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The Time Course of Perisaccadic Receptive Field Shifts in the Lateral Intraparietal Area of the Monkey

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1Laboratory of Sensorimotor Research National Eye Institute Bethesda, Maryland 20892; 2Medical Research Council-Cognition and Brain Sciences Unit and Department of Experimental Psychology, University of Oxford, Oxford OXI–3UD, United Kingdom; 3Keck-Mahoney Institute for Brain and Cognition, Center for Neurobiology and Behavior, and Departments of Neurology and Psychiatry, Columbia University College of Physicians and Surgeons New York, 10032; and 4New York State Psychiatric Institute, New York, New York 10032

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Kusunoki, Makoto and Michael E. Goldberg. The time course of perisaccadic receptive field shifts in the lateral intraparietal area of the monkey. J Neurophysiol 89: 1519–1527, 2003. First published November 20, 2002; 10.1152/jn.00519.2002. Neurons in the lateral intraparietal area of the monkey (LIP) have visual receptive fields in retinotopic coordinates when studied in a fixation task. However, in the period immediately surrounding a saccade these receptive fields often shift, so that a briefly flashed stimulus outside the receptive field will drive the neurons if the eye movement will bring the spatial location of that vanished stimulus into the receptive field. This is equivalent to a transient shift of the retinal receptive field. The process enables the monkey brain to process a stimulus in a spatially accurate manner after a saccade, even though the stimulus appeared only before the saccade. We studied the time course of this receptive field shift by flashing a task-irrelevant stimulus for 100 ms before, during, or after a saccade. The stimulus could appear in receptive field as defined by the fixation before the saccade (the current receptive field) or the receptive field as defined by the fixation after the saccade (the future receptive field). We recorded the activity of 48 visually responsive neurons in LIP of three hemispheres of two rhesus monkeys. We studied 45 neurons in the current receptive field task, in which the saccade removed the stimulus from the receptive field. Of these neurons 29/45 (64%) showed a significant decrement of response when the stimulus appeared 250 ms or less before the saccade, as compared with their activity during fixation. The average response decrement was 38% for those cells showing a significant (P < 0.05 by t-test) decrement. We studied 39 neurons in the future receptive field task, in which the saccade brought the spatial location of a recently vanished stimulus into the receptive field. Of these 32/39 (82%) had a significant response to stimuli flashed for 100 ms in the future receptive field, even 400 ms before the saccade. Neurons never responded to stimuli moved by the saccade from a point outside the receptive field to another point outside the receptive field. Neurons did not necessarily show any saccadic suppression for stimuli moved from one part of the receptive field to another by the saccade. Stimuli flashed <250 ms before the saccade-evoked responses in both the presaccadic and the postsaccadic receptive fields, resulting in an increase in the effective receptive field size, an effect that we suggest is responsible for perisaccadic perceptual inaccuracies.

INTRODUCTION

Since Kuffler first described mammalian visual receptive fields (Kuffler 1953), the important message of a visual neuron has been considered to be the retinal location of the stimulus that activates the neuron, and an immense amount of work has been done plotting the visual receptive fields of neurons throughout the visual cortex (Van Essen et al. 1990). More recently, however, it has become apparent that in some areas of the brain the visual response is not tied to a particular retinal location. This was first demonstrated for visual neurons in the mouth area of premotor cortex, where neurons respond to visual targets close to the mouth regardless of where the eyes are looking (Gentilucci et al. 1983). Under certain circumstances visually responsive neurons in the superior colliculus (Mays and Sparks 1980; Walker et al. 1995), frontal eye field (Goldberg and Bruce 1990; Umeno and Goldberg 1997, 2001), ventral intraparietal area (Duhamel et al. 1998), parietal reach region (Batista et al. 1999), and lateral intraparietal area (Barash et al. 1991; Goldberg et al. 1990) respond to stimuli that are not in their receptive fields as described during fixation.

In particular, the lateral intraparietal area (LIP) has neurons with visual receptive fields that can be studied when a monkey holds its eyes still in a fixation task (Barash et al. 1991; Colby et al. 1996). When gaze changes, the receptive fields as studied during a fixation task move with the retina, thereby moving the receptive field onto a new location in space. Recent work, however, demonstrated that this fixed retinotopy breaks down in the period immediately around a saccade. Whenever a monkey makes a saccade, some neurons discharge before the saccade to stimuli that will enter the receptive field after the saccade. Targets that flash briefly and disappear before the saccade often excite the neuron when the spatial location of the now-vanished target enters the receptive field (Duhamel et al. 1992). This phenomenon represents a transient change in the retinal locus that can excite the cell, so that an object in space that will excite a neuron after a saccade can excite it even though it only appears before the saccade, and therefore, never appears in the retinal receptive field as determined by a fixation.
task. In other words, there is a transient shift of retinal receptive field.

It is not clear if this perisaccadic change in receptive field is a specific change in the receptive field, or a nonspecific change in the visual responsiveness of the neuron. In these experiments, we sought to answer this question by studying the time course of the changes in visual responsiveness of neurons in LIP around a saccade. We found that responsiveness decreases in the current receptive field before the saccade, at the same time that it increases at the retinal location currently occupied by a stimulus that will be brought into the receptive field by the saccade. These data suggest that the retinal locus that can excite a neuron in LIP shifts in a highly specific way whenever a monkey moves its eyes. Preliminary reports of these experiments have appeared elsewhere (Kusunoki et al. 1994, 1997).

METHODS

Animal methods

The subjects for this study were two adult male rhesus monkeys (Macaca mulatta), weighing between 6 and 11 kg. All experimental procedures were approved by the Animal Care and Use Committee of the National Eye Institute in compliance with the Public Health Service Guide for the Care and Use of Laboratory Animals. The monkeys were kept unrestrained in single or paired cages environments. Periodically they were allowed to spend time in a large “playroom” with swings and climbing devices. They were first taught to participate in the pole-and-collar method of transfer from cage to primate chair, and then to sit in a primate chair and accept food and liquid reward. They were then prepared surgically for chronic neurophysiological experimentation. Under ketamine/salurethane general anesthesia using aseptic surgical technique, each monkey was implanted with two plastic recording chambers 2 cm in diameter, each positioned over the lateral intraparietal area at stereotaxic coordinates AP-5 L12; a plastic head holder for restraint of the head during recordings; and subconjunctival eye coils, by which eye position was measured using the magnetic search coil technique (Judge et al. 1980). The plastic devices were anchored in an acrylic cap which in turn was connected to titanium and plastic screws affixed to the skull. The animals were allowed to recover fully from surgery before any experimentation was performed. Animal weights and health status were carefully monitored, and fluid supplements were given as necessary. At several month intervals, the monkeys were anesthetized with ketamine and the dural surface debrided of granulation tissue by suction and surgical excision using a dissecting microscope.

Behavioral paradigms

Each monkey had controlled access to fluids and received most of its intake of fluid during the behavioral sessions. We used standard behavioral paradigms to characterize the responses of each neuron:

FIXATION TASK. The monkey looked at the spot of light and kept his eye in a small window around the fixation point for several seconds. During this period, a peripheral stimulus appeared to which the monkey was not allowed to make a saccade. If the monkey broke fixation, the trial was aborted. The peripheral stimulus could be used to evaluate the baseline visual response of the neuron during fixation (Wurtz 1969).

DELAYED SACCADE TASK. While the monkey looked at the fixation point, a peripheral light appeared and disappeared after a variable interval. After a second variable interval, the fixation point disappeared and the monkey had to make a saccade to where the stimulus had been. If the saccade fell within a window around the stimulus, usually 6°, the stimulus reappeared and the monkey continued to fixate it to earn a liquid reward (Hikosaka and Wurtz 1983). We searched for neurons while the monkey performed the delayed saccade task, controlling the target position with a joystick. We then used this task to study a neuron’s visual and presaccadic responses and to plot out its visual receptive field. In these experiments, we only used neurons that had visual receptive fields with well-defined borders, with the exception of the distal border, which frequently extended past the confines of our tangent screen.

FLASHED STIMULUS TASKS. Once we had ascertained the visual receptive field in the fixation task or the delayed saccade task, we used two versions of a different task, the flashed stimulus task (Duhamel et al. 1992), to ascertain the perisaccadic responsiveness of the neuron (Fig. 1). In each version of the task, the monkey was asked to make a saccade from an initial fixation point (FP1) to a second fixation point (FP2). The second fixation point was always outside the visual responsive and movement fields of the neuron as determined in the delayed saccade task, and generally in the direction opposite of that of the saccade into the movement field. FP1 disappeared at the same time as FP2 appeared. In most trials, an irrelevant stimulus (STIM) appeared for 100 ms. The monkey did not have to use this stimulus for a saccade target, and, if the monkey made a saccade to STIM rather than to FP2, the trial was terminated and the monkey received no reward. STIM could appear in one of two places: the current receptive field or the future receptive field. In the current receptive field task (Fig. 1A), STIM appeared in the receptive field as determined with the delayed saccade task when the monkey fixated FP1. In the future receptive field task STIM appeared in the receptive field as determined when the monkey fixated FP2. In the current receptive field task (Fig. 1A), FP2 was situated so that STIM was outside the receptive field when the monkey fixated FP2. In the future receptive field task (Fig. 1B), FP1 was situated so that STIM was outside the receptive field when the monkey fixated FP1. The positions of STIM, FP1, and FP2 were arranged so that the retinal location of STIM in the future receptive field task when the monkey fixated FP2 was the same as that in the current receptive field when the monkey fixated FP1. The time of appearance of STIM was set to occur randomly between 300 ms before the disappearance of FP1 to 500 ms after. This ensured that the interval from the appearance of the target to the beginning of the saccade would occur at varying times before, beginning, and after the saccade. In the initial experiments, we ran current- and future-receptive field trials in separate blocks, varying only the time of the stimulus flash. In later experiments, we intermixed the trial types. For some experiments, we kept the position of STIM physically identical and varied the direction of saccade in current- and future-receptive field tasks. For others, depending on the geometry of the receptive field, we kept the positions of the initial fixation point and the saccade target constant and moved the STIM position. As control trials, simple saccade trials from FP1 to FP2 and vice versa without STIM, and fixation trials of four possible combinations of a fixation point (FP1 or FP2) and a stimulus (in or out of the receptive field), were also intermixed with current- and future-receptive field trials. Although this laboratory has often used a behavioral task in which the monkey must make rapid sequential eye movements to frequently flashed stimuli (Goldberg and Bruce 1990; Goldberg et al. 1990), neither monkey used in these experiments was initially trained on such a task, and the monkeys rarely if ever made a saccade to the spatial location of the STIM, which was always irrelevant to the task.

Physiological methods

During a recording session, the monkey sat in a primate chair with head restrained and facing a tangent screen 74 cm away. The monkey’s head was restrained but it was free to move its arms and legs. Visual stimuli were red light-emitting diodes (LED) back-projected onto the screen. The screen was nearly dark, illuminated only by background lights from the recording equipment. LED intensities
individual neuron passed through an anti-aliasing low-pass filter at 500 Hz sampled at a rate of 1 kHz by the computer. Horizontal and vertical eye position signals were measured using a search coil system (CNC) and sampled at a rate of 1 kHz. The response of the recorded neuron was monitored on-line with a raster display synchronized to one of a number of events including stimulus appearance and disappearance, saccade start and finish, and trial beginning and end. Unit discharges, eye position, and behavioral indicators were saved on magnetic disk for off-line analysis, with a sample rate of 1 KHz.

Data analysis

Each trial was analyzed off-line, using in-house developed software. Eye position signals were digitally filtered using a FIR filter with a low-pass at 50 Hz. Then the beginning and the end of the first saccade after the disappearance of FP1 were detected using a minimum velocity algorithm and verified by the investigator. The program calculated average spike frequency for a number of intervals, as well as times of saccade beginning and end and stimulation appearance and disappearance times for all visual stimuli. In the analyses shown here spike activity in the 50–350 ms after stimulus appearance and 0–300 ms after saccade end were used. These data were prepared in a format readable by the MATLAB software package (The MathWorks), and final data analyses were performed using MATLAB.

Anatomical methods

Cylinder position was verified using magnetic resonance imaging. The monkey was anesthetized with ketamine, placed in a plastic and titanium stereotaxic device (Crist Instruments), and scanned in a 1.5 T Magnetic Resonance Scanner (General Electric, Signa). We determined the localization of LIP using three criteria. The first was a rough anatomical localization relative to the recording cylinder as provided by the MRI scan. The second was the position of the area relative to the ventral intraparietal area at the floor of the sulcus. VIP was an area deep in the sulcus with characteristic motion-selective visual receptive fields (Colby et al. 1993). LIP was posteromedial to VIP and lay further up the lateral bank of the intraparietal sulcus. The third was the presence of neurons with both visual and presaccadic activity in the delayed saccade task. This placement has been verified histologically in one monkey, which was deeply anesthetized with pentobarbital sodium and perfused with normal saline and then with 10% formalin in normal saline. It was then prepared using standard techniques (Ma et al. 1991) for histological examination of the cerebral cortex. The electrode tracks were found in LIP as was expected from the MRI scans and the physiological criteria.

RESULTS

We recorded 124 LIP neurons in three hemispheres of two rhesus monkeys. Of these 76 neurons had robust visual responses to the appearance of the target in a delayed saccade task. Of these neurons, 19 also had a presaccadic burst. We fully studied 48 visual neurons, which we have described in this paper.

After we ascertained the visual receptive field of a neuron, we studied it in a large series of flashed-stimulus trials. We used future and/or current receptive field trials randomly intermixed and interspersed with control trials in which the stimulus appeared but the monkey was not required to make a saccade, or the stimulus did not appear and the monkey was required to make the saccade. The responses in these control trials did not change significantly throughout the block of trials. The stimulus appeared for 100 ms randomly from 300 ms before the disappearance of the fixation point to 500 ms

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**A** Current RF Task

- **Current RF Task**
- **Future RF Task**

**FIG. 1.** Tasks used. A: current receptive field task. The monkey fixes the fixation point (FP1). The stimulus (STIM) is positioned in the receptive field as determined while the monkey fixes FP1, the current receptive field, outlined with a solid line. FP1 disappears and FP2 appears. The receptive field as determined when the monkey fixes FP2 is the future receptive field, outlined with a dashed line. The spatial location of STIM is in the current but not the future receptive field. STIM appears for 100 ms at a randomly chosen time between 300 ms before the change of fixation point (shown in the example) to 500 ms after the change of fixation point. Depending on when the monkey actually makes the saccade, the stimulus can appear in the neuron’s receptive field, or the saccade can move the stimulus out of the receptive field.

- **B** Future RF Task

- **Future RF Task**

- **Current RF Task**

- **FP1**

- **FP2**

- **STIM**

- **200 ms**

- **Range of Spatial Location**

- **Receptive Field**

- **Eye Position**

- **Saccade**

- **J Neurophysiol • VOL 89 • MARCH 2003 • www.jn.org**
after the disappearance of the fixation point. Figure 2 shows an example of a flashed-stimulus experiment on a single neuron. Responses are shown for trials in which the stimulus appeared and disappeared well before the saccade (left column), just before the saccade (middle column), and well after the saccade (right column). When the stimulus appeared in the neuron’s current receptive field for 100 ms in the interval beginning 200 ms before the saccade, the response evoked by the neuron was significantly less than when it appeared long before the saccade (top rows). After the saccade the stimulus was not in the neuron’s receptive field, and it had no effect. The neuron illustrated in Fig. 2 responded shortly after the saccade to stimuli that had recently appeared in the future receptive field, even when they appeared as long as 300 ms before the saccade (bottom rows, left column). The response increased when the stimuli appeared and disappeared in the interval immediately before the saccade (middle column) and of course, the neuron responded briskly when the stimulus appeared in the future receptive field after the saccade (right column). Comparison of the upper left and lower right panels with the lower middle panel shows that the latency of the response after the beginning of the saccade is much shorter than the visual latency of this neuron, so the neuron would have been classified as having a predictive visual response by the criterion of Walker et al. (1995).

Examining the discharges of the neuron on a trial-by-trial basis illustrates the time courses of these perisaccadic changes in responsiveness in the current and future receptive fields. In Fig. 3, we plotted the spike rate for each trial against the interval from the saccade to the end of the stimulus presentation for the same trial. This is an unusual way of plotting the stimulus presentation. For example, a stimulus whose data on the ordinate is shown at −100 ms appeared in the interval from −200 to −100 ms before the saccade. Figure 3 (same neuron as in Fig. 2) shows activity calculated in two different ways: activity in the 50 to 350 after stimulus appearance (Fig. 3A), and activity that occurs in the 300 ms after the first saccade (Fig. 3B). For all trials in which that interval is <0 ms, the stimulus remained entirely in the original retinal location: in current receptive field trials the stimulus remained in the

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**A Current RF trials**

**B Future RF trials**

**FIG. 2.** Activity of a neuron in current and future receptive field tasks. The diagram to the left of each part of the figure shows the location of the fixation point, saccade target, and current and future receptive fields, and stimuli. In the current receptive field trials the stimulus appeared at STIM and the monkey made a saccade to FP2, which brought the stimulus out the receptive field. In future receptive field trials the stimulus appeared at STIM and the monkey made a saccade to FP2, which brought the STIM into the receptive field of the neuron. Trials were randomly intermixed. Three rasters are shown for each type of trial. Rasters are grouped by rough intervals of saccade onset, from −100 ms before the change of fixation points to 300 ms after. There are 2 rows of rasters in each set. The top row is synchronized on the stimulus appearance (STIM); the bottom on the beginning of the saccade (SAC). Current receptive field trials are shown on first 2 rows of rasters (CRF trials); future receptive field trials on second 2 rows of rasters (FRF trials). In each raster diagram each dot represents a neuronal discharge. Subsequent lines show subsequent trials, each synchronized on the appearance of the stimulus or on the beginning of the saccade shown by the vertical line through each raster and histogram. The histograms beneath sum the activity in the rasters above. The calibration line on the left of each raster is 100 Hz per bin.
responsiveness in the future receptive field increased, even though the stimulus remained entirely in a retinal location that would not be expected to drive the cell in a fixation task. In the interval from 0 to 100 ms, the stimulus appeared for varying times in both the current and the future receptive fields, and transiently in a retinal smear between the two as the eye moved. During this interval, the neuron showed the most activity in future receptive field trials, but little or no response in current receptive field trials. This responsiveness change was explained, at least partly, by the activity just after the saccade (Fig. 3B). In the interval after the saccade, the activity in current receptive field trials (closed circles) continued to be very low, near the level of the neuron’s spontaneous activity. In contrast, the activity in future receptive field trials (open circles) was always high when the stimulus appeared after the saccade, because the future receptive field was now the actual receptive field of the neuron. In Fig. 3B, however, this high activity decreases after the saccade not because of a characteristic of the saccade, but because the stimulus appears too late for its full effect to be exerted during the analysis interval, 0–300 ms after the saccade. This neuron also showed some saccadic suppression, responding less to stimuli in the future receptive field appearing closer to the saccade.

The decrement of responsiveness in the current receptive field could be due to saccadic suppression, and the neuron shown in Figs. 2 and 3 is excited less by stimuli in the future receptive field immediately before the saccade. However, this was not the case for other neurons (Fig. 4). This neuron had a clear decrease in responsiveness to stimuli appearing in the current receptive field before the saccade (Fig. 4A, closed circles). The decrement of excitability required that the saccade remove the stimulus from the receptive field. If the saccade moved the target from one part of the receptive field to another part of the receptive field, there was no net decrement of response (Fig. 4B, closed circles). This neuron also showed a predictive response when the stimulus was presented in the future receptive field (Fig. 4A, open circles). The effect was not a simple nonspecific change in the receptive field. Instead, it required that the saccade bring the stimulus into the receptive field. If the saccade moved the stimulus from a spatial location outside of the receptive field to another location outside of the receptive field, the neuron did not respond (Fig. 4B, open circles).

We studied 45 neurons using the current receptive field task. Of them 29 had a significant ($P < 0.05$ by $t$-test) decrement of response when the stimulus disappeared 100 to 50 ms before the beginning of the saccade, as compared with the response to the same stimulus in the fixation task. This was the second interval closest to the beginning of the saccade in which the stimulus appeared entirely in the current receptive field. We chose this interval rather than the closest interval to eliminate the possibility of nonspecific saccadic suppression. A scatter diagram of the entire sample studied with the current receptive field task is shown in Fig. 5. The responses of the neurons with significant decrement to the stimulus presented just before the saccade decreased 37% on average from the responses when no saccade was intended.

We studied 39 neurons using the future receptive field task. Of them 32 had a significant ($P < 0.05$ by $t$-test) response to flashed stimuli that appeared and disappeared exclusively in the future receptive field. A scatter diagram of the entire

![Figure 3](image-url)

**FIG. 3.** Trial-by-trial analysis of the response of the neuron shown in Fig. 2 to stimuli in the future and current receptive field, as a function of time from saccade onset to stimulus offset. A: each dot is the activity in the interval 50 to 350 ms after the appearance of the stimulus. The vertical line marks the beginning of the saccade. For all points to the left of the vertical line the stimulus appeared and disappeared before the saccade. For all points after about 150 ms the target appeared and disappeared only after the saccade. Open circles: stimulus appeared in the spatial location of the future receptive field as defined at the start of the trial. After the saccade the stimulus is actually in the neuron’s receptive field as defined in a fixation task. Closed circles: stimulus appeared in the spatial location of the current receptive field as defined at the start of the trial. After the saccade the stimulus is no longer in the receptive field as defined in a fixation task. Note that the neuron becomes relatively insensitive to the current receptive field and relatively sensitive to the future receptive field before the saccade. B: each dot is the activity in the 300 ms after the end of the saccade.
sample studied with the future receptive field task is shown in Fig. 6, with the perisaccadic response on the ordinate plotted against the response to the same stimulus in a fixation task. Since the neurons did not respond to the stimulus presented in the future receptive field during the fixation task, the abscissa indicates the neurons’ spontaneous activity. The responses of the neurons with significant predictive response to the stimulus presented in the future receptive field were 2.8 times greater, on average, than their spontaneous activities.

We were able to study 36 neurons with both current and future receptive field tasks. Of these, only one showed neither a predictive response to stimuli in the future receptive field nor a response decrement to stimuli in the current receptive field (Table 1). The results were similar in the two monkeys, so we have pooled the data. To follow the activity across our entire sample, we took the greatest averaged response for each neuron and normalized all the other responses to it. We normalized the average responses for each neuron, and then averaged the averages, giving each neuron equal weight. Figure 7 shows the...
time course of this highly averaged response in the interval 50–350 ms from the onset of the stimulus, plotted as a function of time from saccade onset to stimulus disappearance. For values <0 the stimulus appeared and disappeared before the saccade. Note that across this sample of neurons the responsiveness decreases in the current receptive field before the saccade and increases in the future receptive field at the same time. The shift in responsiveness leads the saccade.

It is more instructive to examine neuronal activity at various times related to the saccade (Fig. 8). The same averaged and normalized data are shown as in Fig. 7, but in this case the activity shown is the response of the neuron in the epoch in the 300 ms after the end of the saccade. When a stimulus appears in the current receptive field well before the saccade, it evokes no activity after the saccade. When it appears at the same time in the future receptive field, it evokes no activity before the saccade, but significant activity after the saccade. However, stimuli that appear in the 200 ms before the saccade evoke activity from the current and future receptive fields. After the saccade only stimuli appearing in the future receptive field evoke activity.

### DISCUSSION

Neurons in LIP respond to visual stimuli, and one can map out their visual receptive fields during a standard fixation task as if they were standard visual neurons. Ordinarily these receptive fields move with the retina: the retinal locus that excites the neuron remains constant, and the spatial location that can excite the neuron changes (Barash et al. 1991; Colby et al. 1996). The perisaccadic activity of neurons in LIP provides an exception to this rule. Most neurons in LIP will respond to a stimulus that flashes and disappears before a saccade if the saccade brings its spatial location into the receptive field of the neuron. Most neurons discharge after the saccade, but some anticipate the visual consequence of the impending saccade and discharge before it (Duhamel et al. 1992). This effect could represent a general, nonspecific enlargement of the receptive field, or it could represent a specific shift in responsiveness. To choose between these two alternatives, we examined the responses of LIP neurons in the perisaccadic interval. We found that responsiveness shifts transiently before the saccade. At the same time that the area of the retina subtending the stimulus that will enter the receptive field (the future receptive field) begins to excite the neuron, the area of the retina subtending the current receptive field loses the ability to excite the neuron. We will discuss the nature of this shift in responsiveness, its perceptual consequences, and its possible role in the maintenance of accurate spatial behavior.

#### The nature of the shift in responsiveness

Whenever a monkey moves its eyes, many neurons in LIP undergo a transient shift of the receptive field on the retina, as if the effective receptive field were to move ahead of the saccade. The experiments reported here demonstrate that this

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**TABLE 1. Distribution of predictive and presaccadic decrement responses**

<table>
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<tr>
<th></th>
<th>Predictive</th>
<th>Nonpredictive</th>
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change in retinal responsiveness is very specific. It does not result from a general enlargement of the receptive field, because stimuli shifted from one part of the retina outside the receptive field to another part of the retina outside the receptive field cannot excite the neuron. This shift of the receptive field does not occur instantaneously. Instead, the responsiveness of the current receptive field decreases as the responsiveness of the future receptive field increases. This results in an effective increase of the receptive field size in the dimension toward the saccade goal. We have not studied intermediate positions, so we cannot distinguish between a decrement in the current receptive field that corresponds to an increment in the future receptive field, or a stretch of the receptive field in the direction of the saccade that begins at the current receptive field and includes the future receptive field.

The shift must arise from a discharge corollary to the saccade because it can occur before the saccade. Some neurons do show a significant saccadic suppression as well as a specific receptive field shift. Other neurons show no suppression at all when a saccade moves a stimulus from one part of the receptive field to another. The sample shows a range of saccadic suppression, and this is perceptible in the analysis of the average activity of the sample.

The receptive field shift consists of two independent phenomena: a response to a stimulus flashed presaccadically only in the future receptive field, and a decrement of response in the current receptive field. Some neurons show both; some only show one. In our sample most neurons had both or neither. We may have underestimated the number of neurons showing a receptive field decrement, because we used a rather stringent criterion for demonstration of suppression. We elected to use only those trials in which the stimulus had disappeared entirely 50 ms before the saccade began, to eliminate nonspecific saccadic suppression. That limited our sample to trials in which the stimulus appeared 150 ms or earlier before the saccade. If we had used a briefer flash, we may have seen an appearance of suppression in neurons that did not show it in the 100-ms interval. This may have resulted in an underestimate of the number of neurons showing a presaccadic response decrement.

The spatially accurate identification of saccade targets by LIP

Since the work of Helmholtz (1909), it has been assumed that the brain constructs a spatially accurate map of the world around it using retinal information and an efference copy of motor commands to construct a supraretinal map. The nature of this map is unclear. For saccadic eye movements the map might even be unnecessary. Neurons in LIP, the frontal eye field (Umeno and Goldberg 1997), and the superior colliculus (Walker et al. 1995) use the dynamics of the impending saccade to calculate a spatially accurate description of the relationship of a stimulus to the fovea. This enables the brain to calculate the displacement vectors of visual stimuli without waiting for the reestablishment of the visual world through new retinal signals and without knowing the absolute location of the target in supraretinal spatial coordinates. This mechanism is imperfect: if the mechanism were perfect, the receptive field would move across the retina like a spotlight and maintain its shape. As we have discussed above, this is not the case. Instead, the receptive field enlarges transiently in the direction of the saccade target. Stimuli that appear in the current receptive field well before a saccade evoke little response after the saccade. However, stimuli that flash suddenly in the current receptive field less than 200 ms before a saccade evoke a significant response even after the saccade. At the same time, stimuli that flash in the future receptive field immediately before a saccade also evoke a response after the saccade. Thus immediately before a saccade, two different populations of neurons are excited by a single recently flashed stimulus: those for which the stimulus is in the current receptive field, and those for which it is in the future receptive field. An example of such a stimulus is the second target in a double-step saccade task: the subject’s performance in the double-step task is determined by how the brain uses these populations of neurons. If the brain were to select only the future receptive field population by a winner-take-all mechanism, any saccade made after the impending saccade would be accurate. If it chose the current receptive field population, then the subsequent saccade would be made using the retinotopic vector of the target. If the brain were to average the signal from the two populations, then stimuli appearing in the perisaccadic interval would be inaccurately localized in an intermediate fashion between that position described by the future receptive field vector and that position described by the current receptive field vector. Such perisaccadic mislocalization has been reported perceptually (Honda 1989; Matin et al. 1970), and also as a systematic saccadic inaccuracy (Dassonville et al. 1995).

Our results can provide an explanation for such errors. We suggest that the message of the visually responsive neurons in LIP is not the presence of a visual target on the retina, but a spatial vector describing the relationship of the stimulus to the current or intended center of gaze. The output message of the neuron does not change in the perisaccadic period. Only the area of the retina which can evoke that message changes, and it does so transiently. After the saccade, the future receptive field is now the current receptive field. If there is a reafferent response, it reinforces the activity evoked by the shift in responsiveness. For stimuli that were present several hundred milliseconds before the saccade, there is no ambiguity. LIP neurons ordinarily do not respond to stable stimuli brought into their receptive fields by a saccade, although they do respond to task-irrelevant stimuli that are rendered salient by virtue of their abrupt onset (Gottlieb et al. 1998). However, stimuli that appear suddenly <250 ms before an impending saccade are so salient that they evoke activity equally in the two sets of neurons, resulting in the specification of two different output vectors which the oculomotor system then averages. Such vector averaging between the current and future receptive fields might explain the results of Dassonville et al. and Honda. However, because the time course of stimulus presentation is so different between these psychophysical experiments and our physiological data, further experiments will be necessary actually to establish a causal relationship between the ambiguous signals recorded in the monkey and the perisaccadic, perceptual errors described in the human.

Dassonville et al. (1995) also showed the curious phenomenon that two targets flashed at the same retinal location but at a different time before a saccade are treated as if they occupy different spatial locations. This result can be understood if one assumes that closer one comes in time to the saccade, the less powerful will be the activation of the neurons whose current
receptive field subsumes the stimulated location, and the more powerful will be the activation of neurons whose future receptive field subsumes that location. The same stimulus will evoke different spatial vectors, according to the weight of activity in the ensembles subsuming the current and the future receptive field. Accordingly the same stimulus at the same point in the retina will be treated as if it occupies two different spatial locations, because of the gradual shift of retinal responsiveness from current to future receptive field.

Another hallmark of perisaccadic mislocalization of recently flashed objects is a compression of the entire visual field, not just an erroneous shift. Morrone et al. (1997) showed that human subjects compress an entire scene toward the goal of a saccade, as if it were painted on a concertina that was squeezed with the saccade goal in the center. We have shown in this study that around the time of a saccade the retinal receptive field enlarges and therefore more of the visual field will localized to the vector of the neuron. This can result in perceived compression of space for the recently flashed object.

This perisaccadic ambiguity may well be the cost of the mechanism whose benefit is the preservation of spatial accuracy around a saccade for objects that did not just recently flash. Beyond the occasional thunderbolt, meteor, and firefly, flashed objects are rare in the natural environment of the macaque, and such flashed objects rarely have behavioral significance for the animal. A major advantage of the predictive mechanism that we have described is that it enables an accurate representation of the stable visual world immediately after the saccade, without the delay that would occur if the brain had to rely on retinal reafference. Inaccuracy in the localization of objects flashed around a saccade may be an acceptable cost for the benefit of more efficient localization of stable objects in the visual environment.

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