STUDIES ON THE DIENCEPHALON OF THE VIRGINIA OPOSSUM

PART III. THE THALAMO-CORTICAL PROJECTION [1]

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NINETEEN TEXT FIGURES AND TWO PLATES (TWO FIGURES)

Numerous detailed studies of the thalamo-cortical connections of several mammals, particularly rodents and primates, have been published, especially during the last decade.[2] This literature has been adequately reviewed in recent years by Walker ('38) and by Lashley ('41). The general plan of the cortical projection of the various thalamic nuclei is clearly revealed by these extensions of the classical studies of von Monakow (1881). Since many details are still obscure, it has been of interest to inquire into the thalamo-cortical relations in the opossum with the object of comparing this animal with higher mammals. Although the available material for this study is not adequate to clear up many remaining uncertainties regarding the details of the mammalian cortical

[1] This study was begun in 1934 at the Department of Anatomy, The University of Chicago, continued in connection with the work described in the first two papers of this series in the Laboratory of Comparative Neurology, Department of Anatomy, University of Michigan, in 1938, and completed in the Department of Anatomy, Western Reserve University. At the University of Chicago the research was supported by a grant from the Wallace C. and Clara A. Abbott Memorial Fund. The work at the University of Michigan was made possible by a National Research Council Fellowship in Medicine; and by the helpfulness of Prof. Elizabeth C. Crosby.

[2] Münzer and Wiener, '02; Nissl, '13; Minkowski, '24; Poliak, '32; Clark, '32, '36; Clark and Boggon, '33 a and b; Waller, '34, '37; Walker, '36, '38; De Haene, '36; Waller and Barris, '37; Gerebtzoff, '37; Stoffels, '39 a and b; Lashley, '41; and others.

projections, it has clearly revealed the general plan of the projection in the opossum, and certain features of the intranuclear localization.

The nomenclature of the cortical areas of the opossum in this report follows that of Gray ('24), and his cortical maps are reproduced in figure 19. It will be obvious that the lamination pattern of cortical areas thus shown is simpler than that in higher forms and that the homologies of cortical areas by the method of cytoarchitectonics are in a number of cases quite obscure. It is hoped that the data on the thalamocortical projections may shed some light on the homologies of the cortical zones functionally related to specific thalamic nuclei. The nomenclature of the thalamic nuclei of the opossum follows that of the first paper of this series (Bodian, '39).

MATERIALS AND METHODS

In addition to numerous normal series of the opossum brain, listed in the previous reports, the material to be described in this paper consists of seventeen selected cases, accumulated between 1934 and 1938, showing retrograde thalamic degeneration following cortical injury by thermocautery or scalpel. Three of these cases had been hemidecorticated; in the others the cerebral lesions were localized to various parts of the neocortex, covering in all most of the extent of the neopallium.

All animals were operated on under morphine ($\frac{1}{2}$ to 1 grain) and ether anesthesia, and were subsequently killed under anesthesia by exsanguination, immediately before perfusion of the fixative through the aorta. Brains were removed, as a rule, 3 to 5 weeks after operation, and were fixed by perfusion with alcohol or formol-acetic-alcohol. Paraffin sections at 20 to 50 μ in complete series were stained with toluidine blue, except in several cases in which two series comprising every tenth section of a 20 μ series were stained respectively with toluidine blue and by Roger's reduced silver method ('31), or by the protargol method (Bodian, '37). In agreement with others (Walker, '38; Lashley, '41) we have

found no evidence that transneuronal atrophy can be confused with retrograde degeneration of cells the axons or cortical terminals of which have been destroyed as early as several months previously.

Several specimens stained by the Marchi method after cortical or thalamic lesions were available, but since this material is limited in the scope of its revelations, it will not be discussed systematically, but only in connection with the analysis of findings in the Nissl material.

DESCRIPTION OF MATERIAL

The lesions in the cases to be described were all placed in the right cortex and are shown in the standard charts accompanying the text, as seen in an evenly spaced series of transverse sections (A) through the neopallium, reading from the rostral to the caudal end. The position of each section of cortex shown is indicated by a bar at the right of the dorsal projection of the neocortex (B), on which the extent of the lesion as seen on the dorsal surface has been carefully charted. In successive rostrocaudal order are then shown ten standard sections of the right dorsal thalamus, with nuclei indicated as in the first paper of this series (Bodian, '39). On these sections the areas showing retrograde degeneration have been carefully plotted, with all possible allowances made for differences in plane and thickness of sections, and for the natural minor variabilities of individual specimens. In the transverse sections through the pallium the depth of the cortex is indicated by the barred line, the hippocampal formation by the dotted lines, and the margins of neocortex by arrows, except where indicated by the hippocampal fissure medially and the rhinal fissure (r) laterally. The orbital sulcus is shown in the fourth and fifth sections (o).

Case 1 (V 80)

Hemidecortication of 5 weeks duration (fig. 1)

Lesion. The entire neocortex was destroyed except the caudolateral pole, but since the internal capsule was completely severed this area

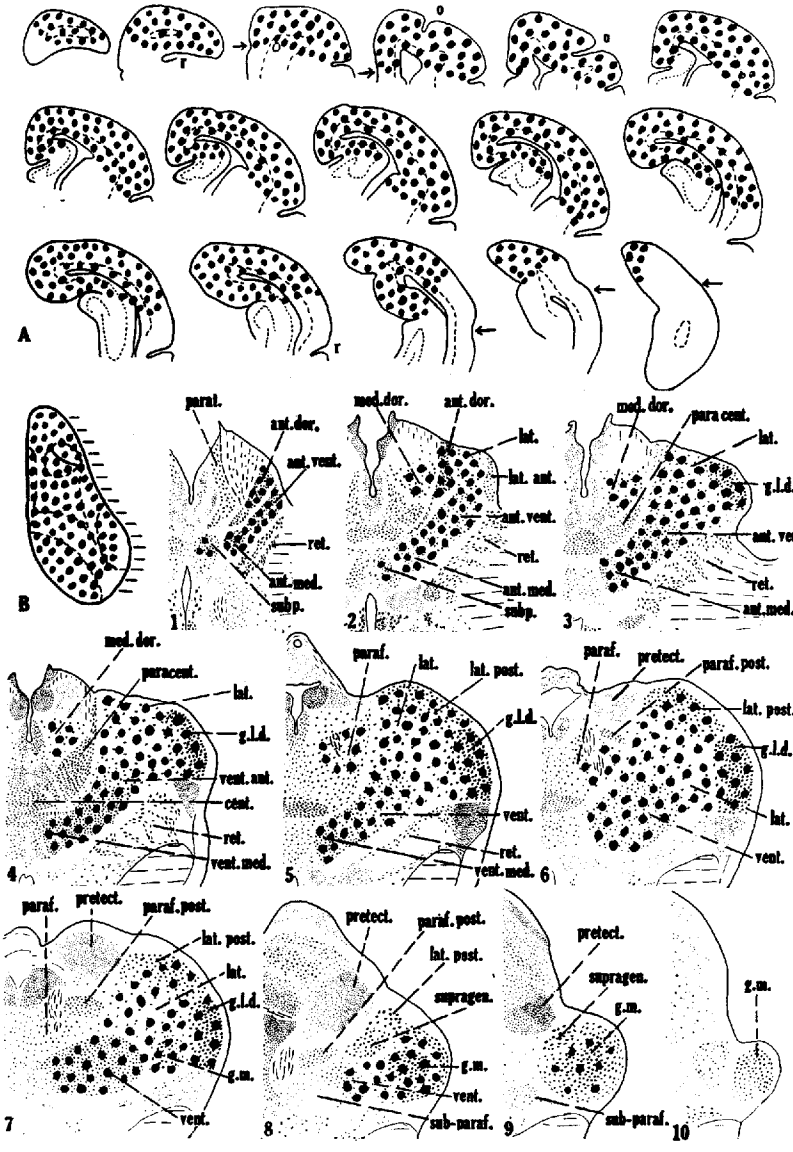

Fig. 1 Case 1. A. Series of transverse sections through the right cerebral cortex, with extent and depth of lesion shown by large dots. Arrows indicate margin of neocortex. *o*, orbital fissure. *r*, rhinal fissure. B. Dorsal projection of right neocortex, showing position of sections in A, and with lesion indicated in similar fashion. 1 to 10. Series of transverse sections through the right dorsal thalamus, drawn from 50 μ toluidin blue series (Bodian, '39). The levels shown represent sections 1, 10, 20, 30, 45, 55, 65, 80, 90, and 105 respectively. Areas showing retrograde degeneration indicated by large dots.

too must be considered as having been separated from its thalamic connections. The lesion includes not only all of the cingular and retrosplenial areas and subiculum, but some of the adjoining hippocampal cortex as well. The gyrus dentatus was spared. Laterally the lesion does not extend below the rhinal fissure at any point, but subjacent to the area insularis and anterior temporal area the lateral edge of the caudate nucleus was destroyed.

Thalamus. The thalamus in this specimen is the site of the most extensive retrograde change seen in any of the cases. Complete or severe degeneration is found in the anterior, medial, lateral, and ventral nuclear groups and in the geniculate nuclei. In addition, moderate cell loss and chromatolysis are found in the nucleus subparataenialis (fig. 20). The details of the retrograde degeneration may be summarized as follows:

Anterior nuclear group. The three nuclei constituting this group all show practically complete loss of nerve cells and replacement gliosis. A few chromatolytic cells remain. *Medial nuclear group.* The nucleus medialis dorsalis is almost completely degenerated, with the exception of a few scattered cells, both chromatolytic and well-staining, at the margins adjoining the midline and commissural nuclei. The nucleus parafascicularis shows severe neurone degeneration and gliosis with, however, many atrophied and chromatolytic nerve cells remaining. The nucleus parafascicularis pars posterolateralis is normal in appearance, as are the nucleus paracentralis and the nucleus parataenialis. The nucleus subparataenialis in its rostral half was severely affected, with considerable nerve cell loss (about 50%) and gliosis, but with many remaining shrunken and chromatolytic neurons (fig. 20). Very little cell loss is apparent in the caudal half of this nucleus, which, however, contains many chromatolytic cells. *Lateral nuclear group.* The nucleus lateralis pars anterior is practically intact, with possibly a slight diminution of cells at its medial border. The nucleus lateralis pars intermedia is almost completely degenerated, with only rare residual chromatolytic cells. The nucleus lateralis pars posterior shows almost complete degeneration except for the caudal pole, which is normal in appearance. *Ventral nuclear group.* All nuclei in this group are almost entirely degenerated, but the margins of the area of cell loss adjoining the nucleus centralis, nucleus paracentralis, and nucleus reuniens are not sharp, because of overlap of normal and degenerated cells. *Geniculate nuclei.* Nucleus geniculatus lateralis dorsalis. This center exhibits almost complete degeneration, with only scattered chromatolytic cells remaining. Nucleus geniculatus medialis: The central part of this nucleus has degenerated almost completely in its rostral half, but caudally many residual cells are apparent, both chromatolytic and normal in appearance. The peripheral part of the

nucleus reveals scattered cell loss and many chromatolytic cells, but caudally, where it forms the caudal pole of the medial geniculate body, it is practically normal. Gliosis is marked in the central and most severely affected part of the nucleus. The degeneration of the medial geniculate nucleus in this specimen is maximal for this series of cases (fig. 21).

The midline and commissural nuclei, the nucleus subparafascicularis, the nucleus suprageniculatus, the nucleus pretectalis, the nucleus parabigeminus, and the nucleus reticularis are all quite normal in appearance.

Case 2 (V 87)

Hemidecortication of 3 weeks duration (fig. 2)

Lesion. All of the neopallium was destroyed except the interhemispheric cortex and a narrow zone bordering the upper lip of the rhinal fissure in the temporal area. However, the white matter and thalamic radiations, except the medial frontal connection, were destroyed down to the margin of the caudate nucleus, so that the only thalamo-cortical fibers passing laterally into the internal capsule and conceivably spared by the lesion are those passing to the upper lip of the rhinal fissure. Similarly, the medial frontal area and its anterior thalamic radiation connections were spared. The hippocampal formation, pyriform cortex, and basal ganglia were all untouched by the lesion.

Thalamus. The retrograde degeneration in this case is severe and practically coextensive with that described in case 1. Two significant differences in this case are, first, the quite normal appearance of the nucleus subparataenialis, and, second, the greater number of cells in various nuclei which are chromatolytic but which had not yet completely degenerated after 3 weeks. Such pale-staining and degenerating cells are most numerous in the nucleus anterior dorsalis, the nucleus parafascicularis, and the nucleus geniculatus medialis. In all the other nuclei which show retrograde change the period of 3 weeks was apparently sufficient for almost total neuronal degeneration.

Case 3 (V 81)

Hemidecortication of 2 weeks duration (fig. 3)

(Horizontal series. Transposed in figure 3 to standard transverse series)

Lesion. The lesion, although large, is entirely confined to the neopallium. It includes both cortex and white matter in most of its extent, so that a narrow strip of neocortex on the interhemispheric surface spared by the lesion has been deprived of afferent connections

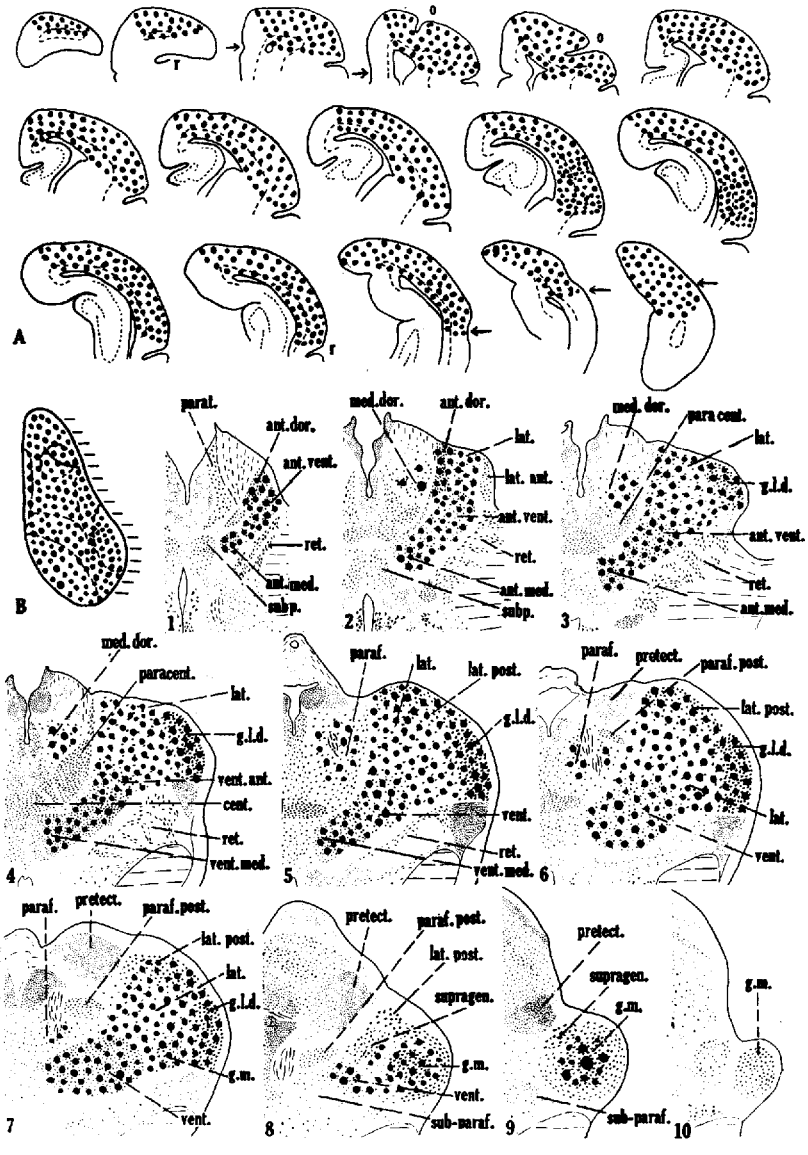

Fig. 2 Case 2. Standard chart as in figure 1.

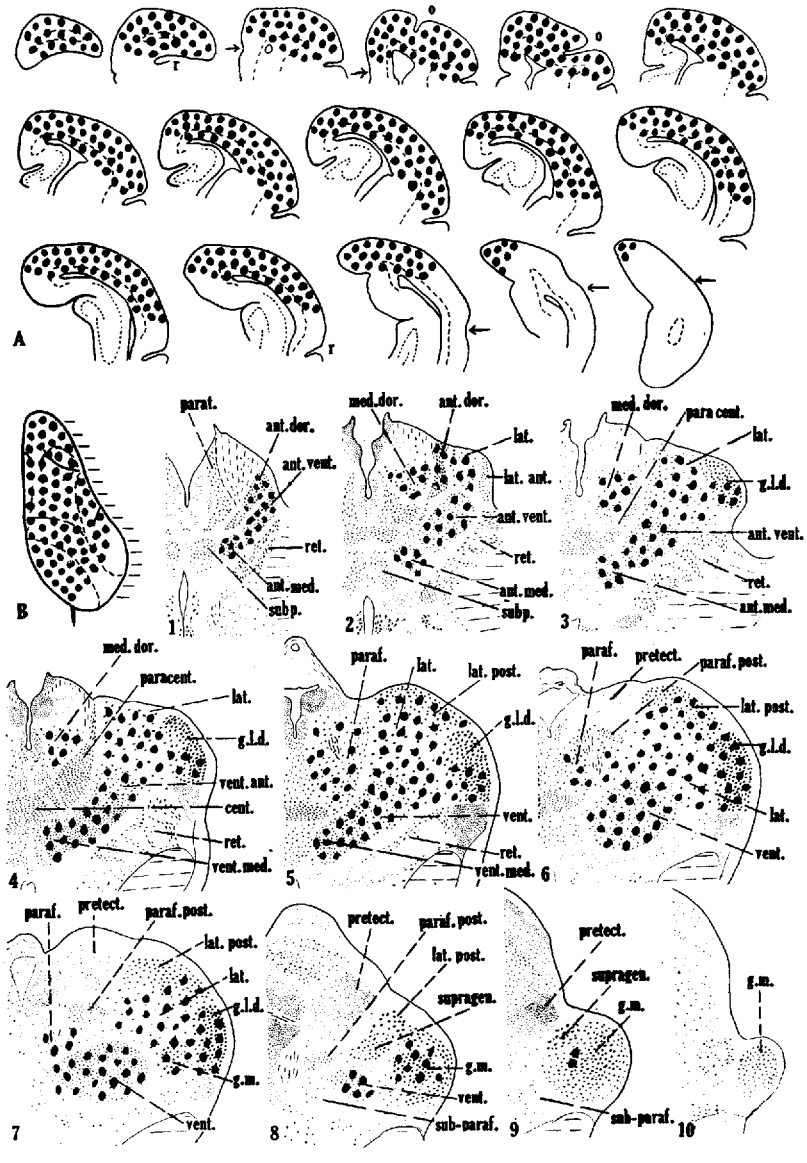

Fig. 3 Case 3. Standard chart as in figure 1.

from the lateral thalamic radiation, but the medial frontal area largely maintains its connections with the anterior thalamic radiation. Moreover, the caudolateral pole of the neocortex, including parts of the area temporalis, area parietalis, and area striata, has been spared, as shown in figure 3, and retains its connections with the caudal part of the internal capsule.

Thalamus. Although the period of degeneration is shorter than that in the previous case, the cell loss and gliosis in most of the affected nuclei are almost equally marked. Nevertheless, more chromatolytic cells and ghost cells are present in this case in the severely affected nuclei. The extent of the degeneration is quite similar to that in case 2, except that the rostrodorsal part of the lateral geniculate nucleus has been spared, the degeneration in the medial geniculate nucleus does not extend so far caudalward, and the unaffected area in the caudal part of the nucleus lateralis pars posterior is larger.

Case 4 (V 90)

Postoperative period 5 weeks (fig. 4)

Lesion. As indicated in the chart, the lesion involves the caudal pole of the neopallium and extends farther rostrally at the lateral and medial margins of the neocortex. It thus includes a large part of the area temporalis, the caudal portion of the area peristriata and the caudal portion of the area cingularis. Most of the area striata has been destroyed, with however a large part of the rostromedial portion of this region spared by the lesion. The borders of the lesion are clear-cut and, because of its caudal situation, there is no possibility of undercutting of more anterior regions. The lesion encroaches somewhat on the lateral edge of the area retrosplenialis, and has probably severed some of its afferent fibers from the thalamus.

Thalamus. The degeneration in the thalamus is severe and involves nuclei of the anterior, lateral, and geniculate groups. In the *anterior nuclear group* the nucleus anterior ventralis is most severely affected in its lateral portion, with a cell loss of about 80%. The medial portion of this nucleus is normal and the line of demarcation between normal and degenerated areas is quite sharp. The nucleus anterior dorsalis has suffered scattered but definite cell loss and there is a large number of chromatolytic cells, especially at its anterior pole. The nucleus anterior medialis is entirely normal. *Lateral nuclear group.* The extent of degeneration in this group is indicated in the chart. The nucleus lateralis pars anterior is intact. The nucleus lateralis pars intermedia in the rostral third of its extent is completely degenerated, but caudally is seen to be normal. Similarly, the nucleus lateralis pars posterior shows fairly severe degeneration rostrally and is

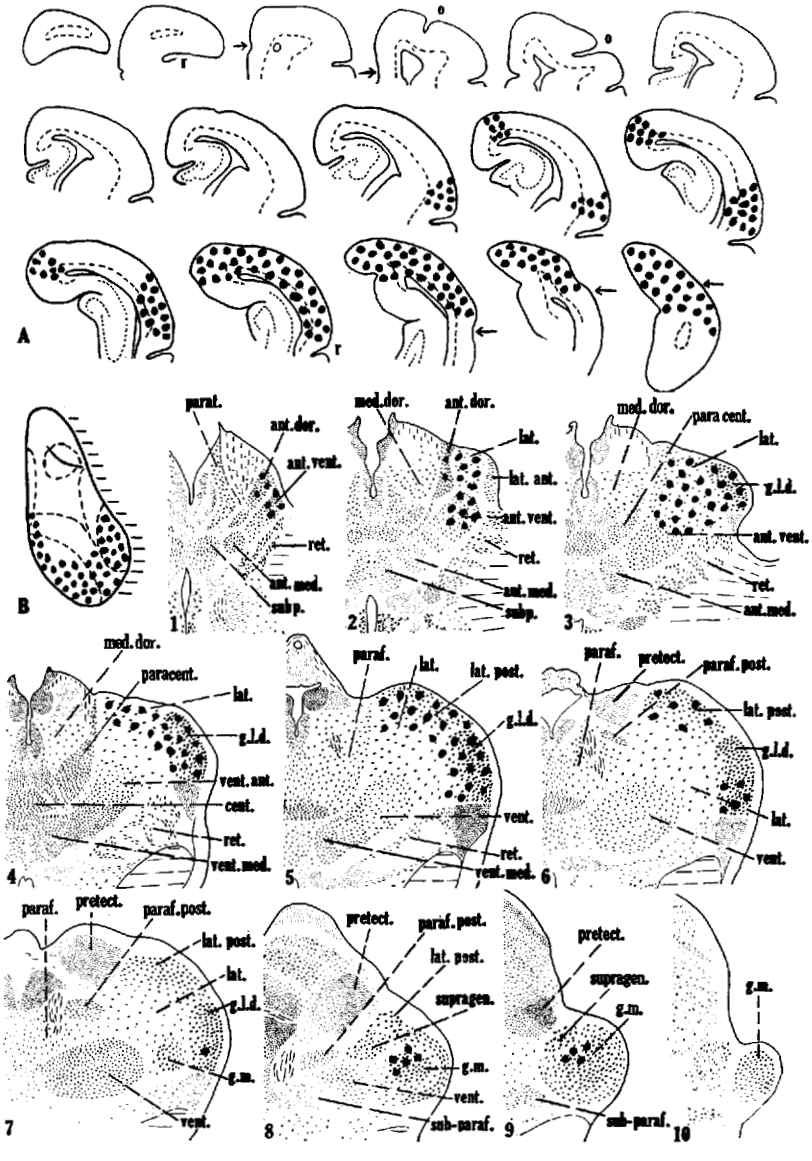

Fig. 4 Case 4. Standard chart as in figure 1.

normal caudally. Between the severely degenerated portion, in which the cell loss is about 60 to 80%, and the normal caudal portion, there is a zone in which the cell loss is only moderate and scattered. The nucleus geniculatus lateralis dorsalis shows extensive degeneration of neurons, and gliosis, in all parts except the dorsocaudal pole. The nucleus geniculatus medialis exhibits severe cell loss in the rostral two-thirds of the central part, with however many chromatolytic cells persisting. The peripheral part and caudal pole are intact. The ventrolateral region of the central part of this nucleus suffered very little cell loss and in some sections appears to be normal as compared with the dorsomedial zone. No other region in the dorsal thalamus shows any retrograde degeneration.

Case 5 (V 89)

Postoperative period 5 weeks (fig. 5)

Lesion. The lesion occupies the region indicated in the chart, with involvement of the striate area, except its caudolateral portion, and of the medial part of the area peristriata on the dorsal surface of the hemisphere. In the region of the peristriate area the lesion is largely superficial to layer V of the cortex. Undercutting of some of the thalamic radiation fibers to the caudal part of the area cingularis probably has occurred.

Thalamus. Severe retrograde degeneration is apparent in the lateral geniculate body except in its rostral and rostrodorsal portions, which are intact, and in the rostral part of the nucleus lateralis pars intermedia. Definite, but scattered, cell loss has occurred in the anterolateral tip of the nucleus anterior ventralis and in the nucleus lateralis pars intermedia adjoining the rostral two-fifths of the lateral geniculate nucleus. No other nucleus of the dorsal thalamus exhibits any retrograde cell change.

Case 6 (V 34)

Postoperative period 6 weeks (fig. 6)

Lesion. The lesion in this case is entirely confined to the area striata and a narrow adjacent zone of the area peristriata. The caudolateral tip of the area striata has been spared by the lesion.

Thalamus. Retrograde degeneration in the thalamus has occurred in the lateral geniculate body and in the nucleus lateralis pars intermedia adjoining the medial surface of the former, as shown in the chart. In the lateral geniculate nucleus many normal cells are present in the anterior pole, mingled with degenerated cells, but the caudal four-fifths of the nucleus shows maximal cell loss comparable

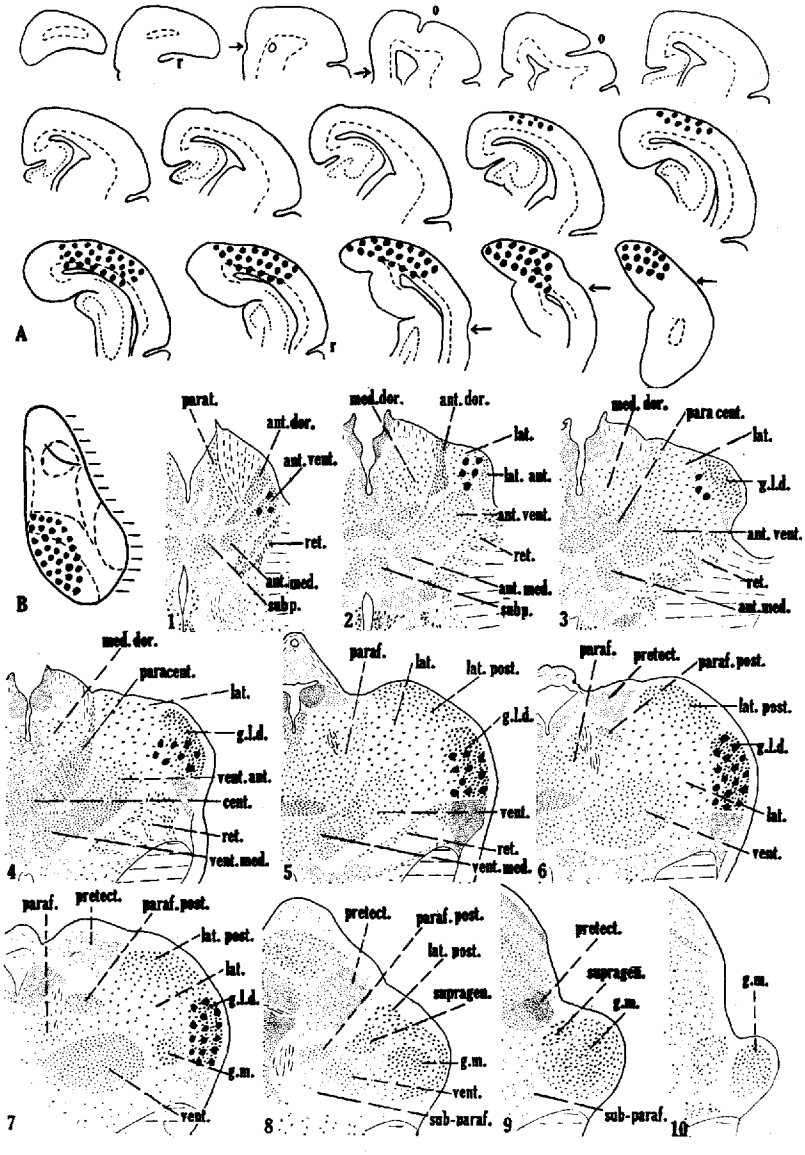

Fig. 5 Case 5. Standard chart as in figure 1.

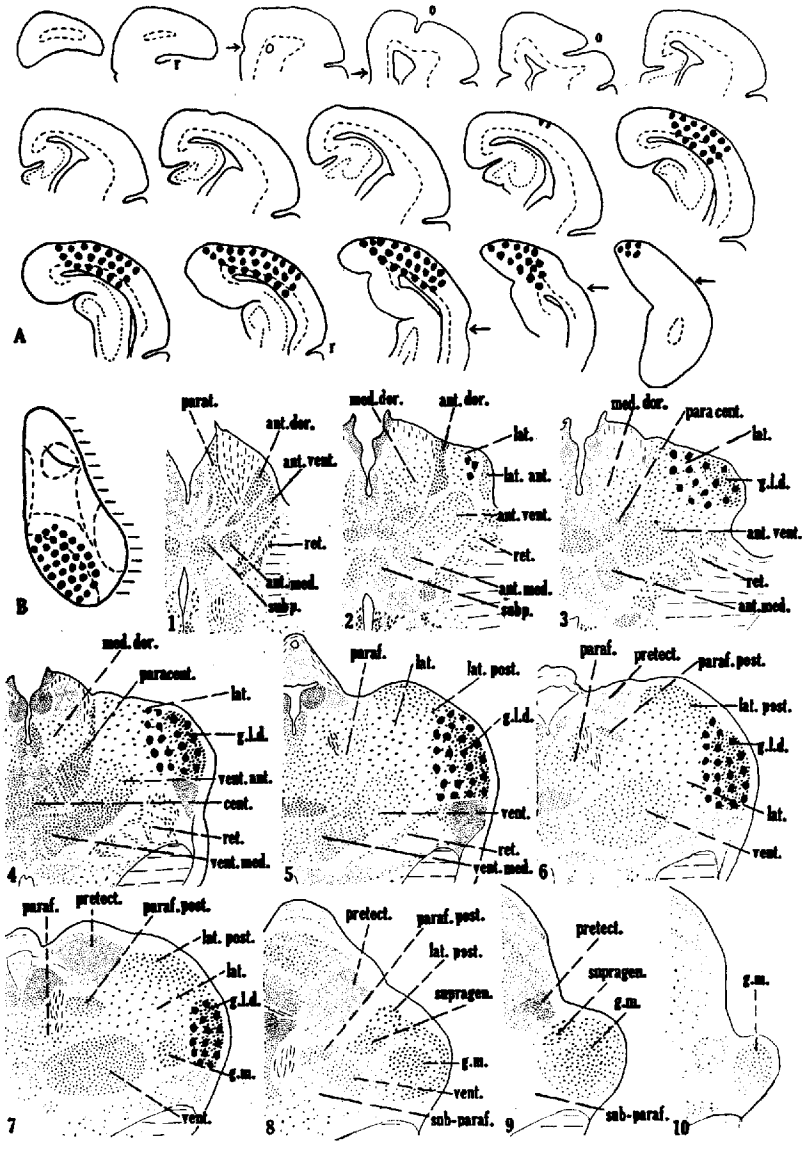

Fig. 6 Case 6. Standard chart as in figure 1.

with that seen after hemidecortication. No other centers in the dorsal thalamus reveal any retrograde change.

An additional case (V 88), practically identical in extent of lesion and in character and extent of the retrograde thalamic degeneration, is available but for the sake of brevity is not described here.

Case 7 (VC 28)

Postoperative interval 8 weeks (fig. 7)

Lesion. The lesion in this case is confined entirely to the neopallium and on its dorsal surface has destroyed most of the area striata, the caudolateral part of the area peristriata, and the caudal tip of the area temporalis. On the interhemispheric surface the caudal part of the area cingularis and the adjacent margin of the area retrosplenialis have also been destroyed.

Thalamus. Severe retrograde degeneration is present in the lateral geniculate nucleus except for the caudal pole, which is normal. Moreover, there is extensive cell loss in the anterior part of the nucleus lateralis pars intermedia and in the nucleus lateralis pars posterior adjoining the dorsal surface of the lateral geniculate nucleus, as well as considerable cell loss in the lateral parts of the nucleus anterior ventralis and nucleus anterior dorsalis. The extent of the degenerated zone, which has fairly sharp borders, can be seen in the accompanying chart (fig. 7). No other centers in the dorsal thalamus show any retrograde changes.

Case 8 (V 83)

Postoperative period 3 weeks (fig. 8)

Lesion. The cortical destruction in this case is restricted to the dorsal surface of the neopallium in the region illustrated in figure 8. Only the caudal part of the area temporalis and a small part of the adjacent area peristriata are directly involved. However, thalamic radiation fibers to the entire caudolateral pole of the neocortex have also been destroyed by the lesion which, in most sections, includes the white matter.

Thalamus. Severe degeneration of cells has occurred only in the nucleus lateralis pars posterior. The extent of the degeneration in this nucleus is almost maximal as compared with hemidecorticated cases, since the majority of the spared cells are at the caudal pole of the nucleus. In addition there is scattered cell loss in the anterior half of the lateral geniculate nucleus. This cell loss is rather small, perhaps 20 to 30%, and indicates that relatively few geniculo-cortical fibers

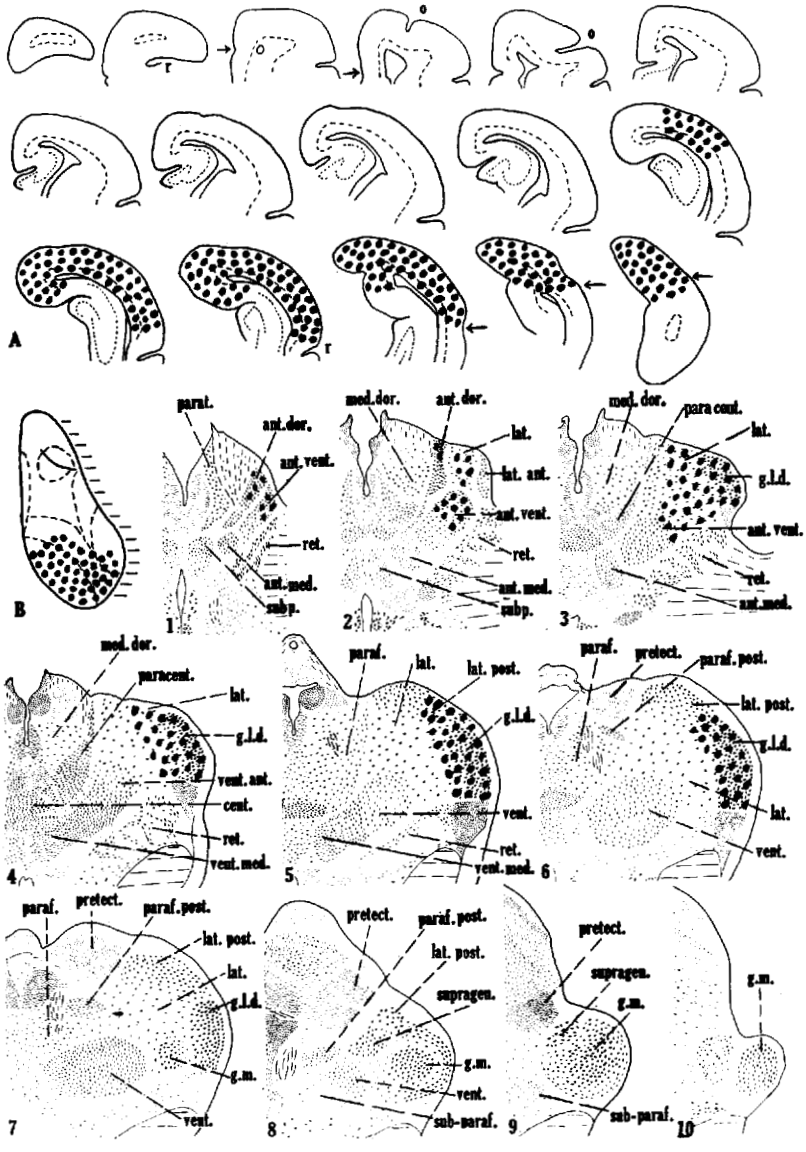

Fig. 7 Case 7. Standard chart as in figure 1.

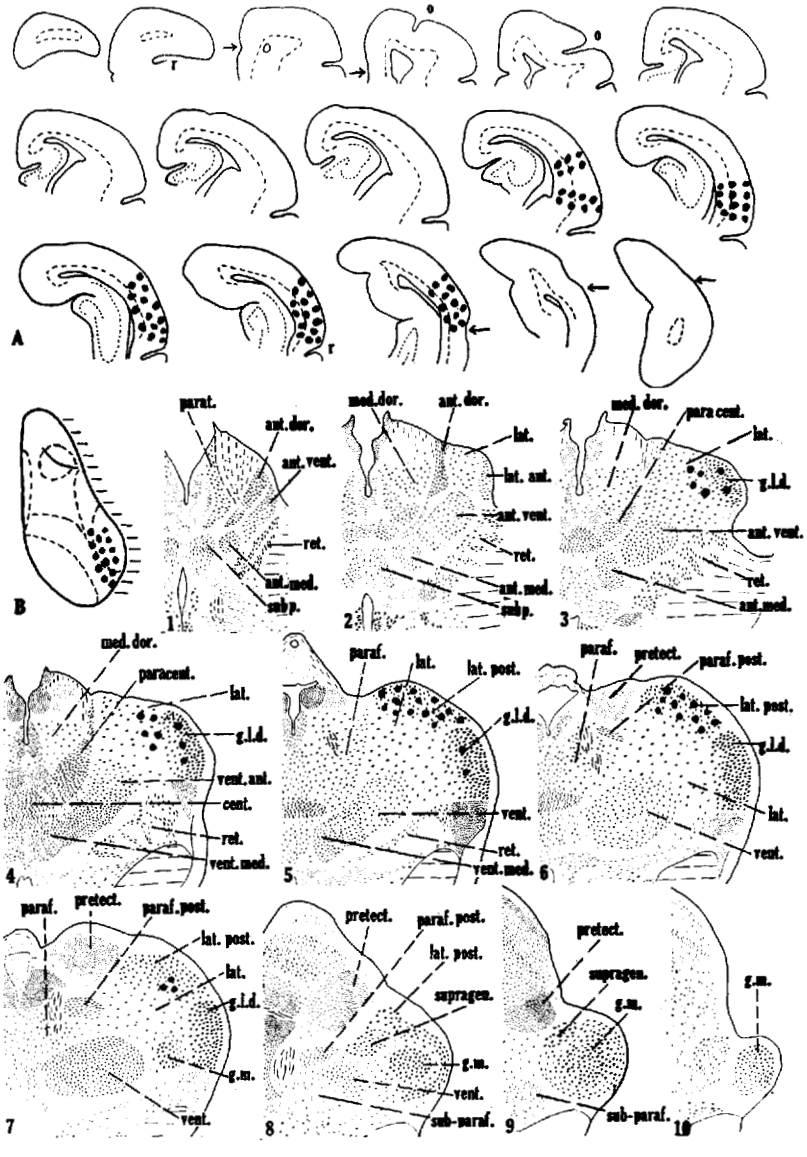

Fig. 8 Case 8. Standard chart as in figure 1.

pass as far laterally as the temporal area. The only other retrograde degeneration in the dorsal thalamus has taken place to a very small extent in the antero-lateral part of the nucleus lateralis pars intermedia.

Case 9 (V 41)

Postoperative period 6 weeks (fig. 9)

Lesion. The cortical destruction in this case is confined entirely to the area temporalis in which, however, the underlying white matter in the caudal part of this region has also been injured. This part of the thalamic radiation contains fibers connected with the caudo-lateral parts of the area peristriata and the area striata.

Thalamus. This case is of interest because, although the lesion is restricted entirely to the area temporalis, the retrograde degeneration in the medial geniculate nucleus is maximal as compared with the hemidecorticated cases. In addition, the undercutting of fibers passing to more caudal areas of the cortex, lesions of which do not affect the medial geniculate nucleus, has produced retrograde cell change in the rostral third of the lateral geniculate nucleus, in most of the extent of the nucleus lateralis pars posterior, and in the rostral part of the nucleus lateralis pars intermedia. The degeneration in the nucleus lateralis pars posterior, except for the caudal pole, which is spared, is severe. It is likewise extensive in the anterior third of the lateral geniculate nucleus. The cell loss in the nucleus lateralis pars intermedia is only moderate, however, with many persisting normal cells. No other centers in the dorsal thalamus show any retrograde changes.

Case 10 (V 84)

Postoperative interval 3 weeks (fig. 10)

Lesion. The extent of the lesion in this case is well shown in figure 10. Only the neopallium has been injured and there has been direct damage to the area insularis, the anterior half of the area temporalis, and the caudolateral part of the area parietalis. However, there is a considerable amount of undercutting of the white matter involving radiation fibers to more medial and caudal regions. This is shown in figure 10, A.

Thalamus. The retrograde degeneration in the thalamus is extensive. *Anterior nuclear group.* In the anterior nuclear group only the nucleus anterior ventralis shows retrograde change, apparently due to cutting of radiation fibers by the lesion. The cell loss is scattered throughout most of the nucleus and involves only about 50% of the cells. *Lateral nuclear group.* The cell loss in the lateral nuclear group is confined to scattered degeneration in the caudal part

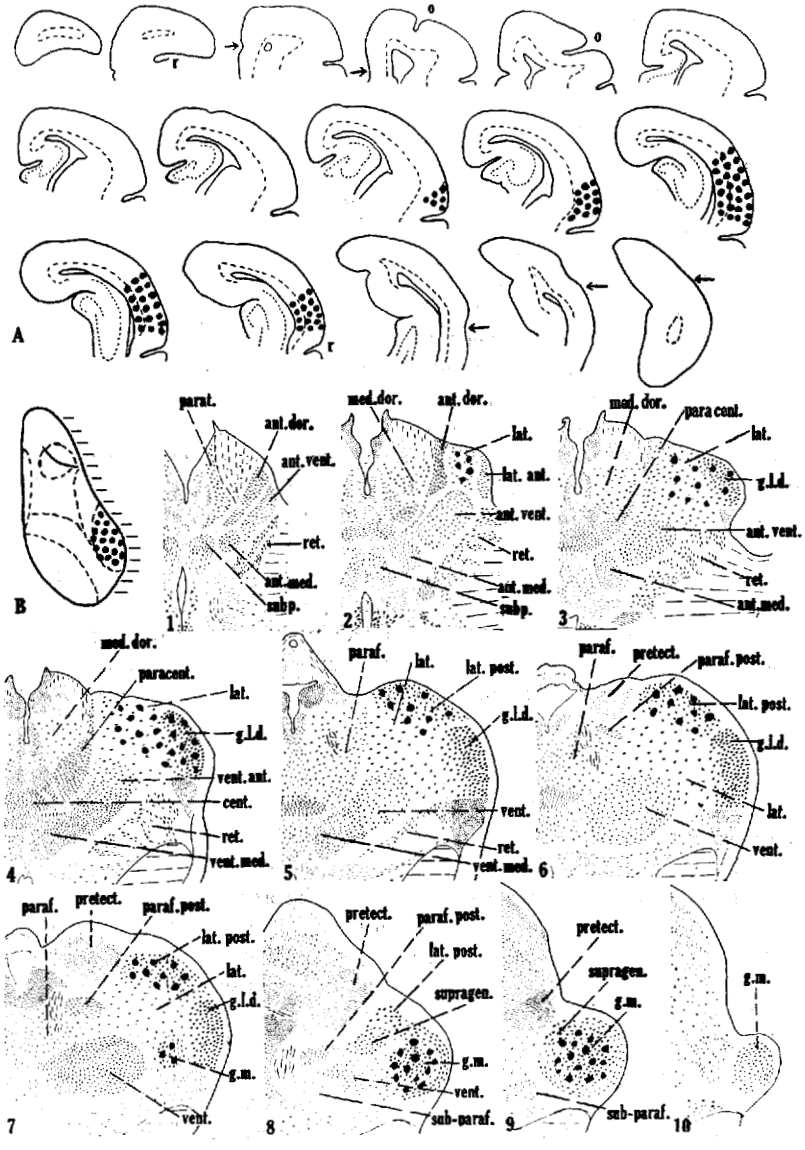

Fig. 9 Case 9. Standard chart as in figure 1.

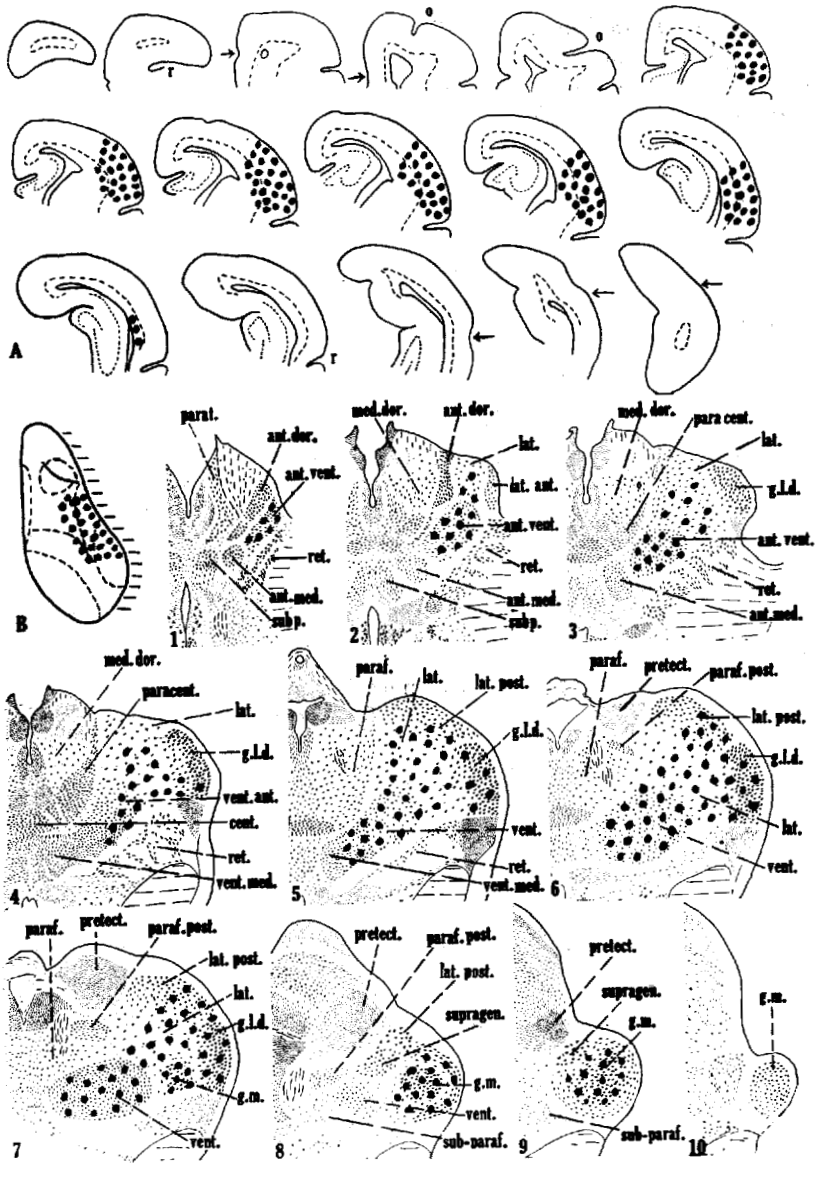

Fig. 10 Case 10. Standard chart as in figure 1.

of the nucleus lateralis pars intermedia and the lateral part of the nucleus lateralis pars posterior. The nucleus lateralis pars anterior is intact. *Ventral nuclear group.* The nucleus ventralis pars principalis has almost completely degenerated. The nucleus ventralis pars medialis is spared, as is also all of the nucleus ventralis anterior, except a narrow lateral zone. *The geniculate nuclei.* The degeneration in the lateral geniculate nucleus is fairly severe, involving as much as 80% cell loss caudally, but scattered normal cells are present everywhere, and the anterior third of the nucleus has been spared entirely. The medial geniculate nucleus shows maximal degeneration as compared with hemidecorticated cases. The character of the retrograde change in this nucleus is entirely comparable with that described in cases 1 and 2. No other centers in the dorsal thalamus show any retrograde changes.

Case 11 (V 40)

Postoperative period 6 weeks (fig. 11)

Lesion. The area of direct cortical destruction comprises the lateral half of the area parietalis and most of the adjoining area insularis. Throughout most of the extent of the lesion, as indicated in figure 11, A, the underlying white matter is also destroyed so that radiation fibers for more caudal and medial areas are probably injured to a certain extent.

Thalamus. The retrograde degeneration in this case is severe and accompanied by considerable gliosis. The borders of the area of cell loss are fairly sharp. The entire ventral nuclear group has degenerated, with the exception of a narrow medial strip of nucleus ventralis pars medialis. In addition, most of the nucleus anterior ventralis is severely affected and also a large part of the nucleus lateralis pars intermedia.

Case 12 (V 42)

Postoperative period 3 weeks (fig. 12)

Lesion. The cortical injury in this case is similar in extent to that of the previously described case. However, it has penetrated to the internal capsule underlying the area insularis, and in addition extends farther medially so as to destroy most of the area parietalis, and its underlying white matter. In the interhemispheric region it undercuts the white matter of the area parietomarginalis and area retrosplenialis. The lesion also extends laterally and anteriorly to the very margin of the rhinal fissure and encroaches slightly on the rostral lip of the orbital fissure.

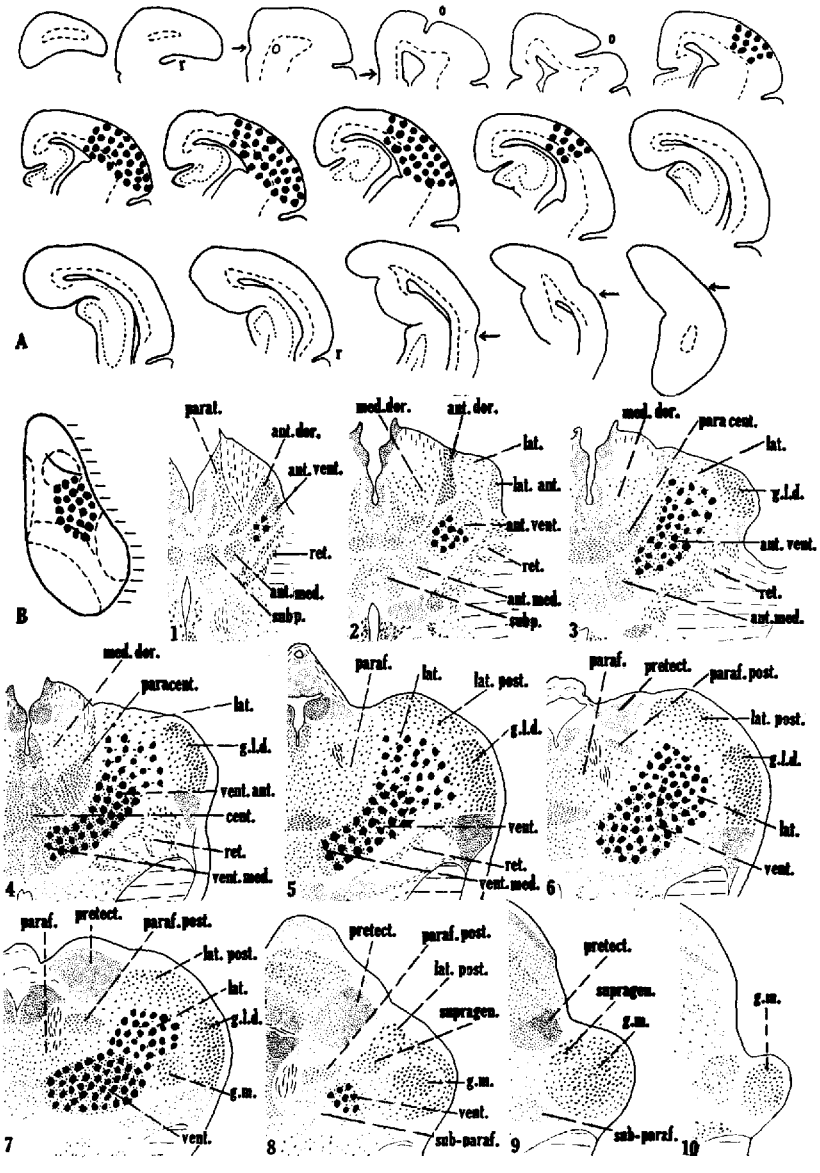

Fig. 11 Case 11. Standard chart as in figure 1.

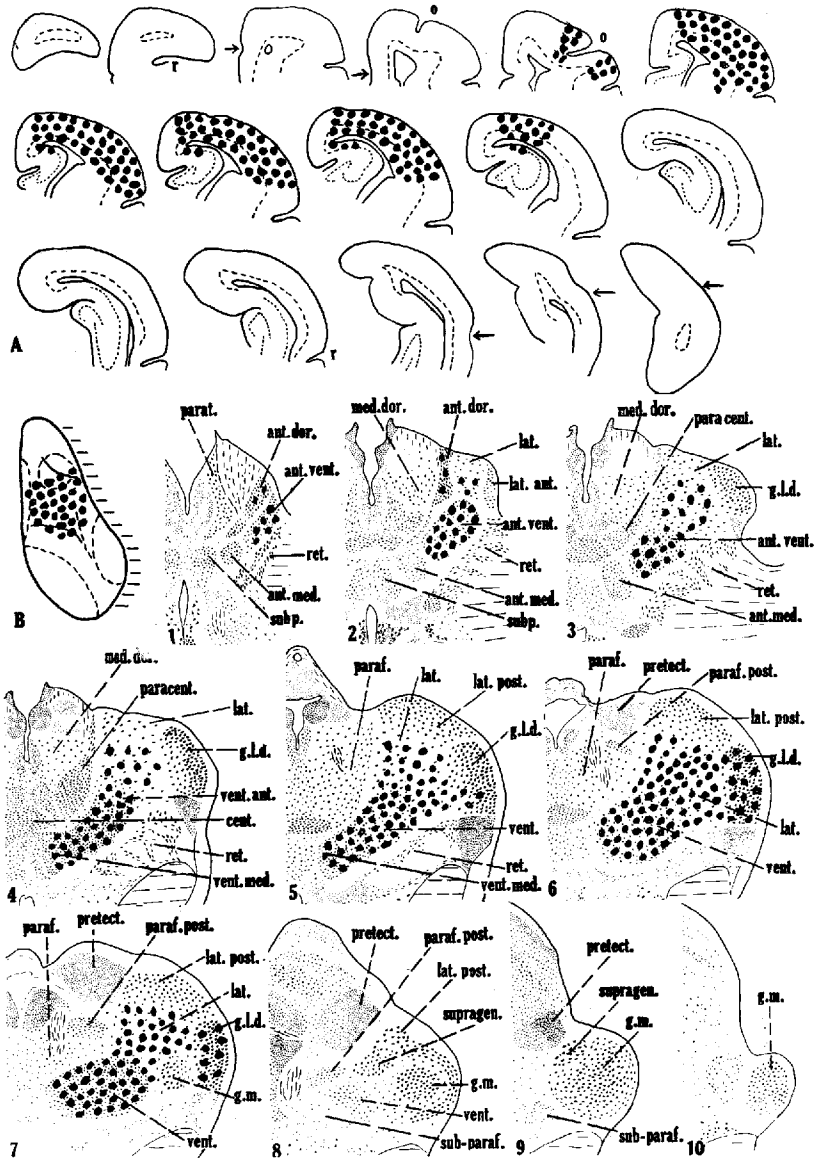

Fig. 12 Case 12. Standard chart as in figure 1.

Thalamus. Severe retrograde degeneration has affected the entire extent of the nucleus anterior ventralis, the nucleus anterior dorsalis, and the entire ventral nuclear group. A narrow medial strip of the nucleus ventralis pars medialis is spared, as is also the caudalmost tip of the nucleus ventralis pars principalis. The caudal pole of the nucleus geniculatus lateralis dorsalis shows moderate degeneration with, however, many residual normal cells present in the degenerated zone. A large part of the nucleus lateralis pars intermedia has also suffered severe degeneration, but no other nuclei of the dorsal thalamus are affected.

Case 13 (V 86)

Postoperative interval 3 weeks (fig. 13)

Lesion. The direct cortical injury is confined almost entirely to the area parietalis, with slight encroachment on the margins of the adjoining area postorbitalis, insularis, and, especially, peristriata. The margins of the injury are sharp and in most sections the lesion extends down to the ventricle so that in addition to complete destruction of the area parietalis there is undercutting of the fibers from areas medial and caudal to it. There is, however, no damage to the hippocampal formation or to the basal ganglia.

Thalamus. Anterior nuclear group. The nucleus anterior ventralis has almost completely degenerated, with a few scattered chromatolytic cells persisting. The nucleus anterior dorsalis shows scattered cell loss but most of the cells are normal in appearance. Similarly the nucleus anterior medialis is largely spared but there is definite and sharply outlined cell loss in its most lateral portion. *Lateral nuclear group.* This group shows retrograde degeneration only in the nucleus lateralis pars intermedia, all parts of which are affected severely. Scattered chromatolytic cells are present in this nucleus, however. *Ventral nuclear group.* The ventral nuclear group has almost completely degenerated with the exception of the nucleus ventralis pars medialis, which is normal except for scattered cell loss at its lateral margin. The caudal tip of the nucleus ventralis pars principalis is also spared. Finally, the caudoventral part of the *lateral geniculate nucleus* shows moderate cell degeneration, and similarly there is apparently slight cell loss in the anteriormost tip of the central part of the *nucleus geniculatus medialis.* No other centers in the dorsal thalamus exhibit any retrograde change.

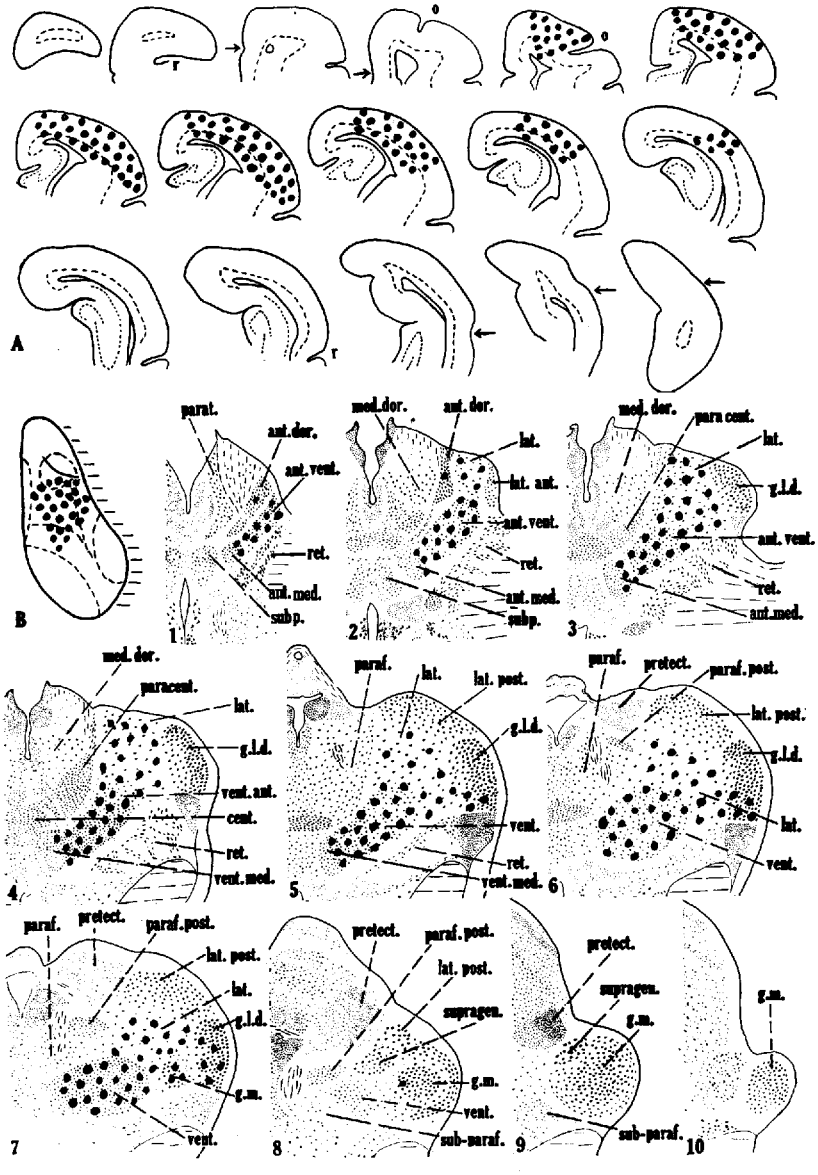

Fig. 13 Case 13. Standard chart as in figure 1.

Case 14 (V 82)

Postoperative interval 4 weeks (fig. 14)

Lesion. The cortex destroyed by the lesion is shown by stippling in figure 14, B, but there is considerable undercutting of white matter in the area shown by heavy outline in the lateral part of the area parietalis and area peristriata. Thus, the lesion in this case may be considered as having involved radiation fibers to the area frontalis, the area preorbitalis, the area postorbitalis, the medial parts of the area parietalis, the area peristriata and the area striata, as well as to the interhemispheric cortex for most of its extent. The lesion, where it undercuts the lateral part of the area parietalis, has impinged also on the margin of the subicular cortex and on the intraventricular alveus.

Thalamus. Anterior nuclear group. There is severe retrograde degeneration of all nuclei in this group, but there are a considerable number of chromatolytic residual cells in the nucleus anterior dorsalis, scattered residual cells in the nucleus anterior ventralis, and there is a definite sparing of the medial part of the middle third of the nucleus anterior medialis. The rest of this nucleus, however, is severely affected. *Medial nuclear group.* The nucleus medialis dorsalis shows severe degeneration caudally, but many residual cells remain in the anterior third of its extent. The nucleus parafascicularis also shows serious cell degeneration, except for the pars posterolateralis, which is quite normal. The nucleus subparataenialis has suffered definite cell loss, as well as chromatolysis of residual cells scattered throughout the nucleus, but most of the cells are normal. *Lateral nuclear group.* In this group there is moderate to severe retrograde degeneration only in the nucleus lateralis pars intermedia, with the cell loss largely restricted to the anterior third of the nucleus and to a narrow zone adjoining the nucleus ventralis pars principalis. *Ventral nuclear group.* The retrograde degeneration in this group is of interest because it is severe and is sharply restricted to two separate portions of this nucleus bridged by a strip of degenerated cells along the ventral margin. The two main foci of degeneration are in the nucleus ventralis pars medialis, which is severely affected (fig. 14, 4 and 5), and in the ventral and ventrolateral margins of the nucleus ventralis pars principalis (fig. 14, 6 and 7). As will be discussed below, the shape of the lesion, which involves the medial part of the area parietalis and the pre- and post-orbital regions, is critical for analysis of the intranuclear localization in the ventral nuclear group. Aside from moderate cell loss in the ventral part of the middle third of the lateral geniculate nucleus, there is no retrograde change in any of the other centers of the dorsal thalamus.

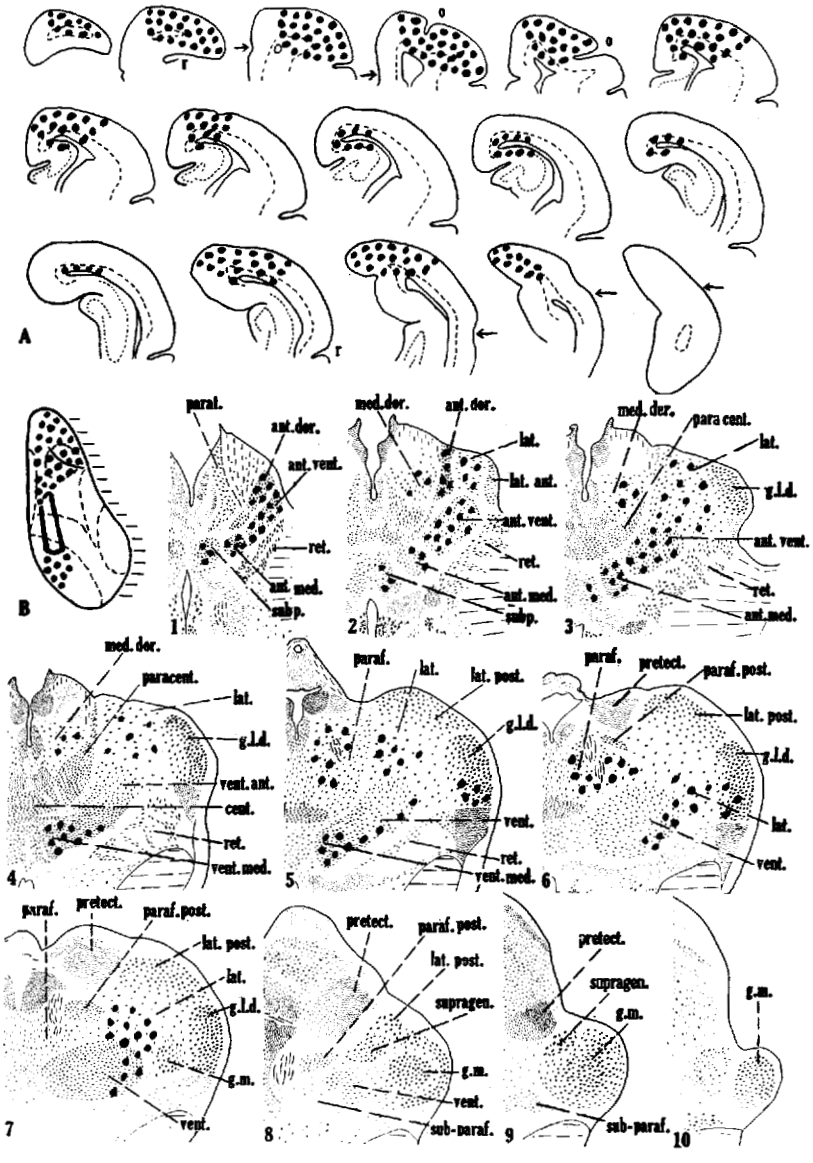

Fig. 14 Case 14. Standard chart as in figure 1.

Case 15 (V 39)

Postoperative interval 6 weeks (fig. 15)

Lesion. The cortical damage in this case is entirely restricted to the neocortex of the lateral two-thirds of the area frontalis, as shown in figure 15.

Thalamus. The only retrograde cell change in the dorsal thalamus is found in the nucleus medialis dorsalis, in which there is definite, but moderate, cell loss and gliosis in most of its extent. The nucleus parafascicularis appears to be intact.

Case 16 (V 85)

Postoperative period 3 weeks (fig. 16)

Lesion. The lesion has destroyed a narrow strip along the medial margin of the dorsal surface of the cerebral hemisphere and includes the lateral part of the area parietomarginalis and adjoining parts of the area parietalis and area peristriata. There is some undercutting of white matter restricted to this zone of cortical injury, but it does not intercept a large number of fibers of the interhemispheric cortical region.

Thalamus. The retrograde cell loss is severe and sharply localized to the ventrolateral margin of the nucleus ventralis pars principalis and a relatively small zone of the nucleus lateralis pars intermedia adjoining the caudal two-thirds of this nucleus. No other centers in the dorsal thalamus show retrograde change.

ANALYSIS AND SUMMARY OF THE THALAMO-CORTICAL PROJECTION

Anterior nuclear group

After hemidecortication, the dorsal, ventral, and medial nuclei of this group degenerate completely after 5 weeks. Most of the neurons of the ventral and medial anterior nuclei disappear 2 weeks after decortication, but many of the cells of the nucleus anterior dorsalis are still present after 3 weeks. Composite findings from partial cortical lesions indicate clearly that the cortical field for the anterior nuclear group lies in the interhemispheric region. This is confirmed by a Marchi series of an opossum (VM 4) with a lesion involving the nucleus anterior ventralis and the adjoining part of the thalamic radiations containing fibers from all of the anterior

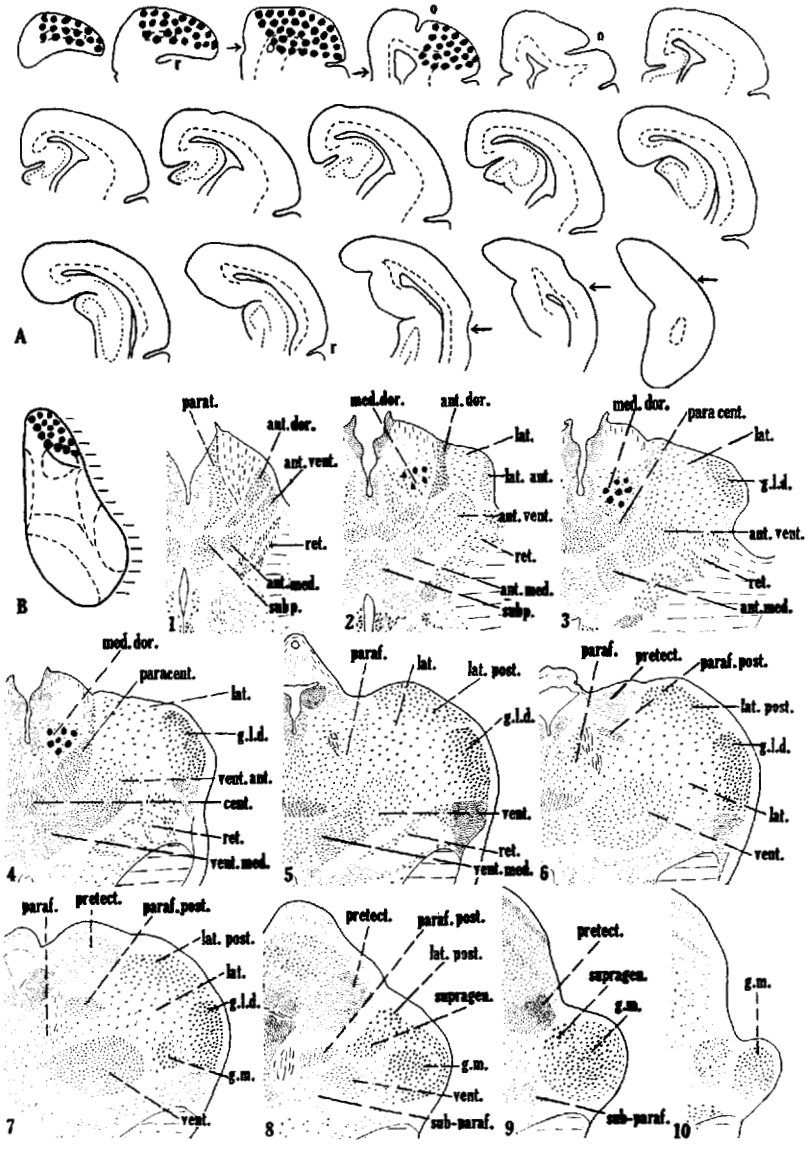

Fig. 15 Case 15. Standard chart as in figure 1.

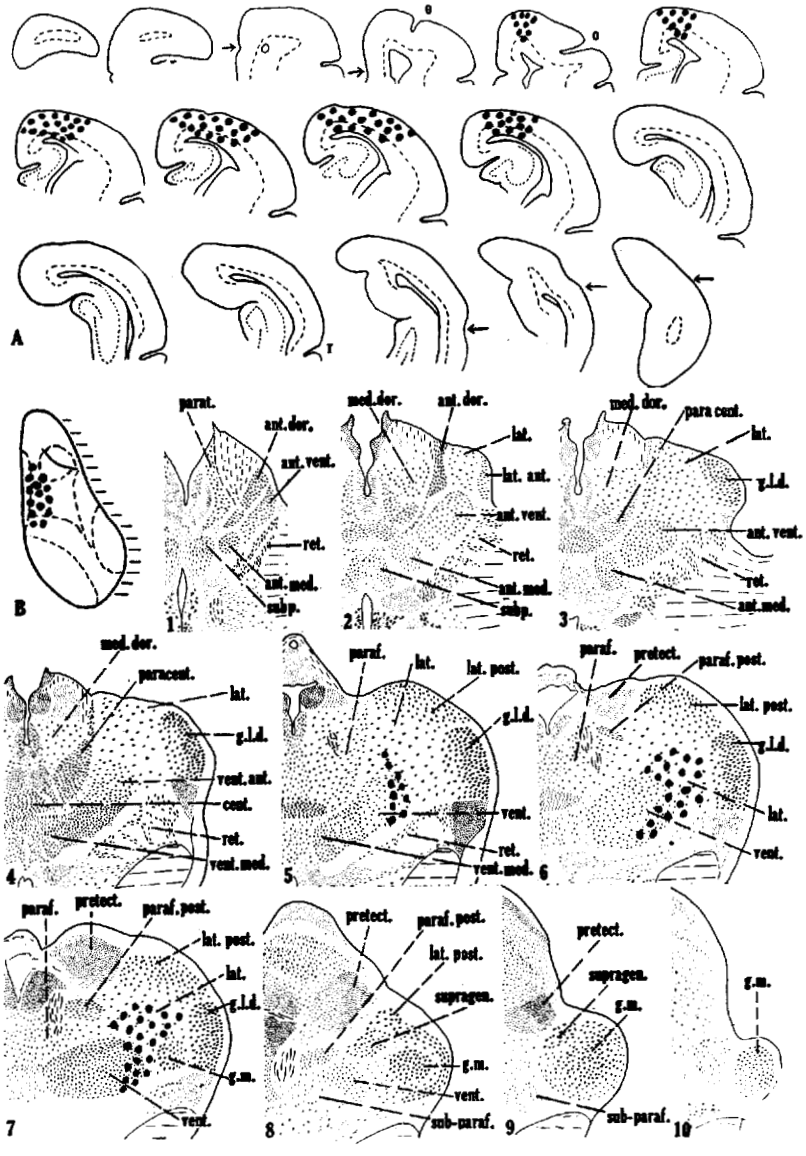

Fig. 16 Case 16. Standard chart as in figure 1.

nuclei. This is the only one of four cases with thalamic lesions, involving in all some part of every thalamic nuclear group, in which Marchi granules were traced to the area cingularis and area retrosplenialis, in their entire extent, and to the margin of the subicular cortex. The available cases, however, are not as satisfactory as could be desired for a determination of the precise fields of representation of the individual nuclei of this group.

Lesions that involve the caudal part of the area cingularis and area retrosplenialis produce retrograde degeneration in the lateral portions of the nucleus anterior dorsalis and nucleus anterior ventralis (cases 4 and 7). Lesions placed on the dorsal hemispheric surface which cut off the afferent fibers to these areas from the internal capsule underlying the area insularis generally produce retrograde degeneration only in the nucleus anterior ventralis (cases 10 and 11). However, when they are placed far enough rostrally to cut off many internal capsule fibers in the white matter under the area postorbitalis, retrograde degeneration occurs also in the nucleus anterior dorsalis (cases 13 and 14). This suggests that the radiation fibers to the nucleus anterior dorsalis lie more rostrally in the internal capsule than those to the nucleus anterior ventralis, although the degeneration in the two nuclei is parallel after direct cortical destruction (cases 4 and 7). The fact that degeneration in the nucleus anterior ventralis was much more severe than that in the nucleus anterior dorsalis in case 4, in which the caudal part of the area cingularis was much more damaged than the adjoining area retrosplenialis, suggests that the latter region is the cortical field for the nucleus anterior dorsalis. This is also suggested by cases 7 and 12, in which the damage to the adjoining areas cingularis and retrosplenialis is similar, and the retrograde degeneration in the two nuclei more nearly comparable in severity. The above-mentioned cases also indicate that the lateral parts of the dorsal and ventral anterior nuclei are represented caudally, and the medial parts rostrally, in the areas retrosplenialis and cingularis respectively. The nucleus anterior

medialis shows severe degeneration in the decorticate cases and in case 14, in which there is destruction of the medial part of the hemisphere from the rostral to the caudal poles. Since it shows no degeneration in cases 15 and 16, in which the cortex of the lateral frontal and medial parietal regions of the dorsal surface of the hemisphere is destroyed, it is extremely likely that its cortical field lies on the interhemispheric surface of the frontal pole, and that radiation fibers pass anteriorly and medially to it under the cortex immediately adjoining the orbital fissure, that is, between the regions destroyed in cases 15 and 16. Since the lesion in case 13 has produced degeneration throughout the nucleus anterior ventralis, but only in a strip of the nucleus anterior medialis immediately adjoining the former, it is likely that the intranuclear organization is similar in both, that is, that the lateral part of the nucleus is connected with the more caudal part of its cortical field. Evidence is presented in connection with the nucleus subparataenialis indicating that the cortical field of the nucleus anterior medialis lies in the upper part of the interhemispheric cortex of the frontal pole.

Medial nuclear group

Following decortication, the nucleus medialis dorsalis degenerates almost completely after 2 weeks. The nucleus parafascicularis exhibits considerable cell loss and cell atrophy after 2 weeks, but even after 5 weeks numerous cells, largely atrophic, persist. The nucleus parafascicularis pars posterolateralis, the nucleus parataenialis, and the nucleus paracentralis are spared. The nucleus subparataenialis shows severe degeneration in case 1 in which the hemidecortication included the medial frontal area, adjoining the septal region, and in case 14, in which undercutting of radiation fibers to this area occurred. It is probable that the thalamo-cortical fibers from this nucleus reach the medial frontal cortex via the anterior thalamic radiation in the medial frontal connection of Loo ('31).

The available cases of partial cortical destruction which bear upon the projection center of the medial nuclear group are few but permit of no doubt that this projection center is the cortex of the frontal pole. In case 15, a lesion confined to the area frontalis on the dorsal aspect of the hemisphere produced degeneration throughout the entire extent of the nucleus medialis dorsalis, and in no other thalamic center. In case 14, this nucleus as well as the nucleus parafascicularis degenerated. Although the lesion is not critical for the latter nucleus, its degeneration suggests, by exclusion, that the cortical field for the nucleus parafascicularis is the cortex medial to the orbital sulcus (fig. 19). The available cases contribute no clear evidence as to the intranuclear localization in these centers, but the relationship of their cortical fields to each other suggests that the anterior parts of these nuclei are represented lateral and rostral to the caudal parts in the cortex of the frontal pole. A single Marchi series of a specimen (VM 3) with a lesion involving in the dorsal thalamus the caudal part of the nucleus medialis dorsalis, the nucleus parafascicularis, and the nucleus lateralis pars posterior, exhibits Marchi granules which can be traced to the frontal area as far forward as the anterior tip. These granules doubtless represent degeneration due to injury of the medial nuclear group.

The nucleus parataenialis did not degenerate in any of our cases, but Stoffels ('39 a) and Lashley ('41) present evidence indicating that this nucleus in the rabbit and rat, respectively, projects to the septal area. This would seem to agree with the present findings of projection of the nucleus subparataenialis (nucleus reuniens of Lashley?) to the medial frontal cortex adjacent to the septal area. In the opossum there is no doubt that the nucleus parataenialis and nucleus subparataenialis are closely related (Bodian, '39 and '40), and indeed they are inseparable at the rostral end of the thalamus. Nissl ('13) appears to have noted degeneration of the parataenial nucleus in the decorticate rabbit.

Lateral nuclear group

Except for the nucleus lateralis pars anterior, the lateral nuclei degenerate almost completely after decortication. The caudal pole of the nucleus lateralis pars posterior, as described in the first paper of this series (Bodian, '39), also remains intact after 5 weeks, so it is possible that this zone should be considered as part of the nucleus suprageniculatus, which similarly is spared after decortication. Most of the cases of partial cortical injury described here contribute to the determination of the cortical fields of the lateral nuclear group, and several of them are critical with respect to intranuclear organization. Although there appears to be some overlapping of the projection from these centers, the boundaries of areas of retrograde degeneration within them are fairly sharp, so that some of the overlap may be only apparent because of the difficulties of accurately delimiting zones in a nuclear group which is so extensive and in which many of the cells are scattered between fiber bundles of the thalamic radiations.

Cases 4 and 14 point to the caudal part of the area parietomarginalis and the medial part of the area peristriata as the cortical field of the rostral end of the nucleus lateralis pars intermedia, and cases 4, 7, 8, and 9 indicate that the cortical field of the nucleus lateralis pars posterior is represented by the caudolateral part of the area peristriata and the caudal half of the area temporalis. However, since all of the lesions involving the caudal half of the temporal area are deep and destroy radiation fibers to the more caudal cortex, it is possible that the cortical field of the nucleus lateralis pars posterior does not include the temporal area. If such were the case, this cortical region would have no thalamo-cortical connections, since it is obvious from cases 7 and 8 that it is not connected with the medial geniculate nucleus.

The radiation fibers to the anterior end of the nucleus lateralis pars intermedia appear to lie rather far caudally in the internal capsule, since they seem to have been undercut

in several cases involving only the caudal fibers of the capsule (cases 4 to 9). Case 16 clearly suggests that the rostral part of the area parietomarginalis receives afferent fibers from the region of the nucleus lateralis pars intermedia which adjoins the lateral margin of the ventral nuclear group, and this is further confirmed by case 14. Cases 5 and 6, in which the area peristriata has been destroyed rostral to the area striata, are clear in associating this region with that part of the nucleus lateralis pars intermedia which adjoins the medial surface of the lateral geniculate nucleus. Cases 10 to 13 are not critical with respect to localization within the lateral nuclear group, since the lesions involve variable amounts of the underlying white matter, but the extent of the retrograde degeneration in these cases in general is not inconsistent with the results of the more critical cases.

Ventral nuclear group

After decortication, all of the nuclei in this group (pars anterior, pars medialis, and pars principalis) degenerate almost completely, but the boundaries between the ventral nuclear group and the nucleus centralis, nucleus paracentralis, and nucleus reuniens are not sharply defined. This is also true of normal specimens. Partial cortical lesions caudal to the area parietalis produce no degeneration in the ventral nuclear group. Case 16, in which the lesion impinges on the medial margin of the area parietalis, shows retrograde degeneration of the ventrolateral border of the nucleus ventralis principalis, and clearly establishes a precise thalamo-cortical relationship, since the borders of the area of retrograde cell loss are sharp. The lateral border of the cortical field of the ventral nuclei is more difficult to establish. However, since lesions which include most of the area insularis as well as the area parietalis (cases 10 and 11) result in retrograde degeneration in the ventral nuclei no more extensive than that seen after lesions involving very little of the area insularis as well as the area parietalis (cases 12 and 13),

it is probable that the lateral border of the cortical field of the ventral nuclei also corresponds more or less to the margin of the area parietalis, except anteriorly. Case 14 exhibits a lesion which involves, in addition to the medial part of the area parietalis (corresponding to case 16), the areas pre- and postorbitalis. Since the retrograde degeneration in the ventral nuclei in this case differs from that of case 16 only in the presence of almost complete degeneration of the nucleus ventralis pars medialis, and cell loss in the ventral margin of the pars principalis, it is likely that the cortical field of the pars medialis coincides with the pre- and postorbital areas. In agreement with this supposition is the fact that lesions which cut off the thalamic radiations to this region (cases 11 and 12) also produce severe degeneration in the nucleus ventralis medialis. A slightly more caudal lesion (case 10) which spares this part of the thalamic radiation produces no retrograde change in the nucleus ventralis medialis, but affects the adjoining medial part of the nucleus ventralis principalis, probably because of damage to the rostrolateral part of the area parietalis. Finally, a lesion (case 13) which injures the caudal border of the area postorbitalis produces cell loss of the lateral margin of the nucleus ventralis medialis. This lesion also results in severe degeneration of the nucleus ventralis anterior, whereas a lesion which spares the anterior end of the areas parietalis and insularis (case 10) also spares most of the nucleus ventralis anterior.

These cases suggest the topographical localization within the cortical projection of the ventral nuclei as shown in figures 18 and 19. A single Marchi series of a specimen (VM 5) in which the lesion destroyed most of the ventral nuclear group and extended back into the midbrain tegmentum is interesting in that it shows degenerated Marchi granules in the cortex confined largely to the pre- and postorbital areas, the parietal area, and the medial margin of the insular area. Marchi granules are also numerous in the interventral commissure of the thalamus. This case, and the other Marchi specimens, clearly confirm the deduction of Loo ('31) from

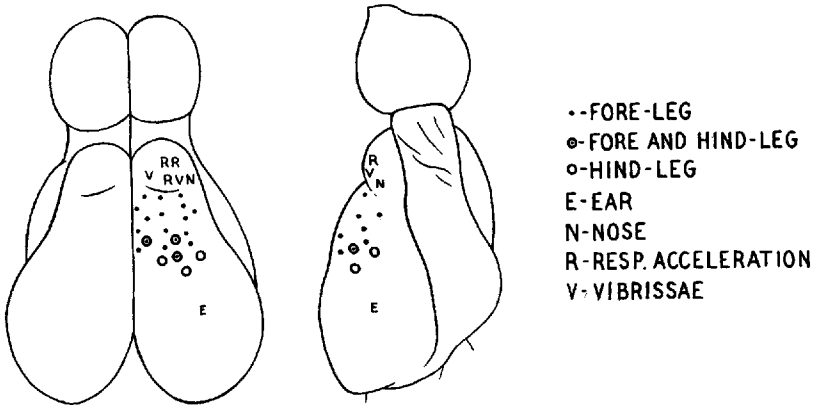

Fig. 17 The excitable cortex of the adult opossum, redrawn from Bromiley and Brooks ('40).

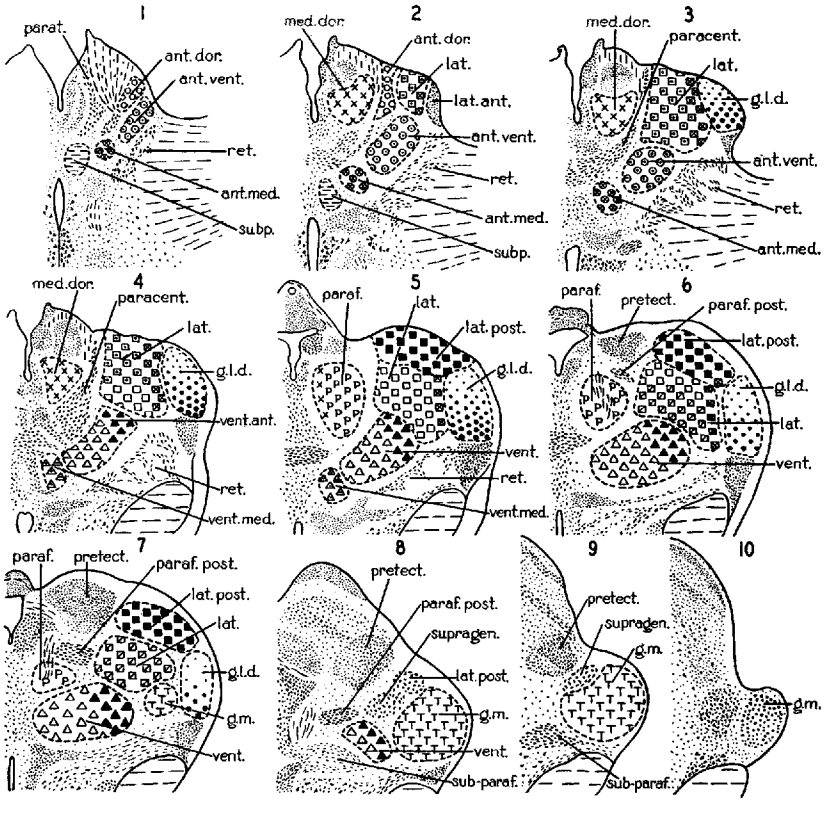

Fig. 18 Standard series of sections through the thalamus, with symbols indicating the nuclei and their segments which undergo retrograde degeneration after destruction of correspondingly marked areas of the cortex shown in figure 19.

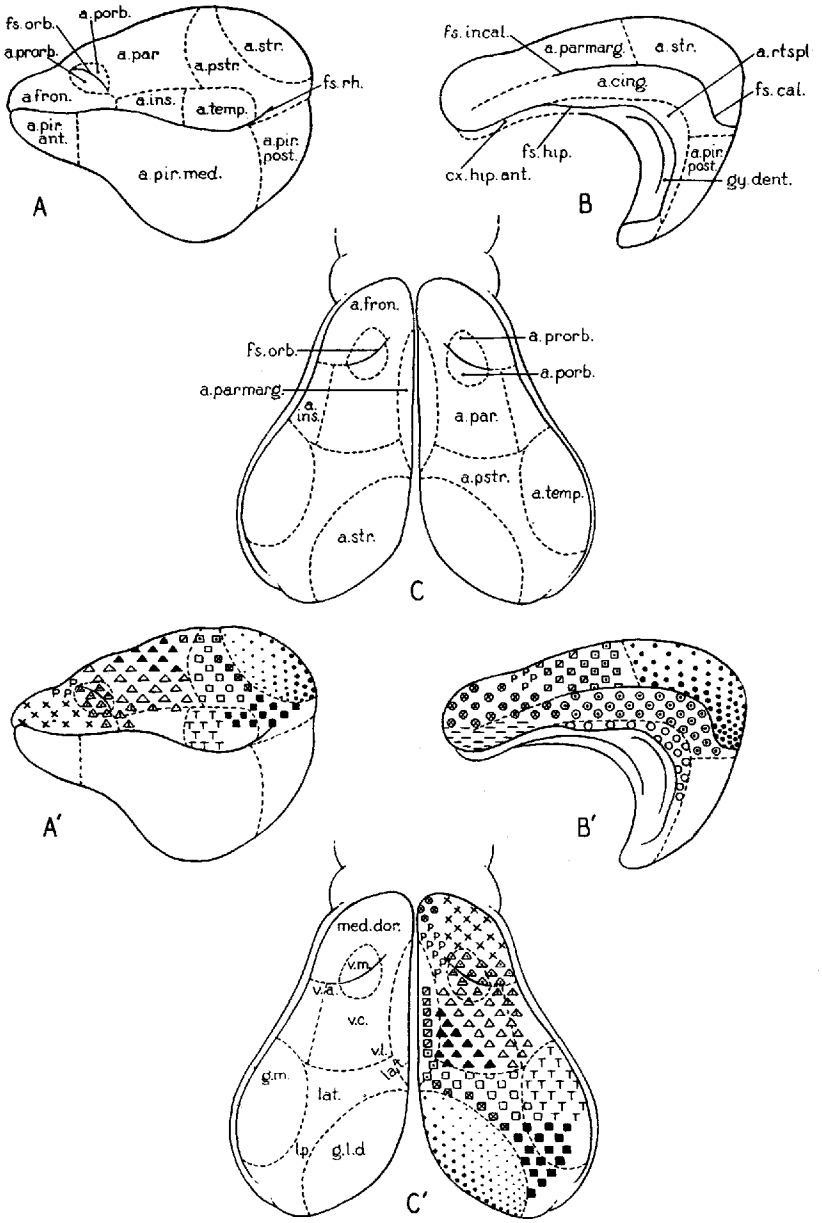

Fig. 19 A, B, C. The cytoarchitectural areas of the cortex of the opossum, according to Gray ('24). A', B', C'. Similar lateral, medial, and dorsal views of the cortex, with cortical fields of thalamic nuclei and their segments indicated with symbols corresponding to those in figure 18. The left hemisphere in C' shows the position of thalamic projection centers on the dorsal neocortex in relation to the outlines of Gray's cytoarchitectural fields. Figures 18 and 19 represent a synthesis of the material described above and are of course partly interpretative, more so with respect to the medial cortical surface than the dorsal.

normal material that the second layer of the white matter of the cortex contains chiefly corticopetal fibers, and the fourth layer chiefly corticofugal fibers. Marchi granules traced from thalamic lesions extend into the second layer of the white matter primarily, and from there into the cortex, whereas such granules traced from cortical lesions extend primarily along the fourth or deepest layer of the white matter toward the internal capsule. It is interesting that 2 weeks after cortical lesions, when cells in the thalamic nuclei are degenerated, the cortical projection fibers of these cells do not as yet stain with the Marchi method. This allows for separation at this time of cortical afferents and efferents in the white matter by differential staining by the Marchi method.

Geniculate nuclei

Nucleus geniculatus lateralis dorsalis. This center degenerates completely after hemidecortication. The details of the localization within the geniculo-cortical projection have been described in an earlier paper (Bodian, '35). The additional cases in this series serve to confirm the previous findings, which are summarized again in figures 18 and 19.

Nucleus geniculatus medialis. After hemidecortication the central part of this nucleus shows severe degeneration, but after 5 weeks many chromatolytic cells remain. More cells persist in the peripheral part, but the caudal fourth of the nucleus shows practically no degeneration. The degeneration within this nucleus after hemidecortication is shown in figure 21. The cortical field of the medial geniculate nucleus is clearly restricted to the temporal area of Gray ('24), since degeneration comparable to that occurring after hemidecortication follows destruction confined to this area (case 9). Lesions in the caudal part of this area, however, produce no discernible retrograde change (cases 7 and 8), so that it is likely that only the rostral part of Gray's area temporalis is concerned in the auditory projection. The available cases with partial lesions of the cortical field of the medial geniculate

nucleus are too few to permit an analysis of the intranuclear topical localization. In agreement with Lashley's ('41) findings in the rat, the degeneration in the medial geniculate nucleus of the opossum is never as complete as that in other nuclei. However, two specimens (cases 3 and 13) in which the retrograde degeneration, although not severe, is partial and localized, suggest that the projection is not completely diffuse.

Midline and commissural nuclei

These centers show no degeneration after purely neocortical destruction.

Nuclei of the di-mesencephalic junction and subthalamus

The nucleus pretectalis, nucleus supragenicularis, nucleus subparafascicularis, nucleus bigeminus, nucleus reticularis, and other subthalamic nuclei do not degenerate after hemidecortication.

DISCUSSION

The previous publications of this series have described in some detail the nuclear structure and fiber connections of the opossum diencephalon, and have made clear that this generalized mammal possesses, in a clearly differentiated way, the principal nuclear groups found in higher mammals (Bodian, '39). As may therefore be expected, the elementary plan of the mammalian thalamo-cortical projection is already clearly established in the opossum. Moreover, the greatest part, if not all, of its simple lissencephalic neocortex receives fibers from some portion of the dorsal thalamus, in well-localized fashion. This localization manifests itself, first, in the remarkably precise association of some of the principal nuclear groups of the dorsal thalamus with specific cortical areas, some of which correspond with the cortical areas as mapped by Gray ('24) on the basis of cytoarchitectural criteria, and, second, in the accuracy of the intranuclear topical projection in many cases (figs. 18 and 19).

In agreement with the findings of Waller ('34) and Lashley ('41) in the rat, one finds in general in the opossum that contiguous thalamic nuclei project to contiguous cortical fields.

The opossum material indicates that there is very little overlap of the projection of adjacent nuclei; uncertainty with regard to the precise border of a cortical field is usually a reflection of the absence of critical lesions. There is little indication of the presence of neocortical regions receiving no thalamic fibers, although the material studied is not critical for narrow "silent" zones between some of the cortical projection fields, in the marginal perirhinal zone, and in the interhemispheric region. There is evidence for good maintenance of localization of projection fibers in the thalamic radiations and in the white matter of the cortex, but localization of the projection in the radiation does not always appear to be as constant or as precise as in the terminal cortical field. Persistence of at least a few residual cells several weeks after decortication or after partial lesions occurs in all thalamic nuclei, but such cells are very scarce in all involved nuclei except the nucleus subparataenialis, nucleus parafascicularis, and nucleus geniculatus medialis. Such residual cells are most often "chromatolytic," and this has resulted in the suggestion that such cells are interneurons which have undergone atrophy due to loss of corticothalamic terminals (Waller, '34; Walker, '38; Lashley, '41). Lashley has also suggested the possibility that neurons of the medial geniculate nucleus send collaterals to all parts of its cortical field and that injury to some of these collaterals may result in a state of permanent atrophy of the parent neurons. However, such residual cells are present even after hemidecortication so that this alternative does not seem plausible. He also suggests that neurons of the medial geniculate nucleus may give off intranuclear collaterals as well as sending axons to the cortex, so that chromatolysis may be due to transneural atrophy due to loss of interconnections within the nucleus itself. Ramón y Cajal ('11), in fact, has described intranuclear collaterals

arising from the cortical axons of some of the cells of the sensory thalamus.

It seems equally likely that the rapid reaction of most of these cells to cortical injury may be due to destruction of cortical terminals, but that they fail to degenerate completely because of the presence of collateral intrathalamic connections. In the case of the medial geniculate body, in which many cells persist, especially in the caudal part where perfectly normal cells are found after hemidecortication, the probability of connections within the thalamus is great. The apparently peculiar response of this nucleus to cortical ablation was noted in previous reports (Bodian, '39, '40), and it was then suggested that the partial degeneration of the nucleus was due to the existence of rich connections with neighboring centers, especially the nucleus ventralis and nucleus subparafascicularis. This explanation still seems a likely possibility, but the problem requires further experimental investigation. Lashley ('41) has also noted incomplete degeneration in the rat, but he has apparently not taken into account my earlier findings. Ramón y Cajal ('11) has emphasized that he does not consider the cells with short axons in the sensory thalamus to be intercalated cells, but rather cells which receive lemniscus fibers and transmit their impulses directly to cells with long axons terminating in the cortex. This suggests that these cells with short axons may atrophy due to degeneration of their cells of termination. Moreover, Ramón y Cajal describes many cortico-thalamic fibers which bifurcate and send collaterals across the midline in the interventral commissure. If these exist in the opossum as well as in rodents, it is interesting that it has not been possible to find any evidence of transneural atrophy or chromatolysis in the contralateral thalamus after hemidecortication. Until further evidence is forthcoming one is inclined to ascribe the chromatolysis or atrophy of residual cells in the thalamus to degeneration of their cells of termination in the same nucleus, if such residual neurons are cells with short axons. If the residual cells have cortical axons,

their persistence following cortical ablation may be due to the existence of thalamic collaterals which serve to maintain the integrity of the neuron, although at a reduced metabolic level. There is evidence that such a situation occurs in the mitral cells of the olfactory bulb, which persist indefinitely at reduced size following olfactory tract section (Howe and Bodian, '42, p. 162). The whole problem of retrograde and transneural reaction of nerve cells needs reinvestigation, in view of the variety of reactions of cells in different nerve centers brought to light in recent years.

The question of the functional significance of localization within the cortical projection of specific thalamic nuclei has been the subject of extensive speculation and discussion, which has been reviewed at length in recent years by Poliak ('32), Walker ('38), Lashley ('41), and others. Lashley casts doubt upon the functional interpretation of solely anatomical demonstrations of spatial localization within the thalamic projections, and states that "the dynamic principles of growth provide a sufficient reason for the topographic arrangement, in that the axons of neuroblasts subjected to the same growth stimulus develop in close contact and consequently in parallel lines." Such an explanation of one of the most striking features of cerebral organization explains little, since the dynamic principles of growth in the central nervous system are far from being clearly established, and are most likely functionally determined in any case. Moreover, it is necessary to question the basis of Lashley's denial of the contrary view that given topographic arrangements within the central nervous system are an expression of functional determinants. For example, Lashley points to the precision of localization within the anterior nuclei as being functionally meaningless in the olfactory system. This presupposes that the function of the anterior thalamic nuclei is "olfactory", which remains to be adequately demonstrated, and fails to deal with the logical necessity of demonstrating the character of the discharges from the anterior nuclei, and how they are determined by the total of afferent messages impinging upon these nuclei,

before attempting to interpret the meaning or lack of meaning of spatial localization on a functional basis. The visual projection, as Lashley ('41) himself points out, clearly shows that "the functional value of a given arrangement" can be inferred from anatomic evidence, providing that we understand sufficiently the nature of the function in question. This is obviously not the case with respect to the anterior nuclei.

Lashley also questions the possibility of a functional interpretation of the projection of the medial geniculate nucleus, since he finds the projection of this nucleus in the rat to be completely diffuse. Since his analysis of the reaction of this nucleus to cortical injury has failed to take into account the complicating factors of the intrathalamic connections, as discussed above, the factual basis of a diffuse cortical projection of this nucleus must be considered in doubt. This is especially true in view of the existence of localization in the auditory radiation, and of contrary findings of Waller ('34).

Studies of the excitable areas of the opossum cortex have been made by many investigators since the early exploratory study of C. L. Herrick and Tight (1890). Gray and Turner ('24) reviewed this work and that of subsequent investigators (Ziehen, 1897; Cunningham, 1898; C. and O. Vogt, '07), and carried out further experiments, which have been extended in more recent years by Rogers ('24), Weed and Langworthy ('25), Langworthy ('27), and Bromiley and Brooks ('40). The results of all of these studies are in substantial agreement, although a hindleg representation was not obtained by all workers. The most recent findings of response to electrical stimulation by Bromiley and Brooks in the adult opossum are shown in figure 17. They are closely comparable with results of stimulation of the cortex of the phalanger, Trichosurus vulpecula, by Goldby ('39), and of various other marsupials by Abbie ('40). Although, as noted by Gray and Turner ('24), the excitable cortex extends over several cytoarchitectural areas, it is interesting to note that the cortical field involved is almost entirely the field of representation of the ventral nuclear group. In general, the face is found to be represented

anterior to the orbital sulcus (nucleus ventralis pars medialis) and in the rostral part of the area insularis (nucleus ventralis pars anterior); the forelimbs are represented behind the orbital sulcus (central part of nucleus ventralis pars principalis); the hindlimbs are represented most caudally, and generally medialward, in the area parietalis (lateral part of nucleus ventralis pars principalis). The orientation of the parts of the projection which correspond respectively to the face, forelimb, and hindlimb representation shows a surprising similarity to that of primates, although the direction of the axis of orientation differs from that of primates.

SUMMARY

1. With the use of the method of retrograde degeneration it has been found that the elementary plan of the mammalian thalamocortical projection is clearly established in the opossum. Localization is precise with respect both to the projection of specific nuclei of the dorsal thalamus and to the projection of segments of most of these nuclei. The details are described.

2. Contiguous thalamic nuclei tend to project to contiguous cortical fields, and there is little neocortex which does not receive thalamic fibers.

3. Residual cells 3 to 6 weeks after hemidecortication are scarce in all but the subparataenial, parafascicular, and medial geniculate nuclei. Such cells are most often chromatolytic, and the problem of their persistence, especially in the medial geniculate nucleus, is discussed.

4. The incomplete degeneration of the medial geniculate nucleus and the normal state of its caudal pole after hemidecortication are believed to be due to strong intrathalamic connections, previously described (Bodian, '39 and '40).

5. The question of the functional significance of anatomical localization in the thalamo-cortical projections is discussed.

6. The excitable area of the cortex of the opossum corresponds very closely to the projection field of the ventral nuclear group, which includes several cytoarchitecturally

different cortical areas. The orientation of the fields of representation of face, forelegs, and hindlegs in the cortex and in the ventral nuclear group is not unlike that of primates.

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PLATES

ABBREVIATIONS

a. cing., area cingularis
a. fron., area frontalis
a. ins., area insularis
a. par., area parietalis
a. parmarg., area parietomarginalis
a. pir. ant., area piriformis anterior
a. pir. med., area piriformis medialis
a. pir. post., area piriformis posterior
a. porb., area postorbitalis
a. prorb., area preorbitalis
a. pstr., area peristriata
a. rtspl., area retrosplenialis
a. str., area striata
a. temp., area temporalis
ant. dor., nucleus anterior dorsalis
ant. med., nucleus anterior medialis
ant. vent., nucleus anterior ventralis
cent., nucleus centralis
cx. hip. ant., cortex hippocampi anterior
fs. cal., fissura calcarina
fs. hip., fissura hippocampi
fs. incal., fissura intercalaris
fs. orb., fissura orbitalis
fs. rh., fissura rhinalis
g. l. d., nucleus geniculatus lateralis dorsalis
g. m., nucleus geniculatus medialis
gy. dent., gyrus dentatus
lat., nucleus lateralis pars intermedia
lat. ant., nucleus lateralis pars anterior
lat. post., nucleus lateralis pars posterior
l. p., nucleus lateralis pars posterior
med. dor., nucleus medialis dorsalis
o., fissura orbitalis
paracent., nucleus paracentralis
paraf., nucleus parafascicularis
paraf. post., nucleus parafascicularis pars posterior
parat., nucleus parataenialis
pretect., nucleus pretectalis
r., fissura rhinalis
ret., nucleus reticularis
subp., nucleus subparataenialis
subparaf., nucleus subparafascicularis
supragen., nucleus supragenículatus
v. a., nucleus ventralis pars anterior
v. c., nucleus ventralis pars principalis (central segment)
v. l., nucleus ventralis pars principalis (lateral segment)
v. m., nucleus ventralis pars medialis
vent., nucleus ventralis pars principalis
vent. ant., nucleus ventralis pars anterior
vent. med., nucleus ventralis pars medialis

PLATE 1

EXPLANATION OF FIGURE

20 Photomicrograph of section of case 1, close to that represented in figure 1, section 2, showing the retrograde degeneration in the anterior nuclei, mediodorsal nucleus, lateral nucleus, and in the subparataenial nucleus after hemidecortication. The degeneration in the nucleus subparataenialis is partial, in the other nuclei almost complete. × 22.

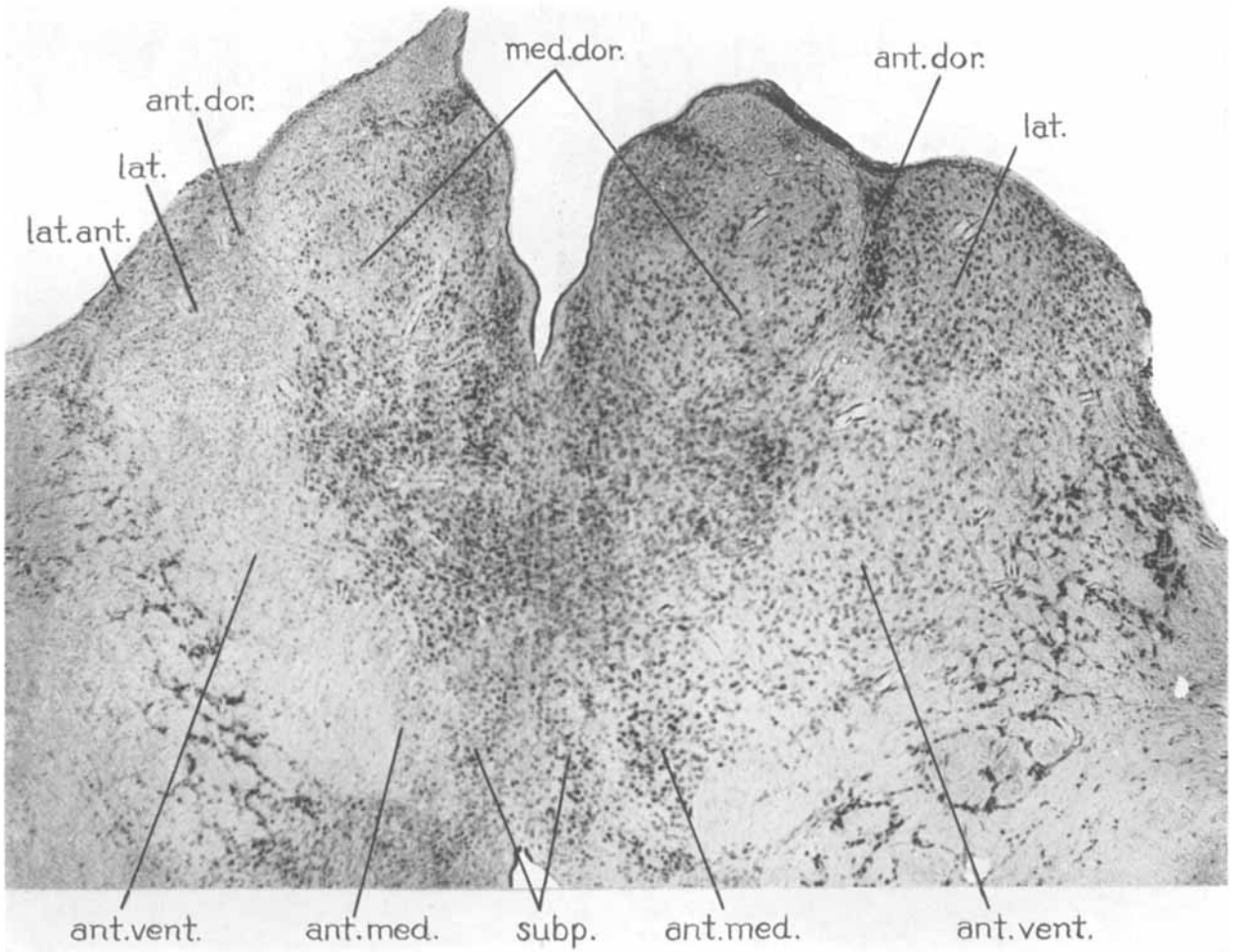
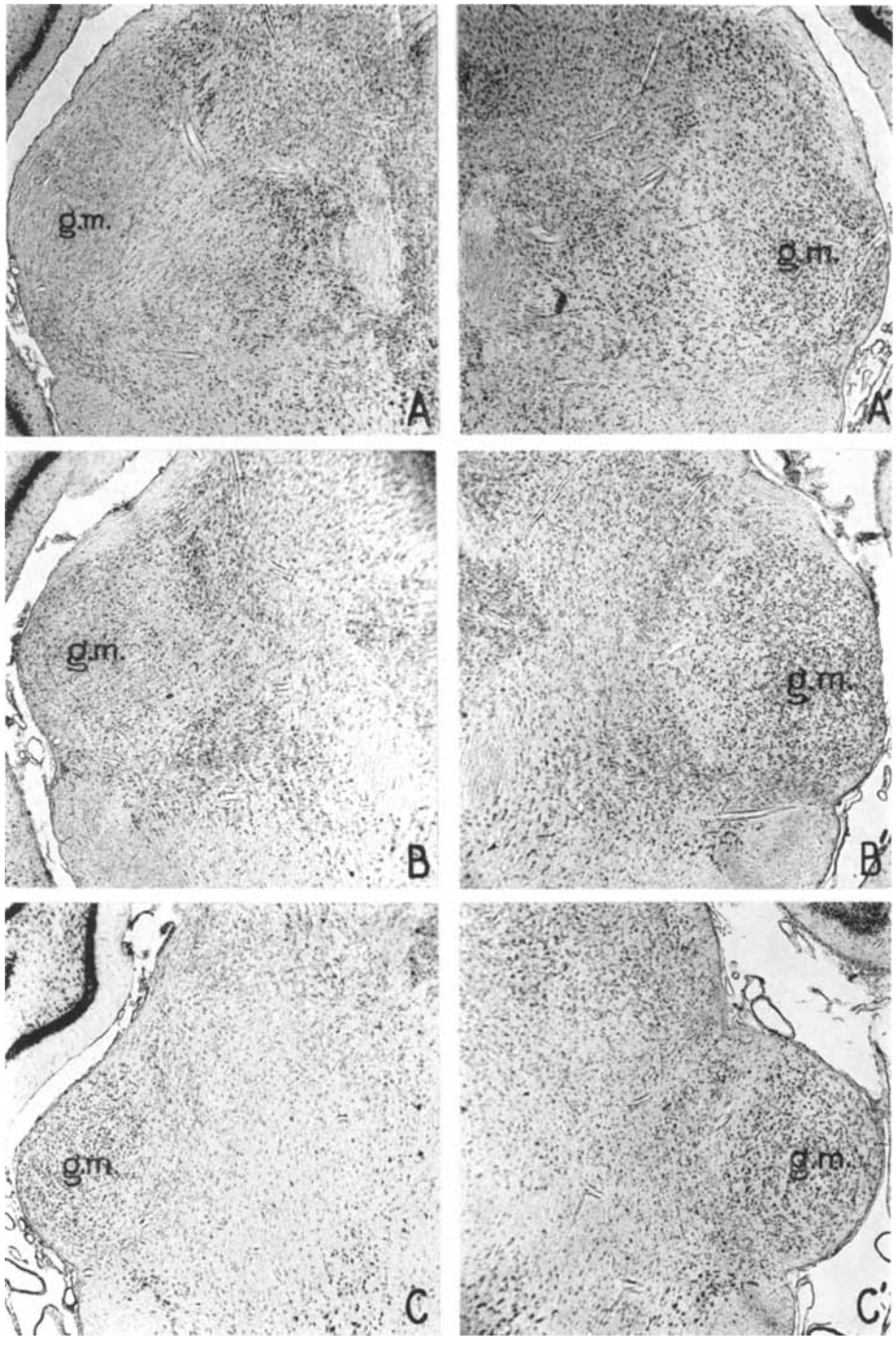

med.dor.
ant.dor.
ant.dor.
lat.
lat.
lat.ant.
ant.vent.
ant.med.
subp.
ant.med.
ant.vent.

PLATE 2

EXPLANATION OF FIGURE

21 Photomicrographs of three levels through the medial geniculate nucleus of case 1, in rostrocaudal order, corresponding roughly to figure 1, sections 8, 9, and 10, showing the severity of cell loss after hemidecortication in the anterior two-thirds of the nucleus, and the sparing of the caudal pole (c). Side of hemidecortication shown at left; normal side at right. × 15.


g.m.
A
g.m.
A'
g.m.
B
g.m.
B'
g.m.
C
g.m.
C'