
Neural enhancement and pre-emptive perception: The genesis of attention and the attentional maintenance of the cortical salience map

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Abstract. One of the stable hypotheses in systems neuroscience is the relationship between attention and the enhancement of visual responses when an animal attends to the stimulus in its receptive field (Goldberg and Wurtz, 1972 *Journal of Neurophysiology* **35** 560–574). This was first discovered in the superior colliculus of the monkey: neurons in the superficial layers of the superior colliculus responded more intensely to the onset of a stimulus during blocks of trials in which the monkey had to make a saccade to it than they did during blocks of trials in which the monkey had to continue fixating a central point and not respond to the stimulus. This enhancement has been found in many brain regions, including prefrontal cortex (Boch and Goldberg, 1987 *Investigative Ophthalmology* **28** Supplement, 124), V4 (Moran and Desimone, 1985 *Science* **229** 782–784), and lateral intraparietal area (Colby et al, 1996 *Journal of Neurophysiology* **76** 2841–2852; Colby and Goldberg, 1999 *Annual Review of Neuroscience* **22** 319–349), and even V1 (Lamme et al, 2000 *Vision Research* **40** 1507–1521). In these studies the assumption has been that the monkey attended to the stimulus because the stimulus evoked an enhanced response. In the experiments described here we show that for abruptly appearing stimuli, attention is not related to the initial response evoked by the stimulus, but by the activity present on the salience map in the parietal cortex when the stimulus appears. Attention to the stimulus may subsequently, by a top–down signal, sustain the map, but stimuli can as easily be suppressed by top–down features as they can be enhanced.

1 Introduction

One of the stable hypotheses in systems neuroscience is the relationship between attention and the enhancement of visual responses when an animal attends to the stimulus in its receptive field (Goldberg and Wurtz 1972; Moran and Desimone 1985). This was first discovered when Goldberg and Wurtz noticed that the visual response of neurons in the superficial layers of the superior colliculus responded more intensely to the onset of a stimulus during blocks of trials in which the monkey had to make a saccade to it than they did during blocks of trials in which the monkey either had to continue fixating a central point and not respond to the stimulus, or when it had to make a saccade to a stimulus which appeared away from the receptive field (figure 1). The authors postulated that this enhancement was related to attention and not to the saccadic eye movements which represented the way in which the attention was manifest, because these neurons did not discharge before eye movements in the dark.

This postulate was wrong: the enhancement of visual responses in the superficial layers of the superior colliculus occurred when the monkey was going to make a saccade to the target, but not when it had to signal the dimming of the peripheral stimulus by a non-spatially related hand movement (Wurtz and Mohler 1976). In fact,

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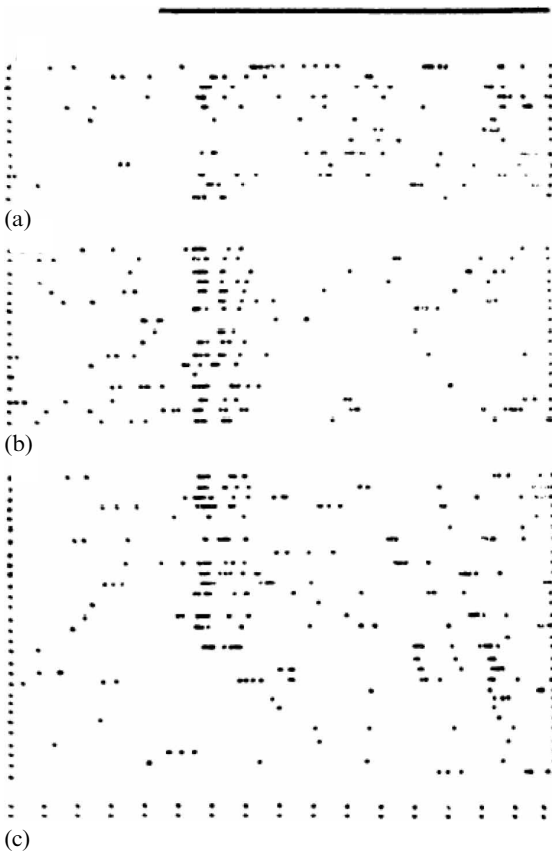


Figure 1. Behavioral enhancement of visual responses in the superficial layers of the monkey superior colliculus. Raster displays when the monkey fixates (a) and a stimulus appears in the receptive field (line at top represents stimulus presentation). Each line represents a single trial. Each dot represents an action potential. Successive lines are synchronized on the appearance of the stimulus. (b) The fixation point disappears and the monkey makes a saccade to the stimulus when it appears. (c) The monkey continues to fixate. Reproduced with permission from Goldberg and Wurtz (1972).

much subsequent work has demonstrated that the superior colliculus has an important role in the generation and motor programming of saccades (Sparks and Hartwich-Young 1989). Nonetheless, the concept of enhancement as a mechanism of attention became enshrined in the literature. Enhancement which was independent of the mode of response was later discovered in the posterior parietal cortex (Bushnell et al 1981), and more specifically in the lateral intraparietal area, LIP (Colby et al 1996). In LIP there is no difference in the enhancement of the visual responses evoked by saccade targets and peripheral attention targets to which the monkey responds with a non-targeting hand movement. These experiments were also done in blocks of saccade, fixation, and peripheral attention trials. This form of enhancement was postulated to be an important component in the neural mechanisms underlying visual attention. In this model, animals attend to stimuli because those stimuli evoke enhanced responses.

However, one critical and rather neglected experiment (Robinson et al 1995) cast doubt on the conventional wisdom. In this experiment, the authors trained monkeys on a cued visual-reaction-time task, in which they had to perform a simple hand movement in response to the appearance of a visual probe. The probe could appear at one of two places in the visual field, in the receptive field of the neuron, or across the vertical meridian from it. On 80% of the trials a valid cue appeared 300 ms before the appearance of the probe at the probe site, and on those trials the reaction time was significantly faster than on the trials in which the cue appeared at the other possible probe location. This cost in reaction time of an invalid cue has been interpreted as cost of an attentional switch: the invalid cue draws attention to the part of visual field where the probe will not appear, and it takes time to switch attention to the actual site of the probe (Posner 1980). If enhancement were ineluctably linked

to attention, the validly cued probe, to which attention had already been allocated, should have evoked an enhanced response. Surprisingly, the validly cued probe often evoked a lesser response than the invalidly cued probe.

Another experiment which cast doubt upon the relationship between enhancement and performance (Grunewald et al 1999) involved intermixed auditory and visually guided saccades. The trials were not run in blocks, and the visual targets evoked the same responses from LIP neurons whether or not they were the targets for the saccade. However, these experiments failed actually to measure attention except by an a posteriori assertion: the authors assumed, but did not prove, that the monkey did not attend to the saccade target. In this review we will examine the role of LIP in the generation of attention, and re-evaluate the enhancement hypothesis.

2 Visual attention does not necessarily require parietal enhancement

Attention has been generally described as having two components: a voluntary, endogenous or top-down form, and an involuntary, or bottom-up form. The typical bottom-up form is evoked by the abrupt onset of a task-irrelevant visual stimulus in the visual field (Yantis and Jonides 1984). The typical top-down form is evoked by some behavior which, a priori, makes the attended spatial location relevant, for example planning a saccadic eye movement to the stimulus (Deubel and Schneider 1996). We (Bisley and Goldberg 2003, 2006) recently studied the interaction between top-down and bottom-up attention in the monkey.

We examined how a monkey's attention was affected by saccade planning and the abrupt onset of task-irrelevant stimuli. We used a contrast sensitivity method. We defined the spatial locus of attention as that area of the visual field with enhanced visual sensitivity (Bashinski and Bacharach 1980). This method enabled us to examine how attention changes over time and under different visual conditions. Furthermore, it allowed us to rule out the possibility that any attentional advantage may be on the motor side of the response, a problem present when defining attention by changes in reaction time.

In the paradigm we used, the monkeys had to plan a saccade to a remembered location and later had to discriminate the orientation of a probe stimulus (figure 2). We measured the contrast sensitivity to the probe. The probe stimulus consisted of three circle distractors and a broken ring whose gap could be on the right or on the left. The orientation of the broken ring instructed the monkey either to cancel (gap on right) or to execute (gap on left) the planned saccade when the fixation spot disappeared. We varied the contrast of the probe, and measured the animal's Go/NoGo discrimination performance to calculate the contrast threshold, which we defined as the contrast at which the animal could correctly discriminate the probe in 75% of the trials. The animal was significantly more accurate when the probe appeared at the saccade goal than when it appeared elsewhere (figure 3a). We interpreted this as the saccade plan endowing the spatial location of the saccade goal with an attentional advantage over other parts of the visual field. The attentional advantage at the saccade goal, illustrated by the enhanced sensitivity, was significant throughout the task ($p < 0.05$ by paired t -test): we used target-probe onset asynchronies from the saccade target to probe of 800, 1300, and 1800 ms, and found enhanced performance in both animals for all target-probe asynchronies that we studied.

The monkey's attention could be also drawn to the spatial location of an abruptly appearing distractor despite the ongoing saccade plan. We flashed a task-irrelevant distractor during the delay to see if it could draw attention away from the goal of the planned saccade (figure 2b). The distractor appeared on half of the trials and was either presented at the saccade goal or opposite the saccade goal (as in figure 2b). The distractor was identical to the saccade target in size, brightness, and duration, but appeared 500 ms after the target. It remained on the screen for 100 ms.

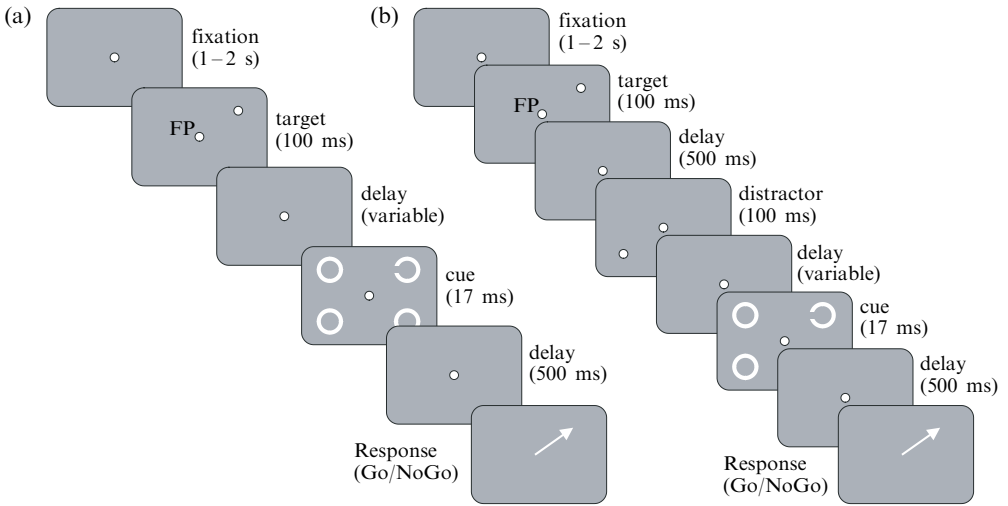


Figure 2. Psychophysical attention task. (a) The monkeys began the trial by fixating a small spot (FP). After a short delay a second spot (the target) appeared for 100 ms at one of four possible positions equidistant from the fovea and evenly distributed throughout the four visual quadrants. The exact target locations varied from day to day, to prevent long-term perceptual learning. This target specified the goal for the memory-guided saccade that the monkey would have to make unless the probe told it otherwise. At some time after the target disappeared, a broken ring (the probe) and three complete rings of identical luminance to the probe flashed for one video frame (~ 17 ms) at the four possible saccade target positions. 500 ms after the probe the fixation point disappeared, and the animals had to indicate the orientation of the broken ring by either maintaining fixation for 1000 ms (when the gap was on the right—a NoGo trial) or making a saccade to the goal and remaining there for 1000 ms (when the gap was on the left—a Go trial). The broken ring could appear at any of the four positions. The luminance of the rings varied from trial to trial, changing the contrast between the probe and the background. (b) In half of the trials a task-irrelevant distractor, identical to the target, was flashed 500 ms after the target, either at or opposite the saccade goal. Reproduced with permission from Bisley and Goldberg (2003).

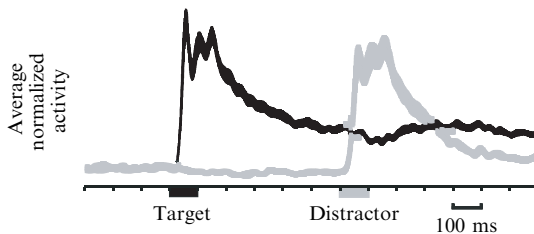


Figure 3. Neural activity in the attention task. Averaged normalized spike density functions from 23 cells, calculated with a sigma of 10 ms. When the target appeared in the receptive field, there was a brisk transient response (black trace) to the target, which then decayed to a relatively level delay period activity. On interleaved trials, the distractor was in the receptive field (gray trace), and the neurons gave a brisk response to the distractor. The activity decayed to a level beneath that evoked by the saccade goal. Reproduced with permission from Bisley and Goldberg, 2003.

When the distractor appeared in the opposite location to the target, and the probe appeared 200 ms after the distractor, the perceptual threshold fell to the attentionally advantaged level at the site of the distractor and rose to the baseline level at the saccade goal. However, 700 ms after the distractor had appeared, the monkey once again had a lower threshold at the saccade goal and a higher one at the distractor location. Thus, as in humans, the abrupt onset of a distractor in the visual field draws

attention. In the monkey this occurs even while the animal is planning a saccade, but the attentional effect of the distractor is transient. The attention advantage lasts for less than 700 ms, by which time attention has returned to the saccade goal. The distractor and the saccade plan had the same effect on the monkey's attention, lowering the contrast sensitivity threshold by the same amount.

Neuronal activity in LIP correlated with the monkey's attentional performance: the activity of LIP neurons in the 100 ms interval before the appearance of the probe predicted the monkey's attention to the site of the probe (Bisley and Goldberg 2003, 2006). We recorded the activity of 41 neurons in LIP with peripheral receptive fields in two hemispheres of the two monkeys from whom we gathered the psychophysical data. All neurons were visually responsive, and the majority had delay-period or peri-saccadic activity as well. The neurons responded both to the saccade goal, and the distractor, but had maintained activity only at the saccade goal (figure 3). The data presented in figure 3 represent a population response to two different events: the appearance of the target and the subsequent generation of the memory-guided saccade, and the appearance of the distractor. Although we recorded the response of each of our neurons to those two events separately, we treated the data as if they came from two different populations of neurons with the same overall properties, whose receptive fields lay at the saccade goal (the 'target population' in black) and the other whose receptive fields lay at the distractor site (the 'distractor population' in gray).

The appearance of the distractor outside of the receptive field had no significant effect on the delay-period activity in the target population. The distractor evoked a brief transient response, which decayed rapidly and soon crossed the level of activity in the target population. This crossing point had behavioral significance. To determine the period in which there was no single significant preponderance of activity in LIP, we compared the activity at the two sites in a 100 ms window that slid across the entire period in 5 ms steps (figure 4, bottom). For each monkey there was a window of neuronal ambiguity of 80 to 90 ms in which there was no significant difference between the activity evoked by the distractor and the activity related to the saccade plan ($p > 0.05$ by Wilcoxon sign rank test).

The activity of the neuronal population in LIP parallels the attentional performance of the monkey. There was a consistent relationship between the activity in LIP (figure 4, bottom) and the behavioral results from the three distractor-probe asynchronies measured previously (figure 4, top). At any given time throughout the trial, the attentionally advantaged part of the visual field was that which lay in the receptive fields of the most active neurons. For example, 200 ms after the appearance of the distractor the greatest activity in LIP was in the distractor population (gray traces), and the attentional advantage lay at the distractor site. 500 ms later the target population again had the greatest activity (black traces), and attention had returned to the saccade goal.

Having determined the average size of this window of neuronal ambiguity over a period of months, we then studied each monkey's contrast sensitivities at the saccade goal and the distractor site at the crossing point in each monkey (455 ms for monkey B and 340 ms for monkey I) and 500 ms later. These times were the center of the window of neuronal ambiguity for each monkey. The top section of figure 4 shows the behavioral data from the original sessions (triangles) and from the sessions recorded after the physiological experiments (circles). At the crossing point (gray column) we found no spatial region of enhanced sensitivity in either monkey, but within 500 ms attention had shifted back to the site of the target in both monkeys, with normalized thresholds similar to those seen in the earlier experiment. This is in stark contrast to the effect of LIP activity on saccades: when there was equal activity in the two populations, even in the 50 ms epoch immediately before the saccade, there was no measurable

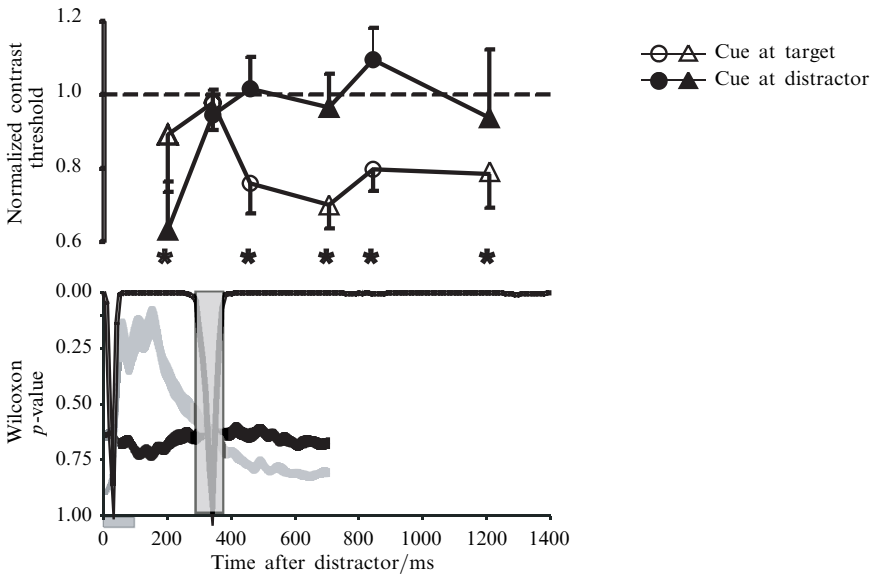


Figure 4. Comparison of neural and behavioral data. The top section shows the behavioral performance of the monkeys when the probe was placed at the saccade goal (open symbols) or at the location of the distractor (closed symbols) in trials in which the target and distractor were in opposite locations. The triangles show data collected before the recording, and the circles show data collected after recording the activity of LIP neurons whose average activity is shown in figure 3, and reproduced in the lower panel. Note that an attentional advantage is a lower normalized threshold. The circle data were recorded at the crossing points of the monkey, 500 ms later, and also collected the crossing point recorded in the other animal. Statistical significance was confirmed with a paired t -test on the pre-normalized data ($*p < 0.05$). The lower section shows a black trace plotting the p -values from Wilcoxon paired sign rank tests performed on the activity of all the neurons for a monkey over a 100 ms bin, measured every 5 ms. A low p -value (high on the axis) represents a significant difference in the activity from the two conditions. The gray column shows when there is no statistical difference between the activity in both populations. 200 ms after the distractor appeared, the attentional advantage lay at the distractor site. When the neural responses were equal, there was no attentional advantage. When there was a small but significant neural advantage at the saccade goal, there was an attentional advantage there. Reproduced from Bisley and Goldberg (2003).

effect on the latency, accuracy, or even early trajectory of the planned saccade (Powell and Goldberg 2000). It is possible that there is a period of time following the distractor when attention is shifting, and this period just happens to coincide with the change in relative activity, while not being related to it. On the other hand, if the activity in LIP were related to attention, then we would expect the behavior to be different in the two animals, because the windows of neuronal ambiguity did not overlap between the two monkeys. We presented the probe to monkey I at the crossing point for monkey B (455 ms) and to monkey B at the crossing point for monkey I (340 ms). We found that the location of the attentional advantage in monkey I had already returned to the saccade goal at the crossing point for monkey B, and that for monkey B the attentional advantage was still at the location of the distractor at the crossing point for monkey I. Note that figure 4 only shows the data for monkey I, but the data for both monkeys have been published elsewhere (Bisley and Goldberg 2003, 2006). These data support the hypothesis that there is indeed a correlation between activity in LIP and the locus of attention.

The absolute level of neural activity did not determine the locus of attention. Instead, the locus of attention lay at the part of the visual field associated with the greatest neural activity in LIP. Thus, the delay-period activity, which determined

the locus of attentional advantage when it was the greatest activity in LIP, could not sustain that advantage when it was swamped by the huge transient response to the distractor. Although at times there was only a small difference in the normalized activity of neurons representing the attentionally advantaged and disadvantaged spatial locations, this difference was extraordinarily robust across the population.

The enhancement hypothesis suggests that the enhanced response evoked by the attended object itself is responsible for the attention to that object (Goldberg and Wurtz 1972; Bushnell et al 1981; Moran and Desimone 1985; Colby et al 1996; Cook and Maunsell 2002). Our results demonstrate, instead, that the attention to be paid to a brief probe is predicted by the activity present in LIP *at the time that the probe appears*. The responses evoked by the probe itself did not correlate with our measure of attention. Remember that on every trial there was either a probe (the broken ring) or a complete ring in the receptive field. We know that the monkey's attention lies at the saccade goal (except soon after the distractor), yet found no difference between the response to the Go probe or the ring in trials in which the saccade plan was directed to the receptive field (figure 5a), or away from it ($p > 0.2$, Wilcoxon paired sign rank test), nor was there any difference in the responses to the probe in correct and incorrect trials. The broken ring (the attended stimulus) and the complete ring evoked the same response despite the fact that the monkey attended to the broken ring. Presumably, since the monkey could only attend to one place at a time in this experiment, there was no attention at the site of the broken ring. For a briefly appearing stimulus, the response evoked by the stimulus is not necessarily related to the attention paid to it.

When the probe was in the receptive field the initial on-responses were identical whether the cue dictated Go to the receptive field, Go elsewhere, or NoGo (figure 5b), or whether there was a complete ring or an intact ring in the receptive field. When the probe signals Go elsewhere the response falls rapidly (dashed trace in figure 5b). When the probe signals Go to the receptive field, the response falls slightly more slowly, and resumes the pre-probe delay-period level (black trace in figure 5b). When the probe signals NoGo and the monkey was planning a saccade to the receptive field, the initial responses to Go and NoGo probes are not different (figure 5c), but the response to the NoGo probe falls far less rapidly, as if the stimulus requiring a cancellation of a saccade plan evokes attention longer than one confirming the saccade plan (gray trace in figure 5b). Across the sample, the late enhanced response to this cancellation of a saccade plan is significantly greater than the response to the continuation signal, both when the saccade plan is to the receptive field (figure 5d) and even more so when the saccade plan and its associated attentional advantage are directed away from the receptive field (figure 5e). The enhanced response is not due to a general arousal evoked by the cancellation of the saccade plan: the enhancement is not seen for the unbroken ring during NoGo trials (figure 5f).

What does the enhanced response to the NoGo probe signify? It could not merely be a signal of attention to the NoGo probe. The monkey also attends to the Go probe—but the Go probe does not evoke an enhanced response. It could not be a non-specific arousal because the unbroken ring does not evoke a similarly enhanced response. Although several groups have suggested that a main function of this brain area is to plan saccades (Platt and Glimcher 1997; Andersen and Buneo 2002), the enhanced response to the NoGo probe renders this interpretation unlikely unless the first step in canceling a saccade is to plan it more. Instead, we suggest that LIP contains a representation of the relative importance of different parts of the visual field, a salience map, and the subsequent enhanced response to an attended stimulus represents top-down maintenance of the importance of the spatial location of that stimulus.

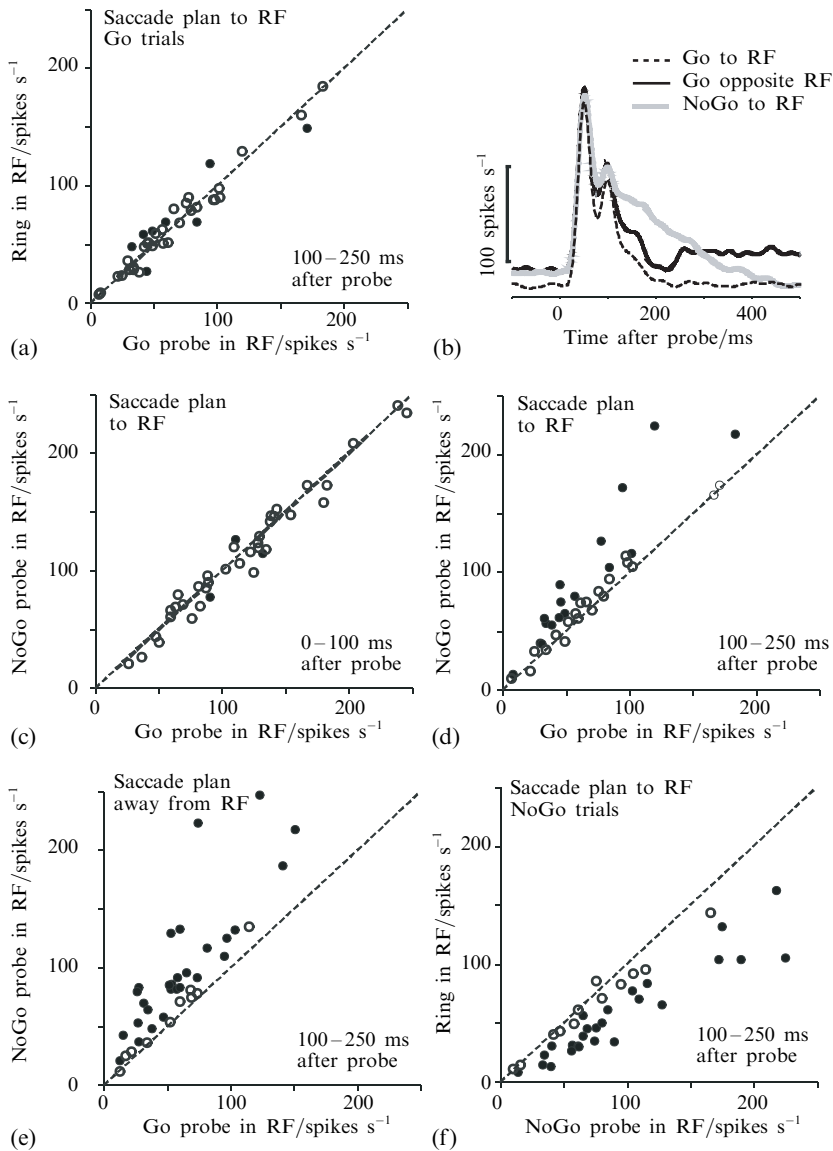


Figure 5. The response to the probe in the receptive field. (a) The response to the complete ring plotted against the response to the Go stimulus in trials in which the monkey was instructed to plan and execute a saccade to the receptive field. Data are from a 150 ms epoch starting 100 ms after the onset of the probe. Across the population there was no difference in the responses to the Go and ring stimuli ($p > 0.6$). (b) Response to the probe. Data are from trials in which the monkey was instructed to plan a saccade into the receptive field and either the Go stimulus (black) or the NoGo stimulus (gray trace) appeared in the receptive field, and from trials in which the saccade goal was opposite the receptive field and the Go probe appeared in the receptive field (dashed trace). The timing of the stimulus presentation is represented by the black bar starting at 0 ms. (c) and (d) The responses to the NoGo stimulus plotted against the response to the Go stimulus in trials in which the monkey was instructed to plan a saccade to the receptive field. Solid circles are from cells in which the difference in activity was significant ($p < 0.05$, t -test), open circles are from cells in which there was no significant difference. (b) Activity for 0 to 100 ms after probe appearance. Across the population there was no difference in response to the two stimuli ($p > 0.15$, Wilcoxon paired sign rank test). (c) Activity from 100 to 250 ms after the onset of the probe. Across the population there was a significant difference in responses (continued over)

3 Top – down factors can suppress responses as well as enhance them

The previous experiment, like the great bulk of studies with eye movements, rewarded the monkey at different times for making or not making an eye movement. In these experiments in which neurons were recorded in monkeys trained to make or not make a particular eye movement the results inevitably reflect some bias of the experimental design. In the real-world, however, primates make saccades to facilitate vision and there is no such thing as a wrong or incorrectly timed eye movement, except for the occasional social taboo. To see if we could garner a better idea of how parietal cortex acts in everyday behavior, we recorded the activity of neurons in LIP of monkeys trained on a visual-search task in which they were free to move their eyes (Sheinberg and Logothetis 2001; Mazer and Gallant 2003; Bichot et al 2005), but in which they reported their decision by a hand movement. There was no reward contingency linked to either fixation or saccade. Under these circumstances neurons in LIP predicted the goal and latency of saccadic eye movements (Ipata et al 2006a), but they also distinguished between plausible and implausible distractors.

Initially, because we wanted to demonstrate the similarity between the monkey's search strategy and that of humans, we often made the pop-out stimulus serve as the target of the search. In one variation of this experiment, we alternated blocks of trials in which the pop-out was always the target, with blocks in which the pop-out was never the target. Under those circumstances, the pop-out distractor often evoked an enhanced response relative to the non-pop-out distractor even on trials in which it was not the target. In the blocks in which the pop-out was the target, the monkeys made their first saccade to the pop-out in almost all of the trials (Ipata et al 2006b). In the blocks in which the pop-out was never the target (figure 6, left columns), monkey R made the first saccade to the pop-out in 148/919 trials (16%), to the target in 520/919 trials (57%), and to a non-pop-out distractor in 251/919 trials (27%). Monkey Z made the first saccade to the pop-out in 517/2438 trials (21%), to the target in 920/2438 trials (37%), and to a non-pop-out distractor in 1001/2438 trials (41%).

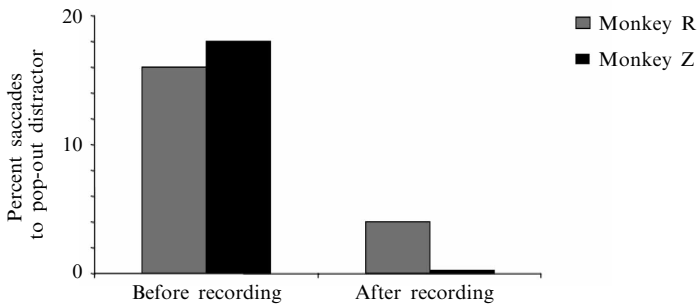


Figure 6. Percentage of first saccades to the pop-out distractor before and during recording. In sessions before recording, blocks in which the pop-out was the target were occasionally presented. The data on the left show the proportion of saccades to the pop-out distractor from these sessions, but only from blocks in which the pop-out was always a distractor. The data on the right were taken from recording sessions, in which the pop-out was never the target. Adapted from Ipata et al (2006a).

Figure 5 (continued)

to the Go and NoGo stimuli ($p < 0.001$). (e) The response to the NoGo stimulus plotted against the response to the Go stimulus in trials in which the monkey was instructed to plan a saccade away from the receptive field. Data are from a 150 ms epoch starting 100 ms after the onset of the probe. Across the population there was a significant difference in responses to the Go and NoGo stimuli ($p < 0.001$). (e) and (f) Response to the NoGo probe plotted against the response to the ring, in trials in which the monkey made a saccade away from receptive field (e) or to it (f). Data are from a 150 ms epoch starting 100 ms after the onset of the probe. Across the population there was a significant difference in the responses to the NoGo and circle stimuli ($p < 0.001$) in both cases. Adapted from Bisley and Goldberg (2003).

Later, because we realized that we were interested in recording from LIP in trials in which the monkey made saccades away from the target, we stopped making the pop-out the target. Under these circumstances (figure 6, right columns) the percentage of first saccades to the pop-out dropped to 4.0% in monkey R (1612/39902) and to 0.2% in monkey Z (150/31923). Monkey R made 22427/39902 (56%) first saccades to the target and 15863/39902 (40%) first saccades to non-pop-out distractors; monkey Z made 14066/31923 (44%) first saccades to the target and 17769/31923 (55%) first saccades to non-pop-out distractors.

The activity of neurons in LIP mirrored this behavioral change. The neurons now usually showed a weaker response to the pop-out than they had when it might have been a target. This weaker response was relative to either the response when the monkey made a saccade to the target in the receptive field, or the response to the non-pop-out distractor on trials in which the monkey made a saccade to a target outside the receptive field (figure 7).

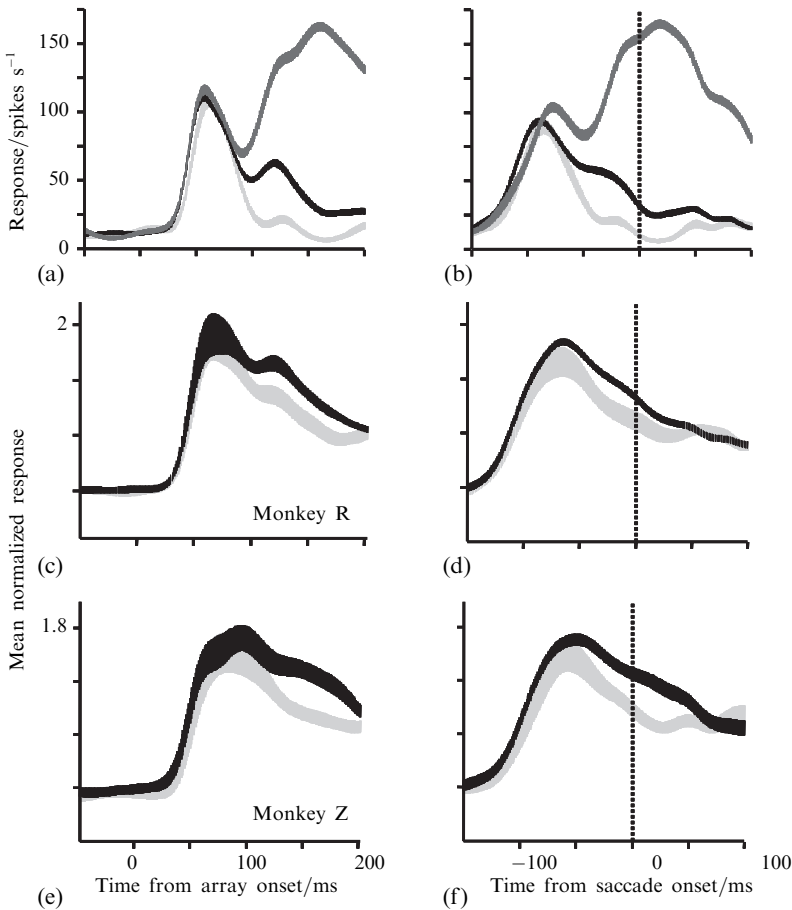


Figure 7. Suppression of response to the pop-out distractor. All data are from trials in which the monkey made the first saccade to the target and released the correct bar. (a) Responses of a single cell to the appearance of an array object in the receptive field plotted against time from target onset. Dark-gray trace: response to the target in the receptive field when the monkey made a saccade to the target. Black trace: response to a non-pop-out distractor in the receptive field when the monkey made a saccade to the target elsewhere. Light-gray trace: response to the pop-out distractor in the receptive field when the monkey made a saccade to the target elsewhere. (b) Same data as in (a), but aligned on saccade onset. (c) and (d) Population averages for monkey R aligned on array onset (c) or saccade onset (d). (e) and (f) Population averages for monkey Z aligned on array onset (e) or saccade onset (f). Reproduced with permission from Ipata et al (2006b).

The monkey's ability to suppress making saccades to the pop-out distractor varied from day to day, as did the neuronal suppression of the response to the pop-out distractor. On days in which the animals were unable to suppress saccades to the pop-out distractor, neuronal responses to the pop-out distractor were equal to, or stronger than, the responses to the non-pop-out distractors.

4 Discussion

These results suggest a new interpretation of the enhancement of activity in LIP. Activity in LIP represents a salience map which can be used to pin visual attention to the peak of the map, or, if appropriate (as in free visual search, but not in a delayed saccade task), drive a saccade to the peak of the map. A number of different signals contribute to this salience map: the response to abrupt onset of a visual target; the generation of a saccade plan to the stimulus in the receptive field; and a top-down control on the visual response which can result in an enhancement of the response to the stimulus in the receptive field, or, as in the pop-out experiment described here, the suppression of that response. Often, when an on-response is enhanced, there is a slight increase in activity before the appearance of the stimulus (Colby et al 1996), which attests to a top-down signal which can drive the cell itself, and serve as a gain-multiplier of the visual response. The peak of the salience map pre-empt perception, especially for stimuli at threshold by virtue of their low contrast or the brevity of their appearance. Enhancement can maintain that peak, but an attended stimulus, especially when attention can be transient, need not evoke an enhanced response. Although a stimulus can be attended without evoking an enhanced response in LIP, this may not be the case throughout the visual system. For example, LIP may serve to bias activity in V4, and the enhancement which occurs as a result of the LIP effect on V4 may actually signify attention.

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