Saccade Target Selection in the Superior Colliculus During a Visual Search Task

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Received 11 March 2002; accepted in final form 26 June 2002

McPeek, Robert M., and Edward L. Keller. Saccade target selection in the superior colliculus during a visual search task. J Neurophysiol 88: 2019–2034, 2002; 10.1152/jn.00181.2002. Because real-world scenes typically contain many different potential objects of interest, selecting one goal from many is clearly a fundamental problem faced by the saccadic system. We recorded from visual, movement, and visuo-movement (VM) neurons in the superior colliculus (SC) of monkeys performing a reaction-time visual-search task requiring them to make saccades to an odd-colored target presented with distractors. First, we compared the responses of SC neurons in search with their responses when a single target was presented without distractors (single-stimulus task). Consistent with earlier reports, initial visual activity was smaller in search than in the single-stimulus task, while movement-related activity in the two tasks was comparable. Further experiments showed that much of the reduction in the initial visual response during search was due to lateral inhibition, although a top-down task-related component was also evident. Although the initial visual activity did not discriminate the target from the distractors, some neurons showed a biphase activity pattern of visual activity. In VM burst neurons, the second phase of this activity was significantly larger when the target, rather than a distractor, was in the response field. We traced the time course of target/distractor discrimination using receiver operating characteristic (ROC) analysis and found that VM burst neurons, VM prelude neurons, and pure movement neurons discriminated the target from distractors before saccade onset but that phasic and tonic pure visual neurons did not. We also examined the relationship between target/distractor discrimination time and saccade latency. Discrimination in VM burst neurons having a biphase pattern of visual activity and in many VM prelude neurons occurred after a consistent delay that did not depend on saccade latency, suggesting that these neurons are involved in target selection as well as movement initiation. In contrast, VM burst neurons lacking a biphase pattern of visual activity, pure movement neurons, and a subset of VM prelude neurons discriminated the target at a time that was well correlated with saccade latency, suggesting that this latter group of neurons is involved in triggering movement execution but not in target selection. Thus a mix of signals likely related to target selection and movement initiation co-exists in different groups of SC neurons. This suggests that certain types of SC neurons participate in the target selection process and that the SC as a whole represents a gateway for target selection signals to be converted into a saccadic command.

INTRODUCTION

Saccadic eye movements rapidly shift the fovea from one area of interest to another in the visual scene. The superior colliculus (SC) is a key structure involved in saccades, and the responses of SC neurons have been studied in detail using tasks in which single eye-movement targets are presented on a homogenous background (single-stimulus tasks) (for review, see e.g., Sparks and Hartwich-Young 1989; Wurtz and Albano 1980). However, most real-world scenes contain many different potential saccade targets, and thus target selection is a crucial process for the saccadic system. Cortical areas believed to be involved in target selection, such as the frontal eye field (FEF) and parietal area LIP, are richly interconnected with the SC (Fries 1984; Leichnetz et al. 1981; Lynch et al. 1985, 1994; Stanton et al. 1988), and recent studies have begun to explore the responses of neurons in the SC and other oculomotor areas using paradigms that require target selection (SC: Basso and Wurtz 1997, 1998; Glimcher and Sparks 1992; Horwitz and Newsome 1999, 2001a,b; Ottes et al. 1987; FEF: Bichot et al. 2001; Burman and Segraves 1994; Schall and Hanes 1993; Thompson et al. 1996; LIP: Platt and Glimcher 1997; Shadlen and Newsome 1996, 2001; prefrontal cortex: Hasegawa et al. 2000; Kim and Shadlen 1999; substantia nigra: Basso and Wurtz 2002; supplementary eye field: Olson et al. 2000; Schiller and Chou 2000; Schiller and Tehovnik 2001; see Schall 2001 for review).

To distinguish neural activity related to selection from activity related to movement initiation, most studies of target selection in the SC have used instructed delay tasks, in which monkeys select a target but are required to withhold execution of a movement until a cue is presented (Basso and Wurtz 1998; Glimcher and Sparks 1992; Horwitz and Newsome 2001b). These studies have found that tonically active “prelude” (or “build-up”) neurons discriminate the target from the distractors even before the monkey has been cued to make a movement, suggesting that prelude neurons are involved in target selection, independent of movement initiation. However, in a reaction-time task, the level of discharge in prelude neurons has also been found to be correlated with saccade latency, indicating that prelude activity may also be related to the readiness to make a saccade (Dorris and Munoz 1998; Dorris et al. 1997). Another common class of SC neuron, the VM burst neuron, produces a burst of activity before saccades into its response field but is inactive during delay periods, suggesting that it is involved in triggering saccade execution but not in target selection (Basso and Wurtz 1998; Munoz and Wurtz 1995).
However, it should be noted that delay tasks are not well-suited to provide information about the possible modulation of VM burst neurons during target selection because these neurons are, by definition, silent during enforced delays.

We used a color-oddbit search task to gain insight into the roles of SC visual, movement, and visuo-movement neurons in a target-selection task that does not impose a delay period. One aim of the current study is to compare the responses of SC neurons in a single-stimulus task and in the search task to determine the extent to which the detailed knowledge of SC function derived from single-stimulus tasks can be generalized to situations requiring target selection. A second aim is to analyze the time course of target/distractor discrimination in SC neurons to determine whether these neurons are modulated by the monkey’s choice of saccade goals, and, if they are, whether this modulation is primarily linked to saccade initiation or could be related to target selection. We used a method developed by Thompson et al. (1996) to determine the temporal relationship between a neuron’s discrimination of the target and the latency of the subsequent movement. If the time at which a neuron discriminates the target is correlated with the time of movement initiation, it provides evidence that the neuron generates, or is a conduit for, the movement command. On the other hand, if a neuron discriminates the target at a time that is unrelated to the initiation of the movement, it provides evidence that the neuron carries signals related to target selection. In the FEF, Thompson et al. (1996) demonstrated that VM neurons discriminate the target from distractors at roughly a fixed time, regardless of the latency of the monkey’s saccade (also see Sato et al. 2001). This indicates that, even in a reaction-time task, selection of the target in visually responsive FEF neurons does not necessarily trigger saccade initiation.

These findings in FEF provide a useful heuristic for separating target selection from saccade-initiation signals in SC neurons during our reaction-time search task. This search task has the advantage that the monkey is not required to withhold a response until a movement cue is presented and thus is somewhat more natural than instructed-delay tasks. Furthermore, it allows us to determine whether neurons that are silent during enforced delay periods (including VM burst neurons, phasic visual neurons, and pure movement neurons) are modulated by the target selection process. Finally, the similarity of our task and analysis to Thompson et al. (1996) facilitates comparisons between SC and FEF neurons using a common target-selection paradigm.

**Methods**

Three 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 isoflurane 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 (12 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.

**Single-unit recording**

We used standard methods to record single neurons in the superior colliculi of three rhesus monkeys. Neural activity was recorded using tungsten microelectrodes with impedances ranging from 0.8 to 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.

**Behavioral procedures**

Testing was performed in a dimly illuminated room. Data collection and storage were 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 with 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 subbending 0.25° in diameter with a luminance of 1.24 cd/m² appeared in the central position against a homogenous dim background of 0.12 cd/m². 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 randomly chosen on each trial to be a red or green disk, chosen to be approximately equiluminant, with measured luminances of 0.90 and 0.92 cd/m², respectively. The target was M-scaled to keep its salience constant across different eccentricities (Rovamo and Virsu
Single-stimulus 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 and an eccentric target stimulus was presented. The target was randomly selected on each trial to be a red or green disk with luminance and size as described for the delayed-saccade task. In each trial, the target stimulus was randomly presented at one of four possible locations. The four possible target locations were all at the same eccentricity and were separated from each other by angles of 90°. The four locations were adjusted for each neuron so that one of the locations fell near the center of the neuron’s response field. Two of the monkeys were given a liquid reward for making a saccade to the location of the target within 275 ms of the onset of the stimuli. The third monkey tended to have slightly longer saccade latencies and was allowed 300 ms to saccade to the target.

Search task

The search task was identical to the single stimulus task described in the preceding text with the difference that three distractor stimuli were presented simultaneously with the target stimulus. In each trial, the distractors were located at the three vacant potential target locations (described in the preceding text). The distractors were identical to each other and were all of the same size as the target. The target differed from the distractors only by virtue of its odd color. In each trial, the colors of the target and distractors were randomly chosen to be red or green.

Data analysis

Off-line analysis of the eye movement data was performed with algorithms that used velocity and acceleration criteria to detect the beginning and end of saccades. Data from each trial were visually inspected to verify the accurate identification of saccades. We analyzed only those trials in which the monkey made a single correct saccade to the target. Discharge rates were calculated by counting spike occurrences during time windows of interest and dividing by the duration of the time window. Unless otherwise noted, significance tests were performed using the Mann-Whitney U test and a criterion level of $P < 0.05$.

Characterization of neurons

We characterized the visual, delay period, and saccade-related responses of SC neurons in the delayed-saccade task. Neurons showing no significant increase in firing rate in the peri-saccadic period (25 ms before saccade onset to the end of the saccade) above the rate in the delay period were characterized as “visual” rather than saccade-related.

To ascertain the presence or absence of tonic delay-period activity in both visual and saccade-related neurons, we compared 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 delay-period activity. This criterion is similar to one described by Basso and Wurtz (1998).

Throughout the text, we will refer to visual neurons lacking delay-period activity as phasic visual neurons, and those having it as tonic visual neurons (see Fig. 1, A and B). The tonic visual neurons were invariably recorded below the deepest phasic visual neurons and above the shallowest neurons with movement-related activity. Based on this position in the SC, as well as their discharge properties in the delayed-saccade task, it seems likely that the tonic visual neurons correspond to the quasi-visual cells of Mays and Sparks (1980). However, we did not perform the requisite double-saccade test to definitively establish this correspondence.

Visuo-movement (VM) neurons lacking delay-period activity will be referred to as VM burst neurons to distinguish them from VM prelude neurons, which have significant delay-period activity in addition to movement-related responses (Fig. 1, C and D). These latter neurons likely correspond to the “prelude bursters” characterized by Glimcher and Sparks (1992) and the “build-up” neurons of Munoz and Wurtz (1995) and Basso and Wurtz (1998). The final category is the movement neuron, which discharges a burst of activity tightly linked to saccade execution but does not have significant visual or delay activity (Fig. 1E).

Poisson spike-train analysis

For some analyses, we identified bursts of visual activity in SC neurons using a Poisson spike train analysis described in Hanes et al. (1995) as modified by Thompson et al. (1996). This analysis was applied to spike trains from individual trials to identify periods during which more spikes occurred than expected (based on a Poisson random process), indicating a significant burst of activity. The onset and offset times of these bursts in each trial were recorded and the
mode onset and offset times were estimated for each cell as described by Thompson et al. (1996).

**ROC analysis of target/distractor discrimination**

The techniques of signal detection theory (Green and Swets 1966) have become increasingly popular for analyzing discrimination at the single-neuron level in a variety of visual and eye-movement tasks (e.g., Bradley et al. 1987; Britten et al. 1992, 1996; Horowitz and Newsome 2001b; Kim and Shadlen 1999; Sato et al. 2001; Shadlen and Newsome 1996; Thompson et al. 1996). The method we used is similar to that used by Thompson et al. (1996) and Sato et al. (2001) to trace the time course of target/distractor discrimination in visually responsive FEF neurons in pop-out search tasks. We used receiver operating characteristic (ROC) analysis to compare the activity of each neuron when the target was presented in the cell’s response field to its activity when the target was presented in the location opposite the response field. Our analysis assumes that for each neuron under consideration, there is a similar “anti-neuron” (Britten et al. 1992), which discharges for saccades in the opposite direction. Theoretically, the brain could weigh the input from the neuron and anti-neuron to arrive at a decision about which stimulus is selected as the saccade goal.

For each trial, we generated a spike density function by convolving the spike train with a Gaussian of sigma 4 ms (Richmond et al. 1987). Use of a longer time constant tended to obscure crucial temporal details such as the “second visual burst” described in RESULTS. We aligned the trials on the presentation of the stimulus array and constructed individual ROC curves at each millisecond by moving a threshold across the entire distribution of firing rates and recording the number of hits and false alarms at each threshold level. Example ROC curves at different time points are shown in the lower insets of Fig. 5C. The area under the ROC curve at each time point (the shaded region in the insets) was integrated to provide an unbiased estimate of the separation between the distribution of firing rates when the target was in the response field versus when it was in the opposite position and a distractor was in the response field. This area can also be interpreted as an estimate of the probability that an observer could correctly predict whether the monkey was going to make a saccade to the stimulus in the neuron’s response field based on the neuron’s firing rate.

As the target selection process evolves in time, the area under the ROC curve typically increases from approximately 0.5 (chance level) to nearly 1.0 (perfect discrimination). To extract a single value for the time of target/distractor discrimination (“discrimination time”) we adopted a method used by Sato et al. (2001). Specifically, we defined the discrimination time as the earliest point at which the ROC area surpassed the 0.75 level, and remained above this level for at least 10 ms of the subsequent 15 ms. However, the results are not critically dependent on the exact definition of discrimination time.

To investigate the relationship between discrimination time and saccade latency, we performed a further analysis in which we partitioned the trials for each neuron according to saccade latency into short-, medium-, and long-latency groups, similar to Thompson et al. (1996) and Sato et al. (2001). First, outliers were eliminated by excluding trials with saccade latencies of less than 125 ms or greater than 300 ms. Then, the three groups were formed by partitioning the distribution of saccadic latencies for each cell into three ranges for which there were approximately equal numbers of trials. Individual ROC analyses were then performed and discrimination times were estimated for each saccade latency group as described in the preceding text.

**RESULTS**

We obtained quantitative data from 111 isolated SC neurons that had spatially restricted response fields and exhibited visual, delay-period, or movement-related activity in the delayed saccade task. A breakdown of our sample by neuron type is shown in Table 1. In the subsequent sections, we will first compare the responses of SC neurons in reaction-time single-stimulus and search tasks, and then proceed with an analysis of the time course of target/distractor discrimination in search.

**Visual activity in search and single-stimulus tasks**

When visual stimuli appear within their receptive fields, most SC neurons exhibit a burst of activity, typically occurring with a latency of 50–60 ms and with an initial phase that lasts approximately 30 ms. We compared this earliest visual activity in SC neurons during the search and single-stimulus tasks. As described in METHODS, we employed a Poisson spike-train analysis method developed by Hanes et al. (1995) for determining the latency of each neuron’s earliest response. For cells that showed a significant visual response (as determined in the delayed-saccade task), we defined the initial visual response as the first 30 ms of the neuron’s activity following this response latency.

Earlier reports studying the visual response properties of SC neurons have shown a lack of color selectivity (Marrocco and Li 1977; Ottes et al. 1987). In agreement with this, across our sample of 96 visually responsive SC neurons (72 recorded in both search and single-stimulus tasks and an additional 24 recorded only in search), we found that the initial visual activity did not reliably distinguish the color of the receptive-field stimulus (red vs. green), in either the visual search task (overall, \( P = 0.38 \)) or the single-stimulus task (overall, \( P = 0.42 \)). Nor did it predict, in search, which stimulus would be selected as the goal of the eventual saccade (\( P = 0.43 \)) or which stimulus was the odd-colored target (\( P = 0.51 \)).

Basso and Wurtz (1998) studied SC discharge using multi-element stimulus arrays and reported that as the number of stimulus elements in their task increased, the initial visual activity of VM burst and VM prelude neurons decreased. In addition to recording VM burst and VM prelude neurons, we also compared the initial visual response in tonic and phasic visual neurons. A typical pattern of results for a single cell is shown in Fig. 2, A and B. We found a significant decrease in the magnitude of the initial visual response in the search task when compared with the single-stimulus task (37% overall reduction across cells, Mann-Whitney U test: \( P < 0.0001 \)). Figure 2D shows a scatter plot of the visual response in our search and single-stimulus tasks by cell type. The suppression of initial visual activity was most prominent in VM burst and VM prelude neurons: for VM burst neurons, the magnitude of

<table>
<thead>
<tr>
<th>Cell Type</th>
<th>( n )</th>
<th>2nd Burst Start, ms</th>
<th>2nd Burst End, ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>VM burst</td>
<td>31</td>
<td>101</td>
<td>128</td>
</tr>
<tr>
<td>VM prelude</td>
<td>39</td>
<td>98</td>
<td>121</td>
</tr>
<tr>
<td>Movement</td>
<td>15</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Phasic visual</td>
<td>13</td>
<td>105</td>
<td>125</td>
</tr>
<tr>
<td>Tonic visual</td>
<td>13</td>
<td>101</td>
<td>126</td>
</tr>
<tr>
<td>All</td>
<td>111</td>
<td>101</td>
<td>126</td>
</tr>
</tbody>
</table>

SC, superior colliculus; VM, visuo-movement.
the suppression was 46% \((P < 0.0001)\), while for VM prelude neurons, it was 42% \((P < 0.00001)\). Suppression was less pronounced in the visual neurons, which were recorded in the more shallow lamina of the SC. Across the population, the phasic visual neurons showed a 15% reduction \((P = 0.006)\), and the tonic neurons showed a 17% reduction \((P = 0.002)\).

Is the decrease in the visual response primarily due to top-down or bottom-up mechanisms?

One possible explanation for this reduction in the visual response is lateral inhibition between neurons with receptive fields in distant regions of the visual field. Alternatively, it is possible that in the context of the search task, the visual responsiveness of SC neurons is reduced through top-down inhibition. In their task, Basso and Wurtz (1998) showed that the initial visual activity of VM prelude neurons was influenced both by stimulus configuration and by the probability that the target would appear in the cell’s response field. In our task, it may be desirable to suppress the tendency of SC neurons to burst, to delay initiation of a saccade until the correct target has been localized. Indeed, the latency of saccades in the search task are generally longer than in the single-stimulus task (McPeek and Keller 2001; Schiller et al. 1987).

To assess the possible presence of a top-down component to the suppression, we recorded the activity of 39 SC neurons in an additional task in which occasional single-stimulus trials (20% probability) were randomly intermixed with search trials (80% probability). The monkeys had no advance warning of when a single-stimulus trial would be presented. Thus if the suppression is primarily due to top-down mechanisms, it should be present for the single-stimulus trials occasionally embedded within search trials. On the other hand, if the suppression is simply due to the presence of more stimulus elements in search, the initial visual activity for single-stimulus trials embedded in search should be identical to that seen for single-stimulus trials presented in a block.

The results show that much of the suppression is due to stimulus-configuration effects (lateral inhibition), although top-down mechanisms also seem to play a role. As shown in the example cell in Fig. 2C, the visual burst is clearly larger for single-stimulus trials embedded in search than for search trials, indicating a bottom-up component to the visual suppression. However, the response in Fig. 2C is also slightly smaller than in B, indicating that there is also a top-down task-related component. The summary results in Fig. 2E show that some of the cells produce a smaller response for single stimuli embedded in search than for single stimuli presented in a block, while

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**FIG. 2.** Initial visual activity in search and single-stimulus reaction-time tasks. A: activity of a visuo-movement (VM) prelude neuron in search when the search target was presented in the cell’s response field. Trials are aligned on the presentation of the stimulus array and saccade onset is indicated in each trial by a thick horizontal tick mark. Inset: the stimulus conditions. The target is represented by a black circle and distractors by gray circles even though the stimuli were equiluminant and differentiated from each other by color. The gray region surrounding the target shows the approximate location of the neuron’s response field. B: the activity of the same neuron in the single-stimulus task. The initial burst of activity beginning about 60 ms after target onset is much larger in this task than in search (A) even though the cell’s response field stimuli were identical in the 2 conditions. C: activity of the same neuron during single-stimulus trials that were embedded within search trials. If the reduced activity in A compared with B were due to a top-down suppression during the search task, this suppression should be seen in single-stimulus trials embedded in search. D: summary plot comparing mean initial visual activity in search and single-stimulus tasks. Activity in search is significantly lower than in the single stimulus task. E: similar plot comparing initial visual activity for single stimuli embedded in search and single stimuli presented in a block. Across cells, activity is slightly lower for single-stimulus trials embedded in search.

The legend to the right shows the plotting symbols used in D and E for different neuron classes.
others show no difference in visual response between the two behavioral contexts. Across the entire sample of 39 cells shown in Fig. 2E, there was a small (13% mean decrease) but significant ($P < 0.01$) decrease in initial visual response for single-stimulus trials embedded in search compared with single-stimulus trials presented in a block, indicating that although lateral inhibition accounts for much of the suppression, there is also a top-down component.

Double-peaked visual response

After the initial visual response declined, in some neurons we observed a second discrete burst of activity in the search task (Fig. 3A). This second burst of activity began about 100 ms after the onset of the response-field stimulus and subsided approximately 25 ms later. Several pieces of evidence imply that this second burst of activity is visual in nature rather than movement related. First, judging from the spike rasters, the timing of the second burst is in better temporal register with the onset of the visual stimuli than with the movement. Second, cells having a second burst typically show this response regardless of whether the subsequent saccade is directed into the cell’s response field or outside the response field (Fig. 3B). Third, we never observed a similar burst of activity in any of the 15 movement neurons we sampled that lacked a visual response. The occurrence of this second burst of activity was not unique to the search task: neurons that showed double-peaked activity in search also tended to exhibit it, typically in a weaker form, in the delayed-saccade task (Fig. 3C). We observed this pattern of activity most prominently in VM burst neurons, although to a lesser extent in the other types of visually responsive SC neurons.

We used the Poisson spike train analysis to quantitatively measure, in individual trials, the presence or absence of two discrete bursts of activity beginning within the first 120 ms after the onset of the search array. The second burst of activity tended to be smaller when the target was presented outside the cell’s response field, and, for that reason, we applied the spike train analysis to trials in which the target was located in the cell’s response field. In neurons having movement-related activity, when shorter-latency saccades are made into the cell’s response field, the saccade-related activity in some trials becomes indistinguishable from the second visual burst. This could be considered analogous to the “merging” of the initial visual response and the movement burst which is seen in VM burst cells for express saccades (Dorris et al. 1997; Edelman and Keller 1996; Sparks et al. 2000). To isolate the second burst, uncontaminated by movement activity in visuo-movement neurons, we examined trials in which saccade latency was 160 ms or longer.

Whenever this analysis detected two discrete, significant bursts of activity in an individual trial that began within 120 ms and ended within 140 ms after the onset of the visual stimulus, we coded that trial as having double-peaked visual activity. Across different neurons, the algorithm’s detection of two discrete bursts of activity ranged from 80% of trials down to 0%. We focused our subsequent analysis on the neurons showing the strongest evidence for double-peaked activity, specifically, those with two discrete significant bursts detected in at least 30% of the individual trials. As shown in Table 1, the VM burst neurons had the largest proportion of cells with a strong second burst. Phasic and tonic visual neurons also often showed double-peaked activity. In contrast, only a small proportion of VM prelude neurons, and none of our movement neurons showed double-peaked activity.

We estimated the beginning and ending times of the second burst of activity for each cell from the individual trial data using the mode test statistic (as described in METHODS). Table 1 shows the estimated onset and offset times for the second burst of activity across our sample of visually responsive neurons. Following identification of the burst times, we calculated the mean firing rate during the second burst in each trial.

We found that cells’ discharge rates during this second burst did not depend on the color of the receptive-field stimulus ($P = 0.54$ across our sample of 34 neurons with a strong 2nd burst). On the other hand, in VM burst neurons, the magnitude of the second burst was significantly larger when the target, rather than a distractor, was located in the cell’s response field ($P < 0.0001; n = 16$). The precise timing of target/distractor discrimination in these cells will be examined in detail in the following sections. In contrast to the VM burst cells, the tonic and phasic visual cells having a second burst of visual activity did not show any significant modulation of their activity when the target was in the cell’s response field versus when a distractor was in the cell’s response field ($P = 0.39; n = 12$). A more complete examination of modulation related to target selection in these cells will also be presented in the following sections.

**FIG. 3.** VM burst neuron with a strong 2nd burst of activity. A: response of the neuron in search when the target was presented in the cell’s response field. Trials are aligned on presentation of the stimulus array. ↑, the onset and offset times of the 2nd burst as estimated from a Poisson spike train analysis (Hanes et al. 1995). B: response of the same cell when a distractor was presented in the response field. The level of activity during the 2nd burst is smaller than in A. C: visual responses of the same cell in the delayed-saccade task. Delay-period and movement-related responses are not shown.

*J Neurophysiol* • VOL. 88 • OCTOBER 2002 • www.jn.org
SACCade TARGET SELECTION IN THE SUPERIOR COLLICULUS

Target/distractor discrimination in VM burst neurons

After comparing the activity of neurons in the search and single-stimulus tasks, we conducted further analyses to determine when individual SC neurons begin to reliably discriminate the target from the distractors in search. We employed ROC analysis, which has been used extensively in perceptual, decision, and target-selection tasks (e.g., Bradley et al. 1987; Britten et al. 1992, 1996; Horwitz and Newsome 2001b; Kim and Shadlen 1999; Sato et al. 2001; Shadlen and Newsome 1996; Thompson et al. 1996), to gauge the probability with which an observer monitoring the neuron’s output could predict the monkey’s eventual saccadic choice. To simplify the analysis, we considered only those trials in which the monkey made a single correct saccade to the target stimulus because we have previously shown that the discharge of some SC neurons in incorrect trials appears to be related to selection of the stimulus for the subsequent corrective saccade (McPeek and Keller 2002). Another simplification was to compare cases in which the target was presented inside the cell’s response field to those in which it was presented in the position opposite the response field; however, we noted that the results are not significantly different if all three distractor locations are included in the analysis. We computed the area under the ROC curve, a measure of the separation between the neuron’s distributions of activity in the two conditions on a millisecond-by-millisecond basis. To extract a specific time for when the neuron first discriminated the target from the distractor, we set a criterion probability of 0.75 and measured the time at which the area under the ROC curve first reliably crossed this level (see METHODS), which we designated the “discrimination time.” This method is very similar to that used previously in studies of visual search in the FEF (Sato et al. 2001; Thompson et al. 1996).

Figure 5 shows this analysis applied to a VM burst neuron. A shows the neuron’s responses aligned on the presentation of the search array when the target was presented in the cell’s response field, and B shows the responses when the target was presented at the location opposite the cell’s response field, relative to initial fixation. Figure 5C plots the area under the ROC curve on a millisecond-by-millisecond basis. The four panels at the bottom show sample ROC curves for this neuron at four different time points, with the shaded regions indicating the area under each curve.

Early in the trial, the area under the ROC curve is near 0.5, indicating that the neuron’s activity level is very similar both when the target is present in the response field and when a distractor is present. Following the cell’s initial visual burst of activity that does not discriminate the target from the distractor, the cell shows a second burst, and the area under the ROC curve begins to grow at a time corresponding to this second burst. Approximately 109 ms after the presentation of the search array, the ROC area crosses the 0.75 criterion level. At the end of the cell’s second burst, the ROC area dips below criterion before increasing again around the time of saccade onset. This biphasic pattern suggests that the timing of target/

Movement-related activity

We compared the magnitude of the saccade-related burst in the search and single-stimulus tasks. Figure 4, A and B, shows this comparison in a typical neuron with movement-related activity. Despite the longer latency of the saccades in the search task, the cell’s activity at the time of movement initiation is very similar in the two tasks. For each cell, we computed a mean discharge rate during a time window beginning 8 ms before the onset of each saccade and ending 8 ms before the end of the movement. This time period has been selected in previous studies of SC saccade-related discharge (Anderson et al. 1998; Munoz and Wurtz 1995; Munoz et al. 1996) because it is thought that the delay from SC discharge to its effect on eye movements is approximately 8 ms (Miyashita and Hikosaka 1996). Figure 4C shows summary data in scatterplot form broken down by SC cell type. In agreement with earlier studies using different paradigms (Basso and Wurtz 1998; Ottes et al. 1987), we found that the saccade-related discharge rate was not significantly different in search versus the single-stimulus task for any of the three types of neuron with movement-related activity (Wilcoxon signed-rank tests: VM burst neurons, P = 0.21; VM prelude neurons, P = 0.11; movement neurons, P = 0.32).

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This biphasic pattern suggests that the timing of target/
distractor discrimination for this neuron is not tightly linked to the timing of the movement. Specifically, the neuron’s discharge is transiently informative about the location of the target during the second burst of visual activity. This transient target/distractor discrimination is followed by a later phase, occurring near movement onset, during which the target is again discriminated from the distractor.

**Relationship of discrimination time to saccade latency**

To extract a more detailed picture of the relationship between the time of target/distractor discrimination and the onset of the subsequent movement, we adopted a method developed by Thompson et al. (1996) in their study of target selection in FEF visuo-movement neurons. Specifically, we divided the trials for each cell according to saccade latency into short-, medium-, and long-latency groups (see METHODS). We then performed the ROC analysis described in the preceding text on each group to determine the time of target/distractor discrimination separately for trials with short, medium, and long saccadic latencies. Using this analysis, Thompson et al. found that the time of target/distractor discrimination in most visually responsive FEF neurons was independent of saccade latency. This indicates that much of the trial-to-trial variation in movement latency observed in search tasks is not due to variations in the time required for visual selection of the saccade target but, rather, is due to delays in the motor output stage. Given this background, we reasoned that if target/distractor discrimination in collicular cells merely reflect the command to move the eyes, discrimination time in these cells should occur later for the longer-latency groups. On the other hand, if the modulation of activity in the SC is related to selection of the target stimulus, discrimination time should not depend on saccade latency.

The results of this analysis for the current cell are shown in Fig. 6. A–C show the cell’s activity for the short-, medium-, and long-latency groups. The solid curve shows mean spike density when the target was in the response field, and the dashed curve shows mean spike density when a distractor was in the response field. The bottom panel plots area under the ROC curve for each of the three groups as a function of time. Dashed lines and downward-pointing arrow heads show the discrimination time for each group, whereas the upward-pointing arrow heads along the abscissa show the median saccade latency for each group. For all three latency groups, ROC area falls. A second increase in ROC area occurs near the time of saccade execution for each group. The primary point of interest is that the time at which the cell’s discharge first discriminates the target from the distractors is virtually the same for all three latency groups, rather than increasing with saccade latency. A further observation is that this discrimination time coincides with the occurrence of the second burst of activity.

Earlier, we noted that some VM burst neurons do not have a strong second burst of activity. Would these neurons show a similar pattern of results? Fig. 7 shows the analysis of a representative VM cell lacking a second burst. For this cell, the target/distractor discrimination occurs at a later time for longer saccade latencies. In other words, the modulation of this cell’s activity appears to be temporally linked to execution of the movement. To examine this relationship across our sample of VM burst neurons, we plotted discrimination time as a function of median saccade latency for the three latency groups. In Fig. 8A, each cell’s data points are connected by lines that are color-coded. Red lines indicate cells that had a strong second burst, whereas blue lines indicate cells with little or no second burst. The slopes of the lines give an indication of the relationship between saccade latency and discrimination time for each cell. If discrimination time is independent of saccade latency, the slope should be near zero. On the other hand, if there is a one-to-one increase in discrimination time with increasing saccade latency, the slope should be near one (parallel to the dashed line). Most of the neurons having a strong
second burst discriminated the target from the distractors at a time which was largely the same regardless of when the saccade occurred. Furthermore, this discrimination time typically fell in the range of 100–130 ms, which corresponds well with the occurrence of the second burst. On the other hand, the discrimination time for most of the neurons lacking a second burst increased as saccade latency increased. This result can be seen more clearly in Fig. 8B, which shows a histogram of slopes. A single slope was computed for each neuron by fitting a least-squares line through the neuron’s discrimination time/saccade latency points plotted above. Neurons having a strong second burst are plotted as red outlined boxes, whereas neurons lacking it are plotted as blue filled boxes. Although there is overlap, neurons having a strong second burst tend to cluster around a slope of 0 (mean slope = 0.23), while the others cluster nearer to a slope of 1 (mean slope = 0.79). A t-test on the slopes of the two groups of VM burst neurons established that they are significantly different ($P < 0.001$).

**Target/distractor discrimination in VM prelude neurons**

We now turn to our sample of VM prelude cells, which show significant delay period activity in the delayed-saccade task. Such neurons have been studied previously in delay tasks requiring target selection (Basso and Wurtz 1997, 1998; Glimcher and Sparks 1992; Horwitz and Newsome 1999, 2001b). On the basis of these studies, VM prelude neurons have been considered to be the collicular cells most likely to be involved in target selection, although, as we have shown in the previous section, some VM burst neurons also carry a signal that seems related to target selection.

Figure 9, A and B shows rasters and spike density functions...
for a representative VM prelude neuron in the search task. As before, A shows activity aligned on the onset of the stimuli when the target was presented in the cell’s response field, whereas B shows activity when a distractor was presented in the cell’s response field and the target was presented at the opposite location relative to the initial fixation point. Figure 9C shows area under the ROC curve as a function of time. This cell was typical of our VM prelude sample in that ROC area rose and eventually crossed threshold but did not decline below threshold until after saccade initiation in contrast to the biphasic pattern seen in some VM burst neurons.

As before, we probed the temporal relationship between discrimination time and saccade latency for our VM prelude neurons by dividing the trials for each cell into three saccadic latency groups and performing separate ROC analyses. The results for this cell are shown in Fig. 10. For all three latency groups, ROC area grows with a similar time course, and discrimination time is nearly independent of saccade latency. Thus the timing of this cell’s modulation is consistent with target selection rather than saccade initiation. Even though the cell does not produce a well-defined second burst of activity, its pattern of earliest discrimination times is similar to that seen in the subset of VM burst neurons having a second burst.

However, other VM prelude neurons showed a different pattern of results. Figure 11 shows a VM prelude neuron for which discrimination time is well correlated with saccade latency: discrimination occurs earlier for shorter-latency movements and later for longer-latency movements. Unlike the result for the VM burst neurons, we could not discern any correlation between the presence of a strong second burst of activity in VM prelude neurons and the temporal relationship between discrimination time and saccade latency. However, it should also be noted that we only observed a strong second burst in 6 of our 39 VM prelude neurons. Summary results for VM prelude neurons are shown in Fig. 12, which plots discrimination time as a function of median saccade latency for each of the three latency groups and shows a histogram of the slopes. Similar to the situation with VM burst neurons, we can see the emergence of two groups of VM prelude neurons: those with discrimination times that are strongly correlated with saccade latency and those with discrimination times that remain fairly constant regardless of latency.

**Target/distractor discrimination in movement neurons**

We next considered the movement neurons, which showed no significant visual or delay activity but which showed strong...
saccade-related bursts in the delayed-saccade task. The activity of a representative movement neuron in search is shown in Fig. 13, A and B. As expected, this neuron shows little visual activity in search but shows a robust burst associated with saccades into its response field. The plot of ROC area in Fig. 13C shows that the cell’s activity predicts the monkey’s saccadic choice. As before, we grouped the trials by saccade latency and performed individual ROC analyses on these subgroups for each cell to determine whether target/distractor discrimination occurred later in trials with a longer latency. As shown in the summary plots of discrimination time versus saccade latency (Fig. 14A) and in the histogram of slopes (Fig. 14B), we found that the time of target discrimination was strongly correlated with saccade latency for nearly all our movement neurons. The mean slope for these neurons was 0.96, which was significantly different from zero (t-test: \(P < 0.00001\)) but not from one (\(P = 0.74\)). This suggests that movement neurons are involved in triggering the onset of saccades and that their activity is not significantly modulated by earlier visual selection in contrast to many visuo-movement neurons.

**Phasic and tonic visual neurons in search**

Finally, we analyzed our sample of phasic and tonic visual neurons in the search task. For both groups of pure visual neurons, we found very little difference in discharge between trials in which the target was presented in the response field and trials in which a distractor was presented in the response field. A typical example of a phasic visual neuron is shown in Fig. 15. The cell shows a robust initial visual response followed by a much smaller second peak and no apparent movement-related activity. The plot of ROC area (Fig. 15C) shows only minor fluctuations around 0.5 (chance level) and never reaches threshold. Results for the tonic visual neurons are quite similar. Although they showed maintained activity throughout the trial that ended only after the saccade was made, the level of this activity did not appear to be modulated by the monkey’s choice of saccade target, and for these neurons, area under the ROC curve did not meet our threshold criteria. Based on our finding that they are not significantly modulated by the monkey’s choice, it appears that neither phasic nor tonic visual neurons play a role in target selection for this task.

**FIG. 10.** Separate ROC analyses of target/distractor discrimination for different saccade latency groups in the VM prelude neuron shown in Fig. 9. Figure conventions are the same as for Fig. 7. Although the cell’s initial activity does not discriminate the target from distractors, discrimination time is virtually the same for all three latency groups, indicating that discrimination in this cell is not related to saccade latency.

**FIG. 11.** ROC analyses of another VM prelude neuron, same conventions as in Fig. 10. In this cell, discrimination occurs later for longer saccade latencies, suggesting that target/distractor discrimination in this cell is related to generation of the saccadic command signal.
DISCUSSION

In a reaction-time pop-out visual search task, we traced the time course of target/distractor discrimination in SC neurons on a millisecond-by-millisecond basis. We found that VM and movement neurons are modulated by the monkey’s eye-movement choice unlike tonic and phasic pure visual cells, which are unmodulated. In a subset of SC visual and VM neurons, we observed a biphasic pattern of visual activity. The second burst of this activity was time-locked to stimulus presentation but, in VM burst neurons, was stronger when the target rather than a distractor was in the response field. As a result, VM burst neurons with a strong second burst discriminated the target from the distractors at a time that was not directly linked to saccade latency. In VM prelude neurons, roughly half of our sample also discriminated the target at a time that was not related to saccade latency. This suggests that the modulation in these two groups of neurons is related to target selection rather than movement production. On the other hand, in VM burst neurons lacking a second visual burst, target/distractor discrimination was fairly tightly linked to saccade latency, suggesting that this subset of SC neurons is involved in triggering movement initiation rather than in target selection. We found a similarly strong correlation between discrimination time and saccade latency in virtually all of our movement neurons and in many VM prelude neurons.

Top-down effects on visual responses

We compared the responses of SC neurons in single-stimulus and search tasks and observed a reduction of the initial visual response in search. We reasoned that this reduced response could be due to the presence of additional stimulus elements in search (lateral inhibition) or to a task-related top-down suppression. We explicitly tested for a top-down component and found that a portion of the suppression in visual response could be attributed to this, although the larger portion of the suppression was due to lateral inhibition. This reduced visual response in the SC appears quite similar to that reported by Schall et al. (1995) for FEF neurons in a color-oddity search task. In the SC, Basso and Wurtz (1998) found evidence for a reduction in the visual response of VM burst and VM prelude neurons with increasing numbers of stimulus elements. In addition to this stimulus configuration effect, they found that the initial visual response of VM prelude neurons was modulated by the probability that the target would appear in the neuron’s response field. Everling et al. (1999) also recently showed that the visual activity of SC neurons can be modulated in a top-down fashion by the task instructions in a pro/antisaccade task and found evidence that this top-down signal is present in FEF neurons projecting to the SC (Everling and Munoz 2000).

We observed that some SC neurons show a biphasic pattern of visual activity. The initial burst of activity has a latency of approximately 50–60 ms and corresponds to the conventional initial visual response, while the second phase begins after a latency of about 100 ms and is more variable in strength. We

FIG. 12. A: for VM prelude neurons, discrimination time is plotted as a function of saccade latency for the 3 latency groups. Similar to that shown in Fig. 8A, the data are connected by lines, and the slope of the lines indicates the relationship between discrimination time and saccade latency. Neurons having slopes near 0 discriminate the target at a time unrelated to saccade latency, whereas neurons having slopes near 1 discriminate the target later when saccade latency is longer. B: histogram showing the slopes for each cell, similar to Fig. 8B. There appear to be 2 populations: 1 that discriminates the target at a time independent of saccade latency and a 2nd that discriminates the target later for longer-latency saccades.

FIG. 13. ROC analysis of target discrimination in a movement neuron. Figure conventions are the same as in Fig. 5.
judged this activity to be visual rather than movement-related because it was time-locked to the onset of the visual stimuli and was present (at a reduced magnitude) even when the subsequent saccade was directed away from the neuron’s response field. Basso and Wurtz (1998) also commented on the presence of two phases of visual response in some SC neurons. They found that both the earlier and later bursts were modulated similarly by their experimental manipulation of target probability.

In our task, we found that most VM burst neurons having a second burst of visual activity discriminated the target from the distractors at roughly the same time, regardless of saccade latency and that this time corresponds to the timing of the second burst. This target/distractor discrimination was transient: after the second burst subsided, VM burst neurons typically showed little activity until shortly before saccade onset. We speculate that the excitability of these neurons is modulated by the target selection process in a continuous fashion but that this modulation becomes apparent in the firing of the neurons only during periods in which the neurons are normally active, such as during the second burst. Our presumption is that these neurons are usually held under strong inhibition until saccade onset, rendering them relatively inactive after the end of the visual response and before the onset of the motor burst (as well as during the waiting period in delay tasks), despite the presence of target-selection related modulation.

Timing of target/distractor discrimination

Our study differed from most prior studies of target selection in the SC in that we used a reaction-time search task. We analyzed the time course of target/distractor discrimination using a method developed by Thompson et al. (1996) that allowed us to determine whether discrimination time in various classes of SC neurons was correlated with saccade latency. We reasoned that if a neuron’s discrimination time is linked to saccade latency, it suggests that the neuron’s activity is related to the saccadic command signal to execute the movement. On the other hand, if discrimination time is independent of saccade latency, it suggests that the neuron’s signal is related to the cognitive process of target selection rather than to movement initiation. The relationship between discrimination time and saccade latency provides clues to the functional roles of SC neurons in our target selection task but obviously does not allow these roles to be definitively established. Other forms of evidence have also been used to probe the relationship between neural activity and target selection. For example, a method that correlates putative selection-related activity with the strength of the sensory cues underlying the selection task has provided valuable insight into target-selection related activity in oculomotor areas such as the SC (Horwitz and Newsome 1999, 2001b), FEF (Gold and Shadlen 2000; Sato et al. 2001), area LIP (Shadlen and Newsome 2000), and prefrontal cortex (Kim and Shadlen 1999).

Earlier studies have hypothesized a role for the SC in saccade target selection. Several studies suggested that some superficial SC neurons could be involved in target selection based on the fact that, in a single-stimulus task, these neurons show an enhanced visual response when their receptive field stimulus is used as a saccade goal (Goldberg and Wurtz 1972; Wurtz and Mohler 1976; Wurtz et al. 1980). More recently,
using tasks that employ a waiting period to separate selection-related activity from saccade-related activity, Glimcher and Sparks (1992), Basso and Wurtz (1997, 1998), Horwitz and Newsome (1999, 2001b), and Munoz and Wurtz (1995) have hypothesized that VM prelude neurons are involved in saccade target selection because their activity discriminates the target even before the signal to initiate a saccade. Furthermore, the discharge of VM prelude neurons has been shown to be modulated by other higher-level factors such as target probability (Basso and Wurtz 1998), movement probability (Dorris and Munoz 1998), and task instructions (Everling et al. 1999).

Given these earlier findings, we expected that the discrimination time for VM prelude neurons in our task would not necessarily be related to saccade latency. In accord with this, we found that about half of our VM prelude neurons discriminated the target from the distractors at a time that was unrelated to saccade latency.

A novel finding of our study is that a subset of VM burst neurons, which are silent during delay periods, also discriminated the target from distractors independently of when the saccade was made, suggesting that they, too, are modulated by target selection. Earlier studies did not explicitly consider the possibility that these neurons are involved in target selection for the simple reason that they required the monkey to select the saccade target during a delay period, and VM burst neurons are, by definition, silent during delay periods. One possibility is that these neurons receive excitation or inhibition related to target selection even in delay tasks but that their overall low activity level during enforced delay periods prevents this modulation from becoming apparent.

We were also somewhat surprised by the fact that in about half of our sample of VM prelude neurons, discrimination time was well correlated with saccade latency, suggesting that some VM prelude neurons are more closely tied to movement initiation than to target selection. Indeed, Dorris et al. (1997) and Dorris and Munoz (1998) have shown that VM prelude activity can be related to the readiness to execute a saccade in the gap paradigm. One possibility is that there are two subpopulations of VM prelude neuron: one that is related to target selection and another that is related to movement readiness. The existence of two types of prelude neuron has been demonstrated by Horwitz and Newsome (1999, 2001a,b) in a motion-discrimination task that requires saccade target selection. They found that one type of prelude neuron shows activity that predicts the monkey’s response early in the trial and depends on the difficulty of the target selection task. The other type identified in their task predicts the monkey’s response late in the trial and shows a stronger saccade-related modulation in activity. It is difficult to directly relate our findings to those of Horwitz and Newsome because they characterized their neurons as prelude neurons on the basis of their responses in a saccadic motion-discrimination task, while we characterized our neurons according to their responses in a delayed saccade task. Furthermore, it is likely that the responses of SC neurons are shaped to some extent by the particular task and training regimen used, as has been demonstrated in FEF by Bichot et al. (1996). Nonetheless, in light of the Horwitz and Newsome results, it is interesting to note that our sample of VM prelude neurons seems to segregate into two groups, one of which is more strongly related to saccade execution and the other to target selection.

Comparison with FEF results in search

The presence of a second burst of visual activity in some SC neurons is reminiscent of the finding by Schall et al. (1995) that in a visual search task, some FEF visual neurons show a second burst of activity when the search target is presented in their response fields. This second burst in FEF visual neurons occurs at a similar time to the second burst identified here and is absent when a distractor, rather than the target, is presented in the response field. The main difference between this finding in the FEF and our finding in the SC is that the FEF results were for pure visual neurons, while we found that the second burst was modulated by target selection only in VM neurons. Although many SC visual neurons also expressed a second burst of activity, these neurons did not discriminate the target from the distractors.

In comparing the time course of target selection in SC and FEF, we note that a subset of SC VM burst and VM prelude neurons discriminated the target from the distractor at a time that was independent of saccade latency. The discrimination times in these neurons (see Table 2) generally agree well with the discrimination times reported for FEF VM neurons by Thompson et al. (1996). This suggests that the two structures are in close communication during the target selection process. Indeed, Sommer and Wurtz (1998) identified the FEF neurons that receive information from the SC and found that virtually all of them are visually responsive. Conversely, Sommer and Wurtz (2000, 2001) showed that the SC receives substantial input from FEF neurons carrying visual and delay-period signals as well as input from FEF movement neurons (Segraves and Goldberg 1987). In addition to this direct pathway from FEF to SC, the FEF and other cortical areas could influence SC activity via the substantia nigra pars reticulata (SNr) (e.g., Hikosaka and Wurtz 1983). In fact, Basso and Wurtz (2002) recently reported that SNr neurons are modulated during target selection in a delay task. Thus it seems that there is extensive communication of visual and presaccadic signals between the SC and FEF.

Our results also reveal some differences in the responses of SC and FEF neurons during visual search. Thompson et al. (1996) found that most visually responsive FEF neurons discriminate the target from the distractors at a time that is independent of saccade latency. In contrast, the SC appears to contain a mix of some VM neurons with discrimination times that are independent of saccade latency and others that are strongly linked to movement onset. Another difference is that in the FEF, many visual neurons that lack a movement-related

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J Neurophysiol • VOL. 88 • OCTOBER 2002 • www.jn.org
We thank J. D. Schall for kindly providing the source code for the Poisson spike train analysis. This work was supported by National Eye Institute Grant EY-08060 to E. L. Keller and by fellowship EY-00881 and a Rachael C. Atkinson Fellowship Award to R. M. McPeek.

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