The lateral intraparietal area as a salience map: the representation of abrupt onset, stimulus motion, and task relevance

Makoto Kusunoki [a,b], Jacqueline Gottlieb [a], Michael E. Goldberg [a,c,*]

[a] *The Laboratory of Sensorimotor Research, National Eye Institute, 49 Convent Drive, Room 2A-50, Bethesda, MD 20892-4435, USA*
[b] *University College, London, UK*
[c] *Department of Neurology, Georgetown University School of Medicine, Washington, DC, USA*

Abstract

Neurons in the lateral intraparietal area (LIP) of the monkey represent salient stimuli. They respond to recently flashed stimuli that enter their receptive fields by virtue of saccades better than they respond to stable, behaviorally irrelevant stimuli brought into their receptive fields by saccades. They respond transiently to abrupt motion onsets, but have no directional selectivity. They respond to stable stimuli that are the targets for saccadic eye movements, but far less before the same saccades without stimuli. LIP is important in the attentional mechanisms preceding the choice of saccade target rather than in the intention to generate the saccade itself. © Published by Elsevier Science Ltd. All rights reserved.

Keywords: Parietal; Saccade; Monkey; Attention; Salience

1. Introduction

The parietal cortex has long thought to be important in the neural mechanisms underlying spatial attention. One parietal area in particular, the lateral intraparietal area (LIP) is important in attentional and oculomotor processes. LIP has reciprocal connections with the frontal eye fields and a direct projection to the intermediate layers of the superior colliculus, from which it receives a disynaptic projection (Andersen, Snyder, Bradley & Xing, 1998). Both the frontal eye field and the superior colliculus are critical in the generation of saccadic eye movements.

LIP also has projections to prestriate and inferior temporal visual areas and parahippocampal gyrus, areas important in vision and spatial memory but which are not known to be involved in the generation of eye movements (Colby & Goldberg, 1999). Neurons in LIP respond to visual stimuli and also discharge, albeit less intensely, before memory-guided and learned saccades, saccades that are made in the absence of visual stimulation (Colby, Duhamel & Goldberg, 1996). Although it is clear that LIP has a visual representation, it is not clear whether this visual representation is dedicated to the processing of saccadic eye movements or has a more general attentional function independent of the generation of any specific movement.

The standard method for determining a visual response of a neuron has been, since the development of the fixation task by Wurtz (1969), the response of the neuron to a stimulus that appears suddenly in its receptive field. This definition has a problem, however. Abruptly appearing stimuli are not only associated with photons exciting rods and cones; they are attentional attractors (Egeth & Yantis, 1997). Stimuli can enter receptive fields in several ways: one is when a light appears suddenly in the receptive field; a second is when a saccade brings a stable object into the receptive field. Since activity in parietal cortex is associated with attention as well as with vision, the question arises as to whether the 'visual responses' of parietal neurons are visual, i.e. responding to photons on the retina, or attentional. In the first of these experiments we assess the difference between the case when the stimulus enters the receptive field by virtue of a saccade, the reafferent case, and the case when the stimulus appears de novo in the receptive field.

* Corresponding author. Tel.: +1-301-4961060; fax: +1-301-4020511.

E-mail address: meg@1sr.nei.nih.gov (M.E. Goldberg).

Another attentional attractor is abrupt stimulus motion (James, 1890). Freezing is a successful evolutionary strategy because predators are less likely to notice still prey than moving prey (Allman, 1999). Areas MT and MST, dedicated to the processing of motion, have strong projections to area LIP. Neurons in those areas are tuned for speed and direction of moving stimuli, and lesions there affect the perception of motion (Newsome & Pare, 1988) and the generation of smooth pursuit eye movements (Newsome, Wurtz, Dürsteler & Mikami, 1985). In this study we asked whether neurons in LIP could be excited by stimuli in their receptive field that, having been quiescent, begin to move. These results have been presented in brief form elsewhere (Gottlieb & Goldberg, 1998; Gottlieb, Kusunoki & Goldberg, 1998).
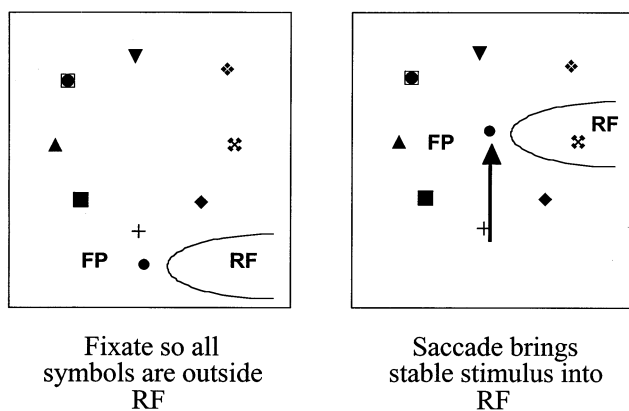

Fig. 1. Stable array task. An array of symbols remains on the screen unchanging throughout the task. Left panel: The monkey looks at a fixation point (Black dot, marked FP) situated so no member of the array is in the receptive field (parabolic solid line, RF) of the neuron. Right panel: The fixation point jumps and monkey makes a saccade (arrow) to follow it, bringing the receptive field onto the spatial location of a symbol (in this case the X).
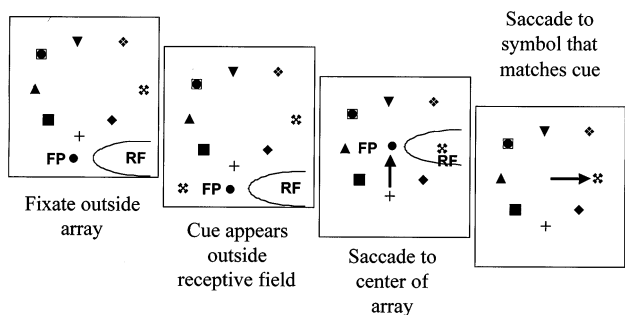

Fig. 2. Stable target task. First panel: the monkey fixates so that all symbols in the array are outside the receptive field. Second panel: a cue appears, also outside the receptive field. Third panel: the fixation point jumps and the monkey makes a saccade that brings a symbol into the receptive field. In this example the symbol in the receptive field matches the cue. Fourth panel: the fixation point disappears and the monkey makes a saccade to the symbol that matched the cue.

2. Methods

2.1. Preparation of animals

Four rhesus monkeys were trained to enter a primate chair voluntarily under pole and collar restraint. They were then prepared for neurophysiological recording under sterile surgical conditions. Anesthesia was induced by ketamine and atropine and maintained by endotracheal isofluorane. We implanted magnetic search coils subconjunctivally (Judge, Richmond & Chu, 1980) and implanted 16–20 titanium bone screws into the skull. We then joined the screws together by an acrylic cap into which we implanted plastic recording cylinders, a connector for the eye coil wires and a plug to fit a head-holder on the primate chair, enabling the animal's head to be held still for recording. All animal protocols were approved as conform to NIH guidelines for animal care and use by the National Eye Institute Animal Care and Use Committee.

2.2. Behavioral methods

The monkeys were trained to fixate a red laser spot that appeared on a tangent screen 86 cm in front of them. They were rewarded for maintaining their eye within a fixation window (2°) in width. When the fixation point moved the monkeys followed it with a saccade (Sparks, 1975). They also quickly learned a memory-guided delayed saccade task: while the monkey looked at the central fixation point, a peripheral stimulus was flashed for 200 ms. After a delay of 500–750 ms, the fixation point disappeared and the monkeys made saccades to the remembered spatial location of the now vanished target (Hikosaka & Wurtz, 1983). Having learned these standard tasks the monkeys were ready to learn more complicated tasks, the stable array tasks and the motion tasks.

In the stable array tasks (Gottlieb et al., 1998) the monkeys were presented with an array of eight stimuli arranged uniformly in a circular array. These stimuli did not appear or disappear from trial to trial. Instead, they were constant for a block of trials. The stimuli were roughly 2° in diameter, and varied in shape and color. They were not equated for luminance. They were positioned so that when the monkey fixated the center of the array at least one stimulus appeared in the receptive field of the neuron under study. In the simplest of these tasks the monkey fixated at a position outside the array so that no stimulus was in the receptive field of the neuron being studied, and then, when the red fixation point jumped, made a saccade to the center of the array (Fig. 1). This saccade brought one of the stable stimuli into the receptive field. In a more complicated version of the task (Fig. 2), the stable target task, the monkey fixated so that the stimulus was not in the receptive field, and a cue appeared during the

1. Monkey achieves central fixation

2. Stimulus appears; remains stationary 1 s.

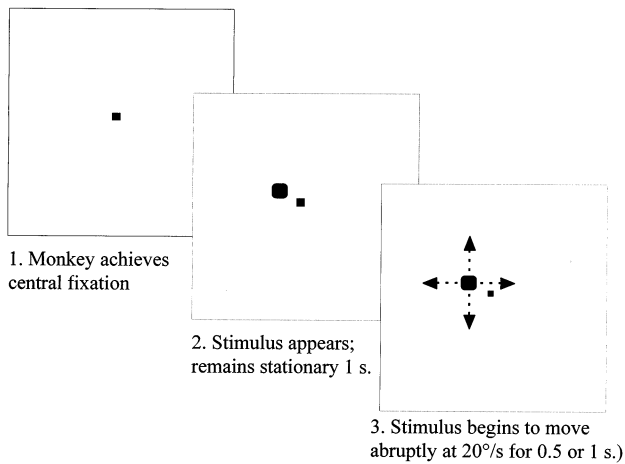3. Stimulus begins to move abruptly at 20°/s for 0.5 or 1 s.)

Fig. 3. Motion task. First panel: The monkey looks at a fixation point. Second panel: The stimulus appears and stays still for 1 s. Third panel: the stimulus suddenly moves at 20°/s in one of four directions: up, down, right, left.

first fixation. This cue matched one of the symbols in the stable array. The fixation point then jumped to the center of the array and the monkey tracked it with a saccade. Finally, when the fixation point disappeared, the monkey made a saccade to the member of the array that had matched the cue. The target indicated by the cue was randomly chosen on each trial among the members of the array. In a third version of the task, the single step stable target task, the trial began with the monkey fixating the center of the screen. The cue could then appear at a location inside or outside the receptive field of the neuron. When the fixation point disappeared, the monkey made a saccade to the symbol that matched the cue. In a fourth version, the black hole task, the array lacked one member. The cue matched the symbol that had been at that location in the previous trials. When the fixation point disappeared the monkey made a saccade to the hole in array. We ran black hole tasks in blocks that followed a block of single-step trials in which the cue always matched the symbol that would be absent in impending black hole trials. This enabled the monkey to learn the saccade that would be required without a visual symbol at the saccade goal.

The motion task began with the monkey fixating a laser spot. Five hundred milliseconds later a peripheral stimulus appeared and remained stationary for 500 ms or 1 s. Then the stimulus began to move 20°/s in one of the four cardinal directions, chosen randomly, for another second and then disappeared (Fig. 3). The monkey never used the stimulus for any part of the task, and if it made a saccade to the stimulus or broke fixation for any reason the trial was terminated. Stimuli were generated by projected LED images whose position was controlled by General Scanning mirror-controlled servo galvanometers.

2.3. Physiological methods

Eye position was measured using the Robinson search coil technique with a 4′ field coil array (CNC Associates) (Robinson, 1963). Single neurons were recorded resin-coated tungsten microelectrodes (FHC, Inc.) inserted into the brain through a guide tube that had partially pierced the dura. Action potentials from the microelectrode were passed through a 6 pole Butterworth filter, discriminated using a BAK time-window discriminator. A Hewlett-Packard Vectra 486-33 computer sampled the pulses from the discriminator at a frequency of 1 kHz. The computer also controlled the monkeys' behavior, sampled eye position at a frequency of 1 kHz and stored all data on disk. The computer was programmed using the REX programming language (Hays, Richmond & Optican, 1982) running under the QNX 5.3 operating system. Video displays were controlled by signals sent via parallel port to the display computer. The monkey chair was placed in the center of the field coils, and the signal evoked in the ocular search coil decoded by a CNC phase detector. The eye position signals were filtered at 500 Hz to eliminate aliasing artifacts from the 1 Khz sample rate.

2.4. Anatomical methods

Electrode penetrations were localized to the posterior bank of the intraparietal sulcus by T1-weighted MRI scans with a tungsten electrode in place at a site that had yielded neurons responsive in the task. MRI estimation of electrode position was verified histologically in two monkeys.

2.5. Data analysis

Rasters and histograms were calculated on-line so we could get an idea of the neuron's responsiveness. Formal data analysis was performed off-line on a UNIX system using special purpose programs written in C and Matlab. Spike density histograms were calculated by convolving the spike train with a Gaussian function with a σ of 10 ms (Richmond & Optican, 1987).

3. Results

A standard visual-memory guided delayed saccade task was used to characterize neurons, and neurons were included in this study if they discharged during this task in response to the stimulus appearance, during the delay period, or immediately before the saccade. We did not explicitly count the number of neurons that we rejected, but they were a small minority of the neurons in LIP, where most neurons have visual responses (Colby et al., 1996). A total of 82 neurons were

recorded in four hemispheres in various aspects of the stable array task and 25 neurons were recorded in three hemispheres in the motion task.

3.1. Stable array tasks

The typical neuron had a brisk response to the sudden appearance of a stimulus in its receptive field during a fixation task (Fig. 4A), and a much smaller response when the same stimulus as a member of the stable array entered the receptive field (Fig. 4B). The decrement of response could have been related to the behavioral irrelevance of the stable target, or, it could have been due to a series of other confounds. For example, the movement of the stimulus into the receptive field by the saccade is not exactly the same as its appearance from the flash; the other members of the array might exert some purely visual local inhibition that suppresses the response. To test if these other factors could be responsible for the diminished response to the stable target, we developed the recently flashed stimulus task. In this task the stable array contained only seven stimuli, but not the one that would be brought into the receptive field by the saccade. This eighth stimulus appeared while the monkey was fixating at the initial position, and remained on throughout the trial. The monkey then made a saccade that brought this recently appeared stimulus into the receptive field. The neuron responded almost as briskly in that case as it did to the abrupt appearance of the stimulus in the receptive field (Fig. 4C, compare with Fig. 4A). Therefore, the difference between the fixation case and the stable target case was not due to the visual or oculomotor differences between the tasks, but to the inconspicu-

ousness of a stable member of the visual environment. Note that the neuron began to respond at or before the end of the saccade. This was a much lower latency than when the stimulus appeared in the receptive field abruptly (compare Fig. 4A with Fig. 4C). Presumably this occurred because of the predictive response described previously (Duhamel, Colby & Goldberg, 1992): neurons in LIP may respond to stimuli that will be brought into their receptive field by saccades earlier than they do to the abrupt appearance of the same stimulus in their receptive fields. The recently appeared stimulus evoked a greater response across the population than did the stable stimulus (using an average response in an interval 200 ms after the end of the saccade: $P < 0.001$ by Wilcoxon signed rank test; 31 neurons), and evoked a statistically significantly greater response in a majority (23/31, $P < 0.05$ by two-tailed t test) of single neurons (Fig. 5).

Salience does not only arise from intrinsic properties of the stimulus. Stable objects can become important by virtue of their relevance to current behavior, and under those circumstances a member of a stable array can evoke a response from a neuron in LIP. We can show this using the stable target task. In this task the monkey knows which member of the array will be the target of the next saccade. Neurons responded strongly to stable stimuli inside their receptive field if these were designated as the target of the next saccade (Fig. 6A1, 6B1). In contrast, if the identical stable stimuli entered the receptive fields but were not designated as the saccade target (the monkey was instructed to saccade elsewhere), neurons responded minimally (Fig. 6A2, B2). The neuron's activity became modulated by the behavioral significance of the stable stimuli only after presen-
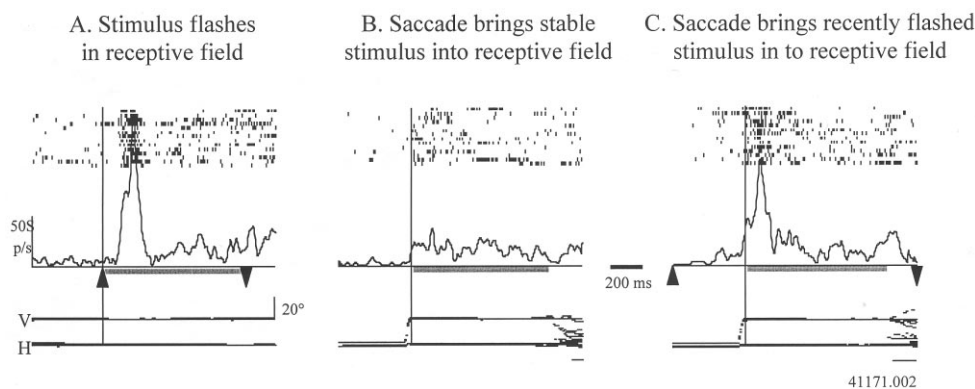

Fig. 4. Effect of recent flash on stable array response. Each diagram is a raster diagram. Each dot is a cell discharge. Each line represents cell activity for one trial. Successive lines are synchronized on an even that occurs at the vertical line. Spike density histograms are shown beneath each raster. The gray bar at the bottom of the spike density histogram shows when, during the trial, the stimulus is in the receptive field of the neurons. Up arrows represent the onset of the flashed stimulus, down arrows represent its disappearance. Horizontal (H) and vertical (V) eye position traces for each raster line are shown superimposed beneath the spike density diagram. (A) Stimulus flashes in receptive field during fixation task; activity synchronized on stimulus appearance. (B) Stable array task: monkey makes saccade that brings stable stimulus into receptive field; activity synchronized on saccade end. (C) Recent stimulus task: monkey makes saccade that begins recently flashed stimulus into receptive field. Stimulus appears at up arrow, roughly 500 ms before saccade; activity synchronized on saccade end. Figure adapted with permission from (Gottlieb et al., 1998)
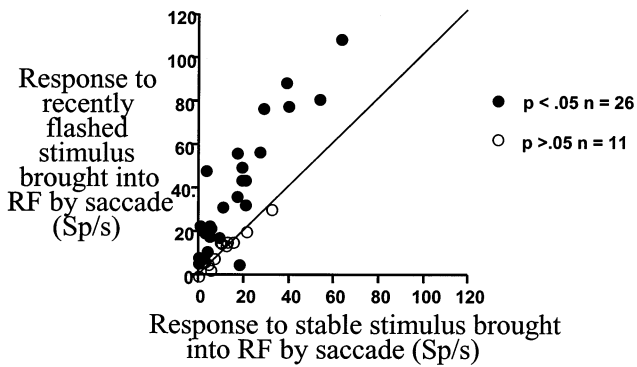
Fig. 5. Scatter population diagram comparing responses in stable array and recent stimulus tasks. Each dot represents the mean response of one neuron in the 200 ms following the end of the saccade when a recently flashed stimulus enters the receptive field by a saccade (ordinate), plotted against the response of the neuron when the stable stimulus enters the receptive field by a saccade (abscissa). The recently flashed stimulus evokes a significantly larger response across the population ($P < 0.001$ by Wilcoxon rank sum). Filled circles are neurons whose discharge was significantly different in one case, open circles are neurons that had equivalent activity in both cases. The solid line is the unity line, $x = y$.

tation of the cue. In a late-cue version of the task the cue appeared only after the first saccade brought the stimulus within the receptive field (Fig. 6B1, 6B2). In this case the differential response to the stable target

began after the cue instead of after the saccade). In the early-cue version, the cue was presented before the first saccade brought the stable stimulus into the receptive field. In this case the response modulation began shortly after the stable stimulus entered the receptive field (after the first saccade).

It is possible that LIP neurons respond in the stable target task because the monkey is planning a purposive saccade (Snyder, Batista & Andersen, 1997), and the activity is less related to the salience of the stable target than it is to the processes underlying saccade planning. To see how much activity in LIP can be allocated to the planning and generation of a saccade itself we used the black hole task in which saccades were made without any target at all. (Fig. 7). We first ascertained the neuron's activity in the stable target task (Fig. 7A). The neuron began to respond after the cue appeared, before the saccade. However, when the monkey made the same saccade in the absence of the stable target the neuron did not respond (Fig. 7B). Multiple regression analysis showed that the difference in response could not be explained by the lower velocity or accuracy of saccades on black-hole trials.

The neuron responded briskly to the cue when it appeared in the receptive field but dictated a saccade elsewhere (Fig. 7C). This shows that the presence of the
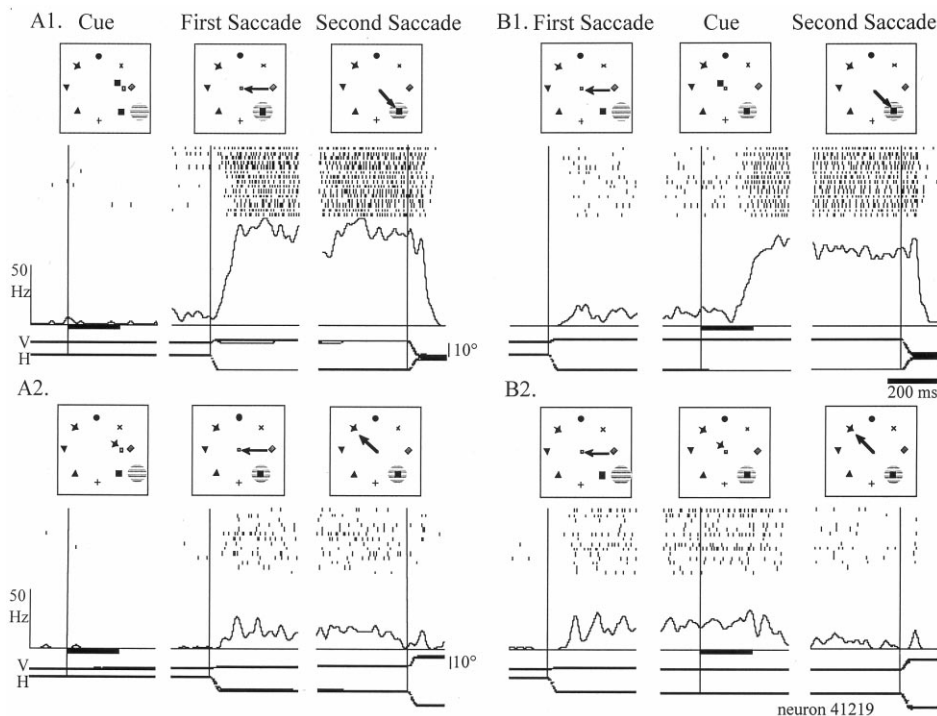

Fig. 6. Response of the neuron in early cue and late cue stable target tasks. (A) early cue task. Each trio of rasters shows the response of the neuron in the same trials synchronized on cue (left), first saccade beginning (middle) and second saccade beginning (right). (A1) Cue appears before the first saccade, and matches stable symbol in the receptive field. (A2) Early cue matches target 180° away from receptive field. (B) Late cue task. Each trio of rasters shows the response of the neuron in the same trials synchronized on first saccade beginning (left), cue (middle) and second saccade beginning (right). (B1) late cue task. Cue appears after first saccade and matches stable symbol in the receptive field. (B2) late cue matches target 180° away from receptive field.

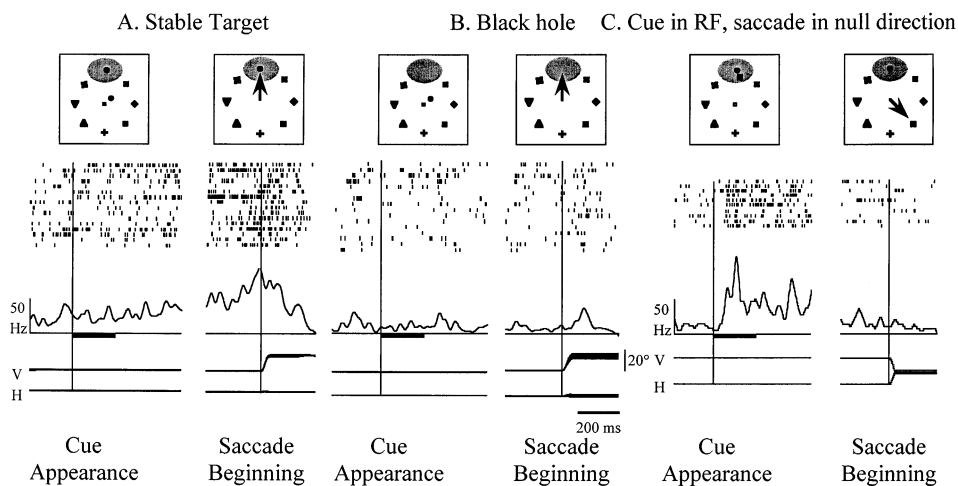A. Stable Target   B. Black hole   C. Cue in RF, saccade in null direction

Fig. 7. Response of the neurons in the single step stable target and black hole tasks. Left rasters synchronized on cue appearance. Right rasters synchronized on saccade beginning. (A) Stable target task. The monkey makes a saccade to the stimulus that matches the cue. (B) Black hole task. The monkey makes the same saccade when the fixation point disappears, but there is no target present. The cue matches the symbol that had been at the saccade target. (C) Stable target task, cue in the receptive field. The cue in the receptive field matches a symbol outside the receptive field, and the monkey makes a saccade in the null direction. Figure modified with permission from (Gottlieb et al., 1998).

stimulus and not the generation of the saccade is responsible for most of the activity evoked in the stable target task. Although such learned saccades are slower and less accurate than visually guided saccades, the difference in response could not be explained by differences in saccade accuracy or velocity. We compared the activity preceding the saccade in the black hole task to the activity associated with a cue in the receptive field that dictated a saccade elsewhere, using a contrast index to describe each cell in the sample (Fig. 8). In the contrast index, $NT/(NT + V)$, NT is the presaccadic response in the black hole task, and V is the visual response to a cue that appears in the receptive field but dictates a saccade elsewhere. A third (6/18) of the neurons had equivalent activity in both cases (indices close to 0.5), suggesting that they encoded a salient location — either the location of a relevant cue or the goal of the next saccade. The remainder discharged significantly less before the saccade in the black hole task than they did to the stimulus that dictated a saccade in a different direction (indices below 0.5). No neuron discharged more prior to the saccade in the black-hole condition than it did in relation to the cue.

3.2. Motion task

In a final task, we asked whether neurons would also respond to stimuli rendered salient by virtue of an abrupt onset of motion. We studied 25 neurons in two monkeys that yielded a phasic response to the sudden appearance of the visual stimulus in the receptive field. Of these neurons, 80% (20/25) also had delay and/or presaccadic activity in the delayed saccade task. The neuron shown in Fig. 9 had such a phasic response that

returned to near baseline several hundred milliseconds after stimulus appearance despite the continued presence of the stimulus. The sudden movement of the stimulus evoked a second response in the neuron. This second response was elicited by all four motion directions, though it was weakest for upward motion. We found that often such apparent directional selectivity was merely a consequence of the location of the stimulus within the receptive field. The neuron in Fig. 10 responded equivalently to the onset of rightward and leftward motion, provided each traversed its receptive field (A and D). If the starting position of the trajectory was held constant, however (left of fixation, as in A and C, or close to center as in B and D) the neuron
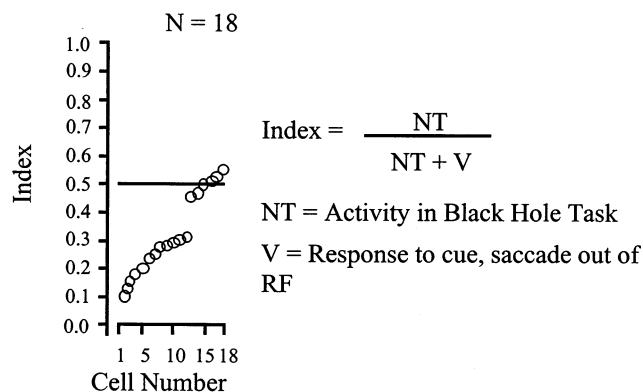

Fig. 8. Scatter population diagram comparing activity in which the monkey makes a saccade without a target (black hole task) and response to a cue that dictates a saccade elsewhere (single step stable target task). We computed an index comparing the response to the cue (V) and the response to the saccade without a target (NT): index $= NT/(V + NT)$. An index of 0.5 means that the responses are equal. An index of 0.33 means that the visual response is twice the presaccadic response in the black hole task.
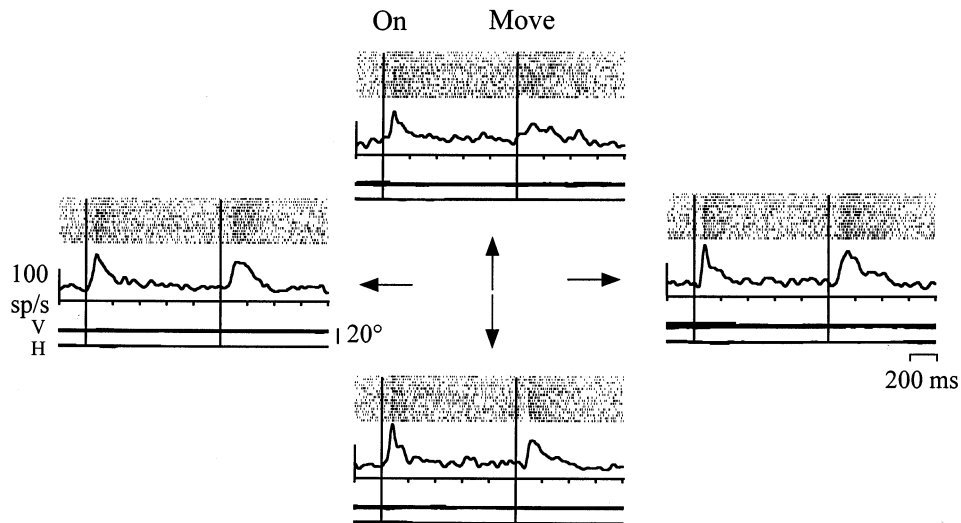
Fig. 9. Responses to abrupt onset and motion during a fixation task. The stimulus appeared at the same point on the screen in each raster, at the first vertical line. After 1 s the stimulus began to move at 20°/s in the direction indicated by the arrow that points at the raster. Rasters synchronized on stimulus appearance.
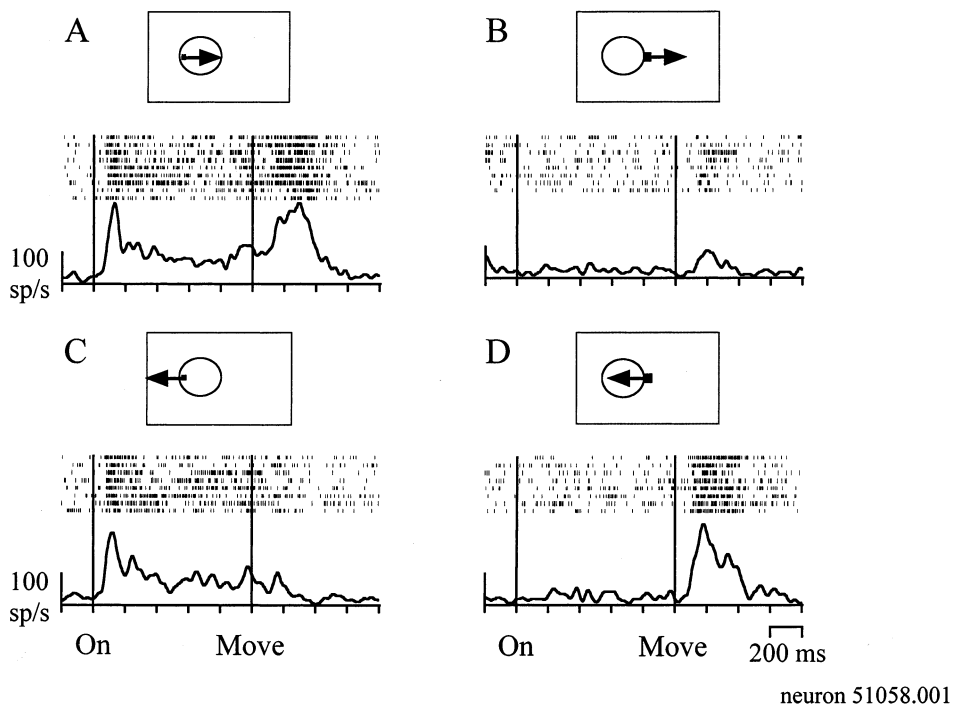

Fig. 10. Dependence of motion selectivity on stimulus location. The cartoon above each raster depicts the site of appearance of the stimulus (square) and the direction of motion (arrow).

appeared to have directionally-selective activity. Note that the receptive field for stimulus motion and the receptive field for abrupt onset of a static stimulus were not identical. The moving stimulus could evoke a weak response even at a spatial location at which it failed to evoke an on-response (Fig. 10B).

By shifting the position of the stimulus within the receptive field for each direction of motion we were able to establish that the difference between the weakest and

strongest response was rather small. We calculated the average spike density in the interval from 100 to 300 ms after motion onset for each neuron in the sample. The median strongest response was 59 sp/s, and the median weakest response was 44 sp/s and the two were strongly correlated (Fig. 11 $y = 0.98x + 20.22$, $r^2 = 0.86$, $P < 0.0001$. The peak motion response was greater than the peak on-response across the population (Fig. 12).

4. Discussion

The role of the lateral intraparietal area in the organization of behavior is not clear. One hypothesis is that it provides a map of salient stimuli in the visual world (Gottlieb et al., 1998; Colby & Goldberg, 1999) without specifying how the stimuli will be used; the second is that it codes the intention to make a saccade to a stimulus (Andersen et al., 1998). In either case LIP must provide its analysis of the visual environment to the areas to which it projects. In these experiments we studied the determinants of the visual response of LIP neurons. We discuss the relationship of these responses to attention and the generation of saccades.

In the 19th century, William James described two different sorts of attention on the basis of introspection. He wrote, "Attention may be divided into various kinds. It is either passive, reflex, non-voluntary, effort-less; or active and voluntary. In passive immediate sensorial attention the stimulus is a sense-impression, either very intense, voluminous, or sudden…big things, bright things, moving things….blood (James, 1890)."

In these experiments we have demonstrated two different aspects of the representation of the visual world in LIP. These different aspects correspond to the objects of James' different kinds of attention. Recently appeared or moving objects evoke James' passive, reflex, or voluntary attention and they also evoke responses in LIP even when they are irrelevant to the ongoing task, whether they appear in the receptive field directly or enter the receptive field by a saccade shortly after their appearance. We found that the sudden motion of a stimulus already in the receptive field, to which the neurons had already habituated, is a powerful stimulus to these neurons. Unlike the motion processing areas which project to LIP (Maunsell & Van Essen, 1983), however, neurons in LIP have little if any selectivity for direction of motion. The difference in activity between stimuli moving in the best direction and stimuli moving in the worst direction was only about 25%. We suspect that had we searched more diligently we might have found trajectories across the receptive field that would have yielded higher responses in the 'least preferred' directions. Neurons in LIP appear to integrate information from afferent neurons in areas MT and MST representing all directions of motion. Another source of a non-directionally selective response to motion salience could be the posterior cingulate cortex. This area projects to the posterior parietal cortex, and has neurons that have a non-directional motion response (Olson, Musil & Goldberg, 1993).

Attended stable objects evoke James' active or voluntary attention. Such objects are also represented in LIP. They are not salient by themselves, but become so by virtue of their relevance to the task. Whether they have just entered the receptive field, or have been in the receptive field already, they evoke a response much larger than that evoked by stable objects that are irrelevant to the animal's behavior. The timing of the enhanced response depends upon when the stimulus becomes salient: if the monkey knows before the saccade that the stimulus is salient, the perisaccadic activity is enhanced. If the monkey learns of the importance of the stimulus only after the saccade, the perisaccadic activity is negligible, and the response only begins after the cue that renders the stimulus in the receptive field salient.

In our experiments we rendered a stable stimulus salient by instructing the monkey to make saccades to it. This raised the question of whether or not the activity was related to the attentional quality of the stimuli or to some aspect of the saccade (Snyder et al.,
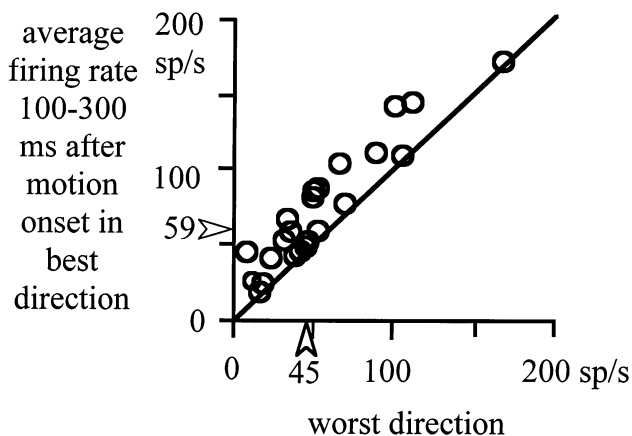

Fig. 11. Directionality of motion response. Each symbol represents the activity of one cell in the interval 100–300 ms after the start of stimulus motion. Activity in the weakest direction is on the abscissa, activity in the strongest direction on the ordinate. Arrows represent the median values for each variable.
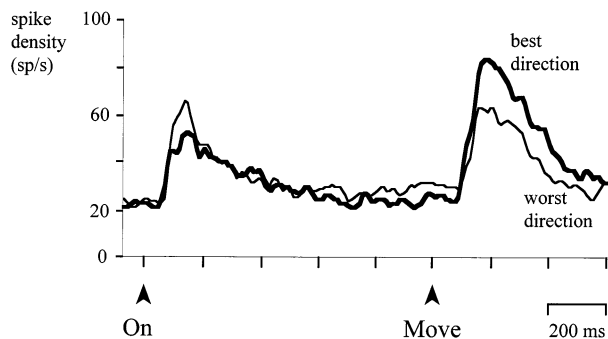

Fig. 12. Temporal pattern of onset and motion discharges. Each line is the average spike density (sp/s) plotted against time for strongest (dark line) and weakest (light line) response directions, synchronized on stimulus appearance (first arrow). Second arrow depicts time of stimulus motion.

1997). In these experiments we show that when the monkey makes a saccade to spatial locations that have no stimuli, most LIP neurons discharge much less than when the monkey makes the identical saccade to a stimulus in the same location. There is a smaller population of neurons that give equivalent responses to salient visual stimuli that are not saccades. We found no neurons that had an unequivocal saccade signal and did not respond also to a salient stimulus that was not a saccade target. In general when there is a conflict between a salient stimulus and an eye movement, neurons in LIP describe the stimulus and not the movement. In these experiments we show that a cue that drives a saccade away from the receptive field drives most cells far better than a saccade made to the receptive field without a stimulus. Those neurons that have a significant presaccadic activity also respond equivalently to stimuli that instruct the animal to make a saccade elsewhere. This is in contradistinction to the frontal eye fields, where movement neurons have little or no visual response, and discharge equivalently for saccades made to spatial locations with or without stimuli (Bruce & Goldberg, 1985; Segraves & Goldberg, 1987). Similarly, LIP neurons respond overwhelmingly to the stimulus in an antisaccade task (Gottlieb & Goldberg, 1999), and respond in an enhanced manner to a stimulus that appears away from the saccade target when a monkey is planning a memory-guided saccade (Powell, Colby, Gottlieb, Kusunoki & Goldberg, 1999). Such results render it unlikely that LIP merely describes intention for saccades. We have shown that LIP neurons respond to the stimuli that are the objects of voluntary and involuntary spatial attention; and, of course, one aspect of spatial attention is the selection of targets in the environment for saccades.

References

Allman, J. M. (1999). Evolving Brains, *Scientific American Library*, 256.

Andersen, R. A., Snyder, L. H., Bradley, D. C., & Xing, J. (1998). Multimodal representation of space in posterior parietal cortex and its use in planning movements. *Annual Review of Neurscience*, *20*, 303–330.

Bruce, C. J., & Goldberg, M. E. (1985). Primate frontal eye fields: I. Single neurons discharging before saccades. *Journal of Neurophysiology*, *53*, 603–635.

Colby, C. L., Duhamel, J.-R., & Goldberg, M. E. (1996). Visual, presaccadic and cognitive activation of single neurons in monkey lateral intraparietal area. *Journal of Neurophysiology*, *76*, 2841–2852.

Colby, C. L., & Goldberg, M. E. (1999). Space and attention in parietal cortex. *Annual Review of Neuroscience*, *23*, 319–349.

Duhamel, J.-R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, *255*, 90–92.

Egeth, H. E., & Yantis, S. (1997). Visual attention: control, representation, and time course. *Annual Review of Psychology*, *48*, 269–297.

Gottlieb, J., & Goldberg, M. E. (1999). The activity of neurons in the lateral intraparietal area of the monkey during an antisaccade task. *Nature Neuroscience*, *2*, 906–912.

Gottlieb, J. P., & Goldberg, M. E. (1998). Neurons in posterior parietal cortex (PPC) encode motion salience. *Investigative Ophthalmology and Visual Science*, *39*, S905.

Gottlieb, J. P., Kusunoki, M., & Goldberg, M. E. (1998). The representation of visual salience in monkey parietal cortex. *Nature*, *391*, 481–484.

Hays, A. V., Richmond, B. J., & Optican, L. M. (1982). A UNIX-based multiple process system for real-time data acquisition and control. *WESCON Conference Proceedings*, *2*, 1–10.

Hikosaka, O., & Wurtz, R. H. (1983). Visual and oculomotor functions of monkey substantia nigra pars reticulata. III. Memory-contingent visual and saccade responses. *Journal of Neurophysiology*, *49*, 1268–1284.

James, W. (1890). *The Principles of Psychology*.

Judge, S. J., Richmond, B. J., & Chu, F. C. (1980). Implantation of magnetic search coils for measurement of eye position: an improved method. *Vision Research*, *20*, 535–538.

Maunsell, J. H. R., & Van Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *Journal of Neurophysiology*, *49*, 1127–1147.

Newsome, W. T., & Pare, E. B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *Journal of Neuroscience*, *8*, 2201–2211.

Newsome, W. T., Wurtz, R. H., Dürsteler, M. R., & Mikami, A. (1985). Deficits in visual motion processing following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. *Journal of Neuroscience*, *5*, 825–840.

Olson, C. R., Musil, S. Y., & Goldberg, M. E. (1993). Posterior cingulate cortex and visuospatial cognition: properties of single neurons in the behaving monkey. *Neurobiology of Cingulate Cortex and Limbic Thalamus: A Comprehensive Handbook*, 366–380.

Powell, K. D., Colby, C. L., Gottlieb, J., Kusunoki, M., & Goldberg, M. E. (1999). Space and salience in parietal cortex., *Current Oculomotor Research*, 25–35.

Richmond, B. J., & Optican, L. M. (1987). Temporal encoding of two-dimensional patterns by single units in primate inferior temporal cortex: II. Quantification of response waveform. *Journal of Neurophysiology*, *57*, 147–161.

Robinson, D.A. (1963). A method of measuring eye movement using a scleral search coil in a magnetic field., *IEEE Trans. Bio-Med. Eng.*, *BME-10*, 137–145.

Segraves, M. A., & Goldberg, M. E. (1987). Functional properties of corticotectal neurons in the monkey's frontal eye field. *Journal of Neurophysiology*, *58*, 1387–1419.

Snyder, L.H., Batista, A.P. & Andersen, R.A. (1997). Coding of intention in the posterior parietal cortex., *Nature*, *VI-386*, 167–170.

Sparks, D. L. (1975). Response properties of eye movement-related neurons in the monkey superior colliculus. *Brain Research*, *90*, 147–152.

Wurtz, R. H. (1969). Visual receptive fields of striate cortex neurons in awake monkeys. *Journal of Neurophysiology*, *32*, 727–742.