A REPRESENTATION OF THE VISUAL FIELD IN THE INFERIOR NUCLEUS OF THE PULVINAR IN THE OWL MONKEY (*AOTUS TRIVIRGATUS*)

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INTRODUCTION

The study of the comparative anatomy of mammalian brains reveals few developments as striking as the expansion in primates of that region of the thalamus referred to as the pulvinar; yet our knowledge of the functional organization of this region is so limited that the pulvinar has been termed the '*terra incognita* of the thalamus'[33]. Portions of the pulvinar have long been suspected of mediating visual functions on the bases of proximity to the known visual centers of the brain stem (the lateral geniculate nucleus and the superior colliculus), early suggestions of direct retinal connections (see ref. 27, pp. 154–155), and deductions from clinical cases[35]. Although ablation experiments have not revealed major visual deficits after pulvinar lesions[9,30], portions of the pulvinar are clearly implicated in visual functions by a number of recent anatomical reports. It now appears that part of the pulvinar is extrinsic, as defined by Rose and Woolsey[28], since it receives a projection from the superior colliculus[13,14,22,23,30]. In addition, parts of the pulvinar project to occipital and temporal areas of cortex[8,10,23,29,32] and there is now anatomical[12,20,31,38], electrophysiological[1,2,11,36,37] and behavioral[24] evidence which indicates that these occipital and temporal cortical areas are involved in visual functions. Finally, photic evoked responses in the inferior pulvinar of the squirrel monkey and bush baby have been recently reported[18].

In view of the evidence that parts of the pulvinar are visual in function, the object of the present investigation was to determine whether portions of the pulvinar are visuotopically organized. In the present study, electrophysiological mapping has revealed evidence for a topographic representation of the visual field which is coextensive with an architectonic entity, the inferior pulvinar. This result is in close correspondence with a recent report that the striate cortex projects topographically onto the inferior pulvinar in the macaque monkey[16].

An abstract of the present findings has been presented elsewhere[3].

METHODS

The methods of electrophysiological mapping of visual structures in the owl monkey have been described previously[1]. In brief, tungsten microelectrodes were used to record from single neurons or small clusters of neurons in the pulvinar of 6 adult owl monkeys (*Aotus trivirgatus*), which were anesthetized with urethane. Receptive fields were determined with small dark bars or slits of light projected on the surface of a translucent plastic hemisphere which represented the visual field. The depth of the microelectrode tip from the surface of the brain was monitored for each receptive field mapped and one or more small electrolytic lesions (20 μA for 10 sec) were made in each penetration to facilitate the reconstruction of microelectrode tracks and the location of recording sites. The experimental brains were perfused and hardened in 10% formol–saline and later frozen, sectioned at 50 μm in either the coronal or parasagittal plane, and stained with cresyl violet for cell bodies. For the photomicrographs of normal material, other brains were perfused with formol–saline, dehydrated, embedded in celloidin, and alternate series of 30 μm sections were stained with thionin for cell bodies or hematoxylin for myelin (Heidenhain–Woelcke technique).

RESULTS

Architectonically, the inferior pulvinar appears as a distinct subdivision of the dorsal thalamus. The nucleus is clearly distinguished from adjacent structures in both Nissl and myelin preparations. Figs. 1–3 illustrate portions of the dorsal thalamus including the inferior pulvinar in 3 standard planes of section. In comparison with dorsomedially adjacent portions of the pulvinar, the cells of the inferior pulvinar are more densely packed and the nucleus has a uniform appearance. Myelinated fibers course through the inferior pulvinar in a caudomedial direction in almost the horizontal plane (see Fig. 3). As Olszewski[25] observed in the macaque, there appear to be two systems of horizontal fibers passing through the inferior pulvinar. The first is represented by the thick fiber bundles seen in the lateral portion of the nucleus. The second is a much more extensive system of small fiber bundles reaching from the rostral border with the lateral geniculate to the caudomedial aspect of the inferior pulvinar.

The inferior pulvinar is bordered ventromedially by the medial geniculate nucleus and rostrally by the lateral geniculate nucleus and is separated from these adjacent structures as well as from the superior pulvinar by bands of myelinated fibers. We have used the term superior pulvinar to denote the remainder of the pulvinar complex excluding the inferior pulvinar.

Visuotopic organization

The visuotopic organization of the inferior pulvinar in the owl monkey was determined by relating receptive field positions to successive recording sites in a number of dorsoventral electrode penetrations. One such penetration near the rostral margin of the pulvinar is shown in Fig. 4. Neurons close to the dorsal junction of the

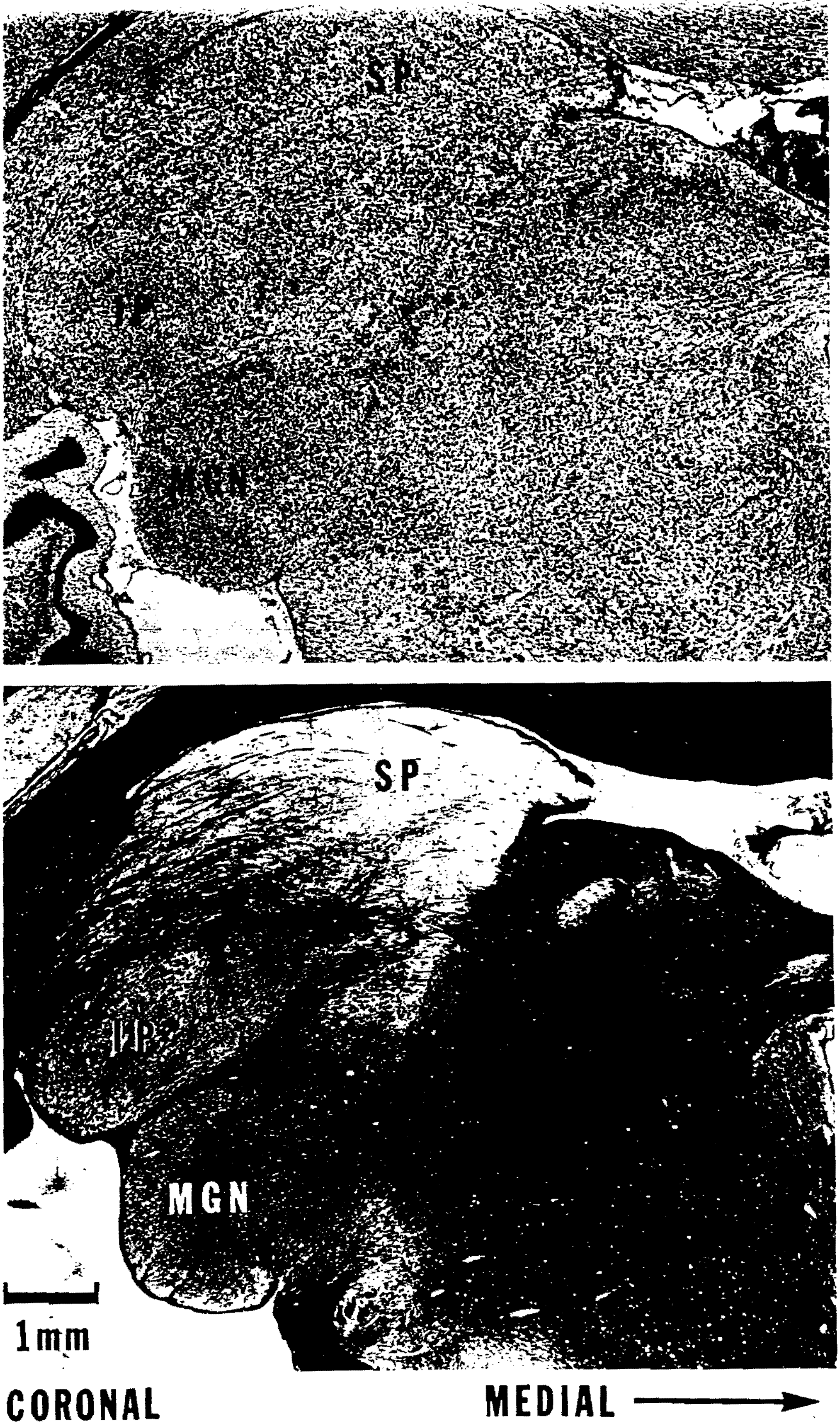
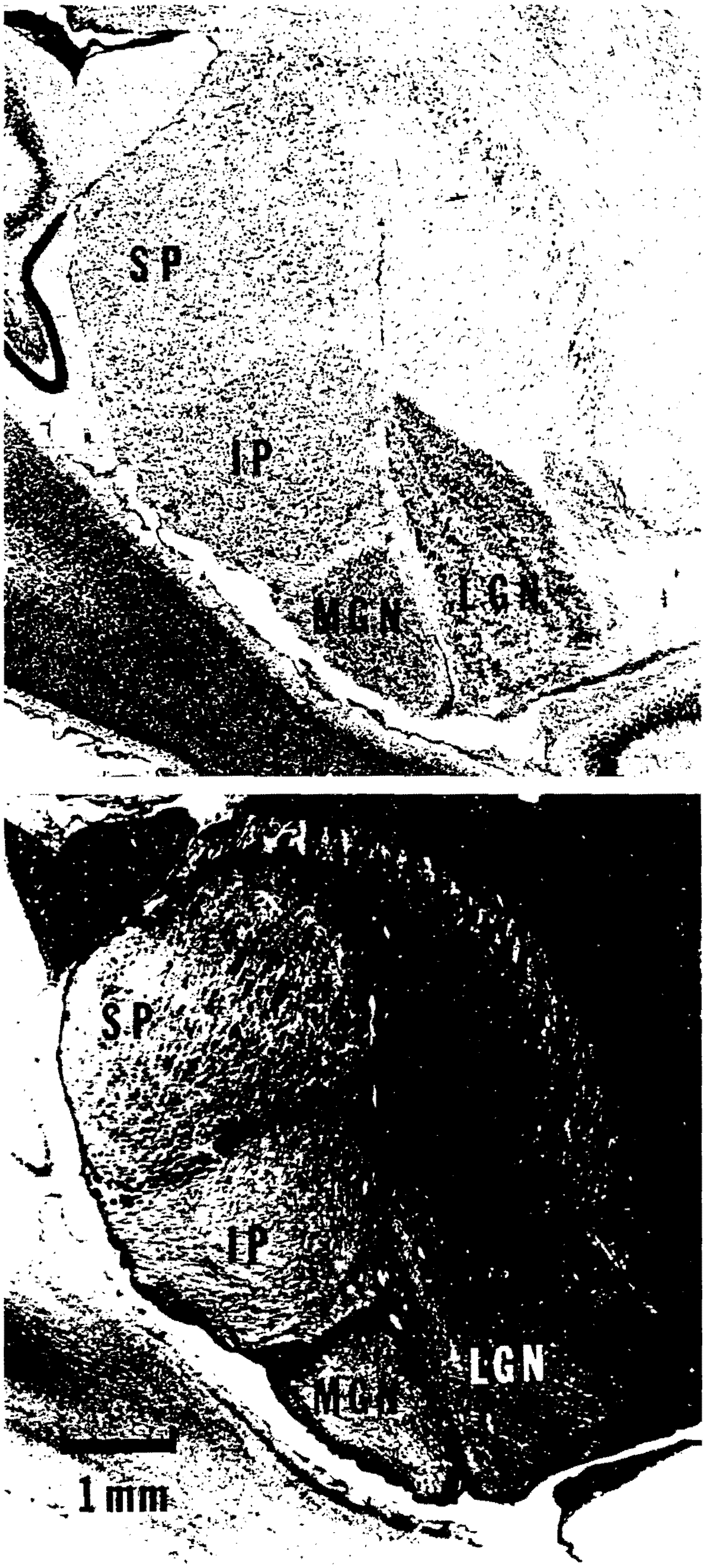


Fig. 1. Adjacent coronal 30 μm sections through the left thalamus of an owl monkey. The upper section was stained with thionin for cell bodies; the lower section was stained with hematoxylin for myelin. IP, inferior pulvinar; MGN, medial geniculate nucleus; SP, superior pulvinar.



PARASAGITTAL ● ROSTRAL →

Fig. 2. Adjacent parasagittal 30 μm sections through the left thalamus of an owl monkey. LGN, lateral geniculate nucleus. Other abbreviations and conventions are the same as in Fig. 1.

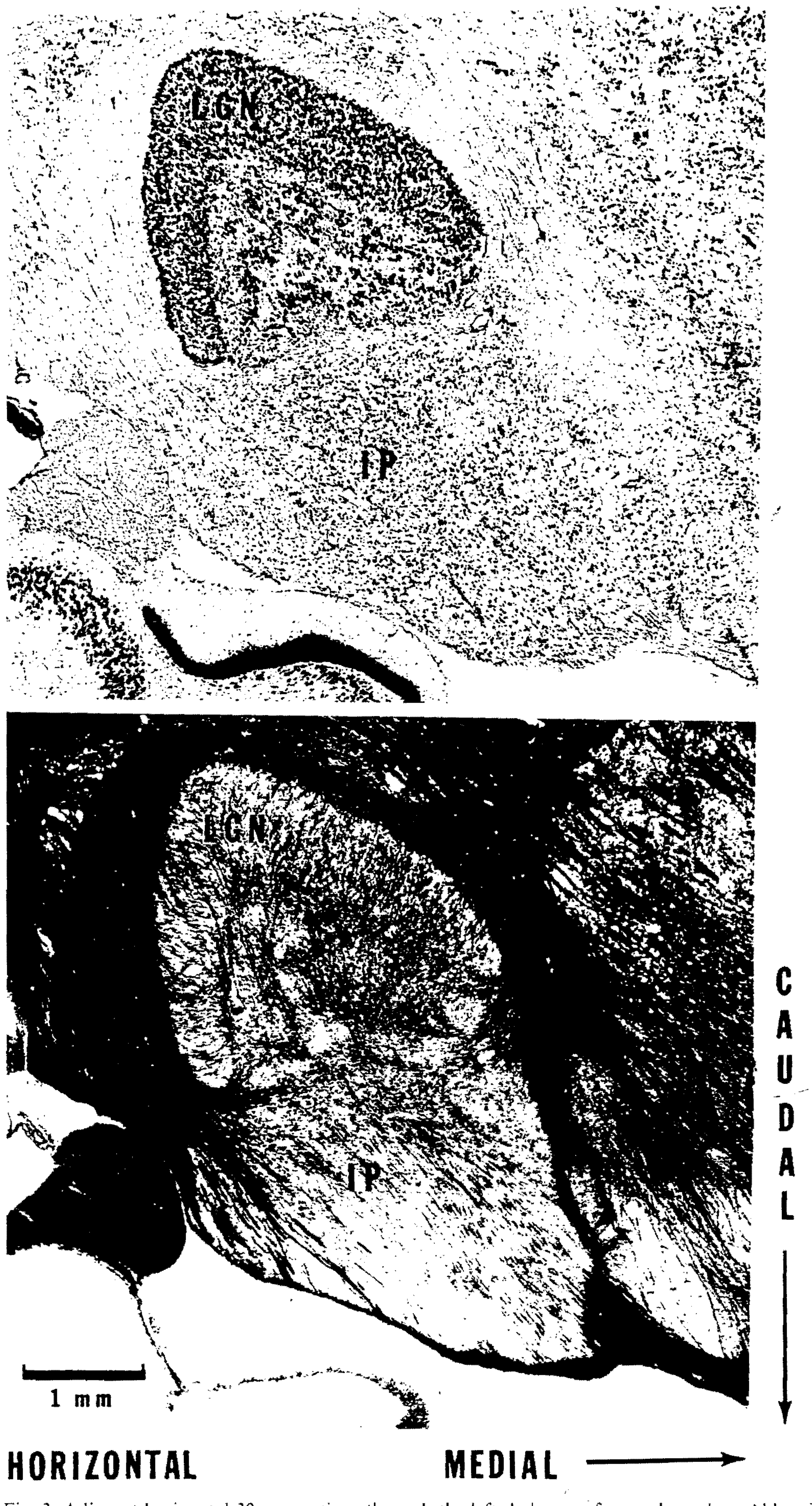


Fig. 3. Adjacent horizontal 30 μm sections through the left thalamus of an owl monkey. Abbreviations and conventions are the same as in Figs. 1 and 2.

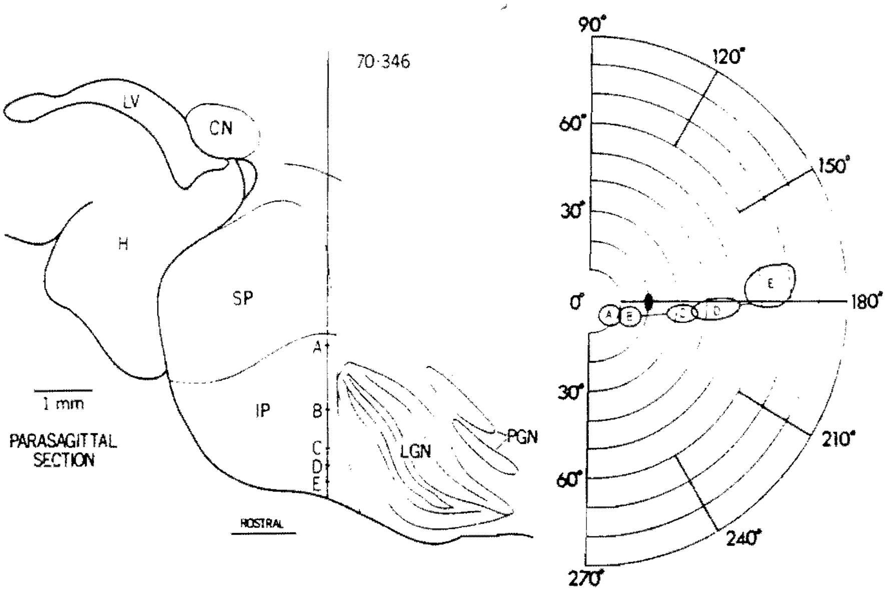


Fig. 4. Receptive fields mapped in experiment 70–346 in a microelectrode penetration through the rostral portion of the inferior pulvinar. The diagram on the left is a drawing of a parasagittal section through the left thalamus. The receptive fields for recording sites A–E are plotted on the perimeter chart of the temporal half of the visual field of the right eye. The solid black oval marked 'OD' indicates the projection of the optic disc in the visual field. CN, caudate nucleus; H, hippocampus; IP, inferior pulvinar; LGN, lateral geniculate nucleus; LV, lateral ventricle; PGN, pregeniculate nucleus; SP, superior pulvinar.

inferior pulvinar with superior pulvinar had small receptive fields located near the intersection of the horizontal and vertical meridians (the center of gaze). Receptive fields for successively deeper recording sites were successively temporal in the contralateral hemifield with the receptive field for the most ventral recording site extending more than 70° from the center of gaze. All receptive fields were near the horizontal meridian. Thus in this portion of the inferior pulvinar, the vertical meridian near the center of gaze is represented dorsally and the temporal periphery is represented ventrally.

A more extensive exploration of the inferior pulvinar is illustrated in Fig. 5. In this experiment, recordings were obtained from a row of 5 electrode penetrations in a parasagittal plane medial to the plane illustrated in Fig. 4. As in Fig. 4, the most dorsal recording sites in the nucleus were activated by stimuli in restricted areas in the central visual field and successively more ventral recording sites related to successively more peripheral receptive field locations. In addition, the experiment reveals that the representation of the upper visual field is caudal and the lower visual field is rostral in this part of the nucleus.

The results of a third experiment are illustrated in Fig. 6. In this experiment, the brain was cut in the coronal plane. As in Figs. 4 and 5, receptive fields near the center of gaze relate to the most dorsal recording sites in the nucleus while more peripheral receptive fields correspond to more ventral recording sites. Receptive fields for electrode penetrations 1–3 show that the representation of the upper visual field is lateral

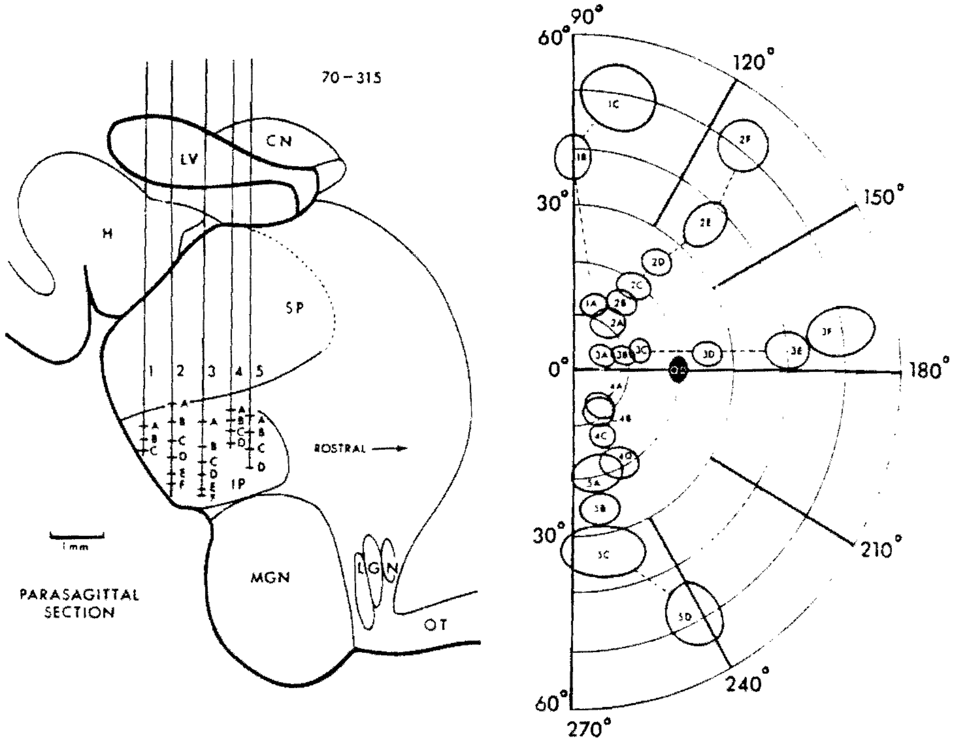


Fig. 5. Receptive fields mapped in a rostrocaudal row of microelectrode penetrations through the inferior pulvinar in experiment 70-315. The diagram on the left is a drawing of a parasagittal section through the left thalamus. Microelectrode penetrations are indicated by numbered vertical lines and recording sites are marked by horizontal bars across these lines and are denoted by letters. The receptive fields corresponding to these recording sites are plotted on the perimeter chart of the temporal half of the visual field of the right eye. OT, optic tract; other abbreviations and conventions are the same as in preceding figures.

to the representation of the lower visual field. Penetration 4 was near the caudomedial margin of the pulvinar and the receptive fields were near the horizontal meridian.

The results from 3 other experiments were consistent with those illustrated in Figs. 4–6. Fig. 7 summarizes our conclusions based on these experiments. The locations of the electrode penetrations in Figs. 4–6 are shown on a dorsal view of the pulvinar in the box on the lower left of Fig. 7. Thus, the reported data can be compared with the summary illustration. Fig. 7 shows 3 coronal sections through the caudal thalamus with coordinates of the visual field superimposed on the inferior pulvinar. The horizontal meridian divides the nucleus into a rostromedial portion in which the lower visual quadrant is represented and a caudolateral portion in which the upper visual quadrant is represented. The horizontal meridian also divides the lateral geniculate in a similar fashion[19]. Much of the dorsal, medial, and lateral margin of the inferior pulvinar corresponds to the vertical meridian. The central 10° of the visual field are represented dorsally and rostrally. More peripheral parts of the visual field are represented ventrally and the extreme temporal periphery is represented near the ventral border of the pulvinar adjacent to the medial geniculate nucleus. The lines of isorepresentation, along which the location of receptive fields of neurons does not

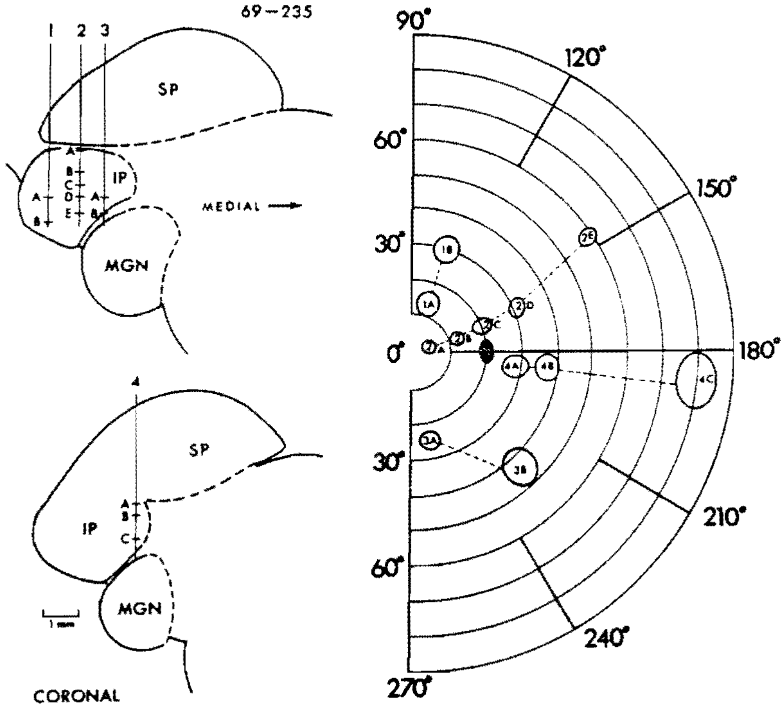


Fig. 6. Receptive fields mapped in microelectrode penetrations through the inferior pulvinar in experiment 69–235. The two diagrams on the left are drawings of coronal sections through the left thalamus. Section A is approximately 500 μm rostral to section B. Abbreviations and conventions are the same as in preceding figures.

change, extend caudomedially and correspond with the small fiber bundle input which also courses caudomedially through the inferior pulvinar.

Response characteristics

The main goal in the present experiments was to demonstrate the visuotopic organization of the inferior pulvinar and no effort was made to isolate and study single units. However, a few comments on properties of neurons in the inferior pulvinar are possible. First, neurons at most recording sites were activated by stimuli to either eye. While the receptive fields in the preceding illustrations were determined with the contralateral eye, the ipsilateral eye also was exposed in three experiments and most recording sites with central and paracentral receptive fields were activated by both eyes; peripheral receptive fields were activated by the contralateral eye. Second, responses were not obtained to stationary stimuli in the receptive fields. Third, responses to the onset or the cessation of a spot of light in the visual field were very poor in comparison to responses to moving stimuli.

DISCUSSION

The results indicate that there is a topographic representation of the contralateral half of the visual field in the inferior pulvinar of the owl monkey. There are

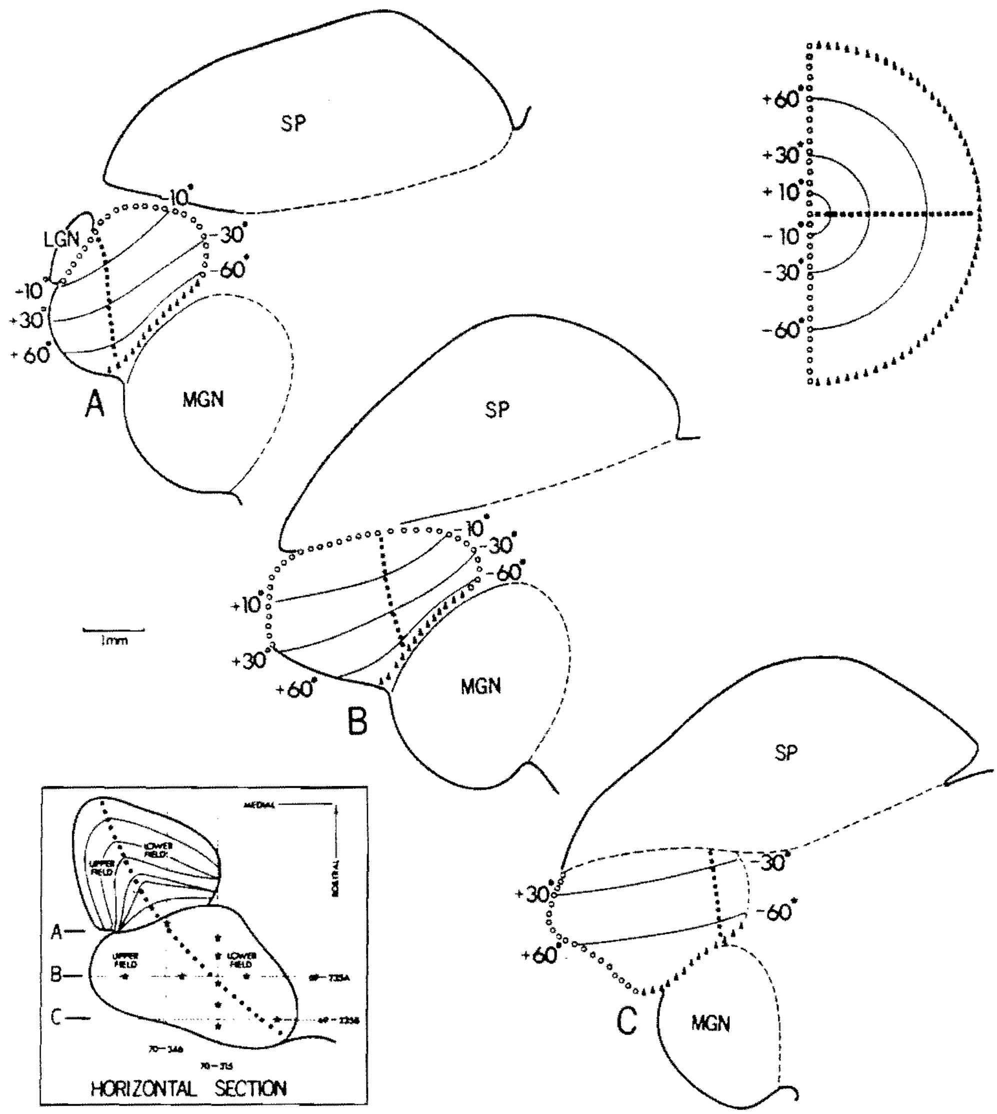


Fig. 7. The representation of the visual field in the inferior pulvinar of the owl monkey. In the box in the lower left corner is a drawing of a horizontal section through the inferior pulvinar and the lateral geniculate nucleus. The horizontal meridian (indicated by the heavy dashed line) divides the inferior pulvinar into a rostromedial portion in which the lower visual quadrant is represented and a caudolateral portion in which the upper visual quadrant is represented. The horizontal meridian continues rostrolaterally and divides the lateral geniculate nucleus in a similar fashion. The light dashed lines correspond to the intersection with the horizontal plane of the parasagittal sections from experiments 70–346 (Fig. 4) and 70–315 (Fig. 5) and the coronal sections from experiment 69–235 (Fig. 6). The stars indicate the positions of the microelectrode penetrations in these experiments, as seen in the horizontal plane. The levels of coronal sections A, B, and C are indicated to the left of the horizontal section. In the upper right corner is a perimeter chart which serves as a key for the projection of the visual field in the inferior pulvinar as shown in coronal sections A, B, and C. The vertical meridian is indicated by small circles; the horizontal meridian by the heavy dashed line, and the extreme temporal periphery of the visual field by the small black triangles.

several potential sources of visuotopic input to the inferior pulvinar. Although direct projections from the retina to the inferior pulvinar have been reported in baboon and macaque monkey[7], these projections are limited to small patches in the rostral part of the nucleus and they cannot account for the complete representation of the visual field. In addition, retinal projections to the inferior pulvinar were not found in the squirrel monkey[5] which is more closely related to the owl monkey than baboons or macaque monkeys. Projections from the superior colliculus to the inferior pulvinar have been described for several primates[13,14,22,23,30], and it is possible that this input provides the visuotopic organization, since a topographical representation of the visual field is found in the superior colliculus of the owl monkey[21]. Another possibility is that the visuotopic organization of the pulvinar depends on input from one or more of the cortical visual areas. A number of topographical representations of the visual field are found in caudal neocortex of the owl monkey, including separate representations in areas 17, 18[2] and part of temporal cortex[1]. Projections from prestriate cortex to the inferior pulvinar have been described in the galago[4], squirrel monkey[23], and macaque monkey[16] and from striate cortex in the macaque monkey[6,16]. The terminations from striate cortex were found to be topographically distributed[16] and the representation of the visual field that would result is very similar to the organization we have described in the present report on the owl monkey. However, a similar projection from striate cortex to the inferior pulvinar has not been found in the squirrel monkey[31].

Another possible source of the visuotopic organization of the inferior pulvinar is input from the lateral geniculate. From normal material, Hassler[15] described fiber projections from the lateral geniculate nucleus to the inferior pulvinar. Because of the juxtaposition of the inferior pulvinar with the lateral geniculate nucleus such interconnections might be expected. Furthermore, the representation of the visual field in the inferior pulvinar mirrors that in the lateral geniculate in that the lower field is medial and the upper field is lateral in both nuclei, while the representations of central vision adjoin. Thus, direct fiber connections could account for the visuotopic organization of the inferior pulvinar. However, experimental evidence of such projections is not available and fiber degeneration studies after lesions of the lateral geniculate[17,34] have been concerned with cortical projections rather than interrelationships with other thalamic nuclei. In addition, retrograde degeneration studies of the lateral geniculate nucleus of primates after striate cortex lesions[26,27] suggest that this nucleus projects exclusively to the striate cortex.

Besides the inferior pulvinar, other portions of the pulvinar may mediate visual functions. Much of the pulvinar complex appears to project to cortex which our work on the owl monkey indicates is visually responsive[1]. In some of our experiments on the inferior pulvinar, we also recorded visual responses for sites in the superior pulvinar. The recordings were too few to reveal the organization of this part of the pulvinar.

SUMMARY

The visuotopic organization of the inferior pulvinar was investigated with microelectrodes by relating receptive field positions to recording site locations in 6 owl monkeys. The central 10° of the visual field are represented dorsally and rostrally.

More peripheral parts of the visual field are represented ventrally and the extreme temporal periphery is represented near the ventral border of the pulvinar adjacent to the medial geniculate nucleus. The lines of isorepresentation, along which the location of receptive fields of neurons does not change, extend caudomedially and correspond with the small fiber bundle input which also courses caudomedially through the inferior pulvinar.

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