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CORTICAL PROJECTION OF THE THALAMIC VENTROLATERAL NUCLEAR GROUP IN MONKEYS[1]

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EIGHT FIGURES

The ventrolateral nuclear group of the dorsal thalamus in the monkey consists of the large cell mass lying between the external and internal medullary laminae rostral to the pulvinar. Fibers from these nuclei terminate on a sector occupying the middle portion of the dorsolateral cerebral cortex. Previous investigators using, in most instances, the method of retrograde degeneration, have determined the cortical projection of various nuclei within this group (Clark and Boggon, '35; Mettler, '47; Walker, '38). Their results show general agreement; however, their published maps differ in detail with respect to the topical arrangement of the projection of separate nuclei. Furthermore, except in the case of n. ventralis posterior, the details of topographical arrangement of the projection to cortex from within an individual nucleus have not been worked out.

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In order to determine the organization of the projection of the entire ventrolateral nuclear mass it is necessary to delimit consistently the various subdivisions. A survey of studies by Crouch ('34), Aronson and Papez ('34), Clark ('32), Krieg ('48), Olszewski ('52), and Walker ('38) on the normal configuration of the Macaque's thalamus indicates that for the ventrolateral nuclear group such delimitation may be difficult.[3] These authors differed from each other in the number of nuclei, their boundaries, designations, and cytoarchitectural characteristics. Thus an attempt to reach conclusive delimitations based on these 6 studies was not successful. An example serves to illustrate some of these difficulties: Crouch reported the largest number of nuclei in the rostral portion of the ventrolateral group; there were 5 nuclei (n. ventralis anterolateralis, n. ventralis anteromedialis, n. ventralis intermedius, n. lateralis anteromedialis, n. lateralis anterolateralis), some with additional subdivisions. Le Gros Clark recognized only two nuclei, one situated medially, and the other laterally (n. ventralis, pars anteromedialis, n. ventralis, pars anterolateralis). Walker and Krieg also listed only two nuclei, but divided them rostro-caudally (n. ventralis anterior, n. ventralis lateralis). Aronson and Papez, and Olszewski considered the anterior tip as one nucleus, but made a mediolateral division at the posterior part. The last author's area X was not identified by any of the others but was included as part of both the n. ventralis lateralis and the n. ventralis posterior.

Table 1 lists the name of the various nuclei and their cell types as described in the 6 studies cited. In constructing this table Walker's study was used as a standard.[4] The subdivision and borderline nuclei and their descriptions were not included. It is apparent that there is some disagreement about the cellular structures of these nuclei. Sometimes myeloarchitecture was used in addition to cytoarchitecture. Again,

[3] The older literature on the monkey's thalamus was reviewed by Aronson and Papez ('34) and Walker ('38).

[4] Walker's designations of the separate nuclei were adopted in later discussions.

TABLE 1

Summary of descriptions used by various authors to delimit the subdivisions of the ventrolateral nuclear group as determined by cytoarchitecture

WALKER	OLSZEWSKI	KRIEG	LE GROS CLARK	ARONSON AND PAPEZ	CROUCH
n. ventralis anterior large, polygonal, well-stained cells in clusters.	*(n. ventralis anterior)* medium-sized, multipolar, plump, rather lightly stained cells in clusters. *(pars magnocellularis)* large dark cells, densely arranged.	*(n. ventralis, pars anterior)* large, dark cells, very widely separated.	*(n. ventralis, pars anteromedialis)* large, polygonal cells, evenly distributed. *(n. ventralis, pars anterior lateralis)* smaller, flattened or fusiform cells in irregular groups.	*(n. ventralis, pars anterior)* large cells in widely separated clusters.	*(n. ventralis anterolateralis) (n. ventralis anteromedialis) (n. ventralis intermedius)*
n. ventralis lateralis medium-sized, polygonal, fairly well-stained cells.	*(n. ventralis lateralis pars oralis)* round or oval, plump, dark cells in large clusters. *(n. ventralis lateralis, pars caudalis)* large, multipolar, plump, slightly light cells, uniformly scattered.	*(n. ventralis, pars ventralis)* cells are denser than n. ventralis anterior, but not darker.	*(posterior parts of n. ventralis anterolateralis and n. ventralis anteromedialis)*	*(anterior parts of n. ventralis, pars lateralis)* fairly large cells scattered. *(anterior parts of n. ventralis, pars ventralis)* medium-sized deep stained cells.	*(n. lateralis anteromedialis, pars anterior, pars posterior) (n. lateralis anterolateralis)* description omitted.
n. lateralis dorsalis medium-sized, fairly well stained, pyramidal cells in compact clumps.	*(n. lateralis dorsalis)* medium-sized, polygonal cells with short dendrites and dark Nissl bodies, evenly and sparsely distributed.	*(n. lateralis doorsalis)* cells are paler than the surrounding cells.	*(n. lateralis, element A)* rather large cells, well spaced.	*(n. lateralis, pars anterior)* medium-sized cells, evenly scattered.	*(n. lateralis dorsalis)* no description.
n. lateralis posterior medium-sized, moderately well stained, cells fairly compact and regularly arranged.	*(n. lateralis posterior)* medium-sized, multipolar cells, evenly and not too densely scattered.	*(n. lateralis, pars anterior)* large, round, dark cells, widely separated, become closer together caudally.	*(n. lateralis, element B)* cells like in Ve, but smaller, less stained, less densely arranged.	*(posterior part of n. ventralis, pars lateralis, n. lateralis, pars inferior and n. lateralis, pars posterior)* medium-sized cells, evenly distributed.	*(n. lateralis posterior, pars dorsalis, pars medialis, pars lateralis)* close, evenly arranged cells. Slightly larger, lightly stained cells. Some large, dark polygonal cells.
n. ventralis posterolateralis large, well stained cells.	*(n. lateralis posterolateralis, pars oralis, pars caudalis)* very large, multipolar, plump, dark cells intermingled with smaller cells caudally.	*(n. ventralis, posterior lateralis)* cells like n. lateralis, pars anterior, but fiber arrangement is not.	*(n. ventralis, pars externa)* large, polygonal, deeply stained cells, diffusely and irregularly spaced.	*(part of n. ventralis, pars lateralis, n. ventralis, pars ventralis and possibly n. ventralis, pars arcuata)*	*(n. ventralis posterolateralis)* small and closely arranged cells.
n. ventralis posteromedialis medium-sized, well-stained, polygonal cells, compactly arranged.	*(n. ventralis posteromedialis)* small and larger cells like n. ventralis posterolateralis, pars caudalis. *(parvocellularis)* small, lightly stained cells, densely packed.	*(n. arcuatus lateralis)* larger, darker cells. *(n. arcuatus medialis)* very small, light cells.	*(n. ventralis pars arcuata)* same size cells as Ve, more irregular and fusiform, some small cells.	*(n. ventralis, pars arcuata)* lateral part — large cells, medial part — small cells.	*(n. ventralis posteromedialis)* no description.
n. ventralis inferior small, polygonal, pale-stained cells, widely scattered lonsely arranged.	*(n. ventralis posterior inferior)* medium-sized, lightly stained, polygonal cells, widely scattered.	*(n. ventralis posterior inferior)* smaller, paler cells, widely spaced.	*(n. ventralis, pars posterior)* medium-sized round, lightly stained cells.		*(n. ventralis posterainferior)* widely scattered cells.

the differences in fiber structures have not been consistently applied by all investigators to all nuclei. Thus, a consistent and universally acceptable criterion for distinguishing separate nuclei within the ventrolateral cell mass has yet to be established.

The present study attempts to determine the cortical projection plan of the ventrolateral nuclear group of monkey's dorsal thalamus. The retrograde degeneration of a large series of monkey's cerebral hemispheres with cortical lesions was examined for this purpose. Partly due to the difficulties encountered in delimiting individual nuclei based on definitions used in previous studies and partly due to the convenience of analysis, a gross topographical criterion of subdivision was adopted. This choice was more or less forced upon us: our material (Nissl stained) often showed severe degeneration which did not permit us to "decide for almost every individual cell whether it should belong to this or that nucleus," as stated by Olszewski (p. 32). It should be emphasized that we do not deny the importance of using regional structural (cellular and fibrous) characteristics to differentiate the separate nuclei of the ventrolateral group. We feel, however, because of the difficulties mentioned, that a gross method will be more useful until a more universally acceptable microstructural analysis based on a large series of monkey brains is available.

MATERIAL AND METHOD

Subdivisions of the ventrolateral nuclear group

Based on a gross topographical criterion, this nuclear group was divided into 6 principal nuclei for the present study: (a) the rostral portion anterior to the beginning of n. medialis dorsalis was considered as one nucleus and designated as V1. It is roughly equivalent to n. ventralis anterior and was further arbitrarily subdivided into a medial and a lateral half. (b) The lateral cell mass between the first appearance of n. medialis dorsalis and the first appearance of the n. centrum medianum was designated as V2 and considered

roughly equivalent to n. ventralis lateralis. It was further subdivided into quadrants: anterolateral, anteromedial, posterolateral, and posteromedial. (c) The cell mass dorsal to the level of the n. centrum medianum and extending from the appearance of this nucleus to the appearance of the n. habenularis was considered roughly equivalent to the n. lateralis posterior. It was called V3 and also subdivided into quadrants: anterolateral, anteromedial, posterolateral, and posteromedial. (d) The ventrolateral portion of the cell mass, co-extensive with the n. centrum medianum, was called V4 and considered roughly equivalent to the n. ventralis posterolateralis; it was subdivided into an anterior and a posterior half. (e) The corresponding ventromedial portion co-extensive with the n. centrum medianum was considered as V5 and is roughly equivalent to n. ventralis posteromedialis. It was subdivided into a lateral and a medial part, the latter roughly equivalent to the parvicellular partion. (f) The nucleus situated between the internal medullary lamina and the striatum zonale (n. lateralis dorsalis) did not clearly degenerate in our preparations and will therefore be omitted from further consideration.

It should be emphasized that the nuclear subdivision designated above are employed solely for pragmatic purposes. They may or may not conform to the architecturally differentiated individual nuclei as described by previous investigators.

Retrograde degeneration of the ventrolateral nuclei

The retrograde degeneration appearing in the ventrolateral nuclear group following cortical ablation was not of the same character throughout. In general, degeneration in the caudal part of this nuclear group showed fairly clear-cut boundaries with marked gliosis. On the other hand, the limits of the degenerated zones in the rostral portion, especially in the nuclear division V1, were difficult to ascertain; less gliosis and more sparsely distributed degeneration were characteristic. For the present study, no attempt was made to differ-

entiate these two types of degenerative changes. They were treated uniformly as indication of retrograde cell-atrophy resulting from the severance of axons. In a few instances, we included a category of "doubtful" degeneration. This category indicates either areas with some pale, or swollen neurons with slight gliosis, or, areas around the borders of definite degeneration which could not easily be assigned to one or another nuclear division.

MATERIAL

Forty-eight cerebral hemispheres of monkeys (Macaca mulatta) with cortical ablations of various loci and extent were used. They are a part of the collection of the Yerkes Laboratories of Primate Biology and the Laboratory of Neurophysiology, Institute of Living. We wish to thank Doctors Semmes, Berman, Robinson and Kruger for making their anatomical materials available to us in this investigation. All the animals have been used in various behavioral studies. Most of the anatomical data have been reported in detail in previous publications (Bagshaw and Pribram, '53; Blum, '51; Blum, Chow and Pribram, '50; Pribram, Kruger, Robinson and Berman, '56). Retrograde degeneration in the ventrolateral nuclear group was analyzed for the present study.

All the brains were embedded in nitrocellulose and cut into serial, coronal sections either in 50 μ or in 25 μ thickness. In the former case every 10th section, in the latter every 20th, was saved and stained with thionin. Thus the stained sections are 0.5 mm apart for all the brains. The cortical lesions of the hemisphere were reconstructed by a standard method of orthogonal projection. The thalamic degenerations were determined microscopically and plotted on drawings of the thalamus projected from the stained sections.

METHOD OF ANALYSIS

The method used to determine the cortical area receiving fibers from a particular nuclear subdivision was similar to

TABLE 2

Summary of thalamic degeneration

Numbers indicate hemispheres. Plus indicates degeneration present in a subdivision of the ventrolateral nuclear group. Minus indicates no degeneration found in this portion. D indicates doubtful degeneration or doubt as to the exact placement of the boundary of definite degeneration. V1: roughly equivalent to n. ventralis anterior; V2: roughly equivalent to n. ventralis lateralis; V3: roughly equivalent to n. lateralis posterior; V4: roughly equivalent to n. ventralis posterolateralis; V5: roughly equivalent to n. ventralis posteromedialis.

M: medial; L: lateral; A: anterior; P: posterior.

NO.	V1		V2				V3				V4		V5	
	M	L	AM	AL	PM	PL	AM	AL	PM	PL	A	P	L	M
1	+	—	+	—	+	—	+	—	—	—	—	—	—	—
2	+	—	+	+	+	—	—	—	—	—		—		—
3	D	+	+	D	+	—	—	—	—	—		—	—	—
4	+	+	+	—	—	—	—	—	—	—	—	—	—	—
5	+	+	+	—	—	—	—	—	—	—		—	—	—
6	+	+	+	—	—	+	+	—	—	—	—		—	—
7	+	+	+	D	+	D	—	—		—	—	—	—	—
8	+	+	+	+	+	+	—	—	—	—	—	—	—	—
9	—	—	—	—	—	+	—	—	—	+	—	D	—	—
10	—	—	—	+	—	+	—	—	—	—	+	—	—	—
11	—	—	—	+	—	—	—	—	—	—	+	+		—
12	—	—	+	+	+	+	+	+	—	+	+	+	—	—
13		—	—	+	—	+	—	—	—	—	—	+		—
14	—	—	+	+	+	+	+	+	—	—	+	+	—	—
15	—	—	—	+	D	+	—	+	—	—	+	—	—	—
16	—	—	—	+	—	+	—	—	—		+	—	—	—
17	—	+	+	+	+	+	+	+	—	—	+	—	—	—
18	—	+	+	+	—	+	+	—	—	—	—	—	—	
19	D	+	—	+	+	+	—	—	—	—	+			—
20	—	+	+	+	+	+	—	—	—	—	+	—	—	—
21	+	+	—	—	+	—	+	+	—	—	—	—	—	—
22	+	+	+	+	+	+	+	—	—	—	—	—	—	—
23	D	+	—	+	+	+	+	—	—		+	—	D	
24	—	—	—	—	+	+	—		—	—	—			—
25	D	+	+	+	+	+	+	D	—	—	D	—	—	—
26	—	+	+	+	+	+	+	+	—	—	+	—	+	—
27	—	—	—	D	—	+	—	—	—	—	D	D	—	—
28		—	—	—	—	—			—	—	—	—	—	+
29	—	—	—	—	—	—	—	—	—	—	—	—	+	—
30	—	—		—	—			—	—	—		—	—	+
31	—	—	—	—	—	—	—	—	—	—	—	—		+
32	—	—	—	—	—		—	—	—	—	D	+	—	—
33	—	—	—		—	—	—	—	—	—	+	+	—	
34	—	—	—	—	—	—	—	—	+	+	+	+	+	—
35	—	—	—		—	—	—	—	+	D	+	+	+	—
36	—	—	—	—	—	—	—	—	—	+	+	+	—	—
37	—	—	—		—	—	—	—	—	+	—	+	D	—
38	—	—		—	—	—	—	—	+	+	+	+	—	—
39		—	—		—	—	—	—	+	+	+	+	—	—
40	—	—	—		—	—	—	—	—	—	—	+	—	—
41	—	—	—	+	—	—	—	—	—	—	—	—	—	—
42	—		—	—	—	—	—	—	+	+	—	D	—	—
43	—	—	—	—	—	—	—	—	—	D	—	—	—	—
44	—	—		—	—	—	—	—	—	D	—	D	—	—
45	+	—	+		—	—	—	—	—	—	—		—	—
46	+	—	D	—	—	—	—		+	+	—	—	—	—
47	+	—	D	—	D	—	D	—	+	—		—	—	—
48	+	—	D	—	—	—	—	—	—	—	—	—	—	—

that described by Chow ('50). In short, it consisted of transposing the reconstructed lesions of all cerebral hemispheres to "standard" brain diagrams. In order to determine the cortical field related to a given subdivision of a nucleus, a common area was mapped by superimposing the "standard" diagrams of all cortical lesions which caused degeneration in this subdivision. The extent of lesions which did not cause degeneration were subtracted from this common area. The minimal extent of the cortical projection field of this selected subdivision was thus obtained. Using this procedure, the minimal extent of the cortical projection field was obtained for each of the 14 subdivisions of the 5 principal nuclear divisions of the ventrolateral group. From these determinations, a general plan of the projection from the entire ventrolateral nuclear group was constructed.

RESULTS

The original reconstructed cortical lesions of the 48 cerebral hemispheres together with representative sections through their thalami showing local degenerations are presented in figures 1 and 2. For easier comparison, left sided diagrams are used throughout. Table 2 summarizes the thalamic degeneration found in these brains.

Limits of the cortical field of the ventrolateral nuclear group

Based both on our earlier studies of the cortical projection of the n. medialis dorsalis, n. pulvinaris and n. anterior (Chow, '50; Pribram, Chow and Semmes, '53; Pribram and Fulton, '54) and the present series of experiments, the boundaries of the cortical sector receiving fibers from this nuclear group may be estimated as follows. Anteriorly, the sector is bound by the limbs of the arcuate sulcus; posteriorly, by a line roughly perpendicular to and bisecting the intraparietal sulcus; medially by the callosomarginal sulcus; and laterally by the Sylvian sulcus.

The cortical projection areas of individual subdivisions

The minimal extent of the cortical termination of the projection of each of the 14 subdivisions of the ventrolateral nuclei as obtained by our method is depicted on a series of "standard" brain maps (figs. 3–7). The legends of these figures describe the results. Listed are the cerebral hemispheres used to construct the diagram of minimal cortical extent of each of the projections, as well as the "exceptional" cases; i.e., those hemispheres which had lesions involving the

Fig. 3 Minimum projection fields of portions of V1, the nuclear division which corresponds roughly to the n. ventralis anterior.

A. Minimal extent of the projection field of the medial portion of V1. This area is made from a composite of the following lesions: Nos. 1, 2, 4, 5, 6, 7, 8, 21, 22, 45, 46, 47, and 48. The following hemispheres have a lesion involving this area but show no degeneration; these are considered as exceptional cases: Nos. 20 and 24.

B. Minimal extent of the projection field of the lateral portion of V1 based on hemisphere Nos. 3, 4, 5, 6, 7, 8, 14, 16, 17, 18, 19, 20, 21, 22, 23, 25, 26, and 41. No. 24 is an exceptional case.

minimal cortical area but had *no* retrograde degeneration in the corresponding nuclear subdivision. Also included are the occasional hemispheres with thalamic degeneration where the lesion did not involve the minimal area correlated with degeneration in that thalamic subdivision. Both the figures and the legends are self-explanatory, and should be read as part of the text. Special mention must be made, however, of the cortical termination of the projection of the anterior portion of the nuclear division V4. The hemispheres were divided into two groups; each yielded a 'common' area. One is predominantly precentral, the other postcentral. If these two

groups had been combined, minimal extent of the projection of this nuclear subdivision would have fallen on the central fissure. For diagrammatic purposes, therefore, we depicted instead the minimal areas obtained from both groups of hemispheres (fig. 6 A, 6 B).

The significance of the "exceptional" cases described above has previously been discussed by one of us (Chow, '50). Ex-

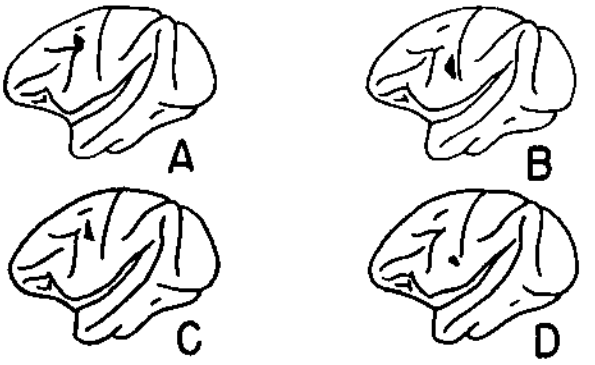

Fig. 4 Minimum projection fields of portions of V2, the nuclear subdivision which corresponds roughly to the n. ventralis lateralis.

A. Minimal extent of the projection field of the anteromedial portion of V2 based on hemisphere Nos. 3, 4, 5, 6, 7, 8, 12, 14, 17, 18, 20, 21, 22, 25, and 26. Exceptional cases are Nos. 1, 2, and 45.

B. Minimal extent of the projection field of the anterolateral portion of V2 based on hemisphere Nos. 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 22, 23, 24, 25, 26, and 41. Exceptional cases are Nos. 2, 6, and 20.

C. Minimal extent of the projection field of the posteromedial portion of V2 based on hemisphere Nos. 4, 6, 8, 12, 14, 17, 18, 19, 20, 21, 22, 23, 24, 25, and 26. Exceptional cases are Nos. 1, 2, 3, and 7.

D. Minimal extent of the projection field of the posterolateral portion of V2 based on hemisphere Nos. 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 23, 24, 25, 26, and 27. Exceptional case is No. 6.

ceptions may result from differences in the size of lesion, the survival time following surgery, the extent of damage to the depths of sulci or the extent of damage to fiber tracts underlying cortex; in addition, inaccuracies in the method of transferring to standard diagrams, and possible variations between individuals in thalamo-cortical projection must be considered. Since no systematic study has been made regarding the pos-

sible factors accounting for exceptions we are compelled, at present, to disregard them in drawing our conclusions.

The general cortical projection plan of the ventrolateral nuclear group

The results indicate, in general, that as these nuclei are defined by us, nuclear division V1 (roughly the n. ventralis

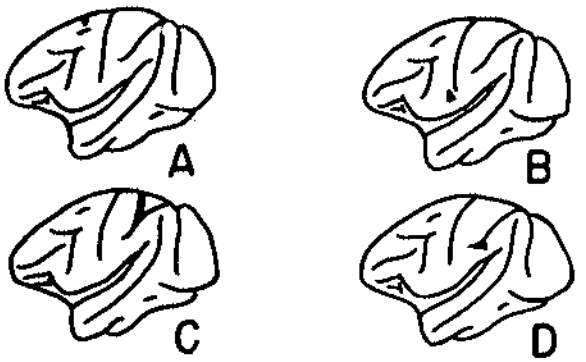

Fig. 5 Minimum projection fields of portions of V3, the nuclear subdivision which corresponds roughly to the n. lateralis posterior.

A. Minimal extent of the projection field of the anteromedial portion of V3 based on hemisphere Nos. 6, 12, 14, 17, 18, 21, 22, 23, 25, and 26. Exceptional cases are Nos. 16, 19, 20, and 24. The lesion of No. 1 does not involve this area but shows degeneration.

B. Minimal extent of the projection field of the anterolateral portion of V3 based on hemisphere Nos. 6, 9, 12, 14, 15, 17, 21, and 26. Exceptional cases are Nos. 23 and 26.

C. Minimal extent of the projection field of the posteromedial portion of V3 based on hemisphere Nos. 34, 35, 38, 39, 42, 46, and 47.

D. Minimal extent of the projection field of the posterolateral portion of V3 based on hemisphere Nos. 34, 36, 37, 38, 39, 42, and 46. Exceptional cases are Nos. 9 and 12.

anterior) projects to a cortical sector dorsal to the superior limb of the arcuate sulcus; V2 (roughly the n. ventralis lateralis) to the precentral gyrus; V3 (roughly the n. lateralis posterior) to a wide U-shaped band of cortex extending from the precentral dimple around the ventral tip of the central fissure, to the cortex on either side of the intraparietal sulcus. V4 (roughly the n. ventralis posterolateralis) sends fibers to

both banks of the central fissure. V5 (roughly the n. ventralis posteromedialis) sends fibers to the fronto-parietal operculum; its parvicellular portion projects to the anterior insula.

Figure 8 depicts the general plan of the central termination of the projection of the entire ventrolateral nuclear group based on the minimal areas described in the previous section. The anteroposterior axis of the nuclear mass corresponds, in

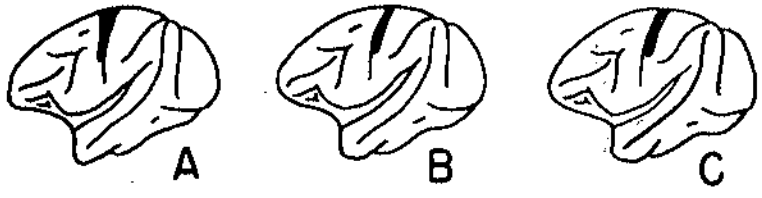

Fig. 6 Minimum projection fields of portions of V4, the nuclear subdivision which corresponds roughly to the n. ventralis posterolateralis. The hemispheres which delimit the anterior portion of V4 fall into two groups: those in which the lesions are predominantly precentral and those in which the lesions are predominantly postcentral. Minimal extent of the projection field would be directly on the central fissure if all brains are used. They are, therefore, separated for diagrammatic purposes.

A. Minimal precentral extent of the projection field of the anterior portion of V4 based on hemisphere Nos. 9, 10, 11, 12, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, and 26. Exceptional case No. 24.

B. Minimal postcentral extent of the projection field of the anterior portion of V4 based on hemisphere Nos. 33, 34, 35, 38, and 39. The lesion of No. 36 does not involve this area but shows degeneration.

C. Minimal extent of the projection field of the posterior portion of V4 based on hemisphere Nos. 11, 12, 13, 14, 32, 33, 34, 35, 38, 39, and 40. Exceptional cases are Nos. 36 and 37.

Fig. 7 Minimum projection fields of V5, the nuclear subdivision which corresponds roughly to the n. ventralis posteromedialis.

A. Minimal extent of the projection field of the lateral portion of V5 based on hemisphere Nos. 24, 27, 28, 34, and 35.

B. Minimal extent of the projection field of the medial (parvicellular) portion of V5 based on hemisphere Nos. 28, 29, 30, and 31.

general, to an anteroposterior dimension of the cortex. The mediolateral axis of nuclear division V1 describes an anteroposterior projection to the cortex. The mediolateral axis of V2 and V3 corresponds to a mediolateral dimension of the cortex. Though our material does not permit a definite determination of the cortical projection of the mediolateral axis of V4 which is roughly equivalent to n. ventralis posterolateralis, previous investigation (Walker, '38) has shown that this axis projects to a *lateromedial* dimension of the cortex. In our material the mediolateral axis of V5 also corresponds

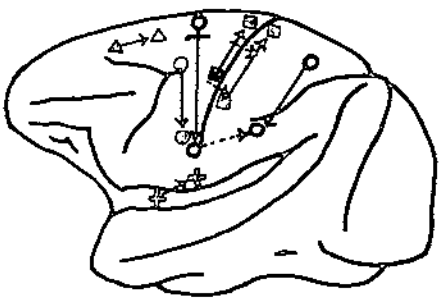

Fig. 8 Diagrammatic drawing to show the general plan of cortical projection of the ventrolateral nuclear group. Straight line with arrow indicates the medial to lateral direction within a nucleus; interrupted line with arrow, the anterior to posterior direction; solid triangle, V1, roughly the n. ventralis anterior; solid circle, V2, roughly the n. ventralis lateralis; open circle, V3, roughly the n. lateralis posterior; solid square, V4, roughly the n. ventralis posterolateralis; cross, V5, roughly the n. ventralis posteromedialis.

to a lateromedial cortical dimension. With the exception of the relation of V3, and V4 which will be discussed below, the dorsoventral axis of the nuclear mass appears to be undifferentiated with respect to the projection.

DISCUSSION

The present results confirm and extend earlier studies delineating the cortical areas which receive fibers from the thalamic ventrolateral nuclei. The retrograde degeneration found in V1 following ablations of restricted cortical areas contrasts with previous reports that the n. ventralis anterior

showed no degeneration even after hemidecortication (Walker, '38). In other primate studies, however, such degeneration does occur (Powell, '52; Mettler, '47). The finding that part of V3 sends fibers to the precentral gyrus confirms Clark and Boggon ('35) who also found that the rostral part of this nucleus (Lb in their nomenclature) projects to regions of the precentral dimple. Our data concerning V4 (roughly the n. ventralis posterolateralis) suggest that its fiber projection concentrates on the banks of the central fissure, and that *pre*central as well as postcentral cortex is involved. The separation of two cortical areas receiving fibers from two subdivisions of V5 (roughly the n. ventralis posteromedialis) supports a similar subdivision made on architectonic and electrophysiological grounds by Rose and Mountcastle for the rabbit and cat ('52): the lateral part of this nucleus projects to the frontoparietal operculum (confirming Clark ('32); Mettler ('47); Walker ('38); the medial, parvicellular part, to the cortex of the anterior insula.

The general projection plan of the ventrolateral nuclear group, in agreement with previous findings, demonstrates an orderly arrangement of projection fibers from the thalamic nuclei to the cortex. It is noteworthy that in spite of the entirely gross topographic criterion we had adopted to separate the nuclear mass, the orderly thalamo-cortical correspondence holds. As in the case of other nuclear groups, the three dimensional nuclear mass forms the projection to a two dimensional cortical surface by failure of differentiation of one axis, in this case the dorsoventral. The anteroposterior dimension of the cortical projection of the entire ventrolateral group appears to be consistent throughout. The mediolateral axis, however, describes different directions on the projection from different nuclear divisions within the group. The medial parts of V4 and V5 send fibers to cortical areas relatively lateral to the cortical areas receiving fibers from the lateral parts of these two nuclei, whereas, the reverse orientation holds for the projections of V2 and V3. These differences may most plausibly be attributed to rotation,

during embryogenesis, of V5 and the adjacent medial portions of V4 from an extreme lateral position to a ventral and medial placement. This hypothesis accounts not only for the apparent discrepancy in the directions of the mediolateral axes of the various nuclear projections but also for the singular dorsoventral differentiation between the nuclei V3 and V4 mentioned above. The possible mechanisms involved in such a nuclear reorientation will be taken up in a subsequent communication together with the question of how the general projection plan of the ventrolateral nuclei fits the results obtained for other thalamic nuclei such as n. medialis dorsalis (Pribram, Chow and Semmes, '53); n. pulvinaris (Chow, '50); n. anterior (Pribram and Fulton, '54).

SUMMARY

Forty-eight monkeys' (Macaca mulatta) cerebral hemispheres with cortical lesions of various loci and extents were serially sectioned and reconstructed. The ventrolateral thalamic nuclear group was divided topographically into 6 principal nuclei roughly equivalent to commonly accepted nuclear divisions. A graphic method was employed to analyze the retrograde degeneration in the ventrolateral cell mass (excepting the n. lateralis dorsalis) resulting from the cortical lesions.

The experimental results indicate that the cortical projection field of the ventrolateral nuclear mass is bounded anteriorly by the limbs of the arcuate sulcus; posteriorly, by a line perpendicular to and bisecting the intraparietal sulcus; medially, by the callosomarginal sulcus; and laterally, by the Sylvian sulcus. Individual nuclei send fibers to limited cortical sectors. Subdivision V1 (roughly the n. ventralis anterior) projects to an area dorsal to the superior limb of the arcuate sulcus, V2 (roughly the n. ventralis lateralis) to the precentral gyrus, V3 (roughly the n. lateralis posterior) to a U-shaped band of cortex extending from the precentral dimple around the ventral tip of the central fissure to the cortex on either side of the intraparietal sulcus. V4 (roughly

the n. ventralis posterolateralis) projects to both banks of central fissure and V5 (roughly the n. ventralis posteromedialis) to the operculum and anterior insula.

A schematic diagram is presented to show the plan of the cortical projection of the ventrolateral nuclear group. The anteroposterior axis of the entire nuclear mass corresponds to an anterior-posterior dimension of the cortex. The cells along the dorsoventral axis of a nucleus terminate on a focal neuronal aggregate in the cortex since this axis remains undifferentiated in the projection. Some apparent discrepancies with regard to the projection of the mediolateral axis of the nuclear mass (which terminate in a predominantly mediolateral dimension in the cortex) are resolved by an hypothesis which states that the medial portion of V4 and V5 has rotated to that position from an extreme lateral origin. Comparison with earlier studies was briefly noted.

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