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A RETROGRADE CELL DEGENERATION STUDY OF THE CORTICAL PROJECTION FIELD OF THE PULVINAR IN THE MONKEY

KAO LIANG CHOW[1]

Yerkes Laboratories of Primate Biology, Orange Park, Florida

ELEVEN FIGURES

The cortical projection field of the pulvinar in primates has usually been ascribed to the posterior parts of the parietal and temporal lobes, but the relatively topographical relationship between various parts of the cortex and pulvinar has not been satisfactorily determined. Experimental results based on secondary cell change in the pulvinar of monkeys following cortical ablation are not consistent. Le Gros Clark and his co-workers ('35, '36, '37) reported that the main part of the pulvinar element pB projects entirely to the lips of the posterior part of the Sylvian fissure (Polyak's posterior Sylvian receptive region, '32), and that another element, pd, projects to the peri-parastriate area. These authors held that a zone of cortex between these two separate areas is devoid of any thalamic connections and that several parts of the pulvinar, the nucleus pa and the caudal pole, do not appear to be affected by lesions in the parieto-temporal region. Walker ('38), on the other hand, favoured a much wider distribution of pulvinar projection fibers. He concluded that the medial and posterior part of the pulvinar projects to the anterior lip of the superior temporal sulcus; that the medial and anterior

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portion projects to the posterior part of the inferior parietal lobule; that the dorsolateral part projects to the posterior half of the superior parietal lobule; and that the n. pulvinaris inferior (Le Gros Clark's pd) projects to the temporo-occipital region.

Not only is there lack of agreement between these authors as to the cortical field of the pulvinar, but there are also individual cases in both Le Gros Clark's and Walker's published anatomic data which do not conform to their own conclusions. In experiment H of Le Gros Clark and Boggon ('35), the cortical lesion encroached upon the "posterior Sylvian receptive region" and yet no degeneration was found in the nucleus pB. Out of 12 cerebral hemispheres that Walker ('38) analyzed for pulvinar degeneration, at least five showed some discrepancies with his generalizations: e.g., in experiments 13A, 14B, 15A the lesions invaded the posterior part of the inferior parietal lobule and yet no degeneration was apparent in the anteromedial pulvinar; in experiment 14A, there should have been degeneration of both the anterior and the posterior medial portions according to his interpretation, yet there was none; in experiment 16A, the presence of retrograde cell change in the lateral parts of the pulvinar, with the superior parietal lobule intact, is inconsistent with Walker's conclusions. With few exceptions, the cortical lesions in these studies were confined to the exposed cortex. It is therefore possible that the inconsistencies in the observed degeneration are the result of differences in the amount of involvement of the depths of the sulci (Sylvian, interparietal, and superior temporal).

The present study was undertaken to reexamine the cortical field of the pulvinar in monkeys by the technique of retrograde cell degeneration. Earlier experimental studies at the Yerkes Laboratories have provided the brains of a number of animals with lesions in the temporal, parietal, and prestriate regions, and these brains have been analyzed for degeneration in the pulvinar with special attention to the medial surface of the parietal lobe, the depths of the sulci, and the possibility of individual variation.

METHODS

Material. Twenty monkeys (Macaca mulatta) with bilateral cortical extirpations of varying location and extent in the parietal and temporal lobes were used. All the operations were performed under nembutal anesthesia with aseptic precautions. The brain tissue was removed by aspiration. The animals were killed at intervals ranging from 32 to 603 days after operation. Their weights at the time of sacrifice ranged from 2.2 to 5.0 kg. All of them except one had been employed in previous behavioral studies. The serial number of the cerebral hemispheres in the present study, the corresponding designation used in previous reports, the body weights of the animals, and the survival days after surgery, are summarized in table 1.

Sketches of the contour of the brain and the fissural pattern of each hemisphere were made by means of a camera lucida. The brains were then fixed in 10% formalin, dehydrated, and embedded in nitrocellulose. They were cut in serial coronal sections at 50 μ thickness. Every 10th section was saved and stained with thionin.

Methods of analysis. In the comparison of different brains, the specification both of points on the cortex and of positions within the pulvinar is difficult. The boundaries of cytoarchitectural areas within the parieto-temporo-occipital region, except for the striate area, cannot be determined with any accuracy and no two descriptions of the pulvinar have agreed with respect to its subdivisions. Until the anatomic connections are known, any division of the cortex or thalamus is likely to be arbitrary and without functional significance.

The fissural pattern is variable but the major sulci are fairly constant and are the most certainly identifiable landmarks available in the cortex. Students of cytoarchitecture who have attempted to parcel the region have generally bounded their areas at the sulci. I have therefore used the sulci as reference points in the description of cortical lesions.

Various ways of dividing the pulvinar in the monkey into separate components have been proposed by several authors (cf. Aronson and Papez, '34; Crouch, '34; Le Gros Clark and

Boggon, '35; Walker, '38; Krieg, '48). No attempt was made here to compare their different elements and to eliminate the discrepancies. For the purpose of examining both the cortical

TABLE 1

Showing the experimental number of the cerebral hemispheres; the corresponding designation employed in previous studies; the weight of the animals at the time of sacrifice; and the surviving days after operation. L, left hemisphere; R, right hemisphere. The anatomic data of nos. 1 to 8, 13, 14, 35, and 36 were given by Blum, Chow and Pribram ('50); of nos. 9 to 12, 21, 22, and 27 to 32 were reported by Blum ('50); and of nos. 15 to 20, 23 to 26, 37, and 38 were reported by Chow ('50). Nos. 39 and 40 were not used previously

HEMISPHERE NO.	PREVIOUS DESIGNATION	WEIGHT OF ANIMAL	SURVIVAL
		kg	*days*
1	PTO-1L	2.5	125
2	PTO-1R		117
3	PTO-2L	2.2	57
4	PTO-2R		70
5	PTO-3L	2.7	340
6	PTO-3R		325
7	PTO-4L	2.9	329
8	PTO-4R		343
9	5L	5.0	603
10	5R		582
11	6L	4.3	603
12	6R		582
13	P-1L	2.1	183
14	P-1R		198
15	3L	2.5	32
16	3R		32
17	5L	2.7	71
18	5R		71
19	4L	3.0	38
20	4R		72
21	4L	3.3	191
22	4R		191
23	1L	2.5	61
24	1R		61
25	2L	2.7	45
26	2R		45
27	3L	3.3	399
28	3R		399
29	2L	3.3	189
30	2R		189
31	1L	3.3	399
32	1R		399
33	7L	2.7	46
34	7R		46
35	T-1L	2.7	236
36	T-1R		228
37	6L	3.0	69
38	6R		69
39		3.8	172
40			194

field of the pulvinar and the topographical relationship of individual parts, the simpler description of Walker was adopted. In his division, the pulvinar consists of three nuclei: n. pulvinaris lateralis, n. pulvinaris medialis, and n. pulvinaris inferior; all of which can be fairly easily distinguished on the basis of topography and cytoarchitecture. Since in my material the pulvinar extends through about 8 sections, the first 4 sections were arbitrarily denoted as an anterior portion, and the last 4 sections as a posterior portion. In the n. pulvinaris lateralis, a dorsal and a ventral part were also separated. The n. pulvinaris inferior usually appeared in two or three sections and was treated as one element without further partition. These divisions of the pulvinar are diagrammatically represented in figure 10. It must be emphasized that aside from those three nuclei as adopted from Walker, the subdivisions of the pulvinar employed here are mostly for the convenience of topographical analysis, with no implication of any necessary cytoarchitectural or functional correlates.

Retrograde degeneration in the pulvinar. Several precautions in interpreting the retrograde cell degeneration picture of the thalamus as discussed by Walker ('38), as well as the possibility of confusing it with the "secondary disuse atrophy" (Le Gros Clark and Boggon, '35), are fully recognized. However, the retrograde cell reaction in the pulvinar is quite characteristic; the nerve cells disappear almost completely, and a marked gliosis develops. Also, the boundary of the affected zone is relatively sharp, and is easily distinguished from the surrounding normal tissue. A second type of cell change, which may be equivalent to Le Gros Clark's partial cell atrophy, was also noted, and labelled as "doubtful." It usually occurred in small areas with vaguely defined boundaries; the cells appeared swollen, shrunken, or poorly stained, and with slight gliosis. Since the cause of this "doubtful" degeneration is uncertain (it may be transneuronal, due to "secondary disuse atrophy," or caused by damage to collaterals), it was disregarded in the final analysis. A set of serial sections of a normal monkey brain was frequently examined, whenever any

difficulty arose in either locating or identifying a degenerated zone.

Graphic method. The most reliable method of defining the correspondences between cortical lesions and thalamic degeneration is that of graphic analysis. A thalamic region is selected for study and the extent of cerebral lesions mapped for all cases which show degeneration within the region. That part of the cortex which is invariably destroyed is determined by superimposing the maps and eliminating all portions of the lesions which are not common to all the maps. This gives the minimal extent of the cortical field of the selected region. Similarly, all available cases which show no degeneration in the selected region are combined into a composite diagram to show that part of the cortex, the damage of which will lead no degeneration within the selected thalamic region. This gives the maximal limits of the field. If a sufficient number of specimens is available the method may be made still more precise by pairing specimens with small overlap of lesions and determining the corresponding region of overlap of degenerated zones in the nucleus. The present series does not include a large enough variety of lesions to permit this, except in a few cases.

For this method it is necessary that the lesions and thalamic regions be reduced to constant dimensions. For this purpose the following procedures were used: the surface extent of the lesions in the cortex was reconstructed by the usual method of orthogonal projection from camera lucida drawings of sections. "Standard" lateral and medial views of a hemisphere were drawn from a brain hardened in 10% formalin. The positions of the fissures and lesions in each of the reconstructions were transferred to the standard outline by proportionally transforming the measured dimensions of the reconstructions to those of the standard. Composite pictures were made by superimposing the adjusted reconstructions and outlining either the common area or the summed areas of lesion.

Damage within the sulci was determined from camera lucida drawings of cross sections. Sections at 2 mm intervals through-

out the length of each sulcus were examined. The destruction of buried cortex was estimated as zero, one-third, two-thirds, or complete; and the estimates tabulated for the Sylvian, superior temporal, and interparietal sulci. Results of these estimates for significant regions are given in tables 2 and 3; and the included loci are shown in figure 2.

The location and extent of retrograde cell change in the pulvinar were determined under the microscope, and marked on the drawings of those cross sections that run through this nucleus. These degenerated zones were then translated proportionally into a series of diagrammatic outlines of the pulvinar for easy comparison. The localization of the degeneration is in accordance with the 7 divisions of the pulvinar. No attempt to construct a composite picture was made, because most of the degenerated zones are fairly extensive, and the position of the smaller cell-atrophied areas can only be approximated, due to the variation and distortion of the shape of the thalamic nuclei. The retrograde degeneration that occurred in other parts of the thalamus in the cases with extensive lesions is not analyzed in the present study.

RESULTS

Descriptions of all the brains except nos. 39 and 40 have been published elsewhere;[2] they are not repeated in detail in this report. Figure 1 gives the reconstructions, as translated to the standardized fissurization, of the cortical lesions of all the cerebral hemispheres.[3] For convenience of comparison, they are represented on the lateral view of the left hemisphere. The adjacent two numbers belong to the same brain, the odd

[2] The reconstruction of location and surface extent of cortical extirpation, the cross sections through the lesion, and the representative drawings of the thalamus of cerebral hemisphere nos. 1 to 8, 13, 14, 35, and 36 were given by Blum, Chow and Pribram ('50); of nos. 9 to 12, 21, 22, and 27 to 32 were included in Blum ('50); and of nos. 15 to 20, 23 to 26, 37 and 38 were reported by Chow ('50).

[3] The retrograde degeneration which resulted from the additional prefrontal ablation of hemisphere nos. 5 to 12 presumably did not involve any part of the pulvinar; therefore, these cortical excisions are not considered in the following discussion.

TABLE 2

The extent of lesion of the walls of the interparietal sulcus in experiments 1 14. The first section starts when the central fissure reaches the midline, and t last section stops in front of the lunate sulcus. Every 4th section is tabulate The degree of damage to the buried cortex is estimated as follows: —, no dama to the depth of the sulcus; +, lesion involves about one-third of the depth; ++ lesion involves about two-thirds of the depth; c, complete destruction

NO.	SECTION NO.				
	1	4	8	12	16
1	—*	—	—*	—	—
2	c*	++	++*	++	+
3	+*	+	+	++*	++
4	+*	+	+	++*	+
5	—*	—	—*	—	—
6	+*	+	++	++	++*
7	++	++*	+*	+	++
8	—	+*	+	+*	++
9	—	—*	—	—*	—
10	—	—*	—*	—	—
11	—*	—	—*	—	—
12	—*	—*	—	—	—
13	c	c*	c*	++	+
14	c	c*	++*	+	+

* These cross sections are shown in figure 2.

TABLE 3

The extent of lesion of the walls of the posterior Sylvian fissure and the poster part of the superior temporal sulcus in experiments 1 to 14. The first sect starts when the central fissure reaches the midline. Every 4th section is tal lated. The degree of damage to the buried cortex is estimated as follows: —, damage to the depth of the sulcus; +, lesion involves about one-third of the dept ++, lesion involves about two-thirds of the depth; c, complete destruction

NO.	POSTERIOR SYLVIAN FISSURE			POSTERIOR SUPERIOR TEMPORAL SUL			
	1	4	8	1	4	8	12
1	—	—	—	—	—	—	+
2	—	—	+	+	+	+	+
3	+	++	c	c	c	c	c
4	+	++	c	c	c	c	c
5	+	++	++	c	c	c	c
6	++	++	++	+	++	++	c
7	—	—	+	—	—	+	++
8	—	+	+	++	++	+	+
9	—	—	—	—	—	+	+
10	—	++	++	—	—	+	++
11	—	—	—	+	+	c	++
12	—	—	—	—	+	+	++
13	—	++	c	—	—	—	+
14	—	++	++	—	—	—	++

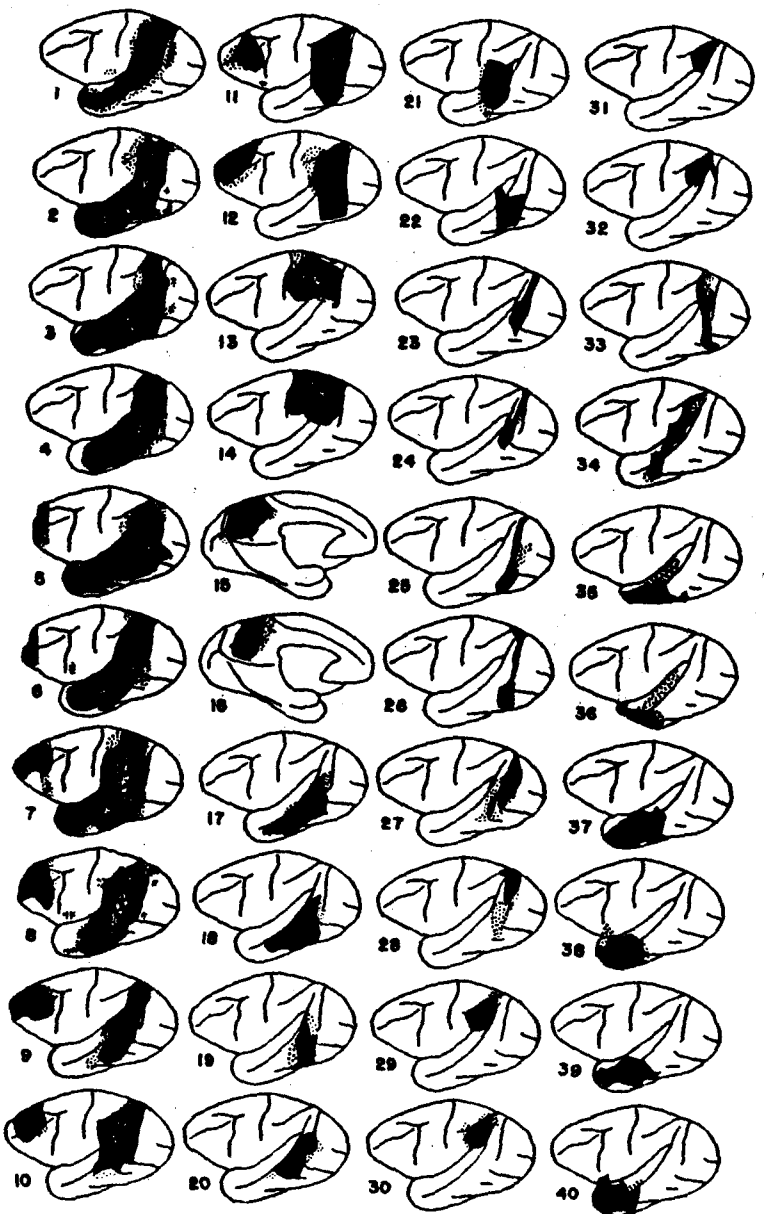

Fig. 1 Reconstruction of surface extent of cortical lesion on the lateral views of the standardized cortical fissural pattern. Complete destruction is indicated by solid black, partial destruction by dots.

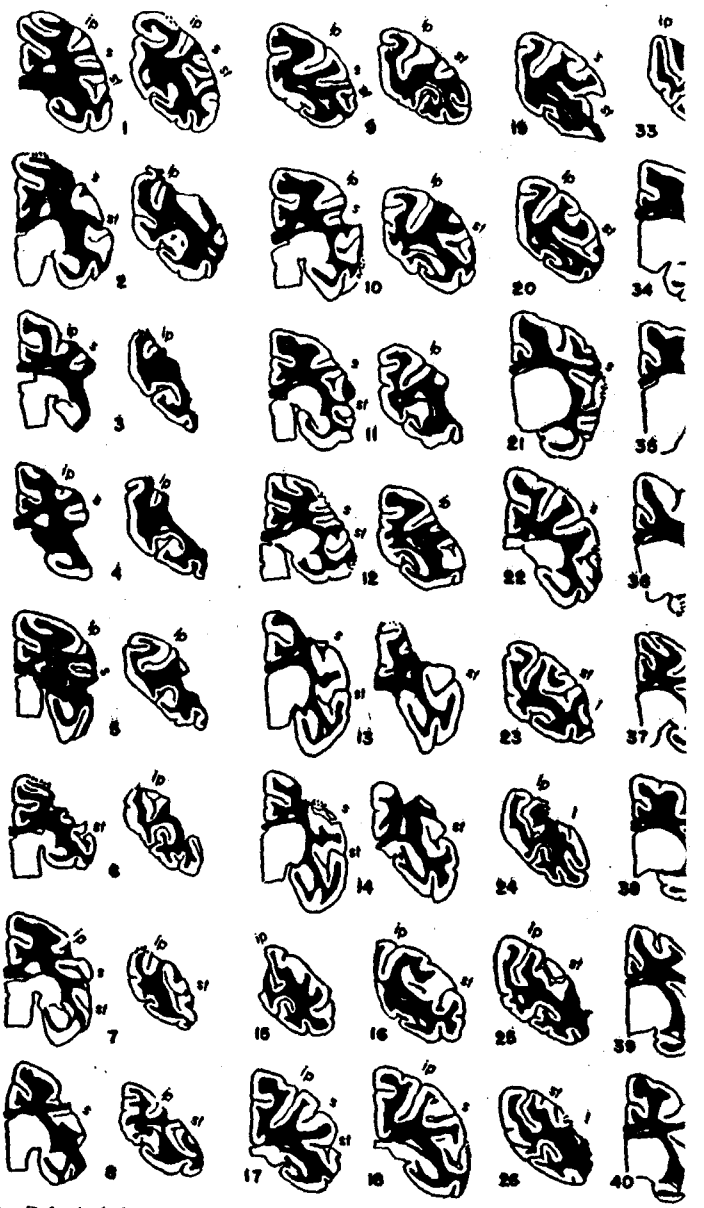

Fig. 2 Selected drawings of the cross sections through the cortical lesi
brain white matter is represented in solid black, and the principle sulci
cated. No cross sections are given for cerebral hemisphere nos. 27 to 32.
parietal sulcus; s, Sylvian fissure; st, superior temporal sulcus; l, lunate s

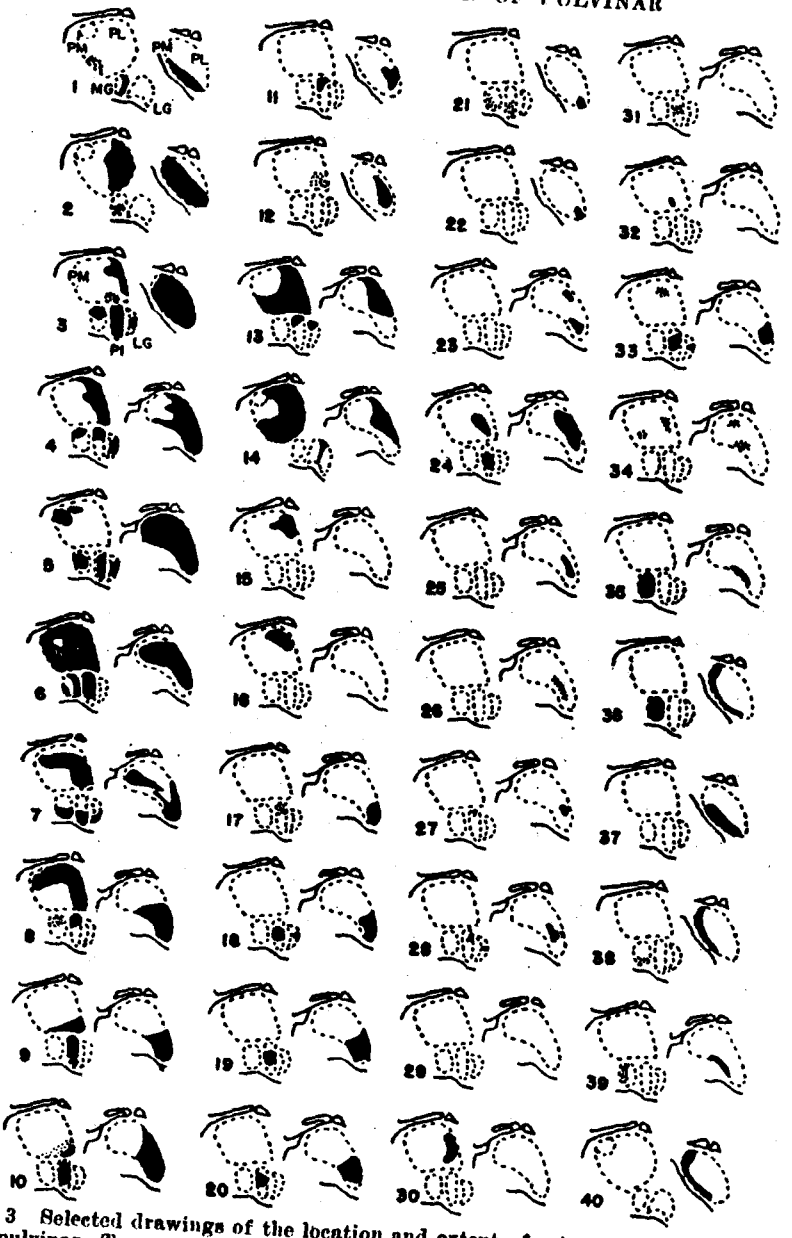

Fig. 3 Selected drawings of the location and extent of retrograde degeneration in the pulvinar. Two cross sections are given for each hemisphere. The first section is either the second or the third after the appearance of the habenular complex; the other section is either the second or the third from the caudal pole of the pulvinar. Complete degeneration is indicated by solid black, doubtful degeneration by dots. LG, lateral geniculate; MG, medial geniculate; PL, n. pulvinaris lateralis; PM, n. pulvinaris medialis; PI, n. pulvinaris inferior.

numbers indicate the left, and the even numbers the right hemispheres. Complete destruction of the cortex is shown by solid black and superficial destruction by dots; the latter was not included in constructing the composite pictures. Figure 2 includes selected drawings of the cross sections through the extirpated region; they are again reproduced as from the left hemisphere. No cross sections are given for nos. 27 to 32, for their lesions were superficial and did not involve the depth of the sulci. Figure 3 shows the retrograde cell degeneration in standardized drawings of the various components of the pulvinar. Two sections are selected for each hemisphere: the first section is either the second or the third after the appearance of the habenular complex; the other section is either the second or the third from the caudal pole of the pulvinar. Completely degenerated area is depicted by solid black, and "doubtful" degeneration by dots. For easier reference, the data on the severity and location of secondary degeneration in the pulvinar are summarized in table 4.

To avoid unduly increasing the length of the present communication, the experimental results are not presented by individual cases; instead, they are subsumed under the following sections, each of which is an attempt to delimitate the cortical projection area of one division of the pulvinar.

The anterior dorsal part of n. pulvinaris lateralis. This part of the pulvinar is continuous with Walker's ('38) n. lateralis posterior, and roughly corresponds to the anterior half of Krieg's ('48) dorsal pulvinar. Ten cerebral hemispheres showed retrograde degeneration in this region: i.e., nos. 2, 3, 4, 6, 7, 8, and 13 to 16 (excluding the "doubtful" degeneration in no. 33). The atrophied zones were all fairly large and extended through the entire length of this division of the pulvinar.

The composite picture of the ablated cortical areas common to 8 out of these 10 hemispheres, i.e., nos. 2, 3, 4, 6, 7, 8, 13 and 14, is shown in figure 4A; and the composite picture of the summed area extirpated in all the other cases that did not show cell atrophy in this division except nos. 1 and 5, is shown

in figure 4B. Figure 4C is constructed by simply subtracting 4B from 4A; and it defines that and *only that* region of the lateral surface of the cortex, the removal of which always is followed by retrograde cell changes in this element. The remaining two cases, nos. 15 and 16, are the only hemispheres

TABLE 4

Approximate location and extent of retrograde degeneration in the pulvinar. PL, n. pulvinaris lateralis; PM, n. pulvinaris medialis; PI, n. pulvinaris inferior; AD, anterior dorsal; AV, anterior ventral; PD, posterior dorsal; PV, posterior ventral; A, anterior; P, posterior. Extent of degeneration is indicated as follows: —, no degeneration; ?, small doubtful; S, small; L, large; C, almost complete

NO.	PL AD	PL AV	PL PD	PL PV	PM A	PM P	PI
1	—	—	—	?	?	S	—
2	C	C	—	L	—	L	?
3	L	S	S	L	—	—	C
4	L	S	L	L	—	L	L
5	—	—	L	L	L	C	C
6	C	L	L	L	L	C	L
7	L	L	—	L	L	L	C
8	L	L	—	C	L	—	L
9	—	S	—	C	—	—	L
10	—	S	S	L	—	—	C
11	—	—	—	L	—	—	L
12	—	?	—	L	—	—	S
13	C	C	L	—	—	—	—
14	C	C	L	—	—	—	S
15	L	—	—	—	—	—	S
16	L	—	—	—	—	—	—
17	—	—	—	L	—	—	—
18	—	—	—	L	—	—	?
19	—	—	—	L	—	—	L
20	—	—	—	L	—	—	L
21	—	—	—	S	—	—	L
22	—	—	—	S	—	—	?
23	—	—	S	S	—	—	—
24	—	L	S	S	—	—	—
25	—	—	—	S	—	—	L
26	—	—	—	?	—	—	—
27	—	—	—	S	—	—	—
28	—	—	—	S	—	—	S
29	—	—	—	—	—	—	S
30	—	L	—	—	—	—	—
31	—	—	—	—	—	—	—
32	—	S	—	—	—	—	?
33	?	—	—	S	—	—	—
34	—	?	—	—	?	?	L
35	—	—	—	—	—	S	—
36	—	—	—	—	—	S	—
37	—	—	—	—	—	S	—
38	—	—	—	—	—	S	—
39	—	—	—	—	—	S	—
40	—	—	—	—	—	S	—

where the medial surface of the parietal lobe was removed. In these cases, atrophy of cells is confined entirely to the anterior dorsal part of the n. pulvinaris lateralis. Therefore, in addition to that lateral cortical sector as depicted by figure 4C, the medial surface of the parietal lobe also receives projection fibers from this part of the pulvinar.

The seemingly exceptional results in nos. 1 and 5, both of which had lesions invading the lateral cortical region (fig. 4C) and yet no retrograde degeneration, can be explained by examining the degree of damage to the buried cortex along the interparietal sulcus. From table 2, it is clear that nos. 1 and 5 are the only ones in which the depth of this sulcus had been left

Fig. 4 A. Composite of lesions common to all cases (except nos. 1 and 5) which showed retrograde degeneration in the anterior dorsal part of the n. pulvinaris lateralis.

B. Composite of lesions of the summed areas of all the other cases.

C. Composite of lesions defining the field of the anterior dorsal part of the n. pulvinaris lateralis.

intact. Similarly the lesions of nos. 9 to 12 reached the interparietal sulcus but did not invade its depth. They also showed no degeneration in the anterior dorsal part of n. pulvinaris lateralis. Consequently, it is very probable that the walls of the interparietal sulcus receive most of the projection fibers.

These experimental results indicate that the anterior dorsal part of n. pulvinaris lateralis projects to the medial surface of the parietal lobe and the posterior part of the superior parietal lobule. On the latter, the projection fibers are concentrated mostly in the walls of the interparietal sulcus.

The anterior ventral part of n. pulvinaris lateralis. This element of the pulvinar is roughly equivalent to Krieg's ('48) anterior half of the lateral pulvinar. All those hemispheres

that showed degeneration in the anterior dorsal part, as described in the previous section, also had degenerated zones in this division, with the exception of the two medial surface lesions, nos. 15 and 16. However, there were 5 additional cases which also showed degeneration restricted to the caudal division; they are nos. 9, 10, 24, 30 and 32 (excluding the "doubtful" cases of nos. 12 and 34). The retrograde degenerations were both large and extended through the entire length in nos. 2, 3, 4, and 7; extensive but limited to the posterior two sections only in nos. 6, 8, 13, and 14; both small and limited to one or two sections in nos. 9, 10, 24, 30, and 32.

For those 8 cases, which also had cell atrophy in the anterior dorsal part of the n. pulvinaris lateralis, the common cortical

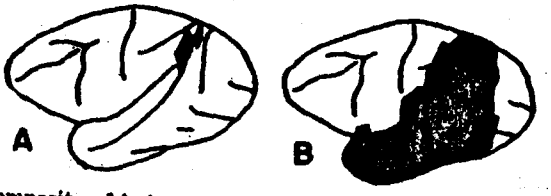

Fig. 5 A. Composite of lesions common to nos. 9, 10, 24, 30, and 32, damage to which produced retrograde degeneration in the anterior ventral part of the n. pulvinaris lateralis.

B. Composite of lesions of the summed areas of all the other cases, which showed no degeneration.

projection area is the same as that of figure 4C. It includes the posterior part of the superior parietal lobule and the depth of the interparietal sulcus. The composite picture of the extirpated area common to the additional 5 cases with degeneration restricted to the posterior region is shown in figure 5A. Figure 5B gives the composite of lesions of all other cases which did not have retrograde degeneration in this part of the pulvinar. The common area in figure 5A consists of the dorsal parts of the inferior parietal and prestriate regions. These are completely included within that of figure 5B. The inconsistency among these cases is difficult to interpret. It appears to be genuine since individual cases with and without degeneration in this region can be matched in nearly identical cortical

lesions, e.g., 23 and 24; 29 and 30. The most plausible explanation of the difference is that the lesions in the positive cases interrupted passing fibers which escaped damage in the negative cases. Such fibers would come from the postero-medial surface of the prestriate region. It is therefore tentatively concluded that the anteroventral part of the n. pulvinaris lateralis projects to the posteromedial part of the parietal lobule, and to the depth of the interparietal sulcus.

The posterior dorsal part of n. pulvinaris lateralis. This division of the pulvinar is roughly equivalent to Krieg's ('48) posterior half of the dorsal pulvinar, especially his pulvinar A and B, which extend to the caudal pole. Nine hemispheres

Fig. 6 A. Composite of lesions common to all cases (except nos. 23 and 24) which showed retrograde degeneration in the anterior ventral part of the n. pulvinaris lateralis.

B. Composite of lesions of the summed areas of all the other cases.

C. Composite of lesions common to nos. 23 and 24.

showed retrograde degeneration: i.e., nos. 3, 4, 5, 6, 10, 13, 14, 23, and 24. The regions of cell atrophy were large and extended to the caudal pole in nos. 4, 5, 6, 13, and 14; small and restricted to one or two caudal sections in nos. 3, 10, 23, and 24.

The composite picture of the cortical lesions common to nos 3, 4, 5, 6, 10, 13, and 14 is shown in figure 6A. This extirpate area is well included within a region, as shown in figure 6B the ablation of which in other cases caused no secondary de generation. It is therefore not possible to differentiate thes 7 cases by their surface lesion alone. When the degree damage to the buried cortex is considered, however, it is foun from table 3, that the severe invasion of the depth of the po terior part of the Sylvian fissure is the common factor. F the remaining two cases, nos. 23 and 24, the ablations we

confined to the prestriate region. The composite of lesions common to these two cases is shown in figure 6C. Needless to say there are other cases with lesions like these two, but showing no secondary degeneration in this pulvinar element.

The posterior dorsal part of n. pulvinaris lateralis projects to the depth of the posterior Sylvian fissure, and possibly, at least in some cases, as evidenced by nos. 23 and 24, also extends to the ventral part of the prestriate region.

The posterior ventral part of n. pulvinaris lateralis. This part of the pulvinar is roughly equivalent to Krieg's ('48) posterior half of the lateral pulvinar, especially the inferior division. Twenty-three hemispheres showed retrograde degeneration: i.e., nos. 2 to 12, 17 to 25, 27, 28, and 33 (excluding the

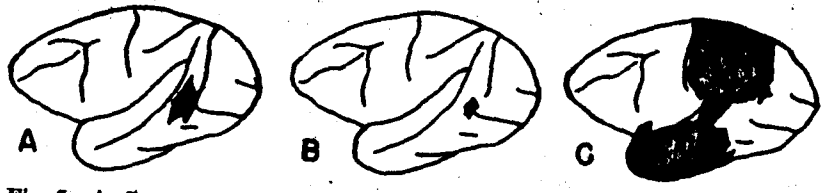

Fig. 7 A. Composite of lesions common to all cases which had large retrograde degeneration in the posterior ventral part of the n. pulvinar lateralis.

B. Composite of lesions common to all cases which had small retrograde degeneration.

C. Composite of lesions of the summed areas of all other cases that have no retrograde cell changes in the posterior ventral part of the n. pulvinaris lateralis.

"doubtful" ones of nos. 1 and 26). The cell-atrophied zones were both large and extended through the entire length in nos. 2 to 12, and 17 to 20; small and restricted to one or two sections in nos. 21 to 25, 27, 28, and 33.

The composite of lesions common to those cases that had large degenerated areas is shown in figure 7A, common to those that had small degenerated areas in 7B. Number 21 is omitted from this composite figure since the lesion in this case did not overlap the area common to the others. Figure 7C gives the composite picture of lesions which produced no degeneration in this part of the pulvinar. It is immediately apparent by examining these three figures that the posterior ventral part of the

n. pulvinaris lateralis projects to the temporo-occipital region. Furthermore, there is indication that the size of the cortical lesion is positively correlated with the size of the thalamic degenerated zone; but further partition of this relationship topologically is not possible with the present limited material. In no. 21, the lesion was superficial and situated in front of these two common zones; it had a small area of cell atrophy in the caudal part of this division of the pulvinar. Whether this indicates a rostral extension of the projection field depicted by figures 7A and 7B, cannot be decided upon from this single case.

The anterior part of n. pulvinaris medialis. This part of the pulvinar is roughly equivalent to Krieg's ('48) anterior half of the medial pulvinar. Only 4 hemispheres showed retrograde degeneration: i.e., nos. 5 to 8 (excluding the "doubtful" one of no. 34). The degenerated areas were all large and extended through the entire length of the nucleus. These 4 cases together with nos. 2, 3, and 4 which did not show corresponding degeneration are the only ones whose lesions invaded the middle part of the exposed cortex of the superior temporal gyrus. The degree of damage to the depth of the sulci, as shown in tables 2 and 3, does not differentiate the cases from those without degeneration, nor is there any other constant difference between the two groups. The cortical field of this part of the pulvinar cannot be definitely determined by the present material. However, it is suggested from the general plan of the pulvinar projection (see discussion below), that the anterior half of the n. pulvinaris medialis may project to the middle part of the superior temporal gyrus, and that hemispheres nos. 2, 3, and 4 are exceptional cases. Further experimentation is needed to verify this conclusion.

It is noteworthy that none of the material of Le Gros Clark and his co-workers ('35, '36, '37) showed retrograde degeneration in this pulvinar element, which they denoted as pa and part of ppB. Walker ('38) reported 4 cases with the region degenerated; the cortical lesions were: one hemidecorticated, one with ablation between interparietal and lunate sulci, and

the remaining two with lesions from the central fissure to the lunate sulcus.

The posterior part of n. pulvinaris medialis. This part of the pulvinar is roughly equivalent to Krieg's ('48) posterior half of medial pulvinar, excluding the inferior nucleus. Twelve hemispheres showed retrograde degeneration: i.e., nos. 1 to 3, 5 to 7, and 35 to 40 (excluding the "doubtful" one of no. 34). The degenerated areas in nos. 2, 3, 5, 6, and 7 were large and extended through the entire length, and in nos. 1 and 35 to 40 were small and restricted to one or two sections.

The composite of lesions common to these 12 cases is shown in figure 8A, and the composite of lesions of all the remaining

Fig. 8 A. Composite of lesions common to all cases which showed retrograde degeneration in the posterior half of the n. pulvinaris medialis.

B. Composite of lesions of the summed areas of all the other cases.

C. Composite of lesions defining the field of the posterior half of the n. pulvinaris medialis.

cases without degeneration summed together is shown in figure 8B. Figure 8C is constructed by subtracting 8B from 8A, and it defines that cortical area the ablation of which is always followed by retrograde degeneration in this division of the pulvinar. Comparison of cases 35 and 36 with nos. 37 to 40 shows that the projection field is restricted to the lateral surface of the temporal lobe, since only the two former involved the medial surface of the lobe and the degeneration in those cases is not greater than in the others. Furthermore, there is indication that the ventral margin of this pulvinar division may be further separated from its medial part (compare nos. 35, 37, and 39 to nos. 36, 38, and 40). The latter projects to the dorsal part and the former projects to the ventral part of the cortical region as depicted by figure 8C. It is clear from these

data that the posterior part of n. pulvinaris medialis projects to the anterior portion of the lateral surface of the temporal lobe.

The inclusion of the neocortex of the temporal lobe as a part of the pulvinar projection field is at variance with the general belief that this part of the brain has no afferent thalamic connection (Le Gros Clark, '37; Walker, '38). Yet the positive findings of this study, together with the case reported by Bucy and Klüver ('40) who found retrograde degeneration in posterior parts of the pulvinar of a monkey following temporal lobectomy, and also two of Walker's experiments ('38; 16A and 17B), provide evidence for the conclusion that the lateral surface of the temporal lobe does receive some projection fibers from the pulvinar.

The n. pulvinaris inferior. This part of the pulvinar is equivalent to Krieg's ('48) inferior nucleus of the medial pulvinar. Eighteen hemispheres show retrograde degeneration: i.e., nos. 3 to 11, 13, 14, 18 to 20, 24, 27, 28 and 33 (excluding the "doubtful" ones of nos. 2, 17, 21, and 31). Table 4 gives the amounts, and figure 3 the locations of the cell-atrophied zones, which usually extended through the entire length except in nos. 10, 11, 13, 14, and 23.

If the 4 cases that had complete retrograde cell changes of this nucleus are excluded (nos. 3, 5, 6, and 9), the remaining ones can be divided into two groups, one with degeneration of the dorsal half, and another with degeneration of the middle or ventral half. The first group consists of hemisphere nos. 4, 8, 11, 13, 14, 27, and 28; and the composite of lesions common to all of them is shown in figure 9A. The second group consists of hemisphere nos. 7, 10, 18, 19, 20, 24, and 33; and the common area is shown in figure 9B. From these figures it can be concluded that the dorsal half of the n. pulvinaris inferior projects to the dorsal part of the prestriate region, and that the middle and ventral parts project to the temporo-occipital and ventral region of the prestriate region. It is noted that there are 6 exceptional cases (nos. 1, 12, 17, 23, 25, 26) whose

lesions invaded these two zones, and yet no retrograde cell atrophy of this nucleus resulted.

If the present result of the topographic arrangement of the projection field of the n. pulvinaris inferior can be upheld in spite of the exceptional cases, then both the conclusions of Le Gros Clark and Northfield ('37), and Walker ('38) are partly confirmed. The former reported that this nucleus (pd in their nomenclature) projects to the prestriate cortex, and the latter that it projects to the temporo-occipital region. Corroborative evidence is also obtained from Lashley's ('48) data; he removed the prestriate cortex, and in some cases also the temporo-occipital region, in a series of spider monkeys (Ateles geoffroyi), and demonstrated retrograde cell degeneration in this nucleus.

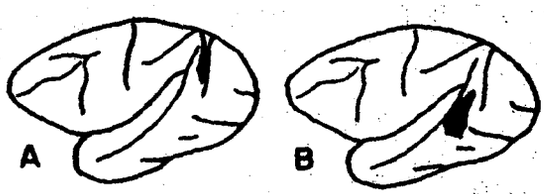

Fig. 9 A. Composite of lesions common to all cases which showed retrograde degeneration in the dorsal part of the n. pulvinaris inferior.

B. Composite of lesions common to all cases which showed retrograde degeneration in the ventral part of the n. pulvinaris inferior.

DISCUSSION

The present series of experiments has demonstrated a much wider cortical projection field for the pulvinar in the monkey than hitherto has been described. Le Gros Clark and Northfield ('37) concluded that the pulvinar projects only to the posterior Sylvian receptive region and the prestriate cortex. Walker ('38) enlarged this field to include the posterior parts of the superior and inferior parietal lobules and the temporo-occipital region, but excluded the dorsal part of the prestriate cortex. My results not only confirm the fact that all the cortical sectors as reported by these authors are connected directly with the pulvinar, but also add the medial surface of the parietal lobe, the lateral surface of the temporal lobe, and the buried

cortices along the posterior parts of the interparietal and Sylvian sulci. They further show a topological arrangement of the cortical fields of the various divisions of the pulvinar. For the n. pulvinaris lateralis, the anterior dorsal part projects to the medial surface of the parietal lobe, the posterior superior parietal lobule and the depth of the interparietal sulcus; the anterior ventral part projects to the posteromedial part of the parietal lobule, and the depth of the interparietal sulcus; the posterior dorsal part projects to the depth of the Sylvian fissure, and the ventral prestriate cortex; and the posterior ventral part projects to the temporo-occipital region. For the n. pulvinaris medialis, the projection field of the anterior half is undetermined, but the posterior half sends its fibers to the lateral surface of the temporal lobe. The fibers of the dorsal half of the n. pulvinaris inferior distribute to the prestriate region, and the fibers of the ventral half to the temporo-occipital area. The boundaries of these cortical sectors are not precise; they both overlap considerably and leave a gap of cortex in between at different places. These results on the delimitation of the cortical projection field of the various components of the pulvinar are summarized in semi-diagrammatic drawings in figure 10. It must be emphasized that the method employed for constructing the composite of lesions gives merely the minimum common area. Since the projection region for the anterior half of the n. pulvinaris medialis is yet to be determined, and since the composite pictures tend to minimize the actual size of these projection areas, it is probable that with additional material available they may prove to be more extensive, overlapping and perhaps including the entire posterior parietal and lateral temporal lobes.

The significance of the exceptional cases. Many cases reported here cannot be incorporated in either Le Gros Clark's or Walker's conception of the projection field of the pulvinar. Also a few cases, as has been pointed out in discussing the several divisions of the pulvinar, are exceptional to my own generalization. The explanation of these discrepancies and the significance of the exceptional cases are not clear. Several

factors which might be responsible for them will be discussed briefly.

The factor of the size of the cortical ablation has been analyzed by measuring some of the cerebral hemispheres with the aid of a planimeter. Although an extensive cortical lesion tends to cause degeneration in several parts of the pulvinar, no correlation between the size of the lesion and either the severity or location of the degenerated zone within a division can be definitely stated (except in the case of the posterior

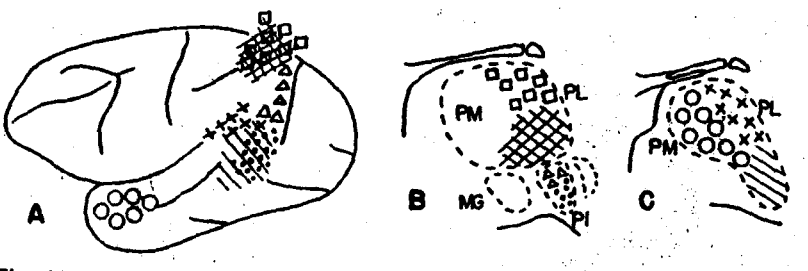

Fig. 10 Semi-diagrammatic drawings to show the spatial arrangement of the cortical projection fields of the various divisions of the pulvinar.
A. Lateral view of the brain with the pulvinar projection fields indicated.
B. Cross section representing the anterior half of the pulvinar.
C. Cross section representing the posterior half of the pulvinar.
PI, n. pulvinaris inferior; PL, n. pulvinaris lateralis; PM, pulvinaris medialis. Squares indicate the anterior dorsal division of the n. pulvinaris lateralis; crosses, the posterior dorsal division; cross-hatched area, the anterior ventral division; and the shaded area, the posterior ventral division. Circles designate the posterior portion of the n. pulvinaris medialis. Triangles show the dorsal half of the n. pulvinaris inferior, and the stippled area, the ventral half.

ventral part of the n. pulvinaris lateralis as reported earlier in this paper). An example of this lack of correlation is seen in nos. 23 and 24. The former had a large cortical lesion with a small cell-atrophied area, whereas the latter had a small lesion with a more severe retograde degeneration.

Another factor is the surviving time after operation. It might be suspected that the longer the time interval, the more distortion or redistribution of cells of the thalamus would obscure the retrograde degeneration. Brodal ('40) reported the influence of this factor on the characteristics of the secondary

cell changes of the inferior olive following cerebellar ablation in newborn mice and rabbits. However, this conclusion may not apply to the present results. The animals used in this study, as judged by their weights, were from 2 to 3 years of age, and the time interval after operation was far greater than that employed by Brodal. He sacrificed his animals a few weeks after surgery, whereas my animals were allowed to survive from several weeks to two years. The data for survival days of all the animals are summarized in table 1; they show no correlation, among animals with approximately the same cortical excision, between the length of the time interval after operation and the severity of retrograde cell changes.

The importance of including the walls along the sulci in determining the cortical field of thalamic nuclei is borne out by the finding that the depth of two principal sulci (interparietal sulcus and Sylvian fissure) are the projection regions for two different parts of the pulvinar. Whereas the significance of damaging the depth of the superior temporal and lunate sulci has yet to be determined, it is possible that some of the exceptional cases can be explained by future knowledge of the role of these buried cortices. Closely related to this problem is the possible damage to fiber tracts which are situated immediately adjacent to the cortical layers. No systematic study of the fiber paths from the pulvinar to cortex is available. Polyak reported from his Marchi material ('32) that only fine, poorly myelinated fibers arise from the pulvinar and that they scarcely reached the cortex. Nevertheless, in examining his figures 52 and 53, it is evident that at least one part of the projection field (the posterior Sylvian receptive region) receives fibers from the pulvinar fairly directly. Further experimentation is needed in order to clarify the importance of this factor. There remains the possibility that the method used for translating the site of cortical lesion to the standard diagram of the hemisphere is not accurate. The individual variation of cytoarchitectural fields (cf. Lashley and Clark, '46) may be so great that the same point between any two principal sulci is not identical among different animals, and that the

constructed composite pictures do not give the common cytoarchitectural areas. However, the fact that a general spatial plan of the pulvinar projection field is demonstrated by the present study suggests the existence of homologous cortical points, at least in the majority of cases.

The presence of exceptional cases both in this and previous studies cannot altogether be satisfactorily interpreted as being caused by the factors discussed above. Further analysis of their significance and of the possible factors involved is needed to determine whether they represent a greater degree of individual variation in the mode of pulvinar projection than has been suspected.

The general plan of the pulvinar projection. For the majority of thalamic nuclei which have been carefully analyzed it has been found that Stoffels' ('39) principle of lamellation holds true. This is the case both within and between functional areas; that is, adjacent points in the thalamus are projected to adjacent points on the cortex, irrespective of their function. My data indicate at least a crude topological relation of parts of the pulvinar to the cortical surface, and this suggests that the projection of the nucleus is to a continuous area and is topologically arranged within each part. The plan of arrangement, as suggested by the available cases, is represented in figure 11. The cephalo-caudal axis of the nucleus is projected along the dorsoventral axis of the cortex; the dorsoventral axis of the nucleus is projected perpendicular to the temporo-occipital axis of the cortex. The lateromedial axis of the pulvinar is not differentiated in the cortex; it corresponds to the direction of the fiber paths which separate the lateral part of the pulvinar into distinct parallel bundles. This rearrangement of the spatial coordinates of the pulvinar to the cortex is different from that reported in Stoffels' study on the thalamic nuclei of the rabbit. He showed that the cephalo-caudal axis of the nuclei is projected to the antero-posterior axis of the cortex, and the dorsoventral axis to the dorsoventral axis of the cortex. The lateromedial axis of the nuclei is again more or less undifferentiated. This difference may be due to

the development and shifting of the pulvinar caudolaterally, as well as to the expansion and displacement of the parietal cortex in the phylogenetically higher monkeys.

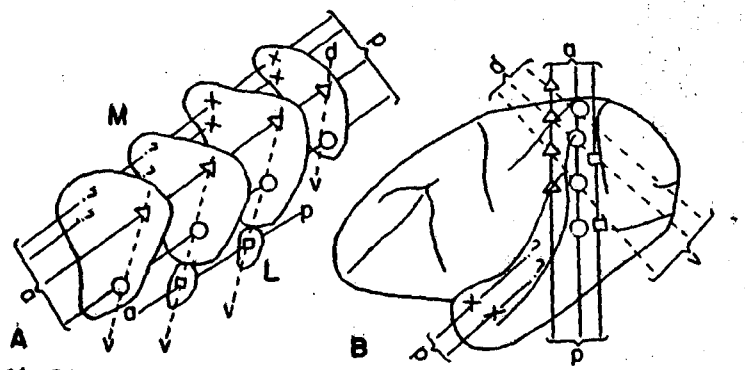

Fig. 11 Diagrammatic drawings to show the general plan of the pulvinar projection.

A. Four representative cross sections through the pulvinar. Straight lines ap indicate the cephalo-caudal axis, interrupted lines dv indicate the dorsal-ventral axis. M, the medial margin. L, the lateral side. Triangles represent the dorsal part of the n. pulvinaris lateralis; circles, the ventral part. Squares depict the n. pulvinaris inferior. Crosses and question marks designate the n. pulvinaris medialis.

B. The lateral view of the cerebral hemisphere with projection plan of the pulvinar indicated. The designations are similar to that of figure 11A.

SUMMARY

Bilateral cortical ablations of varying location and extent within the general region of the parietal and temporal lobes were made on 20 monkeys (Macaca mulatta). The retrograde cell degeneration in the pulvinar of these 40 cerebral hemispheres is analyzed to determine the topological arrangement of the projection field of the designated divisions of the pulvinar. For each of them a cortical projection is mapped by constructing the composite field of lesions. The experimental results indicate that within the n. pulvinaris lateralis, the anterior dorsal part projects to the medial surface of the parietal lobe, the posterior superior parietal lobule, and the depth of the interparietal sulcus; the anterior ventral part projects to the posteromedial part of the parietal lobule and the depth of the interparietal sulcus; the posterior dorsal part projects

to the depth of the Sylvian fissure, and the ventral prestriate cortex; and the posterior ventral part projects to the temporo-occipital region. The projection field of the anterior half of the n. pulvinaris medialis is undetermined, the posterior half sends its axons to the lateral surface of the temporal lobe. The n. pulvinaris inferior distributes the fibers from its dorsal half to the prestriate region, and from its ventral half to the temporo-occipital area.

The pulvinar projection field, as determined by the present study, includes in general those regions described by previous investigators; in addition, it shows a much wider cortical area with more precise delimitation and an orderly spatial arrangement of the various divisions. The need of analyzing the exceptional cases in the determination of the pulvinar projection field is emphasized. Some of the factors that may account for individual variations, such as the size of the cortical lesion, the time interval after operation, the damage to the depth of the sulci, and the interruption of fiber tracts, are briefly discussed.

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