

Covert Orienting of Attention in Macaques. II. Contributions of Parietal Cortex

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SUMMARY AND CONCLUSIONS

1. To understand some of the contributions of parietal cortex to the dynamics of visual spatial attention, we recorded from cortical cells of monkeys performing attentional tasks. We studied 484 neurons in the intraparietal sulcus and adjacent gyral tissue of two monkeys. We measured phasic responses to peripheral visual stimuli while the monkeys attended toward or away from the stimuli or when attention was not controlled. Neurons were tested while the monkeys gazed at a spot of light (simple fixation task), actively attended to a foveal target (foveal attention task), performed a reaction time task (cued reaction time task), made saccadic eye movements to visual targets (saccade task), or responded to a repetitious peripheral target (probability task).

2. In a previous paper we demonstrated that monkeys, like humans, responded more quickly to visual targets when the targets followed briefly flashed visual cues (validly cued targets) (Bowman et al. 1993). It has been hypothesized that the cue attracts attention to its locus and results in faster reaction times (Posner 1980). In the present physiological studies, visual cues consistently excited these neurons when they were flashed in the receptive field. Such activity might signal a shift of attention. Visual targets that fell within the receptive field and that immediately followed the cue evoked relatively weak responses. This response was due to a relative refractory period.

3. Next we tested attentional processes in these tasks that were independent of the visual response to the cue. We placed the cue outside of the receptive field and the target within the receptive field. We found that 23% of these cells had a significant decrease in their firing rate to validly cued targets in their receptive fields under these conditions. Strong responses were evoked by the same target when the cue was flashed in the opposite hemifield (invalidly cued targets). Thus this group of neurons responded best when attention was directed toward the opposite hemifield.

4. For another group of parietal cells (13%) there was an enhanced response to targets in the visual receptive field when the cue was in the same hemifield. For the remaining 64% of the cells there was no significant modulation in this task.

5. The cued reaction time task involved exogenous control of attention; the sensory cue gave spatial and temporal direction to attention. We used several other tasks to test for endogenous control of attention. For some cells, when a monkey simply gazed at a spot of light there was only a modest response to peripheral visual stimuli; when the monkey performed the foveal attention task there was an increase in the intensity of response of the same cell to the same peripheral stimulus. Thus, when attention was directed away from the visual receptive field by endogenous control, there was a similar augmentation of response.

6. When an animal responded repetitiously to targets outside of the visual receptive field (probability task), there was a strong response evoked when the stimulus appeared unexpectedly within the receptive field. Weak responses were elicited at expected locations. The modulations in the cued reaction time, foveal attention,

and probability tasks were quantitatively similar. These observations are also consistent with other data showing that a group of parietal cells responded best when attention was not directed into the visual receptive field. This was true whether attention was manipulated exogenously or endogenously.

7. Approximately 45% of the neurons tested discharged in relation to saccadic eye movements, and the largest number of such cells was located in the posterior bank of the intraparietal sulcus.

8. We conclude from these experiments that parietal cells participate in attentional processes. All respond to the visual cue that directs attention, and this may signal a shift of attention. When the visual cue was positioned near the receptive field, differential activity was produced, all of which may signal attentional shifts. Certain of these cells also had modulations in endogenous tasks that augmented the response when attention was away from the receptive field; such activity could signal a shift of attention to the receptive field. These data provide some mechanisms for contributions of parietal cortex to the dynamics of visual attention.

INTRODUCTION

Parietal cortex has long been associated with attentional processes. The original notion came from the observation that patients with parietal damage have an inability to use sensory data even when their sensory systems are intact. The patients behave as if they have lost the ability to direct their attention to sensory stimuli (Andersen 1987; Critchley 1953; Petersen et al. 1989; Posner et al. 1984; Wurtz et al. 1980).

Two sets of studies have explored neuronal contributions to visual attention. In the first of these, certain neurons within parietal cortex exhibited enhanced responses to peripheral visual stimuli when the animals focused their attention on the stimuli (Bushnell et al. 1981; Goldberg et al. 1990; Robinson et al. 1978). These studies demonstrated a cortical correlate of selective attention. In another set of studies, augmented activity was observed in response to peripheral visual stimuli when the animals' attention was directed to a fixation point, that is, away from the stimulus in the visual receptive field (Mountcastle et al. 1981, 1987). Weak activity was elicited by the same stimuli when they were presented during intervals between trials. These data were interpreted to suggest that attentive fixation facilitated the excitability of parietal neurons.

Unresolved issues from these studies deal with the dynamics of attention and the mode of control of attention. Attention is a continually changing process, and thus the direction of attention can be altered frequently (Bowman et al. 1993; Posner 1980). Previous neurophysiological studies have used long blocks of trials and directed attention to one point

for several seconds (Bushnell et al. 1981; Mangun et al. 1990; Moran and Desimone 1985; Mountcastle et al. 1981, 1987; Richmond and Sato 1987; Robinson et al. 1978; Spitzer and Richmond 1991; Steinmetz et al. 1994). Also, these studies used cognitive manipulations of attention, frequently termed endogenous control. However, attention can be shifted rapidly in response to external sensory events, in which case it is termed exogenous control. Exogenous control produces transient attentional shifts that can change from moment to moment and trial to trial, and that may be mediated by the magnocellular pathways of the visual system (Baizer et al. 1991; Bowman et al. 1993).

The main purposes of the present studies are to evaluate attentional activity in a rapid, dynamic situation and to use exogenous as well as endogenous modes of control. We emphasized a cued reaction time task that incorporates rapid, exogenous control of attention. In this respect we discovered attentional modulations that have transient time courses that parallel the shifts of attention these monkeys have while performing this task. Brief reports of these data have appeared previously (Kertzman and Robinson 1989; Robinson et al. 1991).

METHODS

Animal and tissue preparation

Two rhesus monkeys (6.0–7.5 kg, 1 female, 1 male) were studied. All of the techniques for initial training, surgery, and presentation of stimuli were described in detail in a previous paper (*monkeys M1 and M3*) (Bowman et al. 1993). All procedures were conducted under a protocol approved by the Animal Care and Use Committee of the National Eye Institute and complied with Public Health Service Policy on the humane care and use of laboratory animals. During surgery a stainless steel cylinder was implanted over the intraparietal sulcus (AP +2, L 10). In one animal it was positioned in the vertical, stereotaxic plane whereas in the other it was placed normal to the skull. The cylinder was used in each case to make parallel microelectrode penetrations into various regions of parietal cortex. In both monkeys the sulcus was localized by first physiologically identifying the primary somatosensory cortex and then making successive penetrations in 1-mm steps moving posteriorly (Robinson et al. 1978).

In the second animal (*monkey M1*) we mapped the cortex in detail by first locating the intraparietal sulcus and then closely noting the changes in cortical activity as each penetration progressed. We attempted to establish when the microelectrode passed into and out of the cortex by noting the appearance and disappearance of clear neuronal activity. These transitions marked grey matter, white matter, or sulci. We also noted a limited number of directionally selective visual responses at the depths of the sulcus (Colby et al. 1993). At the conclusion of the studies with this animal we made marking lesions (6 μ A for 20 s) at four different penetration locations so that all penetrations could be reconstructed. Animals were perfused under deep anesthesia and the brains sectioned and stained for fibers or cells on alternate sections.

In reconstructing penetrations in *monkey M1*, the marking lesions were localized from histological sections. Figure 1 illustrates a set of marking lesions from this animal and also the location of the densely myelinated region within the intraparietal sulcus, the ventral region of the lateral intraparietal sulcus (LIPV) (Andersen et al. 1985). The marking lesions in each penetration were separated by set distances (e.g., 0.5 mm) that definitively identified them, and the known distances were used to make calculations to compensate for tissue shrinkage. Next, tracings were made of the cortical area of

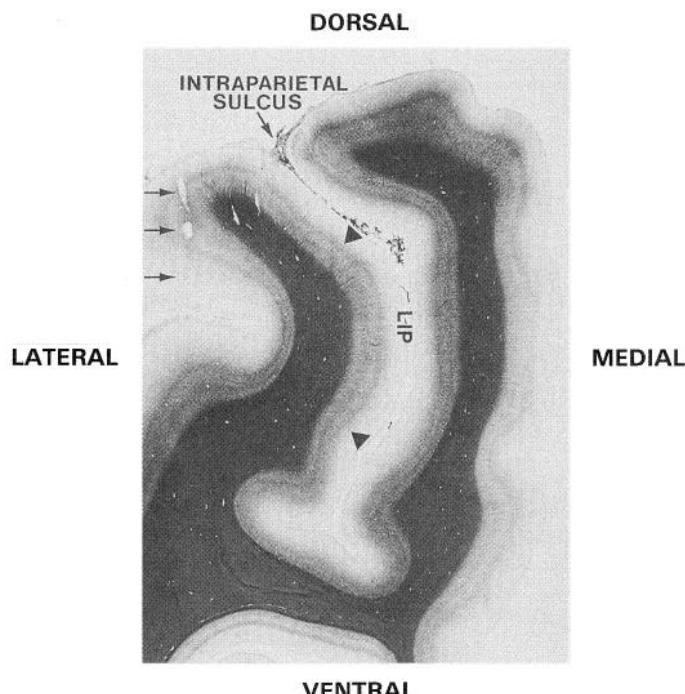


FIG. 1. Histological section of cortical areas sampled. This is a coronal section through a region of the intraparietal sulcus. Far left: 3 arrows indicate a series of marking lesions that show the location of a particular penetration. Arrowheads within the brain section: boundaries of the densely myelinated region within the sulcus, the ventral region of the lateral intraparietal sulcus (LIPV). This section was stained for fibers by the Gallyas method.

interest, and wires were cut and bent to follow this path. This technique was originally developed for studies of prestriate cortex (Gattass et al. 1988). A wire tracing for each section of the brain separated by 1.0 mm was made, and then these were soldered together at the appropriate distances. Once the wire map of the whole area of interest was completed, it was flattened to create a two-dimensional representation of the region. Certain regions within the depths of the intraparietal sulcus had to be cut apart for a complete flattening. An example of this map for the present studies is illustrated on the right in Fig. 2. This figure shows a dorsal view of the brain (left), representative sections and the cortical area sampled (middle), and the flattened map (right). The locations of individual neurons sampled from this animal were then assigned from their distance from the marked penetrations, position within the grid system, and depth from the surface of the cortex. For the first monkey (*monkey M3*), two penetrations were marked, but all penetrations were not reconstructed in detail. Recordings were obtained from the posterior bank of the intraparietal sulcus and dorsal surface after the sulcus was identified physiologically.

Behavioral tasks

We used five tasks: simple fixation, cued reaction time, foveal attention, probability, and saccade. All task images were generated on an IBM AT and back-projected onto a tangent screen with a video system. A trial did not progress until the animal directed its gaze toward the fixation point and positioned its eye within a window (2° square). Eye position was recorded with a scleral search coil, and there were no systematic differences in the fixations for the five different tasks. The same fixation point and eye position window were used in all tasks.

In the simple fixation task, each trial began with the appearance of a fixation light at the center of the tangent screen. After a variable period of fixation, a stimulus was flashed on the tangent

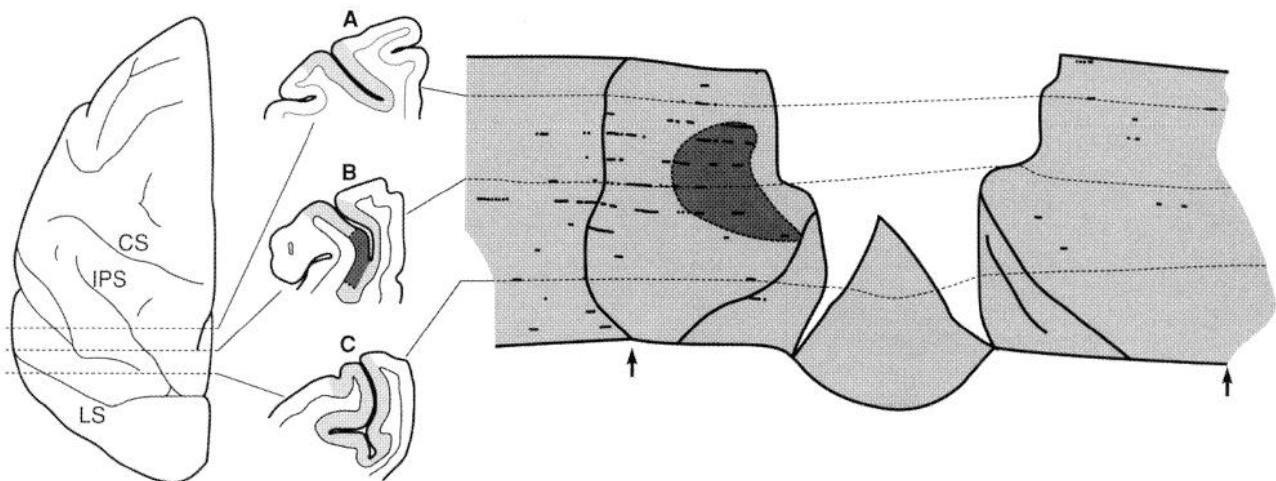


FIG. 2. Area sampled and location of neurons. *Left:* dorsal view of the brain, with dashed lines indicating the locations of coronal sections A–C. The lightly shaded areas in A–C correspond to the area of cortex sampled, whereas the dark shading shows the location of the densely myelinated zone termed LIPv. *Right:* schematic view of the intraparietal sulcus unfolded, with each dot indicating the location of a neuron included in this report. Dashed lines: locations of the sections A–C. Arrows: locations of the dorsal edges of the intraparietal sulcus. See METHODS for the techniques for constructing the flattened map and assigning anatomic locations for the cells. IPS, intraparietal sulcus; CS, central sulcus; LS, lunate sulcus.

screen and then a water reward was delivered automatically. The monkey had to maintain fixation until the reward was presented. In these blocks of trials, the animal did not initiate each trial with its hand but was rewarded for only directing its gaze within the window. Monkeys frequently fixated for several trials, making no exploratory saccades. There was no attempt to control the direction of the animals' covert attention. Visual receptive fields were first located using this task with a hand-held ophthalmoscope. The edges of the receptive fields were estimated by the lack of a consistent, short-latency response at any point outside of the receptive field in three consecutive trials. Computer-generated stimuli were used for the final determination of receptive field edges.

In the cued reaction time task, the monkey started each trial by contacting a bar that turned on a fixation point (Bowman et al. 1993). After the animal fixated, a cue was flashed briefly (83 ms) on one side, and it was followed by a target. The cue was always an open 2° square; the target was generally a filled 2° square, although its size was changed if a clear visual response was not evoked. The side on which the target appeared was randomly varied; cues on the same side as the target (validly cued targets) were presented in 80% of trials, and the cue-target temporal intervals were 100, 400, and 700 ms for *monkey M1* and 50, 150, and 400 ms for *monkey M3*. Targets appeared on either side of the vertical meridian with equal probability; thus only half of the trials had a target presented in the visual receptive field. The background illumination was in the photopic range at 0.3 cd/m², and the fixation point, cues, and targets were 3.0 cd/m². The monkey was rewarded for releasing the bar after the appearance of the target. The animal had to maintain fixation throughout each trial until release of the bar. During study of parietal neurons, the targets were always positioned at the optimal location within the visual receptive field of the neuron and remained on until the monkey responded. In some blocks of trials, cues were placed at the same location as the target. In other blocks of trials, the cue was placed outside of the receptive field. The positions outside of the visual receptive fields were selected individually for each neuron. All data were analyzed after completion of the experiment for confirmation of cue placements with no response.

When the paradigm was changed to the foveal attention task, each trial was started when the monkey contacted the bar at the front of the primate chair. After a variable time a fixation light

appeared at the center of the screen, and the monkey had to have positioned its eye within the window. At variable times after the monkey had maintained fixation, the stimulus was presented in the visual receptive field. After another variable period (from 1 to 3 s), the size of the fixation point increased from 0.4 to 0.8°. The monkey had 500 ms after the expansion of the fixation point to release the bar in order to obtain a water reward. One monkey (*monkey M1*) was trained in this task and performed at >90% correct during the recording experiments.

The probability task was developed to have the monkey (*monkey M3*) respond repeatedly to a target so that the repetitiousness of the task would shift the monkey's attention. Each trial was initiated by the computer and began with the appearance of the fixation point, which the animal had to fixate. After a variable period of time, a second light (target) appeared in the visual receptive field, and the animal had to contact the bar within 500 ms in order to obtain a water reward. In 90% of the trials the target appeared in the visual receptive field, and in 10% of the trials the target was presented at a second location, at the homotopic location in the opposite visual hemifield. Blocks of trials here totaled ≥70 trials. In the next block of trials, the probabilities at the two locations were reversed. For a subset of the neurons tested, the animal's behavioral response was a saccadic eye movement. For these trials, after the monkey fixated the central spot, it was turned off and another light was turned on. Again, this light would appear in the receptive field in 90% of the trials and at a second locus in 10% of the trials. Trials were run in blocks with only one type of response required (bar contact or saccade).

The saccade task began with *monkey M3* initiating each trial with a bar press. After the animal maintained fixation, the central spot was turned off, and a second light was turned on at a location in the periphery. In every trial the target light appeared only within the visual receptive field, and the monkey always made a saccade to the light; all trials included an eye movement, and only the timing of the onset of the target was unpredictable. The monkey was rewarded 200 ms after its eye reached the target position. The computer system monitored the animal's eye position at the central spot and at the target.

Data quantification

All neuronal activity was aligned on a selected trigger event that was chosen for each analysis. Most often this was the onset of the

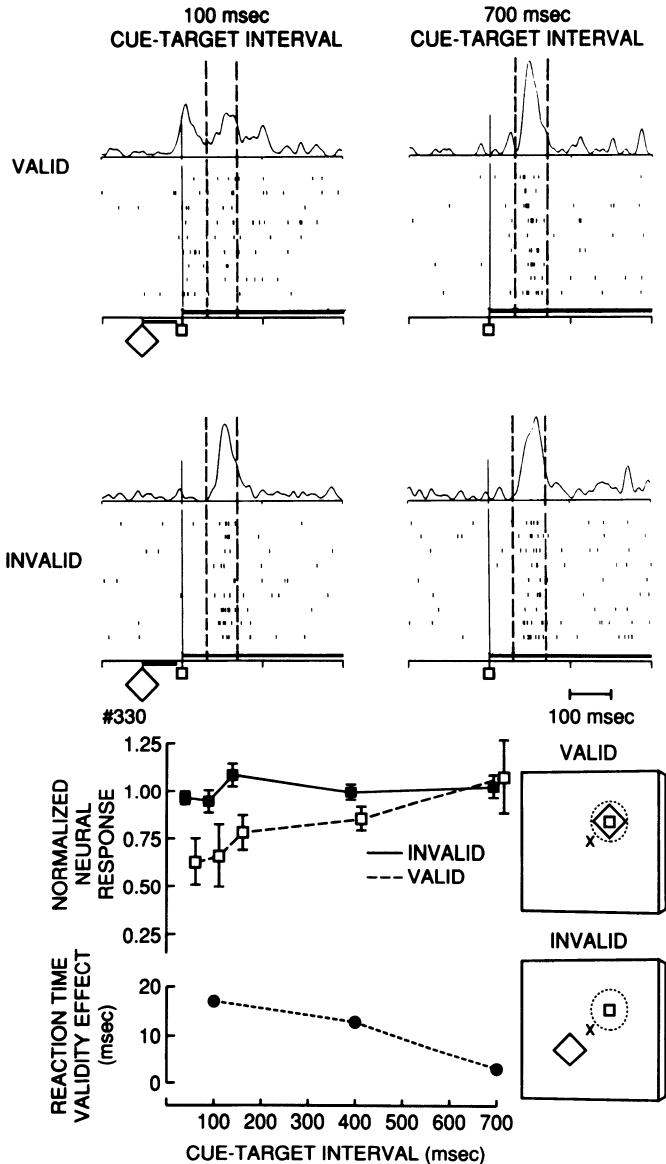


FIG. 3. Refractory responses to the target when the cue was positioned inside of the visual receptive field. *Top of each section*: spike density functions and raster displays showing the response to the stimuli. Vertical dashed lines: windows used for data quantification. Beneath the raster, the diamond indicates the time of onset of the cue, and the horizontal line extending from it shows its duration. Small squares show time of onset of the target, and the horizontal line represents its duration. There was 100 ms between cue and target for data at *left* and 700 ms at *right*. In the raster displays, each dot corresponds to an action potential, and each horizontal row of dots comes from an individual trial. The spike density functions sum only data from the trials displayed in the adjacent raster. The data at the *top* were triggered on the onset of the target; at the *top left* the response to the cue can be seen, and it is followed by a minimal response to the target. For the data labeled *invalid*, there was no response to the cue because the cue was in the opposite visual field. For invalidly cued targets, the responses to the target were uniform as illustrated in the *bottom graph* for the normalized response as solid squares and solid line. The open squares representing the valid means were displaced slightly to the right so that they do not overlap with the invalid means. *METHODS* describes the calculation of the normalized response. Plots show means \pm SE. *Bottom curve*: validity effect of the monkey's reaction times for the trials from which the cellular activity was obtained. Our previous paper contains additional documentation of the transient nature of the validity effect (Bowman et al. 1993). Each monkey was studied with only 3 cue-target intervals, and these intervals differed for the 2 monkeys. Thus the reaction time data have 3 data

targets in the cued reaction time, saccade, or probability tasks or the stimulus in the foveal attention and simple fixation tasks. The neural activity was summed by replacing each discharge with a Gaussian kernel with a standard deviation of 6.0 ms to produce a spike density function (Richmond et al. 1987).

For quantification of the neuronal data, we selected by hand for each cell a response window around the peak discharge (Robinson et al. 1991). Typical window placements are shown in Fig. 3 by the vertical dashed lines. The identical window was used for all conditions and tasks for an individual cell. Background activity was subtracted from the response by creating a window of the same duration positioned at a time after fixation was achieved but before the onset of the stimulus. We used a two-tailed *t*-test to compare responses between any two experimental conditions. Conclusions from such an analysis include the expectation that 5% of such tests will appear significant by chance.

When comparing responses of cells to valid and invalid cueing, significantly different responses between these two conditions were determined by a two-tailed *t*-test. With only one exception, the ratios of invalid to valid visual responses >1.5 or <0.67 were statistically significant (Bushnell et al. 1981).

To make responses equivalent among the various neurons that were sampled, we used a normalization process. All normalization techniques involve comparing individual responses with some standard; which standard is selected is not critical. We observed that there was minimal variation in the response of cells to targets that were invalidly cued (cues and targets in opposite hemifields) (Figs. 3, 4, and 6). Thus for each cell we calculated the mean response to all invalidly cued targets and used this mean to calculate ratios of all of that cell's responses for all targets. Normalized activity is the ratio of one cell's response to a target in one condition to the mean of all the invalidly cued targets for that same cell. Activity from the different cells and animals was normalized before it was combined. One monkey (*monkey M1*) was tested with cue-target intervals of 100, 400, and 700 ms. The other animal (*monkey M3*) was studied with intervals of 50, 150, and 400 ms. For the normalization of the population responses, the data from the two animals were combined, and only the cue-target interval of 400 ms was common to both animals.

RESULTS

We recorded from a total of 484 neurons from the parietal cortices of two monkeys. One hemisphere was sampled in each animal. Neurons were sampled from the dorsal surface, the lateral and medial banks of the intraparietal sulcus, and the densely myelinated region within the sulcus (Fig. 2). The activity of 422 (87%) of the cells was influenced by some experimental manipulation. The remaining 62 (13%) cells were unresponsive. Utilizing techniques described in *METHODS*, we were able to localize 343 neurons in one monkey, and their positions are illustrated in Fig. 2 (*right*). In general, our recordings were posterior to the ventral intraparietal area (VIP), which is located at the depth of the intraparietal sulcus and contains a concentration of visual directionally selective neurons (Colby et al. 1993).

points, whereas the normalized curves come from 4 unique and 1 common cue-target interval. For 1 monkey (*monkey M1*), cue-target intervals were 100, 400, and 700 ms; for the other (*monkey M3*) they were 50, 150, and 400 ms. *Bottom right*: schematic display of the experimental conditions as seen on the tangent screen. Cross: fixation point. Dotted circle: visual receptive field. Diamond: cue. Small square: target.

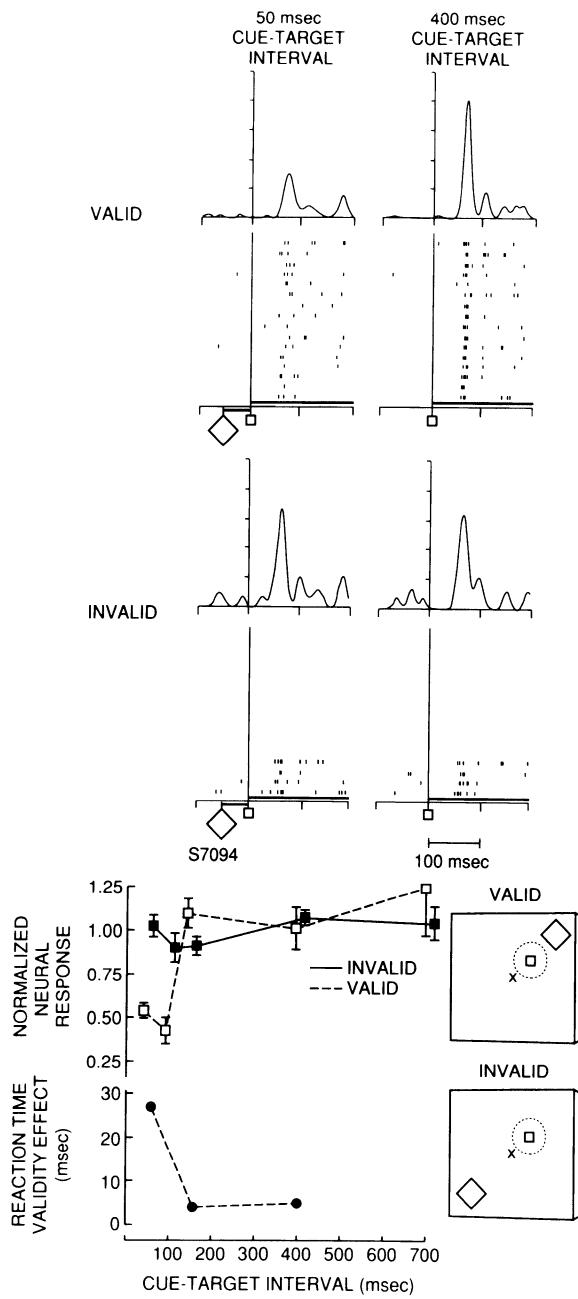


FIG. 4. Responses to the target when the cue was placed outside of the receptive field. In this condition, a group of neurons responded weakly to validly cued targets at short intervals after the cue (*top left*). All other responses were similar. Conventions as in Fig. 3.

Visual activity during cued reaction time task

We studied a total of 126 neurons while the monkeys performed the cued reaction time task. For 25 of these neurons we conducted the experiment so that the cue and target were both positioned at the most effective site within the visual receptive field. Of the remaining cells, 75 were studied with the cue outside of the receptive field, and these will be discussed subsequently. For the other 26 neurons, it was determined by later analysis that the cue was at the edge of the receptive field exciting the cell slightly, and these neurons will not be considered further. In the situation where the cue was centered in the receptive field, there was always

an excitatory burst from the cell at the onset of the cue (Fig. 3). All cells responded transiently to the cue and with uniform responses under all conditions. In validly cued trials, the cue, which is represented in Fig. 3 by the large diamond, fell within the visual receptive field; here, the target, represented by the small square, followed the cue at one of three delays.

For these 25 cells, we analyzed the changes in response to the target. Figure 3 shows that the neuron was refractory to the target just after the cell had discharged in response to the cue. At the *top left* can be seen the response of this neuron to the onset of the cue, which was followed by a weak response to a target; cue and target were separated by 100 ms. At longer intervals (400 and 700 ms) the neuron responded more intensely to the target. When the cue appeared in the visual field opposite to the receptive field, there was a very consistent response to the target (invalidly cued). The sum of the normalized excitability of all 25 neurons tested with the cue and target centered in the receptive field showed a significant effect of the cue (Fig. 3) (analysis of variance, $F(1,4) = 10.25, P < 0.002$). Responses to validly versus invalidly cued targets were different at the first three intervals (50, 100, and 150 ms) (pairwise t -tests). The data

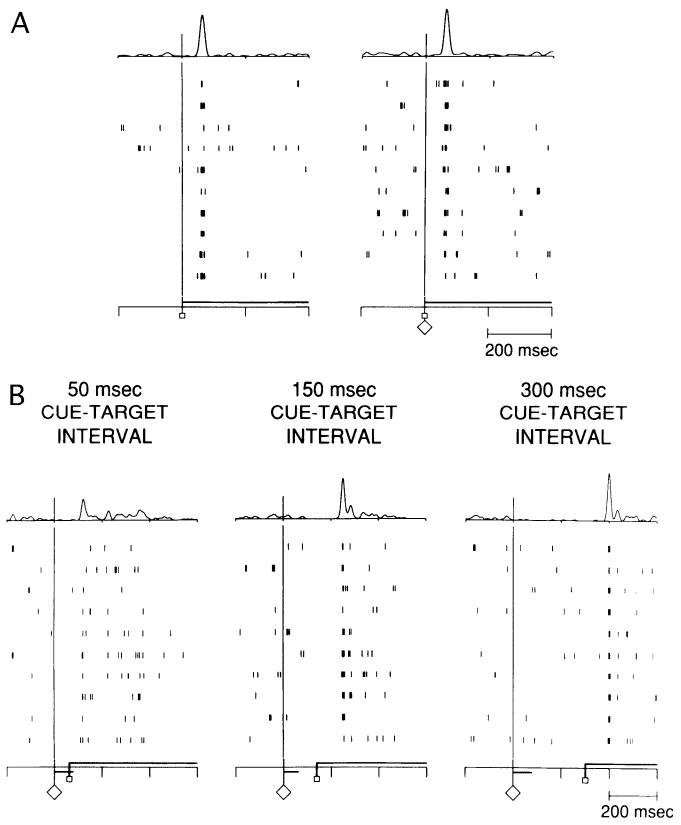


FIG. 5. Lack of visual effects of the cue. *A, top*: data show the response of the cell from Fig. 4 to the target alone (*left*) while the monkey performed the simple fixation task. *A, right*: data show the similar response of this cell to the simultaneous presentation of the cue and target; the target was presented at the same location with the cue positioned just outside of the receptive field. *B*: data show the activity of the same cell to the same stimuli. Here the monkeys were performing the cued reaction time task, and the data are aligned on the cue. Note that the cell discharged in the time interval after the cue, so the cue did not produce a total inhibition. Conventions as in Fig. 3.

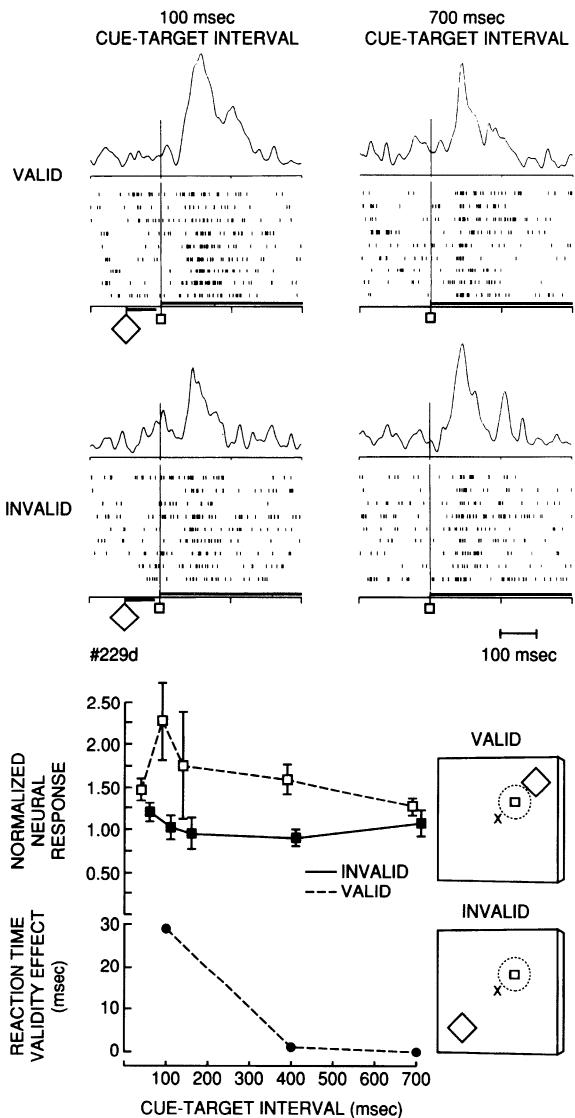


FIG. 6. Neuron responding better to targets at the cued location. *Top*: spike density and raster displays show the enhanced response of this neuron to validly cued targets. There was a consistent response to the target when it was invalidly cued. *Bottom*: plot shows the normalized population activity for those neurons that responded better to validly cued than invalidly cued targets. Conventions as in Fig. 3.

at the *bottom* of the graph in Fig. 3 show the behavioral validity effect during the actual recording of the cell illustrated at the *top*. The validity effect is the difference in reaction times for invalidly and validly cued targets. Each monkey was studied with only three cue-target intervals, and these intervals differed for the two animals. Thus the validity effect values have only three data points, whereas the normalized cellular responses come from the four unique and one common cue-target intervals (see METHODS). We conclude from these results that parietal neurons responded strongly when the cue was flashed in the receptive field. The visual response to the cue produced a relative refractory period such that the cells responded only weakly if the target followed during the next 400 ms. The magnitude and duration of the refractoriness for cells in the superior colliculus was greater under these conditions (Robinson and Kertzman 1995).

Nonrefractory processes during the cued reaction time task

We next wished to learn whether there were other modulations in this task that were independent of the refractory response to the cue. To approach this question, we tested 75 neurons by positioning the cue outside of the receptive field and the target within the receptive field. A schematic of the arrangement of the stimuli for that half of the trials when the target was in the receptive field is illustrated by the tangent screens at the *bottom right* of Fig. 4. Even though cues and targets were not in the identical location, we still refer to valid cues; behavioral validity effects were observed, as illustrated at the *bottom* of Figs. 4 and 6. In this condition the cue did not directly excite the neuron, as illustrated in Fig. 5B. For all of the data to be presented using this approach, there was not a response time-locked to the onset of the cue (Fig. 5B).

A continuum of effects was observed with this arrangement of the task. For all 75 neurons studied in this way, we conducted a two-tailed *t*-test, comparing responses to validly and invalidly cued targets at the shortest cue-target interval. Using this approach, 5% of the neurons would be expected

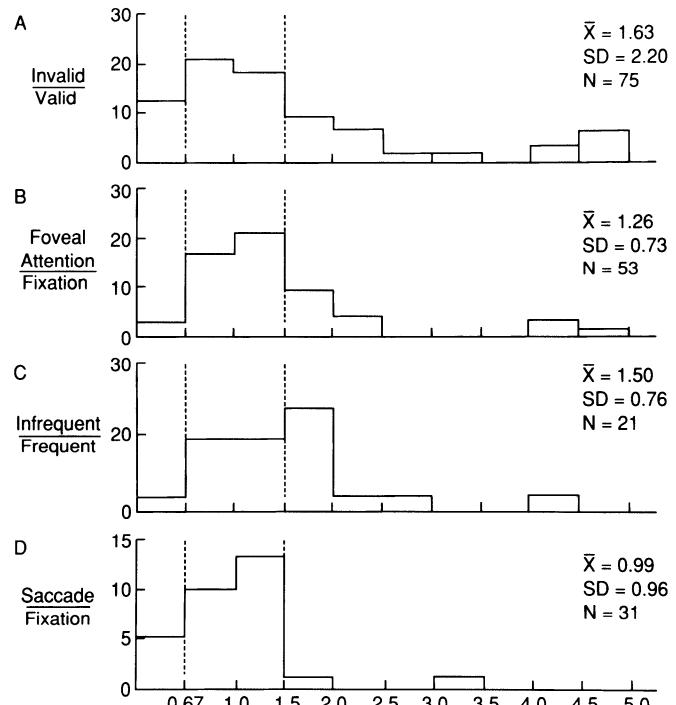


FIG. 7. Ratios of responses in different behavioral conditions. *A*: response of each neuron to an invalidly cued target divided by the response to a validly cued target. Only the shortest cue-target intervals were used. *X*-axis: magnitude of the ratios. *Y*-axis: number of neurons that had each ratio. These data were combined from both monkeys. *B*: ratios were calculated by dividing the response evoked during the foveal attention task by the response during the simple fixation task. These values were obtained from monkey *M1*. *C* was determined by dividing the response for infrequent targets (10%) by the response for frequent targets (90%) during the probability task (monkey *M3*). Data from both bar response and saccade responses were included. *D*: distribution of ratios calculated by dividing the response in the saccade task by the response obtained with simple fixation (monkey *M3*). For every ratio, the data come from the same neuron tested with the identical stimulus. Note that the vertical scales differ in the 4 graphs. \bar{X} , computed mean; SD, standard deviation; N, number of neurons in the sample.

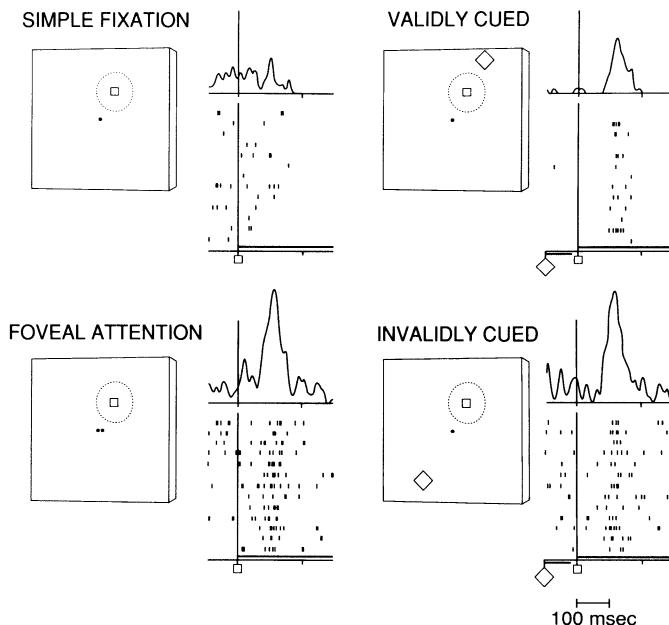


FIG. 8. Differential activity when attention is directed away from the visual receptive field by sensory and task-relevant processes. *Right:* data come from test conditions like those for Fig. 4. *Top left:* for these data the animal was rewarded for maintaining fixation and was not required to respond to the target or fixation point in any other way. As illustrated at *bottom left*, the response of this cell was enhanced when the animal had to attend to the fixation point in order to release the bar when the fixation point increased in size by 0.4°. Conventions as in Fig. 3.

to appear to be changed by chance. One population (48 of 75, 64%) was not significantly influenced by the cueing. However, a second group of neurons (17 of 75, 23%) responded better to invalidly cued targets than to validly cued targets, as illustrated in Fig. 4. For the neuron illustrated at the *top* of the figure, there was a significantly weaker response to the target when it was validly cued at the short interval than when it was invalidly cued at that same interval. The response for the validly cued target at the short interval was significantly different from all the other responses, which were not significantly different from each other.

At the *bottom* of Fig. 4 is the summed, normalized activity for all parietal neurons in this group, those that responded significantly better to invalidly cued targets than to validly cued ones. It was clear from this analysis that the reduction in responsiveness was transient, lasting <100 ms after the cue. The reduced responsiveness was observed only at the shortest intervals, and then the cells returned to their standard level of excitability. Just as the cue had a transient effect on the reaction times, there was a transient effect on these parietal neurons (Bowman et al. 1993). It is possible that the mechanism of the weak response to the validly cued target was due to the shift of attention or to the cue stimulating an inhibitory surround. An inhibitory surround mechanism seems unlikely because simultaneous presentation of both stimuli during the simple fixation task produced no modulation when tested on the cells included in this sample. Figure 5A, *left*, shows the response of the cell to the target alone, and Fig. 5A, *right*, illustrates the comparable response to the cue and target. The data in Fig. 5B show that there was no excitatory response to the cue in the cued reaction time task.

Enhanced responses

A third group of parietal neurons responded best when the cue was flashed near the visual receptive field in the cued reaction time task, and an example of this type of activity is illustrated in Fig. 6. This increased responsiveness began slowly and persisted for ≥400 ms, as illustrated at the *bottom* of Fig. 6. Significantly modulated activity of this type was observed in 10 of 75 (13%) cells. Like the suppressed neurons, the difference between valid and invalid discharges was most pronounced at the short cue-target intervals when the cue effects had their greatest behavioral impact (Fig. 6, *bottom*) (Bowman et al. 1993).

When we made a ratio of the responses for validly and invalidly cued targets, there was a significant shift of the mean of the population toward those responding better to invalidly cued targets. Neurons that responded better to invalidly than validly cued targets had ratios >1.0; those that responded better to validly than invalidly cued targets had ratios <1.0. Figure 7A shows a bar graph of these data and illustrates that the tendency of the population was toward stronger responses to invalidly cued targets. The vertical dashed lines represent ratios >1.5 or <0.67 (Bushnell et al. 1981).

Effects of foveal attention

Because modulation of some parietal visual responses was correlated with attentional effects in the cued reaction time task, we wished to learn whether parietal neurons might also

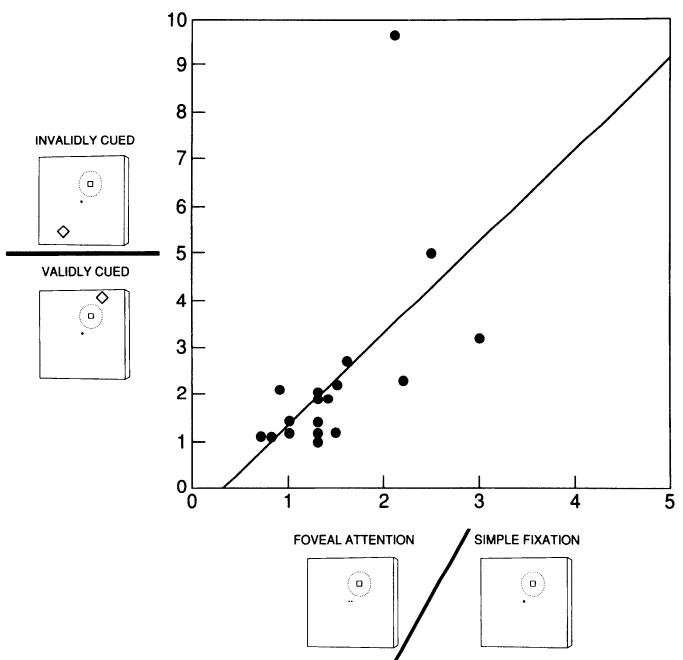


FIG. 9. Correlation of modulations in exogenous and endogenous tasks. Y-axis: ratio of responses at the short cue-target interval for invalidly cued targets divided by the response to validly cued targets. These values are for cells included in Fig. 7A. X-axis: ratio of the response in the foveal attention task divided by that in the simple fixation task. These values are for cells included in Fig. 7B. Line: simple linear regression of the data. These data come from all of the neurons tested in all 4 conditions that also had values of ≥1.0 for invalidly cued target responses divided by validly cued target responses.

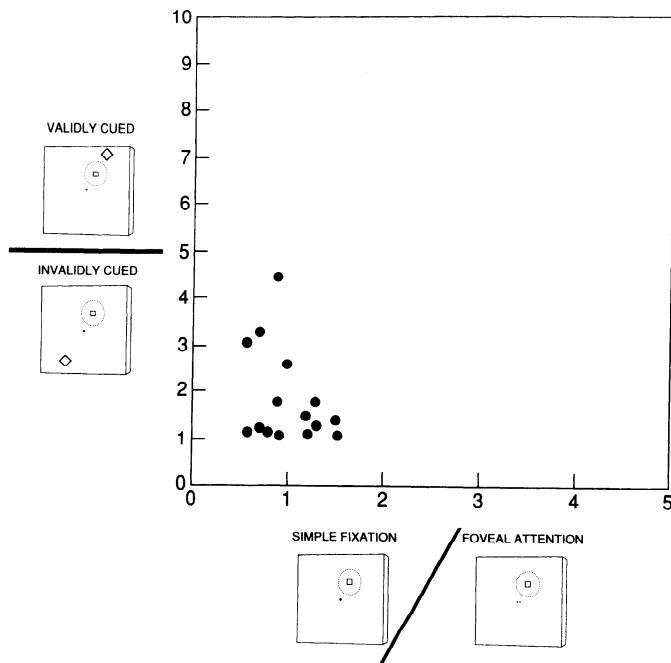


FIG. 10. Lack of correlation for attentional control by different tasks. Data in this plot come from Fig. 7, A and B, and those neurons that responded better to validly cued than invalidly cued targets. Note that the ratios here are calculated opposite those in Fig. 9.

be influenced in other situations that would influence the animals' attention. We studied 53 of the neurons tested in the cued reaction time task during the simple fixation and foveal attention tasks described in METHODS. The data on the *right* in Fig. 8 show the differential activity of one parietal cell during the performance of the cued reaction time task. At the *top left* is illustrated the very weak response of the same neuron to the identical stimulus while the monkey performed the simple fixation task. When we forced the animal to discriminate at the fovea using the foveal attention task (Fig. 8, *bottom left*), there was a great improvement in the visual

response of the same neuron. The two dots at the center of the tangent screen represent the increase in the size of the fixation point that was the monkey's signal to release the bar. The data in Fig. 7B show the ratios of the responses for all cells tested for the simple fixation and foveal attention tasks. There were 10 of 53 cells (19%) with significant enhancements during foveal attention. Here, as in the cued reaction time task, there was a shift toward stronger responses in the population in the foveal attention task. The distributions in Fig. 7, A and B, were not significantly different (χ^2 test). Thus distribution of both ratios might be determined by a single psychological factor, the shift of attention, rather than the simple configuration of stimuli on the tangent screen.

For the 18 neurons with positive ratios for the cued reaction time task, we then plotted those ratios against the ratios for foveal attention and simple fixation tasks (Fig. 9). The Y-axis is the ratio of the invalidly cued target response divided by the validly cued target response (only positive ratios used here); the X-axis is the ratio obtained by dividing the response in the foveal attention task by that obtained during the simple fixation task. There is a significant linear relationship ($P < 0.01$). This relationship suggests that neurons that were strongly modulated during the cued reaction time task were also strongly modulated in the foveal attention task, whereas those that were weakly modulated in one were weakly modulated in the other.

For 16 neurons with enhanced activity to validly cued targets (all cells with ratios of <1.0 when the invalid response was divided by the valid response), we also plotted those values against those from the foveal attention and simple fixation tasks (Fig. 10). Here the ratios were calculated opposite to those for Fig. 9 in order to obtain positive ratios. Cells with enhanced responses in the cued reaction time task showed no simple relationship with their activity in the foveal attention and simple fixation tasks.

Other attentional manipulations

Another way to shift attention is to strongly bias the occurrence of the location of a target. A total of 21 cells were

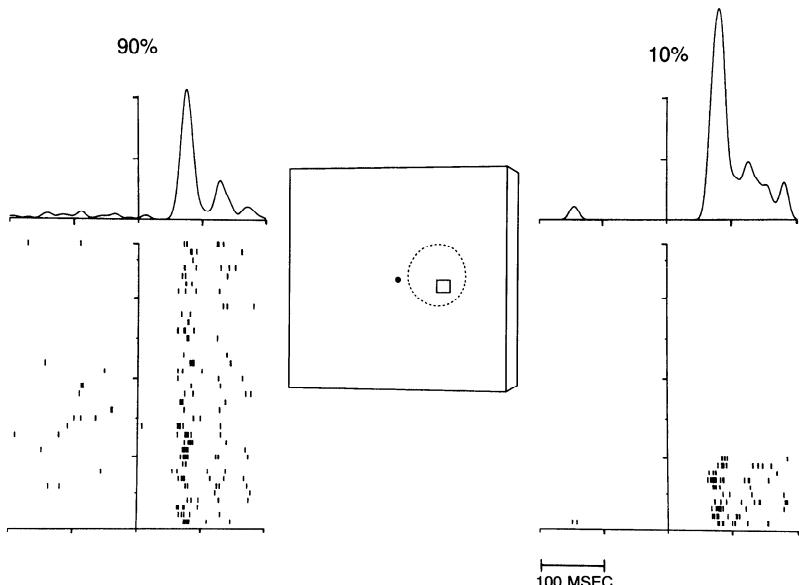


FIG. 11. Differential effect of target probability on visual responses. *Left*: for these data, the target appeared in the visual receptive field in 90% of the trials, and the monkey released the bar when it appeared. In the remaining 10% of the trials, the target appeared in the ipsilateral visual field, and no neuronal response was present. The 1st trials are at the *bottom of the raster*. *Right*: for these data, the same target appeared in the receptive field in only 10% of the trials. In the remaining 90% of the trials, the target appeared in the ipsilateral visual field, and no neuronal response was observed.

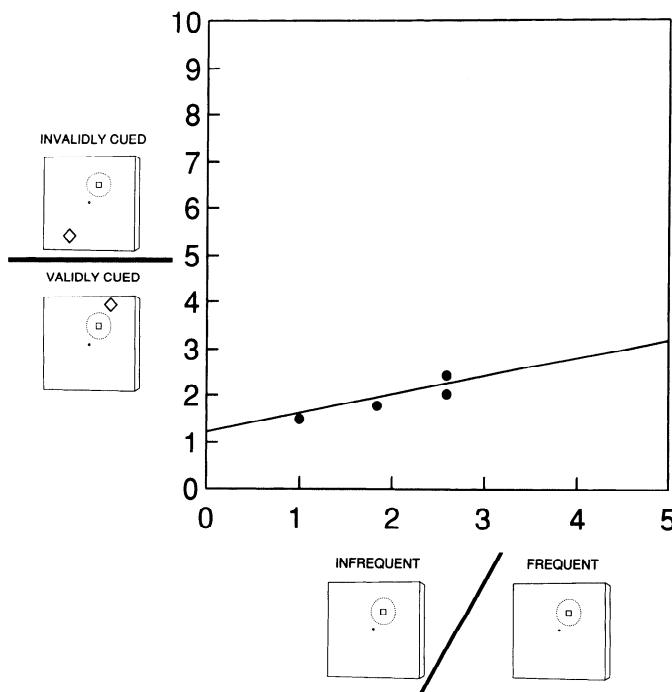


FIG. 12. Correlation of modulations in cued reaction time and probability tasks. The format of this figure is the same as for Fig. 9, and the scales are the same. Only 4 neurons had ratios of ≥ 1.0 in the cued reaction time task and were tested in the probability task.

tested with this approach. We studied 11 neurons in a probability task where the animal had to fixate and release the bar when the target light appeared. We also tested 13 cells in another probability task where the animal's response was a saccadic eye movement. Neurons that were tested in both of these tasks gave similar results. In these two tasks, the target appeared at one location in 90% of the trials and at a second point, in the mirror symmetric location, in the remaining 10% of the trials. In each block of trials, with ≥ 70 correct responses, the probabilities at each location were reversed. The data on the left of Fig. 11 illustrate how a parietal neuron responded well to the initial presentations of the target (bottom of raster) when it appeared at the highly probable location. With repetitions of the trials, the response intensity decreased, as illustrated by weaker responses at the top of the raster. In another block of trials, when the same target appeared seldom (10%) in the receptive field, there was a strong and consistent response. Figure 7C shows the distribution of ratios for these pairs of conditions. The distribution here had a significant shift toward stronger responses to unexpected targets and did not differ significantly from those in Fig. 7, A and B (χ^2 test for 3 samples). In Fig. 12 we plotted the ratios of the cells that had positive values in the cued reaction time task against their ratios in the probability task. For this limited sample, there was a significant relationship ($P < 0.01$). We conclude from these results that the target probabilities shifted the monkey's attention away from the receptive field, and this produced the differential responses.

Preparation for a saccadic eye movement can involve a shift of attention. The data on the right of Fig. 13 show the differential activity of a parietal neuron in the cued reaction

time task. This cell was of the type that responded best to invalidly cued targets. The top left of the figure illustrates the weak response of the same cell during periods of simple fixation (Fig. 13A); at the bottom left are data showing the equally modest response of this cell when this stimulus was the target for a saccadic eye movement (Fig. 13C). We compared 31 cells in this fashion; Fig. 7D shows the ratios of the responses for the simple fixation and saccade tasks. This distribution differs significantly from those in Fig. 7, A-C (χ^2 test; $df = 5$, $P < 0.001$).

Other properties

Figure 14A shows the anatomic locations of the neurons that were modulated in the cued reaction time task. The arrows at the bottom of this flattened portion of the cortex indicate the dorsal surfaces of the intraparietal sulcus. The modulated neurons were predominantly located in the posterior bank of the intraparietal sulcus, which is on the left side of the figure and includes the dark shading that represents the densely myelinated area (LIPv).

During the course of our sampling of parietal cortex, we were able to study cells with receptive fields that included most of the contralateral visual field. Of the 422 excitable

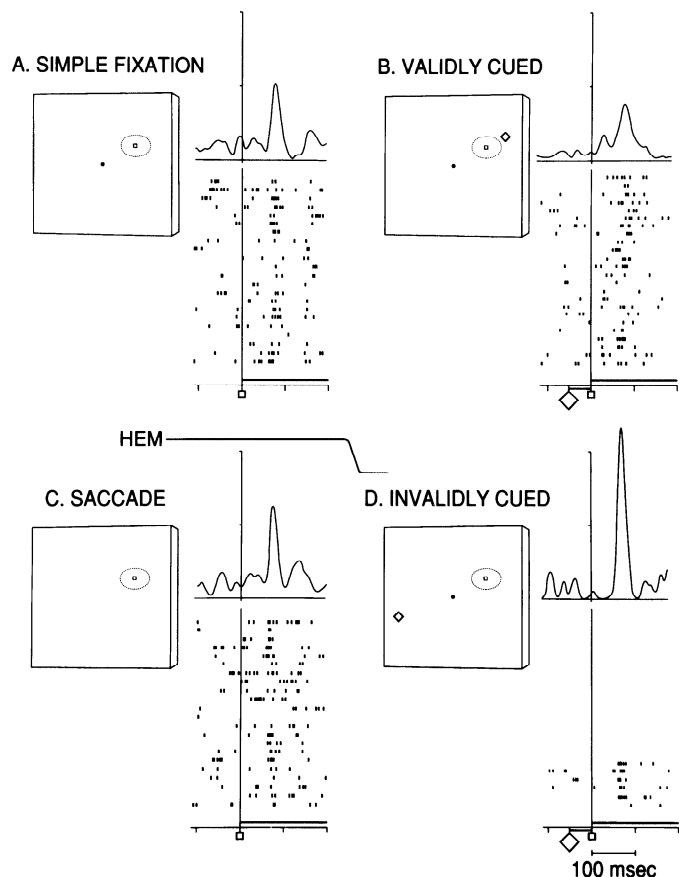


FIG. 13. Influence of saccadic eye movements on cells with attentional modulation. Right: these data show the differential activity of this neuron during the cued reaction time task. Left: at A are the modest responses of the same neuron while the monkey performed the simple fixation task; in C, when the animal was engaged in the saccade task. HEM: schematic horizontal eye movement trace. The conventions here are the same as in Fig. 3.

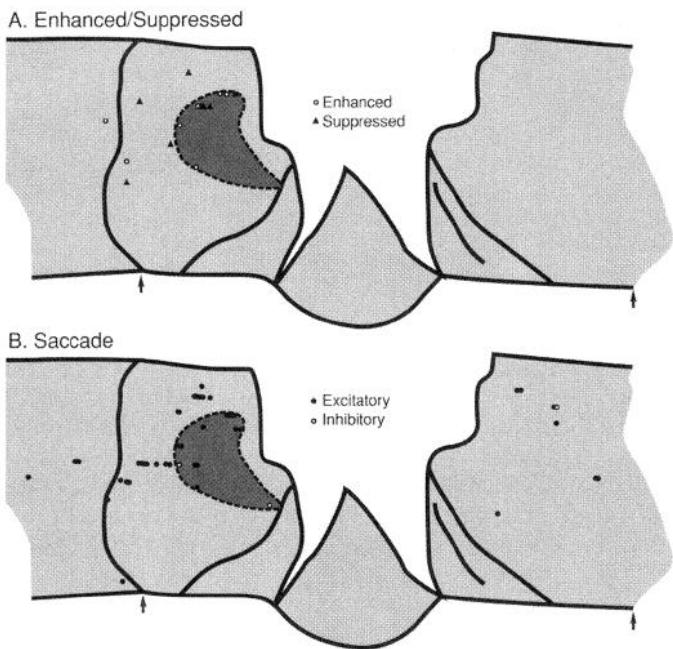


FIG. 14. Anatomic locations of cells with various functional characteristics. The 2 panels correspond to the flattened reconstruction of the cortex as illustrated at right in Fig. 2. *A*: positions of those neurons that were significantly modulated in the cued reaction time task. Arrows at bottom of each map: dorsal edge of the intraparietal sulcus. *B*: cells that discharged with saccadic eye movements.

neurons in our sample, 373 (88%) had solely contralateral visual receptive fields. Of the remaining cells, 29 (7%) had bilateral and 20 (5%) had solely ipsilateral receptive fields. Only 17 cells (4%) had an OFF response.

We tested 125 neurons in relation to visually guided saccadic eye movements in the light, and 50 (40%) were active in this condition. We did not conduct detailed studies of the temporal, spatial, or visual aspects of these properties. Seven neurons with an eye movement relationship were also tested in the cued reaction time task, and five of these responded better to invalidly cued targets. The bulk of active neurons were located on the lateral bank of the sulcus, which is in agreement with previous reports (Fig. 14*B*) (Andersen et al. 1990).

DISCUSSION

Attention is a selection process whereby some stimuli receive higher levels of analysis at the expense of others. Attention can be shifted rapidly or sustained at one point for a period of time. The processes that shift attention may arise externally from the organism—exogenous control—or may be internally mediated with less direct synchronization—endogenous control. In the present studies we describe some response properties of neurons in parietal cortex and analyze changes in these properties during performance in several attentional tasks. All visually responsive neurons discharged to the cue and had differential activity in response to the target depending on validity and cue-target temporal interval (Fig. 3). Many cells had differential activity in other tasks that engaged attention by other modes (Fig. 7). In what follows, first we attempt to integrate these data in terms

of a functional significance of parietal activity to suggest that it signals a shift of attention. Second, we discuss possible physiological mechanisms that the brain might utilize to produce such response properties. Third, we emphasize the parallels between the temporal properties of our physiological observations and the dynamics of attention. Fourth, we relate our data to prior studies using this paradigm with patients with parietal lesions.

Functional significance

BEHAVIORAL RELEVANCE. Many aspects of the present data are consistent with the hypothesis that a component of parietal activity signals a shift of attention to a new location in space. All neurons discharged to the onset of the cue, a situation where attention was probably directed at the fovea before the appearance of the cue (Fig. 3) (Rafal et al. 1988; Robinson and Kertzman 1995). Thus such parietal activity could signal a shift of attention from the fovea to the cued location. Targets that followed the cue at the identical location evoked small responses (Fig. 3), and most likely this weak activity had minimal effect in shifting attention. In those tasks where we attempted to direct the animals' attention away from the receptive field using endogenous paradigms (foveal attention and probability tasks), there were cells that responded optimally when attention was directed away from the receptive field. Here too, their discharge could signal a shift of attention to the location of the visual receptive field.

We also tested many cells with the cue located outside of the visual receptive field (Figs. 4 and 6). Any interpretation of these data is limited by the uncertainty regarding the size of the attentional field, either as measured behaviorally or as such processes might have effects within parietal cortex. Given these limitations, it is possible that all cells studied with cues positioned outside of the receptive field were signaling a shift of attention. For those cells that were suppressed under these conditions, unknown task factors may have positioned attention to include the receptive field plus surround. If such was the case, then this enlarged focus of attention suppressed the visual response. Such suppression would be invoked because attention did not need to be shifted; it included the visual receptive field. For those neurons that were enhanced, different unspecified task conditions may have focused attention to be very localized to the cue alone. Thus attention was not in the receptive field at that time, so that the target evoked an enhanced response signaling a shift of attention into the receptive field. These interpretations require more detailed studies for verification.

We have demonstrated that all cells in the superior colliculus also respond to the cue (Robinson and Kertzman 1995). Thus it is possible that cells at many levels of the visual system play a role in exogenous shifts of attention. Alternatively, responses of some visual cells may be suppressed behaviorally and play no role in exogenous shifts of attention. Parietal cortical cells appear to have a more compelling relationship to attention because many of the same cells responding to the cue also have attentional responses that are invoked in endogenous paradigms (Fig. 8, 9, 11, and 12).

An examination of the ratios in Fig. 7, *A–C*, shows that there was a continuum of modulations of responses for the

different behavioral conditions. For the purpose of making mechanistic interpretations, it is useful to separate the response types into three groups, those suppressed, those enhanced, and those unchanged by these tasks. The largest group of cells were not significantly modulated by any of the present tasks (Fig. 7). However, simple visual processing and/or signaling a shift of attention in exogenous situations might not be their only function. For instance, the monkeys' angle of gaze, intended eye movements, tracking, reaching, or manipulative activities can influence parietal cortical activity (Andersen and Mountcastle 1983; Boch and Fischer 1983; Duhamel et al. 1992; MacKay 1992; Sakata et al. 1983; Taira et al. 1990). The present enhanced cells most likely were the same type as those studied previously with saccadic and attentional enhancement tasks (Bushnell et al. 1981; Goldberg et al. 1990; Wurtz et al. 1980). In those tasks, parietal cells responded best in tasks where the monkeys were required to fixate and attend to the periphery, a type of divided attention task. In both of these different approaches to attention there were strong responses at the focus of attention, and there were objective measures that the animal attended to those stimuli. The suppression of visual responses described here appears comparable with that discovered in inferior temporal cortex during attention to spatial location (Richmond et al. 1983). In these different approaches, there were weak responses at the focus of attention in the periphery.

We observed neurons within parietal cortex that respond weakly to stimuli at the focus of attention and that might signal a shift of attention. There have been demonstrations of better responses for invalidly cued targets in studies of human event-related potentials (Anllo-Vento 1995; Hillyard et al. 1994). Others have suggested a comparable role for the N1 attentional signal from human event-related potentials (Mangun et al. 1990). Some cells were enhanced near validly cued targets, and they appear comparable with the attentional enhancement of the P1 component observed in humans (Mangun et al. 1990).

OTHER ROLES. Andersen and colleagues have proposed that activity within area LIPv is related to the programming of eye movements, because some cells here discharge before eye movements in a wide variety of conditions (Barash et al. 1991a, 1991b; Gnadt and Andersen 1988). It would seem that we have studied different aspects of the activity of these cells. All of the activity we observed was time-locked to the onset of a visual stimulus. Although such activity was frequently present in trials when the animal made a motor response, it preceded such motor responses by hundreds of milliseconds and was not time-locked to them. We have used similar logic to argue for nonmotor roles of other parietal effects (Bushnell et al. 1981; Wurtz et al. 1980).

When two visual stimuli follow each other closely in time, the perception of one is changed by the other (Breitmeyer 1984). There are considerable data on the behavioral and physiological consequences of the close temporal pairing of two stimuli resulting in masking effects (Donchin and Lindsley 1965a,b; Kahneman 1968; Schiller 1968; Schiller and Chorover 1966; Sperling 1965). Targets that follow other stimuli at the same location, generally including foveal vision, are subject to forward masking, an increase in thresh-

old to the target. Targets that follow at disparate locations, again including foveal targets, are subject to paracontrast, resulting in an increase in detection threshold. Aspects of the present experiments might be erroneously considered forward masking and/or paracontrast, although our testing always used peripheral vision. Furthermore, masking experiments deal with the increases in thresholds for the test stimuli, whereas our data show that the animals respond better to the second stimulus (Figs. 3, 4, and 6). In our studies, the behavioral response to the target was enhanced by the cue, not suppressed. This difference may be due to the low intensity and salience of our cue as well as the use of the visual periphery.

In the present physiological studies we tested some neurons with the cue and target separated. As such, these conditions might be erroneously considered paracontrast. As such they might resemble some electrophysiological processes studied in other parts of the visual pathways (Donchin and Lindsley 1965a,b; Schiller 1968). However, we observe a behavioral improvement in performance rather than the U-shaped decline that is characteristic of paracontrast. Even if the underlying physiological mechanisms of masking and paracontrast are similar to the effect in parietal cortex for the cued reaction time task, the two approaches have different qualitative and quantitative effects on behavior.

LIMITATIONS. Although there are many advantages to using the cued reaction time task for studies of attention, there are limitations. First, the task is not very demanding on the attentional system. This is most obvious in Fig. 6 of our previous paper, which showed much greater validity effects for an endogenous task than are present in this approach (Bowman et al. 1993). Second, the behavioral attentional effects that are present are small, however consistent they are. Third, as we have emphasized in this and the prior manuscript, the validity effects are short lived. Thus qualitative and quantitative comparisons between this task and others need to be interpreted cautiously.

Physiological mechanisms

In this part of the discussion we will consider some of the underlying physiological mechanisms and pathways for the several response properties we have observed. It has been known for some time that neurons within parietal cortex respond to visual stimuli, although the detailed anatomy of pathways that connect them with the retina remains unclear (Motter and Mountcastle 1981; Robinson et al. 1978; Yin and Mountcastle 1977). There are neurons within the dorsomedial portion of the lateral pulvinar (area Pdm) that have similar visual properties, and these could be the afferents to parietal cortex (Petersen et al. 1985). The major afferents to parietal cortex include the medial pulvinar as well as various prestriate cortical areas (Andersen et al. 1990; Baleydier and Mauguière 1977; Baleydier and Morel 1992; Cavada and Goldman-Rakic 1989a,b; Yeterian and Pandya 1985). Thus any or all of these sources could provide the visual signals. Because we found that the modulated neurons tended to respond with the short latencies for this sample, it is likely that they are fed via the magnocellular system, which has been suggested to mediate attentional shifts (Baizer et al. 1991; Baleydier and Morel 1992; Maunsell et al. 1990; Van Essen et al. 1992). We have

shown that all parietal neurons respond weakly to the visual target if it follows the cue at the same location (Fig. 3). This effect is due to a relative refractory mechanism that could be initiated within the retina, in parietal cortex, and/or at any other site along the afferent pathway.

For a number of neurons we used endogenous paradigms (foveal attention and probability tasks) and observed enhancement of visual responses. Such effects are probably the result of amplification of sensory responses (Wurtz et al. 1980). The visual signals most likely arrive via pathways just outlined. The modulating inputs could come from such attention-related areas as the Pdm portion of the lateral pulvinar, medial pulvinar, inferior temporal cortex, or prestriate area V4 (Moran and Desimone 1985; Petersen et al. 1985; Richmond and Sato 1987).

Many of our cells were tested with the cue outside of the visual receptive field. We observed various modulations in these conditions. We demonstrated that one group of parietal neurons responded weakly to validly cued targets at the shortest cue-target interval. A simple mechanism by which such an effect might be mediated is through an inhibitory surround; the cue appeared in an inhibitory region of the visual receptive field, and this reduced the response to the target. Whatever the physiological mechanism of this effect, the cells still could signal a shift of attention. Because the cued reaction time task is an attentional paradigm and parietal cortex most likely participates in its performance (Petersen and Robinson 1986; Petersen et al. 1989; Posner et al. 1984), the activity of these cells may mediate attentional effects based on an inhibitory surround mechanism. However, this mechanism seems unlikely for many reasons. First, parietal neurons have minimal or no inhibitory surrounds (Robinson et al. 1978). Second, for these neurons we tested their responses to the target alone and then in simultaneous presentation with the cue (Fig. 5A). Recordings conducted during the simple fixation task showed no inhibitory surrounds for the cells with these effects. For every cell included in this sample, the data were analyzed after completion of the experiment to ensure that no detectable visual response was time-locked with the cue (Fig. 5B). There have been a number of demonstrations of unique surround effects within the visual system, but these do not appear to have the appropriate characteristics to mediate the present effect (Allman et al. 1985; Fischer and Kruger 1974; McIlwain 1964). More compellingly, when these cells were tested in other behavioral tasks that did not include a second, peripheral stimulus, a pattern of activity consistent with attentional modulation of the responses evoked by the target was observed. These tasks included the foveal attention (*monkey M1*) (Fig. 8), probability (*monkey M3*) (Fig. 11), and saccade tasks (*monkey M3*) (Fig. 13). Furthermore, when the activity during the cued reaction time and foveal attention tasks (Fig. 9) was correlated (*monkey M1*) and when activity in cued reaction time and probability tasks (Fig. 12) was correlated (*monkey M3*), there were significant relationships. Only *monkey M1* was studied with the foveal attention task, and these data could be unique for only that animal. However, this seems unlikely because the probability task produced comparable modulations in *monkey M3* (Fig. 7C) and significant correlations with the cued reaction time task (Fig. 12). Because stimulation of an inhibitory surround

could not have been the modulating process in the foveal attention, probability, or saccade tasks, this suggests that it was not the mechanism underlying the differential responses seen in the cued reaction time task. Another study using endogenous control of attention has also shown suppressive effects of attention on parietal neurons (Steinmetz et al. 1994).

An additional control would be to present the cue followed by the target while the monkey performed the simple fixation task. Because no behavioral response would be required to either stimulus, the absence of an interaction would strengthen the argument for an attentional mechanism for the suppression. The lack of an interaction would also exclude apparent motion as a possible mechanism. Because cells were not tested routinely for directional selectivity, it is not possible to relate this possibility to the present data (Motter and Mountcastle 1981; Motter et al. 1987; Steinmetz et al. 1987).

The present discussion deals with the differential activity of this set of neurons as if the modulating process were suppression. This interpretation comes mainly from the observation that there was little change in the excitability of parietal neurons for invalidly cued targets (Figs. 3, 4, and 6). When validly cued trials were analyzed for these cells, the only change was an initial period of diminished responsiveness. Furthermore, for the cells with enhanced responses to validly cued targets (Fig. 6), the increased responsiveness appears to persist for a longer duration than the suppression. Thus the physiological process might be a transient suppression of excitability rather than a much more prolonged period of facilitation. For the enhanced cells, we would propose a more prolonged facilitation in relation to a shift of attention.

For the cells with enhanced responses the mechanism could be a simple visual-visual interaction between the cue and target. This seems unlikely because the cues never directly excited the neurons in any control conditions. It is most likely that some aspect of the direction of attention produced an amplification of the visual signal; this could be mediated via a pulvinar subdivision or a prestriate area.

Dynamics

In a previous report we studied the behavioral effects of the cued reaction time task and concluded that the attentional effects were transient and reproducible (Bowman et al. 1993). After the appearance of the cue there was a rapid change in reaction time performance; validly cued targets were responded to faster than invalidly cued targets. Our data suggest that the major effect is the speeding by the cue and not necessarily slowing by invalidity (Fig. 4 of Bowman et al. 1993). This effect was present with cue-target intervals of only 100 ms. The magnitude of the effect was always reduced at 400-ms cue-target intervals and insignificant at the 700-ms cue-target interval. The time course of the attentional effects changed subtly with various experimental manipulations, but the effect was always present and transient in nature. Thus this is a task with frequent shifts of attention, and there were transient and measurable shifts in reaction times.

In parallel with these behavioral data are the observations that the physiological effects of attention in parietal cortex

arc also transient. Those neurons that were suppressed by attention had a very fast and brief period of reduced response (Fig. 4). Those cells that were enhanced by attention had a facilitation that began more slowly and persisted longer than the suppressive effect but was also transient (Fig. 6). These observations might lend themselves to estimate the time course of various attentional changes.

We also demonstrated that in other behavioral conditions, such as the foveal attention, probability, and saccade tasks, there were comparable attentional modulations. Because the foveal attention task required sustained attention and was conducted in blocks of trials, its temporal dynamics should be different from those in the cued reaction time task. Additional variations might be present in the probability task that could provide insight into other dynamic aspects of attention.

Cued reaction time task and parietal lesions

Several studies have utilized the cued reaction time task to evaluate the abilities of patients with damage to parietal cortex (Baynes et al. 1986; Petersen et al. 1989; Posner et al. 1984, 1987). Several observations are consistent among these various studies. All patients are slow in responding to all targets. In all cases, the patients were slightly but significantly slower to respond to validly cued targets in their affected visual fields than to validly cued targets in the ipsilateral field. These data suggest some sensory problem in the contralateral visual field or a defect in the engagement of attention on targets. These patients were profoundly slowed in responding to targets in the affected visual field when their attention had been drawn to the opposite field by the cue. As such, this demonstration is comparable with the clinical sign of extinction where patients are unable to detect a visual stimulus when it is simultaneously paired with a second stimulus in the intact field. It is important to note that a comparable defect was observed when attention was drawn away from the affected field by a central, symbolic cue. Thus it appears that in these patients an attentional system is damaged. It has been consistently shown that these defects are largest for lesions of right parietal cortex, although they are demonstrable with damage to the left hemisphere. We found that patients were also slow in responding to targets in either visual field after a diffuse cue that weakly illuminated the whole visual field (Petersen et al. 1989). A monkey with a surgical lesion of parietal cortex had similar defects to those of patients tested under identical conditions (Petersen and Robinson 1986). All of these deficits are present for long periods after parietal damage, suggesting that they represent important functions for this part of cortex. In an interesting utilization of this approach it was demonstrated that patients with parietal damage are also slow in attentional shifts made entirely within their affected visual fields (Baynes et al. 1986). It is possible that two types of attentional defects are produced by parietal damage; one would be related to contralateral space and the other related to the movement of attention in the contralateral direction (Posner et al. 1987).

Present and previous data from parietal cortex show the neurons here respond to visual stimuli (Andersen et al. 1990; Motter and Mountcastle 1981; Robinson et al. 1978; Yin and Mountcastle 1977). Most visual receptive fields are on

the contralateral side, although there is a substantial representation of the ipsilateral side. The slowing of responses in humans to validly cued targets presented in the visual field contralateral to a parietal lesion may reflect the loss of these contralateral visual responses. The loss of the cells that respond to stimuli in the ipsilateral visual field may lead to slow behavioral responses for targets in the visual field ipsilateral to a parietal lesion.

It has been proposed that parietal cortex functions to disengage attention, because patients with damage there are profoundly slow in responding to targets in their affected field when their attention has been drawn to their intact field (Posner et al. 1984). It is possible that the neurons studied here, which we have hypothesized signal a shift of attention, are part of the same process. All neurons respond when the cue appears in the receptive field and attention is presumed to be at the fovea. Thus they might signal the need to disengage attention from the fovea. Some cells were suppressed when the cue had drawn attention to the region of the receptive field but were well excited in all other tested conditions. Thus these neurons discharged best when attention was not directed to the receptive field and therefore needed to be disengaged to move to the receptive field. In future studies it will be important to determine whether the processes we have studied here are necessary for attentional shifts. At this point we can only say that they covary.

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