

## Research Reports

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### VISUOTOPIC ORGANIZATION OF THE CEBUS PULVINAR: A DOUBLE REPRESENTATION OF THE CONTRALATERAL HEMIFIELD

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#### SUMMARY

The projection of the visual field in the pulvinar nucleus was studied in 17 Cebus monkeys using electrophysiological techniques. Visual space is represented in two regions of the pulvinar; (1) the ventrolateral group,  $P_{vlg}$ , comprising nuclei  $P\delta$ ,  $P\delta_1$ ,  $P\gamma$ ,  $P\eta$  and  $P\mu_1$ ; and (2)  $P\mu$ . In the first group, which corresponds to the pulvinar inferior and ventral part of the pulvinar lateralis, we observed a greater representation of the central part of the visual field. Approximately 58% of the volume of the ventrolateral group is concerned with the visual space within  $10^\circ$  of the fovea. This portion of the visual field is represented at its lateral aspects, mainly close to the level of the caudal pole of the lateral geniculate nucleus (LGN). Projection of the vertical meridian runs along its lateral border while that of the horizontal one is found running from the dorsal third of the LGN's hilus to the medial border of the ventro-lateral group. The lower quadrant is represented at its dorsal portion while the upper quadrant is represented at the ventral one. In  $P\mu$  the representation is rotated  $90^\circ$  clockwise around the rostrocaudal axis: the vertical meridian is found at the ventromedial border of this nucleus. Thus, the lower quadrant is represented at the lateral portion of  $P\mu$  and the upper at its medial portion. Both projections are restricted to the contralateral hemifield.

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#### INTRODUCTION

It has been shown in mammals that the visual field is represented in an orderly topographical fashion in various cortical and subcortical regions<sup>2,6,8,10,17,33</sup>. The participation of the pulvinar in the analysis of visual information has been suggested by anatomical<sup>9,18,34</sup>, electrophysiological<sup>1,24</sup> and behavioral<sup>28</sup> studies. Available data show that portions of this nucleus include visually driven units<sup>24</sup>, establish reciprocal

connections with cortical visual areas<sup>4,7,25,32</sup>, and receive projections from the superior colliculus<sup>5,21,27</sup>.

A topographic representation of the visual field coextensive with and restricted to the pulvinar inferior was shown in the owl monkey<sup>1</sup>. Although similar results have been reported for the rhesus monkey<sup>3</sup>, anatomical data have shown that both the pulvinar inferior and part of the pulvinar lateralis receive projections from cortical visual areas and from the superior colliculus<sup>4,5,25</sup>. Furthermore, the localization of visual receptive fields recorded from units isolated from both these nuclei in the squirrel monkey<sup>24</sup> led us to reexamine the representation of the visual space in the primate pulvinar.

We have undertaken an investigation of the projections of the visual field onto the pulvinar of the *Cebus* monkey in order to clarify some aspects concerning the number, extent and location of these representations. In the present investigation we have attempted, besides, a correlation between the visual field representation and a cytoarchitectonic subdivision based on Friedmann's analysis of the posterior thalamus of *Macaca mulatta*<sup>12</sup>.

#### MATERIAL AND METHODS

Seventeen *Cebus* monkeys weighing from 1.6 to 4.4 kg were used in acute or chronic preparations. Of these, 5 (4 acute and 1 chronic) were used for multi-unit recordings; the remaining 12, all chronic preparations, are shared with a report on single unit activity in the pulvinar<sup>15</sup>. Topographical data from receptive fields of single units were used to complement the multi-unit analysis.

Five to seven days prior to the recording sessions, a prothesis enabling the orientation of the head according to Horsley-Clarke coordinates was implanted to the skull, under anesthesia. Regression lines relating pulvinar anteroposterior coordinates to anteroposterior dimension of the skull and to body weight were used to estimate coordinates for recording sites<sup>14</sup>.

Before each recording session the animal was anesthetized with ketamine hydrochloride (Ketalar, Parke Davis), 20 mg/kg, and the saphena or femoral vein, as well as the trachea were cannulated. In acute preparations tracheostomy was performed and long lasting local anesthetic (Marcaina, Astra) liberally applied to wound margins. Mydriasis and cycloplegia were obtained by application of both atropine sulfate (1%) and phenylephrine (10%). Immobilization of the animal was initiated by an intravenous injection of 2 mg/kg of gallamine triethiodide (Flaxedil, Abbott) and maintained by a continuous infusion at a rate of 1 mg/kg/h. Artificial respiration was maintained at the rate of 20 strokes/min and the tidal volume adjusted so as to keep expired CO<sub>2</sub> at 5-6% concentration. Except for two animals that were anesthetized by chloralose (Merck), 35 mg/kg, analgesia was achieved by a mixture of 70% N<sub>2</sub>O and 30% O<sub>2</sub>. Rectal temperature was maintained at 36.5 °C through the use of a DC electric heating pad controlled by a telethermometer (Yellow Spring, 73A). EKG and EEG were continuously monitored. To avoid drying of the cornea contact lenses (ØD) fitted by keratometry were employed.

In chronic preparations, at the end of each recording session Flaxedil infusion was discontinued and the animals, still under anesthesia, were allowed to recover from the effect of the paralyzing agent. To facilitate the recovery, neostigmine methylsulphate 0.03 mg/kg (Prostigmine, Roche) combined with atropine sulphate 0.15 mg/kg were administered. Using this procedure it was possible to carry out several recording sessions using the same animal.

At the end of the last recording session, the animal, under barbiturate anesthesia, was perfused with an intra-aortic flow of saline (0.9%) followed by formalin (4%). Following decapitation, the head was kept in fixative overnight. Correlation between recording site and cytoarchitectonic subdivisions was achieved by inspection of 40  $\mu\text{m}$  coronal frozen sections stained with cresyl violet. In two brains a myelin stain method (Weil) was also employed.

The projections of the fovea and optic disc of both eyes, on a tangent screen (Polacoat), were determined by means of a reversible ophthalmoscope. A line joining the projection of the central artery emergence point and of the fovea was taken as the horizontal meridian and the normal to this line at the projection of the fovea as the vertical meridian.

Electrical activity of isolated or of small clusters of neurons was led off by means of glass insulated tungsten microelectrodes (35–75  $\mu\text{m}$  tips) oriented by a LPC-K3 micromanipulator. After amplification signals were monitored using conventional CRO and audio display systems. Control of the electrode position was obtained by performing small electrolytic lesions during a penetration (5–20  $\mu\text{A}$  for 5–15 sec, tip positive).

The data used in the present study was obtained using either small tipped microelectrodes, enabling the isolation of the activity of individual neurons or larger microelectrodes yielding multi-unit recordings. During single unit analysis receptive fields were mapped for the dominant eye and their positions related to the meridians of that eye. When recording multi-unit responses both eyes were left open; by doing so the center of the receptive field of a cluster of binocularly driven neurons reflects the average position of the center of both monocular fields. The positions of the center of the monocular receptive fields were determined in respect to the vertical and horizontal meridians of the corresponding eye. In the determination of the center of binocular receptive fields the vertical meridian was considered to lie half-way between the projection of the two foveae. The positions of each fovea and of the blind spots were plotted before and after each penetration to assure that no drift had occurred. Receptive fields positions were defined in reference to an equatorial, double meridian, gnomonic coordinate system, where their locations are expressed as two angles: azimuth and elevation<sup>6</sup>. The zero azimuth and elevation lines were considered coincident with the vertical and horizontal meridians, respectively.

Visual stimulation was achieved by means of a hand-held projector on a rear projection screen. Receptive fields were mapped using patterned stimuli during animal arousal as identified by fast, low voltage, asynchronous EEG activity.

The center of the tangent screen placed 28.5 or 57 cm away from the anterior nodal point of the eye was made coincident with the zero azimuth. When exploring the

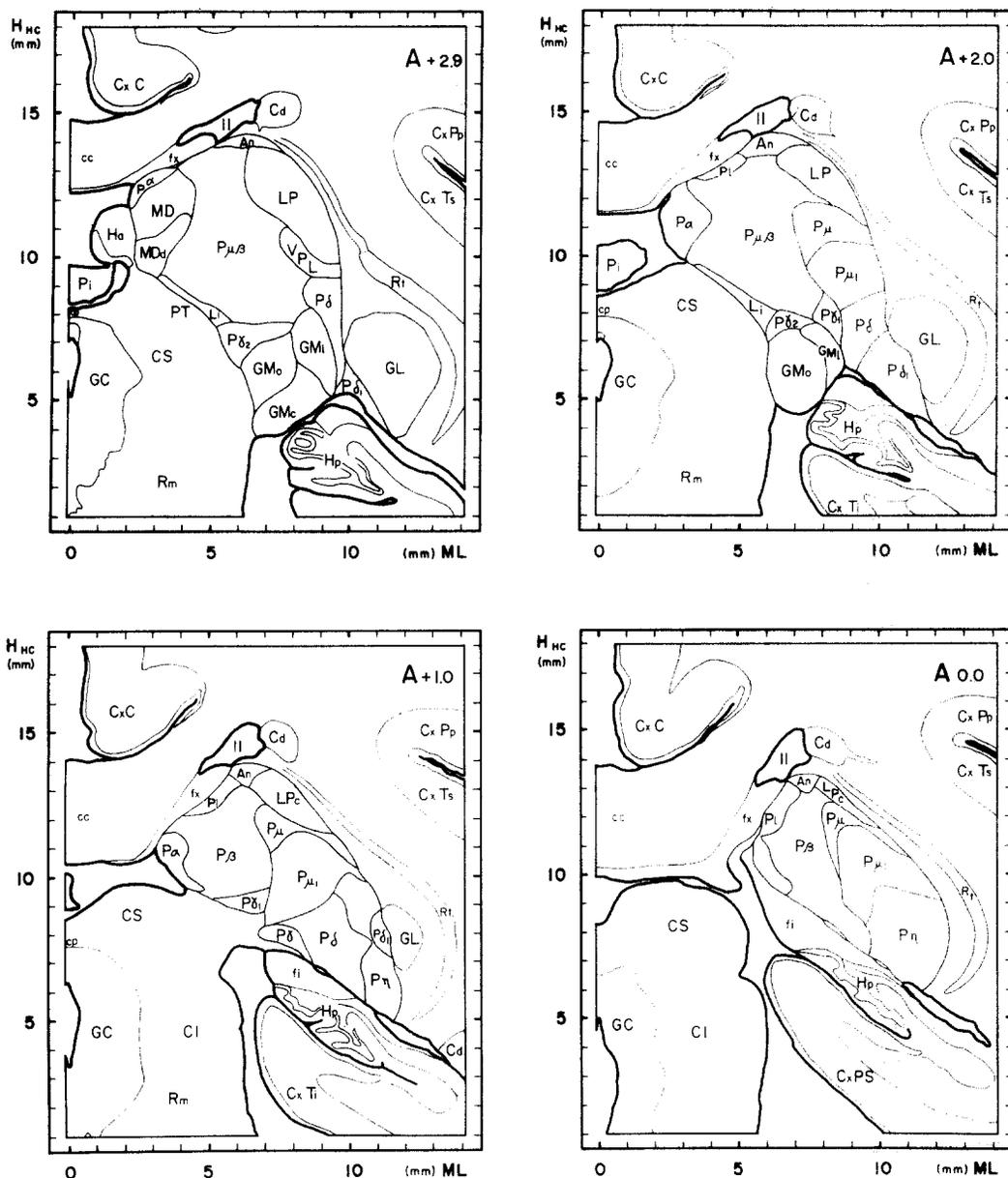


Fig. 1. Architectonic subdivision of cebus monkey pulvinar nucleus in 4 Horsley-Clarke frontal planes. Scales corrected for shrinkage. Abbreviations: An, nucleus angularis; aq, aqueductus Sylvii; cc, corpus callosum; Cd, nucleus caudatus; Ce, cerebellum; CI, colliculus inferior; cp, commissura posterior; CS, colliculus superior; Cx C, cortex cingularis; CxPp, cortex parietalis posterior; CxPS, cortex peristriatus; CxTi, cortex temporalis inferior; CxTs, cortex temporalis superior; fi, fimbria hippocampi; fx, fornix; GC, substantia grisea centralis; GL, nucleus geniculatus lateralis; GM, nucleus geniculatus medialis; GM<sub>0</sub>, . . . . ., pars orodorsalis; GM<sub>e</sub>, . . . . ., pars caudoventralis; GM<sub>1</sub>, . . . . ., pars lateralis; Ha, nucleus habenularis; Hp, hippocampus; Li, nucleus limitans; LP, nucleus lateralis posterior; LP<sub>e</sub>, . . . . ., pars caudalis; MD, nucleus medialis dorsalis; MD<sub>a</sub>, . . . . ., pars densocellularis; P, pulvinar; P<sub>α</sub>, pulvinar pars pulvinalis alpha; P<sub>β</sub>, pulvinar pars pulvinalis beta; P<sub>γ</sub>, pulvinar pars pulvinalis gamma; P<sub>γ</sub><sub>1</sub>, pulvinar pars pulvinalis gamma<sub>1</sub>; P<sub>γ</sub><sub>2</sub>, pulvinar pars pulvinalis gamma<sub>2</sub>; P<sub>δ</sub>, pulvinar pars pulvinalis delta; P<sub>δ</sub><sub>1</sub>, pulvinar pars pulvinalis delta<sub>1</sub>; P<sub>η</sub>, pulvinar pars pulvinalis eta; P<sub>μ</sub>, pulvinar pars pulvinalis mu; P<sub>μ</sub><sub>1</sub>, pulvinar pars pulvinalis mu<sub>1</sub>; P<sub>μ</sub><sub>β</sub>, pulvinar pars pulvinalis mu-beta; P<sub>1</sub>, pulvinar pars pulvinalis 1; Pi, corpus pinealis; PT, regio pretectalis; Rm, nucleus reticularis mesencephali; Rt, nucleus reticularis thalami; VPL, nucleus ventralis posterior lateralis; II, ventriculus lateralis.

periphery of the visual field the screen was laterally displaced so that its center corresponded to azimuth  $45^\circ$ .

The conversion from isoazimuth and isoelevation maps into polar representation was carried out using previously published algorithms<sup>13</sup>. Through this polar representation it became possible to estimate the volume of the nucleus devoted to units of solid angle using a Digitizer (HP 9864A) and a programmable calculator (HP 9810A).

## RESULTS

### *Anatomical considerations*

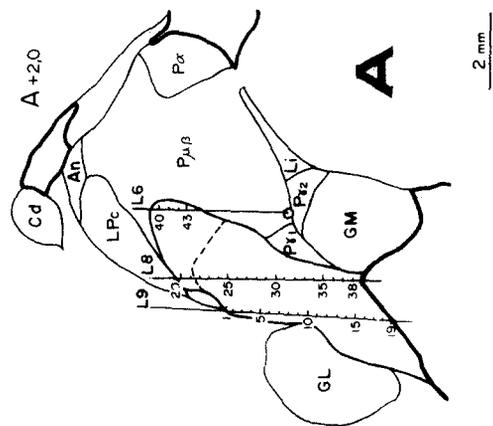
Primates show a striking development of the posterior thalamic region, with a well developed pulvinar nucleus. Friedmann<sup>12</sup> in a detailed analysis of this region proposed a subdivision of the pulvinar, in which 10 subnuclei were identified. The various architectonic subdivisions described for the macaque are also recognizable in *Cebus*<sup>14</sup>. However, based on the study of the myeloarchitecture it was found necessary to subdivide Friedmann's  $P\mu$  into a dorsal and a ventral region, named  $P\mu$  and  $P\mu_1$ , respectively. Fig. 1 illustrates in 4 Horsley-Clarke frontal planes the various subdivisions of the pulvinar and their relations with neighboring structures.

Preliminary results have indicated that the region of the pulvinar which is activated by visual stimulation is located in its lateral portion and includes  $P\delta$ ,  $P\delta_1$ ,  $P\gamma$ ,  $P\eta$ ,  $P\mu$  and  $P\mu_1$  sub-nuclei. Using electrophysiological techniques the topography of projections of the visual field onto this region was analysed. Correlation between recording sites and receptive field positions was carried out for each of several penetrations distributed throughout the whole extent of the nucleus. The data presented in this study was obtained in a total of 64 penetrations; of these 29 were carried out during multi-unit recording experiments. An example of the results obtained in three penetrations carried out in one plane is illustrated in Fig. 2.

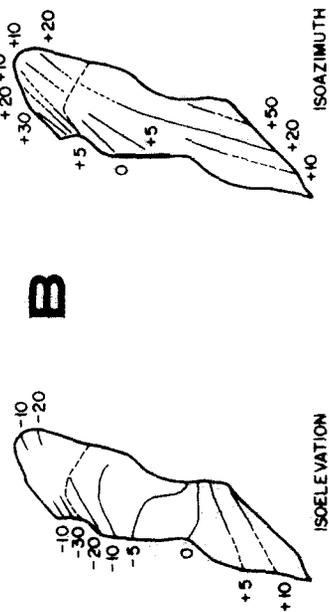
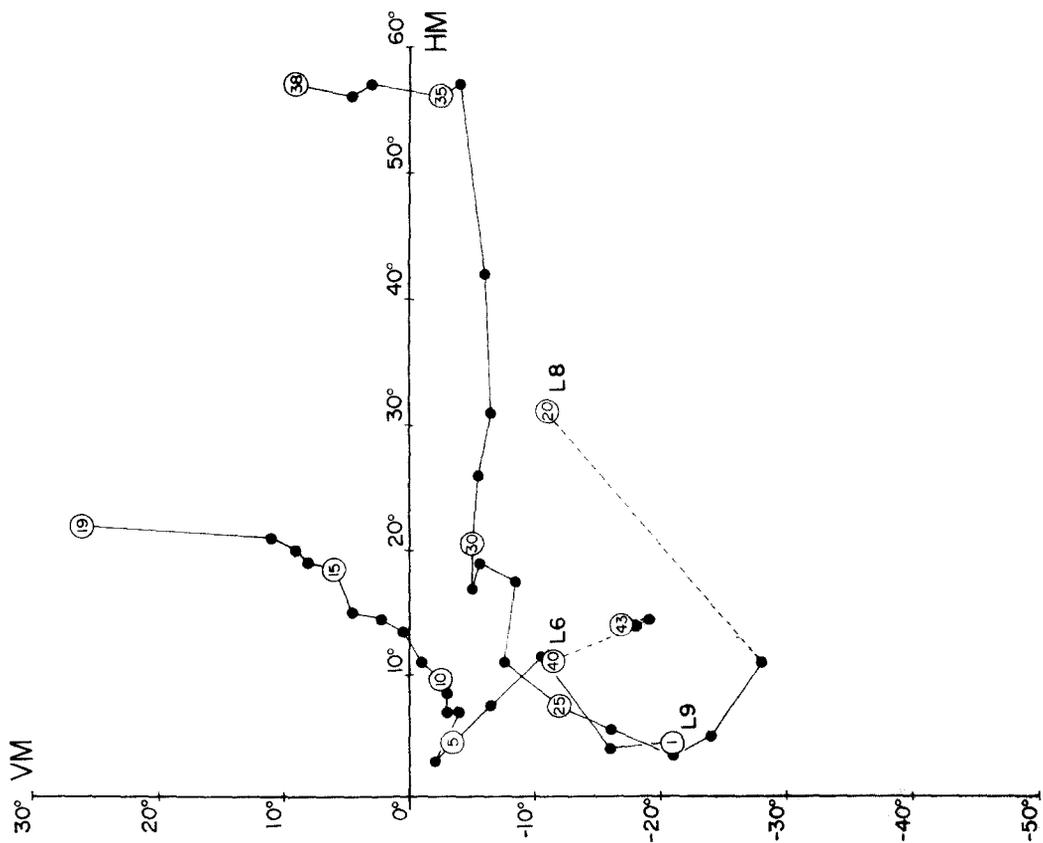
The location of receptive fields corresponding to various recording sites is indicated in an equatorial double meridian gnomonic representation of the contralateral visual hemifield. In the lateralmost penetration, carried out 11 mm from the midline (L 11), the first visually active region corresponds to a receptive field located in the lower visual field, approximately  $9^\circ$  below the horizontal meridian (HM) and lying in the immediate vicinity of the vertical meridian (VM). As the penetration progresses, receptive field centers move upwards. A receptive field with its center located approximately  $8^\circ$  above the horizontal meridian corresponds to the last recording in this penetration. Although receptive field centers stay in the vicinity of VM, a trend to move away from it with increasing distance from the lateral border of the pulvinar is already noticeable in this penetration.

A similar displacement from lower to upper visual field is observed along penetration L 10. Notice that the receptive fields obtained in this penetration are displaced temporally with respect to those of L 11. At the level of the horizontal meridian the representation corresponds to a point  $11^\circ$  temporal to VM.

The most medial penetration L 7, shows a striking difference in the sequence



2 mm



of representation of the visual field when compared to L 10 and L 11. As this penetration proceeds ventralwards, the receptive field centers move from the upper to the lower visual field and approach the vertical meridian. The receptive field centers obtained at the level of HM correspond to a region in space intermediate to that represented in penetrations L 10 and L 11. These observations suggest that the dorso-medial portion of the visually active area of the pulvinar includes a second representation of the visual field. Based on data obtained in these penetrations tentative isoelevation and isoazimuth lines were established as shown in insert B of Fig. 1.

Additional information supporting the presence of a double representation of the visual field in the pulvinar is given in Fig. 3, in which a sequence of three penetrations carried out in a plane approximately 1 mm rostral to that of Fig. 2 is illustrated. In penetration L 9 recording sites 1 to 11 are related to receptive fields located in the lower visual field, in the proximity of the vertical meridian. As the penetration proceeds receptive fields attain HM (point 12), moving towards the upper visual field.

Receptive field centers corresponding to the first two recording sites of penetration L 8 move away from HM. As the penetration crosses the border of  $P\mu$  there is a reversal in this sequence and the receptive fields corresponding to successive recording sites (23–38) move from the lower to the upper field. In both these penetrations, L 8 and L 9, the increasing distance of the recording site from the lateral border of pulvinar results in a temporal shift of receptive field centers (see insert A).

In penetration L 6, restricted to  $P\mu$  the centers of visual receptive fields move in a downward direction along the visual field, as observed in other sequences of recording sites located within the borders of  $P\mu$ , illustrated in Figs. 2 and 4.

In Figs. 2 and 3 we have analysed data obtained in rows of penetrations positioned along coronal planes. The topography of visual field projection along the anteroposterior axis of the pulvinar can be assembled from data gathered in various coronal planes.

The results obtained in five penetrations carried out at Horsley–Clarke medio-lateral plane L 8 are shown in Fig. 4. Insert A indicates the anteroposterior position of these 5 penetrations, together with the position of recording sites and the outline of pulvinar and neighboring structures. A reconstruction of the parasagittal plane L 8 is illustrated in insert B. As in previous figures isoazimuth and isoelevation lines (insert C) were constructed by correlating recording sites with the position of receptive

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Fig. 2. Relationship between receptive field location and recording sites in the pulvinar. Receptive field centers obtained from 3 penetrations are presented in the left side of the figure using an equatorial double meridian gnomonic representation of the visual space. In this representation dashed lines connect receptive field centers of two contiguous recording sites located in the dorsal region; continuous lines being used for the ventral region of the pulvinar. Insert A shows the localization of the recording sites obtained in three penetrations; recording sites are numbered successively for each penetration. The bottom of each penetration is demarcated by electrolytic lesions. Dashed lines in inserts A and B indicate the border between the two representations of the visual field, corresponding to  $P\mu$ , the dorso-medial representation, and  $P_{\text{vig}}$ , the ventrolateral group. In insert B the positions of isoelevation and isoazimuth lines based on data obtained in these penetrations are indicated. For abbreviations see Fig. 1.

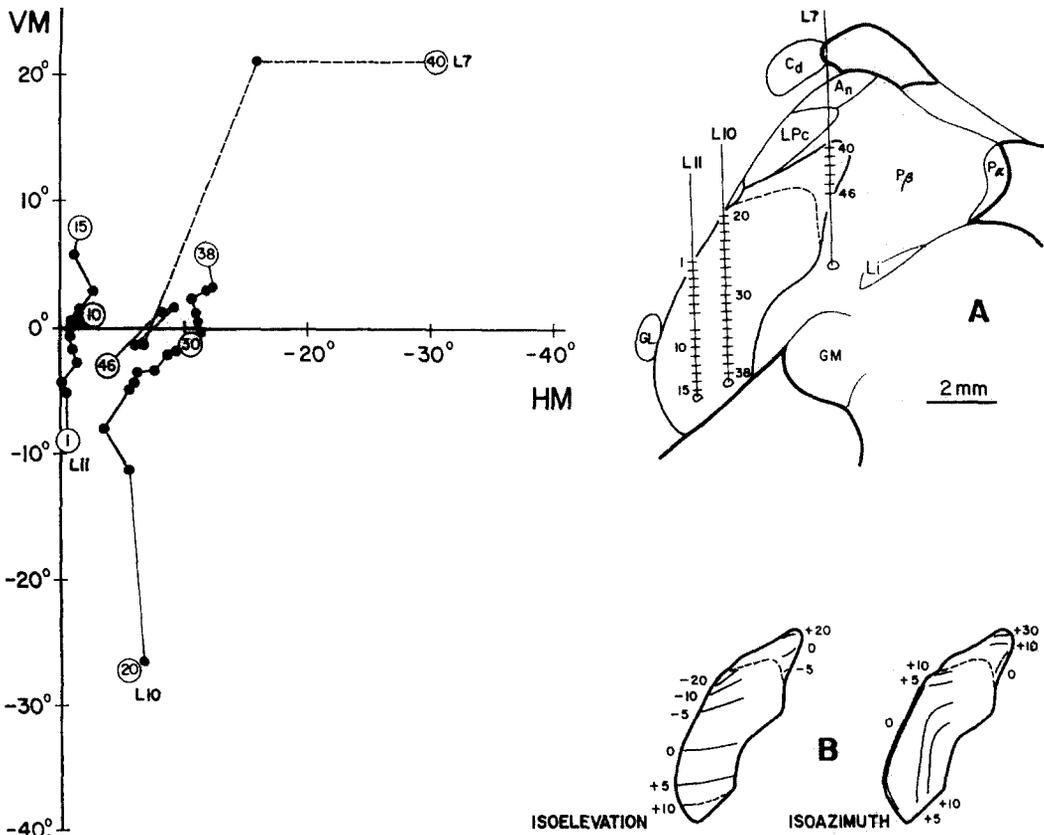


Fig. 3. Topographic representation of the visual space observed in 3 penetrations in a plane approximately 1 mm rostral to that illustrated in Fig. 2. Same conventions as used in Fig. 2. For abbreviations see Fig. 1.

fields centers within the visual field. From the projection of the horizontal meridian (zero isoelevation line) it becomes clear that a larger volume of the nucleus is devoted to the representation of the lower visual field and that there is a considerable expansion of the central portion of the visual field at the central region of the nucleus.

The maps presented in Figs. 2, 3 and 4 were based in 10 penetrations which yielded 114 recording sites. Similar maps were constructed based on data gathered in 19 additional penetrations. The data obtained in these 29 penetrations were confirmed and supplemented by the results obtained in 35 penetrations carried out in the course of a single unit analysis of this region<sup>15</sup>. The topography of visual field representation obtained from the analysis of the receptive fields of units isolated in the pulvinar confirm in all respects the findings obtained from multi-unit recordings. Based on this data a reconstruction of the overall topographic representation of the visual field in the pulvinar was prepared.

In Fig. 5 the visually active region of the pulvinar, localized laterally, is delimited from surrounding structures by a heavier line. Observation of the isoazimuth and iso-

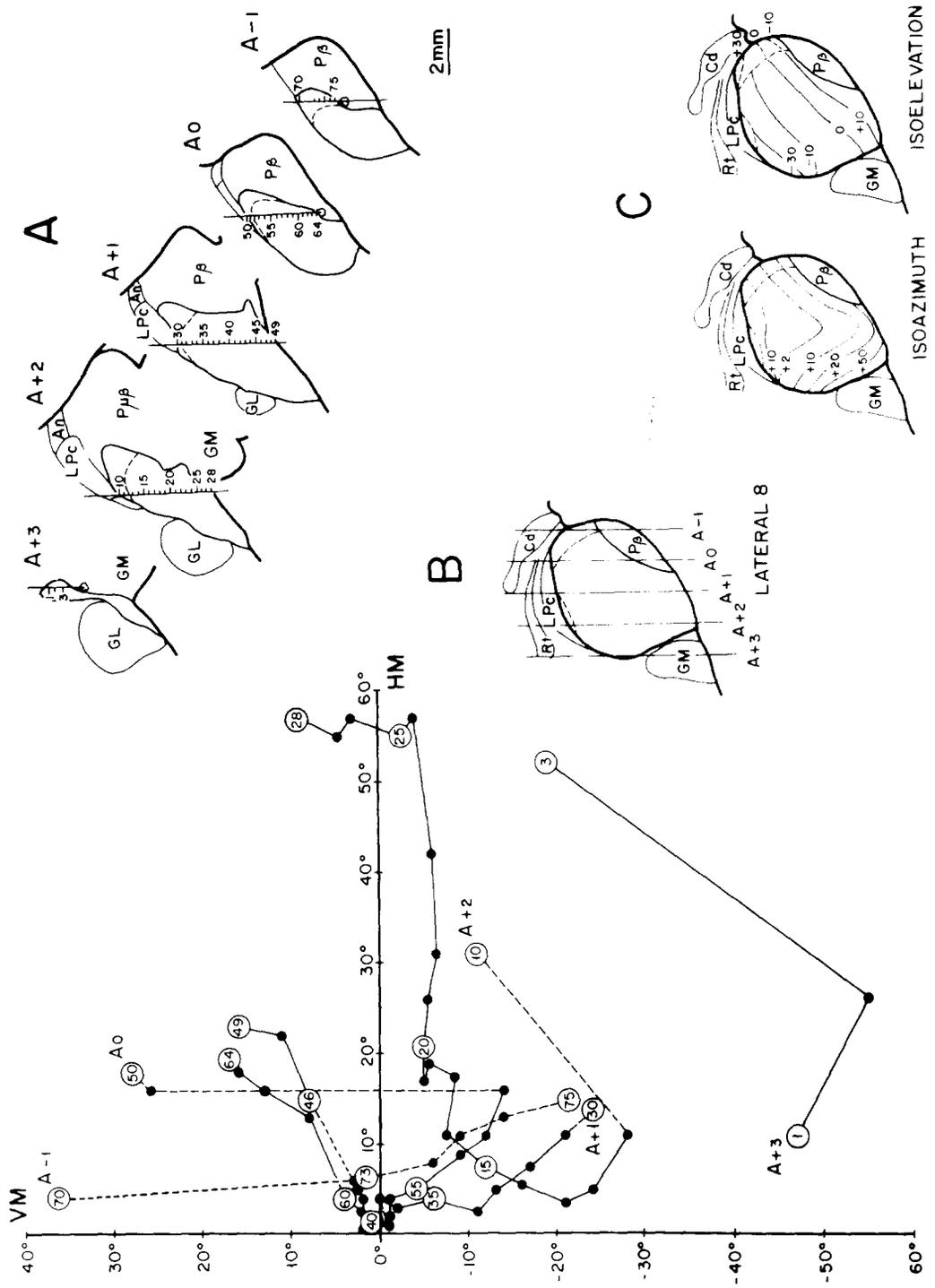


Fig. 4. Receptive field centers obtained in 5 penetrations carried out at a parasagittal plane (L8). Drawings of frontal planes including 5 penetrations carried out in a plane 8 mm from the midline are shown in insert A. Insert B is a reconstruction of this parasagittal plane showing the active region and surrounding structures. Insert C shows isoazimuth and isoelevation surfaces of the visual field constructed based on data obtained in these penetrations. Notice the preponderance of lower visual field representation.

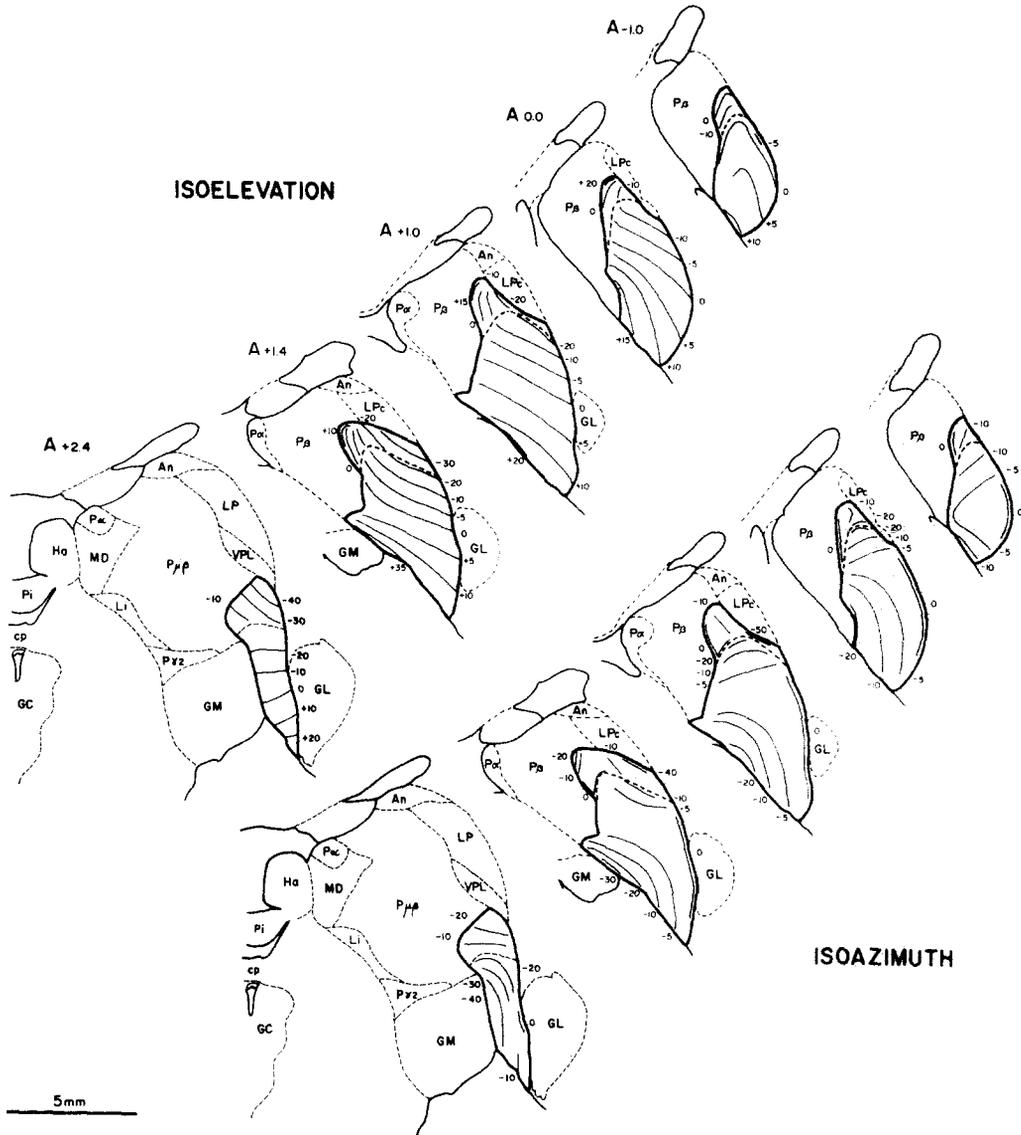


Fig. 5. Diagrammatic representation of the pulvina showing isoelevation and isoazimuth surfaces of  $P_{\mu}$  and  $P_{vis}$  projections in 5 coronal planes. The visually active region is limited by heavy lines, and the dashed line within this region separates the two projection areas. For abbreviations see Fig. 1.

elevation maps clearly indicates the presence of a double representation of the contralateral hemifield that extends along the anteroposterior dimension of the lateral portion of the pulvina. These maps suggest that a point in the visual field projects to an anteroposterior column of cells in the pulvina, similar to the projection lines defined for the dorsal lateral geniculate nucleus of the cat<sup>6</sup>. A dashed line separates the visually active area into two regions which include independent representations

of the visual field: a ventrolateral portion occupying a considerably larger volume, and a smaller dorsomedial region.

In the ventrolateral representation the vertical meridian (zero isoazimuth) is represented along its lateral border; the extent of vertical meridian representation is indicated by a thickening of the line representing the lateral border of the active region. The horizontal meridian (zero isoelevation) at rostral coronal planes is represented in a region lying between the two geniculate nuclei, running from the superior third of the lateral geniculate nucleus towards the inferior third of the medial geniculate nucleus (see Fig. 5, plate A +2.4). Towards the caudal pole the representation of HM is displaced dorsally in the medial region. Thus, the representation of the inferior quadrant predominates at rostral levels, while caudally that of the superior quadrant prevails (see Fig. 5, plate A -1.0). There is a considerable expansion of the projection of the center of gaze in a region lying contiguous to the caudal pole of the lateral geniculate nucleus.

The second, dorsomedial representation of the contralateral visual hemifield shows a different topographic arrangement. In this region the representation is rotated 90° clockwise around the rostrocaudal axis, therefore the vertical meridian is represented at the medioventral border of this region, and the horizontal meridian, represented in the central and caudal portions of this area, runs from the medial third of the ventral border to the dorsal one. The upper visual field is represented medially, while the lower projects to the lateral portion of this region. The rostral pole of the dorsomedial region is entirely devoted to the representation of the periphery of the lower visual field, as shown in plate A +2.4 of Fig. 5. Caudal to this plane a representation of the upper visual field can be observed. Nevertheless the lower visual field still prevails (see isoelevation plates A +1.4 to A -1.0 in Fig. 5).

Our results indicate a greater representation of the inferior quadrant in both the ventrolateral and dorsomedial projection areas. When comparing these projections marked differences in the ratio of the volumes devoted to the central and peripheral portions of the visual field are observed. In order to compare the extent of the representation of central and peripheral vision in these two projection areas the magnification factor was calculated for various eccentricities. We determined the magnification factors in polar representations of the pulvinar visual field projections to allow a comparison of our results with those obtained for the rhesus primary visual system<sup>10, 19</sup>. The isoelevation and isoazimuth maps were combined and transformed into a polar representation, centered at the fovea, as shown in Fig. 6A and B. The magnification factor was determined for each eccentricity by dividing the volume of tissue devoted to the representation of a given eccentricity by the corresponding solid angle of visual field. The magnification factor, expressed in cubic millimeter per stereoradian, for different eccentricities for both the ventrolateral and dorsomedial representations is shown in Fig. 6C. Due to the small size of the dorsal representation and to the limited number of recording sites in this region it was not possible to establish with certainty the magnification factor corresponding to the immediate vicinity of the center of gaze. The data available for points lying between the center of gaze and an eccentricity of 10° were averaged and the result taken as representative for an eccentricity of 5°.

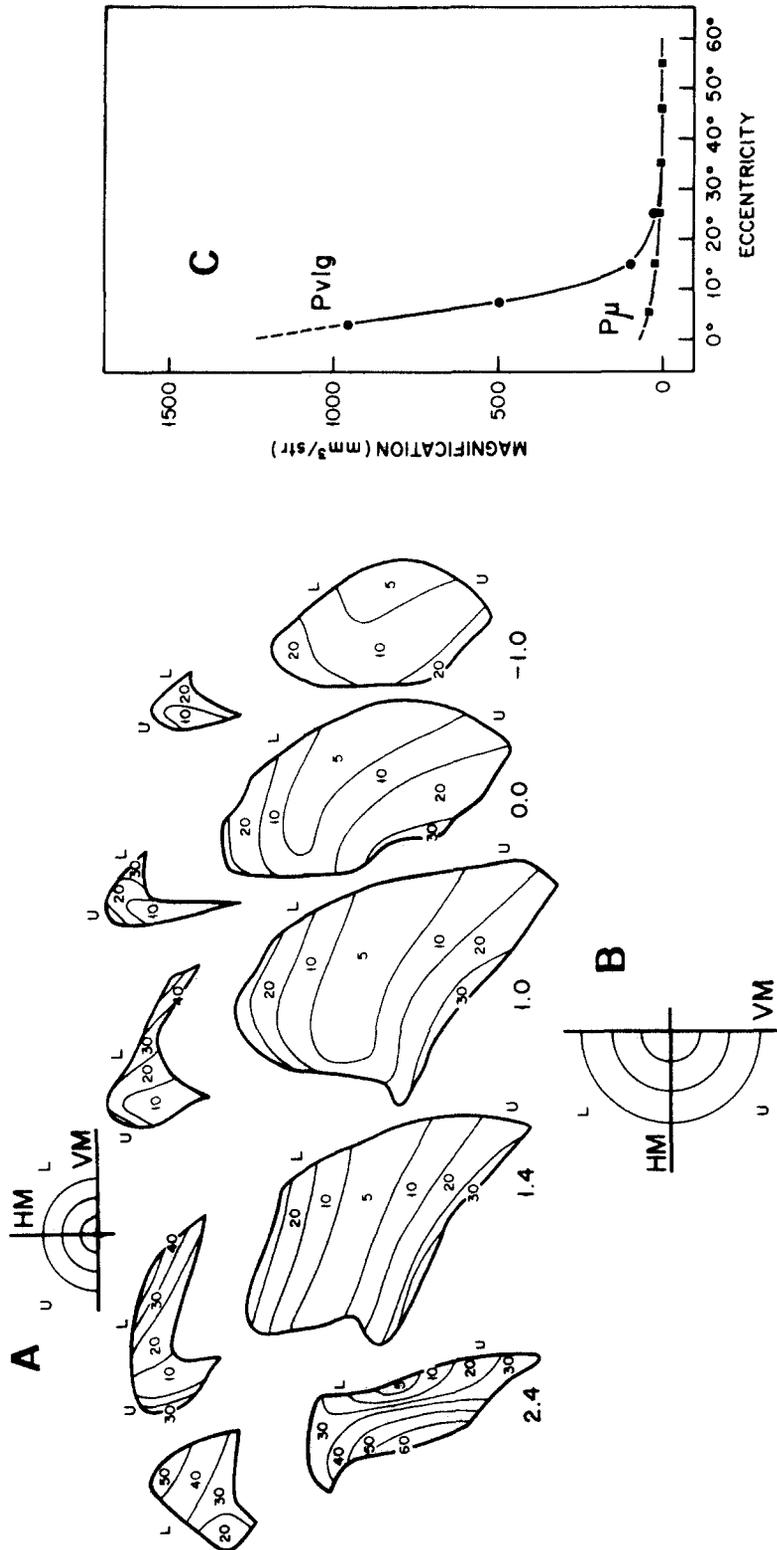


Fig. 6. Diagrammatic representation of the topography of the visual field, in polar coordinates, onto the dorsomedial (A) and ventrolateral (B) projection areas of the pulvinar. U and L denote upper and lower field, respectively. Inserts in A and B give indication of the orientation of the visual field representation.  $P\mu$  and  $P\nu_{lg}$  magnification factors as function of eccentricity are illustrated in C.

In  $P_{vlg}$  averaged values are presented for 2.5 and 7.5°. It is evident that in the ventrolateral projection there is a great expansion in the representation of the center of gaze while in the dorsomedial projection, central and peripheral regions of the visual field are approximately equally represented. Although the precise determination of the magnification factor for the central visual field in  $P_{\mu}$  is not possible, it is interesting to note that the magnification factor for the peripheral portion of the visual field is equal, in absolute values, in both representations.

## DISCUSSION

In the course of a single unit study of the pulvinar we observed that visually driven neurons were restricted to a region extending from its lateral to ventrolateral borders<sup>15</sup>. Since the visually active area includes regions of varying cyto and myelo-architectonic structures we decided to adopt Friedmann's<sup>12</sup> elaborate subdivision of the pulvinar as a guide line for establishing the topography of visual projections in this nucleus.

The results obtained in this study indicate the presence of two independent representations of the visual space. The first, named ventrolateral group ( $P_{vlg}$ ) representation, is coextensive with sub-nuclei  $P\delta$ ,  $P\delta_1$ ,  $P\gamma$ ,  $P\mu_1$  and  $P\eta$ ; while the second, the dorsomedial representation, is coextensive with sub-nucleus  $P_{\mu}$ <sup>16</sup>. It is not easy to establish with certainty a homology between Friedmann's classification of the pulvinar and the division proposed by Olszewski<sup>26</sup>, frequently adopted in studies of the primate brain<sup>11,20,25</sup>. According to our interpretation, Olszewski's pulvinar inferior corresponds to Friedmann's sub-nuclei  $P\delta$ ,  $P\delta_1$ ,  $P\gamma$ ,  $P\gamma_1$  and the rostral part of  $P\eta$ . Sub-nuclei  $P_{\mu}$  and the caudal part of  $P\eta$  are included in pulvinar lateralis. Therefore the  $P_{vlg}$  of this study extends across two of Olszewski's subdivisions, encompassing part of pulvinar inferior and part of pulvinar lateralis. The dorsomedial representation lies within the boundaries of pulvinar lateralis, being coextensive with  $P_{\mu}$ <sup>14</sup>. Consequently the visually active area defined in this study is considerably more extensive than that reported by Allman et al.<sup>1</sup> in the owl monkey and by Bender<sup>3</sup> in the rhesus. According to these authors a single representation of the visual field is observed, being coextensive with and restricted to pulvinar inferior. However, the description of reciprocal connections between striate cortex and both pulvinar inferior and lateralis in *Macaca* and *Saimiri*<sup>25</sup> is compatible with the present findings.

The projection of the visual field onto  $P_{vlg}$  is characterized by an extensive representation of the central visual field at the level of the caudal pole of the lateral geniculate nucleus. It should be taken into consideration that the apparent volume of the region representing the center of gaze is increased by the presence of bundles of fibers that permeate this region, possibly originating from the brachium of the superior colliculus. Even allowing for this, the representation of the center of gaze occupies a larger extent than that reported for the owl monkey<sup>1</sup>. We can attribute this difference to the absence of a well developed region of central vision, for the owl monkey, the only nocturnal New World primate, does not possess a true fovea. The results reported for the macaque<sup>3</sup> are not detailed enough to permit a direct compa-

ri-son. The comparison of our magnification functions for  $P_{vlg}$  with those described for LGN<sup>19</sup> and  $V_I$ <sup>10</sup> of the macaque led us to suppose that there is a smaller predominance of the central visual field upon the periphery representation in  $P_{vlg}$  than in LGN or  $V_I$ . It should be noted that as regards both absolute and relative (% volume/str) values of magnification there is always a prevalence of LGN upon  $P_{vlg}$  values.

In both macaque and owl monkey the vertical meridian was described as originating in the lateral border of pulvinar inferior, then bending inwards following the border between pulvinar inferior and lateralis. This discrepancy may be attributed to a misinterpretation of the extent of representation of the central visual field for, as we have shown, the representation of the center of gaze extends across the whole of the mediolateral dimension of the nucleus. Furthermore, our results are in agreement with the representation of the vertical and horizontal meridians proposed by Ogren and Hendrickson<sup>25</sup>. It is also interesting to notice that the horizontal meridians of the two representations of the visual field are contiguous, which is also largely the case for the multiple cortical visual field maps<sup>2</sup>.

The dorsomedial projection occupies a considerably smaller nuclear volume, and thus it was not possible to establish with equal certainty the relative magnitudes of representation of the central and peripheral visual fields. As in  $P_{vlg}$ , projections of the lower visual field predominate. As postulated by Trevarthen<sup>29</sup> the lower visual field is more directly concerned with the immediate surroundings, therefore this finding points towards a participation of the pulvinar with this aspect of visual information processing.

Our results suggest that a point in space is projected onto a row of cells in the pulvinar which extends along its anteroposterior dimension. This arrangement is similar to that reported in the lateral geniculate nucleus of the cat<sup>6</sup>. This type of anatomical arrangement allows the interaction of various types of projections<sup>25,27</sup> occurring at different anteroposterior planes of the nucleus.

The present study does not rule out the possibility of the presence of other representations of the visual space in the pulvinar. In some penetrations which passed through the mesial border of  $P_{vlg}$  responses were obtained from regions of the visual space that did not conform with the orderly sequence of representation of the visual space in this region. These results were interpreted as due to the activity of the numerous fiber bundles that cross the nucleus at this level. This interpretation is supported by single unit recordings obtained in this region; all units studied presented spike potentials characteristic of soma recordings<sup>15</sup>, and the topographic location of their receptive fields conforms with the overall pattern of representation obtained with multi-unit recordings.

In addition to the visual responses described in pulvinar inferior<sup>1,3</sup>, visually driven units were found in pulvinar medialis<sup>24</sup>, a region which has, in the rhesus, reciprocal connections with the cortical frontal eye fields<sup>30</sup>. Our failure in obtaining responses in this region may be attributed to experimental conditions, since alterations in visually evoked responses were observed in the pulvinar after muscle paralysis<sup>16</sup>.

Visually evoked activity in the pulvinar shows a much greater dependence on

experimental conditions than those recorded in the geniculostriate and retinotectal relay centers. When studying pulvinar single units responses to visual stimuli it became clear that their activation depended on factors other than stimulus characteristics. Some units would respond vigorously to an adequate stimulus, properly oriented in a well defined region of the visual space when the animal presented a desynchronized EEG. The same unit when the animal's EEG displayed slow waves was totally unresponsive. After arousal promoted by somatic or auditory stimulation, the cell would again respond to the adequate stimulus.

Anatomical evidences indicate that pulvinar cells receive synaptic afferences from various sources<sup>21,23,27,31</sup>, and that complex interactions may occur from these various inputs at the level of the glomeruli found in this region<sup>22</sup>.

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*Note added in proof.* After this manuscript was accepted we had access to a study by Wong-Riley (Wong-Riley, M.T.T., Connections between the pulvinar nucleus and the prestriate cortex in the squirrel monkey as revealed by peroxidase histochemistry and autoradiography, *Brain Research*, 134 (1977) 249-268), who suggested that in the squirrel monkey pulvinar lateralis and pulvinar inferior may be functionally closely related. Based on anatomical data, she also suggested the existence of a visuotopic organized map in pulvinar lateralis, with the horizontal meridian represented in a dorsomedial to ventrolateral direction. These findings are in close agreement with the visuotopic organization of PvlG found in the present study.