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# Superior Colliculus Activity Related to Concurrent Processing of Saccade Goals in a Visual Search Task

ROBERT M. McPEEK AND EDWARD L. KELLER

*The Smith-Kettlewell Eye Research Institute, San Francisco, California 94115*

Received 19 June 2001; accepted in final form 20 November 2001

**McPeek, Robert M. and Edward L. Keller.** Superior colliculus activity related to concurrent processing of saccade goals in a visual search task. *J Neurophysiol* 87: 1805–1815, 2002; 10.1152/jn.00501.2001. Saccades are typically separated by inter-saccadic fixation intervals (ISFIs) of  $\geq 125$  ms. During this time, the saccadic system selects a goal and completes the preparatory processes required prior to executing the subsequent movement. However, in tasks in which competing stimuli are presented, two sequentially executed movements to different goals can be separated by much shorter ISFIs. This suggests that the saccadic system is capable of completing many of the preparatory requirements for a second saccade concurrently with the execution of an initial movement. We recorded single neurons in the superior colliculus (SC) during rapid saccade sequences made by rhesus monkeys performing a search task. We found that during the execution of an initial saccade, activity related to the goal of a quickly following second saccade can be simultaneously maintained in the SC motor map. This activity appears to signal the selection or increased salience of the second saccade goal even before the initial saccade has ended. For movements separated by normal ISFIs ( $\geq 125$  ms), we did not observe activity related to concurrent processing, presumably because for these longer ISFI responses, the goal of the second saccade is not selected until after the end of the first saccade. These results indicate that, at the time of an initial saccade, the SC does not necessarily act as a strict winner-take-all network. Rather it appears that the salience of a second visual goal can be simultaneously maintained in the SC. This provides evidence that selection or preparatory activity related to the goal of a second saccade can overlap temporally with activity related to an initial saccade and indicates that such concurrent processing is present even in a structure which is fairly close to the motor output.

## INTRODUCTION

Saccadic eye movements allow the visual system to sample different parts of the visual scene by shifting the fovea. Hence, rapid and accurate saccades are crucial for efficient visually guided behavior. Saccades are typically separated by  $\geq 125$  ms (Becker 1989). During this time, the system must presumably select a stimulus to be the goal of the next movement and complete the motor-preparatory processes that are required prior to executing the movement. After an initial saccade is complete, the selection, preparation, and execution cycle begins anew with information obtained at the new fixation position.

When two sequential saccades are made, the selection and

preparation processes for the second saccade have generally been assumed to begin only after the completion of the initial saccade. However, when strongly competing saccade goals are present in tasks such as visual search (Hooge and Erkelens 1996; McPeek and Keller 2001; McPeek et al. 2000; Theeuwes et al. 1999; Viviani and Swensson 1982), the double-step task (Becker and Jürgens 1979; Corneil et al. 1999; Goossens and Van Opstal 1997), and the anti-saccade task (Amador et al. 1998; Mokler and Fischer 1999), researchers have observed that two saccades to different goals can be executed with a very short inter-saccadic fixation interval (ISFI). It has been hypothesized that these short ISFIs result when some of the necessary presaccadic selection or preparatory processes for a second movement begin even before the initial saccade has been completed (Becker and Jürgens 1979; McPeek and Keller 2001; McPeek et al. 2000; Mokler and Fischer 1999; Morrison 1984; Theeuwes et al. 1999; Viviani and Swensson 1982). This has been dubbed “parallel” or “concurrent” processing of saccade goals.

From the double-step task, in which two visual targets are presented sequentially during the latent period of the subject’s initial saccade, it has been known for some time that visual processing of saccade targets continues even during preparation of a movement (Aslin and Shea 1987; Becker and Jürgens 1979; Findlay and Harris 1984; Hou and Fender 1979; Komoda et al. 1973; Ottes et al. 1984). Furthermore, Becker and Jürgens (1979) found support for the idea that two saccade goals can be processed concurrently by showing that when subjects respond to the double-step stimulus by executing two saccades, the time at which the second saccade occurs is directly related to the time at which the second target step occurs and is independent of when the first saccade or the first target step occurs. This is exactly what would be predicted if the preparation of the two saccades overlapped temporally. McPeek et al. (2000) subsequently replicated this finding in a two-dimensional double step task.

In the monkey, McPeek and Keller (2001) uncovered further evidence for concurrent processing. In a search task in which there is a strong competition between distractor and target stimuli, monkeys, like humans, can generate two saccades directed toward different goals in very rapid succession. When such two-saccade responses were observed, McPeek and Keller found that the trajectories of the initial movements

Address for reprint requests: R. M. McPeek, The Smith-Kettlewell Eye Research Institute, 2318 Fillmore St., San Francisco, CA 94115 (E-mail: rmm@ski.org).

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tended to curve slightly toward the goal of the second movements. This curvature suggests the presence of concurrent neural activity in a motor map at a site corresponding to the goal of the second movement. Preliminary results from recording and stimulation studies have suggested that the presence of strong concurrent activity in the superior colliculus (SC) or frontal eye fields (FEF), peaking immediately before the onset of the initial saccade, can result in curved saccade trajectories (FEF and SC: McPeck and Keller 2000; SC: Port and Wurtz 2000).

McPeck and Keller (2001) hypothesized that when activity related to processing of a second saccade goal becomes strong enough, the salience of the second goal may overtake that of the initial goal during the execution of the initial saccade. This would result in a "re-directed" saccade, which is initially aimed toward the first goal but which changes direction in mid-flight to end near the second goal. Such movements have been observed in a variety of experimental paradigms in which there is competition between two or more saccade goals (Corneil et al. 1999; McPeck and Keller 2001; Minken et al. 1993; Van Gisbergen et al. 1987) or between a saccadic goal and a second goal specified by electrical microstimulation (Schlag-Rey et al. 1989).

The observation of these short (and, in some cases, vanishing) ISFIs has led us to hypothesize that selection and/or preparatory activity related to a second saccade goal can occur even during the execution of a first saccade. This prior processing related to the second saccade goal shortens the time-consuming saccade target selection and preparation cycle, which usually occurs after the end of the first saccade. As a result, it paves the way for a second movement to be generated with minimal delay.

Sparks (1999) has recently discussed the difficulty of empirically isolating the various conceptually distinct saccade preparatory processes, such as shifting focal attention, saccade target selection, and motor preparation. However, distinguishing among these different putative stages in the preparation of a saccade is not the aim of the present study. We merely wish to determine whether there is a neural correlate in the superior colliculus for the proposed concurrent processing of a second saccade goal during an initial saccade. Thus "concurrent processing" could encompass any or all of these preparatory activities.

The finding of concurrent activity in the SC would indicate that when confronted with competing targets, this structure does not act as a strict winner-take-all network. Clearly, the saccadic system as a whole produces a single final output in the form of an eye movement. However, it appears that the SC is capable of representing the salience of a second saccade goal even during the execution of an initial saccade. Our presumption is that by maintaining the representation of the second saccade goal throughout the first saccade, rather than quenching this activity in a winner-take-all fashion, the SC is able to re-map the heightened activity originally present at the site representing the second goal after the initial saccade is complete (Mays and Sparks 1980; Sparks and Porter 1983; Walker et al. 1995). This allows a successive movement to be initiated more rapidly than would be possible if, instead, the target selection/saccade preparation processes had to begin anew without the benefit of a pre-selected second-saccade goal.

## METHODS

Two male rhesus monkeys (*Macaca mulatta*) weighing between 4 and 7 kg were used in this study. All experimental protocols were approved by the Institutional Animal Care and Use Committee at the California Pacific Medical Center and complied with the guidelines of the Public Health Service policy on Humane Care and Use of Laboratory Animals.

### Preparation

A scleral eye coil and a head-holder system were implanted under isofluorane anesthesia and aseptic surgical conditions. Anesthesia was induced with an intramuscular injection of ketamine. Heart rate, blood pressure, respiratory rate, and body temperature were monitored for the duration of the surgery. A coil made of four turns of Teflon-coated stainless-steel wire was implanted under the conjunctiva of one eye using the procedure described by Fuchs and Robinson (1966), as modified by Judge et al. (1980). At the completion of the surgery, animals were returned to their home cages. After 2–3 mo of training in behavioral tasks, described in the following text, the monkeys were prepared for chronic single-unit recording in a second aseptic surgery. A stainless steel recording chamber (15 mm ID), tilted 38° posterior from vertical, was positioned above a craniotomy centered on the midline. Antibiotics (Cefazolin) and analgesics (Buprenex) were administered as needed during the recovery period under the direction of a veterinarian.

### Behavioral procedures

Testing was performed in a dimly illuminated room. Data collection and storage was controlled by a custom real-time program running on a PC. Eye position and velocity were sampled at 1 kHz and digitally stored on disk. A Macintosh computer, which was interfaced with the PC, generated the visual displays using software constructed using the Video Toolbox library (Pelli 1997). Visual stimuli were presented on a 29-in color CRT (Viewsonic GA29) in synchronization with the monitor's vertical refresh. The monitor had a spatial resolution of 800 × 600 pixels and a noninterlaced refresh rate of 75 Hz. The monitor was positioned 33 cm in front of the monkey and allowed stimuli to be presented in a field of view of approximately ±32° along the horizontal meridian and ±30° along the vertical meridian.

The monkeys were seated in a primate chair with their heads restrained for the duration of the testing sessions. They executed behavioral tasks for liquid reward and were allowed to work to satiation. Records of each animal's weight and health status were kept, and supplemental water was given as necessary. The animals typically worked for 5 days and were allowed free access to water on weekends.

### Delayed-saccade task

At the beginning of each trial, a white fixation spot subtending 0.25° in diameter with a luminance of 1.24 cd/m<sup>2</sup> appeared in the central position against a homogenous dim background of 0.12 cd/m<sup>2</sup>. The monkeys were required to keep their eyes within 1.5–2° of the fixation point during an initial fixation interval of 450–650 ms. At the end of this interval, a single target stimulus was presented at a peripheral location while the fixation point remained illuminated. Monkeys were required to maintain central fixation until the disappearance of the fixation point 500–700 ms later. Once the fixation point disappeared, they were rewarded for making a saccade to the peripheral stimulus within 70–400 ms. Early or late responses were not rewarded. Eye position tolerance windows around the target stimuli were made equal to the stimulus eccentricity divided by 5. The target was a red or green disk, with a luminance of 0.90 or 0.92 cd/m<sup>2</sup>, respectively.

### Search task

Trials began with a 450- to 650-ms fixation period as for the delayed-saccade task. However, at the end of the fixation period, the fixation point disappeared. Simultaneously, one target and three distractor stimuli were presented at equal eccentricity from fixation, separated by angles of 90° (see Fig. 1A). The stimuli were red or green disks, which were chosen to be approximately equiluminant, with measured luminances of 0.90 and 0.92 cd/m<sup>2</sup>, respectively. The distractors were all of the same color and the target differed from them only by virtue of its odd color. In each trial, the colors of the target and distractors were randomly chosen.

The locations of the stimuli were adjusted for each neuron so that on every trial, either the target or a distractor was presented near the center of the neuron's response field, as determined using single stimuli. The stimuli were M-scaled to keep their salience constant across different eccentricities (Rovamo and Virsu 1979). At an eccentricity of 15°, each stimulus element subtended 2° of visual angle. Monkeys were given a liquid reward for bringing their eyes to the location of the target within 275 ms of the onset of the stimuli. This allowed the possibility of a reward being given if the initial saccade was incorrect but was followed very rapidly by a correct second saccade. In practice, second saccades usually reached the target too late for the monkey to receive a reward. However, the occasional rewarded two-saccade response encouraged the monkeys not to give up after an initial incorrect response.

### Single-unit recording

We used standard methods to record single neurons in the deeper layers of the superior colliculi of two rhesus monkeys. Neural activity was recorded using tungsten microelectrodes with impedances ranging from 0.8–2.5 MΩ at 1 kHz, lowered into the brain by a hydraulic microdrive. The microelectrode signal was amplified, band-pass filtered, and displayed on a digital storage oscilloscope. Action potentials were discriminated and converted into TTL pulses using a time-amplitude window discriminator. The computer data-acquisition

system registered the occurrence of spikes with a resolution of 1 kHz, and the neural data were stored in register with the behavioral measurements.

### Data analysis

**EYE MOVEMENTS.** Off-line analysis of the eye movement data was performed by algorithms using velocity and acceleration criteria to detect the beginning and end of saccades. The algorithm's identification of saccades was visually inspected for every trial to verify its accuracy. Inaccurate or curved saccades were excluded from analysis even if the monkey had been rewarded for the response. Inaccurate saccades were defined as those landing outside a radius of the goal stimulus equal to 10% of the stimulus eccentricity. For smaller eccentricities from 8° (minimum tested) to 12°, this radius was increased by an additional 0.25°. To determine saccade curvature, we first calculated the mean curvature of all single-saccade responses made to a given stimulus location using a curvature metric described by Smit and Van Gisbergen (1990) to obtain a standard value of curvature for saccades to that location. Curved saccades were defined as those with curvature values outside a range of ±1.5 SDs from the mean curvature value.

**MEASUREMENT OF FIRING RATES.** Discharge rates were calculated by counting spike occurrences during time windows of interest and dividing by the duration of the time window. We defined the "peri-saccadic" interval, our primary epoch of interest, as the 50-ms time period centered on the midpoint in time of the execution of the initial saccade (e.g., for a saccade lasting 30 ms, the time window extended from 10 ms before saccade onset to 10 ms after saccade end). Unless otherwise noted, significance tests were performed using the Mann-Whitney *U* test. For testing the significance of individual cells, we used a criterion level of  $P < 0.05$ . In the summary analyses of the rapid two-saccade responses, we selected error saccades to one of the distractor positions for analysis based on which distractor had the greatest number of error trials. Thus the responses for each cell all had initial saccades directed to the same distractor, followed by a second saccade to the target positioned in the neuron's response field.

**CHARACTERIZATION OF NEURONS.** We ascertained the presence or absence of prelude activity in each SC neuron from its responses in the delayed-saccade task. We compared neural activity during a 100-ms delay-period epoch, occurring 150–50 ms before the signal to execute the saccade, with activity during a baseline epoch beginning 75 ms before the visual stimulus was presented and ending 25 ms after stimulus onset (before the beginning of any SC neural response to the visual stimulus). Neurons that showed significantly greater discharge ( $P < 0.05$  in the Wilcoxon signed-rank test) during the delay-period epoch than during the baseline epoch were classified as having prelude activity. This criterion is similar to one described by Basso and Wurtz (1998).

### RESULTS

In the search task, the monkeys made an initial saccade to the correct target in 64% of trials (chance performance is 25%). This performance is in line with that of humans in a very similar task (McPeck et al. 1999). Our search task is more difficult than standard color-odddity search tasks because the colors of the target and distractor stimuli are interchanged randomly from trial to trial. For example, if several trials in which the target is red and distractors are green are followed by a trial in which the distractors are red and the target is green, both humans (McPeck et al. 1999) and monkeys (Bichot and Schall 1999; McPeck and Keller 2001) have a higher probability of making an erroneous initial saccade to a red distractor.

Initial incorrect saccades are typically followed by second saccades to the correct target. For many of these two-saccade

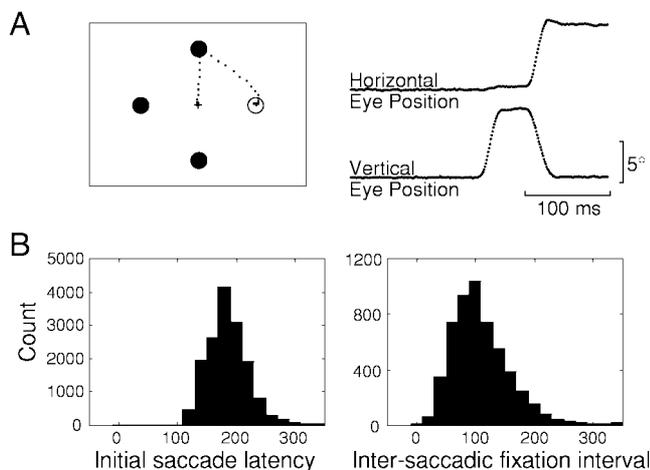


FIG. 1. Diagram of the behavioral task and illustration of short inter-saccadic fixation intervals (ISFIs). *Top left*: a schematic of the stimulus with an eye movement trace superimposed. An initial saccade is made to a distractor, followed by a second saccade to the correct target. In this and all subsequent plots of the visual stimulus, the white disk represents the target stimulus while black disks represent the distractors. In the actual display, the target and distractors were equiluminant and randomly chosen to be red or green on each trial. To the right, horizontal and vertical eye position are plotted as a function of time, making evident the very short fixation interval (~30 ms) between the 1st and 2nd saccades. *Bottom*: histograms of the latency of initial saccades in search (*left*) and of ISFIs when an initial incorrect saccade is followed by a 2nd saccade to the target (*right*). Note that initial saccade latencies fall in the normal range (125–300 ms), while many ISFIs are unusually brief (<125 ms).

responses, ISFI between the first and second saccades is brief. An example of an initial incorrect saccade, followed after a brief ISFI by a second saccade to the target, is shown in Fig. 1A. Histograms of the latencies of all initial saccades (*left*) and the ISFIs between incorrect initial saccades and correct second saccades (*right*) are shown in Fig. 1B. Many of the ISFIs are shorter than the usual primary saccadic latency of 125–300 ms, suggesting that the saccadic system is able to retain information processed during the initial fixation period for use in producing the second saccade.

#### Neural activity: single saccades in search

We recorded the activity of 78 SC neurons that showed a burst of activity for saccades into their response fields in the

delayed-saccade task. The majority (69/78) of these neurons also had visual responses and thus could be classified as visuo-movement neurons. In our search task, SC visuo-movement neurons respond with initial visual activity related to the appearance of a visual target or distractor in their response fields. The neuron shown in Fig. 2 demonstrates a typical pattern of activity. This neuron did not show prelude activity in the delayed-saccade task. The *left column* of Fig. 2 shows the neuron's activity in the search task aligned on the presentation of the visual stimulus array, while the *right column* shows its activity aligned on the onset of the initial saccade. When a saccade is made to the stimulus in the neuron's response field, the cell's activity is more intense near the time of movement onset (Fig. 2A) than when a saccade is made elsewhere (Fig.

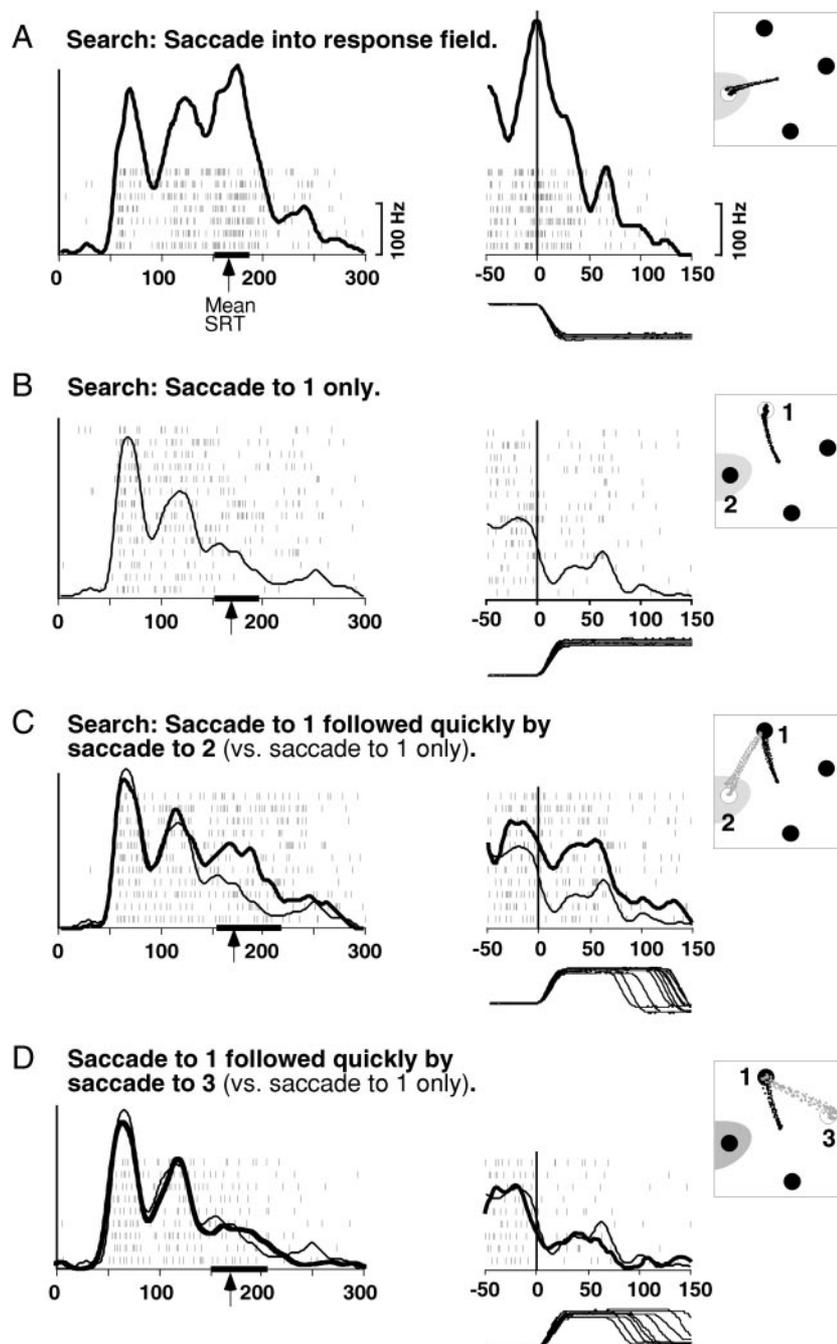


FIG. 2. Activity of a superior colliculus (SC) visuo-movement neuron in the search task. Neural activity is represented by raster plots in which each tick mark signifies the occurrence of an action potential. Mean activity across trials is plotted as average spike density with  $\sigma = 6$  ms (Richmond et al. 1987). Plots in the *left column* are aligned on search array onset, while plots in the *right column* are aligned on the beginning of the first saccade. *Insets* to the right show *xy* spatial plots of eye position across time, superimposed on a schematic showing the positions of the target (portrayed as a white disk) and distractors (portrayed as dark disks). The gray region denotes the approximate response field of the neuron. In the stimulus-aligned plots, the mean time of saccade onset is indicated by the arrow (mean SRT) and the range of saccade onset times is indicated by the thick horizontal bar on the time axis. *A*: activity of the neuron in the search task when single saccades are made to the stimulus inside the neuron's response field. The cell shows initial visual activity followed by a burst occurring around the time of the movement. *B*: activity of the neuron when saccades are made to a search stimulus outside the response field (stimulus 1). The visual discharge is followed by a decline in activity near saccade onset. *C*: when similar initial saccades to stimulus 1 are followed quickly (ISFI < 125 ms) by a 2nd saccade to the stimulus initially in the neuron's response field (stimulus 2), the neuron's activity is maintained at a higher level during the initial saccade. Spike density functions for both single-saccade (thin trace) and double-saccade (thick trace) responses are superimposed for comparison. *D*: neuron's activity when initial saccades to stimulus 1 are followed quickly by second saccades to stimulus 3, which is outside the cell's response field. For such responses, the neuron's activity does not show an increase such as that shown in *C*.

2B). In the former case, a strong movement-related burst of activity peaks around the time of saccade initiation (Fig. 2A, right). In contrast, when a saccade is made to a stimulus outside the neuron's response field, its activity declines near the time of saccade onset (Fig. 2B, right).

#### Rapid two-saccade responses in search

We separately analyzed two-saccade responses in which the initial saccade was directed to a distractor and the second saccade was directed to the correct target. We hypothesized that short inter-saccadic fixation intervals occur when selection or processing of the second saccade goal begins even before the initial saccade has been completed. Specifically, if concurrent processing were occurring in the SC, we would predict that a neuron coding the location of the second goal would show sustained activity around the time of the initial saccade, rather than the normally observed decline in activity, reflecting the fact that the stimulus coded by the neuron has become more behaviorally salient by virtue of being selected as the goal of a future saccade.

In Fig. 2C, we illustrate the activity of the neuron when an initial saccade made to the same upward stimulus shown in Fig. 2B (stimulus 1; outside the cell's response field) will be followed quickly by a second saccade to the stimulus that is initially in the cell's response field (stimulus 2). The spike density functions for the single- and two-saccade cases are directly compared in this figure, with the thin spike-density function showing mean activity for the single-saccade case and the thick spike-density function for the two-saccade case. The initial activity in the two cases is almost indistinguishable (Fig. 2C, left). However, coinciding with the change in the monkey's future behavior, the discharge of the neuron around the time of the initial saccade is maintained at a higher level when a second saccade to stimulus 2 will be made.

The elevated response of this neuron can be better visualized when the trials are aligned on the beginning of the first saccade (Fig. 2C, right): the neuron maintains a slightly higher level of activity before the initial saccade and significantly higher activity during and immediately after the saccade when the initial saccade will be followed rapidly by a future second saccade to stimulus 2, which is inside the neuron's response field ( $P < 0.001$ ). However, this elevated activity is still considerably smaller than the high-frequency burst which accompanies saccades into the cell's response field (Fig. 2A, right). Presumably, a more pronounced discharge could cause the initial saccade to be re-directed toward the response-field stimulus (Schlag-Rey et al. 1989). However, due to their relative scarcity, we excluded such re-directed saccades from analysis as described in METHODS.

#### Dependence on the goal of the second saccade

So far, we have shown that when the monkey makes an initial saccade to stimulus 1 followed quickly by a second saccade to stimulus 2, the neuron's discharge during the initial saccade is elevated. If this elevation in activity is really related to concurrent processing of the goal in the cell's response field, it should be present only when the second saccade is directed to the stimulus inside the cell's response field. To test this prediction, we separately analyzed trials in which the monkey

made an initial saccade to the same upward stimulus (stimulus 1), followed quickly (ISFI  $< 125$  ms) by a second saccade to a stimulus outside the cell's response field (stimulus 3; see the inset of Fig. 2D). As shown in Fig. 2D, the cell's peri-saccadic activity during the initial saccade of this rapid two-saccade sequence is no different from its activity for a single saccade to the same goal ( $P = 0.44$ ). Thus the elevation in activity observed in Fig. 2C is not present for all rapid sequences of saccades. Rather, it is seen only when the goal of the quickly following second saccade lies inside the neuron's response field.

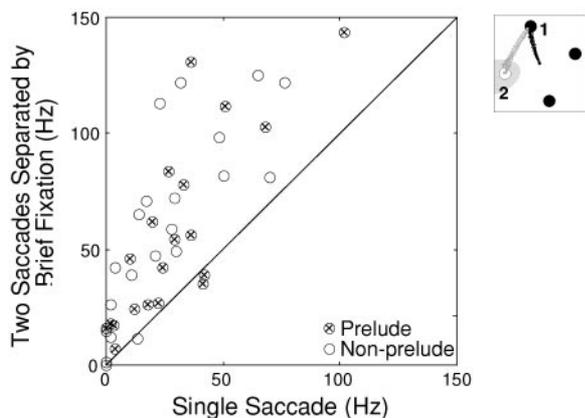
#### Summary data for two-saccade responses

We obtained sufficient data to quantitatively measure concurrent processing activity in 43 cells. For each neuron, we calculated the mean peri-saccadic discharge rate (see METHODS) for the initial saccades of a rapid two-saccade sequence (such as those shown in Fig. 2C) in which the second saccade is directed to the stimulus which was initially presented in the neuron's response field. In Fig. 3A, we plot this rate against the neuron's mean discharge rate during the peri-saccadic interval for similar initial saccades to the same location which are not followed by a second saccade. Across our sample population of neurons, there is a significant increase in activity for the rapid two-saccade case over the single-saccade case (Wilcoxon signed-rank test,  $P < 0.001$ ). On an individual cell-by-cell basis, 49% of our sample (21/43 neurons) show a significant increase in activity.

As argued earlier, if this elevation in activity is due to early selection of the second saccade goal, it should not be seen when the goal of the rapidly following second saccade lies outside the cell's response field. To test this prediction, we compared the mean peri-saccadic discharge rate for each neuron for rapid two-saccade sequences in which both the first and second saccade goals initially lay outside the cell's response field, with its discharge during the same period when a single saccade to the same initial goal was made. Thus this analysis is analogous to that shown in Fig. 3A, with the difference that both the first and the second saccade goals lie outside the cell's response field. As shown in Fig. 3B, for such responses there is little difference in the peri-saccadic discharge rate for the two-saccade versus the one-saccade cases for most cells. On a cell-by-cell basis, three cells showed significantly higher peri-saccadic discharge and one cell showed significantly lower discharge in the rapid two-saccade case versus the single-saccade case. Across cells, there was no significant difference between the two groups (Wilcoxon signed-rank test,  $P = 0.87$ ). This confirms the prediction of the concurrent processing hypothesis that elevated activity during the first saccade should only be seen when the second saccade goal is initially inside the cell's response field. This analysis also eliminates the possibility that the elevation in activity seen in Fig. 3A is some kind of general effect seen for any rapid two-saccade sequence.

Some SC neurons show a low-frequency prelude of activity related to target or movement selection well in advance of saccade execution (Basso and Wurtz 1998; Dorris and Munoz 1998; Glimcher and Sparks 1992; Horwitz and Newsome 1999; Munoz and Wurtz 1995). Of the 43 neurons we analyzed quantitatively in Fig. 3A, 20 showed significant prelude activity in the delayed-saccade task and 23 did not. Surprisingly, we

### A Second saccade goal initially inside cell's response field



### B Second saccade goal initially outside cell's response field

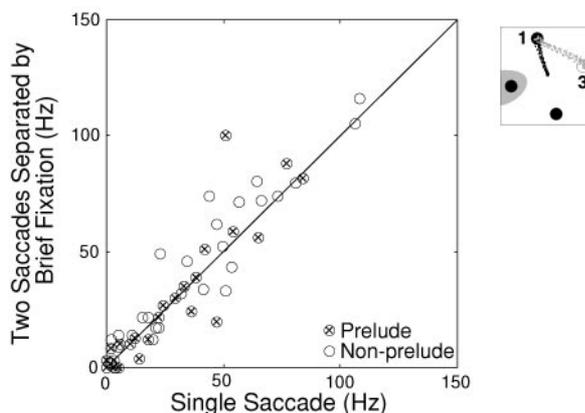


FIG. 3. *A*: scatter plot compares, for each neuron, the mean peri-saccadic discharge rate for saccades to a target located outside the neuron's response field (abscissa) vs. similar initial saccades quickly followed (ISFI < 125 ms) by a 2nd saccade to the stimulus in the neuron's response field (ordinate). If the future occurrence of a rapid 2nd saccade had no effect on a neuron's activity, its plotting symbol would fall along the diagonal line. Nearly all neurons fall above the line, indicating greater activity when an initial saccade is quickly followed by a 2nd saccade. The presence (⊗) or absence (○) of prelude activity for each cell was determined in a delayed-saccade task (see METHODS). We found similar results in both groups of neurons. *B*: scatterplot shows similar comparison for single-saccade responses and rapid double-saccade responses in which the 1st saccade and 2nd saccade goals are both initially located outside the cell's response field. Overall there is no significant difference in discharge for these cases, indicating that the elevation in activity seen in *A* is specific to 2-saccade responses in which the 2nd saccade goal is initially inside the cell's response field.

found that concurrent processing activity is present in neurons lacking prelude activity as well as in neurons having it (see Fig. 3A): 9 of 20 prelude neurons and 12 of 23 non-prelude neurons showed a significant elevation in discharge during the peri-saccadic interval for the two-saccade versus the one-saccade case.

#### Dependence on inter-saccadic interval

In many situations, the goal of a second saccade is selected only after the initial saccade has been completed, using information gathered during the inter-saccadic fixation interval. Thus for movement sequences separated by normal-length ISFIs ( $\geq 125$  ms), we would not expect to see processing of a

second saccade goal during the initial saccade because the second saccade goal would not have been chosen yet. In other words, if the increase in activity seen here represents concurrent processing of a second saccade goal, we should observe it only when two movements are separated by a brief fixation.

To test this prediction, we compared the mean normalized increase in peri-saccadic activity (the "enhancement index") across cells, for two-saccade responses with a very brief ISFI (<125 ms) to those with a more typical ISFI (125–250 ms). For both the short ISFI and the long ISFI groups, the first saccade goal was outside the cell's response field and the second saccade goal was initially inside the cell's response field. The enhancement index for each cell is defined as  $(d_{\text{two}} - d_{\text{one}})/d_{\text{best}}$ , where  $d_{\text{two}}$  is the mean peri-saccadic discharge rate in the two-saccade trials (with ISFIs < 125 ms for the short ISFI case and ISFIs  $\geq 125$  ms for the long ISFI case) and  $d_{\text{one}}$  is defined as the mean discharge rate for similar saccades in search which are not followed by a second saccade. Thus for each cell, the  $d_{\text{two}} - d_{\text{one}}$  term expresses the mean elevation in discharge for the two-saccade cases over the single-saccade cases.  $d_{\text{best}}$  is the mean discharge rate for single saccades when the target was presented inside the neuron's response field and provides a normalization term to equate neurons with different maximum firing rates.

As can be seen in Fig. 4, across our sample of neurons, the enhancement index is significantly higher for responses in which two saccades are separated by a short inter-saccadic fixation interval than for responses in which they are separated by a normal-length fixation period (Wilcoxon signed-rank test,  $P < 0.01$ ). Furthermore, for the responses with a normal inter-saccadic fixation interval, the mean enhancement index does not differ significantly from zero ( $P = 0.68$ ), which is equivalent to the baseline response for single saccades.

#### Activity during the second saccade

It has previously been shown that after the execution of an initial saccade, the loci of activity within the SC are re-mapped to bring them back into registration with the new retinal positions of the stimuli (Mays and Sparks 1980; Sparks and Porter 1983; Walker et al. 1995). Thus after the first movement, the second saccade goal lies outside the neuron's response field (see Fig. 5, left inset). Correspondingly, the discharge of this

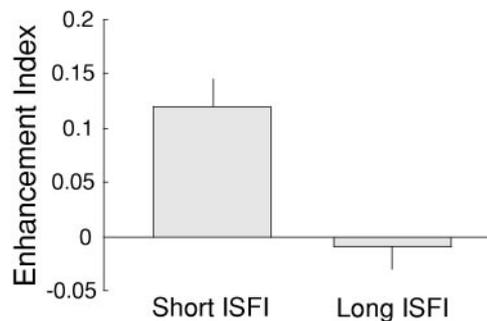


FIG. 4. Compares elevation of peri-saccadic activity for rapid 2-saccade responses (ISFI < 125 ms) vs. 2-saccade responses separated by a normal length ISFI ( $\geq 125$  ms) across our population of cells using an enhancement index calculated for each neuron (see text). Neurons were significantly enhanced when the ISFI was short. When it was longer, neurons showed no significant difference from the discharge observed for comparable single-saccade responses.

## Activity aligned on beginning of second saccade.

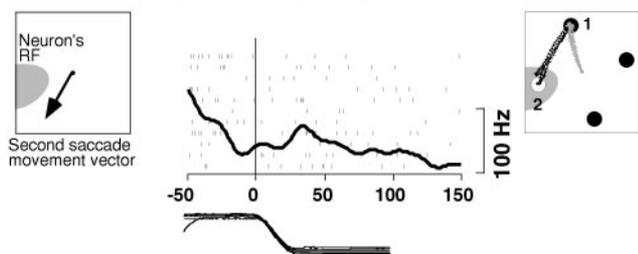


FIG. 5. Activity of the same neuron shown in Fig. 2, aligned on the beginning of the 2nd saccade from stimulus 1 to stimulus 2. The neuron's activity declines to a low level shortly before the beginning of the second saccade, reflecting the fact that the selected goal is no longer inside the cell's response field (see left inset).

neuron declines to a low level before the onset of the second saccade, as shown in Fig. 5, in which the two-saccade trials from Fig. 2C have been re-aligned on the beginning of the second movement. Thus the elevation in SC neural activity described in the preceding text appears to reflect preparatory processing, such as target selection, related to the second saccade goal, but does not directly participate in the eventual execution of the second movement. Across our sample of neurons, we confirmed that there was no unusual elevation in activity during the second saccades in short ISFI trials of the type shown in Fig. 5. Specifically, we compared the discharge during the second saccade for two-saccade responses with a short ISFI to those with a long ISFI as defined in the previous section. In all cases, the initial saccade was directed to a distractor location, while the second saccade was directed to the target that was initially inside the neuron's response field (as in Fig. 2C, for example). We did not find any significant difference in discharge during the second saccade between the short ISFI and long ISFI groups (Wilcoxon signed-rank test,  $P = 0.36$ ). This is the expected result, based on earlier studies (Mays and Sparks 1980; Sparks and Porter 1983), and indicates that, across our sample population of cells, the elevation in activity associated with short ISFIs has subsided by the onset of the second movement, presumably because of the re-mapping of SC activity due to the first saccade.

#### Activity for two different initial saccades

Figure 6 illustrates the discharge during rapid two-saccade responses of a neuron that showed prelude activity in the delayed-saccade task. For this neuron, similar numbers of two-saccade responses occurred in which the second saccades were directed to the stimulus initially inside the cell's response field and the first saccades were directed to the stimulus either in the clockwise or counterclockwise position from the response field. If the elevation in activity we have observed is related to the concurrent processing of the second saccade goal, we would expect it to be present whenever the stimulus in the cell's response field is selected as the goal of a rapidly following second saccade, regardless of which stimulus is the goal of the initial saccade.

Figure 6, left, shows the discharge of the neuron in the search task aligned on the presentation of the search array; whereas Fig. 6, right, shows these responses aligned on the beginning of the movement. Figure 6, A and B, shows responses in which the first saccade is made to the stimulus in the

clockwise position from the response field stimulus, whereas C and D show responses in which the first saccade is made to the stimulus in the counterclockwise position.

The primary point is to show that when two saccades are executed in rapid succession and the second saccade is made to the stimulus which is initially inside the cell's response field, the cell shows a significant increase in discharge slightly before, during, and immediately after the initial saccade regardless of whether this first saccade is made to the stimulus in the counterclockwise (Fig. 6B) or clockwise (Fig. 6D) position from the response field stimulus. In other words, the peri-saccadic elevation in activity does not critically depend on the goal of the initial saccade. Rather it seems to depend on the execution of a rapidly-following second saccade to the stimulus initially in the cell's response field. It should be noted, however, that we were unable to test this result quantitatively across our sample of neurons. For many cells, the monkeys did not produce a sufficient number of appropriately sequenced two-saccade responses to allow us to compare rapid pairs of saccades with different initial goals when the second saccade goal lay inside the cell's response field.

As shown in Fig. 7, this neuron is not directly involved in the eventual execution of the second saccade. Consistent with our findings across our sample of neurons (described earlier), its activity declines to a low level before the second movement begins, reflecting the re-mapping of visual goals. Thus the elevated activity shown in Fig. 6 appears to be related to the early selection of the second saccade goal, occurring even before the first movement has been completed.

#### DISCUSSION

When there is a strong competition between two or more saccade goals, two sequentially executed movements can be separated by surprisingly short ISFIs. We examined such movement sequences in a search task and found that around the time of the initial saccade, there is an increase in activity in SC neurons coding the location of the second saccade goal. A similar increase in activity is not seen for rapid two-saccade sequences in which the second saccade goal lies outside the cell's response field. Thus this elevation in activity is consistent with the idea that the goal of the second saccade has already been selected and has become behaviorally salient even before the end of the first saccade. The results support the idea, first suggested based on behavioral data (Becker and Jürgens 1979), that visuo-motor processing of a competing saccade goal can continue concurrently with the preparation and execution of an initial movement.

We observe this increase in activity at a competing goal site only when two sequential movements are separated by a relatively short ISFI ( $<125$  ms). When two similar movements are separated by a normal-length ISFI ( $\geq 125$  ms), an increase in activity related to the early selection of the second saccade goal is not seen around the time of the first saccade. This observation is also consistent with our interpretation: with longer ISFIs, the elevation in activity is not seen for the simple reason that the second saccade goal has not been selected yet.

Thus our general argument is that rapid two-saccade responses tend to result when there is strong competition between saccade goals. Specifically, one goal may initially reach a higher level of activation and become the goal of the initial

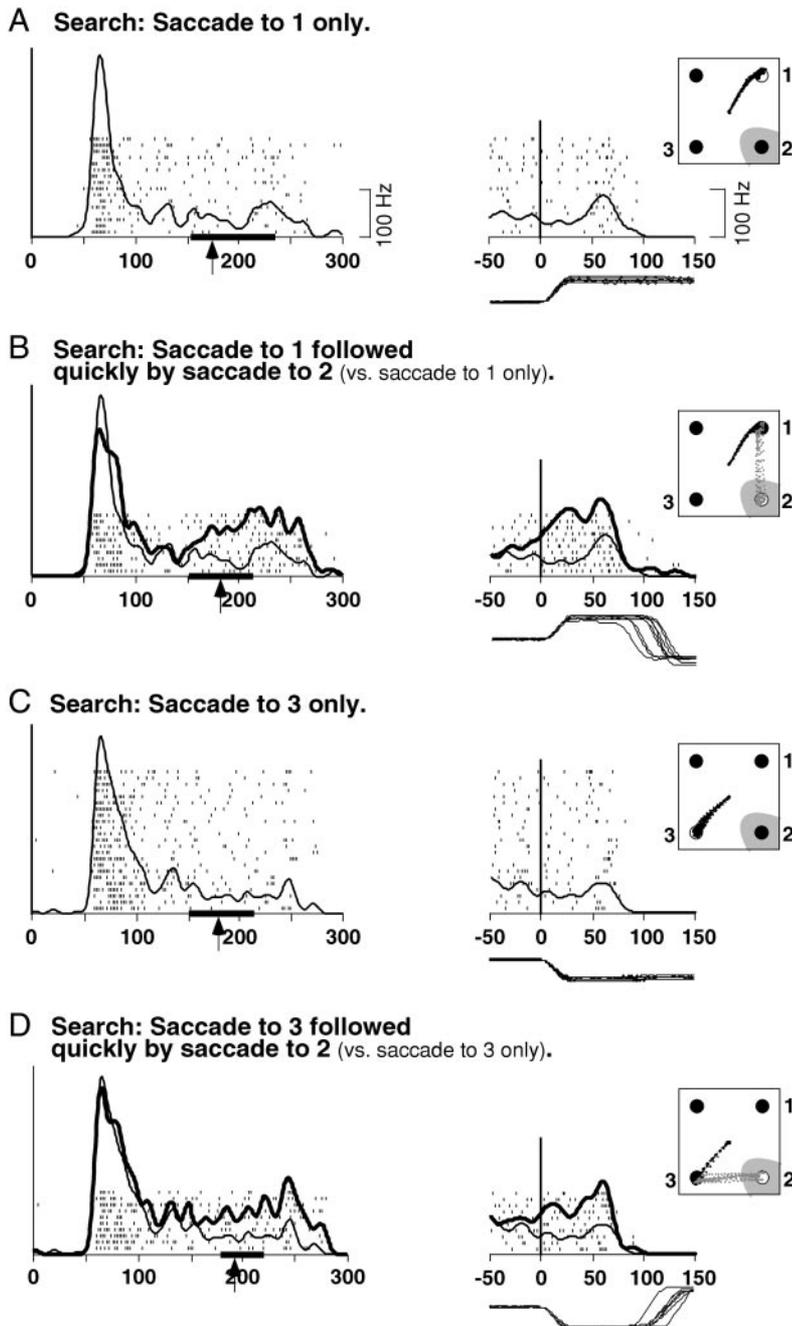


FIG. 6. Activity in a different SC visuo-movement neuron for which we collected 2-saccade responses in which initial saccades were directed to the stimuli in positions either clockwise or counter-clockwise from the response field stimulus. This neuron showed prelude activity in the delayed-saccade task. Format of the figure is similar to Fig. 2, showing activity aligned on the presentation of the search array in the *left column* and aligned on the 1st movement in the *right column*. Responses in which the initial movements were made to the counter-clockwise stimulus are shown in the *top 2 plots* (A and B) and responses to the clockwise stimulus are shown in the *bottom 2 plots* (C and D). B shows that when an initial saccade made to a stimulus outside the cell's response field will be followed quickly by a 2nd saccade to the stimulus initially inside the neuron's response field, the cell's activity around the time of the initial saccade (thick line) is higher than for similar single saccades (thin line). D shows a similar elevation in activity when initial saccades made to a different stimulus outside the cell's response field are followed quickly by a 2nd saccade to the stimulus initially inside the cell's response field.

saccade. However, we theorize that ongoing competition can cause a change in the selected goal. When this change occurs late in the trial, after an initial saccade has already been prepared and can no longer be canceled, we observe, during the initial saccade, an elevation in SC activity at the site coding the second goal, which we argue corresponds to the selection or processing of this target. This advance processing of the second goal allows a second saccade to be produced rapidly after the initial saccade.

#### *Relation to previous studies of target selection in the superior colliculus*

Several studies have examined the discharge of SC neurons during tasks that require selecting one target from among

several stimuli (Basso and Wurtz 1998; Glimcher and Sparks 1992; Horwitz and Newsome 1999; Ottes et al. 1987). In such tasks, visually responsive SC neurons initially signal the presence of all the stimuli with a transient burst of activity related to the presentation of a stimulus in their response field. In most of these studies, delay-period activity was measured before and during target selection. It was found that neurons showing a prelude of activity during the delay period typically fire at a low level for each potential saccade goal. However, as one target is eventually selected to be the goal, activity declines for neurons representing unselected locations and increases for neurons representing the selected goal (Basso and Wurtz 1998; Glimcher and Sparks 1992; Horwitz and Newsome 1999). By the time of saccade execution, this activity has evolved into

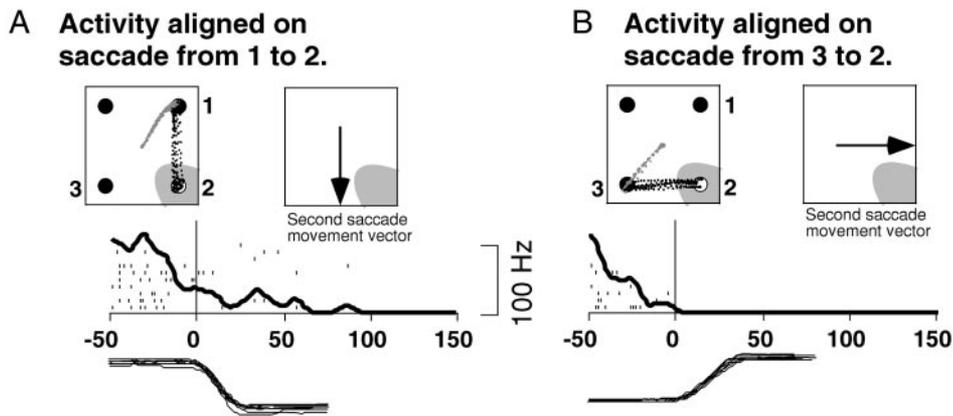


FIG. 7. The activity of the neuron shown in Fig. 6 is aligned on the onset of the second saccade. *A*: 2nd-saccade aligned activity when initial movements are to the stimulus in the position counter-clockwise from the cell's response field stimulus. *B*: 2nd-saccade aligned activity when initial movements are to the clockwise stimulus. In both cases, the cell's discharge declines to a low level before the onset of the 2nd saccade.

a single locus of strong discharge produced by movement-related neurons (including neurons that lack prelude activity) at the site coding the saccade goal. This sequence of events suggests that at saccade onset, the SC tends to operate as a winner-take-all network in which a single selected movement goal is acted on.

However, this view is based on tasks in which a delay period is imposed before the execution of the saccade. The delay period ensures that there is ample time to resolve any competition among potential saccade goals well before the time of the movement. Behavioral evidence and the results we have presented here suggest that the situation may be different when there is a strong competition between two or more saccade goals and the search conditions require an immediate response. Specifically, our results suggest that even during saccade execution, the salience of a non-selected goal can continue to be represented in the activity of superior colliculus neurons. Furthermore, we found that this concurrent processing activity is present in neurons lacking prelude activity as well as in neurons having it. This may be due to the fact that, unlike previous tasks measuring SC activity associated with goal selection, our search task does not impose a delay period. Specifically, the presence of concurrent processing activity in neurons lacking prelude activity may reflect the fact that there is an immediate motor impetus to execute the second saccade as quickly as possible as evidenced by the short inter-saccadic fixation intervals. In contrast, tasks in which the target is selected during a delay period require the suppression of an immediate response, and this requirement may prevent recruitment of non-prelude neurons until a response is permitted.

A recent study by Bichot et al. (2001) showed that the activity of FEF movement neurons coding nonselected distractor locations is greater when the distractor is visually similar to the target or is made salient using visual cues. This increase in activity occurs even though the saccade is made to a stimulus outside the cell's movement field. This finding is consistent with the idea that the population of FEF movement cells, like the collicular visuo-movement neurons shown here, do not form a strict winner-take-all network.

#### Advance preparation and saccade latency

For the two-saccade responses in our task, after the initial saccade is complete, the vector of the second movement no longer coincides with the initial retinotopic position of the target (see Fig. 5, left inset). However, it is known that after an

initial saccade, the locations of potential saccadic goals are re-mapped into their new retinotopic locations (Mays and Sparks 1980; Sparks and Porter 1983). This re-mapping process is very rapid and is not dependent on visual re-afference (Walker et al. 1995). This implies that it is based on stored internal representations of saccadic goals. We argue that these internal representations could also encode the relative salience of the potential goals. An increase in salience of a secondary saccade goal, occurring around the time of an initial saccade, would thus be preserved across the re-mapping process and could influence the production of the second saccade.

Our interpretation assumes that prior target selection and/or preparation can shorten the latency of a subsequent saccade. Recent studies of the neural activity underlying express saccades, which are short latency movements that can be executed under certain stimulus conditions (Fischer and Boch 1983; McPeck and Schiller 1994; Schiller et al. 1987; Sommer 1994), support this view. The occurrence of express saccades is correlated with the presence of motor preparatory activity in the superior colliculus prior to the onset of the visual target (Dorris et al. 1997; Sparks et al. 2000). When this activity is present, the appearance of the visual target seems to trigger a movement-related burst resulting in the initiation of a short-latency saccade (Dorris et al. 1997; Edelman and Keller 1996; Sparks et al. 2000). We hypothesize that the events underlying the short ISFIs we have observed are also the product of advance selection or preparation of the second saccade, in this case, occurring before and during the execution of the first saccade. In our search task, in contrast to the express saccade paradigm, the monkey is not required to await the onset of a visual target before being allowed to initiate the second saccade. Instead, the search stimuli are presented well before the onset of the second saccade and remain visible throughout the trial. This allows the ISFIs between the first and second movements to be even shorter, in some cases, than the latency of express saccades.

The effect of preparatory activity in the SC on saccade latency was also recently investigated by Dorris and Munoz (1998). They examined the correlation between the level of activity in SC neurons before the presentation of a saccadic target with the latency of the subsequent movement. They found that when the level of SC activity in neurons coding a particular movement vector was higher in advance of the presentation of the target, the latency of the resulting saccade was shorter. On the basis of this correlation, they argued that the SC activity could be regarded as motor preparation for a

specific movement vector, acknowledging that “motor preparation” could include attentional mechanisms, target selection, or movement selection. Our interpretation of the present experiments is consistent with the idea that preparatory activity in the SC, in conjunction with the previously demonstrated rapid re-mapping of activity after an initial saccade (Walker et al. 1995), can reduce the latency of a second saccade.

In summary, we present neural evidence supporting the idea that even after one target has been selected and an initial saccade is being executed, selection and processing of a subsequent movement goal can proceed in parallel. The prior completion of such preparatory processes allows the second saccade to be triggered with minimal delay. The presence of this activity in the SC indicates that concurrent processing of saccade goals is not confined to brain areas involved in higher-level, abstract planning, but rather, involves even the lower levels of the oculomotor system.

We thank our colleagues S. Heinen, M. Missal, J. Badler, and R. Larson for helpful comments on the manuscript.

This work was supported by National Eye Institute Grant EY-08060 to E. L. Keller and by National Research Service Award Postdoctoral Fellowship EY-06881 and a Rachael C. Atkinson Fellowship Award to R. M. McPeck.

## REFERENCES

- AMADOR N, SCHLAG-REY M, AND SCHLAG J. Primate antisaccades. I. Behavioral characteristics. *J Neurophysiol* 80: 1775–1786, 1998.
- ASLIN RN AND SHEA SL. The amplitude and angle of saccades to double-step target displacements. *Vision Res* 27: 1925–1942, 1987.
- BASSO MA AND WURTZ RH. Modulation of neuronal activity in superior colliculus by changes in target probability. *J Neurosci* 18: 7519–7534, 1998.
- BECKER W. Metrics. In: *The Neurobiology of Saccadic Eye Movements*, edited by Wurtz RH and Goldberg ME. Amsterdam: Elsevier, 1989, p. 13–67.
- BECKER W AND JÜRGENS R. An analysis of the saccadic system by means of double-step stimuli. *Vision Res* 19: 967–983, 1979.
- BICHOT NP, RAO SC, AND SCHALL JD. Continuous processing in macaque frontal cortex during visual search. *Neuropsychologia* 39: 972–982, 2001.
- BICHOT NP AND SCHALL JD. Saccade target selection in macaque during fixation and conjunction visual search. *Vis Neurosci* 16: 81–89, 1999.
- CORNEIL BD, HING CA, BAUTISTA DV, AND MUNOZ DP. Human eye-head gaze shifts in a distractor task. I. Truncated gaze shifts. *J Neurophysiol* 82: 1390–1405, 1999.
- DORRIS MC AND MUNOZ DP. Saccadic probability influences motor preparation signals and time to saccadic initiation. *J Neurosci* 18: 7015–7026, 1998.
- DORRIS MC, PARE M, AND MUNOZ DP. Neuronal activity in monkey superior colliculus related to the initiation of saccadic eye movements. *J Neurosci* 17: 8566–8579, 1997.
- EDELMAN JA AND KELLER EL. Activity of visuomotor burst neurons in the superior colliculus accompanying express saccades. *J Neurophysiol* 76: 908–926, 1996.
- FINDLAY JM AND HARRIS LR. Small saccades to double-stepped targets moving in two dimensions. In: *Theoretical and Applied Aspects of Eye Movement Research*, edited by Gale AG and Johnson F. Amsterdam: Elsevier, 1984, p. 71–78.
- FISCHER B AND BOCH R. Saccadic eye movements after extremely short reaction times in the monkey. *Brain Res* 260: 21–26, 1983.
- FUCHS AF AND ROBINSON DA. A method for measuring horizontal and vertical eye movement chronically in the monkey. *J Appl Physiol* 21: 1068–1070, 1966.
- GLIMCHER PW AND SPARKS DL. Movement selection in advance of action in the superior colliculus. *Nature* 355: 542–545, 1992.
- GOOSSENS HJLM AND VAN OPSTAL AJ. Local feedback signals are not distorted by prior eye movements: evidence from visually evoked double saccades. *J Neurophysiol* 78: 533–538, 1997.
- HOOGE IT AND ERKELENS CJ. Control of fixation duration in a simple search task. *Percept Psychophys* 58: 969–976, 1996.
- HORWITZ GD AND NEWSOME WT. Separate signals for target selection and movement specification in the superior colliculus. *Science* 284: 1158–1161, 1999.
- HOU RL AND FENDER DH. Processing of direction and magnitude by the saccadic eye-movement system. *Vision Res* 19: 1421–1426, 1979.
- JUDGE SJ, RICHMOND BJ, AND CHU FC. Implantation of magnetic search coils for measurement of eye position: an improved method. *Vision Res* 20: 535–538, 1980.
- KOMODA MK, FESTINGER L, PHILLIPS LJ, DUCKMAN RH, AND YOUNG RA. Some observations concerning saccadic eye movements. *Vision Res* 13: 1009–1020, 1973.
- MAYS LE AND SPARKS DL. Dissociation of visual and saccade-related responses in superior colliculus neurons. *J Neurophysiol* 43: 207–232, 1980.
- McPEEK RM AND KELLER EL. Competition between saccadic goals in the superior colliculus or frontal eye fields results in curved saccades. *Soc Neurosci Abstr* 26: 291, 2000.
- McPEEK RM AND KELLER EL. Short-term priming, concurrent processing, and saccade curvature during a target selection task in the monkey. *Vision Res* 41: 785–800, 2001.
- McPEEK RM, MALJKOVIC V, AND NAKAYAMA K. Saccades require focal attention and are facilitated by a short-term memory system. *Vision Res* 39: 1555–1566, 1999.
- McPEEK RM AND SCHILLER PH. The effects of visual scene composition on the latency of saccadic eye movements of the rhesus monkey. *Vision Res* 34: 2293–2305, 1994.
- McPEEK RM, SKAVENSKI AA, AND NAKAYAMA K. Concurrent processing of saccades in visual search. *Vision Res* 40: 2499–2516, 2000.
- MINKEN AWH, VAN OPSTAL AJ, AND VAN GISBERGEN JAM. Three-dimensional analysis of strongly curved saccades elicited by double-step stimuli. *Exp Brain Res* 93: 521–533, 1993.
- MOKLER A AND FISCHER B. The recognition and correction of involuntary prosaccades in an antisaccade task. *Exp Brain Res* 125: 511–516, 1999.
- MORRISON RE. Manipulation of stimulus onset delay in reading: evidence for parallel programming of saccades. *J Exp Psychol Hum Percept Perform* 10: 667–682, 1984.
- MUNOZ DP AND WURTZ RH. Saccade-related activity in monkey superior colliculus. I. Characteristics of burst and buildup cells. *J Neurophysiol* 73: 2313–2333, 1995.
- OTTES FP, VAN GISBERGEN JAM, AND EGGERMONT JJ. Metrics of saccade responses to visual double stimuli: two different modes. *Vision Res* 24: 1169–1179, 1984.
- OTTES FP, VAN GISBERGEN JAM, AND EGGERMONT JJ. Collicular involvement in a saccadic colour discrimination task. *Exp Brain Res* 66: 465–478, 1987.
- PELLI DG. The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat Vis* 10: 437–442, 1997.
- PORT NL AND WURTZ RH. Two electrode recordings in monkey superior colliculus during curved saccades. *Soc Neurosci Abstr* 26: 297, 2000.
- RICHMOND BJ, OPTICAN LM, PODELL M, AND SPITZER H. Temporal encoding of two-dimensional patterns by single units in primate inferior temporal cortex. I. Response characteristics. *J Neurophysiol* 57: 132–146, 1987.
- ROVAMO J AND VIRSU V. An estimation and application of the human cortical magnification factor. *Exp Brain Res* 37: 495–510, 1979.
- SCHILLER PH, SANDELL JH, AND MANUSELL JHR. The effect of frontal eye field and superior colliculus lesions on saccadic latencies in the rhesus monkey. *J Neurophysiol* 57: 1033–1049, 1987.
- SCHLAG-REY M, SCHLAG J, AND SHOOK B. Interactions between natural and electrically evoked saccades. I. Differences between sites carrying retinal error and motor error signals in monkey superior colliculus. *Exp Brain Res* 76: 537–547, 1989.
- SMIT AC AND VAN GISBERGEN JA. An analysis of curvature in fast and slow human saccades. *Exp Brain Res* 81: 335–345, 1990.
- SOMMER MA. Express saccades elicited during visual scan in the monkey. *Vision Res* 34: 2023–2038, 1994.
- SPARKS DL. Conceptual issues related to the role of the superior colliculus in the control of gaze. *Curr Opin Neurobiol* 9: 698–707, 1999.
- SPARKS DL AND PORTER JD. Spatial localization of saccade targets. II. Activity of superior colliculus neurons preceding compensatory saccades. *J Neurophysiol* 49: 64–74, 1983.
- SPARKS DL, ROHRER WH, AND ZHANG Y. The role of the superior colliculus in saccade initiation: a study of express saccades and the gap effect. *Vision Res* 40: 2763–2777, 2000.
- THEEUWES J, KRAMER AF, HAHN S, IRWIN DE, AND ZELINSKY GJ. Influence of attentional capture on oculomotor control. *J Exp Psychol Hum Percept Perform* 25: 1595–1608, 1999.

- VAN GISBERGEN JAM, VAN OPSTAL AJ, AND ROEBROEK JGH. Stimulus-induced midflight modification of saccades. In: *Eye Movements: From Physiology to Cognition*, edited by O'Regan JK and Levy-Schoen A. Elsevier: Amsterdam, 1987, p. 27–36.
- VIVIANI P AND SWENSSON RG. Saccadic eye movements to peripherally discriminated visual targets. *J Exp Psychol Hum Percept Perform* 8: 113–126, 1982.
- WALKER MF, FITZGIBBON EJ, AND GOLDBERG ME. Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. *J Neurophysiol* 73: 1988–2003, 1995.