Response of Neurons in the Lateral Intraparietal Area to a Distractor Flashed During the Delay Period of a Memory-Guided Saccade

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Powell, Keith D. and Michael E. Goldberg. Response of neurons in the lateral intraparietal area to a distractor flashed during the delay period of a memory-guided saccade. J Neurophysiol 84: 301–310, 2000. Recent experiments raised the possibility that the lateral intraparietal area (LIP) might be specialized for saccade planning. If this was true, one would expect a decreased sensitivity to irrelevant visual stimuli appearing late in the delay period of a memory-guided delayed-saccade task to a target outside the neurons’ receptive fields. We trained two monkeys to perform a standard memory-guided delayed-saccade task and a distractor task in which a stimulus flashed for 200 ms at a predictable time 300–100 ms before the end of the delay period. We used two locations, one in the most active part of the receptive field and another well outside the receptive field. We used six kinds of trials randomly intermixed: simple delayed-saccade trials into or away from the receptive field and distractor trials with saccade target and distractor both in the receptive field, both out of the receptive field, or one at each location. This enabled us to study the response to the distractor as a function of the monkey’s preparation of a memory-guided delayed-saccade task. We had assumed that the preparation of a saccade away from the receptive field would result in an attenuation of the response to the distractor, i.e., a distractor at the location of the saccade goal would evoke a greater response than when it appeared at a location far from the saccade goal. Instead we found that neurons exhibited either a normal or an enhanced visual response to the distractor during the memory period when the target flashed outside the receptive field. When the distractor flashed at the location of the saccade target, the response to the distractor was either unchanged or diminished. The response to a distractor away from the target location of a memory-guided saccade was even greater than the response to the same target when it was the target for the memory-guided saccade task. Immediate presaccadic activity did not distinguish between a saccade to the receptive field when there was no distractor and a distractor in the receptive field when the monkey made a saccade elsewhere. Nonetheless the distractor had no significant effect on the saccade latency, accuracy, or velocity despite the brisk response it evoked immediately before the saccade. We suggest that these results are inconsistent with a role for LIP in the specific generation of saccades, but they are consistent with a role for LIP in the generation of visual attention.

INTRODUCTION

Neurons in the lateral intraparietal area (LIP) discharge in association with a variety of sensory and motor events. During a memory- or visually guided delayed-saccade task, they respond to the appearance of the saccade target, through the delay period, before the saccade, and well after it (Andersen et al. 1987; Colby et al. 1996). They respond to the sudden onset of visual stimuli and give enhanced visual responses when the monkey must respond to the stimulus in some way. Many neurons do not require the presence of a visual stimulus but discharge, albeit weakly before and during the saccades of learned-saccade tasks and even anticipate the appearance of predictable stimuli (Colby et al. 1996). They also respond to auditory stimuli when those stimuli specify the locations for saccades (Stricane et al. 1996).

The significance of this activity is not clear. One hypothesis is that neuronal responses in LIP carry a motor plan and specify the monkey’s intention to make a saccade (Bracewell et al. 1996; Snyder et al. 1997). In this view, activity in LIP is predictive of the monkey’s actually performing a saccade. Sustained and presaccadic activity during the delay period of memory-guided saccade tasks under a variety of conditions has provided evidence for this interpretation (Andersen et al. 1997; Platt and Glimcher 1997).

A second possibility is that neuronal responses are not tied to a particular modality of response but instead specify the salience of an object in a given spatial location. Evidence for this possibility comes from analysis of activity in a number of tasks. LIP neurons respond much more to salient objects that are not saccade targets than to behaviorally irrelevant stable objects. LIP neurons also respond to stimuli that dictate saccades away from those stimuli and discharge much less before saccades made without visual targets (Gottlieb et al. 1998). These experiments show that LIP activity is independent of overt saccade planning. However, in most experiments the stimulus that excited the neuron occurred at a time at which it could have been the subject for covert saccade planning (Andersen et al. 1997).

In this study, we examine the response of LIP neurons to a visual probe during the delay period in a memory-guided saccade task. The stimulus appeared at a time when, presumably, the saccade location had been identified and the saccade plan already formulated. If LIP was dedicated to the planning of saccades, then one might expect the response to the visual probe or distractor to be suppressed when it was irrelevant to saccade planning and when its appearance had no effect on the latency, velocity, accuracy, or trajectory of the saccades. Instead of the response to this saccade-irrelevant stimulus being...
suppressed, we found that LIP neurons responded more intensely when the monkey was preparing a saccade away from the location of the distractor than when the monkey was preparing a saccade to the site of the distractor. The response continued until the time of the beginning of the saccade. A brief description of these experiments has appeared elsewhere (Powell et al. 1998).

METHODS

Animal preparation

Two adult male rhesus monkeys (M. mulatta, 5–10 kg) served as subjects in this experiment. All protocols were approved by the Animal Care and Use Committee of the National Eye Institute and were in compliance with the Public Health Service Guide for the Care and Use of Laboratory Animals. Prior to surgery the monkeys were trained to sit in a primate chair. The monkeys were prepared under aseptic conditions using general anesthesia (induced with ketamine and maintained with isoflurane delivered via a mixture of nitrous oxide and oxygen) for chronic neurophysiological recording. Scleral search coils were implanted to record eye movements (Judge et al. 1980). Bilateral craniotomies were made over the intraparietal sulcus (centered at AP 5 and L12 mm). Recording chambers 2 cm in diameter were placed flush against the skull, allowing an angle of electrode penetration approximately in the plane of the central portion of the intraparietal sulcus. Titanium screws were attached to the skull, and methyl methacrylate resin was used to attach the chambers and head-holding device to the screws. All hardware used was either ULTIMA Resin 1000 Series (GE, Larid Plastics) or titanium to allow magnetic resonance imaging of the recording sites.

Behavioral methods

MEMORY GUIDED TASK. After they recovered from surgery, the monkeys were trained on the memory-guided saccade task (Hikosaka and Wurtz 1983). The monkey sat in a primate chair in a dark room facing a tangent screen 57 cm distant. The trial began when the monkey looked at the fixation point. A target stimulus was presented 750 ms later for 500 ms. The monkey had to maintain fixation throughout the target presentation and hold his gaze until the fixation point was extinguished 750 ms after the target stimulus extinction. The monkey then had to make a saccade to the remembered location of the target stimulus. The location of the target stimulus was placed either in the neuron's receptive field or outside the neuron's receptive field (Fig. 1, A and B). The target stimuli were red light-emitting diode (LED) pinhole images back-projected on a screen using Kodak projection lenses. The stimuli were 0.3° in diameter and had a mean luminance of 2 cd/m². The visual stimuli were produced by back projecting red LEDs or lasers directed by servo controlled mirror galvanometers (General Scanning).

DISTRACTOR TASK. The monkeys were trained to make saccades to the location of a previously flashed target as in a memory-guided saccade task but with the addition of a visual distractor. The monkey maintained fixation of a point of light as a target light was flashed for 500 ms and a visual distractor for 200 ms. The visual distractor appeared 450 ms after the target stimulus was extinguished. The distractor had the same size and luminance as the target and was indistinguishable from it except when it appeared at different locations. Between trials an incandescent background light appeared to prevent dark adaptation and to keep the monkey alert. One hundred milliseconds after the distractor stimulus was turned off, the fixation point disappeared as the signal for the monkey to make a saccade to the location of the target. The monkeys had to ignore the distractor for saccade targeting because it contained no information regarding the location of the required saccade, although conceivably they could have used it as a warning that the saccade was imminent. The monkeys were always rewarded for making a saccade to the remembered location of the target and never rewarded for making a saccade to the location of distractor unless the distractor appeared at the target location. The monkeys used were never trained to perform a double saccade task (Mays and Sparks 1980) and were not rewarded for a second saccade to distractor. We never saw the monkey make a saccade after the trial to the spatial location at which the distractor had appeared. The monkeys did not have a compelling time constraint to make the saccade rapidly (in most cases they were rewarded if they made the saccade within 400 ms); their average saccade latency was 231 ms. There were six combinations of locations for the target and distractor (Fig. 1, A–F). Two tasks were simply visual-memory-guided delayed-saccade tasks without any distractor. Two placed the target and distractor in different locations, with one in the receptive field and the other outside of the receptive field of the neuron. The last two tasks flashed the target and distractor at the same location either inside or outside of the neuron’s receptive field. Each neuron’s dis-

FIG. 1. The 6 variations of the memory-guided delayed-saccade task used to characterize the responses of neurons in the lateral intraparietal area (LIP). Each cartoon represents a task variation and contains a representation of the visual field with the fixation point (FP), the neuron’s receptive field (RF) and saccade (→). The location of the saccade target A–F (●) and distractor stimulus in C–F (○) is also shown. If the saccade target and the distractor target were in the same location, they are marked with a half-filled circle in C and F. The timing of the fixation point and visual stimuli is represented as a running bar plot below the memory-guided and distractor tasks. Each tick mark is 100 ms.
Fig. 2. Magnetic resonance image (MRI) in the coronal plane at the level of LIP. This MRI transects the intraparietal sulcus (S) in both hemispheres. Both grids are visible in this image. The angles of these grids determine the angle of electrode penetration. The image was recorded with an electrode in each grid. The shadow cast by these electrodes is marked by a white line (E).

Physiological methods

Recordings were made with flexible tungsten electrodes (FHC) introduced through stainless steel guide tubes lowered below the surface of the dura but not through it. The guide tubes were held in place by a nylon grid secured in the recording chamber. The grids had holes spaced 1.0 mm apart. Alternate use of two grids, offset from each other by 0.5 mm, enabled penetrations spaced 0.5 mm apart. Magnetic resonance imaging (GE Signa, 1.5 Tesla, T1 sequence) of the monkey’s brain with a tungsten electrode in place was used for anatomic localization (Fig. 2).

Control of the position and timing of the visual stimuli, monitoring of the monkey’s eye position, unit sampling, and on-line data analysis were performed on an Intel-based personal computer running QNX and the REX system (Hays et al. 1982). The electrode signal was passed through a field effect transistor preamplifier and discriminated using two methods. Most neurons were detected by an analog BAK charge was recorded during all trial types, which were presented in a pseudorandomly interleaved fashion.

Data analysis

Responses for each neuron for each trial type were analyzed off-line using in-house software developed in the C and Matlab (MathWorks) programming languages. Neuronal responses were measured for five epochs in each trial: the visual period is the 200-ms epoch from 100 to 300 ms after the appearance of the saccade target; the delay period, from 200 to 400 ms after the saccade target disappeared; the distractor period, from 100 to 300 ms after the distractor appeared; the presaccadic period, 100 ms before the saccade began; and the perisaccadic period, 100 ms after the saccade began. Note that the presaccadic period is not the last 100 ms of the distractor period. The distractor period ended when the fixation point disappears. This was the go cue for the saccade not the saccade onset itself. Neuronal responses were measured as the average spike frequency in the interval. To test for differences in activity in two different tasks in a given epoch, we used the Wilcoxon paired signed-rank test; a test of equality of medians of two matched samples (Matlab). This did not require us to make any assumptions about the normality of spike distributions.

RESULTS

Data set

We studied 28 neurons from three hemispheres of two monkeys. All the cells were tested on all six target and distractor combinations. LIP has a heterogeneous population of neurons. Although 95% of LIP neurons have visual responses (Colby et al. 1996), a lesser proportion have delay and presaccadic activity (Barash et al. 1991). We only used neurons with delay or presaccadic activity in this study. It is important to emphasize that neurons in LIP exhibit a continuum of re-

Fig. 3. Response of a neuron during the delayed-saccade task. A1: visual response of the neuron. In the raster diagram, each line represents a single trial. Each dot is an action potential plotted at the time at which it occurred in the trial. Successive trials are synchronized at the onset of the saccade target (vertical line). The continuous function beneath the raster is a spike probability density function for all the trials in the raster above. Horizontal (H) and vertical (V) eye positions are displayed beneath the spike density diagram, as are the presence of the fixation point (FP) and saccade target (T). A2: presaccadic response. Same data as in A1 synchronized on the beginning of the saccade. The shaded boxes represent the time epochs used to calculate the visual and delay period responses (in A1) and the perisaccadic response (in A2). B, I and 2, shows a different neuron analyzed in an identical manner. The neuron in A has a predominant presaccadic discharge. The neuron in B has a predominant delay-period response.
responses with different neurons showing greater or lesser proportions of delay and presaccadic activity in the memory-guided delayed response task. Both neurons illustrated in Fig. 3 have visual responses. The first neuron (Fig. 3A, 1 and 2) has a strong presaccadic response but a lesser, if significant, activity in the delay period. The second neuron (Fig. 3B, 1 and 2) has a striking delay period response but a lesser presaccadic increase. To characterize the sample rather than merely show averages, we plotted the response of each neuron to the saccade target onset in the memory saccade task against both the summed pre- and perisaccadic and delay-period responses (Fig. 4). In this figure, we have plotted the presaccadic activity (○) and the delay period activity (●) of each neuron against the visual response of that neuron. We connected the presaccadic and delay-period activity of each neuron with a straight line so that the reader could easily perceive the characteristics of each cell. Occasionally the two values overlapped. Most but not all of the neurons in the sample had more visual activity than saccade activity.

Effect of saccade target location on the response to the distractor

To analyze the effect of ongoing saccade planning on the response to a distractor, we studied the responses of neurons to a distractor in the RF during the delay period of a visual memory-guided delayed saccade away from the receptive field (Fig. 5). Surprisingly, most neurons responded more vigorously to the distractor when the saccade target was flashed outside the RF than when it was flashed at the same spatial location at which the distractor appeared. This enhanced response could be seen on neurons with strong presaccadic responses (Fig. 5A1, saccade away from the RF; Fig. 5A2, saccade to RF; same neuron as Fig. 3A) than when it was flashed at the same spatial location at which the distractor appeared as well as in neurons with strong delay period responses (Fig. 5B1, saccade away from RF; Fig. 5B2, saccade to RF, same neuron as Fig. 3B). The population as a whole showed this enhancement of response when the distractor appeared away from the saccade goal (P < 0.001 by Wilcoxon paired signed-rank test). No neuron had a significantly weaker response to the stimulus when the monkey planned a saccade elsewhere (Fig. 6).

The response to the distractor when the monkey planned a saccade into the RF was significantly less across the population than the response to the appearance of the saccade target (P < 0.01 by Wilcoxon paired signed-rank test) as shown in Fig. 7. One possibility for this effect is that the major difference between these two cases was the stimulus order: the neuron responded most at the first appearance in a given trial of a

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**FIG. 4.** Visual, delay period, and perisaccadic responses plotted across the sample. Each symbol represents the activity of a single cell. Presaccadic (○) and delay period responses (●) are plotted against the visual response (ordinate) for each cell. —, connect the responses of the same cell in the 2 conditions.

**FIG. 5.** Response to the distractor appearing near the end of the delay period of a visual memory-guided saccade. A: same neuron as in Fig. 3A shown during 2 types of trials. A1: the distractor was flashed in the RF when the saccade target location was outside the RF. A2: the distractor was flashed at the same spatial location as the saccade target. B: same neuron as in Fig. 3B illustrated in the same trial types as in A.
visual stimulus in the RF regardless of whether the stimulus was the saccade target or the distractor. To see if stimulus order was the only factor, we compared the responses in the two cases when the stimulus in the RF appeared first: when it was a distractor and when it was the saccade target. The response across the population was slightly but significantly greater when the stimulus was the distractor ($P < 0.01$, Wilcoxon paired signed-rank test) in the 100-ms epoch preceding the saccade (Fig. 8).

It is reasonable to expect that an oculomotor signal will be specific to the impending saccade location in the immediate presaccadic epoch. This is not the case for this sample of neurons, despite their presaccadic bursts in the delayed-saccade task. We compared presaccadic activity when the distractor was in the RF but the saccade away (Fig. 9A) to presaccadic activity when the distractor was out of the RF and the saccade to a location in the RF (Fig. 9B). There was no difference in these two cases for the activity of the neuron shown or for the entire sample (by Wilcoxon paired signed-rank test) in the 100-ms epoch preceding the saccade (Fig. 10A). The activity of 10 neurons (those with quite strong presaccadic activity) had slight but statistically significant increases in the presaccadic interval. No neurons were quiescent in the presaccadic interval when the saccade was out of the RF and the distractor in it. Only after the initiation of the saccade was activity significantly greater ($P < 0.001$, Wilcoxon paired signed-rank test) across the sample when the monkey made a saccade to the RF (Fig. 10B).

**Effect of the distractor on saccadic performance**

These results establish that LIP neurons respond vigorously to stimuli flashed in the RF during the delay period of a memory-guided saccade task to a target outside their RFs. Although this suggests that the neuronal discharge is irrelevant to the impending saccade, the possibility exists that this neural activity could result in the degradation of saccadic performance. If this was true, there should be an inverse correlation between distractor appearance and saccade performance. In these experiments, however, the distractor had no effect on saccadic performance. We compared saccade amplitude, velocity, and latency of the 56 sets of saccades in our data set (28 experiments, 2 saccade directions for each experiment) for saccades made in no-distractor trials, using a $t$-test. We found no example where the distractor had any effect on these measures of saccade performance (Fig. 11). We also examined the
trajectories of the saccades and could detect no differences in the initial segment of the saccades.

It is always possible that the numbers of saccades (≥16 for each case) were too low to demonstrate a miniscule but significant effect of the distractor. To rule out this possibility, we combined the latency averages for all saccades. There was still no difference (Fig. 12). Because each experiment had different distractor and target locations, we could not simply average saccade amplitudes. Instead we reasoned that if the distractor were affecting the saccade, then the saccade should be pulled toward the distractor location. We calculated the distance from the end of the saccade to the location of the distractor when it was away from the target (distractor-distance) and compared distractor-distance for distractor away from the saccade target to distractor-distance for distractor at the saccade target (Fig. 12A). There was no difference across the population for this measure, implying that the distractor did not attract the eye either when it was at the target location or away from it.

**Correlation of neural activity to saccade dynamics**

Although in the aggregate the distractor had no effect, it is possible that the response to the distractor could contribute to the variability in the monkey’s saccadic performance. To answer this question, we compared the neural response to the distractor to saccade latency and saccade velocity on a trial-by-trial basis. Only two cells’ distractor responses were correlated to saccade velocity. In both cases, the correlation was only significant ($P < 0.05$) when the saccade target was at a different location than the distractor. For one cell, discharge correlated directly with saccade velocity; for the other, discharge correlated inversely with saccade velocity. Two other neurons had distractor responses that correlated inversely with saccade latency. However, one neuron’s distractor response was only correlated when the saccade target was at the same location as the distractor, while the other neuron’s distractor response was only correlated with saccade latency when the saccade target was at a different location than the distractor. As a population, there was no correlation between the neuronal

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**FIG. 9.** Perisaccadic response when the distractor was flashed at a different location from the saccade target. A: the distractor was inside the neuron’s RF and the saccade target located outside of the RF. B: the distractor was outside the RF and the saccade target inside the RF. Rasters synchronized on saccade beginning. The shaded box prior to the saccade is the 100-ms epoch during which there was no significant different in the neurons response. The light striped box shows the 1st 100 ms during and after saccade, an epoch in which there is a significant difference in the response.

**FIG. 10.** Comparison across the sample of perisaccadic responses when the distractor is flashed in the RF. A: the neural response 100 ms prior to the saccade. The distractor disappeared 100 ms prior to fixation point extinction and an average of 329 ms for saccade away from RF, 328 ms for saccade into RF. There is no significant difference in the response between the 2 conditions across the population (Wilcoxon paired signed-rank test). B: the response of the neurons during the first 100 ms of the saccade into the RF. The 2 populations are significantly different between the conditions ($P < 0.001$, Wilcoxon paired signed-rank test). The line in both plots has a slope of 1.
response to the distractor and either saccade latency or saccade velocity.

We also compared the perisaccadic response of the neurons to the saccade velocity and latency. There was no correlation between the perisaccadic response and any aspect of saccade dynamics.

**DISCUSSION**

The role of LIP in the generation of behavior is not clear. One hypothesis is that LIP is specifically dedicated to the planning or intention to make saccadic eye movements (Platt and Glimcher 1997; Snyder et al. 1997). A second hypothesis is that LIP represents salient objects in the space surrounding the animal (Colby et al. 1996; Gottlieb et al. 1998). This is equivalent to specifying a stimulus to serve as the object for a potential but unspecified behavior or, in other words, specifying attention to that stimulus. In these experiments, we attempted to distinguish between these two hypotheses by examining the visual response of LIP neurons to distracting visual stimuli while the monkey performed a memory-guided delayed-saccade task. We reasoned that if LIP were exclusively related to saccade planning, then the appearance of a distractor at a site far from the saccade goal to which the monkey is already committed should evoke a minimal response in LIP. Paradoxically, we found that LIP neurons with presaccadic and delay period activity responded with higher frequency discharge to distracters when the saccade goal was outside the RF than when the distractor flashed at the saccade goal. Despite this brisk neural response, the distractor had little or no effect on saccadic performance. We will discuss the relationship of our data set to the generally accepted characteristics of LIP neurons and the implication of these results for both intentional and salience interpretations of LIP’s role in the generation of primate behavior.

**Characteristics of LIP neurons**

Almost all neurons in LIP have visual responses. In a visual-memory delayed-saccade task, many neurons respond during the delay and also have a presaccadic response. Many invest...
tigators have emphasized these delay and presaccadic responses in their analyses of LIP (Barash et al. 1991; Bracewell et al. 1996; Platt and Glimcher 1997), although LIP neurons manifest a number of other characteristics. For example, they have very plastic RFs (Duhamel et al. 1992), enhancement of the on response in a peripheral attention task, and presaccadic activity in a learned saccade task (Colby et al. 1996). Platt and Glimcher (1999) have recently shown that some neurons in LIP monitor potential reward and participate in the choice of behavior based on reward contingencies. Neurons in LIP may also be important in describing visual aspects of the stimulus, such as shape (Sereno and Maunsell 1998) or perceived motion (Assad and Maunsell 1995; Eskandar and Assad 1999). Since we did not vary stimulus parameters or reward contingencies, we cannot address these other functions of LIP in this study.

For this study, we concentrated on only those neurons with presaccadic and/or delay activity as well as visual responses. We found enhanced responses to stimuli away from the saccade goal in cells with predominant delay activity and similar enhanced responses in cells with predominant presaccadic bursts. We were concerned that the reader be able to compare the neurons that we studied to those reported in previous studies (Barash et al. 1991; Platt and Glimcher 1997), so rather than give averages of delay-period and presaccadic activity, we report here the values of both activities for every cell we studied (Fig. 4). We must conclude strongly that our population of neurons was no different from those published in previous studies.

Implications for intention

Several investigators have argued that LIP is involved predominantly in saccade intention (Platt and Glimcher 1997; Snyder et al. 1997). This interpretation arose from observations when a monkey simultaneously performed a memory-guided delayed-saccade task and some other behavior (a memory-guided arm reach task or a suprathreshold color discrimination task). Some neurons were more active during the delay period on those trials placing the saccade target in the RF than the arm target or discriminandum in the RF.

Other experiments have established that LIP does not participate in the planning of all-purposive saccades. Neurons respond much more before saccadic eye movements directed to currently present visual targets (Colby et al. 1996; Gottlieb et al. 1998) than they do before learned saccades in which no targets appear during the trial in question. Even LIP neurons that project to the superior colliculus discharge more in a visually guided delayed-saccade task than they do in a memory-guided delayed-saccade task (Paré and Wurtz 1997). This is unlike the frontal eye field, where presaccadic movement neurons burst immediately before all purposive saccades, regardless of visual stimulation (Bruce and Goldberg 1985), and activity predicts that a monkey will make a saccade despite a countermanding order (Hanes et al. 1998). Neurons in LIP report the stimulus position in an antisaccade task, but only a small subset report the saccade direction as well, and almost none report saccade direction exclusively (Gottlieb and Goldberg 1999). Furthermore even neurons that have classical delay-period activity in a delayed-saccade task fail to show such delay-period activity in the antisaccade task (Gottlieb and Goldberg 1999).

We postulated that if a major function of LIP was to support saccade planning, then ongoing saccade planning should suppress the response to a distracting stimulus because the distracting stimulus was unlikely to evoke a saccade plan in competition with the ongoing delayed saccade. We found LIP neurons respond briskly to a stimulus that appears as a distractor during a memory saccade task when a saccade target was presented elsewhere. The response to the distractor continues until initiation of the saccade regardless of actual saccade direction. This response to the distractor when the monkey makes a saccade elsewhere is even greater than the response to the saccade target when it first appears in the visual RF. The neurons respond less intensely to the stimulus when the monkey is already in the process of generating a saccade to its spatial location. It is always possible that at this stage in the generation of memory-guided delayed saccades there is no ongoing planning. However, it is precisely this activity during the delay period that has been used to implicate LIP in intentional processes. Our results are not consistent with an intentional role for LIP. In this sample, no neuron ever demonstrated an unambiguous saccade signal. The population does develop an unambiguous saccade signal after the beginning of the saccade. This may reflect some form of spatial processing, or it may reflect the corollary discharge necessary for the perisaccadic shift of RF (Duhamel et al. 1992). However, a saccade-related signal that appears only after the saccade has begun cannot be responsible for generating the saccade. One possibility is that the monkey transiently intends to make a saccade to the distractor despite the ongoing saccade plan, switching the motor plan (Bracewell et al. 1996; Mazzoni et al. 1996). Then one would expect that the distractor would somehow interfere with saccade performance since the distractor response was often present at the time of the saccade. In these experiments, the distractor had no effect on saccade end point, latency, velocity, or early trajectory. This suggests that the neural response to the distractor was irrelevant to the neural processes underlying saccade planning and generation. The distractor was present 300–100 ms before the fixation point disappeared. The monkey could predict that a saccade would be required soon after the distractor disappeared. This predictability may have contributed to the relatively short mean reaction times for all of the saccades in this study.

Implications for spatial processing

Another interpretation of the role of LIP is that it represents salient objects in the space that we can explore with our eyes without specifying any particular motor plan. This function is consistent with the response of LIP neurons to a distractor. Abruptly appearing novel visual stimuli are inevitably salient (Yantis and Jonides 1984). Although LIP neurons respond weakly, if at all, to stable stimuli brought into their RFs by a saccade, they respond intensely to stimuli in the same spatial location when those stimuli appear immediately before the saccade (Gottlieb et al. 1998). Presumably the abrupt onset of the distractor in our experiments renders the stimuli salient, and the neurons respond to that salience.

In our experiments, LIP neurons discharge more briskly under two conditions that are likely to be associated with a shift of spatial attention: when the monkey first sees the stimulus as the target for a delayed-saccade task and when the distractor...
appears away from the locus of the impending saccade. These results resemble those of other studies of behavioral modulation of parietal neurons: parietal neurons respond more to stimuli flashed in their RFs when the monkey actively attends to a stimulus at the fovea than when the monkey merely has its eye still at an equivalent position in the orbit (Mountcastle et al. 1981). When a monkey performs a cued visual attention task, the response to the reaction-time stimulus is less when its location was cued than when a different location was cued (Robinson et al. 1995). Similar results were found in area 7a, where covert attention to the spatial location of a stimulus also suppresses the response evoked by the stimulus (Steinmetz et al. 1994). These results suggested that parietal signals are more important in shifting attention to a spatial locus than maintaining it. When challenged with a cued visual attention task, patients with right parietal lesions have the longest latency when an invalid cue is ipsilateral to the lesion, suggesting again that the parietal cortex is most critical for shifting visual attention (Posner et al. 1984). Our result, that a stimulus away from the goal of an impending memory-guided saccade evokes a greater response in LIP than a stimulus at the current saccade goal, is perfectly consistent with these other results.

It is always possible, however, that the decrement in response to the distractor at the saccade goal is due entirely to a visual habituation: the response to a stimulus that appears a second time at the same locus as an identical stimulus evokes a lesser response. However, Robinson et al. (1995) showed a similar decrement when they cued the attentional shift from outside the RF. It is therefore more likely that, given the importance of attention in the modulation of visual responses in LIP (Gottlieb et al. 1998) the decrement is attentional.

Saccades and attention

When a human makes a saccade to a visual object, his attention ordinarily shifts to the location of the saccade as measured by a consistent lowering of perceptual thresholds at the site of the saccade target (Deubel and Schneider 1996; Hoffman and Subramaniam 1995; Kowler et al. 1995). It is difficult but not impossible to separate saccadic and attentional processes. If a subject is asked merely to attend to a peripheral location and is then asked to make a saccade elsewhere, attention shifts to the saccade target (Hoffman and Subramaniam 1995). However, if a subject is asked to emphasize the visual discrimination in the periphery and not the accuracy of a concurrent saccade, attention can be allocated to the discrimination location despite the saccade (Kowler et al. 1995).

LIP has connections that are suitable for transmitting information about stimulus salience to both the oculomotor and visual systems. It has projections to and from the frontal eye field and to the intermediate layers of the superior colliculus (Andersen et al. 1985; Lynch et al. 1985; Schall et al. 1995; Stanton et al. 1995). These connections are appropriate for transmitting information about an attended object and potential target to the oculomotor system. LIP also has projections to visual areas such as areas V4, TE, and TEO (Baizer et al. 1991; Webster et al. 1994) which have activity dependent on spatial attention (Moran and Desimone 1985) but are not known to be involved in the generation of saccadic eye movements. It also projects to the parahippocampal gyrus (Suzuki and Amaral 1994), which is critical in spatial memory. A signal that is related to the general aspects of visuospatial attention is useful for all of the projection targets of LIP.

LIP is clearly useful for selecting a salient visual stimulus. The functional significance of that stimulus may be determined more by the areas to which LIP projects. For example, TE and TEO may create an attentional enhancement from information they receive from LIP. The superior colliculus may use the same information as a specification of a possible saccade target. However, the colliculus clearly cannot rely on a signal from LIP to generate a saccade. The frontal eye field sends a signal to the superior colliculus consisting of a powerful specific presaccadic signal or a fixation signal and little or no visual signal (Segraves and Goldberg 1987) in contrast to the strong visual signal LIP sends to the superior colliculus (Paré and Wurtz 1997). When there is a conflict in the superior colliculus between the LIP signal and the frontal signal, as during our distractor paradigm, the frontal signal must predominate.

If LIP is not specifically related to saccade planning but, as we suggest, to a more general attentional function that does not specify a specific movement, why does it discharge less during the delay period of a task when the monkey simultaneously plans a reaching movement to a stimulus in the RF and a saccade elsewhere as reported by Snyder et al. (1997)? The answer to this conundrum may lie in the relationship between saccades and attention. Psychophysical studies have indicated that it is impossible to split extrfoveal attention at a given instant (Joseph and Optican 1996). Given attention’s propensity to stay with saccade targets, it may be that once the monkey chooses a target for the reach, its attention remains at the saccade target locus unless it is disrupted by an event such as the unexpected flash of a stimulus away from the saccade goal. Psychophysical studies will be necessary to determine the locus of attention under such conditions.

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REFERENCES


