Experimental-anatomical Studies on the Cortical Connections of the Anterior Thalamic Nuclei in Carnivores

By

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There has been a diversity of opinion as to whether the anterior thalamic nuclei send fibers to the cerebral cortex. According to Sachs ('09) and Glorieux ('29) the anterior nuclei connect with the caudate nucleus. On the contrary, Clark ('32) described their projections to the cingular gyrus, denying the connections with the caudate nucleus. Many later authors, such as Clark and Boggon ('33), Takeuti ('33-'35), Okuma et al. ('35), Waller ('34, '37), Bodian ('42), and Rose and Woolsey ('48), agreed with Clark. Rose and Woolsey studied the cortical connections of the anterior thalamic nuclei experimentally in detail, and found an intimate relation between the cortical connections of the anterior nuclei and the cytoarchitecture of the cerebral cortex. They concluded that the anteromedial nucleus projects to the anterior limbic region, the anteroventral nucleus to the cingular field, and the anterodorsal nucleus to the retrosplenial area. Rose and Woolsey's view is now accepted by many authors. On the other hand, it has been reported that the anterior thalamic nuclei degenerate after extensive ablation of the lateral cortex (Walker, '35; Waller, '38; Papez, '38; Hirasawa and Okano, '38; Kanagai, '60). Consequently, it may be said that the anterior nuclei project not only to the medial cortex but also to the lateral cortex. However, it has not yet been determined to what lateral cortical area they project.

The present study attempts to elucidate the exact distribution of corticopetal fibers from the anterior thalamic nuclei of the cat and dog by means of the retrograde degeneration method and the Marchi technique.

Material and Methods

The material utilized in this study consisted of 12 cases. In cases 1 and 2 the left lateral cortex of adult dogs were almost completely ablated. After a survival period of 36 days (case 1) and 20 days (case 2), the brains were fixed in 90 per cent alcohol, embedded in celloidin, cut serially at 30 to 35 μ in the transverse plane, and stained with the Nissl method.

Using young dogs (19 days after birth) cases 3 and 4 were prepared in similar manner. However, in these cases the survival period after operation was 89 days (case 4) and 349 days (case 3).

In cases 5 to 10 various circumscribed lesions were made in the medial cortex (limbic area) of adult dogs. After a survival period of 24 to 38 days serial transverse sections were stained by the Nissl method, as in cases 1 to 4.

Cases 11 and 12 were prepared according to the Marchi method using adult cats. In case 11 the dorsolateral part of the anteroventral nucleus was destroyed by electrocoagulation with the aid of the Horsley-Clarke stereotaxic apparatus. After a survival period of 21 days the brain was removed, fixed in 10 per cent neutral formalin, treated with the Marchi technique, and cut serially at 40 μ in the transverse plane.

In case 12 the lesion was placed in the anterodorsal nucleus, involving partly the nucleus anteroventralis, nucleus medialis dorsalis, stria medullaris, and only slightly the nucleus lateralis dorsalis and nucleus parataenialis. The survival period and staining procedure of this case were identical with those of case 11.

As control the Nissl and the Pal-Weigert series of the normal adult cat and dog were also prepared.

Observations

Case 1

In this case the experiment was performed on an adult dog, and the lesion occupied most of the left lateral cortex except for the lower part of the temporal lobe and the anterior and inferior parts of the frontal lobe. Survival after operation was 36 days.

On the operated side retrograde degeneration is found in the anterior thalamic nuclei in addition to the other neothalamic nuclei. Of all of the anterior nuclei the nucleus anteroventralis shows the

most remarkable changes.

The nucleus anterodorsalis shows fairly marked degeneration, but is only slightly affected in rostral levels. Its cells stain less deeply than normal but can hardly be said to present chromatolysis. There is slight gliosis throughout its extent. These changes become somewhat heavier as one passes caudally. In transverse sections the ventromedial part shows a little more pronounced changes than the dorsolateral part. In its caudalmost levels the nucleus anterodorsalis undergoes marked cell loss with gliosis, and contains a number of remaining cells, some of which show chromatolysis.

The nucleus anteroventralis shows marked degeneration, but in rostral levels it undergoes little change. In this nucleus, gliosis and the pale stain of cells are found, but no cells were counted as typical chromatolysis. This nucleus is composed of parvocellular and magnocellular parts. The former appears to be more severely changed than the latter, showing moderate cell loss. The magnocellular part is composed largely of pale stained cells with an admixture of very deeply stained elements, and shows marked gliosis. Traced caudally, these changes become more conspicuous. Gliosis stands out prominently in the magnocellular part and is also found in the parvocellular part, though to a less striking degree. In the latter part some chromatolytic cells are seen. In the caudalmost levels the nucleus anteroventralis shows striking gliosis and marked cell loss which is pronounced in the parvocellular part and the dorsal portion of the magnocellular part.

Degeneration in the nucleus anteromedialis is relatively light compared with that seen in above-mentioned nuclei, and is confined to its dorsolateral part. In rostral levels the dorsolateral part is almost free from degeneration except for its lateral and dorsolateral portions, which show a decrease in intensity of staining of cells with a slight gliosis. Traced caudally this part shows moderate cell loss, especially in its lateral portion. The remaining cells in this part appear to be somewhat smaller than normal control, and do not present the appearance of chromatolysis.

Case 2

In this case the lateral cortex of the left cerebral hemisphere of the dog were ablated extensively as in case 1. The postoperative survival period was 20 days.

The anterior thalamic nuclei of the operated side is only slightly

atrophic, and their changes are somewhat different from those in case 1 with respect to chromatolysis and gliosis. The chromatolytic changes are found more conspicuously but gliosis is less evident; this may be due to the short survival period in this case.

In rostral levels the chromatolytic cells are found sporadically within the nucleus anterodorsalis, especially its dorsolateral part. As one passes caudally, the chromatolytic cells increase in this nucleus, notably in the ventromedial part. In the nucleus anterodorsalis gliosis is seen only slightly.

The nucleus anteroventralis shows less evident chromatolytic reaction and somewhat more conspicuous gliosis as compared with the nucleus anterodorsalis. Proceeding caudally, in this nucleus the cells showing the chromatolytic reaction increase in number. The parvocellular part shows almost the same changes as seen in the magnocellular part, in which fewer chromatolytic cells are found than in the former.

The degeneration of the nucleus anteromedialis is regarded as slight, and confined to its dorsolateral part. Traced caudally, this part shows a little more marked degeneration. Chromatolytic cells are scattered among the practically unchanged cells.

Case 3

In this case a young dog (19 days after birth) was used. The left lateral cortex was ablated in a almost similar manner as in cases 1 and 2, but the anterior extremity of the lesion extended as far as the anterior part of the anterior sylvian gyrus. The survival period of this case was 349 days.

The anterior thalamic nuclei of the operated side are quite atrophic and show marked changes, which are represented by marked cell loss and striking gliosis.

The nucleus anterodorsalis is very atrophic. In rostral levels this nucleus shows cell loss and striking gliosis, both of which are found particularly in the dorsolateral portion. Traced caudally, this nucleus, especially its dorsolateral and ventromedial parts, undergoes more conspicuous changes, showing marked cell loss and striking gliosis. Most of remaining cells are stained lightly, but some are stained very deeply.

The nucleus anteroventralis is also very atrophic and shows great changes, which is particularly conspicuous in the parvocellular part. In rostral levels this nucleus is greatly reduced, and under-

goes cell loss accompanying the deep stain of remaining cells and gliosis. Caudally it shows heavier changes, chief of which is marked cell loss. Within its caudal part there appear small, oval to rounded polygonal, and very lightly stained cells in addition to deeply stained cells which are larger than those in rostral levels.

The nucleus anteromedialis shows fairly marked changes in the dorsolateral part, which is markedly atrophic and undergoes extensive cell loss, though less evident than the nucleus anteroventralis. As its caudal extremity is reached, this part becomes nearly normal except for the presence of slight gliosis. The ventromedial part does not show any noticeable changes.

Case 4

Using a young dog (19 days after birth) the extensive cortical ablation was performed, its extent being almost the same as in the case 3. The postoperative survival period was 89 days.

The anterior thalamic nuclei of the operated side are atrophic, and shows cell loss and gliosis, but these changes are somewhat lighter than those of case 3.

The nucleus anterodorsalis shows marked changes, except for its rostralmost part where only slight changes are found. Traced caudally this nucleus, especially the dorsolateral part, undergoes marked cell loss. In caudal levels the cells remain only in its midportion. Gliosis is relatively light as compared with that in case 3.

The nucleus anteroventralis undergoes severe changes, especially marked cell loss. In its caudal part the changes are more conspicuous than the rostral part, showing more noticeable cell loss and the pale stain of remaining cells. Gliosis is also apparent in caudal levels. In this case the magnocellular and parvocellular parts are similarly changed.

The nucleus anteromedialis shows slight changes which are represented by gliosis and cell loss, and are confined to the dorsolateral part.

Case 5

The dorsal part of the left medial cortex of an adult dog was ablated unilaterally. The dorsal limit of the lesion corresponded to the margo superior, and the ventral limit ran just ventral to the splenial sulcus. The survival period of this case was 28 days.

On the operated side the nucleus anterodorsalis shows no marked changes, but its caudal part undergoes slight cell loss, with a number of pale and small cells remaining. Gliosis can hardly be detected. Cell loss is found especially in the most dorsolateral and ventromedial parts, in both of which chromatolytic cells are also found, though few in number.

Text-fig. 1. Diagrams showing the extent of cortical lesions:
A, case 5; B, case 6.

Of all the anterior thalamic nuclei, the nucleus anteroventralis shows the most remarkable changes, which are found mainly in the magnocellular part and the dorsal portion of the parvocellular part. Changes found in this nucleus are represented by cell loss, a decrease in intensity of staining and chromatolysis of remaining cells, and gliosis. As one passes caudally, these changes become conspicuous.

The nucleus anteromedialis is almost free from degeneration.

Case 6

In this case the ablation of the medial cortex of an adult dog was performed in similar fashion as in case 5. However, this case is different from case 5 in that the lesion extends anteriorly to the upper part of the superior frontal gyrus beyond the cruciate sulcus.

The findings obtained from this case are in principle similar to those from case 5. Therefore, there is no need to give any detailed description.

Case 7

The anterior cingular region (area 24 and the posterior part of area 32 of Gurewitsch et al.) of an adult dog was ablated unilaterally. After a survival period of 28 days the brain was treated in a similar manner as above-mentioned cases.

The nucleus anterodorsalis of the operated side shows no noticeable changes, except for slight gliosis.

The nucleus anteroventralis is only slightly affected. In its rostral part the pale stain of component cells and gliosis are visible, though to a lesser degree. On the contrary the caudal part shows scarcely any noticeable changes other than gliosis.

Of all the anterior nuclei the nucleus anteromedialis shows the most remarkable degeneration. In the rostralmost part severe changes, such as cell loss, a decrease in intensity of staining and chromatolysis of remaining cells and gliosis, are found. These changes are observed mainly in the dorsolateral part, and to a lesser degree in the ventromedial part. Traced caudally, the changes become restricted to the dorsolateral part, in which the changes are conspicuously visible. In caudal levels the dorsolateral part undergoes fairly marked cell loss, containing a number of chromatolytic cells. In the most caudal part the degeneration becomes lighter, though gliosis is conspicuous.

Case 8

The lesion of this case was confined to the left posterior cingular and retrosplenial regions (area 23, 31 and most of area 30 of Gurewitsch et al.). The experiment was performed on an adult dog, and the survival after operation was 32 days.

Retrograde changes can be observed in all of the anterior nuclei on the operated side, especially noticeable in the nucleus anteroventralis.

In rostral levels the nucleus anterodorsalis is only slightly changed. On approaching its middle levels this nucleus shows fairly marked changes, such as cell loss and scattered chromatolysis. These changes are evident in its dorsolateral and ventromedial parts. Gliosis is not evident, but is more or less observed in the caudal part.

The nucleus anteroventralis is severely affected. In rostral levels this nucleus, especially the parvocellular part, shows moderate cell loss. As its middle levels are reached, it becomes degenerated everywhere except for the ventral portion of the magnocellular part, showing fairly marked cell loss and scattered chromatolysis with slight gliosis. In caudal levels this nucleus shows much more evident changes than in rostral levels.

The nucleus anteromedialis is most slightly affected. Its dorso-

Text-fig. 2. Diagrams showing the extent of cortical lesions:

A, case 7; B, case 8; C, case 9; D, case 10.

lateral part, especially in caudal levels, represent scattered cell loss, a decrease in intensity of staining and smaller size of cells, and slight gliosis.

Case 9

Using an adult dog the lesion was placed in the left retrosplenial region corresponding to the posterior part of area 30 and a part of area 19 of Gurewitsch et al. The survival after operation was 24 days.

On the operated side the nucleus anterodorsalis shows very scattered chromatolysis even in its rostralmost levels. Traced caudally, this nucleus becomes fairly markedly degenerated and shows cell loss, chromatolysis, the pale stain and small size of residual cells. These changes are conspicuous in its ventromedial part. In the most caudal part the degeneration is rather slight.

Fairly severe changes are also found in the nucleus anteroventralis except for its rostralmost part in which only a little degeneration is seen. This nucleus is affected mainly in the dorsal portion of the parvocellular part and the medial and dorsomedial portions of the magnocellular part. In these parts there is moderate cell loss with gliosis. In caudal levels the nucleus anteroventralis becomes more conspicuously degenerated, showing marked cell loss,

a decrease in intensity of staining and small size of remaining cells, and marked gliosis. Its ventrolateral portion, however, does not show any degeneration except for slight gliosis.

The nucleus anteromedialis is slightly affected. In middle and caudal levels the dorsolateral part of this nucleus shows slight cell loss, a decrease in intensity of staining and very scattered chromatolysis of remaining cells, and slight glial reaction.

Case 10

In this case the experiment was performed on an adult dog. The lesion destroyed a small part of the left medial cortex, extending from the posterior part of the retrosplenial region to the most posterior part of the splenial gyrus (a part of area 30 and a small part of area 17 of Gurewitsch et al.). The survival period of this case was 15 days.

The nucleus anterodorsalis of the operated side is severely affected. Although this nucleus is only slightly changed in rostralmost levels, it undergoes marked degeneration in most of its extent. Within this nucleus chromatolytic cells are found abundantly everywhere, particularly in the dorsolateral and ventromedial parts. In addition to chromatolysis, the pale stain of cells and slight gliosis are also found.

In the nucleus anteroventralis the degeneration is relatively light compared to that seen in the nucleus anterodorsalis and is found in most of its extent except for the rostralmost part. Chromatolytic cells are scattered in the parvocellular as well as the magnocellular part, but are very few in the ventral and ventrolateral portions of the latter part. Gliosis is only suggested.

The nucleus anteromedialis is not affected.

Case 11

In this case the lesion was produced by electrocoagulation in the dorsolateral part of the left nucleus anteroventralis of an adult cat with aid of the stereotaxic apparatus. After survival of 21 days the brain was treated by the Marchi technique.

Tracing the Marchi series from rostral to caudal, the degenerated granules are found at the rostralmost level of the corpus callosum of the operated side. In this level the granules are scattered in the white matter lying just dorsal to the corpus callosum. From there the granules radiate toward the gyrus rostralis, the cortex of

Text-fig. 3. Diagram showing the extent of the electorolytic lesion of the nucleus anteroventralis in case 11.

which is free from granules. The gyrus fornicatus contains a few granules, but the gyrus splenialis is devoid of degenerated granules.

At the level of the rostral part of the lamina terminalis, the degenerated granules become more concentrated along the dorsal surface of the corpus callosum. The degenerated granules in the gyrus rostralis increase somewhat in number, and are directed toward the cortex. The gyrus fornicatus contains a number of granules which do not reach the cortex. A few number of granules can be followed to the gyrus splenialis and also to the gyrus lateralis in which the granules are very few in number.

In sections through the caudalmost part of the optic chiasm, the gyrus rostralis is about to disappear, being replaced by the gyrus fornicatus. The degenerated fibers increase considerably in number, and form a dense mass along the dorsal surface of the corpus callosum. From this mass the degenerated fibers can be traced to the gyrus fornicatus, in which the granules are found not only in the white matter but also in the deepest layer of the cortex. Within the gyrus splenialis and gyrus lateralis the degenerated granules are found in the white matter and also in the deepest layer of the cortex. Moreover, the white matter of the gyrus suprasylvius medius contains very few granules.

At the middle level of the anterior thalamic nuclei, the small lesion is seen in the most dorsolateral part of the nucleus antero-

ventralis. This corresponds to the rostral pole of the electrolytic lesion. The degenerated granules are concentrated around the lesion, especially in the nucleus anteroventralis, stratum zonale and stria terminalis. The degenerated fibers swing laterally, dorsolaterally and then dorsomedially to reach the gyrus fornicatus, gyrus splenialis, gyrus suprasplenialis and gyrus lateralis. The amount of degenerated granules is most abundant in the gyrus fornicatus, and least abundant in the gyrus lateralis. Within these gyri a few granules can be recognized not only in the white matter but also in the deepest layer of the cortex. Moreover, very few granules can be followed into the white matter of the gyrus suprasylvius medius. The mamillo-thalamic tract is not degenerated in this case.

In sections through the caudalmost part of the nucleus antero-dorsalis, degenerated granules are found distributed most abundantly. The nucleus lateralis dorsalis contains scattered degenerated granules which may correspond to the fibers connecting the nucleus anteroventralis with nucleus lateralis dorsalis and nucleus pulvinaris. In this level the degenerated granules are also found in the stria terminalis and the stratum zonale covering the nucleus lateralis dorsalis dorsally and dorsolaterally. From there the degenerated fibers sweep dorsomedially looping about the caudate nucleus. The degenerated fibers go to the gyrus fornicatus, gyrus splenialis, gyrus suprasplenialis and gyrus lateralis. The degenerated granules are found most abundantly in the gyrus fornicatus. A lesser amount of granules is seen in the gyrus splenialis and suprasplenialis and a few granules are also visible in the gyrus lateralis. Within these gyri the granules are present not only in the white matter but also in the deepest layer of the cortex. Moreover, careful observation reveals that the gyrus suprasylvius medius contains very few degenerated granules in the white matter.

At the rostral level of the dorsal nucleus of the lateral geniculate body, the degenerated granules decrease in number all over the section. The granules can hardly be seen within the nucleus pulvinaris, but are scattered in the stria terminalis, and to a lesser degree in the stratum zonale lying dorsal to the nucleus pulvinaris. The degenerated granules in the stria terminalis are continuous with the fibers which swing dorsomedially around the tail of the caudate nucleus. At this level the degenerated granules are found in the gyrus fornicatus, gyrus splenialis, gyrus suprasplenialis and gyrus lateralis, though fewer in number than the previous section.

Also very few of the degenerated fibers are visible in the gyrus suprasylvius medius.

At the section passing through the middle of the posterior commissure the degenerated granules are fewer in number, especially in the gyrus splenialis, gyrus suprasplenialis and gyrus lateralis. Within the gyrus suprasylvius medius the granules can hardly be observed.

Text-fig. 4. Diagrams showing the cortical projections of the nucleus anteroventralis in case 11.
A, medial aspect; B, dorsal aspect.

In levels of the splenium corporis callosi, the degenerated granules are few in number even in the gyrus fornicatus. The gyrus splenialis, gyrus suprasplenialis and gyrus lateralis contain very few granules.

As the caudal pole of the corpus callosum is reached, the degenerated granules decrease greatly in number. Even in the gyrus fornicatus the number of granules are very few, especially in its ventral part.

In this case the lesion is not confined to the nucleus anteroventralis, involving a small part of the nucleus lateralis dorsalis. Consequently, the findings described above cannot be excluded from the influence of destruction of the nucleus lateralis dorsalis. However, it may be said that the fibers from the nucleus anteroventralis project mainly to the posterior-cingular region, some fibers to the medial cortex above the splenial sulcus and very few fibers to the lateral cortex, gyrus lateralis and gyrus suprasylvius medius.

Case 12

This case was also treated by the Marchi method using an

adult cat. The lesion was placed in the left nucleus anterodorsalis except its rostralmost part, involving partly the nucleus anteroventralis, nucleus medialis dorsalis, stria medullaris, nucleus lateralis dorsalis and nucleus parataenialis. The survival period of this case was 21 days.

Text-fig. 5. Diagram showing the extent of the electrolytic lesion of the anterodorsal part of the thalamus in case 12.

On tracing the Marchi series from rostral to caudal, the degenerated granules appear in the white matter of the cerebral hemisphere of the operated side at the rostralmost level of the corpus callosum. At this level degenerated granules are found fairly abundantly in the white matter of the gyrus rostralis, and are scattered in the gyrus splenialis, but are not present in the gyrus fornicatus. Moreover, they are scattered along the dorsal surface of the corpus callosum.

At the rostral level of the lamina terminalis the distribution of degenerated granules is almost the same as the previous section. In this level, however, the degenerated fibers are observed more abundantly and are also found in the gyrus fornicatus in addition to the gyrus rostralis and gyrus splenialis. In the dorsomedial periphery of the internal capsule lying close to the caudate nucleus, only a few degenerated granules are scattered.

At the rostral level of the anterior commissure, the degenerated granules are found most profusely in the gyrus rostralis. A fair

number of the granules are seen in the gyrus fornicatus, and only a few granules in the gyrus splenialis.

As the rostralmost level of the anterior thalamic nuclei is approached, the degenerated granules as well as fibers gradually increase in number. Especially the stria medullaris, and the surrounding and limiting medullary laminae of the anterior thalamic nuclei contain an abundant amount of degenerated granules. In the nucleus anteroventralis and nucleus anterodorsalis the degenerated fibers of passage are abundantly observed. These degenerated fibers can be followed laterally, and then swing dorsomedially along the ventral and lateral margin of the caudate nucleus. At this level the degenerated granules are found fairly abundantly in the gyrus fornicatus, to a lesser degree in the gyrus splenialis, gyrus suprasplenialis and gyrus lateralis.

At the caudalmost section of the nucleus anteroventralis the electrolytic lesion is seen most conspicuously. The lesion destroys the whole extent of the nucleus anterodorsalis, involving the most dorsal part of the nucleus dorsomedialis and the medialmost part of the nucleus anteroventralis. The degenerated granules are found abundantly in the stratum zonale, and to a lesser degree in the nucleus lateralis dorsalis and the nucleus anteroventralis. These granules as well as fibers pass laterally to reach the stria terminalis. Looping around the tail of the caudate nucleus, they course dorsomedially and finally run chiefly into the gyrus fornicatus, to a lesser amount into the gyrus splenialis, gyrus suprasplenialis and gyrus lateralis, and only a few into the gyrus suprasylvius medius.

At the level of the centre médian nucleus of L u y s, scarcely any degenerated granules were seen in the dorsal thalamus, but a fair amount of granules is present in the stria medullaris. The degenerated fibers coursing to the cortex are smaller in number than in the previous section, and are found mainly in the white matter of the gyrus fornicatus, and to a lesser amount in the gyrus splenialis and gyrus suprasplenialis. The gyrus lateralis and gyrus suprasylvius medius can hardly be said to contain any degenerated granules.

At the section through the splenium corporis callosi the degenerated granules as well as fibers decrease in number, and are found only in the gyrus fornicatus.

At the level a short distance caudal to the corpus callosum, the degenerated granules are found in the gyrus fornicatus, especially

in the retrosplenial region in which the granules decrease ventrally in number. As one passes caudally, the granules become restricted to the retrosplenial region.

This case is not appropriate for analysis of the cortical connections of the anterior thalamic nuclei, because the lesion is not confined to the anterior nuclei. However, it is worthy of note that in this case the retrosplenial region contains a large number of degenerated granules.

Discussion

Formerly, it was thought that the anterior thalamic nuclei project to the subcortical centers rather than to the cerebral cortex. Sachs ('09) studied the fiber connections of the thalamic nuclei using the cat and monkey, and stated that the nucleus dorsalis magnus corresponding to the nucleus anteroventralis does not send fibers to the cerebral cortex, but connects with the head of the caudate nucleus. Glorieux ('29) investigated the connections of the thalamic nuclei of the dog experimentally by means of the Marchi method, and arrived at a similar conclusion.

On the other hand, von Monakow ('95) reported that the anterior thalamic nuclei may project to the anterior and middle parts of the "erste äussere Windung." Minkowski ('24) believed the connections of these nuclei were with the frontal cortex. Clark ('32) studied the connections of the anterior nuclei of the rat by means of the Marchi method and found that the nucleus anteroventralis connects with the cingular area of the neopallium by the thalamofugal fibers. Thereafter, Clark and Boggon ('33) concluded from their experiment on the cat using the Marchi method that the anterior nuclei are related to the entire extent of the gyrus cingularis, and send no fibers to the caudate nucleus. Moreover, they found cell atrophy of the anterior nuclei in cases having lesions placed in the gyrus cingularis. Takeuti ('33-'35) studied the fiber connections of the anterior thalamic nuclei of the rabbit by the Marchi technique, and found that the anterior nuclei (nucleus anterodorsalis and nucleus anteroventralis) contribute fibers to the area retrosplenialis angularis (Rsg) of Brodmann; the lateral part of the anterior nuclei projects to the posterior half of area Rsg β , the medial upper part to the posterior part of Rsg α and to Rsg γ , and medial lower part to the anterior part of Rsg α ,

β . However, he did not state definitely on what cortical area each anterior nucleus depends. Okuma et al. ('35) traced the cortical connections of the nucleus anteromedialis, and stated that this nucleus connects with the cingular region.

Recently, Rose and Woolsey ('48) described the relations existing between the cytoarchitecture of the cortex and the cortical connections of the anterior thalamic nuclei, and concluded that the nucleus anterodorsalis projects to the retrosplenial area, the nucleus anteroventralis to the cingular field, and the nucleus anteromedialis to the anterior limbic region. The findings in the present paper (cases 7 to 10) agree in essentials with theirs.

In cases having lesions in the medial cortex above the splenial sulcus (cases 5 and 6), the nucleus anteroventralis is fairly severely degenerated, and the nucleus anterodorsalis is only little changed. The lesions of these cases graze the dorsal margin of the gyrus fornicatus, so that the findings mentioned above are not excluded from the influence of grazed lesions in the gyrus fornicatus. However, it may be said that the nucleus anteroventralis and a part of the nucleus anterodorsalis are considered to project also to the gyrus splenialis and gyrus suprasplenialis. The findings of case 11 (Marchi series) confirms more or less this view. Akimoto et al. ('56) followed the retrograde degeneration of the thalamic nuclei of the cat after lesions of the various parts of the cerebral cortex, and stated that the nucleus anteroventralis and nucleus anterodorsalis project to the gyrus cinguli and gyrus splenialis. This statement is roughly consistent with our findings.

It has long been known that the anterior thalamic nuclei show marked retrograde degeneration after extensive ablation of the lateral cortex. Waller ('38) traced the retrograde degeneration after hemidecortication in the cat, and stated that the nucleus anteroventralis represents complete degeneration but the nucleus anterodorsalis and nucleus anteromedialis degenerate only partially.

The experiments concerning the ablation of the lateral cortex on young animals have been undertaken in considerable detail by some authors. Hirasawa and Okano ('38) removed in new-born rabbits the lateral cortex extensively, and traced the ensuing changes after 3 to 10 months. They stated that after 10 months the nucleus anteroventralis and nucleus anterodorsalis disappear almost completely and the nucleus anteromedialis shows severe changes. Kanagai ('60) reported the ablation experiment of the lateral cortex

in a young dog, and stated that the nucleus anterodorsalis, nucleus anteroventralis, and nucleus anteromedialis pars dorsolateralis exhibit fairly heavy changes, but the nucleus anteromedialis pars ventromedialis is less severely changed.

As mentioned above, the anterior thalamic nuclei are thought to depend not only on the medial cortex but also on the lateral cortex. However, no author has presented definitely as yet to what lateral cortical areas these nuclei project. Von Monakow supposed that the cortical region corresponding to the anterior thalamic nuclei may be the "erste äussere Windung," but this cannot be regarded as definitely established. Cases 11 and 12 of the present paper are considered to contribute in some degree to clarification of this problem. These cases, especially case 11, show that the nucleus anteroventralis, especially its dorsalateral part, probably sends fibers to the lateral cortex, gyrus lateralis and gyrus suprasylvius medius, in addition to the medial cortex.

The precise localisation of the fiber connections of the nucleus anteroventralis has not been fully known. The extensive ablation experiments of the lateral cortex in this paper reveal that this nucleus is almost wholly affected, especially more markedly in the parvocellularis than in the magnocellular part. In cases destroying the gyrus splenialis and gyrus suprasplenialis, it degenerates for the most part except its ventral portion. The ablations of the gyrus fornicatus result also in the degeneration of the nucleus anteroventralis, except for its ventral and ventrolateral parts. In these cases the parvocellular part appears to be affected more severely than the magnocellular part. From findings mentioned above it may be said that the whole extent of the nucleus anteroventralis connects with the cerebral cortex, but its ventral part, especially that of the magnocellular part, sends only a few fibers to the cerebral cortex and is considered to connect predominantly with the mamillothalamic tract. Case 11, having the lesion in the dorsolateral part of the nucleus anteroventralis, shows no degeneration in the mamillothalamic tract. Takasu ('58) described the myeloarchitecture and fiber connections of the dog thalamus using the normal myelin preparations, and stated that the parvocellular part of the nucleus anteroventralis appears to have nothing to do with the mamillothalamic tract.

Lashley ('41) studied the cortical projections of the thalamic nuclei in the rat, and concluded that all of the dorsal thalamic

nuclei with the exception of the medial geniculate body have sharply localized topographical projections. Rose and Woolsey ('48) described the minimal overlap of the cortical connections of the thalamic nuclei. According to our observations, however, it can be stated that the cortical projection fields of the anterior thalamic nuclei overlap not only with each other, but also with the other projection systems.

As the above-mentioned cortical ablation experiments indicate, the anterior thalamic nuclei are apparently cortical dependencies. According to von Monakow the cortical dependencies are recent phylogenetically. However, it has been thought that the anterior thalamic nuclei are old phylogenetically. If so, von Monakow's view is incompatible in this respect. Hirasawa and Okano ('38), based on their ablation experiments on the rabbit, concluded that the "direkte Grosshirnanteile" is not always recent phylogenetically, and that in this respect von Monakow's view needs substantial revision. The question now arises; are the anterior thalamic nuclei really old phylogenetically? A series of comparative-anatomical and embryological investigations carried out in our laboratory reveal that the nucleus anterodorsalis, nucleus anteroventralis and a large part of the nucleus anteromedialis are regarded as relatively recent when viewed from the standpoint of vertebrate phylogeny. It is not until the mammalian stage in phylogeny that these nuclei appear, although a large part of these nuclei show a regression in the ascending mammalian scale. Consequently, von Monakow's view appears to us quite justified.

Summary

1. The retrograde degeneration in the anterior thalamic nuclei of the dog following localized ablations of the limbic cortex indicates that the nucleus anteromedialis projects mainly to the anterior cingular region, the nucleus anteroventralis to the posterior cingular region, and the nucleus anterodorsalis to the retrosplenial region.

2. By ablation of the medial cortex above the sulcus splenialis of the dog, the nucleus anteroventralis and nucleus anterodorsalis, especially the former, show retrograde degeneration.

3. When the lateral cortex of the cerebral hemisphere is almost completely ablated unilaterally in adult and young dogs, considerably severe changes are found in the nucleus anteroventralis, nucleus

anterodorsalis and nucleus anteromedialis pars dorsolaterals. This fact may indicate that these nuclei project also to the lateral cortex.

4. On studying the Marchi preparations of the cat in which the electrolytic lesion has been made in the dorsolateral part of the nucleus anteroventralis, the degenerated fibers can be traced mainly to the posterior cingular region, a part of the anterior cingular region and the anterior part of the retrosplenial region. In addition to these regions, a small number of degenerated fibers can be followed also to the gyrus splenialis, gyrus suprasplenialis, gyrus lateralis and gyrus suprasylvius medius.

5. The cortical projection fields of the anterior nuclei overlap more extensively than generally assumed. These projection fields overlap not only with each other, but also with the other projection systems.

6. From the above-mentioned findings it may be concluded that the anterior thalamic nuclei send fibers mainly to the limbic cortex, but a few fibers run dorsalward to the medial cortex above the sulcus splenialis, and the lateral cortex, especially the gyrus lateralis and the gyrus suprasylvius medius.

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Explanation of Plates

- Fig. 1. Case 1. Transverse section through the middle level of the nucleus anteroventralis. Nissl stain. $\times 45$.
 Fig. 2. Case 1. Transverse section through the caudal level of the nucleus antero-dorsalis and nucleus anteroventralis. Nissl stain. $\times 45$.
 Fig. 3. Case 2. Transverse section through the middle level of the nucleus antero-dorsalis and nucleus anteroventralis. Nissl stain. $\times 45$.
 Fig. 4. Case 3. Transverse section through the rostral level of the anterior thalamic nuclei. Nissl stain. $\times 23$.
 Fig. 5. Case 3. Transverse section through the middle level of the anterior thalamic nuclei. Nissl stain. $\times 23$.
 Fig. 6. Case 3. Transverse section through the caudal level of the anterior thalamic nuclei. Nissl stain. $\times 23$.
 Fig. 7. Case 4. Transverse section through the rostral level of the anterior thalamic nuclei. Nissl stain. $\times 23$.
 Fig. 8. Case 4. Transverse section through the caudal level of the anterior thalamic nuclei. Nissl stain. $\times 23$.
 Fig. 9. Case 5. Transverse section through the rostral level of the nucleus antero-dorsalis and nucleus anteroventralis. Nissl stain. $\times 40$.
 Fig. 10. Case 5. Transverse section through the caudal level of the nucleus antero-dorsalis and nucleus anteroventralis. Nissl stain. $\times 40$.
 Fig. 11. Case 6. Transverse section through the caudal level of the nucleus antero-dorsalis and nucleus anteroventralis. Nissl stain. $\times 40$.
 Fig. 12. Case 7. Transverse section through the rostral level of the anterior thalamic nuclei. Nissl stain. $\times 18$.
 Fig. 13. Case 7. Transverse section through the middle level of the anterior thalamic nuclei. Nissl stain. $\times 23$.
 Fig. 14. Case 8. Transverse section through the middle level of the anterior thalamic nuclei. Nissl stain. $\times 40$.
 Fig. 15. Case 8. Transverse section through the caudal level of the anterior thalamic nuclei. Nissl stain. $\times 40$.
 Fig. 16. Case 9. Transverse section through the middle level of the anterior thalamic nuclei. Nissl stain. $\times 23$.
 Fig. 17. Case 11. Transverse section through the cerebral hemisphere at the rostral level of the nucleus anteroventralis. Marchi method. $\times 8$.
 Fig. 18. Case 12. Transverse section through the cerebral hemisphere at the level slightly caudal to the splenium corporis callosi. Marchi method. $\times 8$.

Abbreviations

Ad	Nucleus anterodorsalis
Am	Nucleus anteromedialis
Av	Nucleus anteroventralis
Cc	Corpus callosum
Cf	Corpus fornicis
Gf	Gyrus fornicatus
Gl	Gyrus lateralis
Gsp	Gyrus splenialis
Gpsm	Gyrus suprasylvius medius
Gssp	Gyrus suprasplenialis
Hip	Hippocampus
Ladl	Nucleus laminaris, pars dorsolateralis
Ld	Nucleus lateralis dorsalis
Lv	Nucleus lateralis ventralis
Md	Nucleus medialis dorsalis
Nc	Nucleus caudatus
Pt	Nucleus parataenialis
Sm	Stria medullaris
Ssp	Sulcus splenialis
Vl	Ventriculus lateralis

Fig. 2.

Fig. 4.

Fig. 1.

Fig. 3.

Fig. 6.

Fig. 8.

Fig. 5.

Fig. 7.

Fig. 10.

Fig. 12.

Fig. 9.

Fig. 11.

Fig. 14.

Fig. 16

Fig. 13.

Fig. 15.

Fig. 18

Fig. 17