VII—The Thalamic Connections of the Parietal and Frontal Lobes of the Brain in the Monkey

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[Plates 23–27]

It is well known that a large proportion of the thalamus proper functions as a relay station through which sensory impulses are projected on to the cerebral cortex. With the exception of the lateral geniculate body (whose detailed relations to the *area striata* have recently been worked out with great accuracy by Poliak (1933)) the precise relation of the various thalamic nuclei and their subdivisions to the different cortical areas still remains to be established. The investigation of which this communication represents a report was undertaken in the first place in order to define precisely the manner in which the main sensory nucleus of the thalamus (nucleus ventralis) is projected on to the sensory areas of the cortex. We have, however, extended our original plans to include a survey of the thalamo-cortical connections of the greater part of the frontal and parietal regions of the cerebral cortex. The work of previous investigators which bears on this question we will leave for consideration in the discussion at the end of this paper.

Methods

For the purpose of our studies we used the ordinary macaque monkey, *Macaca mulatta* (= *Macacus rhesus*). Our observations are based on thirteen experiments. In each, the animal was subjected to an operation in which a small block of cortex was excised. The lesions were usually quite localized and, so far as possible, were planned to involve not more than one or two of Brodmann's cortical areas. As the records of the experiments show, the lesions were relatively superficial, being limited to the gray cortex and the immediately subjacent white matter. We can confidently affirm, therefore, that there was never any possibility of damage to the vascular supply of the thalamus which might conceivably vitiate the observations on the ensuing degeneration in the thalamic nuclei.

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Operative technique—The animals were anæsthetized by an intraperitoneal injection of sodium ethyl barbiturate (nembutal), using 0·8 cc of a 5% solution per kilogram of body weight. In a few animals an additional 0·2 cc of the solution was required. Anæsthesia occurred rapidly and recovery was not prolonged beyond 4 to 5 hours.

A coronal incision was made on one side through the scalp. The skull was opened by a trephine hole and, after sufficient bone had been chipped away, the dura was incised and the brain exposed. The portion of the brain to be removed was excised by means of a fine sharp scalpel. Actual bleeding points were controlled by cautery and a hot saline plug assisted in stopping most of the capillary oozing. The cavity remaining was usually filled with a muscle graft obtained from the temporal muscle. The scalp wound was closed by a continuous running stitch and the wound left undressed. After the operation, the animal was kept in a warm cage and provided with a warm coat. The stitches were not removed, and the wounds healed well.

Eighteen animals were submitted to operation. Of these, three died prematurely, two from post-operative shock and one from pneumonia. In two others, the lesions were found to be unsuitable for detailed study.

Examination of the experimental material—The animals were allowed to survive for approximately three months. Our previous work has shown us that at the end of this time the retrograde degeneration of the cells of origin of thalamo-cortical fibres is complete and localized, and gives a sharply defined picture in microscopical preparations. The animals were killed by an overdose of anæsthetic and the brain immediately removed. The lesion was first studied macroscopically, measured, and as accurately as possible reproduced diagrammatically. It should be noted that these diagrams of cortical lesions (reproduced below) make the lesions appear rather less extensive than they actually were at the time of the operation, owing to the subsequent contraction of the tissues during the process of healing. In each animal, the area of cortex containing the lesion was embedded in paraffin, sectioned, and stained with hæmatoxylin and eosin or methylene blue. In this way the precise extent of the damage to the cortex could be ascertained, with special reference to the different cortical areas which had been involved.

As soon as the cortical lesion had been studied macroscopically, a block was removed from the brain containing the whole extent of the thalamus. This was placed in 70% alcohol for one or two days until sufficiently hardened, when it was cut into separate blocks 2 or 3 mm in thickness, each of which was embedded in paraffin after dehydration in absolute alcohol and clearing in cedar wood oil. Complete serial sections were cut throughout the length of the thalamus in a coronal plane at a thickness of 20μ, and were stained with Borell's methylene blue. This staining method gives a very striking contrast between the normal and abnormal cytoarchitecture. Cells whose cortical connections had been severed by the operative lesion had undergone complete cytolysis and this was always accompanied

by a marked gliosis. Areas of direct retrograde cell atrophy in the thalamus could thus be defined with accuracy and certainty (as the microphotographs reproduced in the plates amply demonstrate). It must be emphasized that, with longer intervals than three months after operation, there may be a slight cell shrinkage in thalamic nuclei not directly connected with the area of cortex involved by the lesion. This is a secondary disuse atrophy depending on the fact that the various nuclei of the thalamus are to a greater or lesser extent functionally related to each other, and it must be rigorously distinguished from the *complete* atrophy of the cells directly connected by thalamocortical fibres with the injured cortex. Failure to make this distinction has possibly led to erroneous interpretations in the past. We would emphasize that, in our experiments, we have had no difficulty in defining quite sharply the areas of direct retrograde degeneration. We wish to point out, also, that it is most important that the investigator should be thoroughly familiar with the normal cytoarchitecture of every part of the macaque thalamus before attempting to define regions of cell degeneration. For example, in the rostral planes of the thalamus, the cells of the ventral and lateral thalamic nuclei may be rather scattered and separated into isolated groups between which are relatively large acellular areas. It is possible for these latter areas to be mistaken for regions of cell atrophy even though, of course, the absence of an accompanying gliosis should make such an error at once apparent. Again, the density and arrangement of the cells of the centre median nucleus show variations from one brain to another, and an irregular spacing of cells may then also be suggestive of a diffuse atrophy, which, in fact, is not really present. It should be noted, further, that there is some individual variation in the degree of definition of some of thalamic nuclei (especially the different elements of the ventral and lateral nuclei), and even in their relative extent. For these reasons it is very essential that studies of this kind should be accompanied by the objective demonstration of clearly defined microphotographs which can leave little possibility of doubt in regard to the results and their interpretation.

We must point out that the method we have used can clearly give positive results only when it is possible to recognize areas of degeneration where cells have undergone atrophy in definite circumscribed groups, or where there is a conspicuous and fairly wide-spread diffuse atrophy. This, in fact, occurred in all but one of our experiments. For instance, following lesions of the post-central gyrus (area post-centralis), well-defined patches of complete cell atrophy were always found in the pars externa of the ventral nucleus. On the other hand, no definite areas of degeneration could be detected in the lateral nucleus after these cortical lesions. It is, of course, possible that isolated and scattered cells of the lateral nucleus may be directly connected with the area post-centralis even though the nucleus as a whole is predominantly related to other parts of the cortex. For the determination of this question the method of retrograde cell degeneration is not adequate, as it is not possible to detect with certainty the atrophy of a few scattered single cells in the midst of normal cells.

ABBREVIATIONS USED IN THE FIGURES

Ac, Anterior colliculus.
Ad, Nucleus antero-dorsalis.
Am, Nucleus antero-medialis.
Av, Nucleus antero-ventralis.
C, Nucleus caudatus.
Cm, Centre median nucleus.
Cp, Posterior commissure.
Dm, Nucleus dorso-medialis.
Dm', parvicellular element.
Dm'', magnocellular element.
Ed, Edinger-Westphal nucleus.
Gl, Lateral geniculate body.
Gm, Medial geniculate body.
Hb, Nucleus habenulæ.
Lm, Nucleus of the medial medullary lamina.
La, *Lb* } Elements of the lateral nucleus.
M, Meynert's bundle (fasciculus retroflexus).
Mth, Mammillo-thalamic tract.
pa, *pβ*, *pd*, *pμβ*, } Elements of the pulvinar.
Pf, Nucleus parafascicularis.
Prt, Nucleus pretectalis.
Pt, Nucleus parataenialis.
PP, Pes pedunculi.
R., Nucleus reticularis.
Sb, Nucleus subthalamicus.
Sbm, Nucleus submedius.
Sm, Stria medullaris.
Val, Nucleus ventralis, pars antero-lateralis.
Vam, Nucleus ventralis, pars antero-medialis.
Var, Nucleus ventralis, pars arcuata.
Ve, Nucleus ventralis, pars externa.
Vp, Nucleus ventralis, pars posterior.
3, Nucleus of the third nerve.

THE ELEMENTS OF THE VENTRAL AND LATERAL NUCLEI OF THE THALAMUS IN *Macaca*

A general account of the nuclei of the thalamus has been previously published by one of us (CLARK, 1932, *a*). It is necessary to give here an amplified account of the ventral and lateral nuclei of the macaque thalamus so that the ensuing descriptions of experimental results may be clear. The cytoarchitecture of the thalamus of *Macaca* corresponds extremely closely with that of *Cercopithecus* as described and figured by FRIEDEMANN (1911–12).

The ventral nucleus of the mammalian thalamus is situated in the ventral part of the pars dorsalis diencephali, extending medially almost to the mid-line and laterally to the lateral medullary lamina which separates it from the nucleus reticularis. Ventrally it lies in contact with the ventral medullary lamina, while dorsally it is indistinctly separated from the lateral nucleus. By many authors, the lateral and ventral nuclei are not distinguished from each other. On the basis of cell and fibre architecture, however, these elements may be separately (though not always sharply) defined and, as we shall see, they are rather different in their fibre connections. Although the ventral nucleus is often termed the " fillet nucleus," not all the elements of this nucleus are concerned with receiving the terminal fibres of the fillet system (p. 348). It is well established, however, that at least a part of the ventral nucleus represents a relay station for the passage of sensory impulses from lower levels to the cerebral cortex.

Our own studies of a number of complete sets of serial sections through the thalamus of *Macaca*—stained with Borell's methylene blue—have enabled us to recognize all

the elements of the ventral nucleus which were defined by FRIEDEMANN. These elements are the nucleus ventralis, pars externa (*Va* + *Va'* of FRIEDEMANN, *Vent. A* and part of *Vent. C* of VON MONAKOW, nucleus ventralis postero-lateralis of other authors), nucleus ventralis, pars arcuata (*Vb* of FRIEDEMANN and VON MONAKOW, nucleus arciformis, noyau semi-lunaire, noyau arqué, schälenformiger Körper,

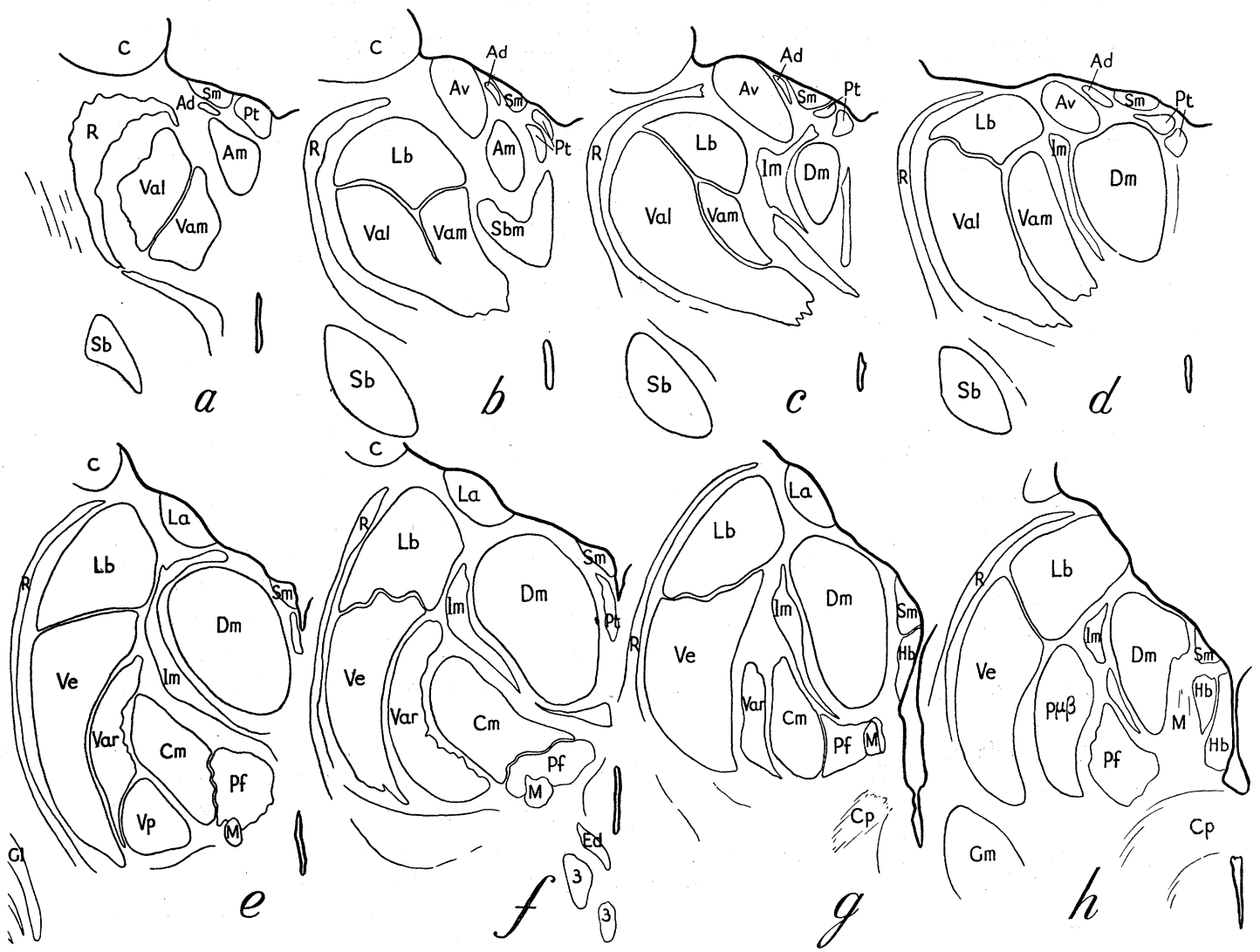


FIG. 1—Transverse sections through the thalamus of *Macaca mulatta* showing the constituent nuclei. × 6.

nucleus ventralis postero-medialis of other authors), nucleus ventralis, pars posterior (*Vp* of FRIEDEMANN), nucleus ventralis, pars antero-medialis, and nucleus ventralis, pars antero-lateralis, fig. 1, and fig. 28, Plate 23.

Nucleus ventralis, pars externa—This comprises the largest element of the ventral nucleus in the monkey. It occupies the caudal two-thirds of the whole length of the thalamus, reaching back to the level of the medial geniculate body

with the dorsal aspect of which it lies in immediate relation, fig. 1, *h*. Rostrally it passes over into continuity with the pars antero-medialis, the transition between the two elements being quite gradual. Ventrally it is in contact with the ventral medullary lamina, laterally with the lateral medullary lamina which separates it from the reticular nucleus, while medially it is separated from the centre median nucleus by the pars arcuata or, in caudal planes, by an element of the pulvinar (nucleus *pμβ* of FRIEDEMANN). Dorsally the pars externa merges with an element of the lateral nucleus of the thalamus (nucleus *Lb*) from which it is separated by no well-defined boundary. Nucleus *Lb* is to be distinguished on the whole by the fact that its cells are smaller, less deeply stained, and less densely arranged than those of the pars externa of the ventral nucleus. Moreover, no fibres of the fillet system have been demonstrated to reach the lateral nucleus.

The cells of the pars externa are large and polygonal, deeply stained, and with many branching processes. They are disposed in diffuse and irregular laminæ which are related to the numerous fasciculi of medullated fibres which penetrate the lateral margin of the nucleus in a ventro-medial direction.

Nucleus ventralis, pars arcuata—This nucleus is unusually well defined both by its cytoarchitecture and by the medullary laminæ which surround it, fig. 28, Plate 23. It extends over a little more than the caudal half of the thalamus, forming a compact group of cells which insinuates itself between the ventral part of the pars externa and almost the whole length of the centre median nucleus, fig. 1, *e* to *g*. Caudally it is first apparent (as the sections are traced forwards) at the medio-ventral extremity of the pars externa, lying at this level immediately ventral to nucleus *pμβ*. Further rostrally, it extends in a dorsal direction so that it reaches up to the nucleus of the medial medullary lamina in the middle of the thalamus. Here its boundary is not always distinct, and it may grade insensibly into the nucleus of the medial medullary lamina.

The cells of the pars arcuata are in general of the same size as those of the pars externa but rather more triangular or fusiform in shape, and they are mingled with smaller cells which are not seen in the pars externa. The cells are all very deeply stained and closely packed, and they are arranged in clumps so as to give a somewhat lobulated appearance to the whole nucleus. The intercellular matrix also takes up the stain to a slight degree, which still further emphasizes the distinctness of this element.

Nucleus ventralis, pars posterior—This element apparently corresponds to FRIEDEMANN'S pars parvicellularis which is shown quite distinctly in his microphotographs of the thalamus of *Cercopithecus*. In *Macaca* it is poorly defined and varies in different specimens. It is composed of medium, rather lightly stained and rounded cells, and appears as an oval mass situated below the middle part of the pars arcuata, fig. 1, *e*, lying in close relation to the ventral extremities of the latter element and the pars externa.

Nucleus ventralis, pars antero-medialis—This element is really a forward extension of the pars externa (morphologically speaking) and is found in the rostral third of the thalamus immediately ventro-lateral to the nucleus of the medial medullary lamina, fig. 1, *a* to *d*. Its medial part is pierced by the mammillo-thalamic tract. It consists of large polygonal cells which are deeply stained, evenly arranged, and intermingled with smaller cells.

Nucleus ventralis, pars antero-lateralis—This element is present in the rostral third of the thalamus lying between the pars antero-medialis and the lateral medullary lamina, fig. 1, *a* to *d*. It consists of cells which are very distinctly smaller than those of the antero-medial element, and flattened or fusiform in shape. They are disposed in somewhat irregular groups separated by fairly wide acellular areas.

The lateral nucleus of the thalamus can be separated into two quite distinct elements, *La* and *Lb*. The former is particularly well defined, and in cross-sections through the whole length of the thalamus between the levels of the anterior nucleus and the base of the pulvinar appears as a small oval group of cells at the dorsal surface, circumscribed by medullary laminæ and consisting of rather large cells well spaced out, fig. 1, *e* to *g*. Caudally this nucleus becomes continuous with one of the elements of the pulvinar (*pa*). The element *Lb* is less well demarcated. It lies at the dorso-lateral aspect of the ventral nucleus from which it is not sharply separated, especially at its oral extremity, fig. 1, *a* to *h*. Its distinctness also varies from one individual brain to another. As mentioned above, it is mainly to be distinguished from the ventral nucleus in Nissl preparations by the size and arrangement of its constituent cells. Caudally, nucleus *Lb* merges with certain elements of the pulvinar. A small subdivision of this nucleus is in many macaque monkeys rather sharply defined at the extreme dorso-lateral angle of the thalamus—the nucleus angularis. FRIEDEMANN and VOGT have divided nucleus *Lb* into several elements which they define by slight differences in fibre and cell architecture. Owing to the difficulty of delineating these subsidiary parts anatomically, we have not attempted to define them in the present investigation. We would again emphasize that the whole nucleus *Lb* is extremely ill-defined at its ventral border where it may grade insensibly into the pars externa of the ventral nucleus. Thus it has been found a matter of considerable difficulty when cell degeneration occurs at the junctional area of these two nuclei to determine whether it is the dorsal extremity of the ventral nucleus or the ventral margin of the lateral nucleus which has been affected.

EXPERIMENTAL RESULTS

Experiment A—Monkey No. 10. Operated March 28, 1933, killed June 19, 1933.

Examination of the fresh brain after death showed the lesion to be situated in the upper part of the post-central gyrus, being evidently limited to the " leg area " as defined by DE BARENNE, fig. 2 *a*. Superficially it measured 7 mm in sagittal diameter.

The margin of the lesion was 5 mm from the sulcus centralis in front, 2 mm from the intraparietal sulcus behind, and 2·5 mm from the upper margin of the brain medially.

Sections of the lesion showed that it was quite superficial, only just extending through the thickness of the cortex, fig. 2 *b*. As far as could be judged from an examination of these sections, it was practically confined to the area post-centralis (BRODMANN'S areas 1, 2, and 3).

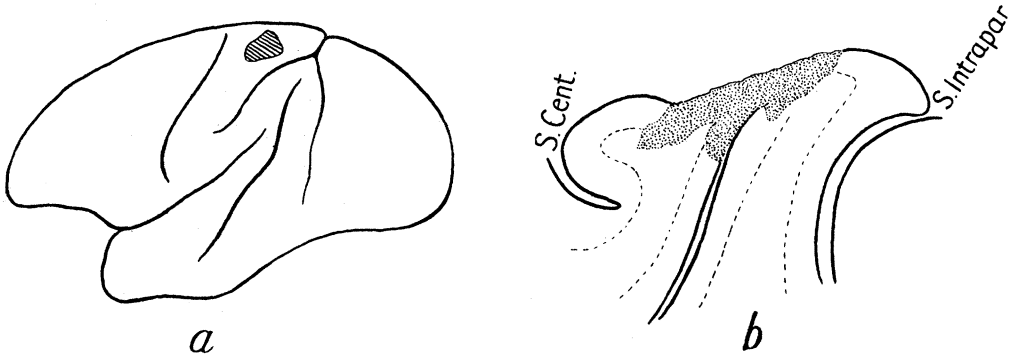


FIG. 2 *a*—The cortical lesion in experiment *A*. × ⅔. *b*—Sagittal section through the middle of the lesion in experiment *A*. × 3⅓. In this and similar diagrams, the extent of the cortical destruction is indicated by the stippled area.

The thalamus—In describing the changes seen in the thalamus in these experiments, the serial sections will be traced in a caudo-cranial direction. The most caudal section of the first block in this case passes through the tip of the projecting pole of the pulvinar, the medial geniculate body and the rostral margin of the anterior colliculus. At this level, the cytoarchitecture of the thalamus is quite normal. At the level of sections through the middle of the lateral geniculate body (*e.g.*, section 90 of the first block) there is a small patch of total cell atrophy accompanied by a gliosis at the lateral margin of the posterior end of the pars externa of the ventral nucleus where it comes into relation with the dorsal aspect of the medial geniculate body. Twenty sections further rostrally the area of atrophy has expanded somewhat, occupying at this level a considerable proportion of the lateral half of the pars externa, extending to the lateral margin of the thalamus and dorsally to the margin of nucleus *Lb*. The gliosis is very distinct and accentuates conspicuously the area of degenerated cells. The extent of this area in section 116 is shown in fig. 3 *a* and fig. 29, Plate 23. It is fairly sharply circumscribed at this level, being demarcated abruptly from the surrounding zone of normal cells, and it should be noted that it is confined to the pars externa of the ventral nucleus, not involving at all the lateral nucleus or the nuclei of the pulvinar. About ten sections further forward, normal cells begin to appear scattered in the degenerated area, and the latter becomes more limited to the lateral margin of the pars externa. The appearance in section 178 of the first block is shown in fig. 3 *b*, where it may be

seen that the area of total cell atrophy is limited to a small patch near the dorsal extremity of the nucleus. Extending a little up and down from this area, and close to the lateral margin of the nucleus, is a zone in which also normal cells are found scattered. The other elements of the ventral nucleus at this level (pars arcuata and pars posterior) are quite normal in appearance. In the most rostral section of the first block, section 200 (which passes through the rostral extremity of the lateral geniculate body and the middle of the centre median nucleus), the thalamus appears to be normal except that there is some glial proliferation, which shows up by its darker staining, along the lateral margin of the dorsal extremity of the pars externa. There is no definite evidence at this level, however, of cellular degeneration.

The second block consists of 184 sections and extends from the level of the maximum development in cross-section of the centre median nucleus as far forwards as the rostral end of nucleus *La* and of the dorso-medial nucleus. Throughout this region of the thalamus there is no sign of cell atrophy and all the elements of the ventral nucleus—as well as other diencephalic nuclei—are entirely normal.

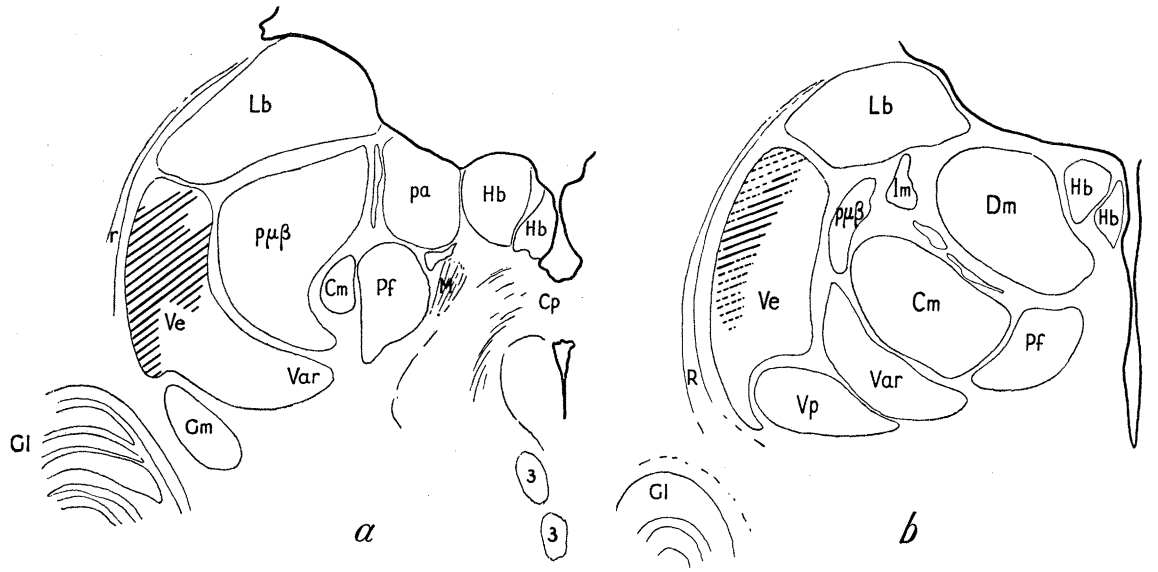


FIG. 3, *a* and *b*—Transverse sections (Nos. 1.15.6 and 1.22.2) through the caudal third of the thalamus in experiment *A*, showing the extent of cellular atrophy. In this and similar diagrams, areas of total cell atrophy are indicated by hatching, while areas in which cell degeneration is partial are marked by interrupted lines.

The most posterior section of the third block passes through the caudal margin of the anterior nucleus. At section 84 the anterior extremity of the ventral nucleus is reached, while section 126 marks the rostral limit of the anterior nucleus of the thalamus. In none of these sections is there any abnormal change in the cyto-architecture of the thalamus.

The area of cell atrophy is thus limited in this case to the lateral part of the pars externa of the ventral nucleus and lies between sections 90 and 200 of the first block,

that is to say, it extends forwards from the caudal extremity of the nucleus for a distance of 2·2 mm (the sections having been cut at 20 μ). The whole antero-posterior extent of the ventral nucleus covers 378 sections, which gives a sagittal diameter of 7·6 mm (not taking into account loss of tissue at the surface of the blocks in the process of sectioning). Hence the atrophic area is limited to rather less than the caudal third of the whole ventral nucleus. It may be emphasized that although the lesion involved the " leg area" component of the post-central gyrus in this experiment, the cellular atrophy is confined to the ventral nucleus and does not affect the lateral nucleus.

Experiment B—Monkey 16. Operated June 20, 1933, killed September 27, 1933.

The lesion lay in the middle part of the post-central gyrus, reaching to within 1 mm of the central sulcus anteriorly, and to the rostral lip of the intraparietal

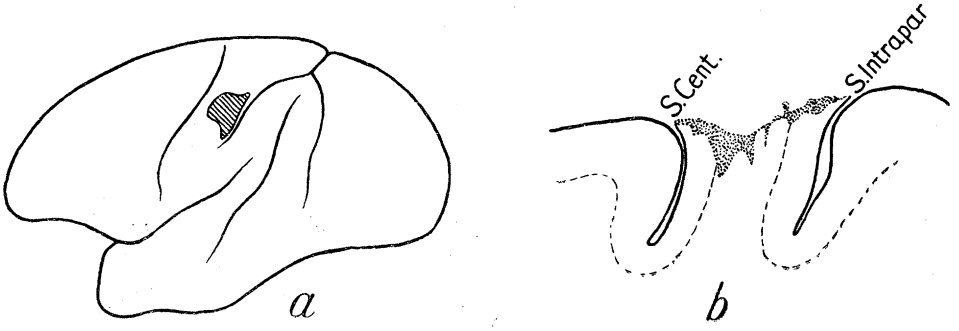


FIG. 4 *a*—The cortical lesion in experiment *B*. × ⅔. *b*—Sagittal section through the middle of the lesion in experiment *B*. × 3⅓.

sulcus posteriorly. It measured 4·5 mm in sagittal diameter and 7·5 mm in transverse diameter, and was situated 12 mm from the upper margin of the brain, fig. 4 *a*. Microscopic section showed the lesion to be superficial, involving no more than the exposed cortex lying between the central and intraparietal sulci (BRODMANN'S area post-centralis). Moreover, it was situated approximately at the junction of the arm and face areas of DE BARENNE, fig. 4 *b*.

The thalamus—The sections of the first block of the thalamus pass through the projecting pole of the pulvinar and the medial geniculate body. The cytoarchitecture of these regions is quite normal, nor is there any gliosis among the fibres of the cortico-tectal facsciculus passing to the anterior colliculus.

The most caudal section of the second block cuts through the middle of the medial geniculate body. At this level the cells of the thalamic nuclei are normal, but in the medial part of the pars externa of the ventral nucleus there is present some diffuse gliosis. A little further forwards, at the level of the caudal pole of the lateral geniculate body (section 19 of the second block), this gliosis is accentuated and accompanied by a distinct cellular atrophy which involves a small patch at the

middle of the medial margin of the pars externa where the latter lies in contact with nucleus $p\mu\beta$. At the level of the middle of the lateral geniculate body (*e.g.*, section 50) the patch of atrophy, which is here quite sharply circumscribed, extends ventrally so that it comes to occupy the ventral half of the medial margin of the pars externa. The accompanying gliosis renders this degenerated area still more conspicuous, fig. 5 and fig. 30, Plate 24. The area at this level measures 3 mm in vertical diameter and is 0·8 mm wide. The normal and well-stained cells of the adjacent nuclei (*e.g.*, the pars arcuata of the ventral nucleus, the centre median

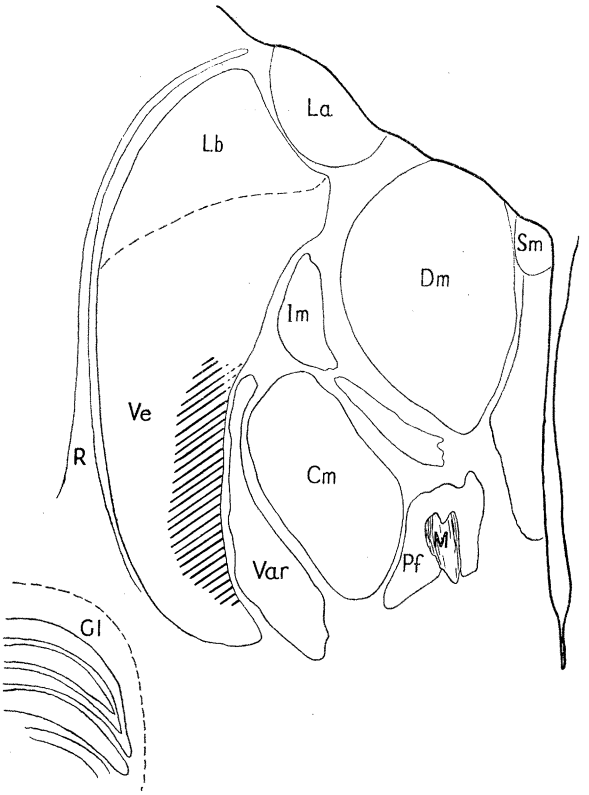


FIG. 5—Transverse section (No. 2.10.4) through the caudal third of the thalamus in experiment *B*, showing the area of cell atrophy in the medial part of the pars externa of the ventral nucleus.

nucleus, and nucleus *Lb*) stand out in strong contrast with the atrophied cells. At section 97 the patch of atrophy has disappeared, the cells of the pars externa at this level being normal. In the region of the pars externa involved by cellular atrophy at more caudal levels, however, there is still to be seen some gliosis. A few sections further forwards, the whole nucleus appears completely normal.

A study of sections through the more rostral planes of the thalamus fails to show any cell atrophy, all the nuclei (including the pars posterior of the ventral nucleus) being normal.

The whole length of the ventral nucleus in this specimen extends over 361 sections. This gives it a sagittal diameter of 7·2 mm (not taking into account loss of tissue

at the surface of the blocks during the process of sectioning). The area of cell atrophy is limited to a small patch at the medial margin of the pars externa of the ventral nucleus and extends over 78 sections or approximately 1·6 mm. Counting from the caudal pole of the ventral nucleus, the area extends from section 35 to section 113, and thus occupies roughly the rostral two-thirds of the caudal third of the ventral nucleus as a whole.

Experiment C—Monkey 15. Operated June 20, 1933, killed September 19, 1933.

In this case (which represents approximately a combination of experiments *A* and *B*) two small and localized circular lesions about 5 mm in diameter were made in the upper and lower parts of the post-central gyrus or area post-centralis, fig. 6 *a*. The upper lesion involved the caudal lip of the central sulcus and extended

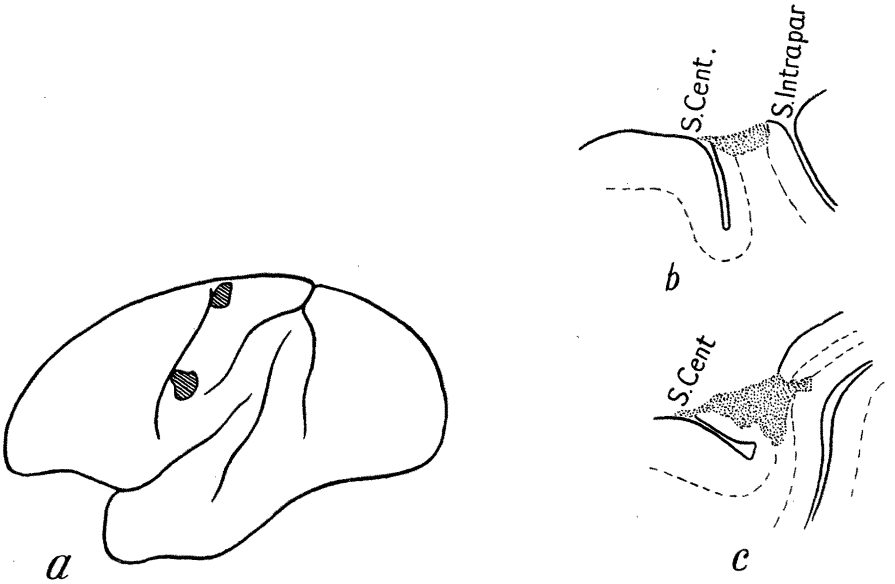


FIG. 6 *a*—The cortical lesions in experiment *C*. × ⅔. *b*—Sagittal section through the middle of the lower lesion. × 3⅓. *c*—Sagittal section through the middle of the upper lesion. × 3⅓.

back for 3·5 mm, its upper margin being 7 mm from the upper margin of the brain. Section of this lesion, fig. 6 *c*, showed it to be quite superficial, involving little more than the thickness of the cortex. The lower lesion also reached to the caudal lip of the central sulcus, extending back to the lower extremity of the intraparietal sulcus. This lesion was situated 16 mm from the upper margin of the hemisphere. Histological examination showed that it was practically confined to the thickness of the cortex, fig. 6 *b*. It may further be noted that these two small lesions were situated in the leg and face areas of DE BARENNE.

The thalamus—The most caudal section of the first block of the thalamus passes through the middle of the medial geniculate body, the pulvinar and the anterior colliculus. At this level, the cytoarchitecture of the thalamus is quite normal.

A little further forwards, at the level of the caudal pole of the lateral geniculate body (section 31), a small area in which the cells have undergone complete atrophy is seen at the ventro-lateral angle of the pars externa of the ventral nucleus immediately dorsal to the rostral pole of the medial geniculate body. Tracing the sections forwards, this patch of atrophy expands until, at section 63, it extends up almost to the middle of the lateral border of the pars externa and occupies the lateral half of the nucleus at this level, some normal cells remaining, however, at the lateral margin. The cellular atrophy is accompanied by a marked gliosis. The elements of the pulvinar and lateral nucleus are quite normal.

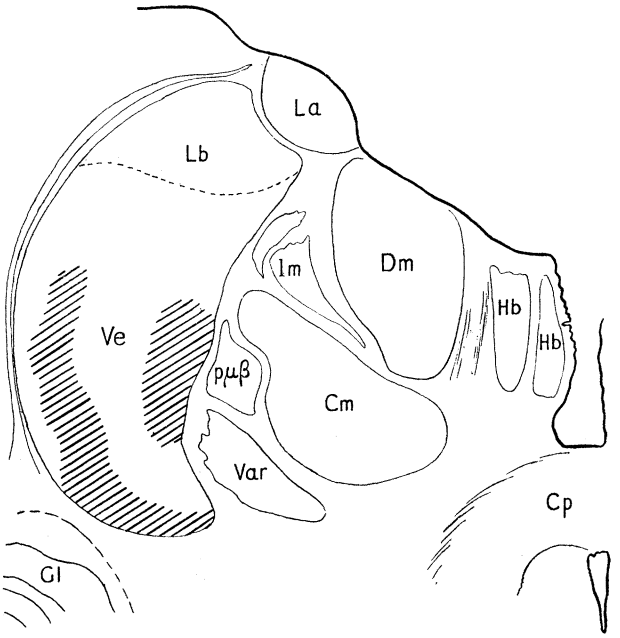


FIG. 7—Transverse section (No. 2.14.5) through the caudal third of the thalamus in experiment *C*, showing two areas of atrophy in the pars externa of the ventral nucleus.

The most caudal section of the next block passes through the middle of the lateral geniculate body. The patch of atrophy in the lower part of the lateral margin of the pars externa is here very well circumscribed, being about 3 mm in vertical diameter and 0·6 mm wide. At this level, also, there is another isolated patch of cell atrophy at the medial margin of the pars externa of the ventral nucleus, where this lies in contact with the lateral margin of nucleus *pμβ*, fig. 7. Twenty sections further rostrally this medial patch is much more distinct and reaches up to the caudal margin of the centre median nucleus. The medial and lateral atrophic areas are separated by the middle part of the pars externa in which the cytoarchitecture is normal, but at the ventral extremity of the nucleus they appear to become continuous. The pars arcuata of the ventral nucleus is normal. By section 41 of this block, the pars arcuata has extended dorsally so as to separate the medial

patch of atrophy from the centre median nucleus, and at this level both patches (especially the lateral one) are becoming smaller. At section 60 the lateral patch has disappeared, the medial patch being still present in the medial margin of the ventral half of the pars externa. Finally, at section 90 the medial area of degeneration is no longer visible.

All the other elements of the thalamus—including the elements of the lateral nucleus—are perfectly normal in their cytoarchitecture.

The ventral nucleus in this specimen extends over 457 sections, and thus has a sagittal diameter of approximately 9·1 mm. The atrophic areas lie between section 31 and section 190 of the whole series, extending therefore over 159 sections or 3·2 mm. Thus they are limited to the caudal two-fifths of the whole ventral nucleus, reaching almost to its caudal extremity. The lateral area of atrophy extends further caudally than the medial area, while the latter extends further rostrally. The results of experiments *A* and *B* indicate that the lateral area is related to the upper cortical lesion, and the medial area to the lower lesion.

Experiment D—Monkey 21. Operated November 21, 1933, killed February 5, 1934.

The lesion in this animal was situated at the upper extremity of the central sulcus, cutting into the upper border of the hemisphere, fig. 8 *a*. It extended 8 mm behind

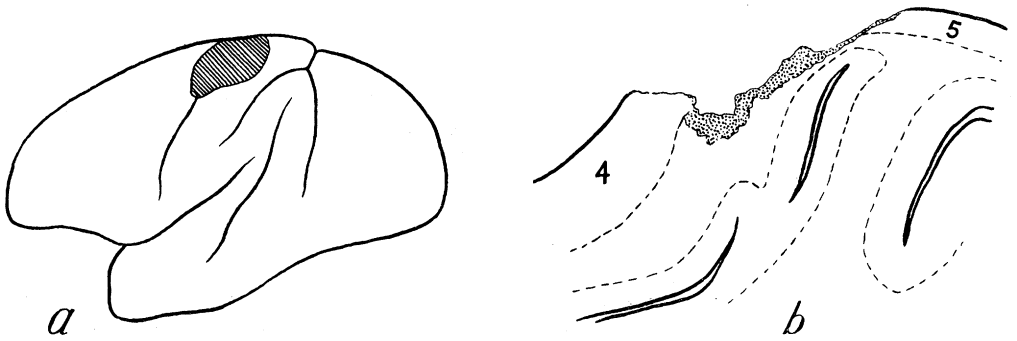


FIG. 8 *a*—The cortical lesion in experiment *D*. × ⅔. *b*—Sagittal section through the middle of the lesion in experiment *D*. The numbers refer to BRODMANN's cortical areas. × 3⅓.

the sulcus and also involved its anterior lip. In sagittal diameter the lesion measured 14 mm, and in transverse diameter 15 mm.

Fig. 8 *b* represents a sagittal section through the lesion close to the upper margin of the hemisphere. The section cuts through the depths of some of the sulci on the medial surface of the brain. The cortical areas on either side of the lesion are indicated in the diagram by BRODMANN's numbers. These sections show that the upper extremity of the general sensory cortex and the caudal margin of the corresponding region of the motor cortex have been destroyed. It is apparent, also, that the fibre connections of that part of the sensory cortex which extends on the medial surface of the hemisphere have been interrupted (at least in their greater

part). It is probable, therefore, that most of the leg region of the area post-centralis as well as a part of the corresponding region of the caudal margin of the motor area have been involved.

The thalamus—The most caudal section of the first block passes through the middle of the medial geniculate body, the posterior end of the lateral geniculate body, the anterior colliculi and the pulvinar. The cytoarchitecture at this level is quite normal. At the level of the extreme caudal end of the ventral nucleus (section 101) there is no gliosis or cell atrophy. Immediately in front of this level (in section 130) a patch of complete cell atrophy appears in the lateral part of the dorsal half of the pars externa of the ventral nucleus, accompanied by a pronounced gliosis. This area of degeneration is sharply limited above by the ventral margin of the lateral nucleus (element *Lb*), the latter nucleus being entirely normal in appearance. More rostrally, by section 180, the area of atrophy becomes more extensive and is so sharply circumscribed that it can readily be defined by naked-eye inspection of the section. Here the whole of the pars externa is completely devoid of recognizable nerve cells except along its medial border where the cells remain intact. The pars arcuata of the ventral nucleus and the lateral nucleus are normal. The first section of the second block passes through the rostral end of the centre median nucleus and the caudal third of the nucleus dorso-medialis. Here the patch of cellular atrophy is sharply limited to the lateral part of the pars externa of the ventral nucleus, fig. 9 and fig. 31, Plate 24, extending dorsally as far as the nucleus *Lb*. All other

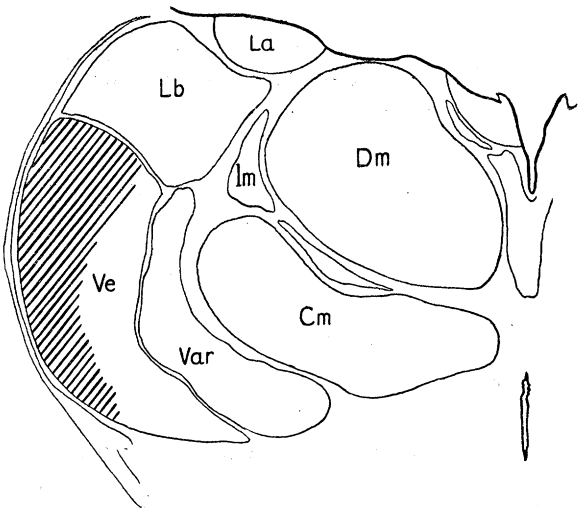


FIG. 9—Transverse section (No. 2.3.4) through the middle of the thalamus of experiment *D*.

thalamic elements at this level are normal. In section 40 of this block, scattered normal cells begin to put in an appearance throughout the atrophic area, and by section 90 the pars externa is relatively normal except for a certain degree of gliosis. A few sections more rostrally this gliosis disappears and beyond this level the cyto-architecture of the thalamus is completely normal.

In this experiment, therefore, the cell degeneration is confined to the pars externa of the ventral nucleus. The whole extent of the ventral nucleus covers 412 sections, which gives a sagittal diameter of approximately 8·2 mm. The area of cell atrophy is confined to 190 sections, and is thus limited to a little less than the caudal half of the whole ventral nucleus. Again it should be noted that the lateral nucleus of the thalamus appears to be intact and the cell degeneration limited to the ventral nucleus, although the leg area of the post-central gyrus has been extensively involved by the lesion.

Experiment E—Monkey 17. Operated October 3rd, 1933, killed December 28, 1933.

Macroscopic examination of the brain at death showed a relatively large lesion situated in the anterior half of the parietal lobe, fig. 10 *a*. The sagittal diameter of the lesion was 15 mm, and the transverse diameter 20 mm. Anteriorly it extended

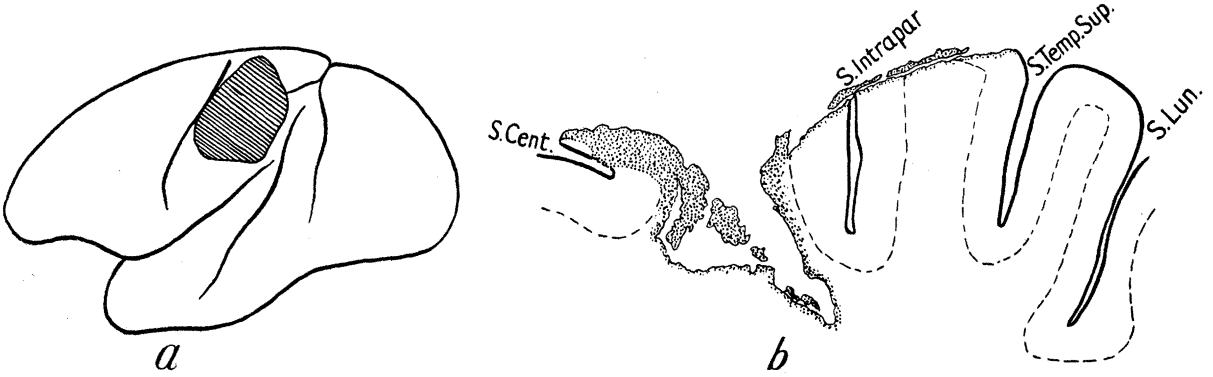


FIG. 10 *a*—The cortical lesion in experiment *E*. × ⅔. *b*—Sagittal section through the middle of the lesion in experiment *E*. × 3⅓.

into the caudal lip of the sulcus centralis, above to within 5 mm of the upper border of the hemisphere, and behind to the rostral lip of the upper extremity of the parallel sulcus.

Microscopical sections, fig. 10 *b*, showed the lesion to be relatively superficial, and limited rostrally by the bottom of the central sulcus. The cortex in the depths of the intraparietal sulcus was left intact. From a study of the histology of the cortex in the immediate neighbourhood of the lesion it can be demonstrated that the latter has involved BRODMANN'S cortical areas 1, 2 and 3 in most of the upper two-thirds of the post-central gyrus, the oral part of area 7, and a relatively small portion of area 5.

The thalamus—The most caudal section of the first block of the thalamus passes through the pulvinar, the anterior colliculus, and the geniculate bodies. At this level there is no degeneration of the nuclear elements, and there is no gliosis in the cortico-tectal fasciculi. All the nuclei of the pulvinar (including nucleus *pd*) are normal. At section 17 of this block, the caudal end of the ventral nucleus becomes

apparent, lying immediately dorsal to the rostral end of the medial geniculate body, and consists here of normal well-stained cells. At section 57, which cuts through the rostral part of the geniculate bodies, the upper end of the fasciculus retroflexus, and the caudal end of the habenular ganglion, there is a small sharply circumscribed patch of atrophy in which the complete disappearance of the cells is accompanied by a conspicuous gliosis. This patch is approximately 1 mm in diameter at this level, and is situated immediately lateral to the caudal part of the nucleus parafascicularis in the medial portion of a group of cells which appears to correspond to the rostral end of FRIEDEMANN'S nucleus $p\mu\beta$. There is some doubt in the identification of this group, however, for the presence of cellular degeneration makes the definition of the thalamic elements in this transitional region between the pulvinar and the main part of the thalamus more than usually difficult. The main element of the pulvinar at this level (FRIEDEMANN'S nucleus $p\beta$) and the parafascicular nucleus are quite normal.

Further forward, at the level of the caudal end of the centre median nucleus (*e.g.*, section 100 of the first block), the patch of atrophy has extended laterally below the main element of the pulvinar to involve the caudal region of the pars externa of the ventral nucleus which is here completely degenerated except for a vertical band of cells at its lateral margin along the lateral medullary lamina, fig. 11 *a*. The cell atrophy and gliosis also extend into the ventral part of the posterior end of the lateral nucleus (*Lb*) where, however, the degeneration is not so complete, for in this region scattered normal cells persist. The centre median nucleus and the arcuate nucleus (which also appears at this level) are normal. By section 116, at the level of the maximum development of the centre median nucleus, the atrophic area is somewhat larger and much more distinct. It remains sharply circumscribed so that, indeed, it can be recognized in the section by the use of a hand lens, appearing as a pale area surrounded by the dark blue of the normally stained regions. It involves here the whole of the pars externa of the ventral nucleus except for a thin layer of cells at its lateral surface, and also the pars posterior except for its medial extremity where a few normal cells persist. The area of atrophy, further, sends a narrow extension dorsally through the middle of the nucleus *Lb* (which it divides into medial and lateral normal portions), but not quite reaching to the dorsal surface of the thalamus. Thus the dorsal part of the degenerated area is here separated from the centre median nucleus by the medial part of nucleus *Lb*.

The most caudal section of the second block passes through the middle third of the thalamus at the level of the rostral end of the centre median nucleus. Here the whole of the large pars externa is completely atrophied, and the region of this nuclear element appears as a blank space (as far as nerve cells are concerned) abruptly outlined by the normal nuclear elements which surround it, fig. 11 *b* and fig. 32, Plate 25. Throughout the pars externa there is a diffuse gliosis. Nucleus *Lb* is also involved by the atrophy but here the cell degeneration is not total, for isolated normal cells are scattered evenly through the matrix of the nucleus, and the accompanying gliosis is not so dense. By these differences in the degenerative

reaction, the lateral nucleus contrasts rather strongly with the pars externa of the ventral nucleus in this experiment. The arcuate nucleus, the dorso-medial and centre median nuclei, and the nucleus of the medial medullary lamina are all normal. On the other hand, the cells of the nucleus reticularis in the lateral medullary lamina overlying the pars externa of the ventral nucleus have all disappeared.

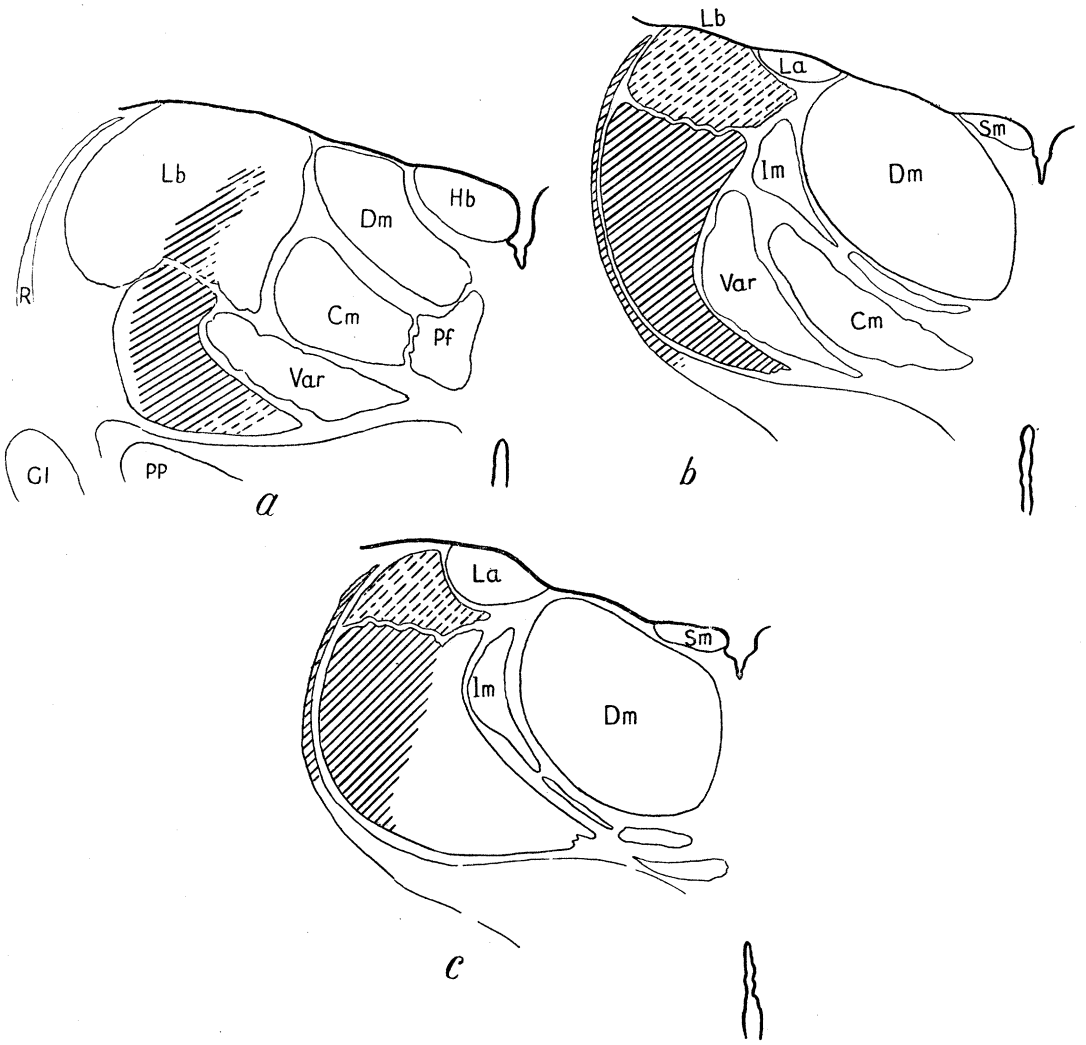


FIG. 11, *a*, *b* and *c*—Transverse sections through the thalamus of experiment *E* (section Nos. 1.15.5., 2.5.5., and 2.9.2.).

At section 41 of the second block the caudal end of the nucleus *La* appears at the dorsal surface of the thalamus. This nucleus (throughout its whole extent) contains normal cells. At this level, also, normal and well-stained cells are evident in the medial tail-like process of the pars externa of the ventral nucleus (where it lies ventral to the arcuate nucleus), and coincidently with this, normal cells are present in the ventral end of the reticular nucleus. As the sections are traced

forwards from this point, the area of atrophy in the pars externa and the reticular nucleus rapidly shrinks. By section 65 of this block it is limited to the dorso-lateral part of the ventral nucleus and a corresponding extent of the reticular nucleus, while nucleus *Lb* is still greatly degenerated except for scattered cells, fig. 11 *c*. At the rostral end of this block (section 102) the area of cell atrophy lies at the dorso-lateral extremity of the ventral nucleus (the anterior end of the pars externa) and is approximately 2 mm wide and 3 mm in vertical diameter. Nucleus *Lb* is practically normal at this level.

The most caudal section of block 3 passes through the anterior third of the thalamus immediately caudal to the anterior nucleus. There is no degeneration in the thalamus at this level, or further rostrally. The cells of the antero-lateral and antero-medial elements of the ventral nucleus, as well as those of this part of the nucleus reticularis are quite normal.

The ventral nucleus of the thalamus in this case extends over 360 sections. Thus the nucleus is approximately 7·2 mm in sagittal diameter. The area of atrophy extends from section 40 (counting from the posterior extremity of the ventral nucleus) to section 224. The atrophy therefore involves practically the caudal two-thirds of the ventral nucleus except for its posterior extremity. It should be exphasized that in this experiment the pars arcuata of the ventral nucleus was entirely normal in appearance. On the other hand, the greater part of the lateral nucleus (*Lb*) in its caudal half showed a general but partial atrophy, while the element *La* was intact. Lastly, a considerable extent of the reticular nucleus had undergone degeneration and also (possibly) the medio-rostral part of the nucleus *p*μβ of the pulvinar.

The lesion in this experiment differs from the lesions in experiments *A*, *B*, *C* and *D* in that a considerable part of cortical area 7 (area parietalis) and a small part of area 5 (area preparietalis) were involved in addition to the area post-centralis. In contrast with the previous experiments, also, there is (besides an atrophy affecting the ventral nucleus) considerable degeneration of the lateral nucleus (*Lb*). It may be inferred therefore that nucleus *Lb* is related to cortical area 7 and perhaps also to area 5.

Experiment F—Monkey 22. Operated December 5, 1933, killed February 19, 1934.

The lesion was made in the upper and posterior part of the parietal lobe. Examination at death showed that it involved the lip of the occipital operculum behind (cutting here into the area striata) and in front reached as far forwards as the caudal lip of the small post-central sulcus, fig. 12 *a*. Above, the lesion reached into the upper margin of the hemisphere. It was approximately circular in shape, measuring 18 mm in diameter.

Microscopical sections of the lesion showed that it was superficial, not reaching down into the depths of the sulci, fig. 12 *b*.

The thalamus—The thalamus was cut in four blocks, The most caudal section of the first block passes through the tip of the pulvinar and the posterior margin

of the medial geniculate body, while the most rostral section cuts the middle of the medial geniculate body and the posterior commissure. Throughout this block there is complete absence of cell degeneration except at its extreme anterior limit. Here the caudal end of element *Lb* of the lateral nucleus appears, where it enters the base of the pulvinar, and in this nucleus there is a small patch of gliosis accompanied by a partial cell degeneration. The main element of the pulvinar (nucleus *pβ*) is apparently unaffected.

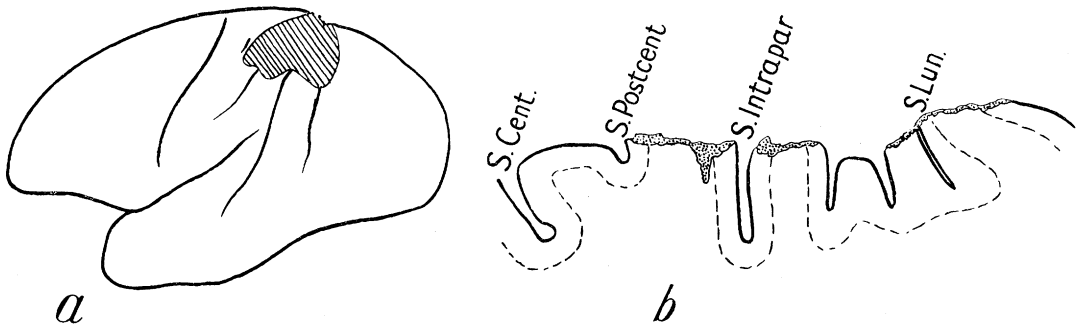


FIG. 12 *a*—The cortical lesion in experiment *F*. × ⅔. *b*—Sagittal section through the middle of the lesion in experiment *F*. × 3⅓.

The first sections of the second block pass through the rostral fibres of the posterior commissure and the habenular ganglion. Here there is marked atrophy involving almost the whole of element *Lb* and also the medial part of the nucleus *pd* of the pulvinar, fig. 13 *a*. This atrophy is accentuated by an unusually dense gliosis. All the component parts of the medial geniculate body are quite normal. A little more rostrally (section 25 of this block) the atrophic areas become rather more extensive and more clearly circumscribed. At this level the whole of the element *pd* is completely degenerated, the outline of the nucleus being sharply marked out by the glial proliferation which has replaced the damaged cells. A slight degree of gliosis extends into the lateral margin of nucleus *pβ*, but there is no certain evidence of any loss of cells in this element. The caudal end of the lateral geniculate body appears in these sections, and as it is traced forwards, it is seen that a sector of this body immediately to the medial side of its central axis has undergone complete degeneration, fig. 13 *b*. This area received fibres from the upper half of the macular region of the retina, and is related to the small involvement by the lesion of the upper part of the area striata close to the sulcus lunatus. This observation corresponds closely with POLIAK's work on the projection of the lateral geniculate body on the visual cortex in monkeys.

The degree of cell atrophy in section 72 is shown in fig. 13 *b*. Here the whole of the element *Lb* is degenerated except for a thin layer of cells at the dorsal surface of the thalamus. This atrophy extends as far medially as the nucleus of the medial medullary lamina. The element *La* does not appear to have suffered any loss of cells, though in its outer part there is a slight degree of gliosis. The caudal extremity

of the ventral nucleus in this section is quite normal, as also are the other thalamic elements such as the centre median, parafascicular and dorso-medial nuclei. At the level of the rostral end of the lateral geniculate body a small group of cells appears in the centre of the atrophic area affecting the lateral nucleus, and when the most rostral sections of the second block are reached (*e.g.*, section 125, fig. 33,

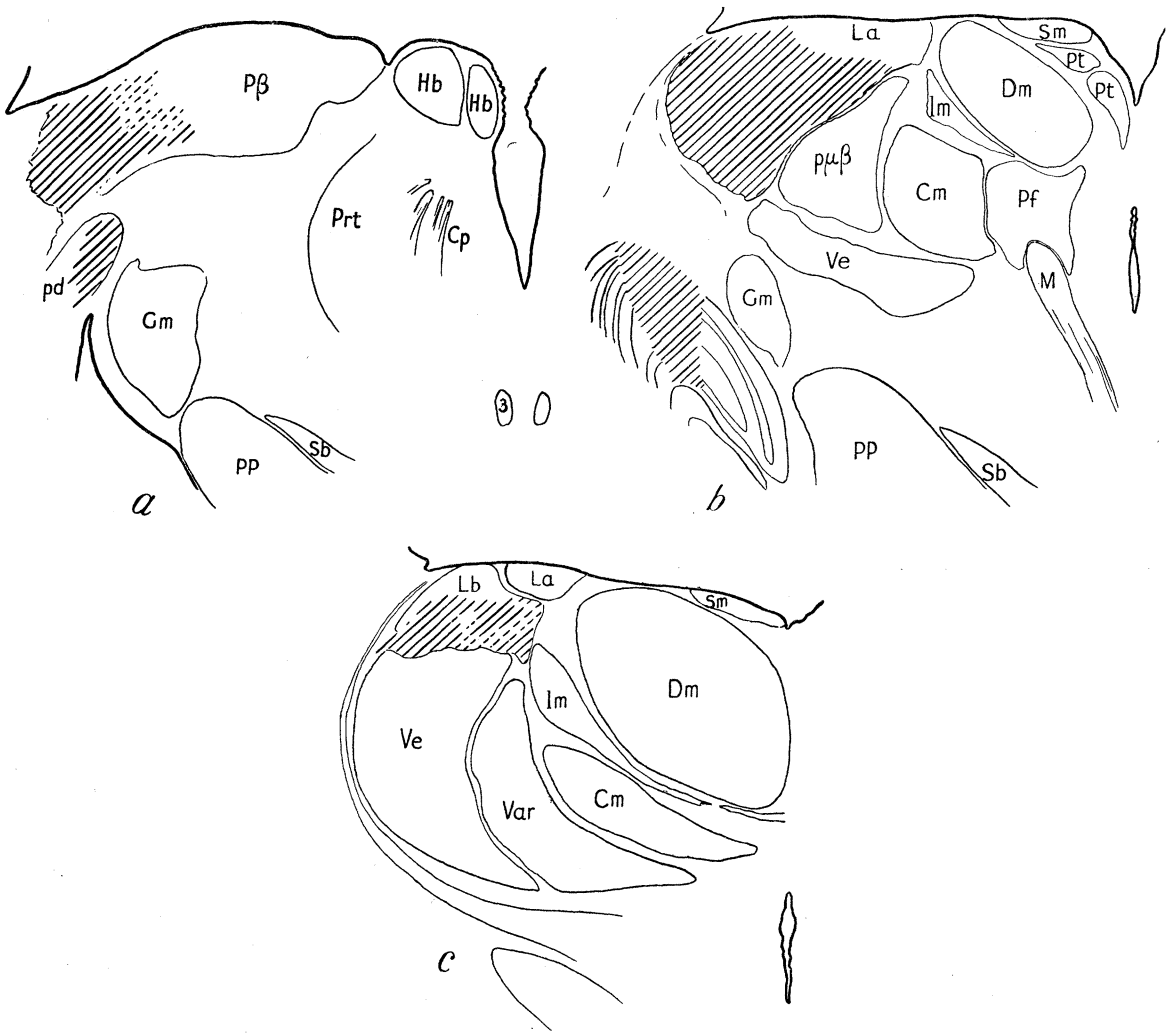


FIG. 13, *a*, *b* and *c*—Transverse sections (Nos. 2.1.8., 2.9.8., and 3.2.6.) through the thalamus in experiment *F*, showing areas of degeneration in nucleus *Lb*, nucleus *pd*, and the lateral geniculate body.

Plate 26) this area has become divided into medial and lateral parts by a zone of normal cells.

The first sections of the third block pass through the middle of the dorso-medial nucleus, the rostral part of the centre median nucleus, and the maximum development of the pars arcuata of the ventral nucleus. Here there is a sharply localized patch of cell atrophy which involves the ventral half of the lateral nucleus (*Lb*),

reaching from the lateral to the medial medullary lamina, fig. 13 *c*. Nucleus *La* and the angular nucleus are normal. The elements of the ventral nucleus are also quite intact. By section 32 of this block, cell degeneration has disappeared, and in front of this level the cytoarchitecture of the whole of the thalamus is normal.

In this experiment, the lesion involves practically the whole superficial extent of the area preparietalis (BRODMANN's cortical area 5), as well as a small portion of the upper part of the area parietalis (area 7), the striate cortex, and the peristriate areas (18 and 19). Cell atrophy in the thalamus is confined to the caudal half of nucleus *Lb*, to the greater part of the nucleus *pd* of the pulvinar, and to a median sector of the lateral geniculate body. The main nucleus of the pulvinar ($p\beta$) and all the elements of the ventral nucleus are normal.

Experiment G—Monkey 20. Operated November 14, 1933, killed February 5, 1934.

Superficially the lesion was found to lie in the posterior part of the inferior parietal lobule, mainly confined to the angle between the intraparietal and the lunate sulci, fig. 14 *a*. Above, it reached almost to the upper border of the hemisphere close

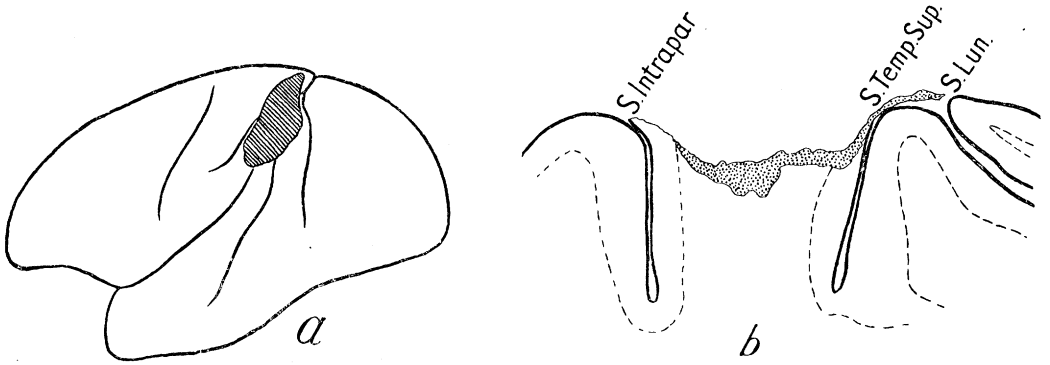


FIG. 14 *a*—The cortical lesion in experiment *G*. × ⅔. *b*—Sagittal section through the middle of the lesion in experiment *G*. × 3⅓.

to the parieto-occipital fissure, and behind to the rostral lip of the lunate sulcus. Its anterior margin was 11 mm behind the central sulcus. The sagittal diameter of the lesion was 18 mm, and the transverse diameter 15 mm.

Sections showed that the lesion was not quite so extensive as inspection of the surface of the brain had suggested. It was confined almost entirely to BRODMANN's area 7, reaching slightly into area 19 behind, and into the lower margin of area 5 above, fig. 14 *b*.

The thalamus—The most caudal sections of the first block pass through the middle of the lateral geniculate body and the oral part of the medial geniculate body, the posterior commissure and the pulvinar. At this level there is a conspicuous gliosis throughout the element *Lb* extending as far medially as the margin of element $p\beta$ of the pulvinar, but no definite cell degeneration is evident. A few sections further forwards, however, the gliosis becomes more distinct and localized, and at section 28

a circumscribed but quite small patch of cell atrophy (not more than 1 mm in diameter) is present close to the dorsal surface of the thalamus in the boundary between the medial edge of the element *Lb* and the lateral margin of *pβ*, fig. 15. A few sections further rostrally this patch of atrophy has disappeared.

Except for this small area at the caudal end of the thalamus, the thalamic nuclei (including nucleus *pd* of the pulvinar) are all entirely normal throughout their whole extent. The slight degree of cell atrophy in the thalamus in this experiment is evidently related to the fact that the cortical lesion was mainly confined to an area of the parietal lobe which, as shown by POLIAK's researches (1932), does not

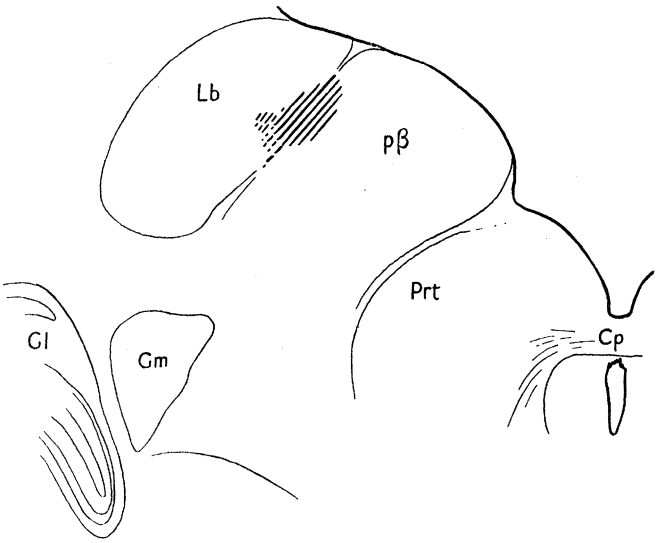


FIG. 15—Transverse section (No. 1.3.8) through the caudal end of the thalamus in experiment *G*.

receive thalamo-cortical fibres. The degeneration in the caudal end of the lateral nucleus may be secondary either to the involvement of the caudal margin of POLIAK's " somatic sensory " region, or to the involvement of the upper end of his projection area of unknown significance, which he found in immediate relation to the posterior part of the Sylvian fissure. This experiment confirms the results obtained by the previous experiments, *i.e.*, that the main part of the lateral nucleus (*Lb*) is essentially related to the posterior part of the parietal cortex (area parietalis, or area preparietalis, or both) and not to the area post-centralis.

Experiment H—Monkey 25. Operated March 13, 1934, killed May 13, 1934.

A fairly extensive lesion was made in the posterior part of the parietal lobe in this experiment. Macroscopically at death it appeared oval in shape, measuring 24 mm in sagittal diameter, and 16 mm in transverse diameter. Rostrally it reached up to 3 mm from the middle of the central sulcus, above up to 5 mm from the mid-line, and behind it extended into the upper part of the occipital lobe. Below, the lesion involved the upper extremity of the Sylvian fissure, fig. 16 *a*.

Microscopically, the lesion was found to be fairly deep, but confined to the cortex and the subjacent white matter. A very large proportion of the parietal lobe excluding the area post-centralis had been involved. The greater part of areas 5 and 7 on the lateral surface of the hemisphere was directly destroyed, as well as the upper part of areas 18 and 19 and a considerable portion of the upper half of the rostral part of the area striata. In addition, the lesion was sufficiently deep above to have interrupted most, if not all, of the fibre connections of those parts of

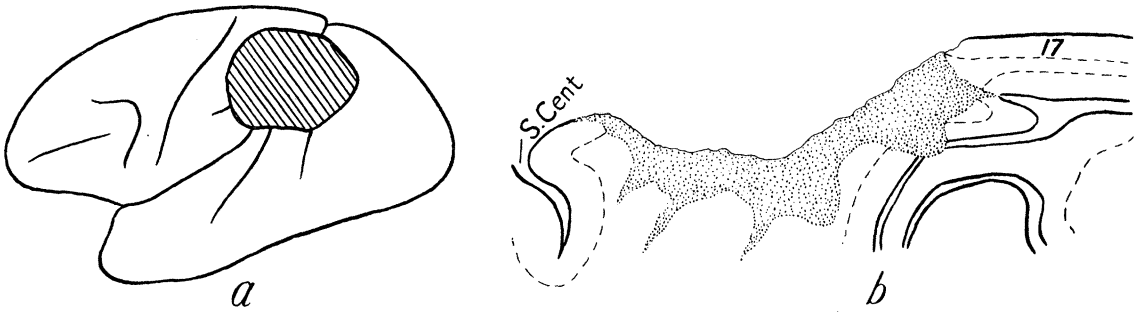


FIG. 16 *a*—The cortical lesion in experiment *H.* × ⅔. *b*—Sagittal section through the middle of the lesion in experiment *H.* × 2⅔.

areas 5 and 7 which extend on to the medial surface of the hemisphere. On the other hand, the sections show that the area post-centralis and its connections were left intact except perhaps for a small portion of its caudal border in about the middle of its length, fig. 16 *b*.

The thalamus—The thalamus was sectioned serially in three blocks. The most caudal section of the first block passes through the anterior colliculus and the projecting pole of the pulvinar. The latter is here formed by the main element of the pulvinar, nucleus *pβ* of FRIEDEMANN, and it is interesting to record that it shows no certain evidence of cellular degeneration. It appears to contain its normal density of cells, and if there is any cell atrophy it is too slight and too diffuse to be detected. At the level of sections passing through the medial geniculate body (*e.g.*, section 40 of the first block) a conspicuous patch of atrophy with an accompanying dense gliosis appears at the dorso-lateral angle of the pulvinar in the position of the caudal extremity of the lateral nucleus (element *Lb*), and extending out to the lateral medullary lamina, fig. 17 *a*. The medial geniculate body is normal. As the sections are traced forwards, the patch of atrophy increases in size, reaching ventrally to a position just lateral to the medial geniculate body where it involves the region of the nucleus *pd* of the pulvinar. The cells of this nucleus have completely disappeared. By section 100 the area of degeneration begins to extend medially along the dorsal surface of the thalamus, but it is here confined to element *Lb*. The other elements of the pulvinar at this level, *pβ* and *pa*, contain normal cells and show no gliosis. In section 140, the whole area of nucleus *Lb* is still completely atrophied, while nucleus *pβ* which appears at this level is normal. It may also be

noted that the cells of the medial half of the lateral geniculate body have undergone complete atrophy, in relation to the cortical injury involving the upper half of the area striata. In section 170, the caudal extremity of the pars externa of the ventral nucleus appears. It contains normal cells and stands out in contrast with the area of gliosis and cell atrophy in the lateral nucleus immediately dorsal to it. The other thalamic elements which are visible at this level, element *La* of the lateral nucleus, the dorso-medial and centre median nuclei, are quite intact. Fig. 17 *b* shows the degree of atrophy in section 180 of the first block. Here it is seen that the cell atrophy is confined to nucleus *Lb* and that in the dorso-medial part of this nucleus the degeneration is partial, for at this level scattered normal cells begin to appear here.

The first section of the next block passes through the middle of the thalamus at the level of the maximum development of the dorso-medial nucleus and the centre

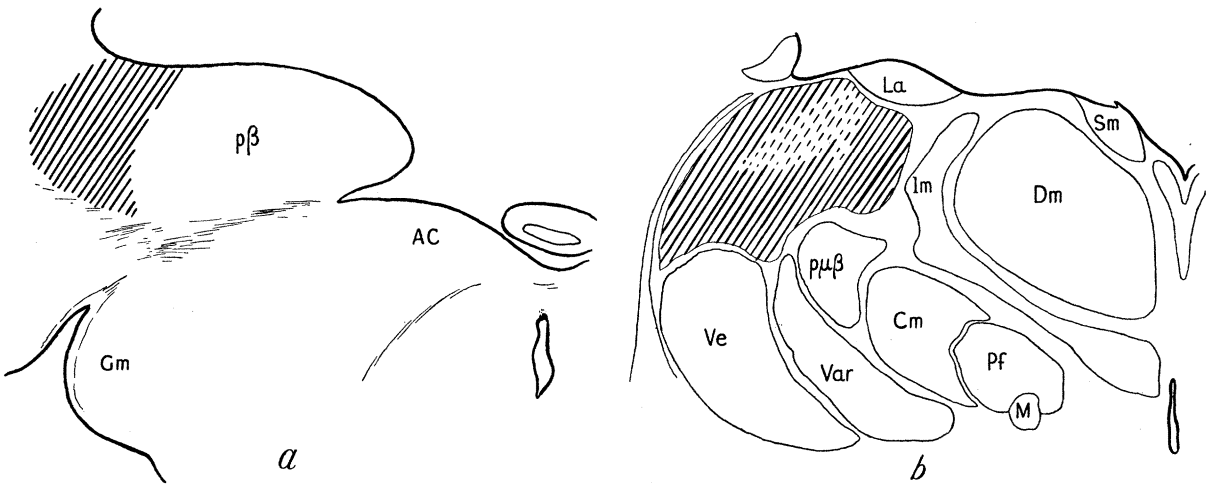


FIG. 17, *a* and *b*—Transverse sections (Nos. 17.7.4., and 1.19.2.) through the caudal and middle parts of the thalamus in experiment *H*.

median nucleus. Here, the nuclear elements of the thalamus all appear normal except for a small and localized patch of atrophy and gliosis at the lateral margin of the junctional region between the pars externa of the ventral nucleus and nucleus *Lb*. This small patch disappears by section 50 of this block. Rostral to this level, the cytoarchitecture of the thalamus is completely normal.

In this experiment, therefore, cell atrophy is confined to the posterior half of nucleus *Lb* and to element *pd* of the pulvinar and the medial half of the lateral geniculate body. That is to say, it corresponds closely with, but is a little more extensive than, the atrophy found in experiment *F*. It may be emphasized again that, although almost the entire caudal part of the parietal cortex had been involved in the operative lesion, the main element of the pulvinar, nucleus *p*β, showed no definite evidence of cellular atrophy, while the elements of the ventral nucleus likewise present a normal cytoarchitecture.

Experiment I—Monkey 18. Operated October 3, 1933, died October 13, 1933.

This monkey died ten days after the operation, and was thus not available for the study of retrograde cellular degeneration. The opportunity was taken of studying the centrifugal connections of the parietal lobe by using the Marchi technique.

The lesion in this case was situated in the caudal half of the upper part of the parietal cortex, fig. 18 *a*. Macroscopically it was found to be broadly oval, measuring 12 mm in sagittal, and 9 mm in transverse diameter. The upper margin was 5 mm from the upper margin of the hemisphere, and the anterior margin 9 mm from the central sulcus. Caudally the lesion reached back to the rostral lip of the sulcus lunatus, involving the upper ends of the intraparietal and parallel sulci, and not quite reaching the upper extremity of the exposed part of the Sylvian fissure.

Microscopical sections showed the lesion to be superficial, extending only to a slight degree beneath the cortex, fig. 18 *b*. A considerable degree of inflammatory

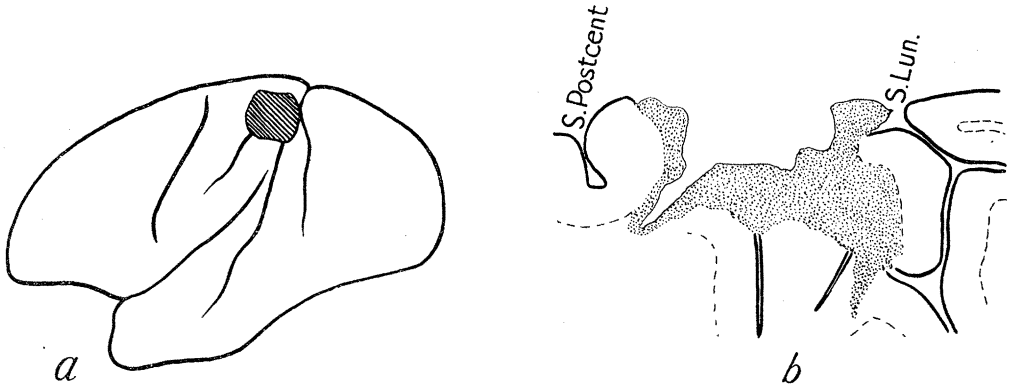


FIG. 18 *a*—The cortical lesion in experiment *I*. × $\frac{2}{3}$. *b*—Sagittal section through the middle of the lesion in experiment *I*. × $3\frac{1}{3}$.

reaction was noticed in the area of the lesion, but the surrounding region of the hemisphere was quite normal in appearance. A comparison with BRODMANN's charts indicates that the lesion had involved the most dorsal part of his cortical areas 18, 19, and 7, and also the caudal part of area 5.

The thalamus—The thalamus was cut into a series of blocks and stained for Marchi degeneration in the usual way. Every fourth section was preserved. Sections through the rostral part of the thalamus (at the level of the anterior nucleus) show an abundant but scattered deposit of coarse Marchi granules in the fibres of the internal capsule of the left side, but no trace of Marchi degeneration in the thalamus itself. The great majority of the degenerated fibres in the internal capsule can be traced in continuity to the lateral third of the crus cerebri. They pass down into the upper part of the pons where they begin to terminate in the pontine nuclei in which a fine sprinkling of Marchi granules is apparent. This demonstration of cortico-pontine fibres taking origin in the parietal cortex (which confirms the observations of MINKOWSKI (1919)) deserves emphasis, for by many authorities they

do not seem to be recognized. BIEMOND (1930) has also noted that after occipital and parietal lesions in monkeys, degeneration in the so-called temporo-pontine tract is unmistakeable.

In tracing the sections of the thalamus caudally, at the level of the middle of the lateral geniculate body scattered degenerated fibres are seen to leave the medial aspect of the internal capsule and pass into the lateral medullary lamina of the thalamus. A few of these penetrate into the lateral margin of the pars externa of the ventral nucleus. Further caudally most of these degenerated fibres accumulate in the most ventral part of the posterior extremity of the pars externa where they form rather a conspicuous deposit. Moreover, the fasciculi which penetrate the whole of the lateral margin of the pars externa at this level (as far dorsally as nucleus *Lb*) also contain isolated fibres showing definite Marchi degeneration. On the other hand, the fasciculi of the thalamic radiations which enter the lateral nucleus (elements *La* and *Lb*) are entirely free of osmic deposit. Marchi degeneration in the ventral extremity of the pars externa of the ventral nucleus becomes more dense posteriorly and involves the bundles of fibres which course dorso-medially and caudally towards the tectum, penetrating here the caudal end of the ventral nucleus.

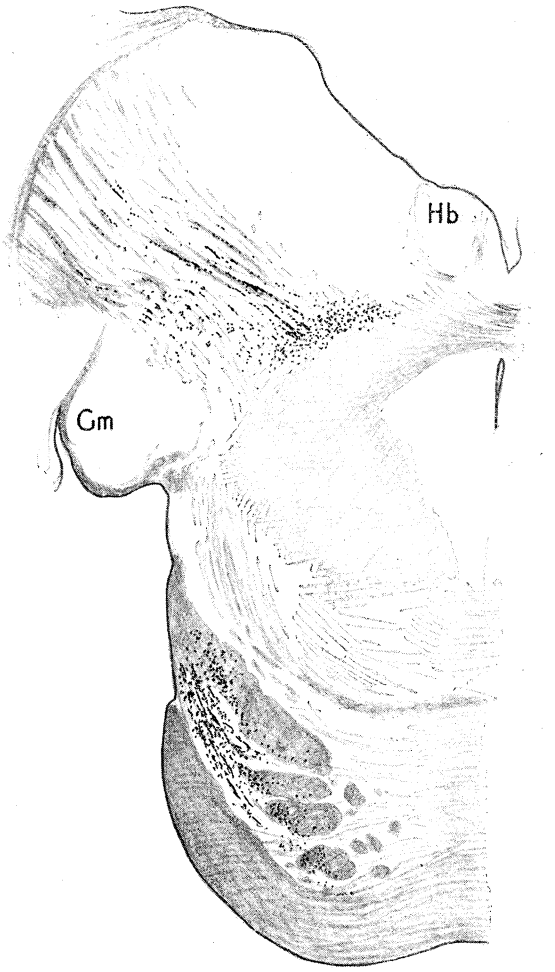


FIG. 19—Transverse section through the caudal end of the thalamus and the pons in experiment *I*, showing Marchi degeneration extending along the cortico-pretectal fasciculi and the parieto-pontine fibres.

In sections through the pulvinar region, at the level of the medial geniculate body, conspicuous Marchi degeneration is present in the slender fasciculi which stream medially between the pulvinar and the tegmentum of the mid-brain towards the anterior colliculus. These degenerated fibres join those which penetrate the ventral extremity of the pars externa of the ventral nucleus, and all of them can be traced without difficulty into the stratum album medium of the anterior colliculus where they terminate, fig. 19. The area of terminal degenerated fibres extends along and under cover of the rostral margin of the anterior colliculus as far as the dorso-medial margin of the medial geniculate body. This area marks the position of the pretectal nucleus, an element which is much better defined in the brains of

lower mammals (CLARK, 1932, *a*) and, in the monkey, lies at the tecto-thalamic junction in close relation to the nucleus limitans.

The degenerated fibres penetrating the caudal extremity of the thalamus are therefore to be regarded as cortico-pretectal rather than cortico-tectal fibres. They correspond entirely with the cortico-pretectal fibres which were demonstrated by one of us in the rat's brain after a lesion involving the parietal region of the cortex immediately in front of the area striata (CLARK, 1932, *b*). No degenerated fibres are present in the stratum opticum of the anterior colliculus. Degeneration in this layer has been recorded by several observers (PROBST, 1900, BEEVOR and HORSLEY, 1902, BOUMANS, 1905, POLIAK, 1932 and BIEMOND, 1930) after injury to the striate area of the cortex.

It has been remarked that in our experiment many scattered degenerated fibres were found to penetrate the caudal part of the ventral nucleus. Whether any of these terminate in this nuclear element or whether they are all fibres of passage aiming for the pretectal nucleus cannot be determined in this case. It is possible that a similar experiment with a subsequent sectioning of the thalamus in a horizontal plane might lead to a decision.

It may be noted that nowhere in the whole series of sections was there any trace of Marchi degeneration in the caudate or lenticular nuclei, or in any other elements of the thalamus besides the pars externa of the ventral nucleus.

Experiment J—Monkey 19. Operated October 10, 1933, killed January 1, 1934.

In this animal the lesion was confined to the upper half of the precentral gyrus, fig. 20 *a*. Dorsally it cut the upper margin of the hemisphere and extended down

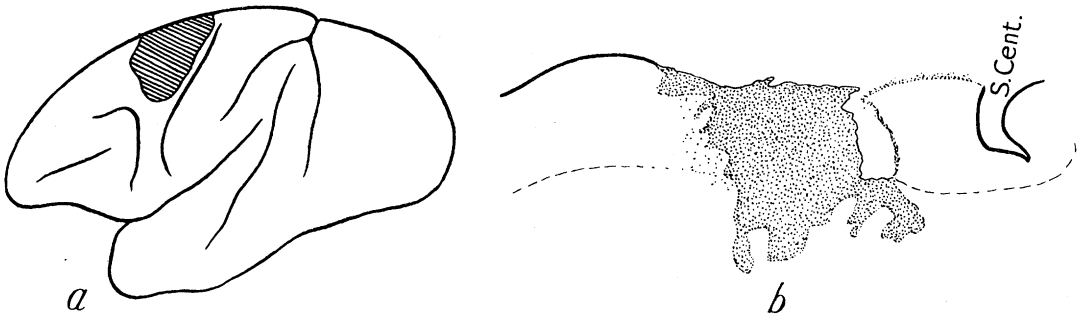


FIG. 20 *a*—The cortical lesion in experiment *J*. × ⅔. *b*—Sagittal section through the middle of the lesion in experiment *J*. × 3⅓.

on to the medial surface for 5 mm. Caudally it reached to the rostral lip of the sulcus centralis, and anteriorly extended forwards for 15 mm. The lesion was approximately 13 mm in transverse diameter. Its position evidently corresponds to the leg area and part of the arm area of the motor cortex. Histologically the lesion was found to be quite superficial, and practically limited to the gray cortex,

fig. 20 *b*. It did not extend back quite as far as the bottom of the central sulcus, and was confined practically entirely to BRODMANN's area 4 (area gigantopyramidalis).

The thalamus—The most caudal section of the first block passes through the projecting pole of the pulvinar and the anterior colliculus, while the most rostral section is at the level of the habenular ganglion and the caudal extremity of the lateral geniculate body. Throughout this block the cytoarchitecture of the thalamus is quite normal, and there is no gliosis present in the cortico-tectal fasciculi.

The caudal section of the second block cuts through the caudal end of the dorso-medial nucleus, centre median nucleus, the element $p\mu\beta$ of the pulvinar, and the middle part of the lateral geniculate body. All the nuclei of the thalamus at this level are normal. In section 29 of this block a small patch of cell atrophy with accompanying gliosis is seen immediately dorsal to the rostral pole of nucleus $p\mu\beta$. There is also some partial degeneration of the cells of the nucleus of the medial medullary lamina. On the other hand, the cells of the pars externa of the ventral nucleus are here all well stained and normal, and no change is to be observed in the lateral nuclear elements (*Lb* and *La*) or in the centre median and dorso-medial nuclei. A little further forwards, fig. 21 *a*, the patch of atrophy extends ventrally along the lateral margin of the centre median nucleus (which it sharply circumscribes) and on the medial aspect of the pars externa of the ventral nucleus. It thus involves the arcuate nucleus which lies in this position. This nucleus at this level is affected by a diffuse atrophy, practically all its cells having disappeared except for a few in its medial half and at its ventral extremity. The pars posterior of the ventral nucleus is normal. By section 82, fig. 34, Plate 26, this atrophic area (in which, however, a few normally stained cells are scattered infrequently) has become very distinct and is confined to the pars arcuata and the dorsal end of the pars externa of the ventral nucleus, as well as the dorsal half of the reticular nucleus. Along the medial border of the ventral half of the pars externa there is considerable gliosis and perhaps also some partial cell degeneration, but the latter is uncertain for many normal cells are to be seen in the midst of the gliosis. At the junctional region of the pars externa of the ventral nucleus and nucleus *Lb* there is considerable gliosis and a partial cell atrophy, but it seems probable that there is little if any cell atrophy in the main mass of element *Lb*, and certainly none in its dorso-medial part. The nucleus of the medial medullary lamina and nucleus *La* are normal. At the level of the rostral pole of the centre median nucleus (section 105 of this block) the area of cellular atrophy is fairly extensive, involving here the whole of the anterior extremity of the pars externa of the ventral nucleus except for the lateral half of its ventral third. The arcuate nucleus now contains a large proportion of normal cells, a partial atrophy being confined to its dorsal moiety. The cells in that part of the nucleus reticularis which overlies the degenerated region in the pars externa have disappeared. The most anterior section of block 2 (section 168) passes through the caudal pole of the anterior nucleus. At this level the rostral

elements of the ventral nucleus are found, pars antero-lateralis and pars antero-medialis. The former is completely degenerated except at its medio-ventral extremity, while the latter contains normal cells and is free of gliosis. In element *Lb* there is towards the front of this block very evident gliosis at its ventro-lateral margin and extending up to its dorso-lateral angle, and at the level of the caudal pole of the anterior nucleus there is some cell atrophy in this region. The dorso-medial part of *Lb*, however, contains normal cells.

The first section of the third block cuts through the caudal part of the anterior nucleus of the thalamus. Here, again, the area of total cell atrophy involves the whole of the pars antero-lateralis of the ventral nucleus except at its medio-ventral extremity, but there are two circumscribed patches of normal cells at its dorsal

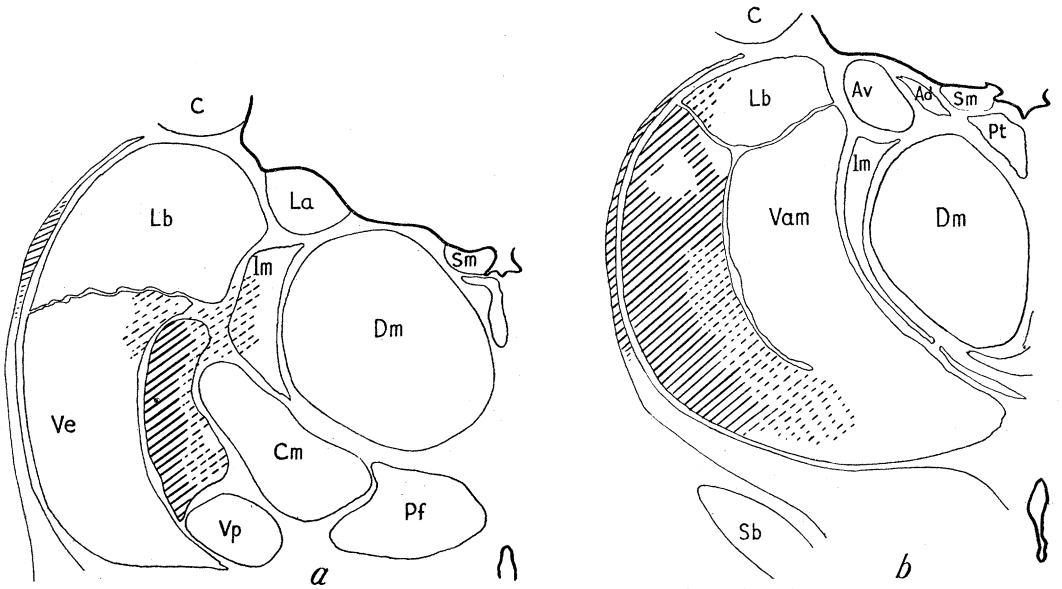


FIG. 21, *a* and *b*—Transverse sections (Nos. 2.7.5. and 3.1.6.) through the middle part of the thalamus in experiment *J*.

extremity, fig. 21 *b*. The reticular nucleus over a corresponding extent is partially degenerated. The antero-medial element is normal. In front of this level, the area of atrophy shrinks rapidly, and by section 50 it no longer exists. At this level, also, the nucleus reticularis is quite normal.

The ventral nucleus in this specimen extends over 430 sections and thus has a sagittal diameter of approximately 8·6 mm. The cellular atrophy extends between section 139 and section 328 of this series. It is therefore situated in approximately the middle two quarters of the whole length of the ventral nucleus. Further, the cell degeneration is limited to the pars arcuata, the dorsal part of the anterior extremity and slightly along the medial border of the pars externa, and the pars antero-lateralis of the ventral nucleus, as well as a corresponding extent of the nucleus reticularis. A small area in the ventro-lateral part of nucleus *Lb* (just rostral to its central point) should be included among the atrophic areas. As

indicated above, the limits between the ventral and lateral nuclei at this junctional region are difficult to define, and at least the greater part of nucleus *Lb* seems to contain normal cells.

Experiment K—Monkey 13. Operated June 13, 1933, killed September 5, 1933.

The lesion was situated in the frontal lobe of the right hemisphere and on death was found to measure 7·5 mm in sagittal diameter, and 5 mm in transverse diameter. It reached up to within 5 mm of the upper margin of the brain, and was separated from the central sulcus behind by a distance of 10 mm. Below and in front, it extended down to 2 mm from the upper limb of the arcuate sulcus, fig. 22 *a*.

FIG. 22 *a*—The cortical lesion in experiment *K*. × ⅔. *b*—Sagittal section through the middle of the lesion in experiment *K*. × 3⅓.

Histological examination showed that the lesion was quite superficial and was confined to cortical area 6. The motor area (4), the rostral limit of which is indicated by an arrow in figure 22 *b*, was intact.

The thalamus—Some gliosis is present in the anterior part of the internal capsule, but nowhere in the whole extent of the serial sections through the thalamus was any evidence of cell atrophy or gliosis found. A careful study of the elements of the ventral and lateral nuclei showed no cellular change.

Experiment L—Monkey 24. Operated January 24, 1934, killed April 5, 1934.

The cortical lesion in this case was made in the upper part of the frontal lobe above the sulcus arcuatus and (as far as could be determined) in front of the motor area, involving almost the entire extent of the area frontalis agranularis (area 6 of BRODMANN). Superficially, the lesion was found to extend laterally for 10 mm from the medial border of the hemisphere, reaching to the dorsal lip of the sulcus arcuatus, and having a sagittal diameter of about 12 mm, fig. 23 *a*. It also extended down on the medial surface of the hemisphere for a distance of 5 mm.

Coronal sections were taken through the lesion, fig. 23 *b*. From these sections it was found to be practically confined to area 6 on the lateral surface of the brain. Medially, at one point, it extended down almost to the corpus callosum, involving

here a part of the gyrus cinguli. Moreover, the subjacent white matter had been cut through as far down as the roof of the anterior horn of the lateral ventricle. The caudate nucleus, however, was quite intact.

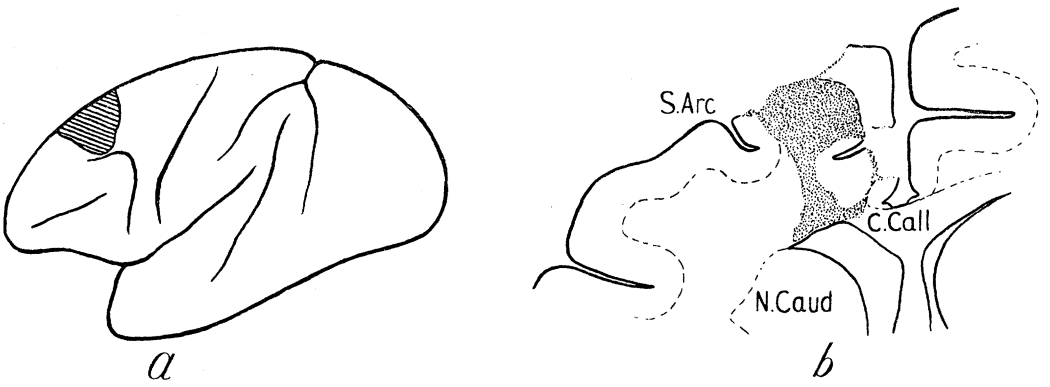


FIG. 23 *a*—The cortical lesion in experiment *L*. × ⅔. *b*—Coronal section through the middle of the lesion in experiment *L*. × 3⅓.

The thalamus—The whole length of the thalamus was serially sectioned in four blocks. The first two blocks include the pulvinar and the caudal part of the thalamus. No degeneration could be detected in these regions. The nuclei, including the centre median nucleus, the dorso-medial nucleus, and the lateral nucleus (elements *La* and *Lb*), are completely normal in their cytoarchitecture. The third block passes through the middle of the thalamus. In the caudal sections of this block, no cell changes are to be observed. In section 108, at the level of the caudal pole of the antero-ventral nucleus, there is a slight degree of cellular atrophy and accompanying gliosis at the dorsal margin of nucleus *Lb*. Tracing the sections forwards, this atrophy becomes more distinct and forms a fairly circumscribed patch at the dorsal extremity of the nucleus lateralis *b* in which, however, scattered normal cells still remain. Further forwards, the atrophic area descends ventro-medially to involve the dorsal extremity of the antero-medial element of the ventral nucleus, immediately alongside the nucleus of the medial medullary lamina. The cells of the latter nucleus are quite normal and deeply stained. By section 140, the patch of atrophy is mainly confined to the dorsal angle of the nucleus ventralis, pars antero-medialis, fig. 24 and fig. 35, Plate 27. It forms a relatively small area, but is rendered very conspicuous by the disappearance of the cells and the gliosis. The

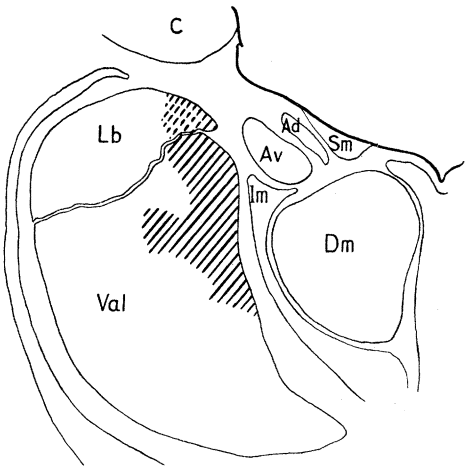


FIG. 24—Transverse section (No. 3.19.8.) through the anterior third of the thalamus in experiment *L*.

most caudal section of the fourth block passes through the caudal part of the antero-ventral nucleus. Here the localized area of degeneration and the accompanying gliosis are still distinct, involving the dorsal margin of nucleus lateralis *b* and extending ventro-medially into the ventral nucleus. In a few sections it begins to shrink, and by section 33 it has become quite indistinct. Immediately in front of this level, evidence of atrophy is apparent in the anterior group of nuclei. The antero-dorsal nucleus is very shrunken in cross-sectional area and contains but few normal cells, standing out thus in strong contrast with the normal antero-dorsal nucleus of the right side of the thalamus. Moreover, the medial half of the antero-ventral nucleus in this plane also shows a diffuse cell atrophy accompanied by a distinct gliosis. At the rostral pole of the anterior nucleus there is no longer any cell degeneration or gliosis to be observed.

In this case, then, cell atrophy is confined to the rostral extremity of the antero-medial element of the ventral nucleus, a small part of the rostral extremity of the lateral nucleus (*Lb*), and to the rostral half of the antero-dorsal and of part of the antero-ventral nucleus. The cell atrophy in the antero-dorsal and antero-ventral nuclei is of slight extent. We have no doubt that it is directly related to the involvement by the cortical lesion of a part of the gyrus cinguli on the medial surface of the hemisphere, for we have previously demonstrated the existence of a connection between the anterior nucleus and this gyrus in the rat and cat. On the other hand, the cell degeneration in the rostral end of the ventral and lateral nuclei is certainly the result of the extensive destruction of area 6 of the cortex. This cell atrophy, however, is of rather small extent in comparision with the area of the cortical lesion. It may be inferred, therefore, that BRODMANN's area 6 receives relatively few fibres from the thalamus. In this connection it may be noted that in experiment *K* in which a small part only of this cortical area was involved by the operative lesion, we failed to find any evidence of cellular atrophy or gliosis in the thalamus.

Experiment M—Monkey 23. Operated January 23, 1934, killed April 5, 1934.

The cortical lesion in this experiment was limited to that part of the lateral surface of the frontal lobe which lies anterior to the sulcus arcuatus, fig. 25 *a*. Superficially it measured 17 mm in sagittal diameter, and 15 mm in vertical extent. Above and behind, the lesion reached the rostral lip of the arcuate sulcus, while in front it extended to a distance of 10 mm from the frontal pole of the hemisphere. The whole length of the sulcus rectus, with the exception of its anterior extremity, was involved.

Microscopic sections were made in the horizontal plane through the lesion, fig. 25 *b*. They showed that the lesion was limited to the cortex and the immediately subjacent white matter, involving the greater proportion of the area frontalis granularis (areas 8 and 9 of BRODMANN).

The thalamus—The whole length of the thalamus was serially sectioned in three blocks. A close study of these sections shows that cell degeneration is entirely confined to the dorso-medial nucleus (nucleus medialis *a* of other authors) and a

small area of the nucleus ventralis, pars antero-medialis. All other thalamic elements, including the centre median nucleus, parafascicular nucleus, lateral nucleus and anterior nucleus, are completely normal with well-staining cells. The atrophy in the dorso-medial nucleus is particularly well-defined and very sharply circumscribed. It occupies the whole of the parvicellular element (approximately the lateral two-thirds of the nucleus) and extends throughout the entire length of the nucleus from the level of the mammillo-thalamic tract in front to the level of the

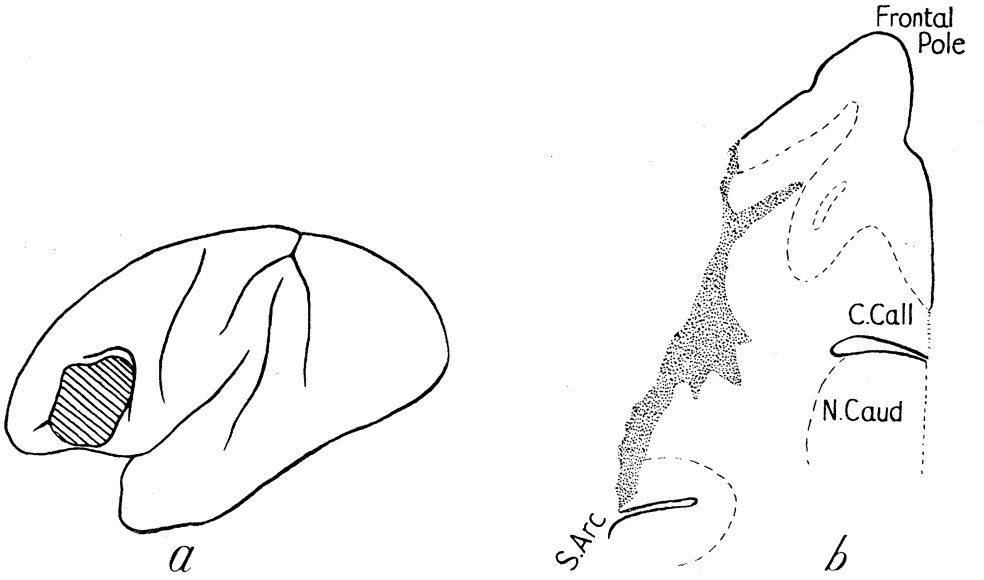
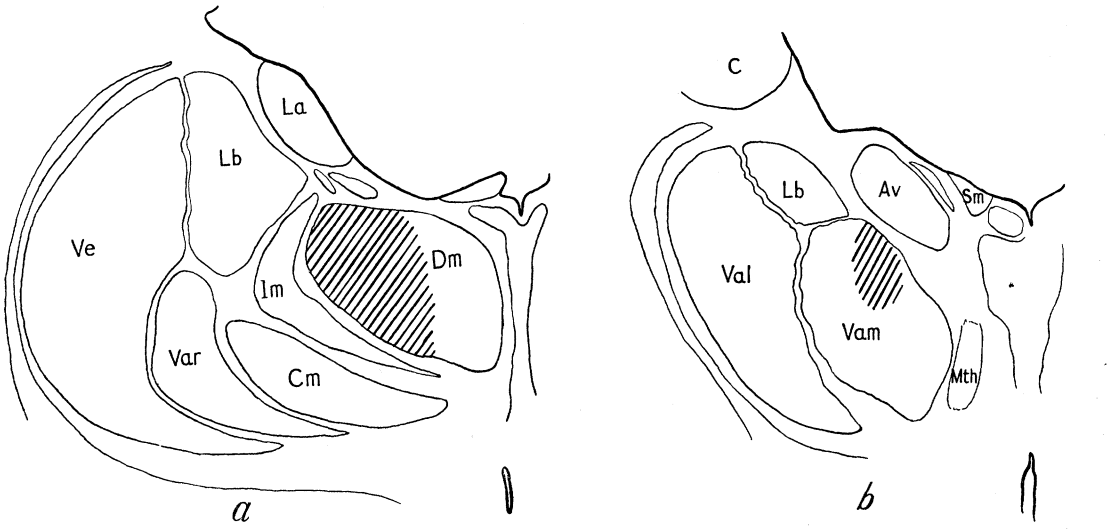


FIG. 25 *a*—The cortical lesion in experiment *M*. × ⅔. *b*—Horizontal section through the middle of the lesion in experiment *M*. × 3⅓.

fasciculus retroflexus behind. In this region, the cells have undergone complete degeneration (except at the very caudal extremity where a few scattered cells persist), and the area of atrophy is accompanied by a rich gliosis which renders it even more conspicuous. Medially the atrophic area is limited by the magnocellular element of the dorso-medial nucleus in which the cells are normal in size and number, but stain less intensely than those of the opposite side, while laterally it is bounded by the nucleus of the medial medullary lamina in which, also, the cells are quite normal, fig. 26 *a* and fig. 36, Plate 27. The only other cellular degeneration is found in the antero-medial element of the ventral nucleus, just rostral to the dorso-medial nucleus and at the level of the upper end of the mammillo-thalamic tract. Here, there is a small circumscribed patch of complete cell atrophy (approximately 1 mm in diameter at its maximum development) lying immediately ventral to the antero-ventral nucleus, fig. 26 *b*. It extends over some 60 sections and is associated with distinct gliosis. The most rostral part of the antero-medial element shows some gliosis in the same region, but it shows no definite evidence of cell degeneration at this level.

The extensive and complete cell atrophy in the dorso-medial nucleus is evidently related to the cortical lesion which involved the greater part of the granular cortex of the frontal lobe. The small atrophic patch in the pars antero-medialis of the ventral nucleus may possibly be related to the same cortical area, but is more probably the result of a slight involvement by the lesion of the fibre connections of the agranular frontal cortex which lies above and immediately adjacent (see experiment *L*). We would emphasize again that all the other thalamic nuclei



FIGS. 26, *a* and *b*—Transverse sections (Nos. 2.5.8. and 3.4.7.) through the middle and anterior parts of the thalamus in experiment *M*, showing the areas of cell atrophy in the dorso-medial nucleus and the pars antero-medialis of the ventral nucleus.

(some of which, such as the centre median nucleus and the lateral nucleus, have been asserted to have connections with the frontal cortex) are quite intact. It is also of interest to note that no change could be detected in the red nucleus and sub-thalamus.

DISCUSSION OF RESULTS

Our experiments have demonstrated in some detail the ascending connections between certain of the thalamic nuclei and the cortex of the parietal and frontal lobes of the cerebral hemisphere. Before considering separately the connections of these nuclei with the cortex, it is convenient to refer to the evidence bearing on the question of the precise termination of the various sensory tracts which reach the thalamus from lower levels. We may thus be able to indicate or, at least, to suggest how the impulses which these tracts carry are projected on to the cortex.

There is some clinical evidence to show that on their approach to the thalamus sensory tracts become progressively segregated in accordance with the nature of the sensory impulses which they carry, and thus it is probable that the different elements of sensation are represented in different topographical regions of the

thalamus. But the details of this localization have yet to be conclusively worked out. It is generally believed that the fibres of Edinger's spinal lemniscus come to occupy the most lateral part of the main fillet in the mid-brain and are therefore likely to be distributed to the lateral part of the thalamus, while the trigeminal fillet probably terminates in the more medial parts. It is at least fairly certain now that the fillet system ends entirely in the ventral nucleus of the thalamus and the cells of some of the intralaminar nuclei which encapsule this nucleus (as well as in the nucleus pretectalis and possibly in the region of the subthalamus). In spite of statements to the contrary, there is no real evidence that any part of this system is terminally related to the lateral, dorso-medial or centre median nuclei.

As the result of numerous degeneration experiments carried out over thirty years ago, PROBST (1900) demonstrated that fibres of the medial and spinal fillets end in a region of the ventral nucleus which (judging from his figures) corresponds to the nucleus ventralis, pars externa. WALLENBERG (1900) found that fibres from the cuneate and gracile nuclei end in the ventral nucleus, while fibres from the posterior horn of the cervical part of the spinal cord end in a region between the termination of the nucleus cuneatus fibres and the medial geniculate body (*i.e.*, in the caudo-lateral margin of the pars externa of the ventral nucleus). Following a lesion of the cuneate nucleus, C. VOGT (1909) found degenerated fibres passing to the caudal region of the pars externa. Some of the more medially situated fibres were also seen to enter the capsule of the centre median nucleus and to penetrate the pars arcuata of the ventral nucleus. It is probable, however, that they all eventually terminated in the pars externa. In Marchi experiments carried out by one of us on the rat's brain (CLARK, 1932, *b*), lemniscus fibres were not found to extend further than the ventral nucleus of the thalamus. In a recent paper (1932), Ranson and INGRAM have defined very clearly the precise termination of the medial fillet and the brachium conjunctivum in the thalamus of the cat, confirming to a considerable extent the conclusions of previous workers such as VOGT and ALLEN. They found that the two systems of fibres do not intermingle to any marked extent in the thalamus. The medial fillet ends in the whole of the pars externa of the ventral nucleus except for its rostral pole, some of its fibres penetrating the caudal pole of the pars arcuata *en route*. On the other hand, the brachium conjunctivum fibres terminate almost entirely in the pars arcuata of the ventral nucleus, some, however, ending in the nucleus parafascicularis, nucleus centralis lateralis, and the rostral pole of the pars externa of the ventral nucleus.

Studies of myelogeny have also contributed some data regarding the termination of sensory tracts in the thalamus. We may refer to LANGWORTHY's recent contribution on this subject (1933). He found that in the brain of a two months' old infant " myelinated spino-thalamic fibres end in the ventral nucleus as do also fibres of the medial lemniscus and brachium conjunctivum." On the other hand, at this age there are no myelinated fibres in the anterior, medial and lateral nuclei, or in the pulvinar. In 1906, O. VOGT recorded that in an infant of 81 days sections of the brain showed coarsely medullated fibres of the medial lemniscus streaming

into his nucleus *va* (which corresponds with the main part of the pars externa of the ventral nucleus), while, more orally, the distinctly finer fibres of the " Haubenstrahlung " could be seen entering his nucleus *va'* (which apparently corresponds to the rostral end of the pars externa). In a comprehensive review of their work in 1920, C. and O. VOGT referred to their recognition of nucleus *va* as the end station of the fillet fibres and nucleus *va'* as that of the brachium conjunctivum fibres.

All these observations indicate that the termination of the fillet system is limited to the ventral nucleus of the thalamus, and in higher mammals it is probable that only the pars externa of this nucleus receives the fibres of this system. None have been traced to the lateral nucleus, or to the dorso-medial nucleus (medial nucleus of human anatomy). In spite of these consistent results, there still remain some authorities who include the ventral and lateral nuclei under one term—the ventro-lateral nucleus, regarding it as a single entity the whole extent of which receives lemniscus fibres. This assumption, however, appears to rest upon the indirect evidence of thalamo-cortical connections.

On the basis of experimental work by VON MONAKOW and MINKOWSKI, the conception has arisen that the lateral nucleus is related to the " leg area " of the central convolutions, while the ventral nucleus is related to the " arm area." POLIAK (1932) believes that it is " probable that the afferent sensory tracts attain all parts of the lateral nucleus including the dorsal portion close to the zonal stratum." But this statement is apparently made on the basis of an extensive intra-thalamic lesion (his experiment No. 2) in which far more than the fillet system has been involved. Later in his monograph (p. 70) POLIAK makes the more definite statement that the afferent tracts from the spinal cord, bulb, pons, and cerebellum spread " almost over the entire ventro-lateral and dorso-lateral nucleus " and " the lateral nucleus receives afferent fibres in its entire transverse extent or width." On p. 72, again, he affirms that " it is at least the lateral nucleus of the thalamus in its entire dorso-ventral and medio-lateral extent situated between both medullary laminæ which is the terminal station for the lower ascending somatic sensory tracts as well as the point of departure of the uppermost link of the afferent somatic sensory system, the thalamo-cortical radiation." The fact remains, however, that in experiments in which the lesion has been confined to the *fillet system*, degenerated fibres have not hitherto been traced to the lateral nucleus of the thalamus, and this evidence is in accordance with the pictures afforded by a study of Weigert sections of normal mammalian brains. O. VOGT (1906) records that three weeks after a lesion affecting the post-central gyrus, secondary fibre degeneration is confined to his nucleus *va* (main part of pars externa of the ventral nucleus), while after a similar lesion in the precentral gyrus, the degeneration is found in the thalamus immediately oral of *va* (*i.e.*, in the rostral end of the pars externa of the ventral nucleus).

WINKLER (1933) has recently suggested that the ventral nucleus of the thalamus receives the termination of the medial fillet (conveying proprioceptive impulses) while the lateral nucleus receives exteroceptive impulses by way of spino-thalamic fibres. In figure 713 of his book, he demonstrates the termination of degenerated

fibres in the ventral nucleus after destruction of the posterior column nuclei of both sides in the rabbit's brain. But he does not adduce evidence for his statement concerning the lateral nucleus. Thus the direct relation (if any) of the lateral nucleus of the thalamus to the sensory somatic paths ascending from lower levels remains still to be established.

We may now proceed to a consideration of the evidence afforded by our own experiments on the relation of the ventral and other nuclei of the thalamus to the cerebral cortex.

The cortical connections of the thalamic nuclei—Nucleus ventralis, pars arcuata.—This exceptionally well-defined element of the thalamus was consistently normal after all cortical lesions involving the parietal lobe of the cerebral hemisphere. On the other hand, a lesion of the precentral gyrus involving the leg and arm regions of the motor cortex was followed by an extensive cellular degeneration of almost the whole nucleus (except for its medio-ventral extremity and its anterior end). This is demonstrated objectively in a sufficiently convincing manner by comparing fig. 34, Plate 26 (which shows the atrophied nucleus in experiment *J*) and fig. 32, Plate 25 (in which the nucleus is shown unaffected after an extensive parietal lesion in experiment *E*). The nucleus was unaffected by lesions of the premotor and prefrontal areas of the cortex (areas 6, 8 and 9). It may be inferred with confidence, therefore, that the pars arcuata of the ventral nucleus probably projects entirely on to the precentral or motor cortex. In this connection, it is interesting to refer to the evidence (cited above) that the arcuate nucleus is the end-station of the brachium conjunctivum fibres which reach the thalamus from the dentate nucleus of the cerebellum. Considering its predominantly motor functions, it is perhaps not surprising that the precentral cortex should receive impulses from the cerebellum by way of the arcuate nucleus. The functional significance of the pars arcuata of the ventral nucleus has, however, been interpreted otherwise. The researches of WALLENBERG and PROBST (among others) have suggested that this nucleus receives the terminal fibres of the trigeminal fillet and thus ultimately receives sensory impulses from the facial region. SAGER's conclusions in his recent paper (1933)* seem to confirm this conception, for he states that the arcuate nucleus is mainly connected by ascending fibres with the face region of the post-central cortex and slightly with the arm region. But this statement is based on two cases in which the precentral cortex (*as well as* the post-central cortex) had been involved by the experimental lesion. Our own experiments have demonstrated that the

* A copy of SAGER's monograph reached us when we had completed our series of experiments. By methods somewhat similar to ours, he studied the retrograde degeneration in the thalamus following cortical lesions in the monkey. His conclusions are based on four experiments in each of which the lesion was relatively extensive, involving several of BRODMANN's areas. This author has been rather seriously handicapped (we think) by the staining method which he elected to use—van Gieson. This stain is not very appropriate for the study of cellular degeneration and does not give a picture which can be readily reproduced photographically as an objective demonstration. We have found it a little difficult, therefore, to judge of the validity of some of his interpretations.

arcuate nucleus is connected with the precentral and not with the post-central gyrus. Moreover, the results of experiment *J* (see fig. 21 *a* and fig. 34, Plate 26) show that the nucleus is by no means predominantly related to the face area of the cortex as SAGER supposes.

Nucleus ventralis, pars externa—Experimental evidence shows (*vide supra*) that this element is the terminal station of at least the greater part, and probably the whole, of the thalamic fibres of the medial fillet. Our experiments indicate that it is related exclusively to the cortex immediately adjacent to the sulcus centralis. Lesions limited to the area post-centralis are consistently followed by cell atrophy limited to the pars externa of the ventral nucleus. Lesions involving other parietal cortical regions (areas 5, 7, 18 and 19) are not followed by changes in this nuclear element. Our data show, indeed, that except for its rostral extremity, the whole of the pars externa (and, through it, the medial fillet) projects on to the post-central gyrus (area post-centralis). Moreover, it is possible to localize different regions of this cortical area in the pars externa and, by employing the observations of DE BARENNE on the sensory regions of the cortex in *Macaca* (1924), to define in the same way the topographical representation of the body. Thus, the lower extremity is represented most laterally and caudally in the nucleus, and the face most medially and rostrally. It appears, therefore, that the length of the post-central gyrus from above downwards is reproduced in the pars externa of the ventral nucleus in a latero-medial direction, and not in a dorsi-ventral direction as some authors have supposed.* We would particularly emphasize that the upper end of the post-central gyrus is related by thalamo-cortical fibres to the lateral margin of pars externa, reaching to its inferior extremity, and not to the lateral nucleus (see experiments *A*, *C* and *D* and figs. 3, 7, 9, and figs. 29 and 31, Plates 23 and 24). The rostral end of the pars externa of the ventral nucleus, especially at its dorsal part, is connected with the motor cortex of the precentral gyrus (experiment *J*). It is this part of the nucleus which, on the evidence of VOGT, ALLEN, and RANSON and INGRAM (*vide supra*), receives brachium conjunctivum fibres (and perhaps, also, tegmental fibres). We have already noted that the pars arcuata of the ventral nucleus (the main termination of the thalamic fibres of the brachium conjunctivum) is also related to the precentral gyrus.

Nucleus ventralis, pars antero-lateralis—In experiment *J*, following an extensive lesion of the precentral area of the cortex, massive degeneration was found in this nuclear element, not reaching, however, to its rostral extremity. On the other hand, lesions involving the other cortical areas of the frontal lobe were followed by no demonstrable

* [*Note added in proof, November* 14, 1934—Since our paper was received for publication, a report on the thalamic projections to the central gyri in *Macacus* has appeared in the 'Journal of Comparative Neurology' (vol. 60, August 15, 1934), by A. EARL WALKER. This author also found that the vertical length of the general sensory cortex from above downwards is represented as a latero-medial arrangement in the ventral nucleus of the thalamus. He also confirmed our own observations that the lateral nucleus does not project on to the area post-centralis.]

change in its constituent cells. The afferent connections of the antero-lateral part of the ventral nucleus are not certainly known, but it may be noted that there is no convincing evidence that any fibres of the fillet system terminate in it.

Nucleus ventralis, pars antero-medialis—Experiment *L* indicates that at least the dorso-medial region of this element projects fibres on to the area frontalis agranularis (premotor area) of the cortex. The remainder of the nucleus has not been fully accounted for. It remains intact after lesions involving the greater part of the motor cortex (area precentralis) and the area frontalis granularis, and is also unaffected by injuries to any part of the parietal lobe. It is possible, however, that it may be related by corticipetal fibres to the inferior extremity (face region) of the motor cortex, for this part of the cortex was not injured in any of our experiments.

Nucleus lateralis—The lateral nucleus of the thalamus consists of two quite distinct elements *La* and *Lb*. The former is particularly well defined, being circumscribed by a medullary capsule. In none of our experiments was any cell degeneration detected in this element, though in experiment *F* there was noted a slight degree of gliosis in its outer margin. We may conclude, therefore, that element *La* either has no cortical connections with the frontal and parietal lobes at all, or, if they are present, they must be very few and scattered.

Element *Lb* lies at the dorsal surface of the thalamus and can with difficulty be differentiated morphologically from the subjacent ventral nucleus (pars externa). However, it is distinguished from the latter by certain features of its cytoarchitecture and by the fact that fillet fibres have not hitherto been traced into it. In all our experiments in which the cortical lesion in the parietal lobe has been confined to the area post-centralis (experiments *A*, *B*, *C*, and *D*), cell degeneration has been limited to the pars externa of the ventral nucleus. On the other hand, in experiment *E*, in which the lesion involved the post-central area and portions of areas 5 and 7, cell atrophy was found in the pars externa of the ventral nucleus and also in the caudal half of nucleus *Lb*. Further, in experiments *F*, *G*, and *H*, in which the cortical lesions lay behind the area post-centralis, cell degeneration was found in nucleus *Lb* while the ventral nucleus remained intact. These experiments show that the post-sensory areas of the parietal lobe (by which we understand all that part of the parietal cortex lying caudal to the area post-centralis, and including BRODMANN's areas 5, 7, 18 and 19) receive fibres from the caudal half of element *Lb*. Moreover, these corticipetal connections of *Lb* are most abundant at its caudal extremity, and at more rostral levels they become progressively less numerous. Towards the middle of the nucleus, scattered normal cells persist even after extensive cortical lesions of the parietal lobe. This demonstration of the relation between the lateral nucleus and the parietal " association " areas of the cortex confirms some of our previous observations. It has been shown, for instance, that in the rat the lateral nucleus of the thalamus projects on to the postero-superior part of the parietal cortex, a region of the cortex which we suppose to be homologous with the much

more extensive parietal " association " areas of higher mammals (CLARK 1932, *b*, CLARK and BOGGON 1933, *a*).

Our experiments also indicate that the rostral half of element *Lb* of the lateral nucleus is related, at least in part, to the cortex of the frontal lobe. Thus, following a lesion of the motor cortex (experiment *J*) a small degree of partial cell degeneration was found in the ventro-lateral part of *Lb*, while a lesion of the premotor cortex (area 6) was accompanied by partial degeneration in its medial border at its anterior end. In both these experiments the greater part of the rostral half of nucleus *Lb* remained normal. It thus appears that the cortical connections of the rostral half of *Lb* with the frontal cortex are quite slight. No degeneration in *Lb* was noted after injury to the prefrontal cortex (areas 8 and 9).

The pulvinar—The term " pulvinar " is a descriptive term of macroscopic anatomy applied to the posterior projecting pole of the thalamus in Primates. It comprises several fairly distinct nuclear elements. In the lateral part of its base is an extension of the caudal extremity of the lateral nucleus (element *Lb*). The main part of the pulvinar is formed by a relatively large nucleus, *pβ* of FRIEDEMANN. This continues forwards into another element, *pμβ*, which insinuates itself between the pars externa of the ventral nucleus and the nucleus parafascicularis, fig. 1. At the dorsal surface of the base of the pulvinar is a small nucleus, *pa*, continuous rostrally with nucleus *La*, while between the geniculate bodies is another small and compact element, *pd* (area intergeniculata). In none of our experiments was any cellular degeneration detected in the main element *pβ* (with the possible exception of a very small patch at the extreme lateral margin of the nucleus in experiment *G*). It appears, therefore, that the main part of the projecting pole of the pulvinar has little if any direct connection with the parietal cortex. This conclusion is in accordance with the observations of POLIAK in the report of his Marchi experiments on the monkey's brain. Elements *pa* and *pμβ* remained likewise intact in these experiments (with the possible exception of the rostral pole of the latter in experiment *E*). As recorded above, the caudal extremity of *Lb* where it enters into the base of the pulvinar projects on to the post-sensory areas of the parietal lobe. In two experiments (*F* and *H*) the nuclear element *pd* had undergone partial or complete atrophy. In experiments *E* and *G*, on the other hand, this nucleus was unaffected. In the former two cases, the cortical lesion of the parietal lobe extended further backwards than the other parietal lesions, involving a considerable part of areas 18 and 19 as well as areas 5 and 7. It can be inferred, therefore, that nucleus *pd* is rather related to areas 18 and 19. It may be noted that these areas lie in part between the auditory and visual areas of the cortex, and thus occupy a topographical position analogous to that of the nucleus *pd* which is interposed between the medial and lateral geniculate bodies.

Nucleus dorso-medialis (*nucleus medialis of human anatomy*)—This nucleus is composed of two parts, a medial large-celled element and a lateral small-celled element (of which the latter comprises approximately the lateral two-thirds of the nucleus in

Macaca). It has before been pointed out that this nucleus undergoes a progressive expansion as it is traced up through the mammalian series, and that in Man it attains to its highest development. Moreover, it is the lateral parvicellular element which is almost entirely involved in this increasing elaboration (CLARK 1932, *a*). In 1909, SACHS affirmed that this nucleus has no cortical connections, and this statement has unfortunately been repeated for many years. It is, however, well established that the dorso-medial nucleus is in direct fibre relation with the frontal

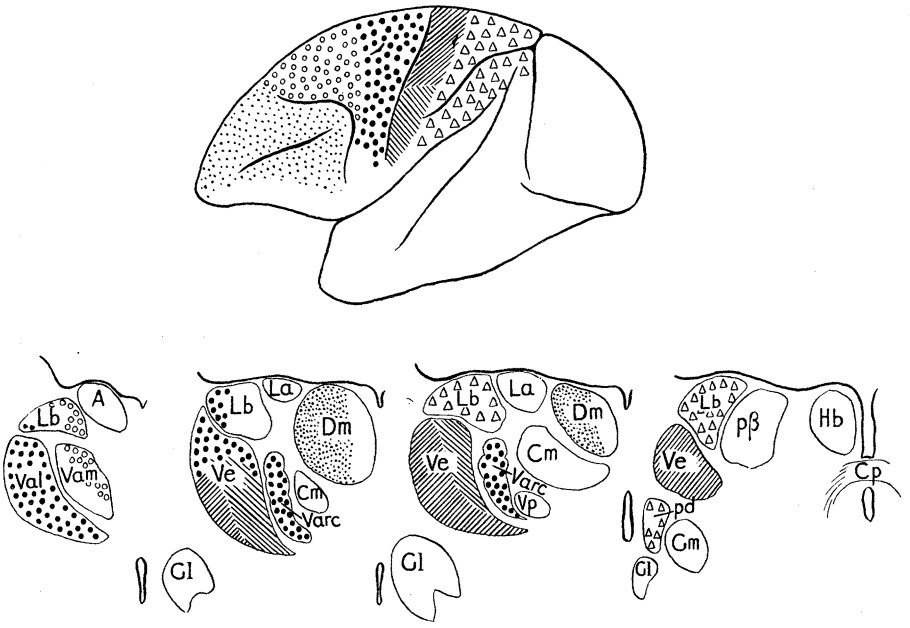


FIG. 27—Diagram showing the connections between different thalamic nuclei and different cortical areas as worked out by the experiments recorded in this paper.

Fine dots = area frontalis granularis (areas 8 and 9), coarse dots = motor area (area 4), circles = area frontalis agranularis (area 6), hatching = area post-centralis (areas 1, 2 and 3), triangles = post-sensory areas of the parietal cortex (areas 5, 7, 18 and 19).

cortex. This has been demonstrated in the rat by Marchi experiments (CLARK 1932, *b*) and retrograde cell degeneration (CLARK and BOGGON 1933, *b*) and by both methods in the cat (CLARK and BOGGON, 1933, *b*). In the latter animal, it was shown that the granular cortex of the frontal pole receives fibres from the whole of the lateral parvicellular element of the dorso-medial nucleus, while the medial (and smaller) magnocellular component is evidently unrelated to the cortex. This conclusion has been entirely corroborated by the present series of experiments on the monkey's brain. In experiment *M* a cortical lesion involving the greater part of the area frontalis granularis was followed three months later by the complete disappearance of practically the whole of the parvicellular element of the dorso-medial nucleus, fig. 36, Plate 27, the region of the atrophied cells being taken by a dense gliosis. The magnocellular element, on the contrary, remained intact.

Cortical lesions involving other parts of the frontal lobe (area precentalis, 4, or area frontalis agranularis, 6), or the parietal lobe, were accompanied by no change in the dorso-medial nucleus. It may be concluded, therefore, that the area frontalis granularis comprises a projection area of the cortex for the parvicellular portion of the dorso-medial nucleus, and that this nucleus sends fibres to no other part of the frontal cortex. SAGER (1933) recently found evidence of a direct connection between this nucleus and the frontal cortex. In neither of his experiments, however, was the granular cortex of the frontal lobe injured to more than a slight extent. Consequently, he found only slight degeneration in the most lateral part of the dorso-medial nucleus and was led to the erroneous conclusion that the greater part of this nucleus is not related to the cortex. He infers also (p. 115) that the nucleus is partly in relation with the agranular frontal cortex (area 6 of BRODMANN), although in both his experiments in which this cortical area was injured (monkeys 454 and 455) a portion of the granular cortex (areas 8 and 9) was also involved. Our own experiments, in which the cortical lesions were limited to area 6, are not in accord with this inference.

Centre median nucleus—In every one of our experiments the centre median nucleus was carefully studied in serial sections throughout its extent, and in every case it had preserved its integrity. It remained consistently normal in its cytoarchitecture and its definition, even when adjacent elements such as the ventral nucleus and the dorso-medial nucleus were grossly degenerated, and in no instance was it affected by a gliosis. These observations are in full accord with our previous studies on the cat's brain (CLARK and BOGGON 1933, *a*, and 1933, *b*), in which we failed to find any evidence of corticipetal connections by the Marchi method after localized electrolytic lesions involving the nucleus, or by the method of retrograde degeneration after a lesion of the frontal cortex. Hence we can state with confidence that the centre median nucleus is almost certainly not connected directly with the cerebral cortex. It may also be noted that one of us has argued, on the basis of comparative anatomical studies, that this nucleus is probably to be regarded as an intra-thalamic mechanism concerned with the integration of the activities of other thalamic elements (CLARK 1932, *a*).* SAGER (1933) reports cytological changes of very slight degree in the centre median nucleus after lesions of the frontal lobe in two monkeys, and concludes " qu'il est en relation d'une part, avec l'écorce frontale et d'autre part, avec la zone corticale correspondent à la face." His microphotographs, however, are far from convincing and we think it probable that his conclusion rests on an error of interpretation, related to the fact that the centre median nucleus in normal brains shows a certain degree of individual variation in the density and spacing of its constituent cells. Until and unless more convincing evidence of a positive nature is forthcoming, the conception of a direct cortical connection of the nucleus should be abandoned.

* SAGER (1933, p. 115) is in error in attributing to one of us the statement that the centre median nucleus is in relation with the frontal cortex.

The anterior nucleus—In 1909, SACHS concluded, on the basis of experimental work, that the anterior nucleus of the thalamus has no cortical connections. This opinion has commonly been held for many years. However, it has recently been demonstrated in the cat and the rat (CLARK 1932, *a*, CLARK and BOGGON 1933, *a*) that the cells of this nucleus project fibres on to the area cingularis of the cortex which extends along the upper aspect of the corpus callosum. In only one of the present experiments on the brain of the macaque monkey was the gyrus cinguli involved by the cortical lesion (experiment *L*), and in this experiment the injury to this region of the cortex was quite small. Nevertheless, subsequent histological examination of the thalamus showed definite evidence of degenerative changes in the antero-dorsal and the antero-ventral element of the nucleus (especially the former). This experiment, therefore, serves to corroborate our previous studies of the connections of the anterior nucleus.

Nucleus pretectalis—In lower mammals, this nucleus is well defined and relatively large. In the higher Primates it is much less distinct and is represented by a rather diffuse collection of small cells lying under cover of the nucleus limitans along the rostro-lateral margin of the anterior colliculus (CLARK 1932, *a*). If the nucleus limitans is taken as marking the boundary between the diencephalon and the mid-brain, the pretectal nucleus should properly speaking be regarded as a mesencephalic element. No evidence was found in our experiments of any corticipetal connections of this nucleus. On the other hand, experiment *I* shows that corticifugal fibres arising from the posterior part of the parietal cortex terminate in it. These observations confirm previous studies on the rat's brain in which, also, cortico-pretectal fibres were found to arise from the post-parietal region of the cortex, while no evidence of pretecto-cortical fibres could be demonstrated (CLARK 1933, *b*).

Other thalamic nuclei—Besides the centre median and pretectal nuclei, element *La* of the lateral nucleus, and the main element of the pulvinar, the following cell groups showed no change as the result of the cortical lesions produced in this series of experiments : nuclei of the mid-line, nucleus submedius, paratænial nucleus, habenular nuclei, nucleus parafascicularis, and the zona incerta of the subthalamus. Our previous studies have led us to conclude that none of these elements give off corticipetal fibres.

The expenses of this research were met by a grant from the Royal Society, which we wish gratefully to acknowledge. We should like, also, to express our thanks to our technical assistant, Mr. E. THOMPSON, for his care in the preparation of the large numbers of Nissl sections which this investigation involved.

SUMMARY

By way of summarizing the results of the experiments recorded in this paper, we may note briefly the origin of the thalamo-cortical fibres passing to the several areas of the parietal and frontal lobes of the monkey's brain.

Parietal lobe—The most massive cell atrophy in proportion to the extent of cortical injury has been found after lesions involving the area post-centralis. This is in accord with POLIAK's observation that the greatest density of projection fibres in the parietal cortex is found immediately adjacent to the central sulcus. The area post-centralis receives fibres entirely from the pars externa of the ventral nucleus.

The post-sensory areas of the parietal lobe (areas 5, 7, 18 and 19) receive fibres from the caudal half of the lateral nucleus (element *Lb*), mainly from its posterior extremity, and also from nucleus *pd* of the pulvinar. The evidence indicates that *Lb* is related to areas 5 and 7, while the element *pd* projects on to area 18 or 19 or both.

Frontal lobe—The area precentralis (motor area) receives projection fibres from the whole of the pars arcuata of the ventral nucleus, the dorsal and medial part of the rostral end of the pars externa of the ventral nucleus, and the pars antero-lateralis of the ventral nucleus. Its lower end may possibly receive fibres from the pars antero-medialis of the ventral nucleus, but our experimental data do not allow a definite statement on this point. In addition, a small region at the lateral margin of the rostral end of the lateral nucleus (*Lb*) and a part of the nucleus of the medial medullary lamina are also connected by corticepetal fibres with the precentral area.

The area frontalis agranularis (area 6 of BRODMANN, premotor area) receives comparatively few thalamic projection fibres. These originate in the pars antero-medialis of the ventral nucleus and in the medial and dorsal part of the rostral end of the lateral nucleus (element *Lb*).

The area frontalis granularis (prefrontal area, areas 8 and 9) is pre-eminently the projection area of the large dorso-medial nucleus. It receives fibres from the whole length of the lateral two-thirds (parvicellular element) of this nucleus.

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DESCRIPTION OF PLATES

PLATE 23

FIG. 28—Transverse section through the middle of the normal thalamus of *Macaca mulatta* to show the normal appearance of many of the thalamic nuclei in sections stained with methylene blue. × 15.

FIG. 29—Transverse section (No. 1.15.6.) through the caudal third of the thalamus in experiment *A*, showing the area of atrophy in the lateral part of the pars externa of the ventral nucleus, following a cortical lesion in the upper part of the post-central gyrus. × 18.

PLATE 24

FIG. 30—Transverse section (No. 2.10.4.) through the caudal third of the thalamus in experiment *B*, showing the area of atrophy in the medial margin of the pars externa of the ventral nucleus, following a cortical lesion in the lower part of the post-central gyrus. × 45.

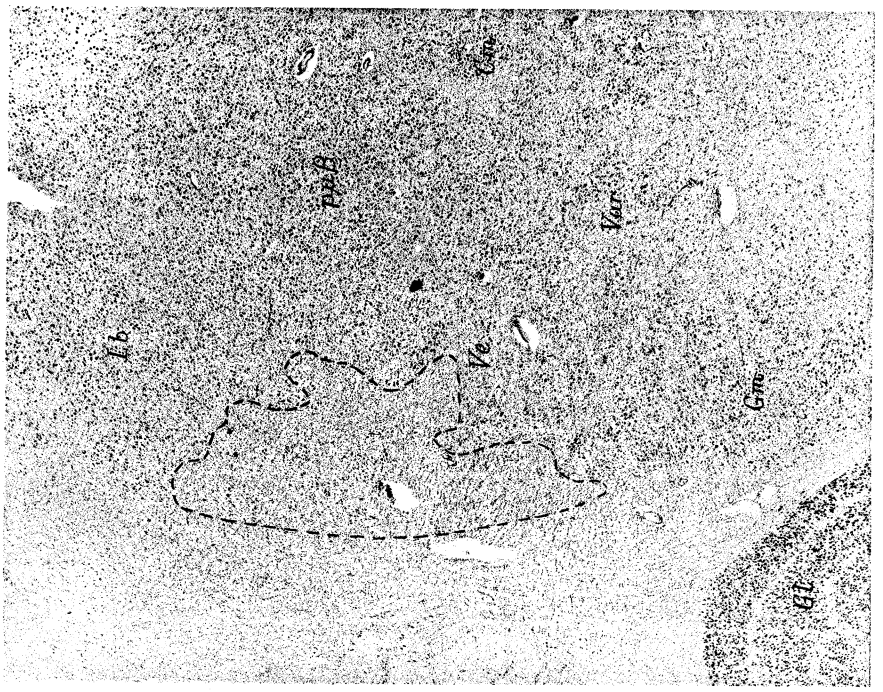
FIG. 31—Transverse section (No. 2.4.4.) through the caudal third of the thalamus in experiment *D*, showing the area of atrophy in the lateral half of the pars externa of the ventral nucleus following a lesion involving the lips of the upper end of the sulcus centralis. Note the normal cells in the nucleus lateralis (*Lb*). × 28.

PLATE 25

FIG. 32—Transverse section (No. 2.4.3.) through the middle of the thalamus in experiment *E*, showing the atrophy in the pars externa of the ventral nucleus and in the lateral nucleus (element *Lb*). In the latter the atrophy is partial, and normal cells are sparsely scattered throughout the nucleus. Note the complete absence of cell atrophy in the pars arcuata of the ventral nucleus. In this experiment, the cortical lesion involved the area post-centralis (sensory cortex) and the rostral part of the post-sensory cortex of the parietal lobe. × 22.

PLATE 26

FIG. 33—Transverse section (No. 2.16.8.) through the caudal part of the thalamus in experiment *F*, showing two patches of atrophy in the lateral nucleus (element *Lb*), following a cortical lesion involving the postero-superior part of the parietal lobe. × 40.



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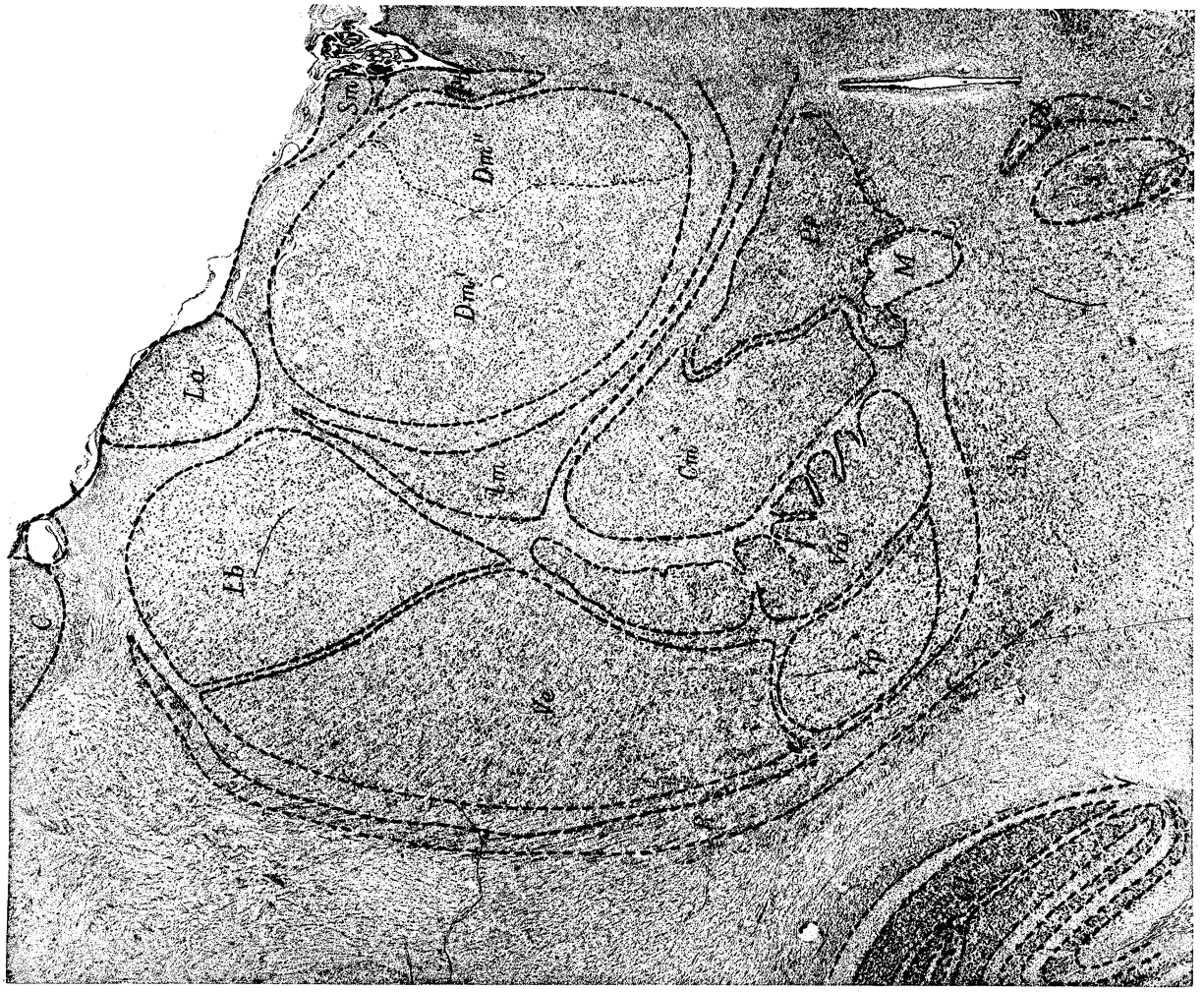

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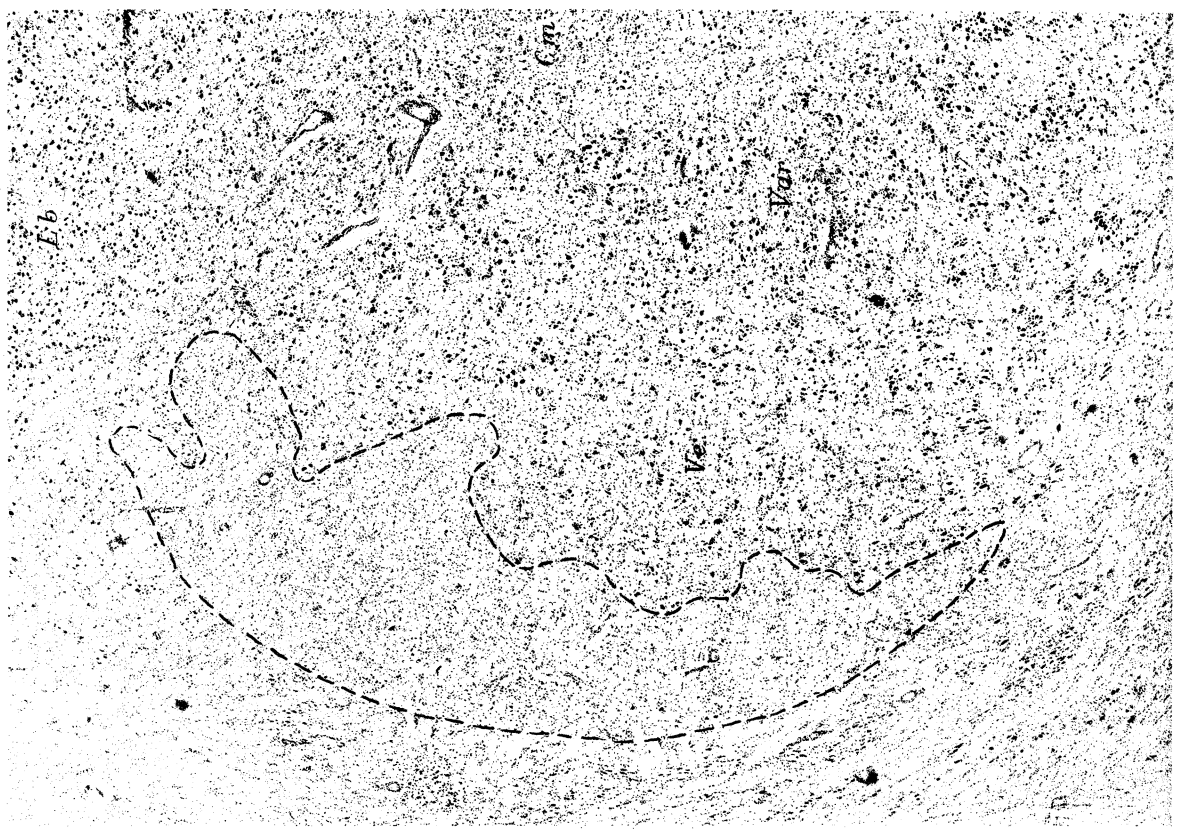

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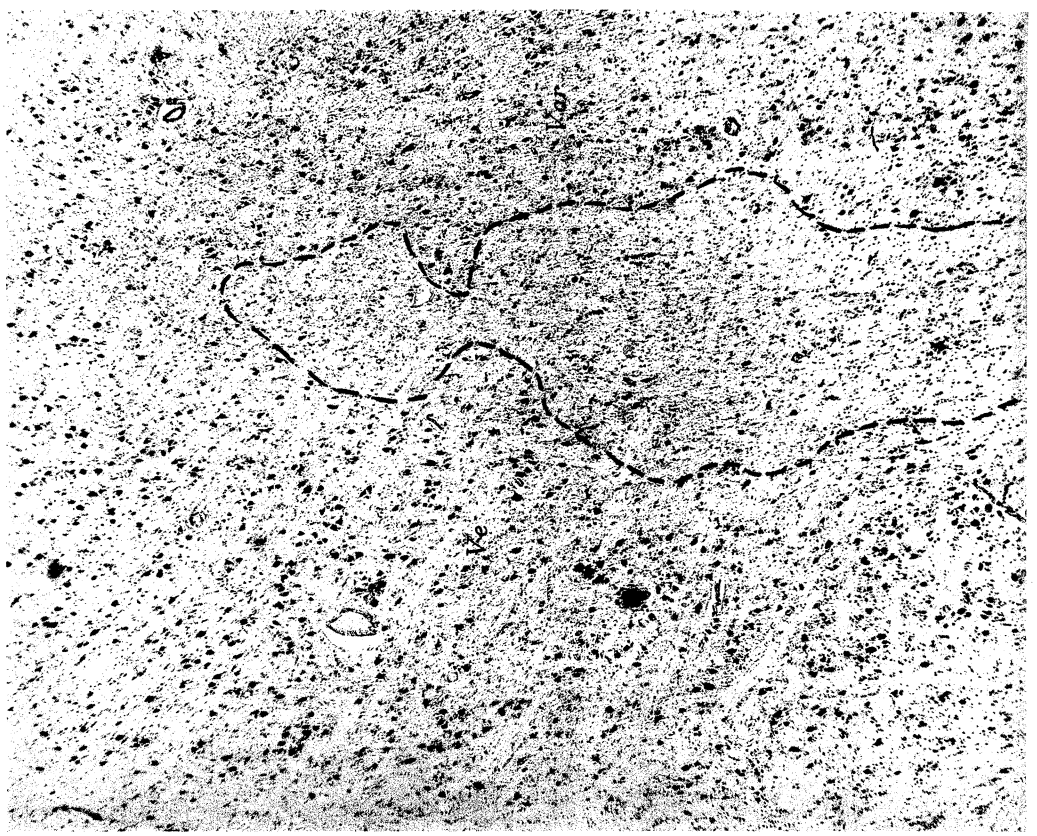

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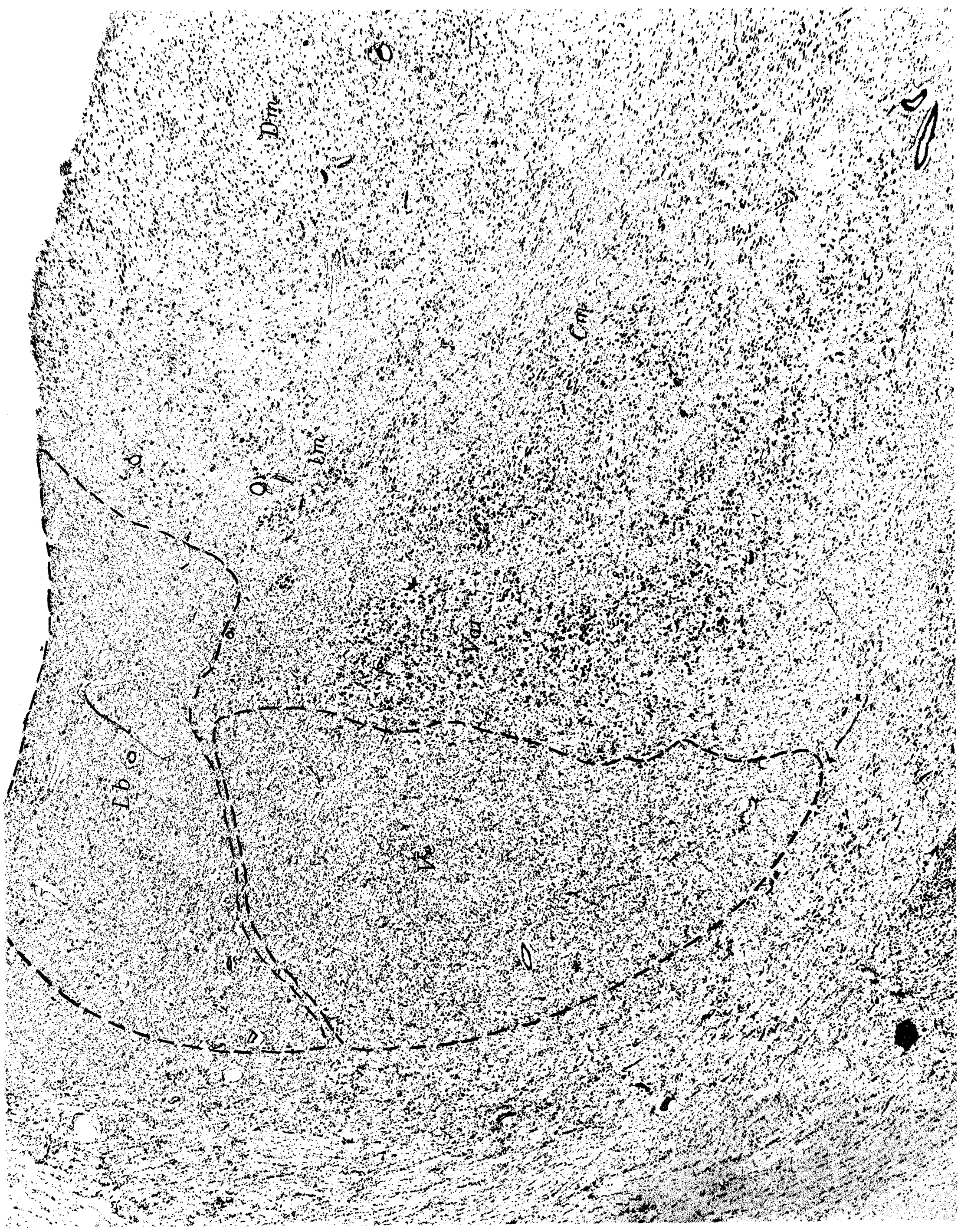

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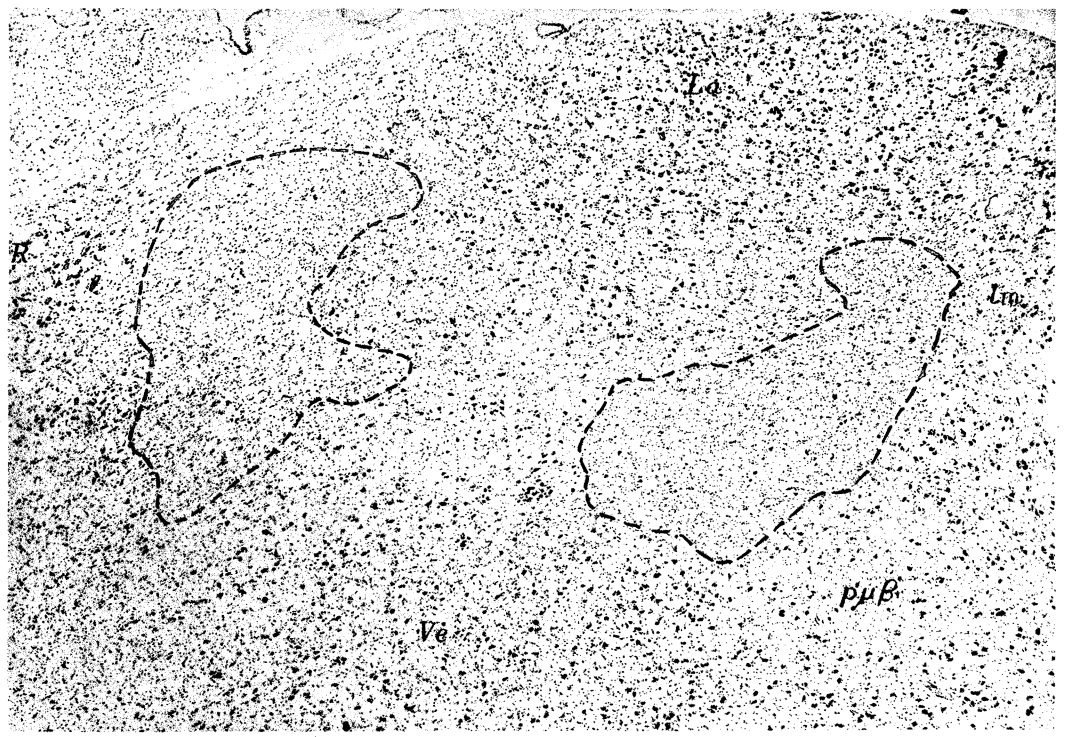

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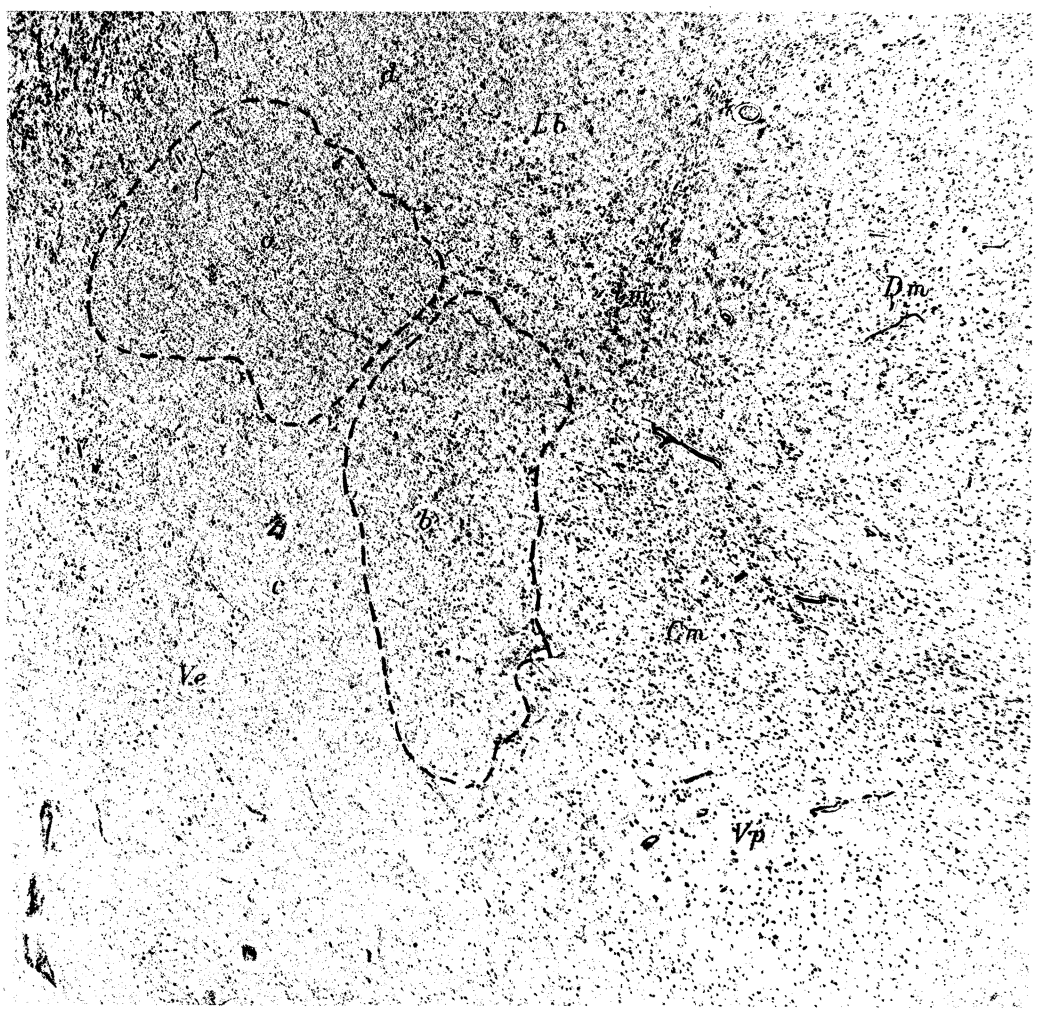

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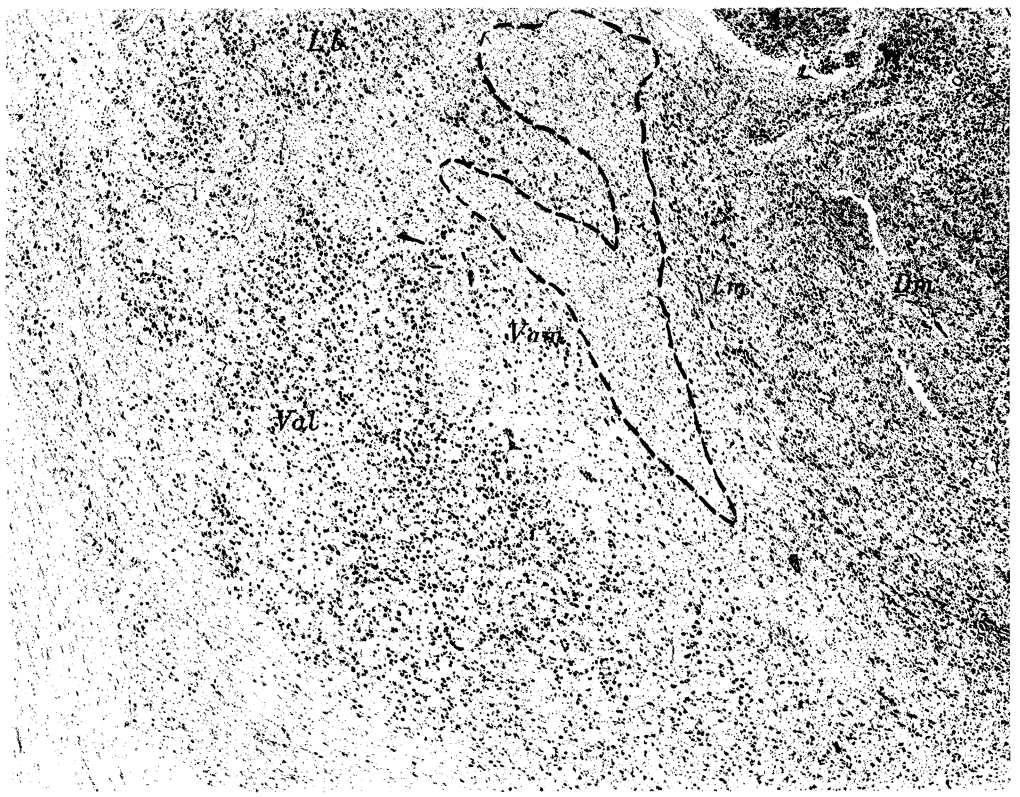

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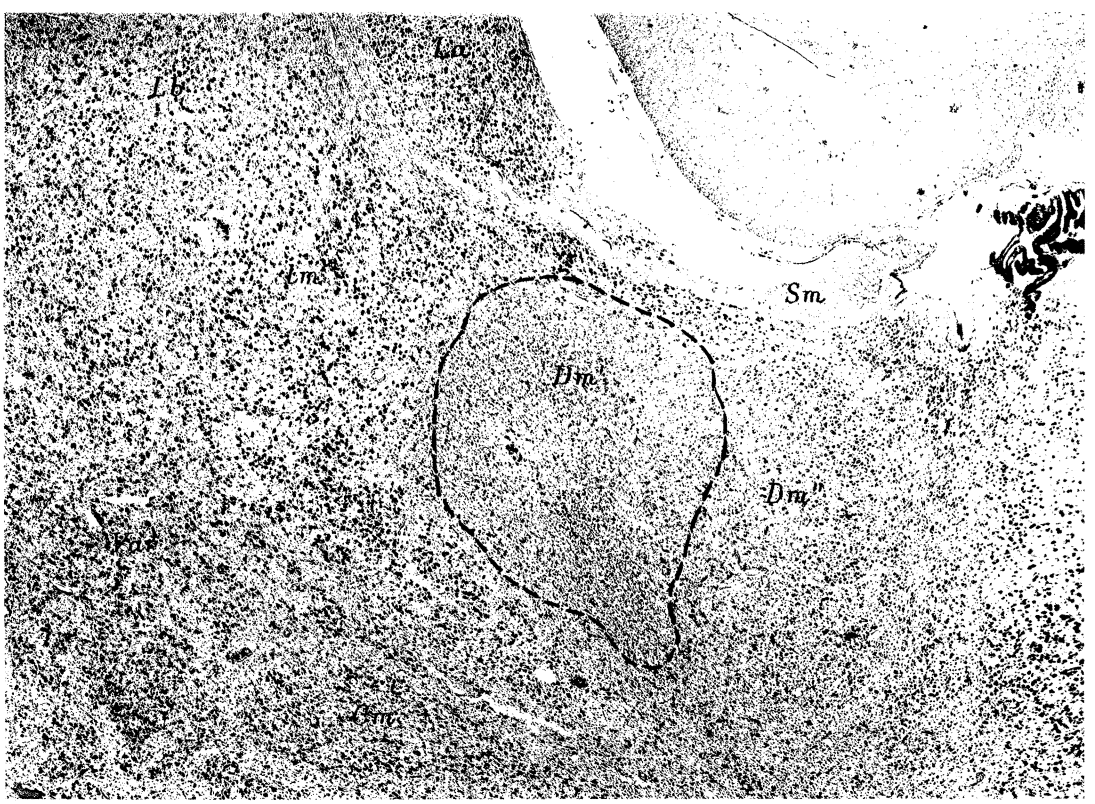

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FIG. 34—Transverse section (No. 2.11.2.) through the middle of the thalamus in experiment *J* showing the area of atrophy following a cortical lesion involving the upper half of the motor cortex (area 4). *a*. Area of cell atrophy and gliosis in the dorsal extremity of the pars externa of the ventral nucleus. *b*. The pars arcuata of the ventral nucleus showing gliosis and partial cell atrophy. *c*. Area along the medial border of the pars externa of the ventral nucleus showing gliosis and partial cell atrophy. *d*. Area at the junctional region of the pars externa of the ventral nucleus and the lateral nucleus (*Lb*) showing gloisis and partial cell atrophy. × 22.

PLATE 27

FIG. 35—Transverse section (No. 3.18.8.) through the rostral part of the thalamus in experiment *L* showing the area of cell atrophy in the medial margin of the pars antero-medialis of the ventral nucleus and the medial margin of the lateral nucleus (element *Lb*). × 20.

FIG. 36—Transverse section (No. 2.7.6.) through the middle of the thalamus in experiment *M* showing the area of atrophy in the lateral two-thirds (parvicellular element) of the dorso-medial nucleus, following a cortical lesion involving the greater part of the area frontalis granularis (areas 8 and 9). Note that the cells of the medial magnocellular element of this nucleus remain undegenerated, but stain rather lightly. × 20.

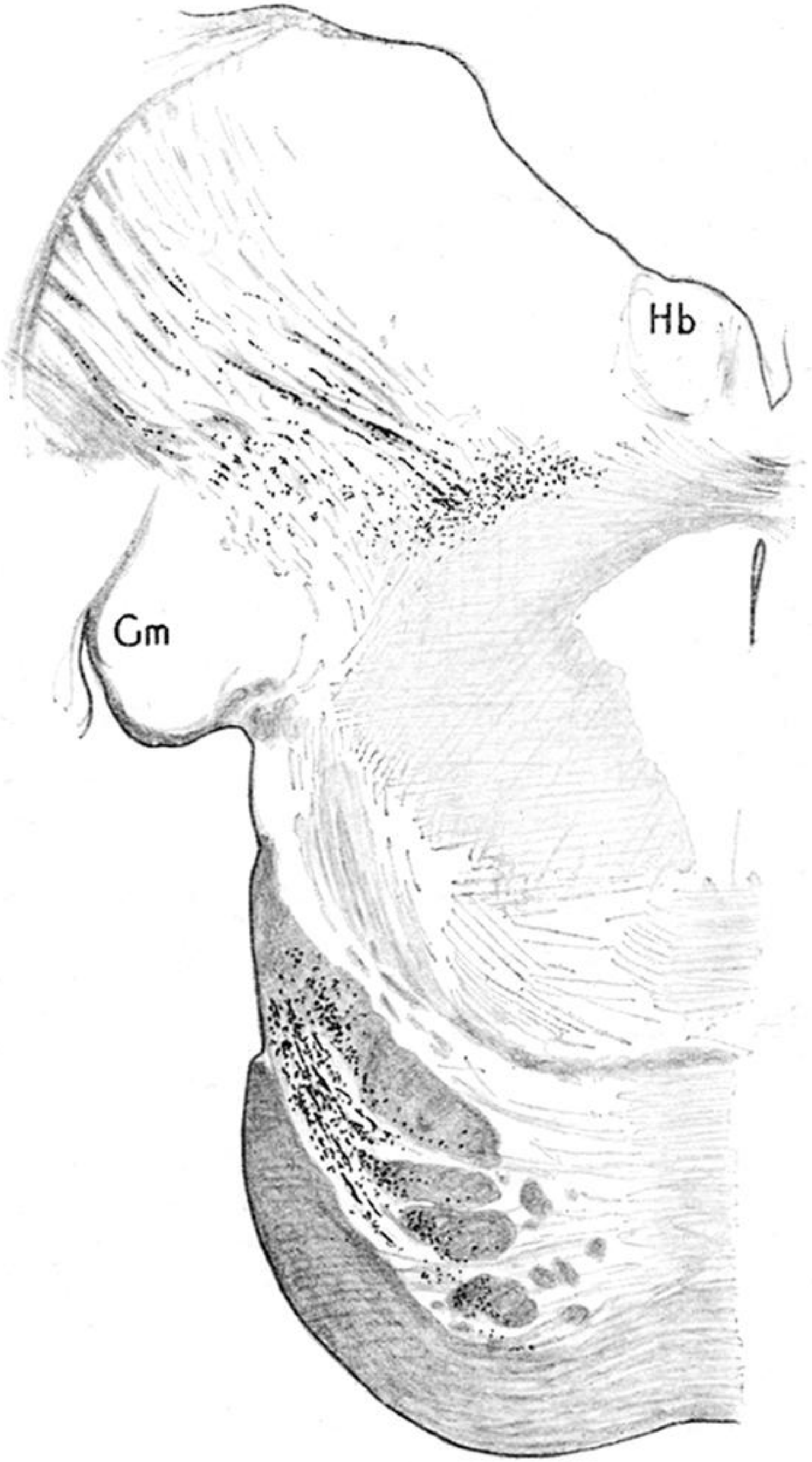
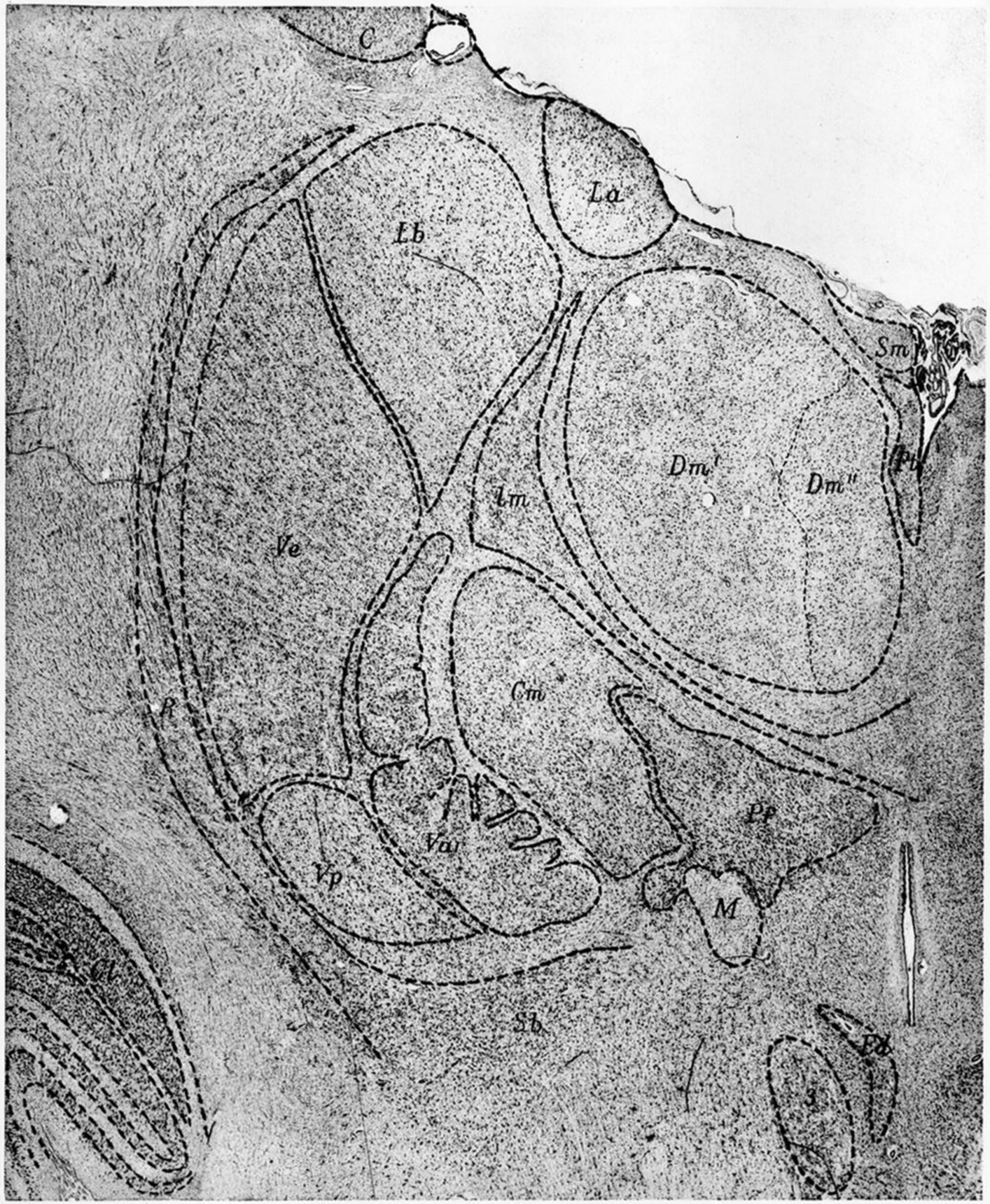


FIG. 19—Transverse section through the caudal end of the thalamus and the pons in experiment *I*, showing Marchi degeneration extending along the cortico-pretectal fasciculi and the parieto-pontine fibres.



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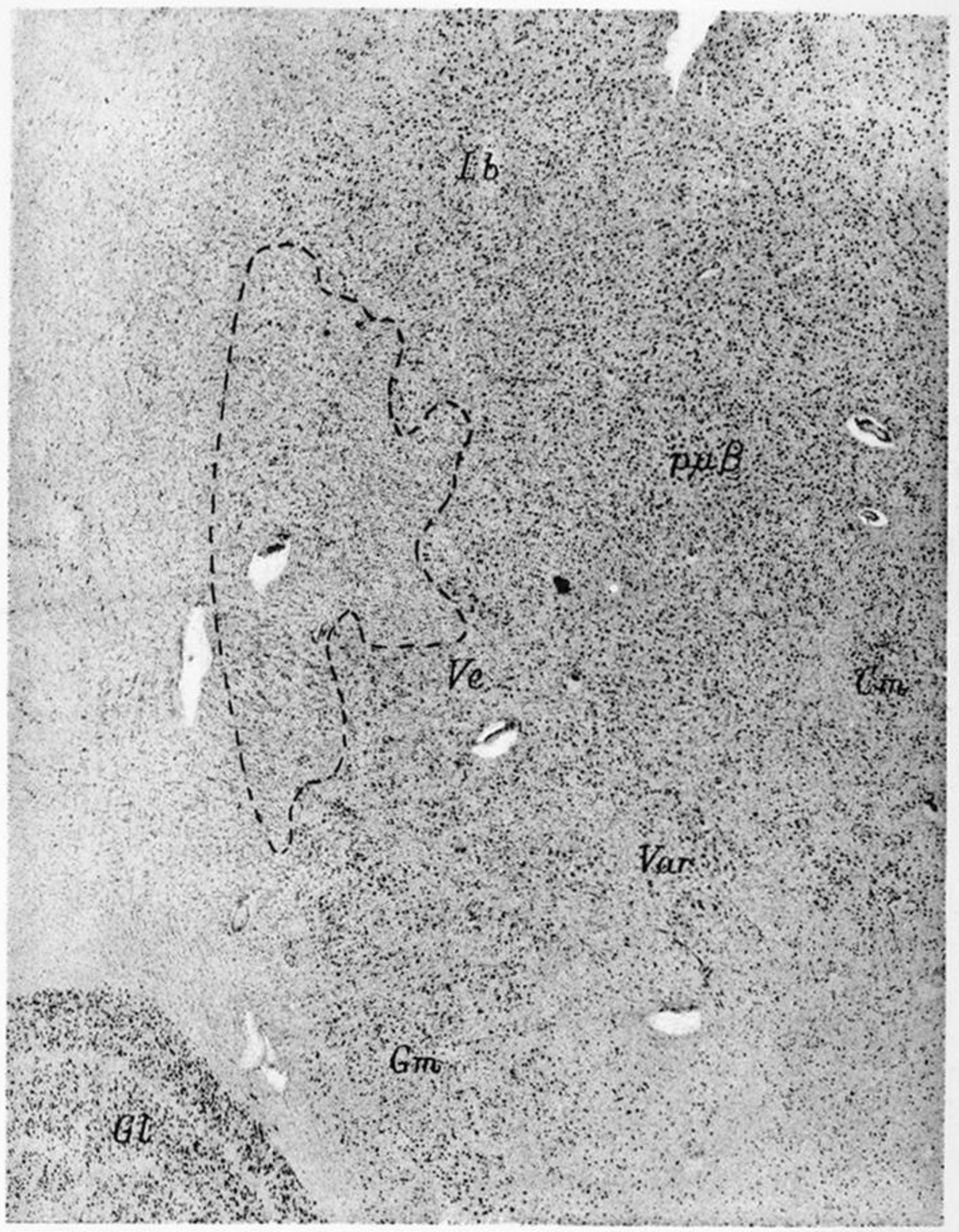

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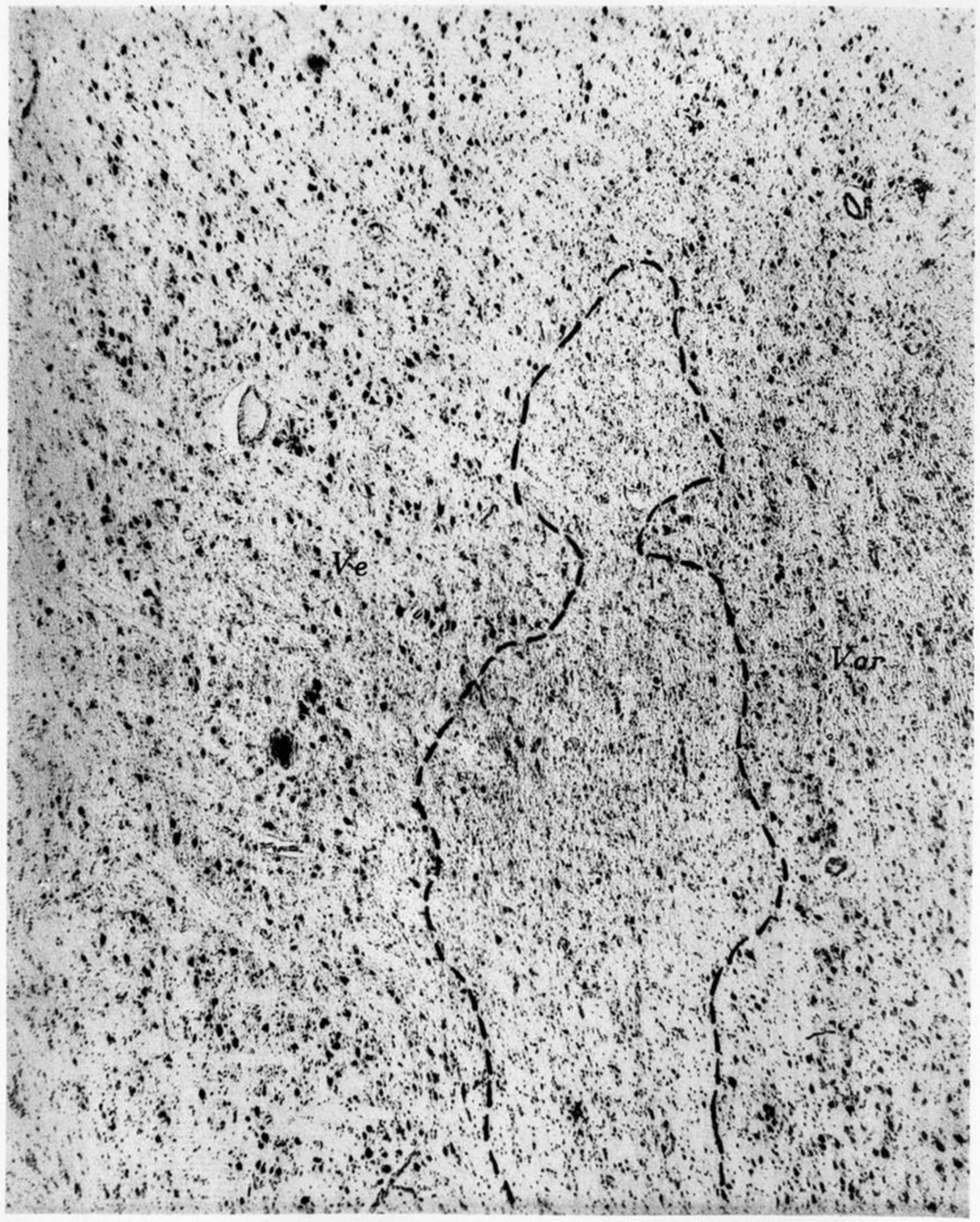
PLATE 23

FIG. 28—Transverse section through the middle of the normal thalamus of *Macaca mulatta* to show the normal appearance of many of the thalamic nuclei in sections stained with methylene blue. × 15.

FIG. 29—Transverse section (No. 1.15.6.) through the caudal third of the thalamus in experiment *A*, showing the area of atrophy in the lateral part of the pars externa of the ventral nucleus, following a cortical lesion in the upper part of the post-central gyrus. × 18.



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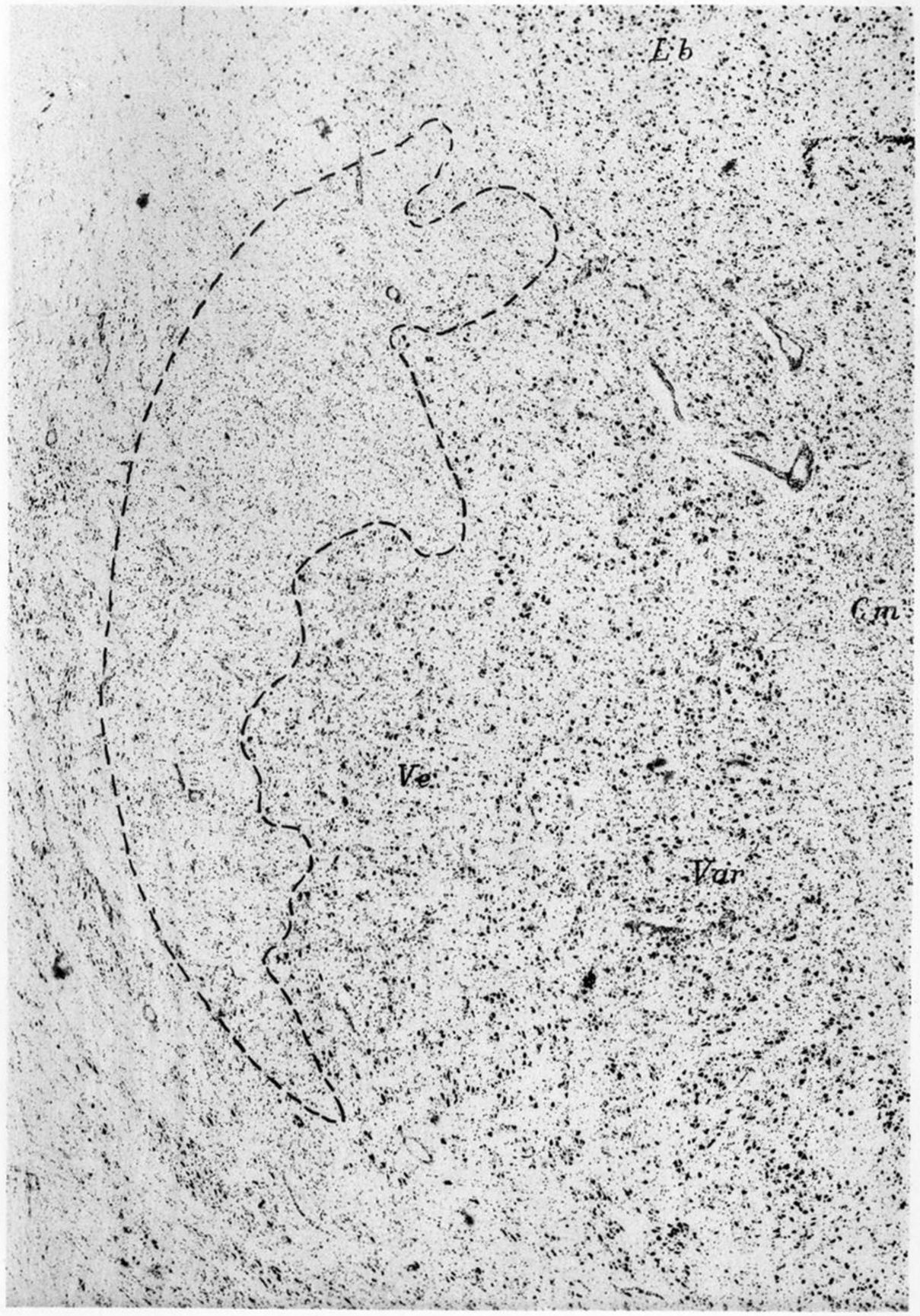

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PLATE 24

FIG. 30—Transverse section (No. 2.10.4.) through the caudal third of the thalamus in experiment *B*, showing the area of atrophy in the medial margin of the pars externa of the ventral nucleus, following a cortical lesion in the lower part of the post-central gyrus. × 45.

FIG. 31—Transverse section (No. 2.4.4.) through the caudal third of the thalamus in experiment *D*, showing the area of atrophy in the lateral half of the pars externa of the ventral nucleus following a lesion involving the lips of the upper end of the sulcus centralis. Note the normal cells in the nucleus lateralis (*Lb*). × 28.

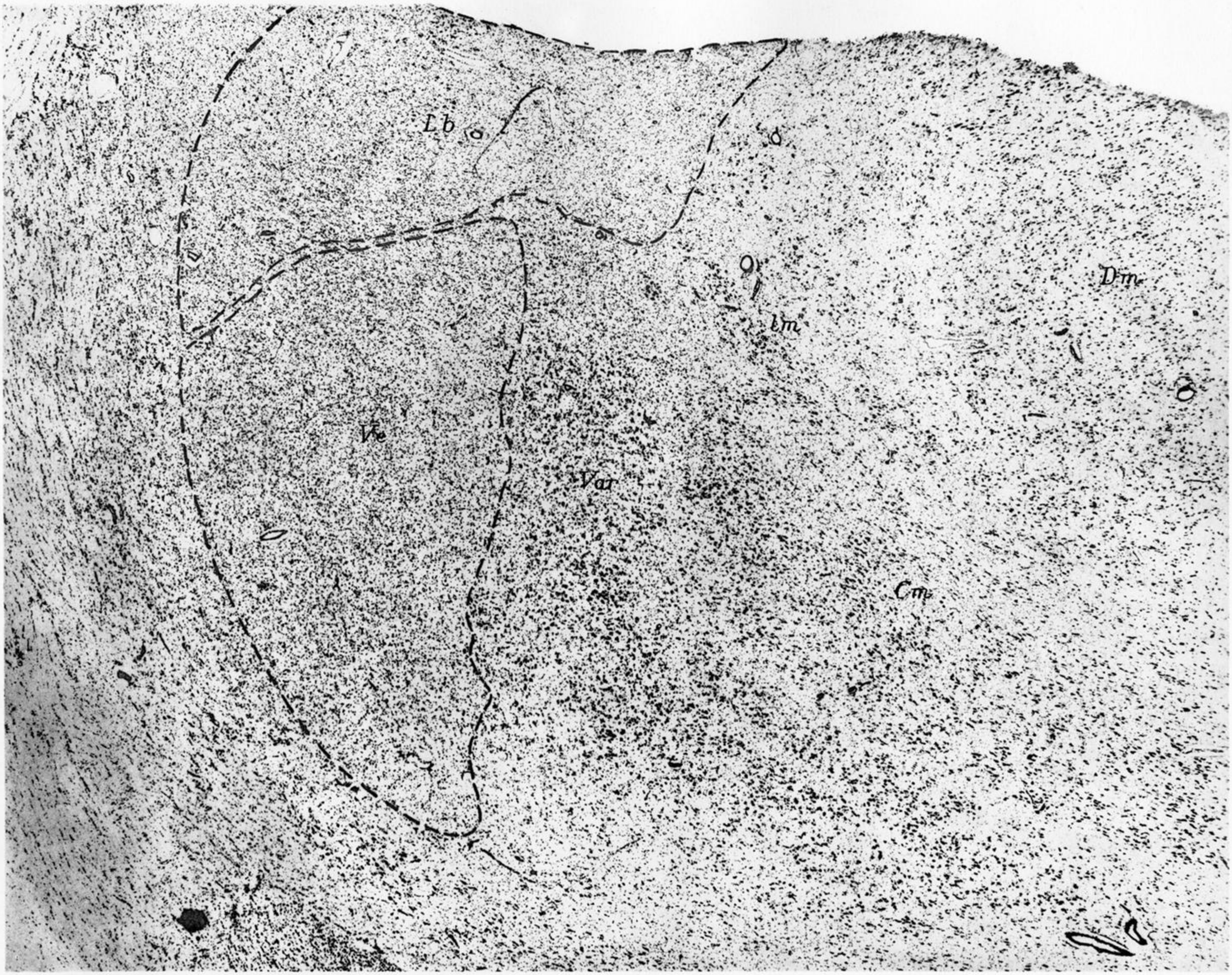
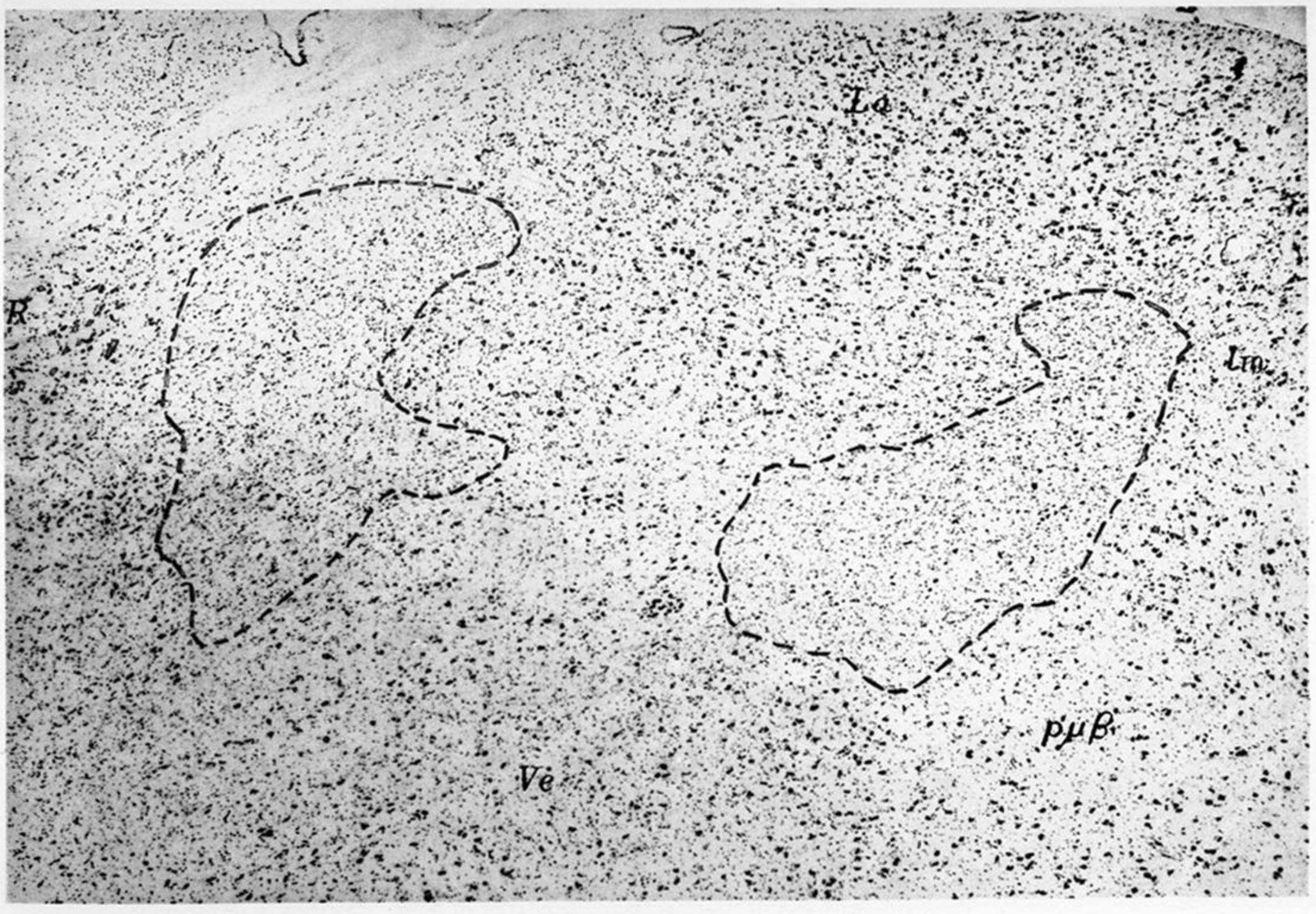


PLATE 25

FIG. 32—Transverse section (No. 2.4.3.) through the middle of the thalamus in experiment *E*, showing the atrophy in the pars externa of the ventral nucleus and in the lateral nucleus (element *Lb*). In the latter the atrophy is partial, and normal cells are sparsely scattered throughout the nucleus. Note the complete absence of cell atrophy in the pars arcuata of the ventral nucleus. In this experiment, the cortical lesion involved the area post-centralis (sensory cortex) and the rostral part of the post-sensory cortex of the parietal lobe. × 22.



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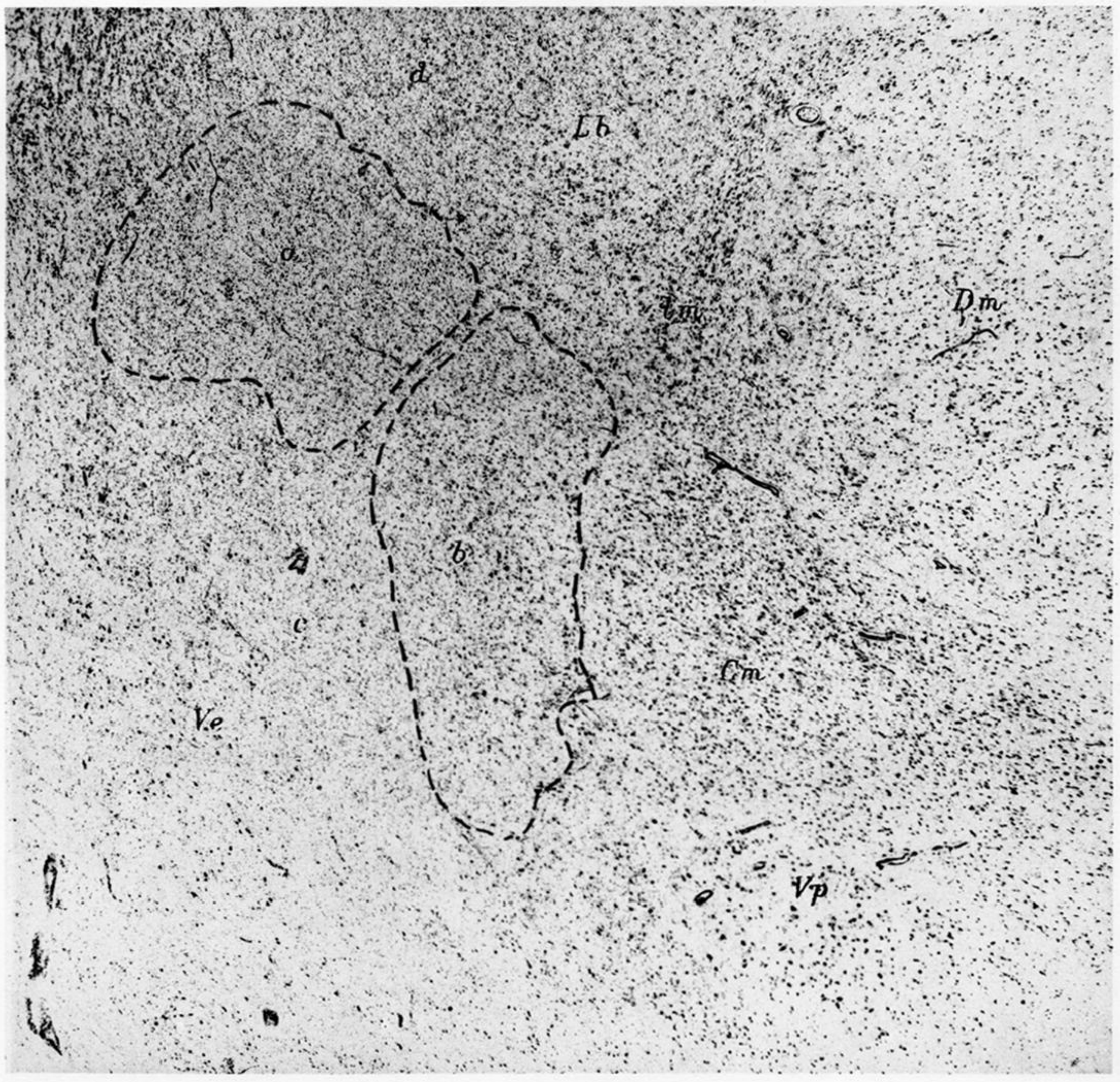

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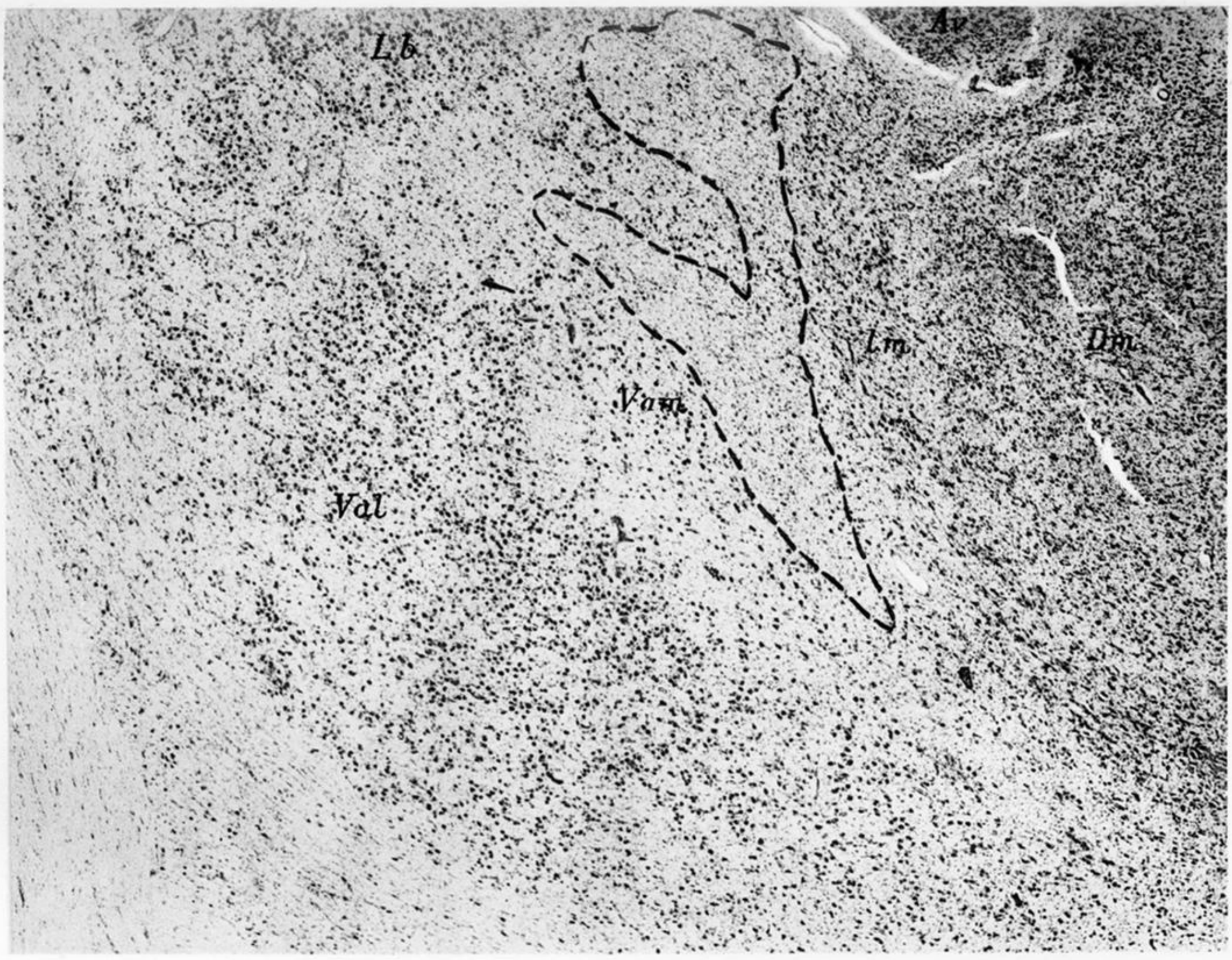
PLATE 26

FIG. 33—Transverse section (No. 2.16.8.) through the caudal part of the thalamus in experiment *F*, showing two patches of atrophy in the lateral nucleus (element *Lb*), following a cortical lesion involving the postero-superior part of the parietal lobe. × 40.

FIG. 34—Transverse section (No. 2.11.2.) through the middle of the thalamus in experiment *J* showing the area of atrophy following a cortical lesion involving the upper half of the motor cortex (area 4). *a*. Area of cell atrophy and gliosis in the dorsal extremity of the pars externa of the ventral nucleus. *b*. The pars arcuata of the ventral nucleus showing gliosis and partial cell atrophy. *c*. Area along the medial border of the pars externa of the ventral nucleus showing gliosis and partial cell atrophy. *d*. Area at the junctional region of the pars externa of the ventral nucleus and the lateral nucleus (*Lb*) showing gloisis and partial cell atrophy. × 22.



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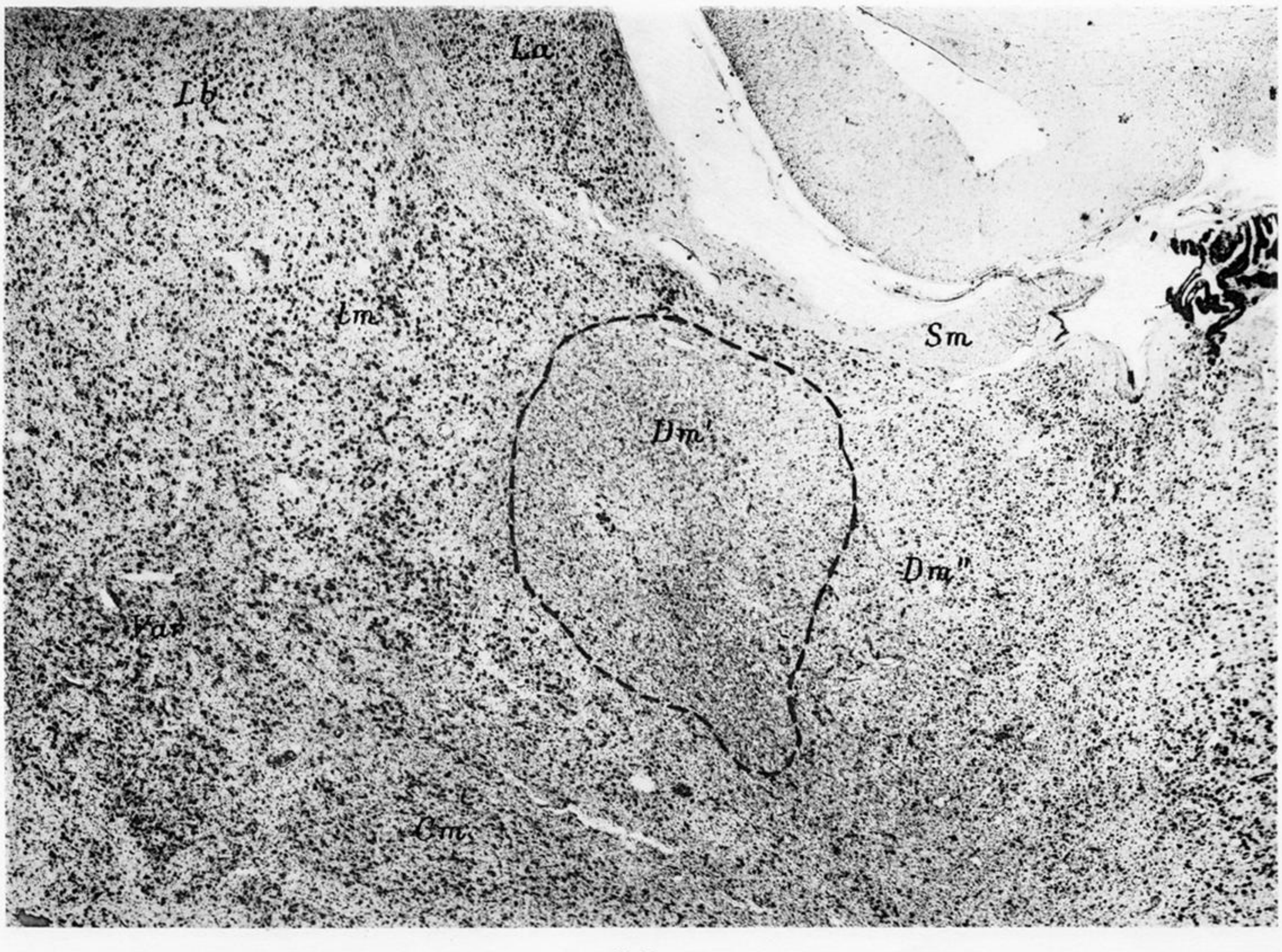

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PLATE 27

FIG. 35—Transverse section (No. 3.18.8.) through the rostral part of the thalamus in experiment *L* showing the area of cell atrophy in the medial margin of the pars antero-medialis of the ventral nucleus and the medial margin of the lateral nucleus (element *Lb*). × 20.

FIG. 36—Transverse section (No. 2.7.6.) through the middle of the thalamus in experiment *M* showing the area of atrophy in the lateral two-thirds (parvicellular element) of the dorso-medial nucleus, following a cortical lesion involving the greater part of the area frontalis granularis (areas 8 and 9). Note that the cells of the medial magnocellular element of this nucleus remain undegenerated, but stain rather lightly. × 20.