area cingularis, while in the opposite hemisphere in which the antero-ventral nucleus was intact, this cortical area was free of deposit. In a third case (rat *Th.* 6), the antero-ventral nucleus was also injured, together with the main part of the lateral nucleus, the dorso-medial nucleus, and the dorsal margin of the ventral nucleus. Here, also, Marchi degeneration was found in the fibres of the upper part of the internal capsule extending into the cingular cortex. These cases, with the negative evidence provided in cases in which other thalamic elements had been subjected to injury with a complete absence of Marchi degeneration in the area cingularis, appear to demonstrate that corticipetal fibres extend from the antero-ventral nucleus to the whole extent of the area cingularis of the cortex in the rat. This conclusion is not in accord with the generally accepted idea that the anterior thalamic nuclei send no projection fibres to the cortex—and especially with the experimental findings of Sachs and Glorieux. These authors, however, carried out their studies with carnivores in which these connections may be less obtrusive.* Winkler (1921) states definitely that it is easy " au moyen de la suppression de l'écorce dans la region tout à fait médiane de la surface externe de l'hemisphere " to produce in the rabbit complete atrophy of the anterior nucleus of the thalamus and the disappearance of all its cells. Thus we believe it to be established that—at least in rodents—there is a reciprocal fibre relation between the antero-ventral nucleus and the cingular cortex. As regards the antero-medial nucleus, the experiments provided no evidence that it either receives or sends off cortical fibres. A study of this element in sections of normal material also indicates that it is independent of the cortex. It is probably the only part of the anterior group of nuclei which can in any way be regarded as a representative of the " palæothalamus," and it may be noted that there is evidence to show that it is derived phylogenetically from the nucleus dorso-medialis anterior of the reptilian thalamus, a nucleus which is not related to the somatic areas of the lateral part of the fore-brain. Weigert sections of the brains of lower mammals indicate that the antero-medial nucleus is connected by short fibres with the antero-ventral nucleus, the nucleus medialis ventralis, and the nuclei of the mid-line (periventricular system). None of the experiments were suitable for the investigation of the possible cortical connections of the antero-dorsal nucleus. This question requires further study with the use of larger brains. I have elsewhere

* Since writing this, Mr. R. H. Boggon, M.S., and the author, working in collaboration, have succeeded in producing a small localised electrolytic lesion in the anterior nucleus of the cat's thalamus. Our Marchi preparations of this specimen demonstrate quite definitely a fibre connection between this nucleus and the whole length of the cingular area of the cortex.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(Clark, 1929) stated that comparative studies show a relation between the development of this nucleus and the extent of the peculiar granular cortex found in the retrosplenial area. It is desirable that this suggestion should be followed up experimentally.

Nucleus lateralis, pars principalis.—The main part of the lateral nucleus in the rat's brain is a small element, confined to the more rostral planes of the thalamus. It is this nucleus which expands to such a marked degree in the brains of higher mammals and its large size is characteristic of all Primate brains—even in the smallest representatives of this order. In none of the experiments in which the lemniscus system was involved by the lesion were degenerated fibres traced into the lateral nucleus. This observation is in accord with the results of other investigators and in harmony with the conception that the lateral nucleus—as compared with the ventral or fillet nucleus—represents a higher functional level of the thalamus. Moreover, it lends no support to the thesis advanced by von Monakow's school that the lateral nucleus is related to the "leg" areas of the general sensory cortex while the ventral nucleus is related to the "arm" areas. Most regions of the cortex have been injured by localised lesions in the course of these experiments on the rat's brain, but in one instance only was subsequent Marchi degeneration traced into the substance of the main part of the lateral nucleus. This was in the case of rat *C* 2, fig. 6. It will be seen by reference to fig. 1, *C* 2, that the lesion here involved the most dorsal part of the parietal region of the cortex, just anterior to the area striata. Topographically, this part of the cortex in the rat's brain would seem to correspond with the parietal association areas which expand so enormously in the brains of higher mammals. It is significant, therefore, that comparative studies show a close parallel between the expansion and elaboration of the lateral nucleus of the thalamus and the parietal association areas of the cortex.

The experiments provide some evidence of the distribution of corticipetal fibres from the main part of the lateral nucleus, although in no case was this nucleus alone involved by a local lesion. Thus, in rat *Th.* 5, the dorsal part of the ventral nucleus was injured on one side, and Marchi degeneration traced in the upper part of the parietal area of the cortex as far dorsally as a level 2·5 mm. from the mid-line. On the opposite side, the main part of the lateral nucleus and the antero-ventral nucleus were involved, and on this side degenerated fibres were traced up in the parietal area as far as the mid-line and also into the cingular cortex. Having established the relation between the latter cortex and the antero-ventral nucleus, we are left with the presumption that the degenerated fibres in the most dorsal part of the parietal area (*i.e.*, extending out from the mid-line for a distance of 2·5 mm.) are derived from the lateral nucleus. Similar evidence is provided by rat *Th.* 3. The conclusion is thus reached that the main part of the lateral nucleus of the thalamus is related by reciprocal fibre connections with the most dorsal limit of the parietal area on the lateral surface of the neopallium (probably in its more posterior part), close to the mid-line. This conclusion fits in with the conception that the great expansion of the main part of the lateral nucleus in higher mammals is associated directly with the progressive elaboration of the parietal "association" areas in these forms.

Nucleus lateralis, pars posterior.—This thalamic element is continuous rostrally with the main part of the lateral nucleus, and it extends downwards and backwards immediately above and behind the dorsal nucleus of the lateral geniculate body. There is abundant evidence to show that this element is homologous with at least a part of the "pulvinar" in higher forms (CLARK, 1930). In the experiments recorded in this paper there is no case in which an intrathalamic lesion localised to the pars posterior of the lateral nucleus was produced. In one case (rat *Th.* 7), the element was involved by the lesion, and the Marchi sections suggest that it is connected with the lower and anterior part of the area striata and with a strip of cortex immediately below and in front of this area. This conclusion accords with the appearance indicated in Weigert sections of normal material. Horizontal sections of the brain of lower mammals show cortical fibres leaving the medial aspect of the pars posterior of the lateral nucleus and passing forwards immediately medial to the optic radiations which leave the lateral geniculate body. Entering the internal capsule, they turn laterally in front of the optic radiations, and appear to be distributed to the cortex just anterior to the area striata. The experiments were not adequate for the determination of the corticifugal connections of the pars posterior. The investigation of the connections of this element is rendered difficult by the fact that it is traversed by fibres of passage—cortico-tectal fibres and optic tract fibres. Marchi material of the rat's brain after enucleation of one eye shows that while many of the optic tract fibres of retinal origin penetrate the pars posterior on their way to the anterior colliculus, none appear to terminate in it (CLARK, 1931).

Nucleus dorso-medialis.—The dorso-medial nucleus is the equivalent of the "medial nucleus" of human descriptive anatomy, and of the nucleus medialis dorsalis of recent authors. It has by many been regarded as a "palæothalamic" centre and classed among the "medial" group of nuclei which are credited with a great phylogenetic age. I have elsewhere (CLARK, 1932) pointed out that the dorso-medial nucleus is in reality one of the more recently developed elements of the thalamus, that it belongs to the upper functional levels of the thalamus, and that it reaches its most pronounced development in Man. On these grounds, it is desirable that the nucleus should not be included in the medial nuclear group and more especially so since the term "nucleus medialis" has been applied by different authors to so many thalamic elements that it has led to considerable confusion. It is largely as a result of this inconsistency in terminology that the "medial nucleus" is still stated to be an important terminal nucleus of the fillet system—and especially the trigeminal fillet.

In the three experiments in which the lemniscus system was injured (rats *Th.* 1, *BS* 1, and *BS* 2), the degenerated fillet fibres were traced into the ventral nucleus of the thalamus (as well as the anterior colliculus and the pretectal nucleus). In rat *Th.* 1 (in which the fillet had been cut across at its entry into the thalamus), there was a slight Marchi deposit in the caudal end of the dorso-medial nucleus, but in this case the lesion had involved the nucleus parafascicularis immediately behind, which is connected with the dorso-medial nucleus by short fibres, and the main part of the dorso-medial nucleus

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

contained no Marchi granules. With this exception, the dorso-medial nucleus in these experiments was entirely free of osmic deposit. These observations are in accord with the experimental studies of Probst (1900), who never found lemniscus fibres terminating in the dorso-medial nucleus (nucleus medialis *a* of his account).

In two experiments in which the cortex of the frontal pole was injured by a localised lesion (rats *F* 2 and *F* 3), Marchi degeneration was traced along the most medial fibres of the internal capsule in close relation to the septal region, and up the course of the inferior thalamic radiations into the medial medullary lamina and the dorso-medial nucleus, fig. 7. Such a cortico-thalamic connection was not found after lesions involving other parts of the cortex. In two cases (rats *Th.* 4 and *Th.* 6), the dorso-medial nucleus was involved by an intrathalamic lesion. In both degenerated fibres were traced from the site of the lesion into the most medially situated fasciculi of the internal capsule, occupying the same position as the cortico-thalamic fibres from the frontal pole to the dorso-medial nucleus just mentioned. In one, rat *Th.* 4, sections through the frontal pole showed that the Marchi deposit extended from the dorso-medial nucleus into the cortex of this region. The experiments thus show a reciprocal fibre connection between the frontal cortex and the dorso-medial nucleus in the rat. It is interesting to note here that there seems to be a relation between the relative size and differentiation of the dorso-medial nucleus in different mammalian brains and the elaboration of the cortex of the prefrontal areas. It may also be recalled that the dorso-medial nucleus is in fibre connection with the peri-ventricular system of fibres, and it thus provides a structural link through which it is theoretically possible for the prefrontal cortex to be brought into functional relation with hypothalamic centres.

Nucleus pretectalis.—There is some doubt as to whether this element should be included in the thalamus. It appears to occupy a position at the junction of the mid-brain and the diencephalon. Evidence is provided by rat *P* 2, fig. 3, *b*, that corticifugal fibres arising from the caudal part of the parietal area of the cortex terminate in the pretectal nucleus, while the evidence of rat *Th.* 1 suggests (but does not conclusively show) that it gives off no corticipetal fibres. This is in accord with the statement of Winkler (1921) to the effect that the pretectal (prebigeminal or posterior) nucleus remains unaffected by ablation of the greater part of the neopallium. On the other hand, Papez (1930) believes, on the basis of Marchi preparations, that corticipetal fibres arise in the pretectal nucleus of the rat, but he was unable to follow them to their termination. There is evidence to show that the pretectal nucleus receives fibres from the optic tract, but that these fibres are probably not of retinal origin (Clark, 1932). In the experiments in which the medial and trigeminal fillets were involved by the lesion, a few degenerated fibres were traced to the pretectal nucleus.

Nuclei of the Mid-line.—In several of the intrathalamic lesions the periventricular system was cut across, and in these cases a fine Marchi degeneration could be followed down for a short distance in a subependymal position. Evidence was also found in this material to indicate that descending fibres from the habenular nuclei and the dorso-

medial nucleus contribute to this system. In no case, however, could degeneration be certainly traced down from the mid-line nuclei into the hypothalamus. Normal Weigert sections show that such a connection does exist, but it is probably by short neurones in relays. Glorieux (1929), however, by the Marchi method in dogs' brains, followed fibres from the nucleus centralis medius (his "noyau réunissant") into the hypothalamus as well as into the substance of the dorso-medial nucleus. This author found no thalamo-cortical fibres from the mid-line nuclei, and the absence of such a connection is indicated in the case of rat *Th.* 3, in which a lesion on one side was confined at one point to the nucleus reuniens. Cajal described cortical connections for the nuclei of the mid-line in his rodent material, but this observation has not been borne out by experimental evidence. In none of the cases in which cortical lesions were produced was it possible to trace degenerated fibres as far as the mid-line nuclei.

Corticifugal Connections.—In all the experiments in which neopallial lesions were produced an ensuing Marchi degeneration was traced to some part of the thalamus. It appears that in the rat cortico-thalamic fibres terminate in all the principal nuclei of the thalamus with the exception of the nucleus antero-medialis, nucleus medialis ventralis and the nuclei of the mid-line. The wide distribution of cortico-thalamic connections was described by Cajal in rodents. It is interesting to note that in higher mammals such connections are apparently very insignificant. Thus, in the monkey, Minkowski (1924) and Biemond (1930) were unable to trace any corticifugal fibres to the ventral nucleus, and only a few doubtful fibres (from the region of the frontal lobe) to the lateral nucleus. It is necessary that such observations should be taken into account, since such cortico-thalamic connections have been postulated in man to explain the cortical control of thalamic activities, and thus to account for the contrast between thalamic and cortical types of sensation (see Head and Holmes (1912) and Stopford (1930)).

Our experiments on the rat indicate that cortico-tectal fibres only arise from the occipital lobe of the cerebrum, and thus accord with the findings of other investigators. The evidence of rat *P* 2 shows that cortico-pretectal fibres arise from the caudal part of the parietal area.

In rat *F* 3 a conspicuous cortico-subthalamic connection was demonstrated after a lesion involving the frontal pole, fig. 7, *c*. Such a connection was not found after cortical lesions elsewhere, though in all cases corticifugal fibres were traced down in the crus cerebri to the mid-brain and towards the pons. They were not followed down further than this level.

In none of these cortical lesions has it been possible to demonstrate convincingly the presence of cortico-striate connections. The sections indicate, indeed, that Marchi degeneration found in the putamen and the caudate nuclei is confined to fibres of passage.

Corticipetal Connections.—The experiments lead to the conclusion that, in the rat, all the principal nuclei of the thalamus proper send off projection fibres to the neopallium

with the exception of the antero-medial nucleus, nucleus medialis ventralis and nuclei of the mid-line. It would appear, therefore, that these are the only thalamic elements which have any title to be included in what has been termed the "palæothalamus."*

Descending Thalamic Tracts.—No evidence was provided by the experiments in which lesions were made in the thalamus proper that any descending thalamic tracts reach down below the level of the rostral part of the mid-brain. Within recent years it has been shown that descending fibres once supposed to spring from the thalamus really have their cells of origin in the globus pallidus of the corpus striatum. The pallido-olivary and the pallido-reticular tracts belong to this category.

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* Since the manuscript of this paper was completed, there has come to hand a recent monograph by S. Poliak on "The Main Afferent Fibre Systems of the Cerebral Cortex in Primates" (University of California Press, 1932). This investigation, however, concerns itself primarily with the delineation of the auditory, visual, and general sensory areas of the cortex by tracing Marchi degeneration after lesions involving the *internal capsule* of the monkey's brain. The precise relation of the nuclear elements of the thalamus to different parts of the cortex has not been considered in detail (with the exception of the lateral geniculate body). Important though this monograph certainly is, its results are not sufficiently closely related to this report on the connections of the rat's thalamus to require consideration here.

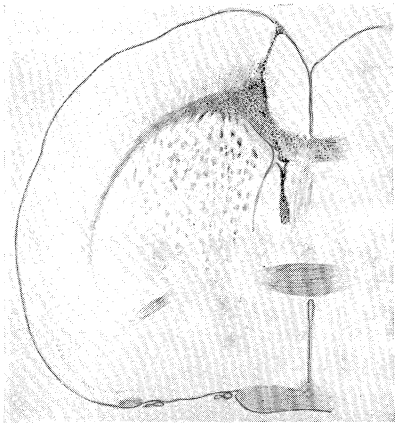

FIG. 2*a*.—Rat P 1.

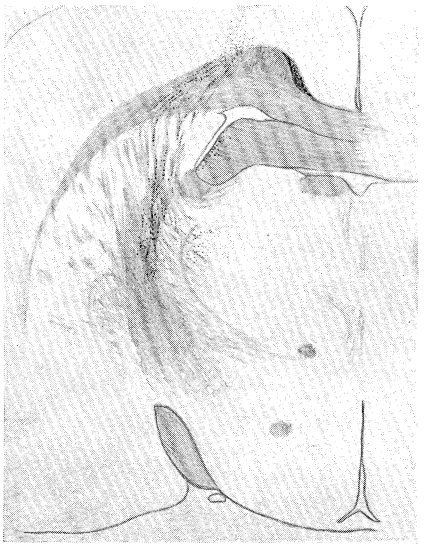

FIG. 2*b*.—Rat P 1.

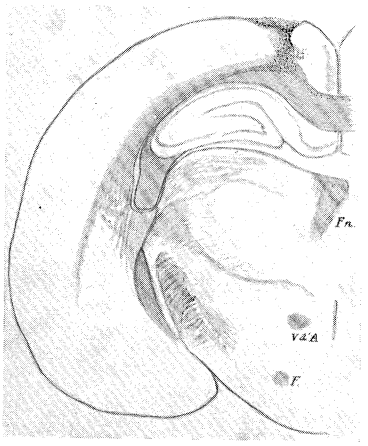

FIG. 5*a*.—Rat C 1.

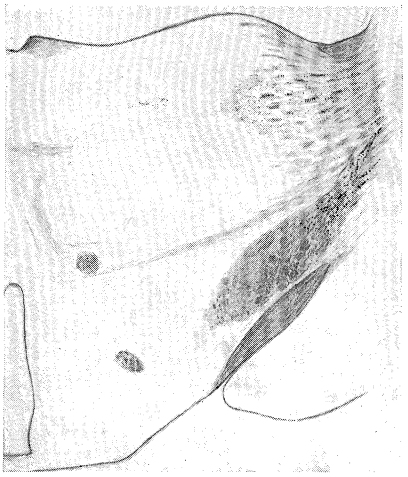

FIG. 3*a*.—Rat P 2.

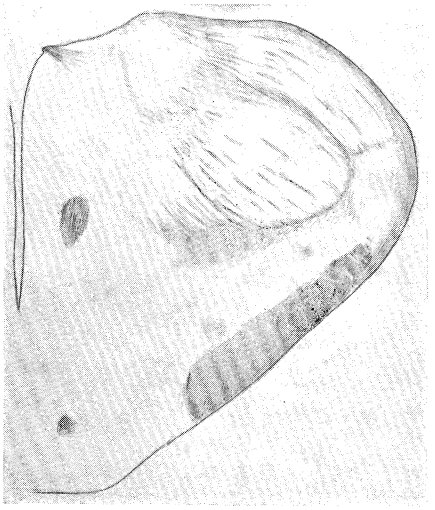

FIG. 3*b*.—Rat P 2.

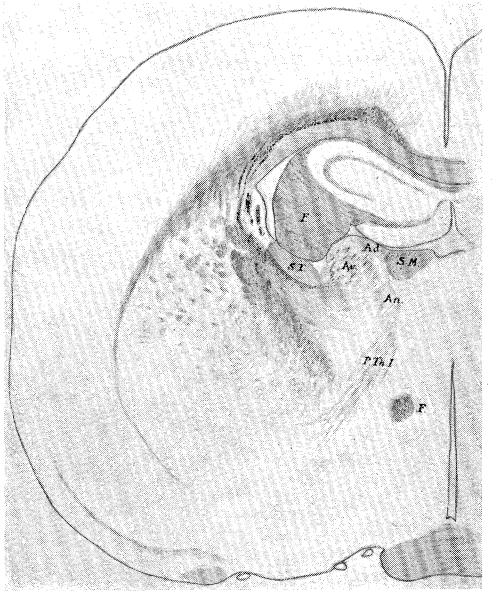

FIG. 5*b*.—Rat C 1.

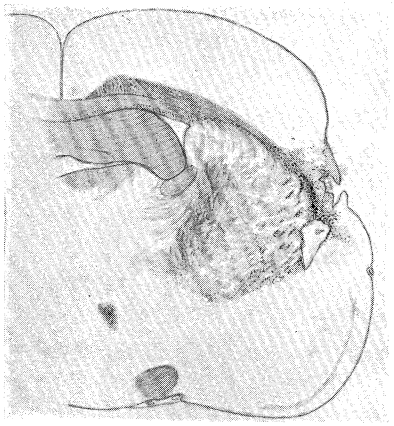

FIG. 4*a*.—Rat T.

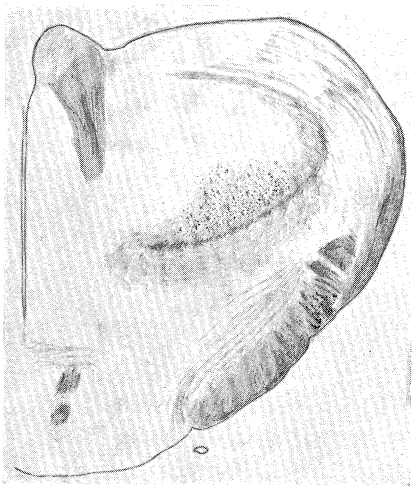

FIG. 4*b*.—Rat T.

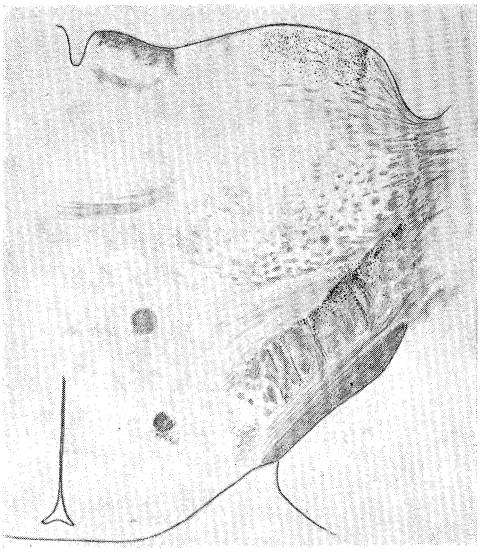

FIG. 6.—Rat C 2.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

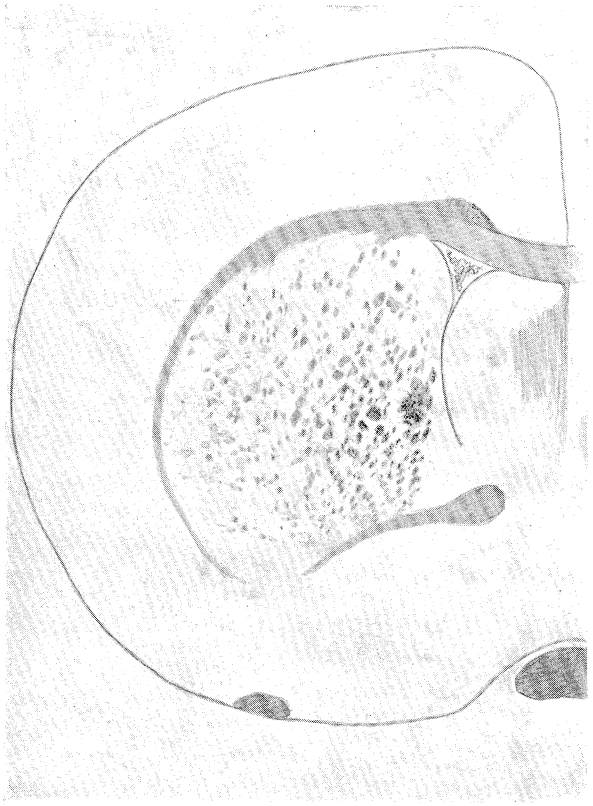

FIG. 7*a*.—Rat F 3.

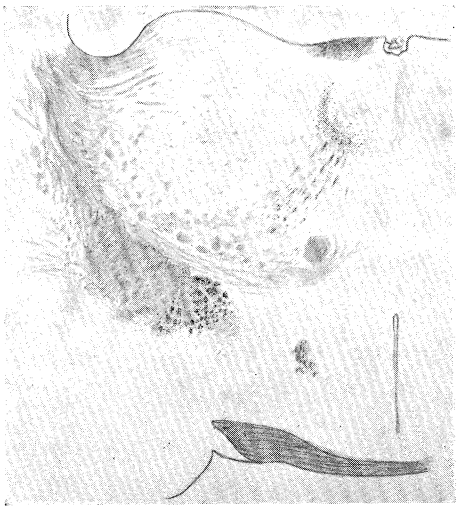

FIG. 7*b*.—Rat F 3.

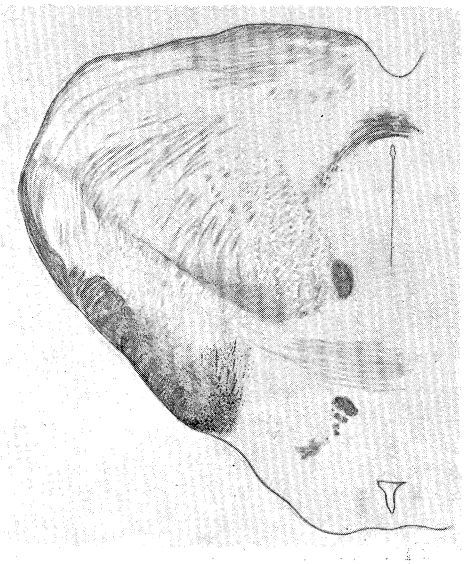

FIG. 7*c*.—Rat F 3.

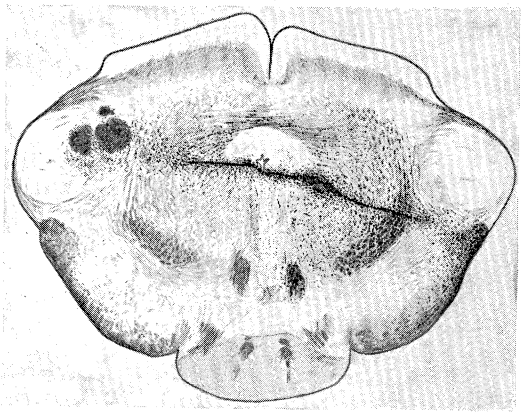

FIG. 8*a*.—Rat Th. 1.

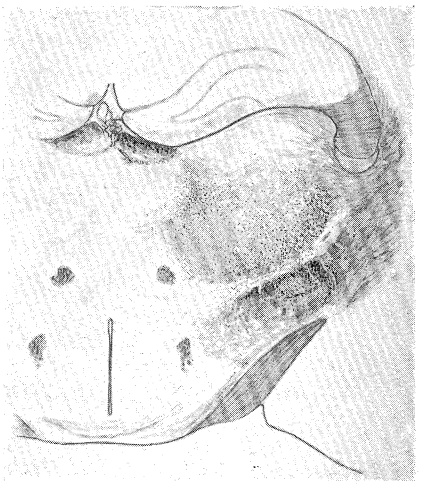

FIG. 8*b*.—Rat Th. 1.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

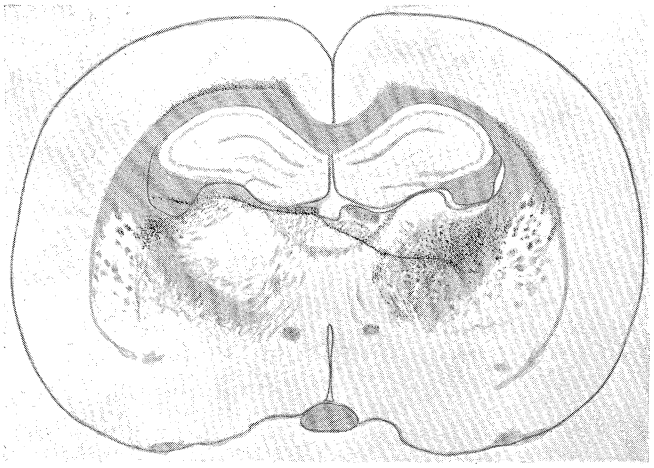

Fig. 9*a*.—Rat Th. 2.

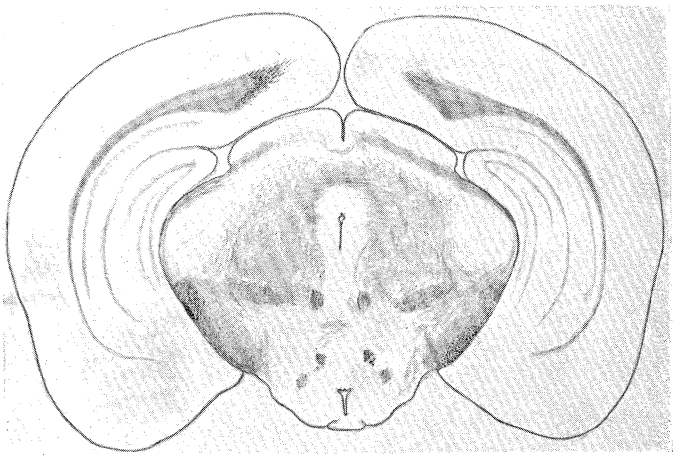

Fig. 9*b*.—Rat Th. 2.

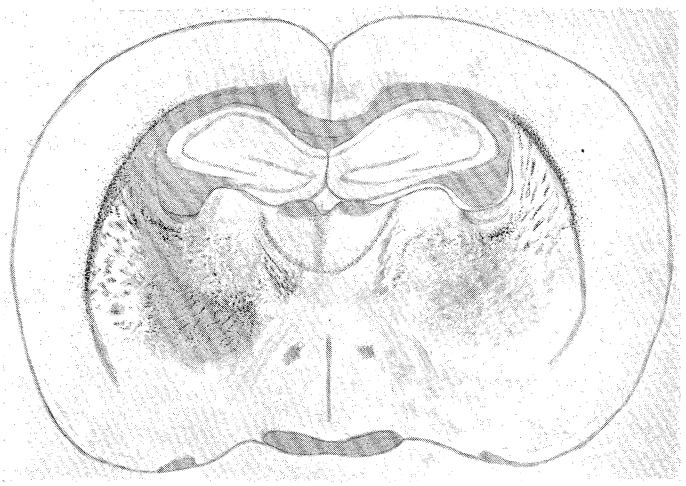

Fig. 10*a*.—Rat Th. 3.

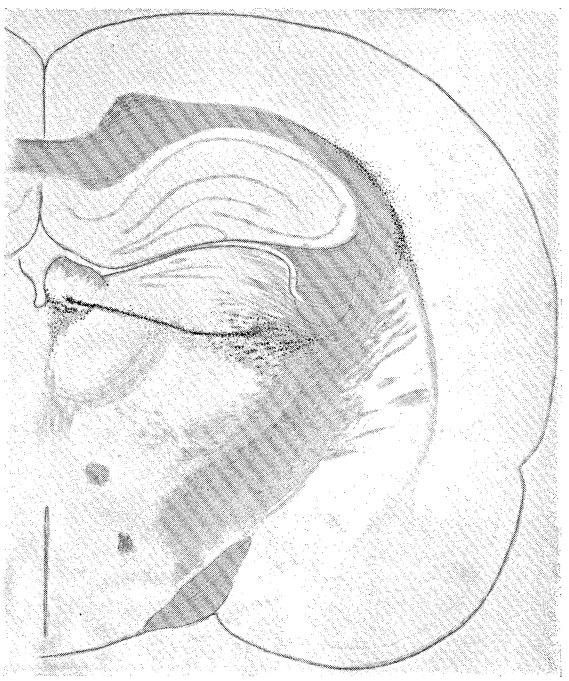

Fig. 10*b*.—Rat Th. 3.

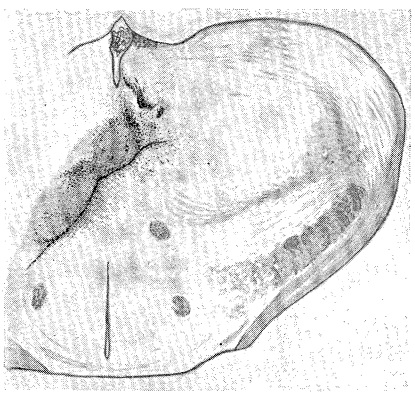

Fig. 11*a*.—Rat Th. 4.

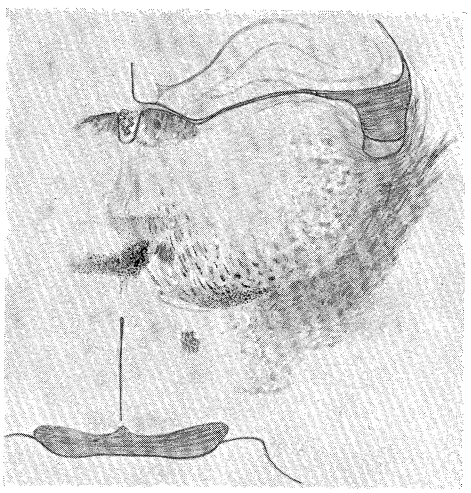

Fig. 11*b*.—Rat Th. 4.

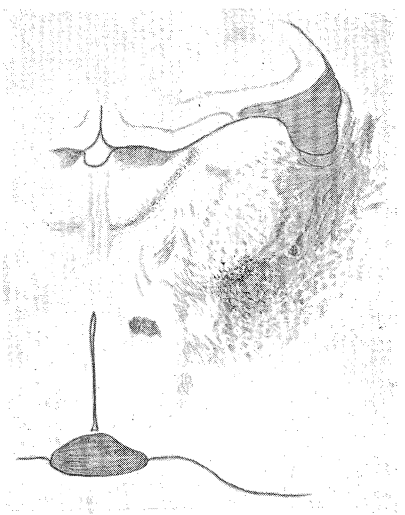

Fig. 11*c*.—Rat Th. 4.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

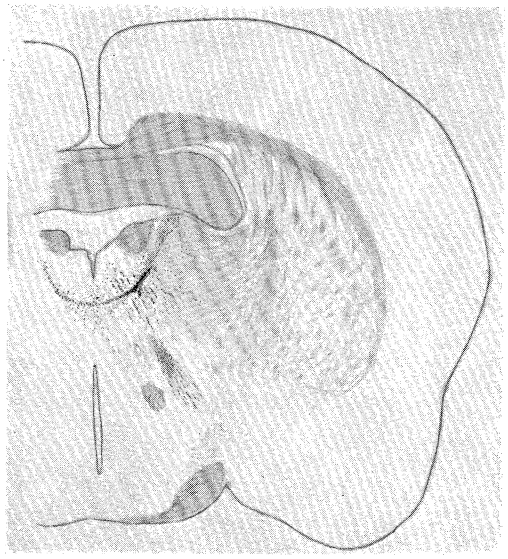

FIG. 12*a*.—Rat Th. 6.

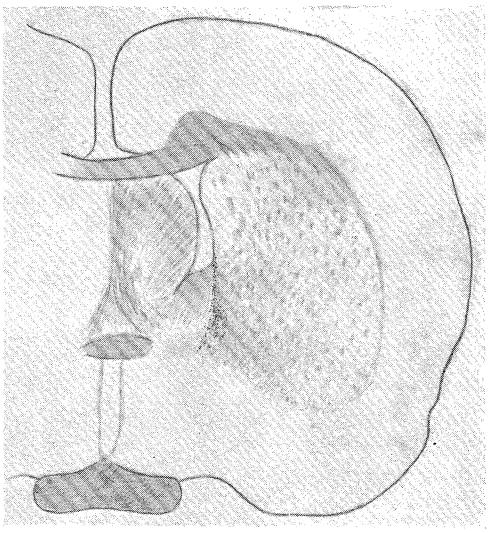

FIG. 12*b*.—Rat Th. 6.

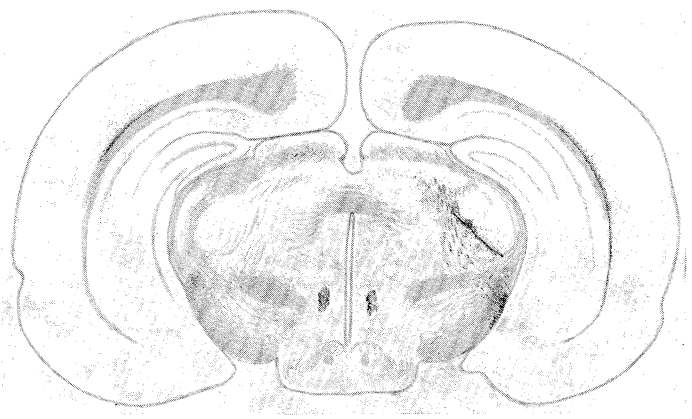

FIG. 13.—Rat Th. 7.

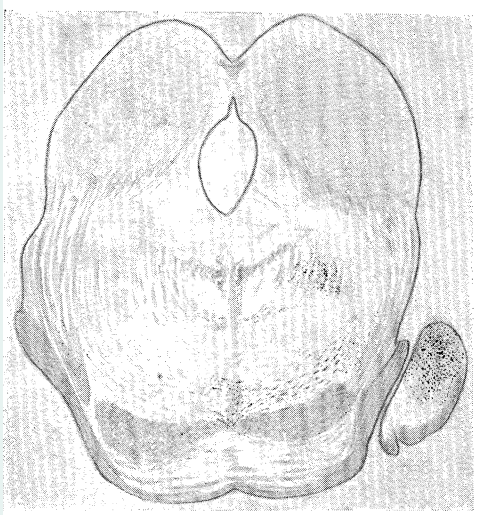

FIG. 14*a*.—Rat BS 1.

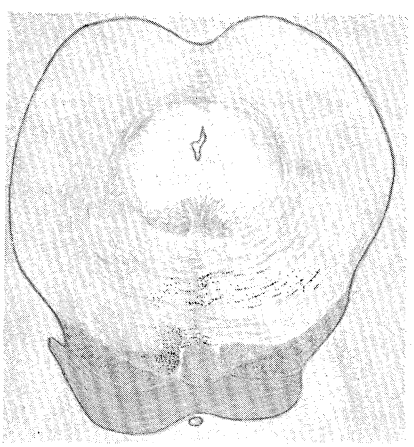

FIG. 14*b*.—Rat BS 1.

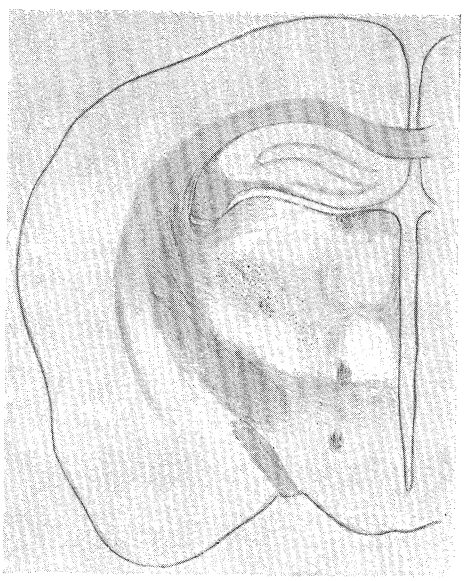

FIG. 14*c*.—Rat BS 1.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

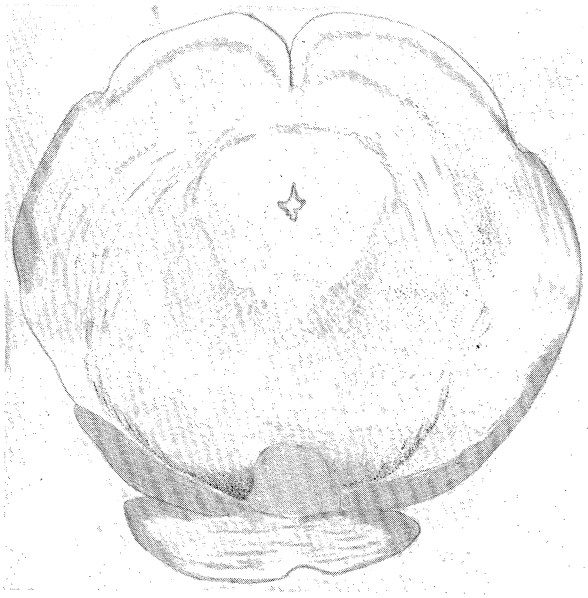

FIG. 15*a*.—Rat BS 2.

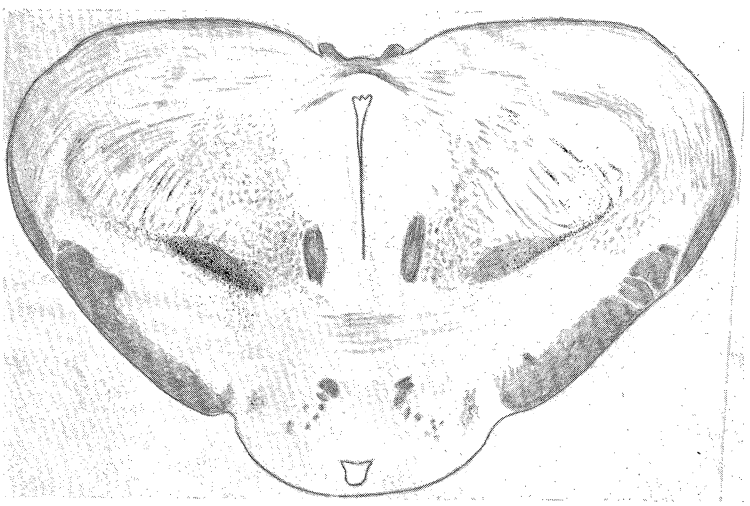

FIG. 15*b*.—Rat BS 2.

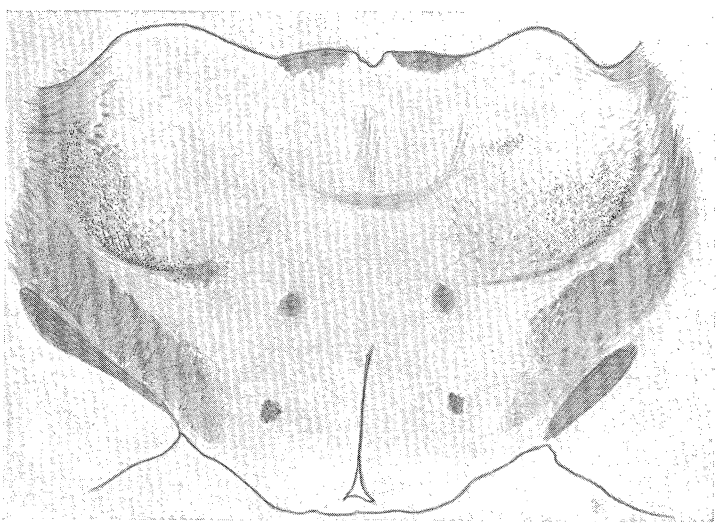

FIG. 15*c*.—Rat BS 2.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

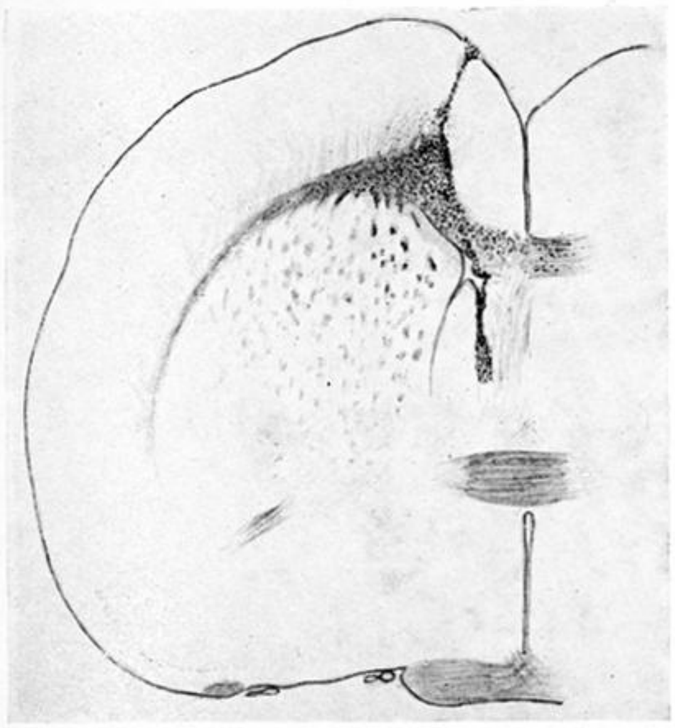

FIG. 2*a*.—Rat P 1.

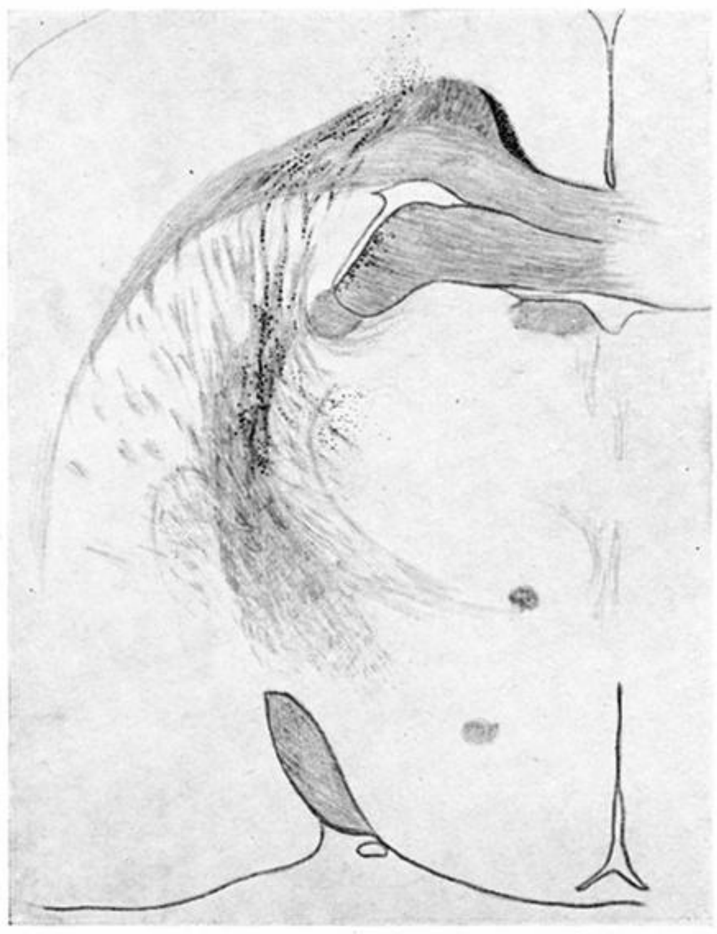

FIG. 2*b*.—Rat P 1.

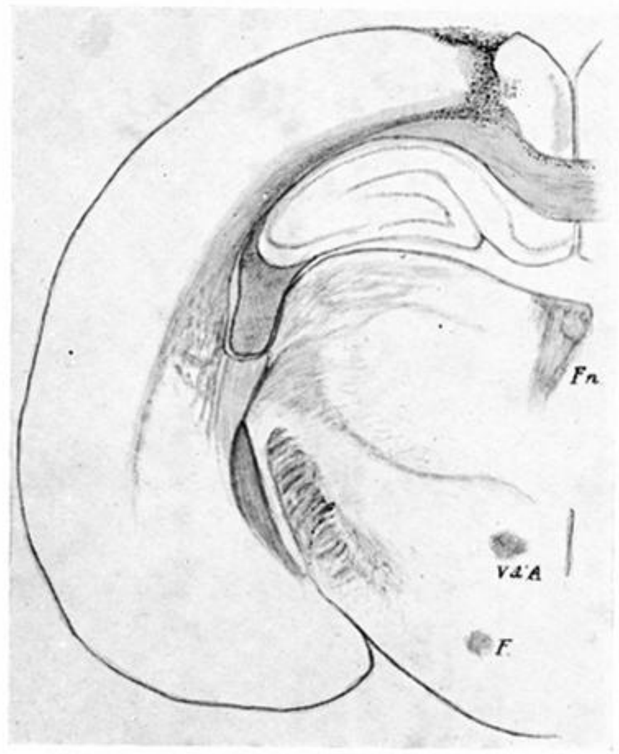

FIG. 5*a*.—Rat C 1.

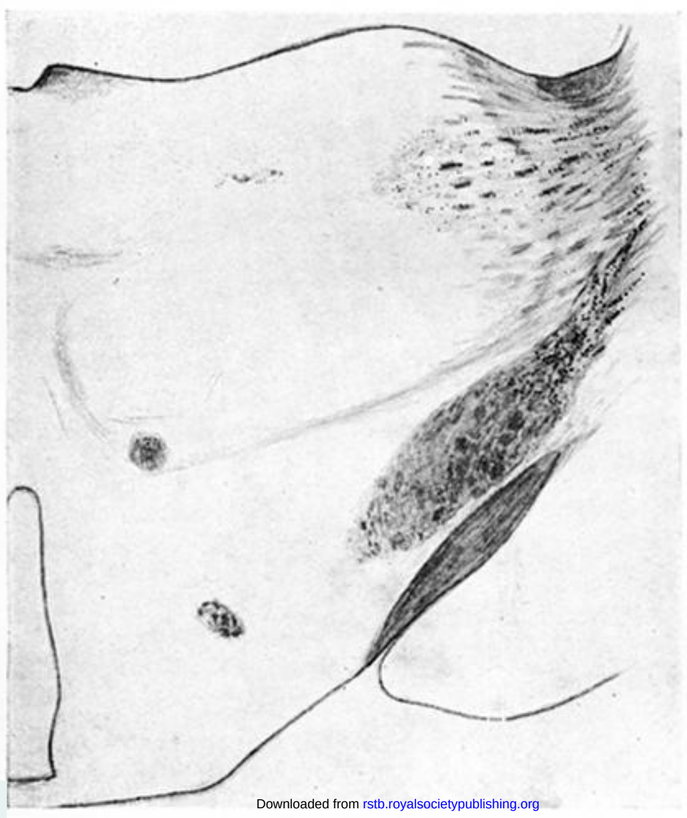

FIG. 3*a*.—Rat P 2.

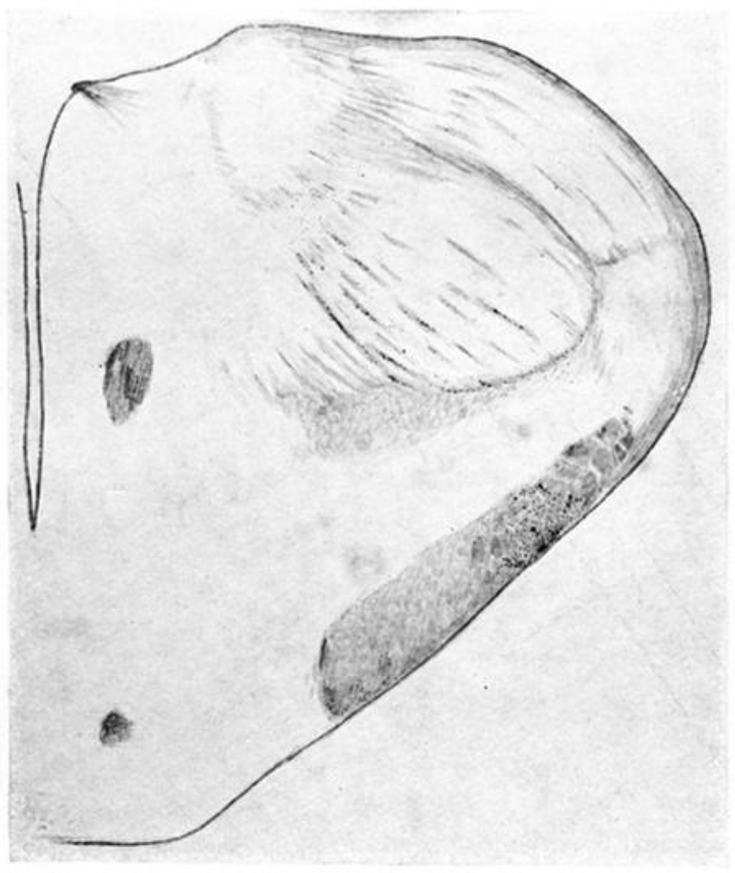

FIG. 3*b*.—Rat P 2.

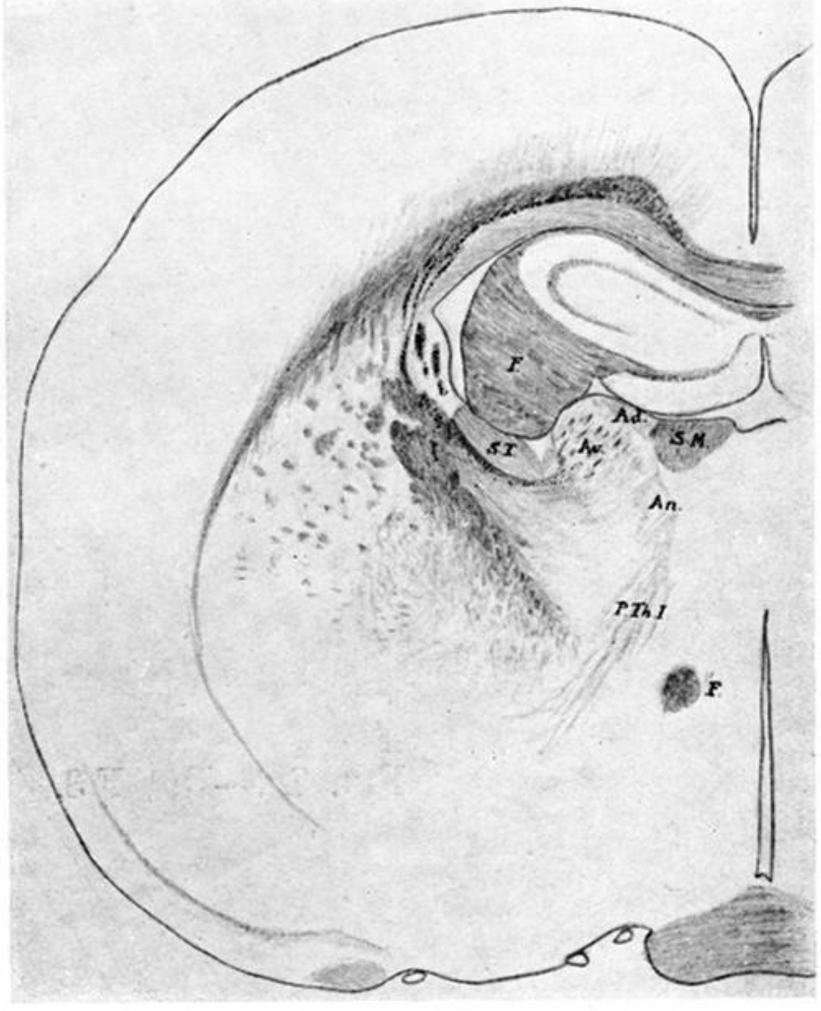

FIG. 5*b*.—Rat C 1.

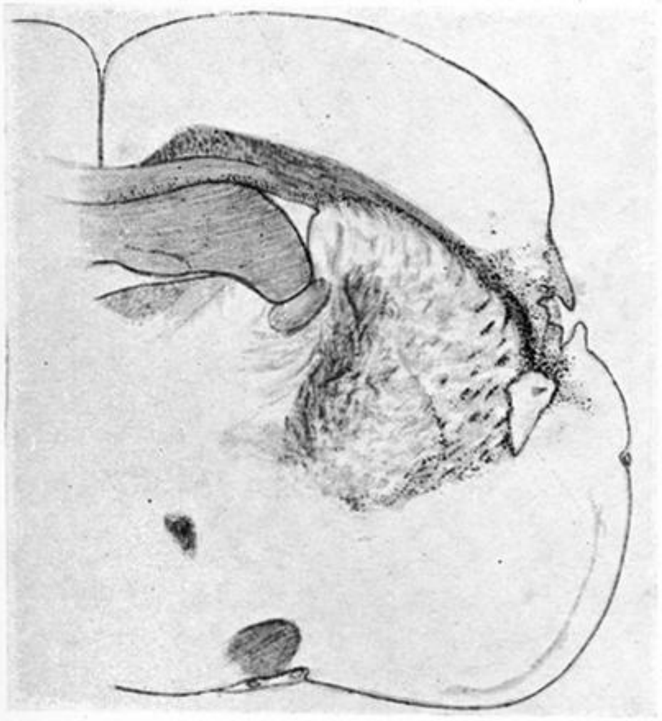

FIG. 4*a*.—Rat T.

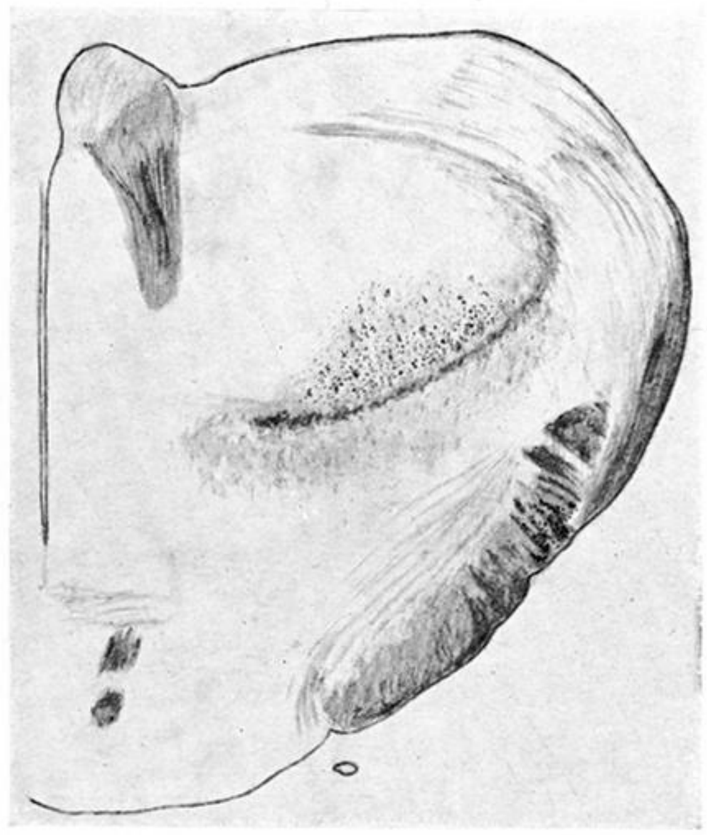

FIG. 4*b*.—Rat T.

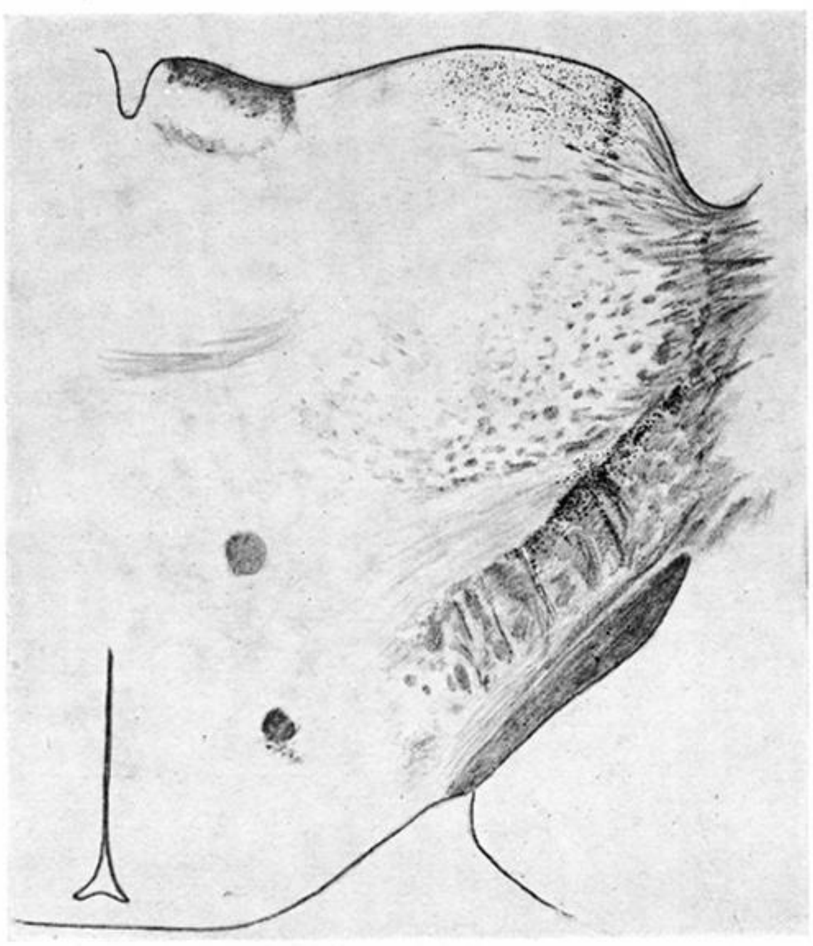

FIG. 6.—Rat C 2.

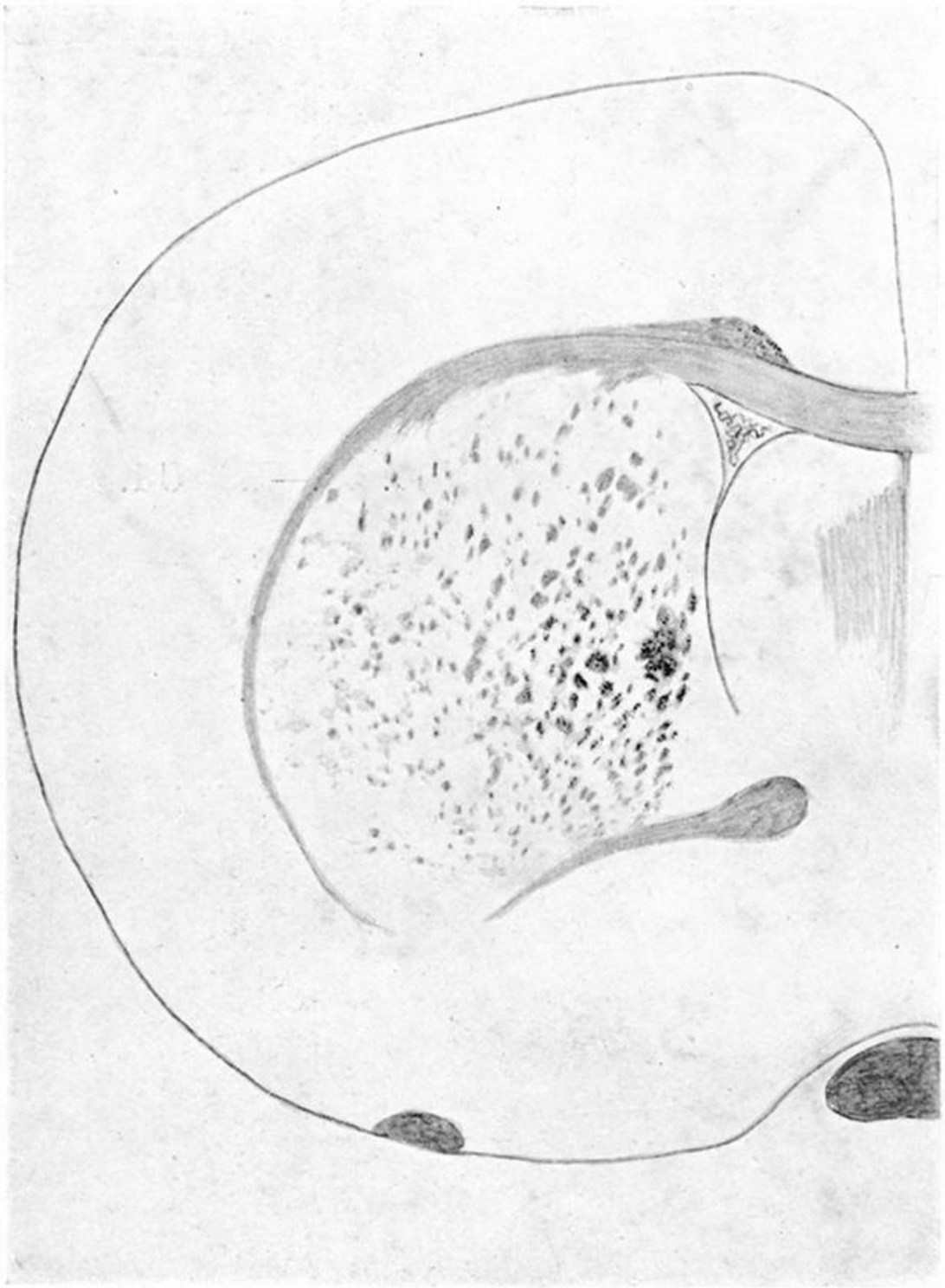

FIG. 7*a*.—Rat F 3.

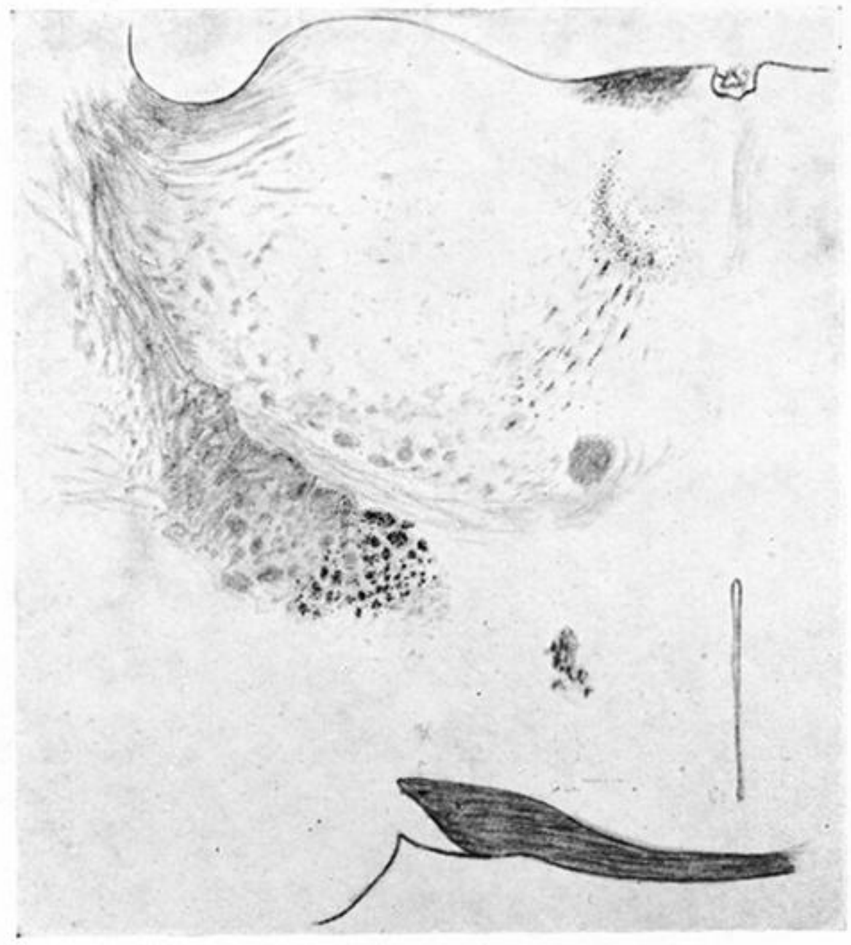

FIG. 7*b*.—Rat F 3.

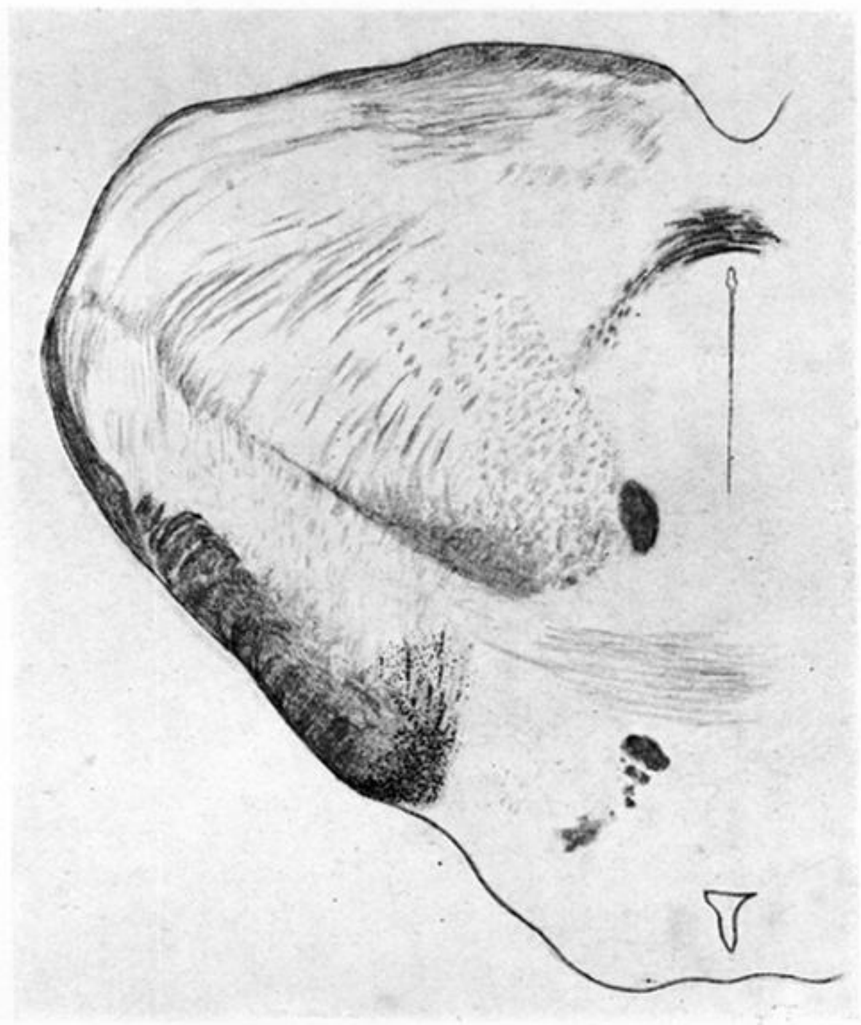

FIG. 7*c*.—Rat F 3.

FIG. 8*a*.—Rat Th. 1.

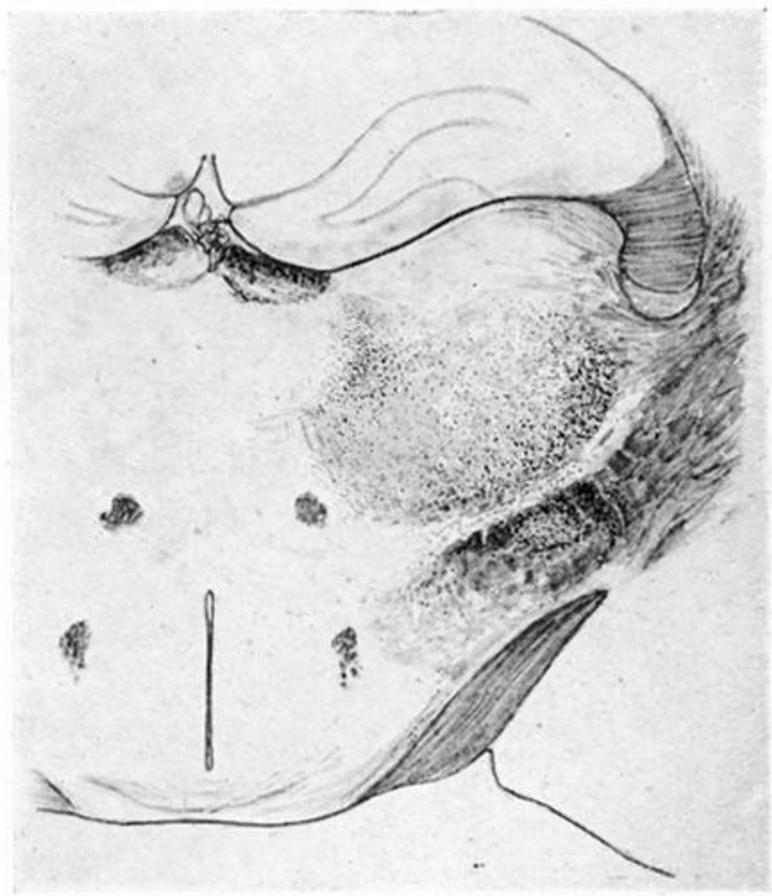

FIG. 8*b*.—Rat Th. 1.

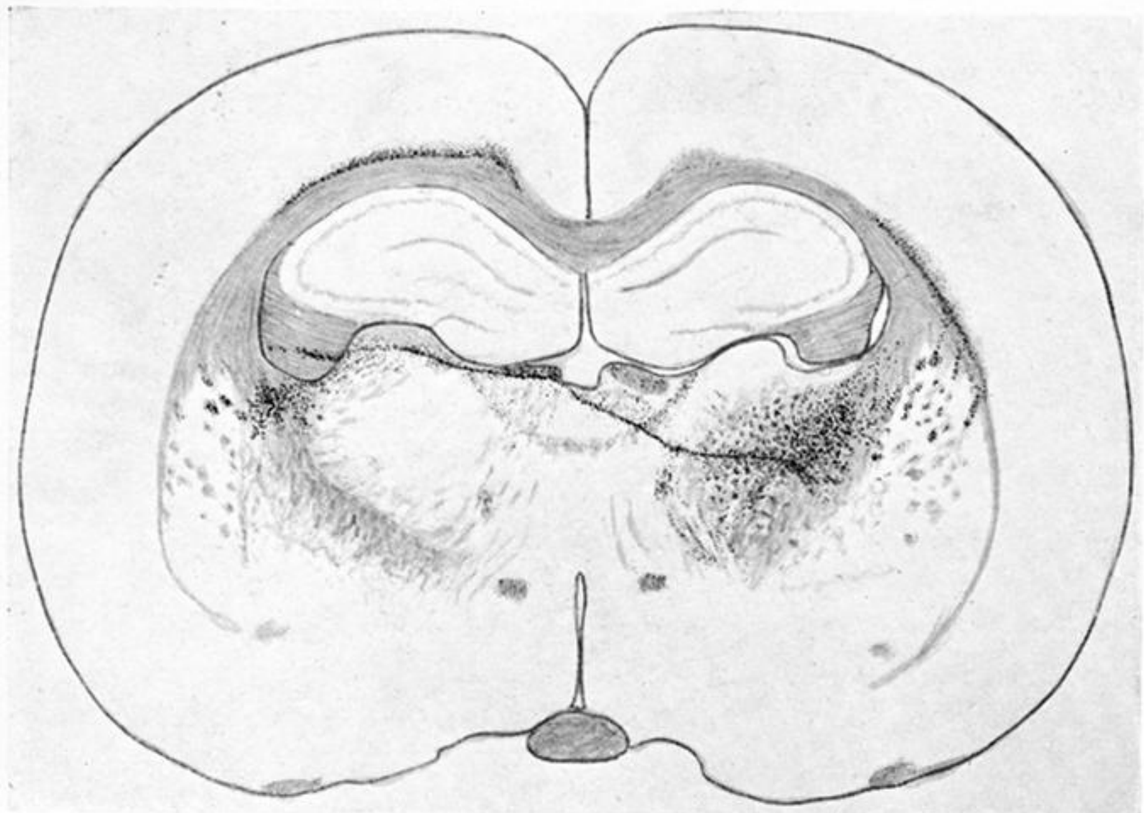

FIG. 9*a*.—Rat Th. 2.

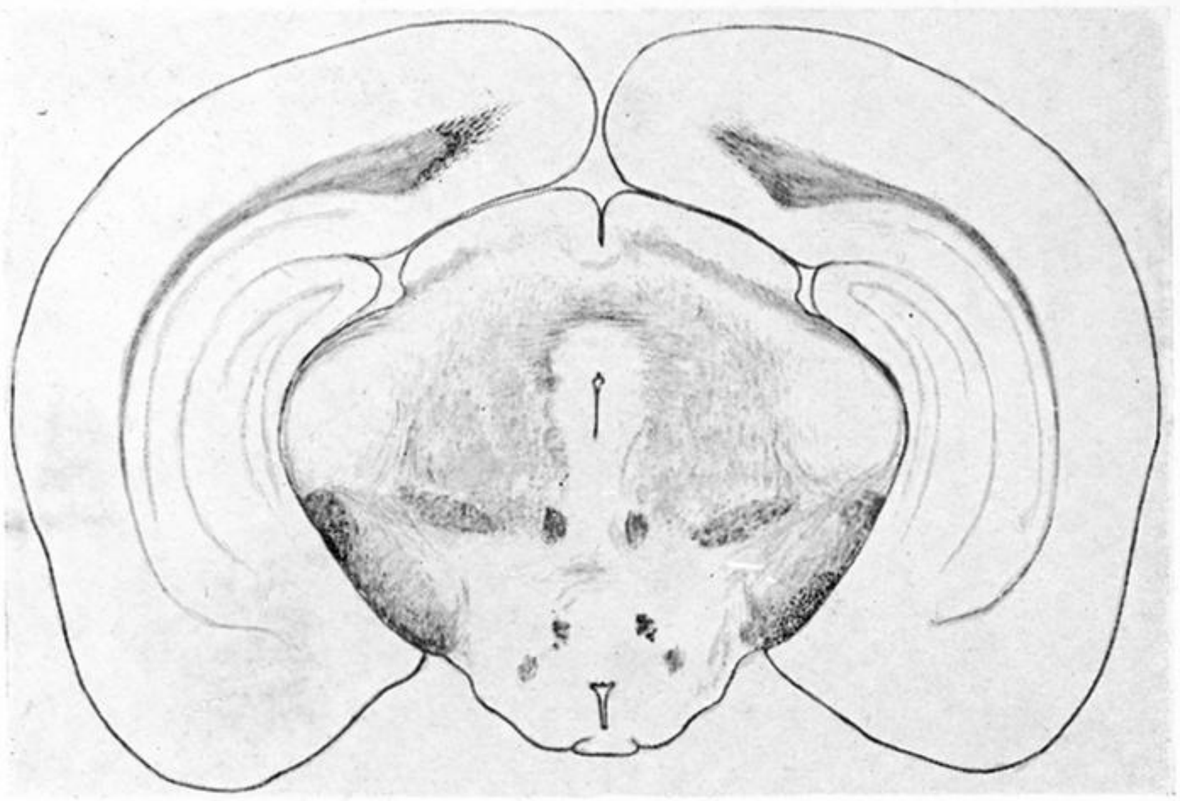

FIG. 9*b*.—Rat Th. 2.

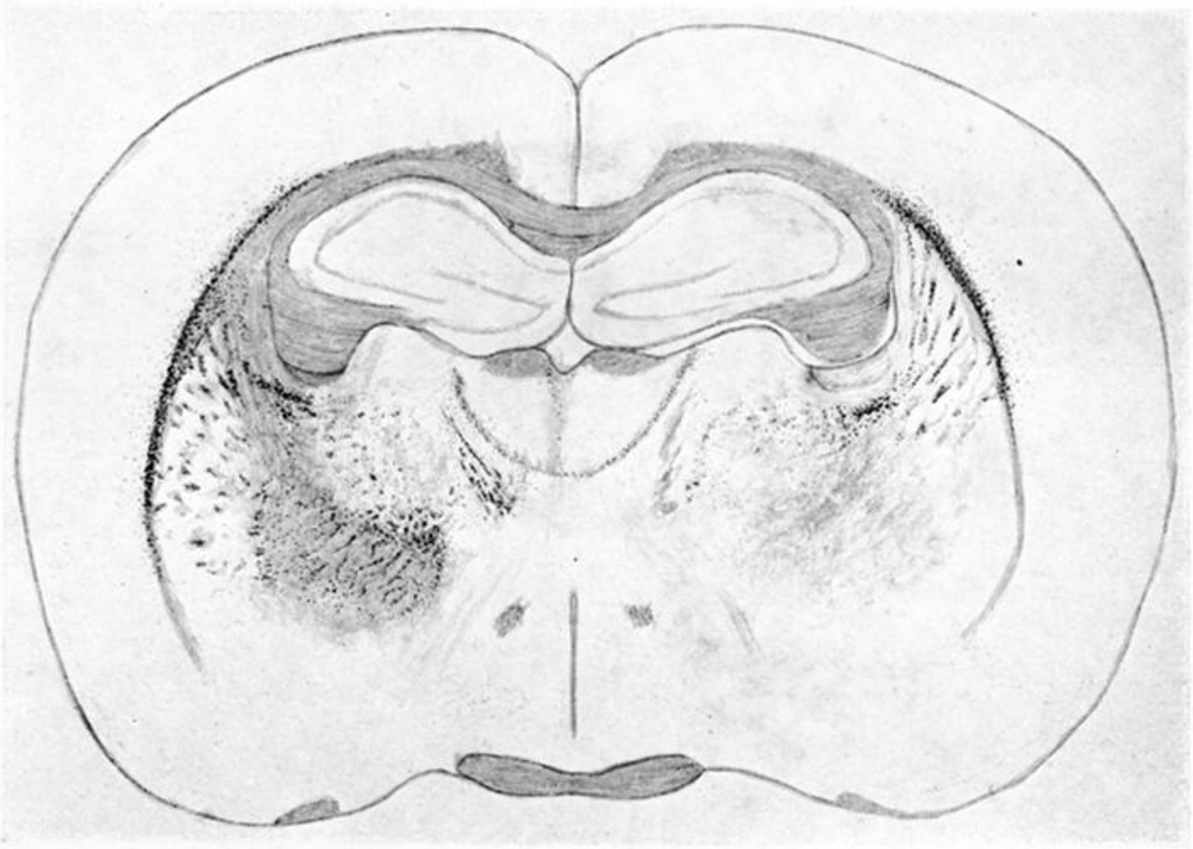

FIG. 10*a*.—Rat Th. 3.

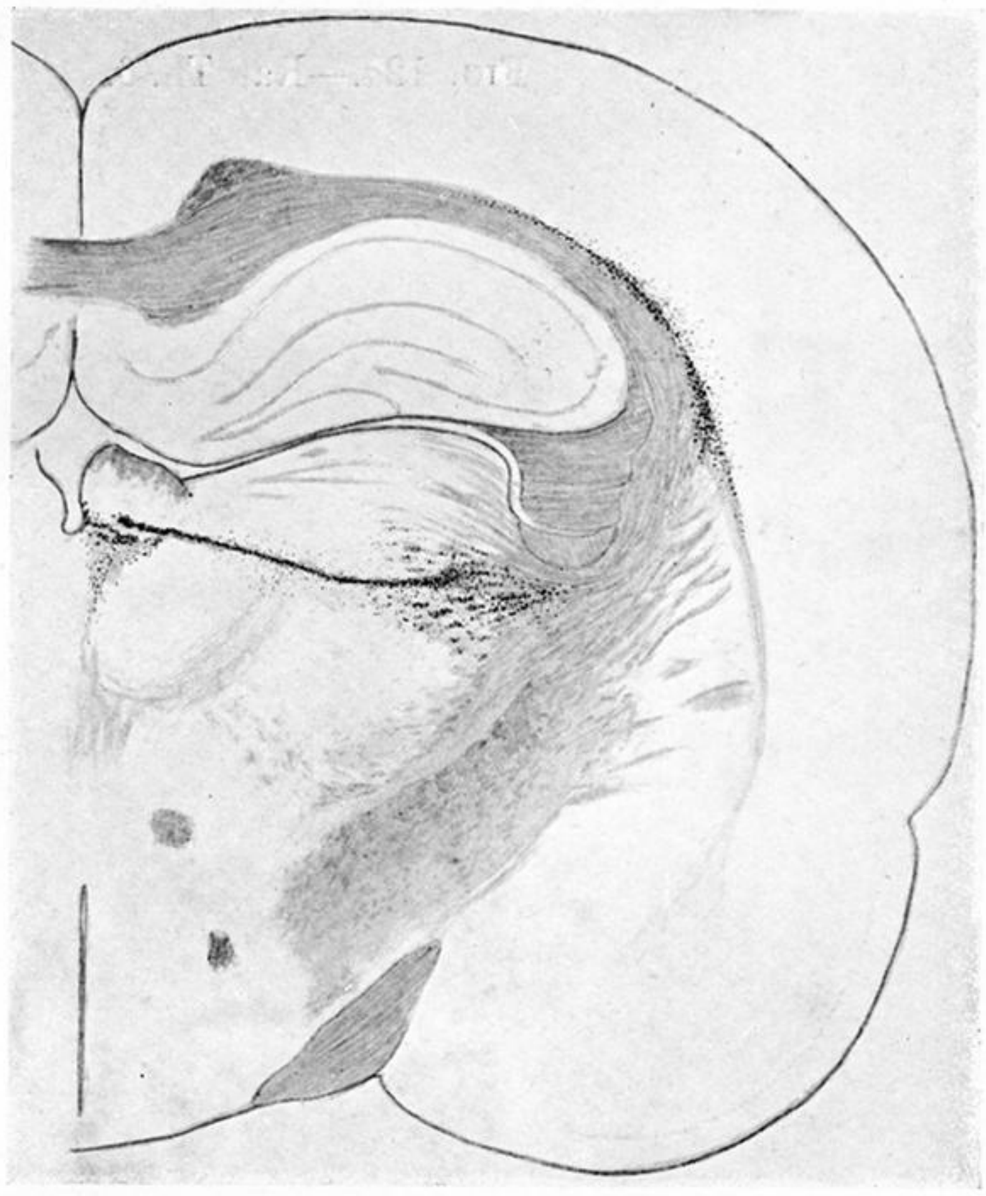

FIG. 10*b*.—Rat Th. 3.

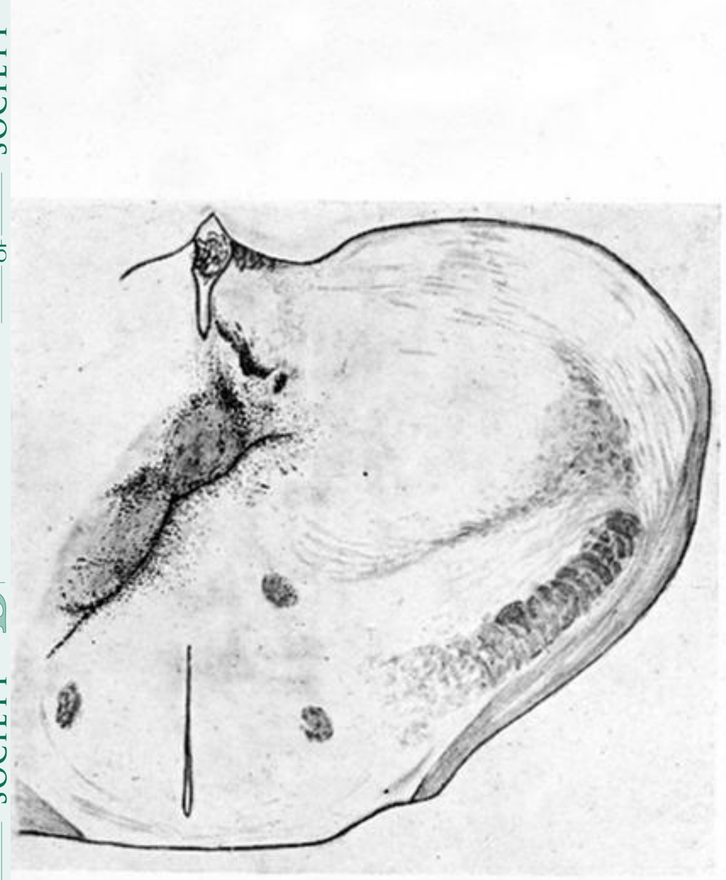

FIG. 11*a*.—Rat Th. 4.

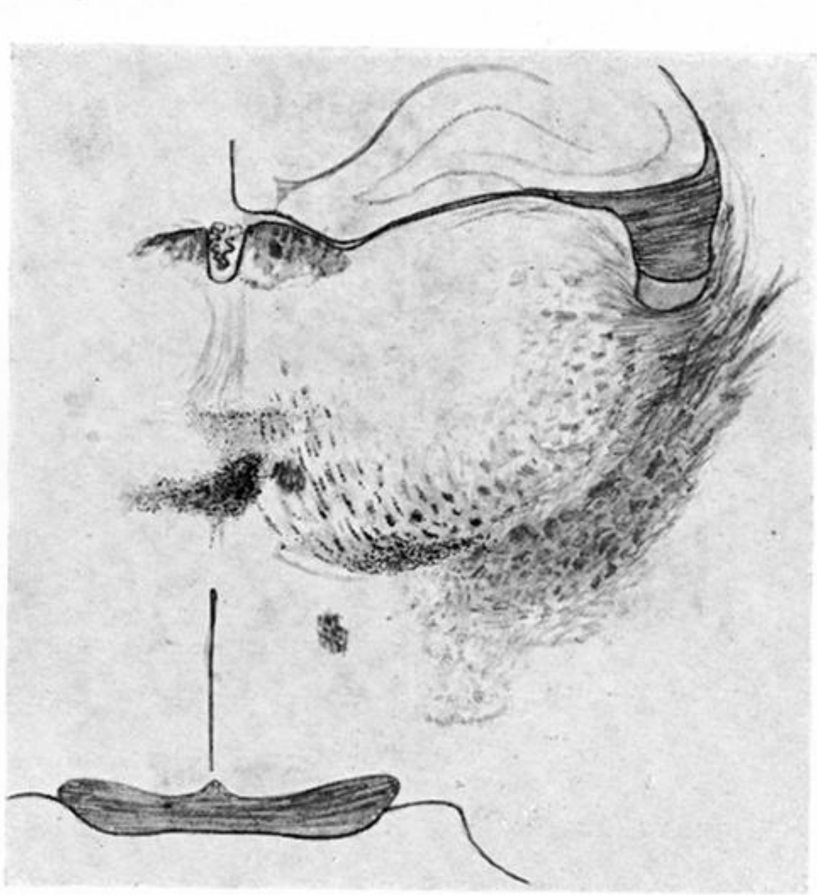

FIG. 11*b*.—Rat Th. 4.

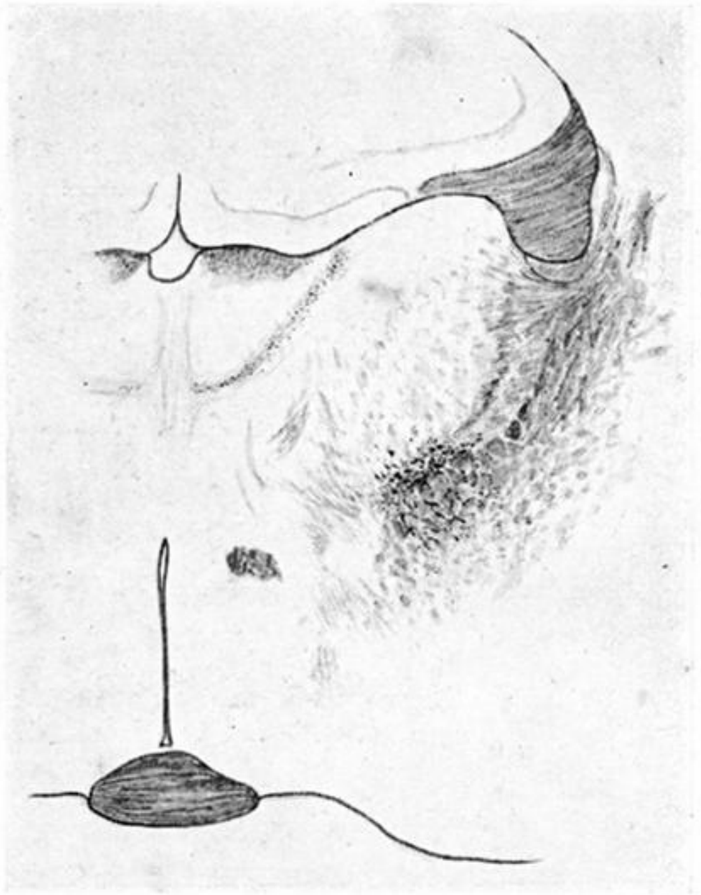

FIG. 11*c*.—Rat Th. 4.

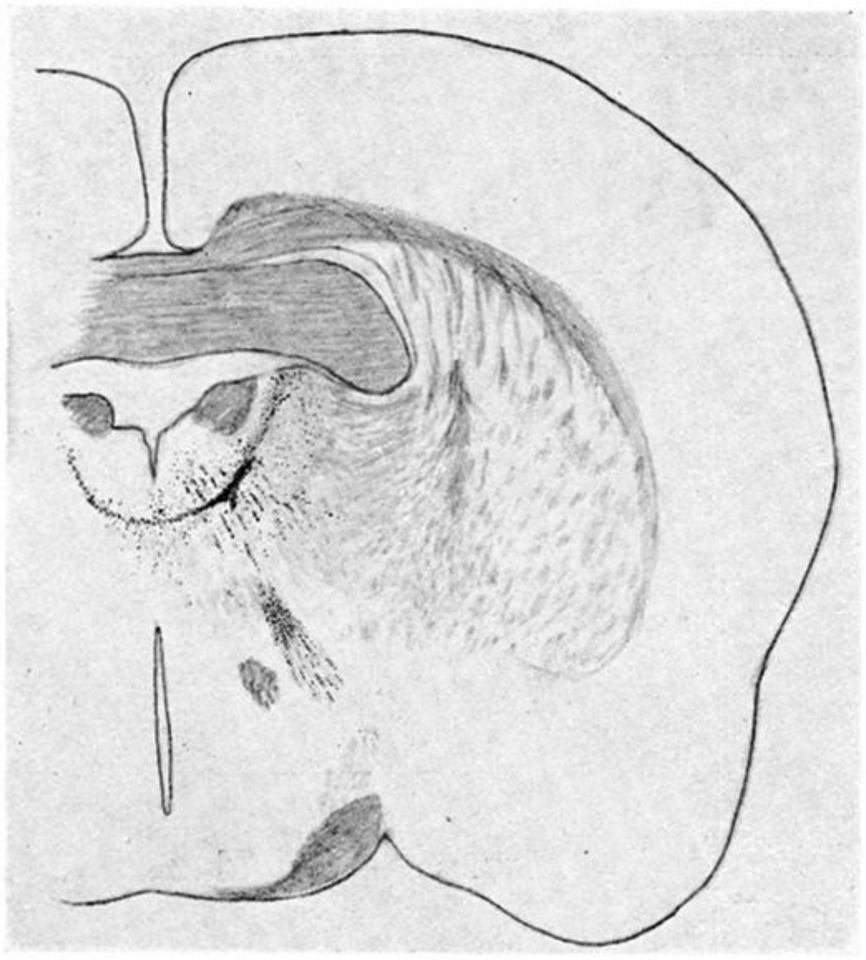

FIG. 12*a*.—Rat Th. 6.

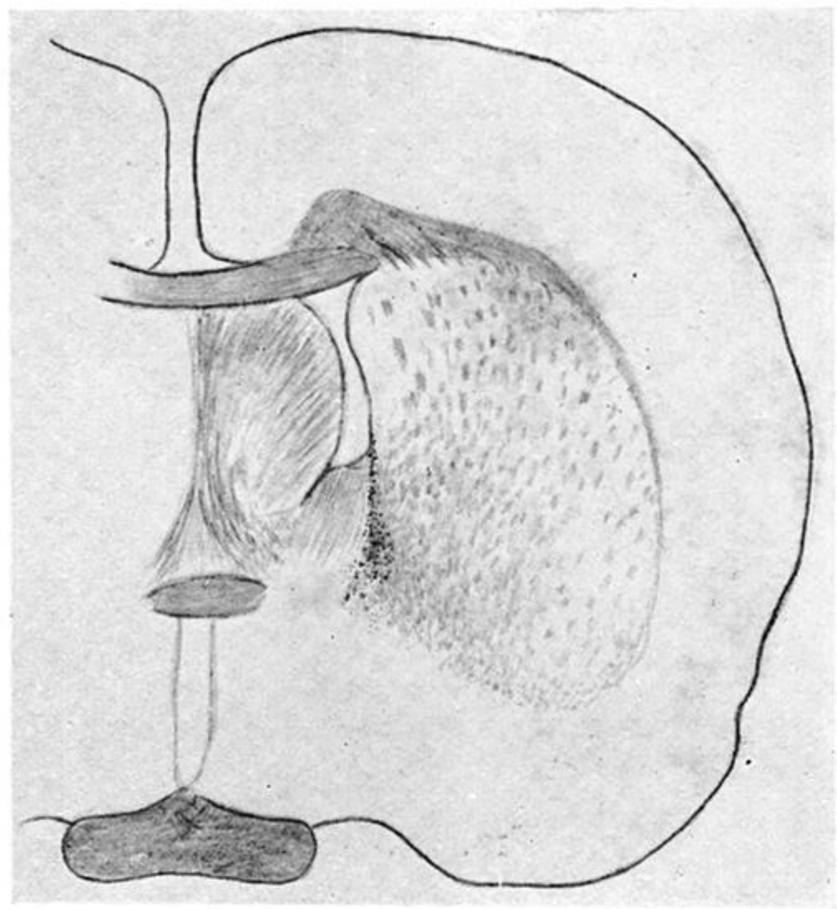

FIG. 12*b*.—Rat Th. 6.

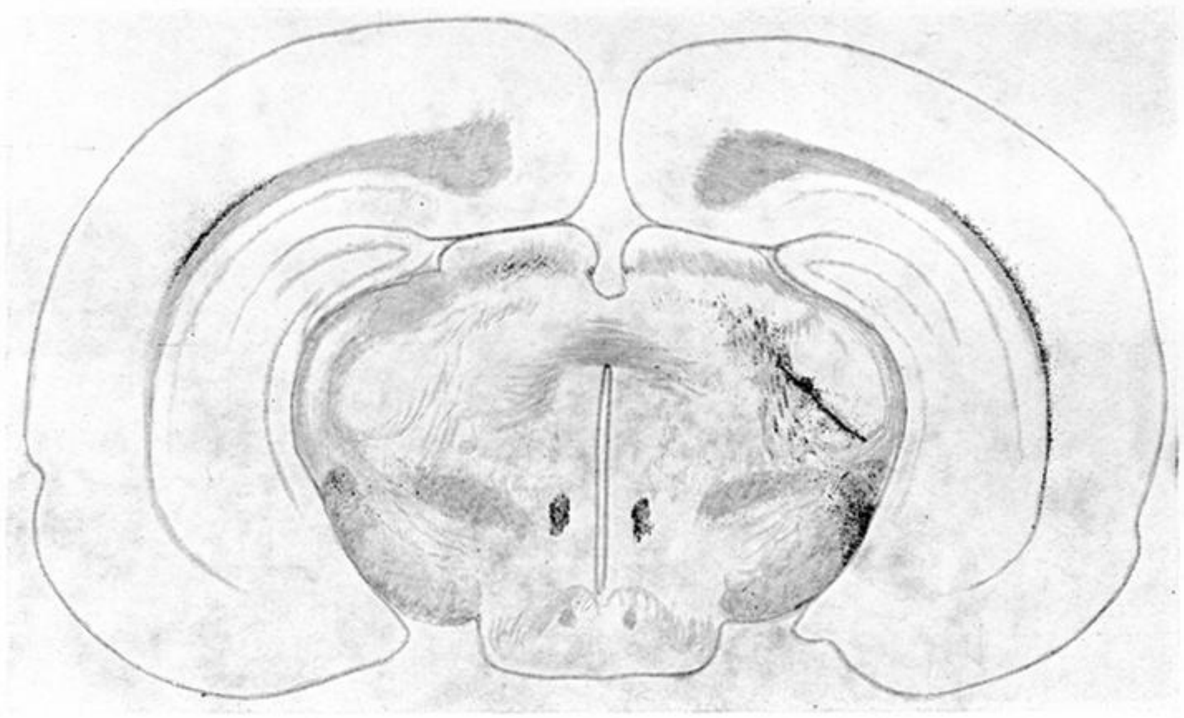

FIG. 13.—Rat Th. 7.

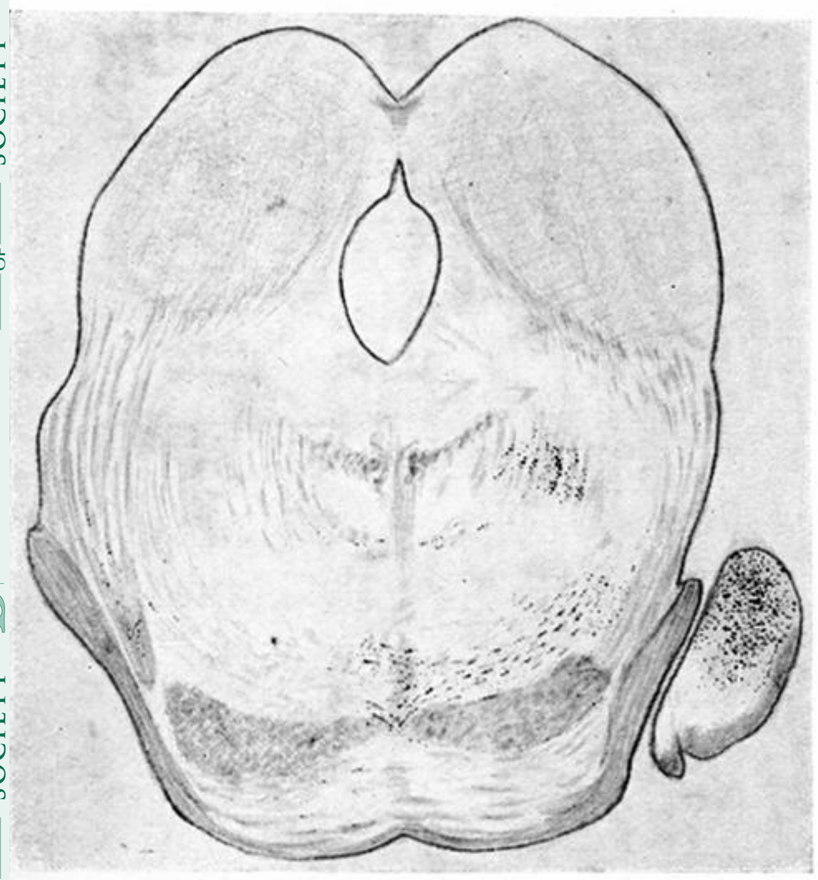

FIG. 14*a*.—Rat BS 1.

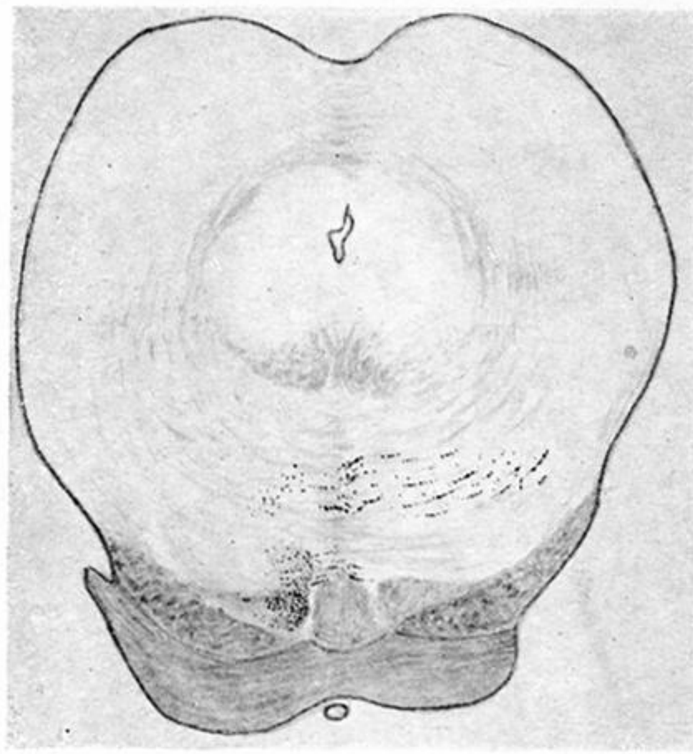

FIG. 14*b*.—Rat BS 1.

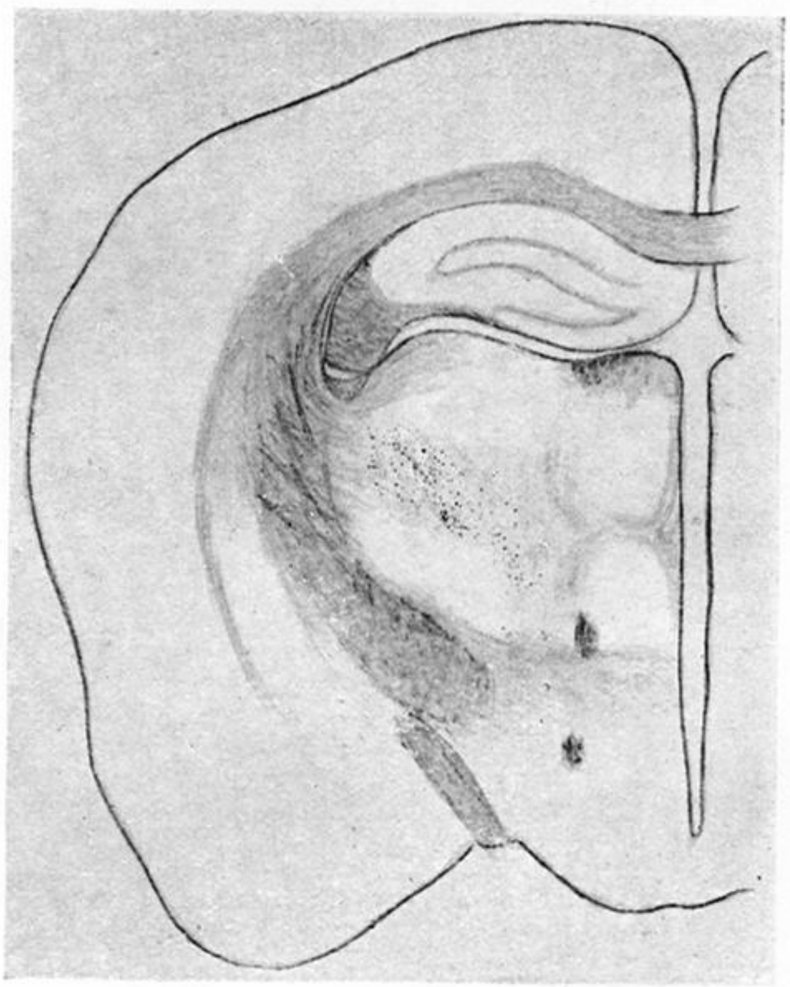

FIG. 14*c*.—Rat BS 1.

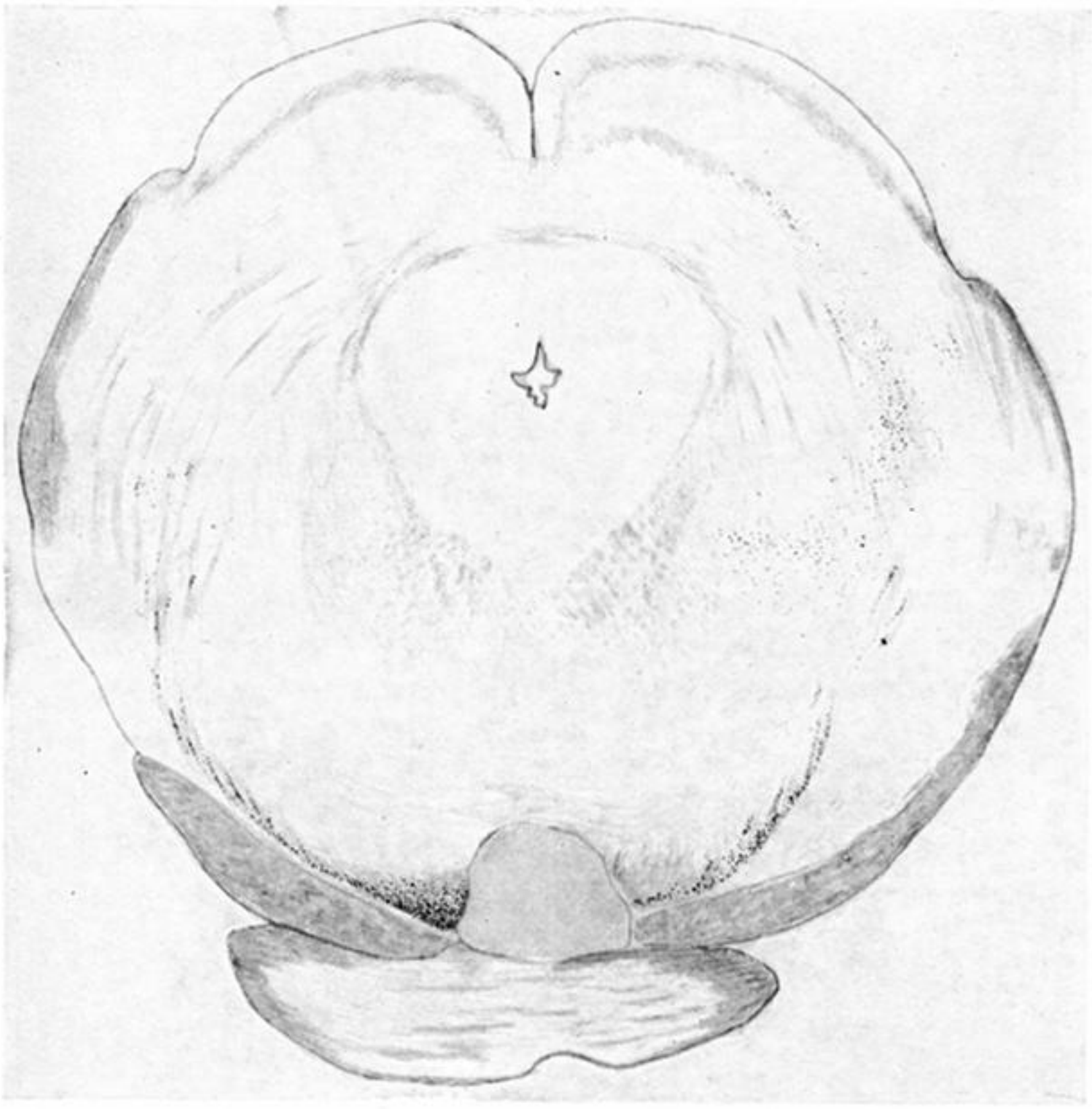

FIG. 15*a*.—Rat BS 2.

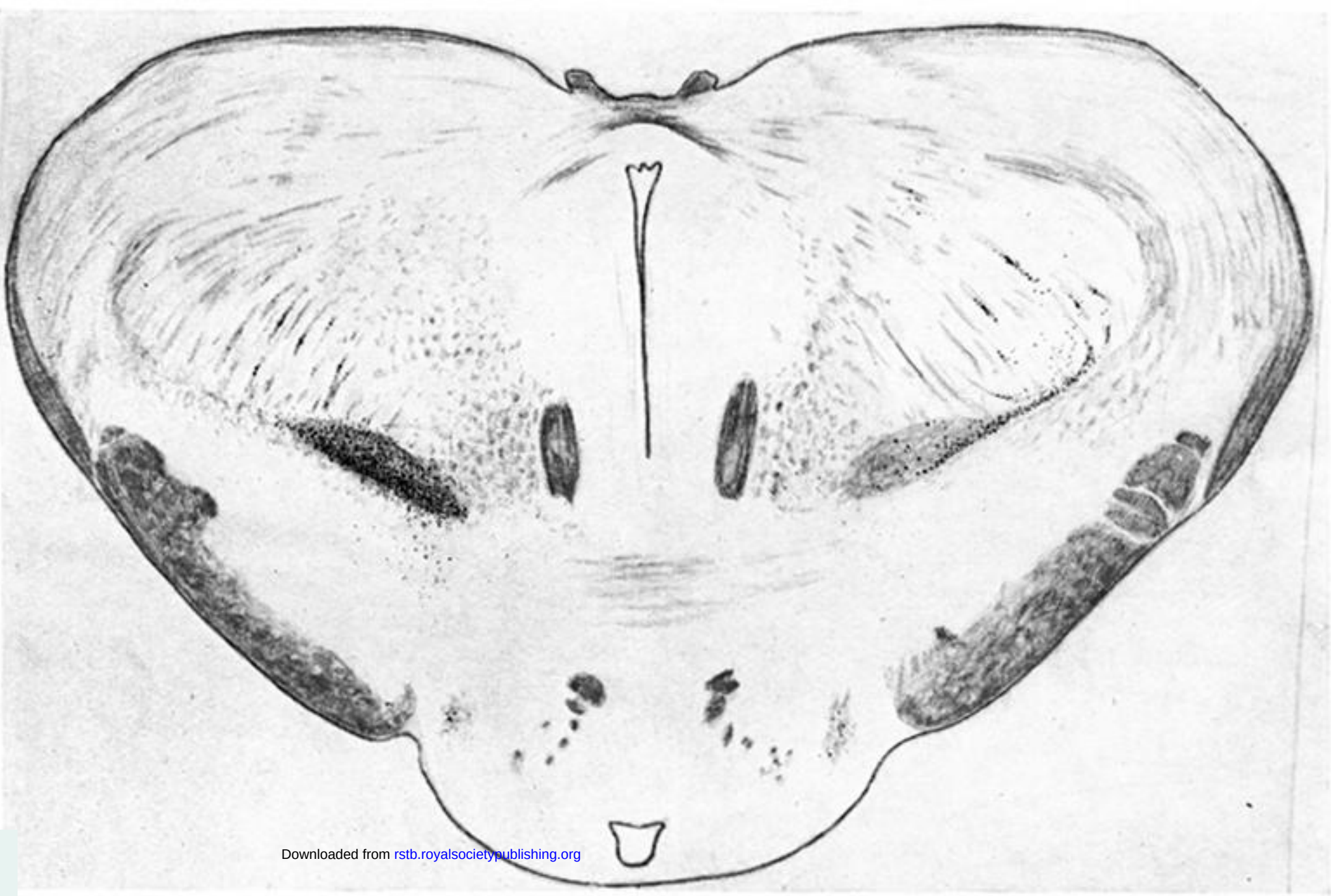

FIG. 15*b*.—Rat BS 2.

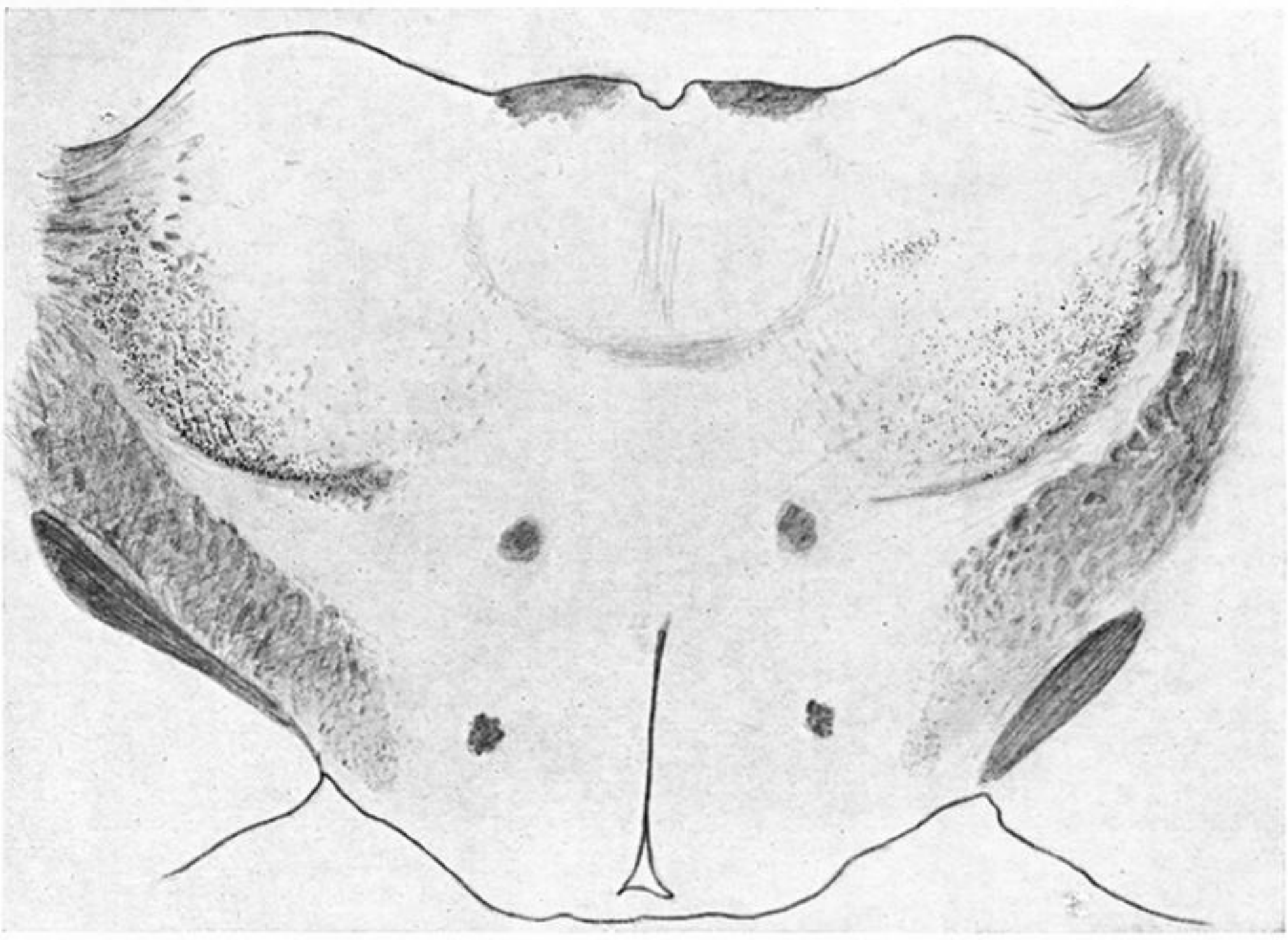

FIG. 15*c*.—Rat BS 2.