Pulvinar Nuclei of the Behaving Rhesus Monkey: Visual Responses and Their Modulation

STEVEN E. PETERSEN, DAVID LEE ROBINSON, AND WILLIAM KEYS

Laboratory of Sensorimotor Research, National Eye Institute, National Institutes of Health, Bethesda, Maryland 20892

SUMMARY AND CONCLUSIONS

1. We have examined the properties of neurons in three subdivisions of the pulvinar of alert, trained rhesus monkeys 1) an inferior, retinotopically mapped area (PI), 2) a lateral, retinotopically organized region (PL), and 3) a dorsomedial visual portion of the lateral pulvinar (Pdm), which has a crude retinotopic organization. We tested the neurons for visual responses to stationary and moving stimuli and for changes in these responses produced by behavioral manipulations.

2. All areas contain cells sensitive to stimulus orientation as well as neurons selective for the direction of stimulus movement; however, the majority of cells in all three regions are either broadly tuned or nonselective for these attributes. Nearly all cells respond to stimulus onset, a significant number also give a response to stimulus termination, and rarely a cell gives only off responses. Nearly all cells increase their discharge rate to visual stimuli.

3. Receptive fields in the two retinotopically mapped regions, PI and PL, have well-defined borders. The sizes of these receptive fields show a positive correlation with the eccentricity of the receptive fields. The receptive fields in the remaining region, Pdm, are frequently very large, but with these large fields excluded, show a similar correlation with eccentricity.

4. All pulvinar cells tested (n = 20) were mapped in retinal coordinates; the receptive fields are positioned in relation to the retina. We found no cells with gaze-gated characteristics (2), nor cells mapped in a spatial coordinate system.

5. The response latencies in PI and PL are shorter and less variable than the latencies in Pdm.

6. Active use of a stimulus can produce an enhancement or attenuation of the visual response. Eye-movement modulation was found in all three subdivisions in about equal frequencies. Attentional modulation was common in Pdm and was rare in PI and PL. The modulation is spatially selective in Pdm and nonspecific in PI for a small number of tested cells.

7. These data demonstrate functional differences between Pdm and the other two areas and suggest that Pdm plays a role in selective visual attention, whereas PI and PL probably contribute to other aspects of visual perception.

INTRODUCTION

The pulvinar represents the largest nuclear mass in the primate thalamus, and its selective phylogenetic enlargement parallels that of the parietal, temporal, and occipital association cortices. Recent studies have provided physiological, anatomical, and behavioral data linking parts of the pulvinar to visual behavior (13). An understanding of the visual function of the pulvinar is important for two reasons. First, it is through the pulvinar that information from the superior colliculus reaches the cortex. Second, the pulvinar has extensive connections with visual cortical areas and thus has the potential for significant influences on all of these areas.

The pulvinar nucleus can be divided in several ways. It has been separated on cytoarchi-
tectonic criteria into inferior, lateral, medial, and oral subdivisions (36). On the basis of electrophysiological experiments, Bender (4) identified three visual regions within the anterior portions of the cytoarchitectonically defined inferior and lateral pulvinar nuclei (Fig. 1). The first of these functional areas, PI, includes all of the cytoarchitectural inferior pulvinar along with a small amount of the adjacent cytoarchitectural lateral pulvinar. This area has a complete and organized map of the contralateral visual hemifield (4). A second retinotopic map, PL, confined to the adjacent cytoarchitectural lateral pulvinar, forms a "second-order transformation" (1) of the visual hemifield; it has a split representation of the horizontal meridian and wraps around PI. The boundary between the two maps can be seen in the myeloarchitecture (4). An adjacent part of the cytoarchitectural lateral pulvinar, which we have termed Pdm, lies dorsal and medial to these maps and has been shown to be visually responsive (4). We have physiologically identified these three subdivisions, and they are the focus of our present experiments.

Because no consensus has been reached on the boundaries of the subdivisions of the pulvinar nucleus or on the associated terminol-

---

FIG. 1. BSC, brachium of the superior colliculus; CC, corpus callosum; HIPP, hippocampus; PI, inferior pulvinar map; PL, retinotopically organized region of the lateral pulvinar; Pdm, a dorsomedial part of the lateral pulvinar; SC, superior colliculus. Microelectrode penetration in Pdm marked with lesions. Solid lines, outline of part of a section of a rhesus monkey brain. Within the line drawing is a photomicrograph of the pulvinar nuclei and adjacent brain. Penetration was above the initial marked site (indicated by large arrowhead). Insert at top right shows boundaries of the 3 pulvinar areas studied (PI, PL, Pdm). + corresponds to the upper contralateral visual field, – to lower field. At left of the photomicrograph is the trace of an electrode penetration into the superior colliculus.
ogy, we have adopted the following nomenclature: the inferior map will be referred to as PI, even though it crosses the classically defined cytoarchitectonic border, the adjacent lateral map will be termed PL, even though this does not include all of the cytoarchitectural lateral pulvinar, and the dorsomedial portion of the lateral pulvinar will be called Pdm.

The exact contribution of the pulvinar to visual behavior has been hard to define. Most of the initial experiments that tested for losses of visual capacities after damage to the pulvinar yielded no significant deficits (15, 32). Such animals were able to identify and remember the characteristics of diverse visual images. This suggests that the visual function of the pulvinar is not in the realm of passive visual sensation. Experiments by Chalupa, Coyle, and Lindsley (14) showed that monkeys with damage to the inferior pulvinar have difficulties in learning visual discriminations when the images are presented very briefly. These animals appear to have trouble in rapidly scanning the visual scene during periods of fixation. This interpretation is supported by studies showing that monkeys and humans with pulvinar lesions have visual neglect, prolonged fixations, and fewer eye movements while learning and performing visual discriminations (51, 52, 55). These data are confounded by the fact that lesions of this region damage fibers of passage, often including those in the brachium of the superior colliculus (7). Thus, Nagel-Leiby, Bender, and Butter (34), after attempting to assess function following kainic acid lesions, suggested that previously reported effects of pulvinar lesions may be due to fiber damage.

We studied the contribution of the pulvinar to visual behavior by recording from single cells in awake, trained monkeys. After determining some of the visual properties of the neurons in three subregions (PI, PL, and Pdm), we explored how the response properties could be influenced by different types of oculomotor and attentional behavior. The results of the experiments suggest that there are functional differences in these subdivisions of the pulvinar and that the areas contribute to different categories of attention and perception.

Brief reports of these experiments have been presented previously (38, 39, 45, 47).

**METHODS**

Many of the details of our experimental techniques have been described in previous reports (11, 24, 44). We recorded from nine rhesus monkeys (Macaca mulatta, 7 male and 2 female) and studied 11 hemispheres. The animals were 2–3 yr old and weighed 4–6 kg.

After an animal had undergone preliminary training, we implanted several devices under surgical anesthesia with barbiturates. A scleral search coil was attached to one eye using the technique of Judge, Richmond, and Chu (25). Next, a stainless steel well was connected to the skull over the stereotaxic locus of the inferior pulvinar (AP +3.5; L +10.0). Finally, bolts were attached to the lateral aspect of the skull and a metal sleeve cemented to the cylinder and bolt mass for restraining the animal’s head during recording. For 1–2 days after surgery, the animal was given small analgesic doses of morphine.

About a week after the initial surgery, we began recording multiunit activity to locate the superior colliculus and lateral geniculate nucleus in the recording chamber as guides for localizing the pulvinar subnuclei. In our early experiments, all recordings were made with glass-insulated, platinum-iridium microelectrodes. After the colliculus and geniculate were located, we controlled the water intake of the animal so that it would perform a fixation task. Monkeys were weighed daily to ensure adequate hydration and food intake. After all training and experimental sessions, animals were returned to their cages for the evening.

While the animal directed its gaze to a point of light (fixation point) on a tangent screen, spots and bars of light were moved in the animal’s visual field. Stimuli were front- or back-projected from a quartz-iodide lamp and were 1–2 log units above a background of 1 cd/m². Infrequently, responses to colored stimuli were tested by placing Wratten filters in the light path. Receptive field progressions were noted to generate a preliminary topographic map of the lateral geniculate nucleus and the pulvinar subnuclei. By observing the orderly progressions of the receptive fields in a penetration, we determined whether we were recording in the lateral geniculate nucleus, the inferior retinotopic map (PI), or the lateral retinotopic map (PL) (Fig. 2) (4, 27). The dorsomedial region of the lateral pulvinar (Pdm) was identified by its position in relation to the maps (lateral geniculate nucleus, PI and PL) and the observation of large, varied fields with no obvious regular progression (Fig. 2).

When an area of interest had been delineated, an 18-gauge, stainless steel guide tube was lowered through the dura and cortex overlying the pulvinar and cemented to the recording chamber. The tip of the tube was placed ~4 mm dorsal to the nucleus.
of interest. Tungsten electrodes were threaded through the guide tube for the recording of single neurons. The guide tube allowed for continued recording within a previously ascertained area and permitted us to make 15–25 penetrations into a restricted region. The flexibility of the long tungsten wire apparently improved the recording stability, as well. There are two reasons for assuming that recordings with these electrodes were from cells rather than fibers of passage: no discernable signals were recorded when passing through apparent white matter, and most signals were similar after slight changes in electrode position.

The animals were trained on several behavioral tasks to determine the influence of different types of behavior on the visual responses of pulvinar neurons. In the basic task, the animal initiated a trial by pressing and holding down a bar, which illuminated a fixation point on the tangent screen. The animal would fixate the light because it would subsequently dim as a signal for a bar release. A timely response to the dimming produced a drop of water as reward. During fixation other lights could be flashed onto or moved over the tangent screen to test the visual properties of the cells.

The animals were also trained to saccade or attend to targets under several conditions. Detailed descriptions of these tasks appear in the results section where appropriate. Different behavioral tasks were run in blocks of trials.

After studying a particularly interesting cell or completing a productive penetration, six μA of anodal current were passed through the electrode for 30–60 s to make marking lesions. Figure 1 shows marking lesions identifying a penetration in Pdm. These lesion patterns were subsequently reconstructed from histological sections of the brain alternatively stained with cresyl violet for cells, and Weil or Gallyas stains for fibers. The myelin stained sections were especially helpful in determining the border between the PI and PL maps (4). We confidently reconstructed 27 penetrations in nine monkeys. This was accomplished by utilizing marking lesions in histological sections and the physiologically determined maps. Of these 27 penetrations, 10 were histologically located in PI, 6 were marked in PL, 7 were localized in Pdm, and 4 in adjacent brain areas.

An on-line digital computer controlled all lights, detected the responses of the animals, evaluated eye-movement traces, and analyzed neuron firing patterns in relation to a variety of experimental events. The experiments were analyzed on-line as rasters and histograms, but data were also stored for future analysis such as calculation of latencies and indices (11, 24).

**Fig. 2.** Progression of visual receptive fields with increasing depth in pulvinar. Plots on left are from a penetration through PI, those on the right are from Pdm. Open circle, geometric center of the visually responsive region that is indicated by the rectangle about it. Boundaries of the visually responsive regions were determined by flashing and moving stimuli near the field borders and listening to the unit activity. Each test point is numbered in sequence and was determined by advancing the microelectrode 0.25 mm through the pulvinar. For the penetration through PI, visual receptive field no. 1 was recorded dorsally in PI. For the Pdm penetration, receptive field no. 1 was recorded in dorsal Pdm, and no. 6 was tested ventral in Pdm. Cross at top left of each illustration indicates the point of fixation (fovea). Note that scale for the penetration through Pdm is 5 times that of the PI penetrations. For definitions, see Fig. 1 legend.
RESULTS

We studied the properties of 412 cells in the pulvinar. Based on histological and/or topographic criteria, we were able to clearly assign 304 neurons into specific subdivisions: 83 in the inferior mapped area (PI), 119 in the lateral mapped region (PL), and 102 in another visual region of the lateral pulvinar (Pdm). In PI, 90% of the cells were visually responsive, in PL

<table>
<thead>
<tr>
<th>TABLE 1. Pulvinar visual properties</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mapping:</strong></td>
</tr>
<tr>
<td>Visual responsiveness</td>
</tr>
<tr>
<td>Latency</td>
</tr>
<tr>
<td>On only</td>
</tr>
<tr>
<td>Off-on</td>
</tr>
<tr>
<td>Off only</td>
</tr>
<tr>
<td>Multiple-response pattern</td>
</tr>
<tr>
<td>Antagonistic interactions</td>
</tr>
<tr>
<td>Excitatory</td>
</tr>
<tr>
<td>Inhibitory</td>
</tr>
<tr>
<td>Phasic only</td>
</tr>
<tr>
<td>Tonic only</td>
</tr>
<tr>
<td>Phasic-tonic</td>
</tr>
<tr>
<td>RF Size vs. eccentricity</td>
</tr>
<tr>
<td>Mapped in retinal coordinates</td>
</tr>
<tr>
<td>Direction preference</td>
</tr>
<tr>
<td>Directionally selective</td>
</tr>
<tr>
<td>Bidirectional</td>
</tr>
<tr>
<td>Behavioral modulation‡</td>
</tr>
<tr>
<td>Eye movement modulation</td>
</tr>
<tr>
<td>Attentional modulation</td>
</tr>
<tr>
<td>Eye-movement and attentional modulation</td>
</tr>
<tr>
<td>% Modulated cells</td>
</tr>
<tr>
<td>Attenuated</td>
</tr>
</tbody>
</table>

PI, an inferior, retinotopically mapped area; PL, a lateral, retinotopically organized region; Pdm, dorsomedial visual portion of the lateral pulvinar. r, coefficient of correlation; SD, standard deviation. * NS, no statistical significance. † Without lg fields. ‡ Modulation, a change of 3/2 or 2/3 from control condition (see text).
there were 74%, and in Pdm there were 57%.
We examined responses to stationary stimuli
for latency, size selectivity, and receptive-field
size; also we studied responses to moving
stimuli and the influence of behavioral con-
ditions on visual responses. Table 1 contains
the number of cells tested for the properties
we studied as well as statistical measures where
appropriate. In one animal we placed a re-
cording chamber over the intraparietal sulcus
and recorded cells in cortical area 7. We stud-
ied 123 neurons and for 38 of these cells de-
determined a visual response latency.

One of the features that distinguished Pdm
from the other two areas of the pulvinar was
its crude retinotopic organization. When we
made penetrations in PI or PL for mapping
or single-unit studies, the progression of re-
cceptive-field locations was regular (4) (Fig. 2).
Fields were adjacent and moved in a system-
atic way. Penetrations that traversed Pdm were
quite different. Here the fields did not move
in simple ways and were seldom adjacent (Fig.
2). The retinotopic organization in Pdm was
much cruder than that in PI and PL.

Responses to stationary stimuli

Although the three regions of the pulvinar
have visually responsive neurons and are an-
tomically contiguous, there are functional
properties that distinguish them. Some of these
differences are revealed by their responses to
stationary stimuli, and others are demonstra-
ble by changing behavioral tasks to alter the
responses to stationary stimuli.

The distributions of response latencies to
the onset of stationary visual stimuli are shown
in Fig. 3. The mean response latencies and
their standard deviations in PI and PL were
similar to each other, and these values differ
markedly from those of Pdm (Table 1). Using
Scheffe’s multiple comparisons, Pdm latencies
were significantly different from those in PI
and PL. (P > 0.001). Since these distributions
appeared to deviate from the normal, the dis-
tributions were also tested with a Kruskal-
Wallis one-way analysis of variance, and the
samples were found to differ (40). In Pdm the
mean response latency was comparatively
long, and the distribution had a very broad
range of latencies. The distribution for Pdm
was quite similar to that found for the visually
responsive cells of cortical area 7, which we
studied in one animal. A comparison of Pdm
and area 7 distributions is also shown in Fig.
3, the similarities being consistent with the
known interconnections between the two areas
(31, 49, 50, 53). The differences among the
three pulvinar subnuclei were also maintained
in the off-response latency distributions; the
means for PI and PL were short relative to the
latency distribution for Pdm. The mean la-
tency for the superior colliculus is 43.5 ms (33); for transiently responsive cells in striate cortex it is 28 ms; and for cells with sustained responses it is 38 ms (30). The afferents from either of the areas could easily drive pulvinar cells.

Most pulvinar cells (216/221, 97%) rapidly changed their firing rate in response to the onset of a visual stimulus. A significant minority (22%) of the cells had a response to stimulus termination (Fig. 4), but it was rare to see an example of a cell with only an off response (Table 1). The great majority of pulvinar neurons gave an increased response (214/221, 97%), but there were examples of response decrements in each of the pulvinar subdivisions (Fig. 4).

Pulvinar neurons responded to changes in illumination or to the continual presence of light. We used the term tonic to describe any change in a firing pattern that persisted for the duration of stimulus presentation (Fig. 4). Phasic referred to responses which were time locked to the stimulus onset (or termination) and lasted less than the stimulation time. The majority of cells in all regions (Table 1) gave a phasic response to the onset of a visual stimulus, although cells having tonic responses made up about one-fifth of cells in all the subdivisions. The most dramatic examples of tonic responses were inhibitory (Fig. 4). A few cells had both phasic and tonic components (Fig. 4) and a special subset of these cells had multiple pattern responses (see below).

A small number of cells in the lateral pulvinar subdivisions [PL (n = 4) and Pdm (n = 2)] gave qualitatively different responses when presented with different stimulus configurations. For the cell in Fig. 5, the phasic burst of the response was present for both small and large stimuli, but the tonic component of the response was demonstrable only when smaller stimuli were presented. We also saw such changes associated with stimulus intensity and saw more complicated patterns with changes in stimulus configuration (such as a 3-peaked response that varied in more complex fashion with changes in stimulus size). This type of multiple pattern response is reminiscent of the variable patterns of responses of neurons in area TE of the inferior temporal cortex (42).

Within a visual receptive field, there were various interactions between excitatory and inhibitory influences. Some of these were due to simple center-surround antagonism, whereas others reflect more complex internal relations. Some pulvinar cells responded most vigorously to stimuli that were smaller than the whole receptive field or smaller than the excitatory region of the receptive field. Similar cells had been found in other cortical and subcortical visual structures (see Refs. 3 and 37). Figure 6 illustrates three different types of relations. Some cells had weak summation within their receptive fields and antagonistic surrounds, as shown in Fig. 6A. Figure 6B shows a size-selective cell; it responded better to stimuli that were smaller than the excitatory area of the receptive field. Other cells had both size selectivity and antagonistic surrounds (Fig. 6C). Some cells had no significant
antagonistic interaction. PL had very few cells that exhibited the inhibitory effects, whereas size selectivity and/or antagonistic surrounds were more frequently found in PI and Pdm (Table 1).

Each time the eye moves, an image from the external visual scene excites a different part of the retina. In spite of such changes in retinal location, the perception of objects remains stationary. Thus, a visual response of a neuron may encode a location of a stimulus in real space (as they are perceived) or in reference to the retina as it moves with the eyes. Twenty cells in the pulvinar were tested to ascertain if the responses were mapped in retinal coordinates. A visual receptive field was mapped in retinal coordinates if it moved in tandem with the position of the retina: it was mapped relative to the retina and not in external spatial coordinates or other more complex frame of reference. An example of a cell mapped in retinal coordinates is shown in Fig. 7. This cell was inhibited by light and had a slight off response at stimulus termination (Fig. 7A). The activity to the left of the trigger line shows suppression when the stimulus was on; activity to the right shows the off response and return of spontaneous activity. In each figure the cross mark indicates the straight-ahead position on the tangent screen, and the small circle indicates the direction of gaze. The square is the stimulus, and the dashed circle is the visual

![Diagram showing visual receptive fields and stimulus configurations](image-url)

**FIG. 5.** Multiple pattern response to different stimulus configurations. This cell has both phasic and tonic characteristics to its response to a small stimulus but only a phasic response to a large one. The area enclosed by the dashed line is the visual receptive field as mapped with small spots of light; FP indicates the fixation point. Stimulus remained on for duration of rasters illustrated. Vertical scale equals 100 spikes/trial. This neuron was located in the dorsomedial visual portion of the lateral pulvinar.
FIG. 6. Cells with and without size selectivity and antagonistic surrounds. Each vertical column of data is taken from a different cell; diagrams, left, are schematics to indicate a stimulus much smaller than the excitatory region of receptive field (top), a stimulus that fills most of the receptive field (center), and one that far exceeds the receptive field (bottom). Cell in A had equivalent responses to both stimuli within the field but a much weaker response to the large stimulus. This cell had a clear antagonistic surround. Neuron in B had responses to a spot in the receptive field and no response to stimuli that filled the field; it has size selectivity. Cell in C responded well to the spot, weakly to a larger stimulus; there was no response to stimuli that exceeded the receptive field. This cell has size selectivity and an antagonistic surround. Vertical scales indicate 275 spikes/s/trial in A; 135 in B; and 150 in C. All 3 of these cells were recorded in the dorsomedial visual portion of the lateral pulvinar.

receptive field. Whether the animal was looking straight ahead (Fig. 7A) or upward (Fig. 7B), the receptive field was in the same place relative to the retina; the inhibition and return of firing was of the same general strength. We conducted similar experiments observing on responses, off responses, antagonistic surrounds, and responses to moving stimuli. All 20 cells were tested with two different fixation points, and 4 cells were studied with three gaze directions. All of the visually responsive cells of the pulvinar we tested were mapped in retinal coordinates, and none showing obvious gaze dependence (2), nor indications of being mapped to a less-conventional frame of reference. A further test of this type of organization showed that stimuli presented at the same location on the tangent screen with the animal looking at different fixation points (Fig. 7, C and D) elicited a response only when the eye was aligned on the appropriate location (Fig. 7, A and B). Only a small number of cells in Pdm were tested in this way ($n = 5$), and it is possible that eye-position effects could be found here because related processes are present in area 7 (2), an interconnected part of cortex (31, 49, 50, 52).

For PI and PL, the sizes of receptive fields were clearly scaled with the eccentricity of the field (Fig. 8). Field boundaries were determined by assessing the response to a stationary stimulus over several trials. We used the geometric center of the receptive field for the eccentricity and excluded cells for which we found no lateral border. The fields in PL were slightly larger than those in PI of the same...
Fig. 7. Test of coordinate mapping of visual responses. Data in A show the activity of this cell to a stimulus in its receptive field while the animal fixates straight ahead. Cross, straight-ahead position on the tangent screen; small circle, direction of the monkey's gaze; dashed circle, cell's receptive field; small square, stimulus. The light came on before the start of these rasters and histograms, and the trigger indicates the time of stimulus offset. The cell is suppressed by the light and has a slight off response at end of the stimulation. For B the monkey has its gaze on a spot 7° lateral and 19° up, and the cell is inhibited by the light just below this point. In C the animal fixates the same eccentric location; the cell does not respond to the light in the same position as A. The cell is not suppressed by the light here if the monkey gazes straight ahead (D). This cell was recorded in the inferior, retinotopically organized region.

Eccentricity. Making such a comparison for the cells in Pdm was complicated by the presence of extremely large (represented by triangles in Fig. 8) or small (represented by diamonds in Fig. 8) receptive fields. For these cells it was frequently difficult to determine the actual boundaries of the receptive field because they were so large or were confined to the region of the fixation point. In addition, it was hard to establish the lateral edge of the large

Fig. 8. Correlation of visual-receptive field size with eccentricity. Each circle corresponds to a single cell whose receptive field size and eccentricity were studied. Most often stationary spots of light were used to map fields; occasionally moving lights were utilized. Rasters were taken for several trials to determine the edges of the receptive fields. The geometric center of the visual receptive field was used as the measure of eccentricity. Triangles, top of each plot, denote cells that had receptive fields that had no lateral border and could not be accurately positioned on these plots. Receptive field size is the square root of the area calculated by multiplying length by width by a factor to account for oval shape. Diamonds, cells with very small receptive fields at the fovea; n, number of cells used in computing the correlation coefficient; r, correlation coefficient for the plot (unbounded cells not included); P, level of significance.
receptive fields. With such cells excluded from analysis, there was a clear correlation in Pdm between receptive field size and eccentricity. The correlation coefficient is significant, as it is for PI and PL (Fig. 8), and the fields in Pdm are slightly larger than PI and PL.

**Responses to moving stimuli**

Most of our testing for directionality was done qualitatively with stimuli moved by a joystick in several directions through the visual field. A small number of cells in each area were tested quantitatively with computer-generated motion, and these quantitative runs generally agreed with our qualitative assessments. All of our quantitative testing of responses to movement utilized stimuli smaller than the receptive field to decrease the effects of stimulus orientation; directions were pseudorandomly presented.

Most of the cells of the pulvinar were pan-directional (Table 1); they responded clearly and consistently to stimuli moving in all directions (Fig. 9). Although many of these cells did not have identical responses to all directions of motion, they had strong activation for all directions. Such activity provides the visual system with data about the location of a moving image, but little else.

A small number of the cells in PI, PL, and Pdm had a directional preference in that they respond clearly to one direction of motion and
FIG. 10. Directionally selective response to a light swept through the receptive field. This cell responded well to upward and rightward movement and poorly to the other directions. The visual receptive field was centered at 13° contralateral, 14° down, and was 10° wide and 12° high. The histogram vertical axis represents 300 spikes/s/trial. Stimulus speed was 25°/s, the stimulus was a 3.8° circle, and the cell was recorded from the inferior, retinotopically organized region.

poorly to its opposite (Table 1). Generally, these cells responded to a broad range of directions (Fig. 10).

The final qualitative response to motion was bidirectionality: cells that favored one direction and its opposite over those orthogonal to the preferred directions (Fig. 11). Few of the cells that we tested in any area were clearly bidirectional (Table 1). Cells with bidirectional responses to movement are often assumed to be orientation selective. Although we did not quantitatively test pulvinar cells for orientation selectivity (using stationary bars at several orientations, or some other test), bidirectional cells generally responded well to stationary stimuli oriented orthogonally to the best direction. However, it was rare that an elongated, stationary bar of a particular orientation was the only stimulus able to evoke a vigorous response from a cell. Even cells with clear orientation selectivity were driven quite well by other stimuli. Our data are consistent with the reports of Bender (5) who found broad tuning for cells in PL, which he classified as orientation selective. In addition, our cells may be more broadly tuned than Bender's cells because we used shorter stimuli than he did, which have been shown to broaden tuning in pulvinar cells (5).

Behavioral modulation

In active vision, some images are used to initiate movements, some evoke a shift of attention, and others are ignored. We found that many cells in the pulvinar had different responses to the same stimulus when it was actively used in a behavioral context. An example is shown in Fig. 12. This cell from PL
FIG. 11. Bidirectional response to stimulus motion. Cell responded well to vertical movements as well as some close diagonals. Horizontal motion as well as its diagonals produced suppression or little response. The visual receptive field was 2° up, 0.5° contralateral, 5° × 5°, stimulus a 3.8° circle, and speed 40°/s. Vertical scale is 300 spikes per s per trial. Cell was located in the inferior, retinotopically mapped area.

Cells in the pulvinar that were modulated in the saccade task were also tested for modulation under different behavioral conditions. First, we determined if the modulation required an eye movement or could be produced by attention to a peripheral stimulus. We also tested for the spatial selectivity of the modulation, that is, whether the modulation was dependent on the direction of the saccade or attentional locus. Detailed descriptions of these tasks and the interpretation of their results have been published (11, 54). When modulated cells in the pulvinar were tested for spatial selectivity and eye-movement dependence, two of the four possible pairings tended to associate: spatial selectivity with eye-movement independence and spatial nonselectivity with eye-movement dependence.

A comparison of the visual responses during the performance of three tasks was used to assess the relationship of the response modulation to saccadic eye movements and attention. In the first, a simple fixation task (Fig. 12B), the monkey gazed at a central spot of light while other stimuli were flashed on the tangent screen to obtain a visual response. The monkey responded to the dimming of the fixation point by releasing a bar. An adequate stimulus for location and size was chosen, and the response to this stimulus was used as a basis for comparison to the responses during the other tasks.

The second task was a "peripheral attention" procedure (Fig. 12D). Again, the animal fixated the central spot. The same visual stimulus was illuminated on the tangent screen, and after a random interval the peripheral stimulus would dim. The monkey was prevented from making an eye movement to the stimulus but was rewarded for releasing the bar during the stimulus dim. For cells of the type shown in Fig. 12, there was little or no change in response between the fixation and attention tasks and never of the magnitude of influence of eye movements. In this task, it was assumed that the monkey attended to the peripheral stimulus if the dimming was correctly detected. If the monkey moved his eyes from the fixation point during the performance of any of these two tasks, the trial was aborted by the computer and the data from these trials were not used.

The third task was a saccadic eye-movement paradigm (Fig. 12C). The animal fixated the same point, but on some trials, the fixation
light was turned off and simultaneously the same stimulus appeared on the tangent screen. The offset of the fixation point signaled the monkey to make a saccadic eye movement from the fixation point to the stimulus since this new light would dim as a signal for a bar release. Figure 12. C and D, illustrates the eye-movement dependence of this enhancement. In Fig. 12B, the response during the fixation task was small. The response when the animal attended to the stimulus in the peripheral attention task was also weak (Fig. 12D). However, when the animal used the stimulus as the target for a saccadic eye movement, the response to the stimulus was much greater (Fig. 12C). The data show that this enhancement indicates that an eye movement is about to occur and does not signal the attention shift that precedes the eye movement.

The pulvinar cells with eye-movement dependence tended to lack spatial selectivity (1/6 cells tested in PI and PL show spatial selectivity). Figure 12B shows a response during fixation with two stimuli flashed on the tangent screen, one in the receptive field and one distant from the receptive field. Figure 12C shows the response when the animal made a saccade to the stimulus lying within the receptive field. The response was enhanced by the saccadic eye movement. But, as is evident in Fig. 12A, the response was also enhanced by a saccade to a stimulus distant from the receptive field. An enhanced response from these cells signals that an eye movement is about to occur but does not indicate in which direction the eye movement will be made. This type of modulation was found in PI (Table 1). We do not have enough data to fully characterize enhanced responses in PL, but we have found that 60% of the PL cells tested were enhanced in the saccade task. In a separate population of PL neurons, only 1 neuron in 14 was enhanced on the peripheral attention task. These data suggest that enhancement in PL is eye-movement dependent, as it is in PI.

It could be proposed, for spatially nonselective modulation, that the termination of the fixation point, coupled with the onset of a stimulus in the receptive field, yielded the enhanced response. In control experiments,
simple termination of the fixation point was insufficient to produce a response in these cells, so a foveal off response alone was not responsible for this modulation.

Most cells in Pdm, in contrast to those in PI and PL, paired the attributes of spatial selectivity and eye-movement independence. The response to a stimulus presented during simple fixation is represented in Fig. 13A. This discharge was smaller than the response to the same stimulus when the animal attended to it (Fig. 13B). When the animal attended to a stimulus outside of the visual receptive field (Fig. 13C) there was no clear modulation. These data show that this enhancement is spatially selective; it is not related to task difficulty or general arousal. Comparable spatial selectivity was also demonstrable for this group of cells using a saccade task instead of an attention task. The data in Fig. 13D show that this same cell was also enhanced when the animal used the stimulus as the target for a saccadic eye movement. Since the modulation was demonstrable with both saccadic and attentive use of the stimulus, we conclude that it is eye-movement independent.

Attenuated responses

Although all of the above examples have been of enhanced responses, 16% of the modulated cells had attenuated discharges (Table 1). The cell in Fig. 14 gave a greater response during fixation (left) than when the animal attended to the identical stimulus (right). This effect was not due to fatigue or habituation because the original response always returned when the fixation condition was reinstated. These observations are comparable with an effect studied in cortical area TE (43) and are seen occasionally in area 7 (11, 39, 44).

Response variability

Bender (5) reported that most (86%) of the cells in PI have a "moment-to-moment fluctuation in their visual responsiveness." We have also noted such variability, but in some
cases the variability was affected by changing behavioral conditions. For some of our cells there was a large fluctuation in response for a series of trials during the fixation task. These observations were not due to cell damage or suboptimal stimulations. For about half of such cells, the variability was decreased during a saccade or peripheral attention task; an example is shown in Fig. 15B. These observations indicate that factors such as arousal, attention, and saccadic readiness can influence pulvinar cells. However, not all variability was controllable with our stimuli and paradigms, indicating that there were other undetermined influences on pulvinar cells (Fig. 15A).

Comparison of the visual areas of the pulvinar

Our results indicate that regions of the pulvinar have distinct physiological characteristics and most likely contribute to different aspects of visual behavior. The most dramatic differences are between the properties of cells in a dorsomedial region of the lateral pulvinar (Pdm) and the two retinotopically organized areas, PI and PL.

The work of Bender (4) and our observations show that PI and PL have simple retinotopic organizations, whereas Pdm has a poor retinotopic arrangement. The size of the receptive fields of these areas differ; for the cells in PI and PL there is a regular relationship between receptive field size and eccentricity (Fig. 8). A poorer correspondence is present for Pdm when all cells are included. The response latencies are different in these populations as well (Fig. 3). Taken together these data suggest that the visual extractions done by PI and PL are qualitatively different from those done in Pdm.

In addition to the differences in sensory responses noted, there are nonvisual influences that distinguish Pdm. Cells in Pdm are enhanced when a monkey uses a stimulus as the target for attentive or saccadic behavior. In

DISCUSSION

Several general points emerge from these experiments, and they will be the focus of our discussion. The differences in the properties of neurons in these three areas will be highlighted. Next, we will propose functional roles for the subdivisions based on physiological properties. We will then compare our data with other studies of pulvinar neurons in primates. Finally, we will consider how properties of the PI could be mediated by some of its known afferents.
contrast, the cells in PI and PL are enhanced only with saccadic use of target lights. The enhancement in Pdm is spatially selective; it is present for use of a light only when it is in the visual receptive field. These various properties suggest that Pdm is performing a different function than that done in PI and PL.

**Functional significance**

The results of our experiments lead us to propose different functions for the different subdivisions of the pulvinar. The properties found in Pdm suggest that this region functions in selective visual attention. The properties found in PI and PL are more consistent with those parts of the pulvinar being organized to deal with the visual effects of eye movements.

Cells in Pdm have several properties useful in selective visual attention. First, many are visually responsive and thus signal the presence of visual images. Second, they respond differently to stimuli that are the focus of active behavior. This modulation is spatially specific; the effect is part of a selection process and not related to generalized phenomena. The process is independent of the exact motor response of the animal; it is dissociable from movement as is attention (41). Third, there are cells (not reported here) that discharge during and after saccadic eye movements made spontaneously in total darkness (saccade cells) (47). Such information about the conclusion of an eye movement could be of use to an attentional system in indicating that an attentional search and shift has been completed. Pdm can signal that a target has been detected (visual response), it was selected for attention (spatially-selective, movement-independent enhancement), and the saccade to examine it has been completed (saccade cell activity).

Humans with lesions that include the pulvinar have visual neglect (55) similar to that seen in humans with lesions of the inferior parietal lobe (16). In spite of having intact visual fields, they have difficulty responding to stimuli that are presented contralateral to their lesions if other stimuli are presented simultaneously. Taken together, these physiological and clinical lines of evidence provide support for a role for Pdm in selective visual attention.

We have proposed that PI and PL may contribute to the processing of the visual effects of eye movements. Cells here have four properties relevant to this function. First, they are visually responsive (5, 47) and discharge over a wide range of stimulus velocities (46). Second, these cells have an enhanced response when a visually guided eye movement is about to occur (Fig. 12). Next, we have found in other studies (46) some cells that discharge to moving stimuli have a mechanism that prevents many of them from responding to retinal stimulus motion, generated by an eye movement. This process is probably not a visual effect. Finally, a population of cells in PI, not described here, has activity that is concurrent with the end of an eye movement (47). Their activity is present even with eye movements made spontaneously in total darkness. All of these properties of cells in PI and PL show that they process information related to eye movements and the events surrounding saccades.

**Visual properties of pulvinar from other studies**

Our data are in general agreement with other physiological studies of the visual properties of the pulvinar of the primate. Bender (5) recorded from PI of paralyzed, nitrous oxide-anesthetized macaques, and his studies, like our own, found well-defined visual receptive fields that increased in size with increases in eccentricity. Both reports described populations of nonoriented, directionally selective, and broadly tuned, oriented cells; response latencies and receptive field sizes are basically the same. Although Bender (5) reported a larger proportion of directionally selective and oriented cells than we present here, many of his cells most likely would have been classified as pandirectional by us since their responses are clear to all directions of motion (Fig. 9). Also in our study, we tended to use shorter stimuli, which Bender has shown to broaden tuning. These differences in proportions between Bender's study and ours probably reflect experimental approaches rather than functional differences.

Benevento and Miller (10) studied the visual properties of cells in the caudal part of the lateral pulvinar, which they called PLγ. This part of the pulvinar is posterior to the areas we have tested and is strongly interconnected with the inferior temporal cortex. Several of the properties of the cells here are similar to those we found for Pdm. Both areas have cells with large receptive fields, neither area has a precise retinotopic organization, and the re-
ceptive fields can be unbounded. However, PLγ frequently has ipsilateral and bilateral receptive fields, and we have not found such fields in Pdm. Recently Felsten et al. (18) reported a few cells in PLγ and other parts of the pulvinar that are selective for colored stimuli. We have not noted cells that are selectively responsive to colored test patterns, but our study of this property is largely anecdotal. The observations that PLγ has different connectional and physiological properties suggest that it may represent an additional subdivision of the pulvinar with a different role in visual behavior.

Gattass and colleagues (20, 21) studied two retinotopically organized areas of the pulvinar in the Cebus monkey, a New World primate. They described a ventrolateral group of subnuclei that probably corresponds to PI and an area, Pγ. Cells with oriented visual receptive fields are common in these nuclei as are cells that have a directional selectivity for moving stimuli. The visual receptive-field properties of these two pulvinar areas in the Cebus monkey are similar, and they are comparable to Bender’s (5) and our own data for PI and PL. Although cells with directionally selective responses to moving stimuli have been described in the squirrel monkey (29), they appear to be less common than in the macaque or Cebus monkeys. In general, these comparisons do not suggest clear differences between species given the differences in experimental approaches.

**Cortical and collicular contributions to PI**

PI receives afferents from the superficial layers of the superior colliculus and cortical visual areas (8, 9, 12, 23, 26, 35). It is of interest to know what characteristics of the cells in PI are derived from which of these afferents (28). When retinal eccentricity is taken into account, the receptive fields in PI are at least twice as large as the corticocollicular cells in striate cortex (19) and almost one-third larger than the smallest fields in the superior colliculus (17). Either of these afferents could account for the size of the receptive fields in PI. The colliculus could account for some, but not all, of the receptive field types in PI. However, Bender (6) has reported that lesions of striate cortex dramatically reduce the visual responsiveness of cells in PI. He also showed that lesions of the superior colliculus have little effect on visual properties. Thus, it appears unlikely that the colliculus simply contributes visual characteristics to PI.

We have demonstrated that the modulation of responses in PI requires that the monkey make an eye movement to the stimulus (Fig. 12). This is similar to the eye-movement dependence seen in the modulation of collicular responses. However, spatial selectivity of enhancement, which is characteristic of collicular responses, is rare in PI. Because the enhancement in PI is different from that in the colliculus (spatially selective, eye-movement dependent) (22, 54), there is not a simple transmission of this effect from the colliculus to the thalamus.

A clearer similarity between the properties of PI and collicular neurons is in their response to stimulus motion during saccades. Many cells in PI respond to stimuli that are rapidly swept across their receptive fields while an animal fixates. Many of these same cells do not discharge to comparable stimulus motion when it is generated by the animal’s eye movement (46). Because some of the cells in the superficial layers of the colliculus have this same property (48), the process that eliminates visual responses during saccades may be transmitted from the colliculus to PI. While it appears that the visual properties of cells in PI are determined by the input from striate cortex, the collicular inputs to this region could well contribute to changes in this visual responsiveness in different behavioral situations.

Received 5 November 1984; accepted in final form 23 April 1985.

**REFERENCES**


