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LIMIT AND ORGANIZATION OF THE CORTICAL PROJECTION FROM THE MEDIAL THALAMIC NUCLEUS IN MONKEY

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THIRTEEN FIGURES

The projection of n. medialis dorsalis on the anterior part of the frontal cortex of primates is established, but evidence concerning extent and internal arrangement of this nuclear projection provides an insufficient guide to finer cortical parcellation. In the course of experiments designed primarily to investigate the effects on behavior of partial frontal ablation, we have analyzed retrograde thalamic degeneration in 40 cerebral hemispheres of Macaca mulatta. Our results, supplemented by those of other investigators, indicate the topology of thalamo-cortical correspondence.

On the basis of its cellular appearance, Walker ('38, '40) divides the nucleus into a lateral paralamellar part, an anteromedial magnocellular part, and a main parvicellular part. He assigns the projection of the paralamellar and lateral parvicellular portions to the cortex anterior to the arcuate sulcus; the magnocellular and medial parvicellular parts to the orbital surface. He finds that the paralamellar division projects more posteriorly than the lateral parvicellular part, but he is unable to differentiate between magnocellular and me-

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dial parvicellular projections. In addition, he suggests that a dorsoventral organization is maintained in the projection from thalamus to cortex. The relationship of the anteroposterior nuclear plane to the cortex remains uncertain.

Mettler ('47) also finds an organized projection of n. medialis dorsalis on the frontal cortex, and interprets this relationship in terms of Brodmann's cortical areas. The most rostral portion of the nucleus projects to area 12; somewhat more caudally, the lateral portions of the nucleus project to areas 9 and 10, the ventromedial to area 11, and the dorsomedial to area 12; still more caudally, the entire medial portion projects to area 11, the central parts to areas 9 and 10, and the most lateral portions to area 8; at the level of the beginning of n. centrum medianum, only the dorsomedial part of the nucleus projects to area 11, while the rest of the nucleus projects to areas 10, 9, and 8, medial to lateral, respectively. At the caudal tip of the nucleus, only a projection to area 8 remains. In general, Mettler's conclusions appear to agree with those of Walker, with the following exceptions: whereas Walker does not specify any change in the dorsoventral arrangement of fibers from the posterior part of the nucleus, Mettler suggests that the dorsal part of this projection goes to the orbital cortex, and the ventral part to the lateral cortex. Moreover, Mettler places the origin of the projection to the cortex within and around the arcuate sulcus entirely in the lateral nuclear group, whereas Walker assigns it to the paralamellar portion of n. medialis dorsalis.

In order to clarify the precise relation of the orbital cortex to the nucleus, von Bonin and Green ('49) made a series of orbital and ventrolateral cortical lesions in the macaque. The ventrolateral lesions encroached upon the orbital surface and resulted in gliosis in the central and ventral portions of the nucleus. The caudal extremity of the nucleus was undegenerated. Their small orbital lesions failed to produce retrograde changes in the thalamus. They conclude that they "have confirmed . . . the thalamo-cortical relations between 'orbital cortex' and (the medioventral part of the) medial thalamic

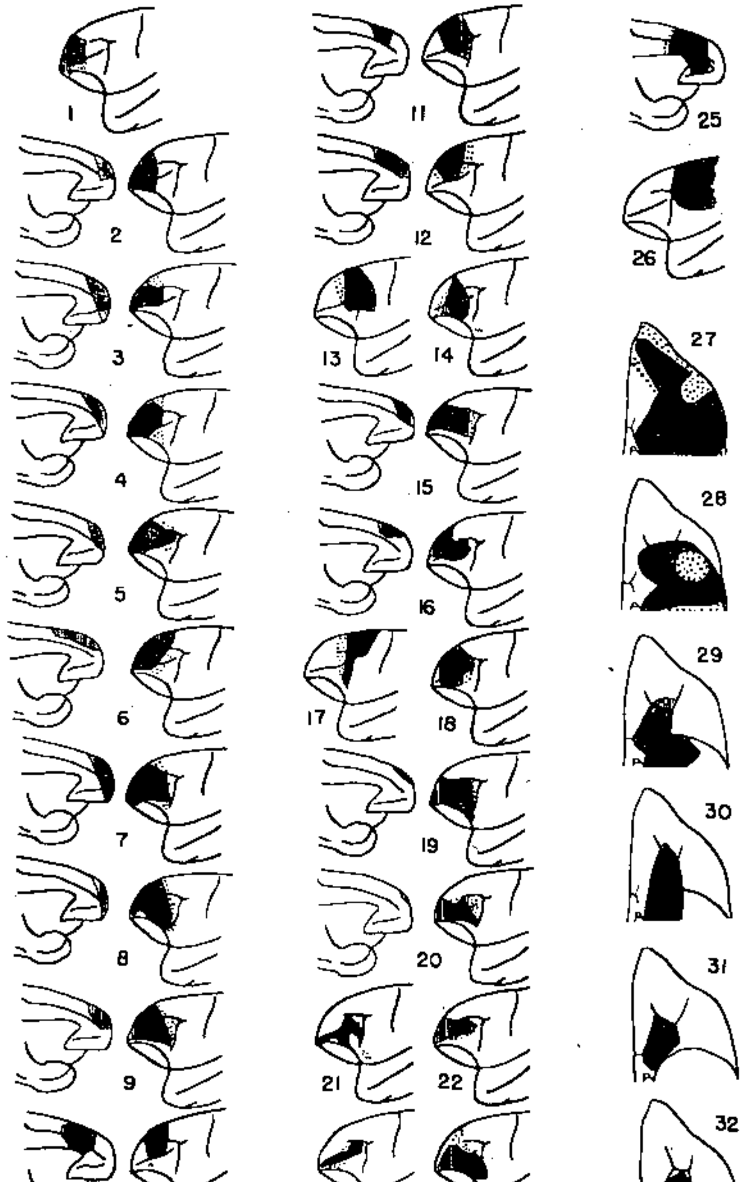

Fig. 1 Representation on standard diagrams of frontal lesions resulting in degeneration in n. medialis dorsalis. Whenever a surface is not represented, the extent of lesion on this surface is negligible. Black indicates complete, stippling partial destruction. The lesion in hemisphere no. 26 includes some of the anterior bank of the sulcus arcuatus.

nucleus." The absence of any thalamic changes following the lesions restricted to the orbital surface casts some doubt, however, on the existence of a thalamic projection to this cortex.

METHODS

Forty cerebral hemispheres from 20 monkeys (Macaca mulatta) were used. Two months to two years prior to sacrifice, surgical ablations of frontal cortex had been made. The brains were fixed in 10% formalin, dehydrated in alcohols, and embedded in nitrocellulose. They were cut in serial coronal sec-

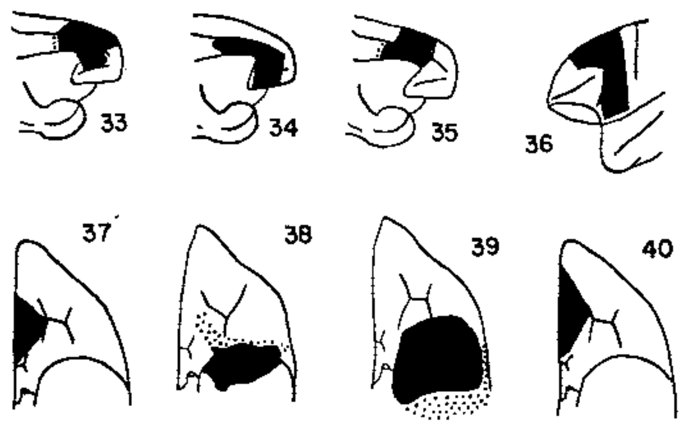

Fig. 2 Representation of frontal lesions resulting in no degeneration of n. medialis dorsalis. The lesion in hemisphere no. 36 does not extend to the anterior bank of the sulcus arcuatus.

tions at 25 μ or 50 μ thickness. Sections 500 μ apart were stained with thionin and used to make medial, ventral, and lateral reconstructions of the cortical surface.

The reconstructed lesions were transposed to a "standard" brain diagram, as described by Chow ('50) (figs. 1 and 2). The position and extent of retrograde degeneration in the thalamus were plotted on drawings of the appropriate sections (figs. 3 and 4). For the purpose of analysis of thalamic degeneration, we adopted the divisions of n. medialis dorsalis outlined by Walker: paralamellar, parvicellular, and anteromedial magnocellular. We further subdivided the parvicellular portion into 4 quadrants by dorsoventral and mediolateral lines, and examined the nucleus in its anterior, middle, and posterior parts (table 1). "Anterior" was considered to be that part of the nucleus rostral to the level of n. centrum medianum. "Posterior" was considered to be caudal to the level of the beginning of the habenular complex. All cortical lesions which caused degeneration in a given subdivision of the nucleus were superimposed, and the area of overlap was plotted. All lesions which did not cause degeneration in the selected subdivision were superimposed. Any area of encroachment of this composite area on the area of overlap of lesions causing degeneration was eliminated from the latter. The residual area of overlap defines the minimal extent of the cortical projection field of this part of the nucleus. These procedures were followed for each of the 14 subdivisions of the n. medialis dorsalis.

RESULTS

Our data show that the projection of n. medialis dorsalis is concentrated in and around the frontal pole, sulcus principalis, sulcus arcuatus, and sulcus orbitalis. They exclude cortex caudal to the sulcus arcuatus, medial to the sulcus orbitalis, and caudal to a line joining the anterior extremities of the sulci rostralis and callosomarginalis.

The paralamellar portion of the nucleus projects to the cortex of the anterior bank of the sulcus arcuatus, especially along its inferior limb (fig. 5). The anteromedial magnocellular part projects to the rostral portion of the posterior orbital gyrus (fig. 6). Within the parvicellular division, the entire lateral portion projects along the sulcus principalis. The caudal extremity of the lateral parvicellular nucleus projects just dorsal to the caudal extremity of the sulcus principalis (fig. 7); the rest of the lateral parvicellular projection lies rostrad and somewhat ventrad (figs. 8, 9). The projection from the medial parvicellular portion of the nucleus reaches the anterolateral orbital cortex and the ventral and medial pole (figs. 10, 11). The most caudal fibers of this projec-

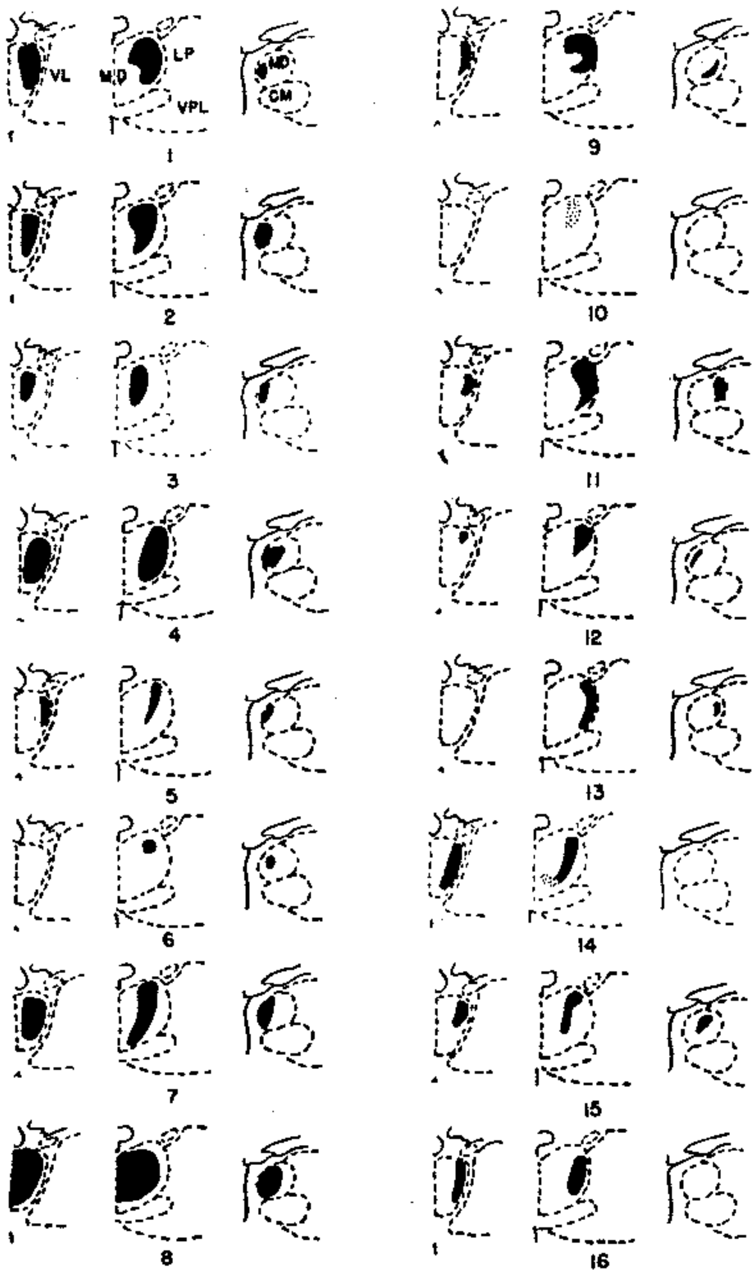

Figure 3

Fig. 3, Fig. 4 Representation of thalamic degeneration in anterior, middle, and posterior sections of the n. medialis dorsalis. Numbers correspond to number of hemisphere diagrammed in figure 1. Degenerated zones are indicated by solid black.

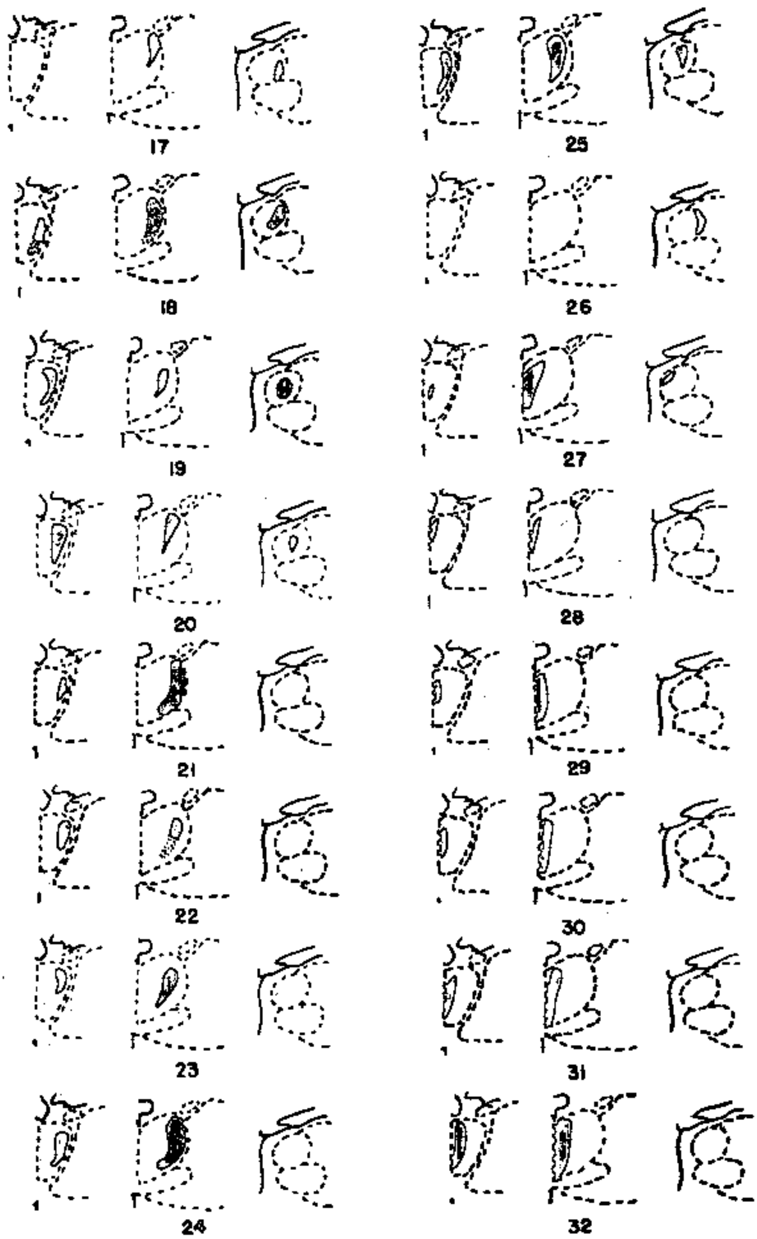

Figure 4

tion end on the medial surface somewhat dorsally to the remainder (fig. 12).

Comparison of figures 8 and 9 and of figures 10 and 11 reveals no distinctions between anterior and middle parts of the

TABLE 1

Numbers indicate hemispheres. Plus indicates degeneration present in portion of n. medialis dorsalis; minus indicates no degeneration found in this portion. D indicates doubtful degeneration. (Paralam., paralamellar; LS, lateral parvicellular; MS, medial parvicellular; ML, medial magnocellular.)

	PARALAM.	LS Ant.	LS Mid.	LS Post.	MS Ant.	MS Mid.	MS Post.	ML
1.	—	+	+	—	—	—	+	—
2.	—	+	+	—	—	—	+	—
3.	—	+	+	—	+	+	+	—
4.	—	+	+	—	+	—	+	—
5.	—	+	+	—	—	—	+	—
6.	—	+	+	—	—	—	+	—
7.	—	+	+	—	+	—	+	—
8.	—	+	+	—	+	+	+	+
9.	+	—	+	+	—	—	—	—
10.	—	—	D	—		—	—	—
11.	+	+	+	+	—	—	—	—
12.	—	+	+	—	—	—	+	—
13.	+	—	+	+	—	—	—	—
14.	—	+	+	—	—	—	—	—
15.	—	+	+	+	—		—	—
16.	—	+	+	—	—	—	—	—
17.	+	—	+	+	—	—	—	—
18.	—	+	+	+	—	—	—	—
19.	—	+	+	+	—	—	—	—
20.	—	+	+	+	—	—	—	—
21.	+	+	+	—		—	—	—
22.	—	+	+	—	—	—	—	—
23.	—	+	+	—	—	—	—	—
24.	+	+	+	—	—	—	—	—
25.	—	+	+	+		—	—	—
26.	—	—	—	+	—	—	—	—
27.	—	—	—	—	+	+	+	+
28.	—	—	—	—	+	+	—	+
29.	—	—	—	—	+	+	—	+
30.	—	—	—	—	+	+	—	+
31.	—	—	—	—	+	+	—	+
32.	—	—	—	—	+	+	—	+

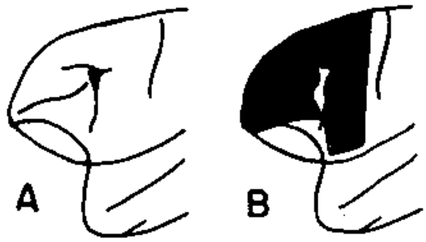

Fig. 5 A Area of overlap of lesions resulting in degeneration of the paralamellar portion of the n. medialis dorsalis. The partial destruction of cortex in hemisphere no. 9 was included to make this diagram.

Fig. 5 B Composite area of lesions resulting in no degeneration in this portion of the nucleus. The partial destruction of cortex in hemisphere no. 15 was included to make this diagram. The two areas A and B show no coincidence except for a small section just caudal to the posterior extremity of the sulcus principalis.

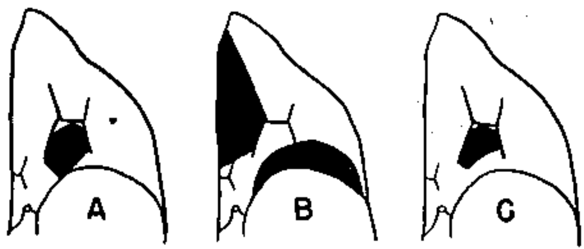

Fig. 6 A Area of overlap of lesions resulting in degeneration of the medial magnocellular portion of the n. medialis dorsalis. Hemisphere no. 8 was not included and considered an exception.

Fig. 6 B Composite area of lesions resulting in no degeneration of this portion of nucleus.

Fig. 6 C The area resulting when the overlap of B on A is subtracted from A. This diagram represents the minimal area of the projection field of the medial magnocellular portion of the n. medialis dorsalis.

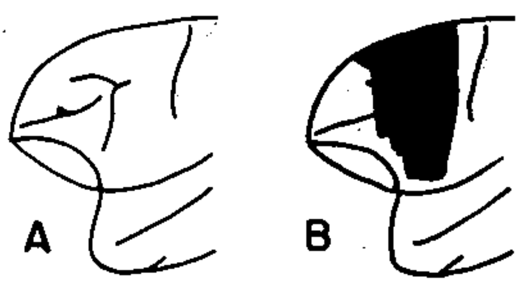

Fig. 7 A Area of overlap of lesions resulting in degeneration of lateral small celled portion of n. medialis dorsalis in anterior sections.

Fig. 7 B Composite area of lesions resulting in no degeneration of this portion of the nucleus. The two areas (A and B) do not coincide.

Fig. 8 The area of overlap of all lesions resulting in degeneration of the lateral small celled portion of n. medialis dorsalis in middle section. All lateral surface lesions anterior to the arcuate sulcus resulted in degeneration of this portion of the nucleus.

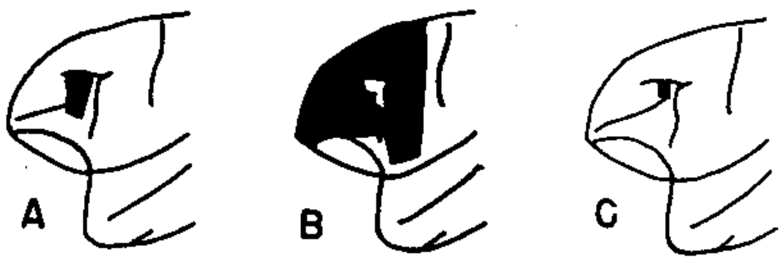

Fig. 9 A The area of overlap of all lesions resulting in degeneration of the lateral small celled portion of n. medialis dorsalis in posterior sections. Number 6 was excluded and considered an exception. The partial destruction of cortex in hemisphere no. 9 was included in obtaining this area.

Fig. 9 B The composite area of all lesions resulting in no degeneration of this portion of the nucleus. Hemispheres no. 5 and no. 23 were not included and considered exceptions.

Fig. 9 C The area resulting when the overlap of B on A is subtracted from A. This diagram represents the minimal area of the projection field of the lateral small celled portion of the n. medialis dorsalis in posterior sections.

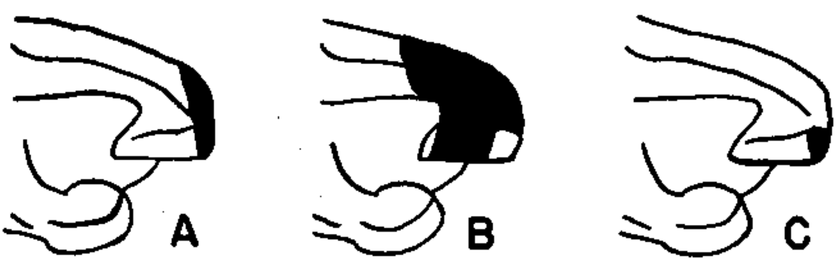

Fig. 10 A Area of overlap of lesions resulting in degeneration of the medial small celled portion of the n. medialis dorsalis in anterior sections.

Fig. 10 B Composite area of lesions resulting in no degeneration of this portion of nucleus.

Fig. 10 C The area resulting when the overlap of B on A is subtracted from A. This diagram represents the minimal area of the projection field of the medial small celled portion of the n. medialis dorsalis in anterior sections.

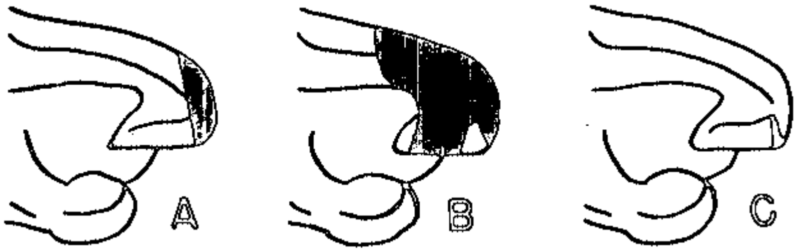

Fig. 11 A Area of overlap of lesions resulting in degeneration of the medial small celled portion of the n. medialis dorsalis in middle sections.

Fig. 11 B Composite area of lesions resulting in no degeneration of this portion of the nucleus.

Fig. 11 C The area resulting when the overlap of B on A is subtracted from A. This diagram represents the minimal area of the projection field of the medial small celled portion of the n. medialis dorsalis in middle sections.

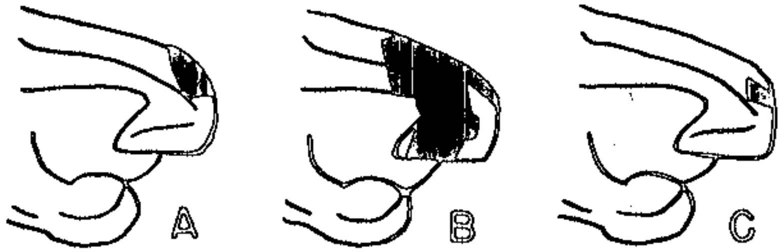

Fig. 12 A Area of overlap of lesions resulting in degeneration of the medial small celled portion of the n. medialis dorsalis in posterior sections.

Fig. 12 B Composite area of lesions resulting in no degeneration of this portion of the nucleus.

Fig. 12 C The area resulting when the overlap of B on A is subtracted from A. This diagram represents the minimal area of the projection field of the medial small celled portion of the n. medialis dorsalis in posterior sections.

parvicellular projection. Likewise, no distinction appeared between the projection fields of dorsal and ventral divisions of this projection.

DISCUSSION

On the basis of our material the projection of n. medialis dorsalis in monkey is bounded by the superior and inferior limbs of the sulcus arcuatus posteriorly, the sulcus orbitalis ventrally, and a line connecting the anterior ends of the sulci callosomarginalis and rostralis medially. Thus, only the cortex of the superior and inferior frontal gyri, lateral and posterior orbital gyri, and the polar cap (medially, ventrally, and laterally) receives such projection. Within these limits an orderly arrangement of fibers exists as has been stated. Our

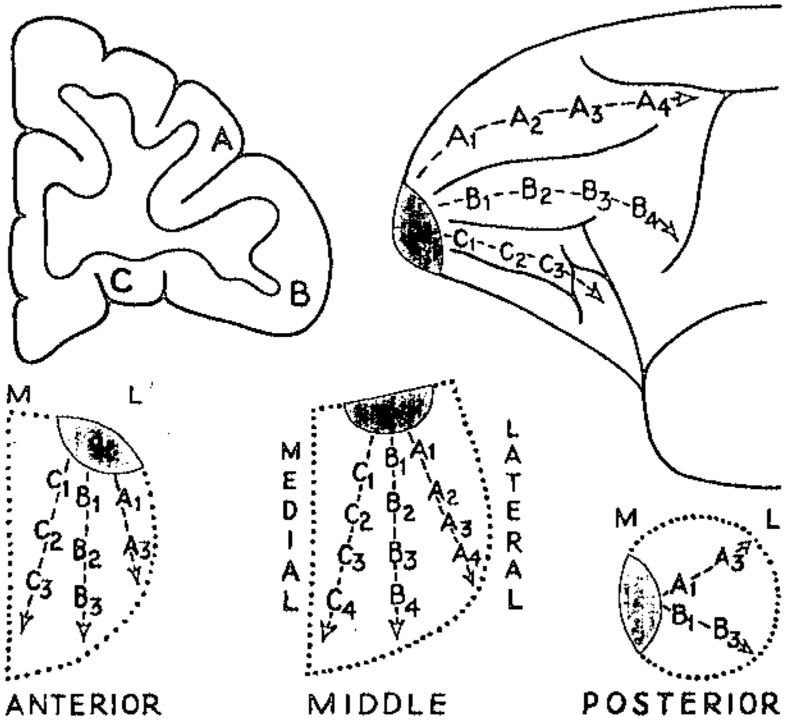

Fig. 13 Diagrammatic representation of the nuclear origin and cortical termination of the projections of the n. medialis dorsalis in monkey demonstrating the axial arrangement from eccentric core to periphery in anterior, middle, and posterior sections of the nucleus and corresponding cortical axes extending caudally from the frontal pole.

results, supplemented by those of others when necessary, suggest the following conception of this arrangement.

The frontal polar cap is represented throughout the length of the nucleus. In anterior and middle sections, the polar cap is represented centrally in the dorsal half; in posterior section, in the medial half. Our evidence suggests that the lateral portion of the parvicellular projection centers on the sulcus principalis. Moreover, it confirms Walker's conclusion that the most lateral part of the nucleus, the paralamellar portion, projects to the anterior bank of the arcuate sulcus. The results of ventrolateral lesions reported by von Bonin and Green, together with our own which do not involve this region, indicate that the central part of the nucleus projects to the ventrolateral cortex, centering on the lip of the hemisphere. Our data further confirm all previous reports that the orbital cortex receives a projection from the medial parvicellular portion. Extending Walker's conclusion that at least part of the anteromedial magnocellular part of the nucleus projects to the orbital surface, we find that this part degenerates completely when the lesions include the anterior part of the posterior orbital gyrus.

These results make possible a systematization of the relationship of the n. medialis dorsalis to the frontal cortex: if in anterior and middle sections we consider the thalamic origin of the polar projection as a dorsally placed eccentric core, and draw radiating lines from this core, the lines radiating medially describe the successive origin of the projection on the cortex from the polar cap along the sulcus orbitalis; the lines radiating ventrally in the nucleus describe the origin of the projection along the lateroventral edge of the hemisphere; whereas the lines radiating laterally in the nucleus describe the origin of the projection along the sulcus principalis. In posterior thalamic sections, the core is medial rather than dorsal; lines radiating ventrolaterally describe the origin of the projection along the sulcus principalis, whereas lines radiating dorsolaterally describe the origin of the projection on the cortex between the pole and the superior ramus of the sulcus arcuatus.

From these considerations it is apparent that the rostrocaudal axis of the n. medialis dorsalis is undifferentiated with respect to the origin of the cortical projection. On the other hand, the rostrocaudal dimension of the frontal cortex is reflected in the axial distribution from core to periphery in the nucleus. The circumferential dimension of the frontal cortex described by a line parallel to the sulcus principalis and sulcus orbitalis, moving in a lateroventral to medial direction, corresponds to the circumferential distribution described by a line in the nucleus moving in a lateral to ventral to medial to dorsal direction around the core. Thus, an anteroposterior file of cells projects to a focal neuronal aggregate in the cortex.

Recently, psychosurgical material has become available for study of the frontal projections from n. medialis dorsalis in man. Conclusions are based almost exclusively on section of the white matter of the frontal lobe rather than on cortical ablations. Comparison of the systematic organization of the projections in man with that of monkey shows general agreement with respect to limit and gross relationship of the medial projection to orbital cortex and lateral projection to the lateral cortex. There is difference of opinion as to the presence and origin of the projection to the human frontal pole. Some investigators doubt if it exists at all (McLardy, '50); others assign the origin of its projection to the central portion of the nucleus (Freeman and Watts, '47). McLardy's interpretation perhaps implies that the cortex homologous to monkey's frontal pole is anterolaterally placed in man. Other discrepancies appear, however. McLardy's material permits him to state that the medial magnocellular projection terminates in the medial half of the orbital cortex. This conclusion differs from our findings in monkey that the medial orbital gyrus receives no such projections. There is more agreement with respect to the projection to the posterior orbital cortex. In both monkey and man only the rostral portions receive a projection, the more caudal (and less granular) parts do not. A further point of difference is that McLardy finds in his material no retrograde degeneration in the rostral tip of n. medialis dorsalis, nor in the dorsal part of this nucleus in middle sections, nor of its medial magnocellular portions. This finding might be attributed to the surgeon's inability to sever all fibers fanning out to a highly convoluted cortex. Finally, the anteroposterior axial organization which McLardy believes to characterize the human projection cannot be discerned in our material. Conversely, there is no evidence presently available that the simian dorsoventral or "core-periphery" arrangement of the projection exists in man. More restricted frontal lesions in both monkey and man will be necessary before the reasons for these discrepancies can be clarified.

SUMMARY

Forty cerebral hemispheres (Macaca mulatta) with partial ablations of frontal cortex were serially sectioned and reconstructed. Retrograde degeneration in the thalamus was analyzed in relation to locus and extent of cortical lesion.

The projection of n. medialis dorsalis is concentrated in and around the frontal pole, sulcus principalis, sulcus arcuatus, and sulcus orbitalis. Throughout the greater extent of the nucleus, the most lateral parts project to the anterior bank of the sulcus arcuatus; the most medial parts, to the posterior orbital gyrus; the most ventral parts, to the ventrolateral edge of the hemisphere; the most dorsal parts, to the pole. In posterior sections, the polar representation is medial in the nucleus, and that of the dorsolateral cortex is lateral.

Thus a rostrocaudad axis in the cortex corresponds in the nucleus to lines radiating peripherally from the polar representation. That circumference of cortex described by a line moving in an arc extending from above the sulcus principalis around the ventrolateral edge of the hemisphere to the sulcus orbitalis corresponds in the nucleus to a line moving in an arc in a lateral → ventral → medial → dorsal direction and centering on the polar representation. An anteroposterior file of nuclear cells, therefore, projects to a focal neuronal aggregate in the frontal cortex.

Similarities and discrepancies with published conclusions regarding the projection of the n. medialis dorsalis in man are noted.[3]

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