Competition Between Saccade Goals in the Superior Colliculus Produces Saccade Curvature

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McPeek, Robert M., Jae H. Han, and Edward L. Keller. Competition between saccade goals in the superior colliculus produces saccade curvature. J Neurophysiol 89: 2577–2590, 2003. First published January 22, 2003; 10.1152/jn.00657.2002. When saccadic eye movements are made in a search task that requires selecting a target from distractors, the movements show greater curvature in their trajectories than similar saccades made to single stimuli. To test the hypothesis that this increase in curvature arises from competitive interactions between saccade goals occurring near the time of movement onset, we performed single-unit recording and microstimulation experiments in the superior colliculus (SC). We found that saccades that ended near the target but curved toward a distractor were accompanied by increased presaccadic activity of SC neurons coding the distractor site. This increased activity occurred ~30 ms before saccade onset and was abruptly quenched on saccade initiation. The magnitude of increased activity at the distractor site was correlated with the amount of curvature toward the distractor. In contrast, neurons coding the target location did not show any significant difference in discharge for curved versus straight saccades. To determine whether this pattern of SC discharge is causally related to saccade curvature, we performed a second series of experiments using electrical microstimulation. Monkeys made saccades to single visual stimuli presented without distractors, and we stimulated sites in the SC that would have corresponded to distractor sites in the search task. The stimulation was subthreshold for evoking saccades, but when its temporal structure mimicked the activity recorded for curved saccades in search, the subsequent saccades to the visual target showed curvature toward the location coded by the stimulation site. The effect was larger for higher stimulation frequencies and when the stimulation site was in the same colliculus as the representation of the visual target. These results support the hypothesis that the increased saccade curvature observed in search arises from rivalry between target and distractor goals and are consistent with the idea that the SC is involved in the competitive neural interactions underlying saccade target selection.

INTRODUCTION

Natural scenes typically contain a multitude of different objects that could serve as targets for saccadic eye movements. Target selection is thus an important process in the generation of accurate goal-directed saccades. In behavioral studies, it has been found that when there is strong competition between target and distractor saccade goals, the trajectories of saccades to the target may show significant curvature toward the distractor (Findlay and Harris 1984; McPeek and Keller 2001; Minken et al. 1993; Port and Wurtz 2000; Van Gisbergen et al. 1985; Viviani et al. 1977) in contrast to the relatively straight trajectories seen when only a single saccade goal is present (Bahill and Stark 1977; Keller 1980; King et al. 1986; Quaia et al. 2000; Van Gisbergen et al. 1985; Viviani et al. 1977). This curvature suggests that in some circumstances, execution of a movement may begin before selection of a single saccade goal is finalized. Specifically, in a visual search task, McPeek and Keller (2000, 2001) hypothesized that ongoing competition between saccade goals in visuo-motor structures such as the superior colliculus (SC) or frontal eye field (FEF) results in saccade curvature due to the presence of simultaneously active, but spatially separated, populations of neurons corresponding to different candidate saccade goals in these topographically organized motor maps. In a double-step task, Port and Wurtz (2000, 2001) similarly hypothesized that the highly curved and averaging saccades that they observed resulted from temporally overlapping bursts of activity at two sites within the SC.

In the present study, we used two different methods to assess the validity of the hypothesis that competition between saccade goals gives rise to curved saccades. First, we recorded from neurons in the SC while monkeys performed a visual search task in which they were rewarded for making a saccade to an odd-colored target presented simultaneously with distractors. In most trials, the monkeys made a single saccade with a rather straight trajectory to the location of the target. However, in some trials, they executed curved saccades (McPeek and Keller 2001). These saccades were initially directed between the target and a distractor but underwent a smooth change in direction during the movement and ended near the location of the target. In the present paper, we show that such curved saccades are associated with increased presaccadic activity in the SC at the site coding the distractor toward which the saccade curved. Near the time of saccade initiation, this activity at the distractor location is rapidly suppressed. In contrast, neurons at the target site show a stereotypical high-frequency burst of activity for saccades to the target, regardless of whether the movements have curved or straight trajectories. These results support the idea that trajectory curvature is produced by temporally overlapping presaccadic activity at two sites in the SC.

To test this hypothesis directly by establishing a causal link between competing activity at two SC sites and saccade curvature, we performed a second experiment in which we used...
electrical microstimulation of the SC to induce curvature in saccades made to single visual stimuli. Specifically, during the reaction time before a saccade was made to a single visual stimulus, we delivered a train of electrical pulses at a SC site that would have coded a distractor in the search paradigm. We shaped the temporal envelope of the stimulus train so that it closely resembled the activity profile recorded in the SC at distractor sites during curved saccades in search. The stimulation trains were subthreshold for evoking movements, but we found that optimally configured presaccadic trains, delivered to sites in the SC that were not at the location activated by the visual stimulus, produced highly curved saccades. These latter results provide additional support for the hypothesis that competing activity at separate sites in the SC can produce saccadic curvature.

The data presented here have appeared previously in preliminary form (McPeek and Keller 2000).

METHODS

Four male rhesus monkeys (Macaca mulatta) weighing between 4 and 7 kg were used in this study. Monkeys H, G, and M participated in the recording experiments and monkeys G, M, and F participated in the stimulation experiments. 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.

A detailed description of the general methods and behavioral tasks has been published recently (McPeek and Keller 2002a). Briefly, a scleral coil (Fuchs and Robinson 1966; Judge et al. 1980) and a head-holder system were implanted under isofluorane anesthesia and aseptic surgical conditions. After training in behavioral tasks (described in the following text), a second surgery was performed to position a stainless steel recording chamber (15 mm ID), tilted 38° posterior from vertical, above a craniotomy centered on the midline. Antibiotics (Cefazolin sodium) and analgesics (Buprenorphine hydrochloride) were administered as needed during the recovery period under the direction of a veterinarian.

Testing was performed in a dimly illuminated room. 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 access to water on weekends.

Single-unit recording

We used standard methods to record single neurons in the deeper layers of the SC. Neural activity was recorded using tungsten microelectrodes with impedances ranging from 0.8 to 2.5 MΩ at 1 kHz, advanced by a hydraulic microdrive. Action potentials were identified using a time-amplitude window discriminator. The computer data acquisition system recorded the occurrence of spikes and sampled eye position and velocity with a resolution of 1 kHz.

Delayed-saccade paradigm

At the beginning of each trial, a white fixation spot subtending 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/m. 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 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/m², respectively. The size of the target was M-scaled to keep its salience constant across different eccentricities (Rovamo and Virsu 1979). At an eccentricity of 15°, the target subtended 2° of visual angle.

Single-target paradigm

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 (RF) as determined in a preliminary on-line analysis using single stimuli. Two of the monkeys were given a liquid reward for bringing their eyes to the location of the target within 70–275 ms of the onset of the stimuli. The third monkey tended to have longer saccade latencies and consequently was allowed 70–300 ms to reach the target.

Search paradigm

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, at equal eccentricity from fixation, separated by angles of 90° (see Fig. 1, top). The distractors were identical to each other and differed from the target only by virtue of the target’s odd color. In each trial, the colors of the target and distractors were randomly chosen.

The data were separated into four types of response, illustrated in Fig. 1: into field (the target appeared in the response field of the neuron); ipsi location (the target appeared at the array location separated 90° in direction from the center of the response field and in same visual field as the response field of the neuron); contra location (the target appeared at the array location separated 90° in direction from the center of the response field and in the opposite visual field from the response field of the neuron); and opposite location (the target appeared at the array location that was diametrically opposite in direction to the response field).

Stimulation paradigm

In this paradigm, a microelectrode was lowered into the deeper layers of the SC as determined by monitoring multi-unit activity. The evoked saccade vector for the site was then determined by delivering a short pulse train of high-frequency (400 Hz), biphasic (0.25 ms for each phase) electrical stimulation through the electrode. Current was initially set at the minimum level that would evoke a saccade in every trial. We increased the duration of the stimulation pulse train until the maximal site-specific fixed vector saccade (FVS) was obtained (Stanford et al. 1996).

In the experimental trials, the monkeys performed a simple single-target visually guided saccade paradigm. At the beginning of each trial, the white fixation spot appeared in the central position. 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
Competing Saccade Goals

This interval, the fixation point was turned off, and a single target stimulus appeared at one of two peripheral locations. Monkeys were rewarded for making a saccade to the peripheral stimulus within 70–400 ms. The two possible locations for target appearance were at the same eccentricity as the amplitude of the FVS and at directions 90° displaced from the FVS (ipsi and contra locations; see Fig. 1, bottom). In 50% of trials (randomly selected), we delivered a sub-threshold pulse train of electrical stimuli through the microelectrode. The onset of the stimulation occurred a short interval after target appearance (30–80 ms). The frequency of pulses in the stimulation train began at 10 Hz and increased linearly over a period of 125 ms to a maximum frequency of either 200 or 250 Hz. The train was terminated either by saccade onset or after 125 ms, when it had reached its preset maximum frequency. Current was adjusted to produce smoothly curved saccade trajectories that terminated near the visual target and was always less than or equal to the threshold current value required to evoke the FVS using high-frequency (400 Hz) stimulation. We verified that the stimulation parameters were sub-threshold for evoking saccades by repeatedly stimulating at the maximum train frequency (200 or 250 Hz) for a duration of 125 ms and observing an absence of evoked movements in every instance. We separately analyzed saccades made with and without stimulation.

Data analysis

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. The monkeys performed the search task correctly in 74% of trials, well above chance-level performance (25%) and comparable to human performance in a similar task (McPeek et al. 1999). In a previous report based on different data from those analyzed here, we examined the behavioral characteristics of correct and erroneous saccades in the search task (McPeek and Keller 2001). In this study, erroneous saccades were excluded from analysis as were saccades that were directed toward the correct target but were inaccurate. Inaccurate saccades were defined as those landing outside a circular region centered on the target stimulus with a radius equal to the greater of 2° or 15% of the mean saccade amplitude, where mean saccade amplitude was computed separately for each cell and each stimulus location. As a result of this criterion, we eliminated 229 saccades (~3%) of a total of 7,335 movements directed toward the correct target location. Saccades that were eliminated included hypometric and averaging saccades that landed in between stimulus locations (see McPeek and Keller 2001 for examples of such movements in a similar search task). In the stimulation paradigm, we intentionally adjusted the current level to produce smoothly curved saccades that landed near the visual target. In our analysis of the eye movements in this task, we applied the same accuracy criterion used in the search task. This resulted in the elimination of ~5% of stimulated responses (56 of a total of 1,175) across the 22 stimulation sites.

We calculated the mean curvature of all accurate saccades made to a given stimulus location using a curvature metric described by Smit and Van Gisbergen (1990). In analyses comparing neural discharge for curved and straight saccades (Figs. 2–4), curved saccades were defined as those with curvature values outside a range 0.75 SD from the mean curvature value computed. The mean curvature value was determined using accurate saccades made in the search task and was separately calculated for each of the four stimulus locations used with each neuron.

Measurement of firing rates

We calculated discharge rates by counting spike occurrences during a time-window that began 30 ms before saccade onset and ended with the start of the saccade. The number of spikes in each such presaccadic interval was divided by the duration of the time window. We chose this particular time window because SC movement-related activity typically precedes the onset of the movement (Munoz and Wurtz 1995; Sparks 1978). In the summary analyses comparing neural discharge for curved and straight saccades, significance tests were performed using the Wilcoxon rank-sum test. Unless otherwise noted, significance was defined as a criterion level of \( P < 0.05 \).

Characterization of neurons

We used the delayed-saccade task to characterize each neuron according to the presence or absence of visual, delay-period, and movement-related activity. We analyzed only those cells with movement-related activity, as determined by the presence of a significant \( P < 0.05 \) in the Wilcoxon signed-rank test) increase in firing rate averaged over a period from 25 ms before saccade onset to the end of the saccade, compared with mean activity during the delay period (150–50 ms before the signal to execute the saccade). We measured the presence or absence of delay-period activity in each SC neuron by comparing neural activity during the 100-ms delay-period epoch.
described in the preceding text 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 ($P < 0.05$) during the delay-period epoch than during the baseline epoch were classified as having delay-period activity. These neurons will be referred to as prelude neurons (Glimcher and Sparks 1992) and likely correspond to the build-up neurons described by Munoz and Wurtz (1995). Movement-related cells lacking prelude activity will be called burst neurons (Munoz and Wurtz 1995). All of the neurons included in this report showed visual responses to stimuli in their response fields. Although movement-related neurons lacking visual responses are also found in the SC, we encountered such cells relatively infrequently and, hence, did not include them in the analysis.

**Determination of saccade curvature and “corrected curvature”**

We defined the curvature of saccades as the maximum deviation from a straight-line trajectory divided by the amplitude of the movement (Smit and Van Gisbergen 1990). Because saccades made to different parts of the visual field by different individual animals can have idiosyncratic natural curvature values, we also computed a “corrected curvature” measure that allowed us to collapse the curvature data across different target positions and different monkeys. To compute corrected curvature, we first converted the curvature measures for each target location in each animal into deviation scores. Specifically, for each cell or stimulation site, we computed the mean curvature for saccades made to each target location in the single-stimulus task. We took these means as the natural curvature values for saccades made to those locations. Because we are interested in deviations from the baseline natural curvature, we subtracted these means from each individual curvature value for saccades made to the same location by the same animal in the search or stimulation paradigms. Finally, we adjusted the sign of curvature so that saccades that curved toward the response field of the cell being recorded (or toward the FVS of the stimulation site) had positive values of curvature and saccades that curved away from the response field (or FVS) had negative curvature values. In the analyses that follow, we call this new curvature measure “corrected curvature,” to distinguish it from the raw curvature values.

**RESULTS**

**Neural recordings in the SC**

**Occurrence of trajectory curvature during the search task.** Previously, we reported that the trajectories of saccades made in search tend to show greater curvature than those made to single visual stimuli appearing at the same locations in visual space (McPeek and Keller 2001). In the present study, we found that the mean value of unsigned curvature for all saccades made in our search task was 0.052, while the mean unsigned curvature measured when saccades were made to single targets appearing at the same locations was 0.035. Curved and straight saccades did not appear to form two distinct populations of response: for any particular target location in the search task, saccades showed a continuum of curvature values. We also did not find any systematic difference in the distribution of the curvature metric for saccades made to targets located in the cardinal or oblique directions.

**Differences in SC neural response for curved versus straight saccades.** Here we report on the activity of 24 burst cells and 39 prelude cells in the deeper layers of the SC during the visual search paradigm. During delay periods, burst and prelude neurons show quite different patterns of activity; but both types of SC neurons produce a saccade-related burst of activity beginning shortly before movement onset. In our analysis of the SC activity associated with curvature, we found that the critical determinant of saccade curvature was SC activity in the period immediately preceding the onset of the saccade. Because we found similar presaccadic modulation of activity associated with curvature in both burst and prelude neurons, we combined the two groups in the analyses that follow.

We examined the discharge of each cell for curved and straight saccades for each target location. We only included the analysis of a particular direction for each cell if there were at least two curved saccades in the set of movements for that direction. Typically the number of curved movements included in each of the four directional sets of data was 6 and the number of straight movements was usually ≥20. Representative results for one cell recorded in the right SC are shown in Fig. 2. The center of this cell’s response field was located down and to the left at an eccentricity of 20°. Figure 2, left, shows the neuron’s activity for saccades made into the response field.
saccades, the cell’s presaccadic discharge began to decline approximately 50 ms before saccade onset and was near zero by movement onset. However, when saccades were curved toward the optimal movement field, the activity increased sharply beginning 30 ms before saccade onset before declining rapidly near saccade onset. The difference in discharge during the 30-ms presaccadic interval for this cell was significant (P < 0.05). Much of the earlier presaccadic discharge in Fig. 2 results from the unaligned visual responses of the cell. We have previously reported on the visual responses of SC neurons in the color oddity search paradigm (McPeek and Keller 2002a), and all of the neurons described in the present report showed visual as well as motor responses, as determined in the single-target, delayed saccade paradigm.

Figure 3 compares the discharge for straight and curved saccades across the population of neurons included in this report. The mean spike density aligned on saccade onset for straight and curved saccades was computed for each cell. The schematic diagrams (right) show the response types included in each spike density plot. The actual centers of the response fields of the recorded neurons were located in various different regions of the visual field, spanning amplitudes of 6–30° in a range of different directions. In Fig. 3, left, the mean spike density over all the cells for straight saccades is shown (- - -) as is the mean for saccades curved toward the response field (—). The spike densities for the individual trials were first normalized by the maximum discharge rate for each cell in the 30-ms presaccadic interval for straight saccades made to the RF. The normalized traces for each cell and condition were then averaged to yield a population mean for each type of trajectory over all the cells.

As shown in Fig. 3A, the mean normalized population activities for curved (—) and straight trajectories ( - - -) are almost identical for the presaccadic time period and during the saccade, for movements made to the into field location. In the 30-ms presaccadic time window (□), there was no significant difference in activity for curved versus straight movements (P = 0.37).

If curved saccades arise from competition between the saccade goal and a distractor, we expect neurons coding distractor stimuli to show higher discharge rates when saccades made to the ipsi or contra locations curve toward the cell’s response field than when they are relatively straight. Figure 3B shows that, for saccades made to the ipsi location, the population discharge for saccades curved toward the response field is, indeed, higher in the presaccadic time window, and this difference is significant (P < 0.05). When saccades were made to the contra target location (Fig. 3C), the presaccadic population discharge also appears higher for saccades curved toward the response field, but this difference did not quite reach significance (P = 0.065).

To examine the possibility that SC activity is higher at all distractor locations during curved saccades, we also plotted results comparing discharge for curved and straight saccades to the opposite location (Fig. 3D). We found no significant difference (P = 0.63), indicating that the increase in activity for

**Fig. 3.** Comparisons of averaged population discharge for curved and straight saccades. In each temporal plot, - - -, the normalized population mean spike density for straight saccades; ——, the same for curved saccades. All responses are aligned on saccade onset (time = 0), □, the time interval that was used for quantitative analyses of the difference in discharge for straight and curved saccades. Right: schematic representations of the target (○) and distractor (●) locations. A: the target appeared in the response field (RF) and saccades with curvature in either direction were included in the computation of mean discharge for curved saccades. B: the target appeared at the ipsi location (in the same visual hemifield as the RF) and discharge for straight saccades was compared with discharge for saccades curved toward the RF. C: the target appeared at the contra location (neighboring location in the opposite hemifield). Again, discharge for straight saccades is compared with discharge for saccades curved toward the RF. D: the target appeared in the Opposite location, and discharge for saccades with curvature in either direction was compared with discharge for straight saccades.
curved saccades is spatially restricted as expected if curvature results from competition between neighboring goals.

As described in METHODS, we excluded inaccurate saccades from analysis. As a further check to verify that the differences in neural discharge seen for curved and straight saccades to the ipsi and contra locations are not due to differences in the endpoints of the movements, we compared the mean landing positions of straight and curved saccades. Specifically, we computed the radial differences in saccade end point for curved and straight saccades for each target position in each of the 63 cells. The differences were small (maximum difference for any cell = 1.95°, mean difference over all cells = 0.53°), indicating that the saccades differed primarily in the trajectory they used to reach similar end points.

Figure 4 shows scatter plots that compare the discharge of the individual cells for straight and curved saccades. For each neuron, we computed the mean discharge rate in the 30-ms presaccadic period for curved saccades and plot this rate against the neuron’s mean discharge in the same interval for straight saccades. Figure 4A compares these rates for saccades made into the cell’s RF. Saccades curved in either direction were included. Sufficient numbers of curved saccades were found so that all 63 cells could be included in this analysis. Across the population of cells there was no significant difference in presaccadic discharge between straight and curved saccades (P = 0.42).

Figure 4B makes a similar comparison for saccades made to the target when it was presented at the ipsi location. In this analysis, we only included curved saccades that initially deviated in the direction of the response field, and we had sufficient data to examine 60 cells. In contrast to the situation found for saccades directed into the RF, when saccades were directed to the ipsi location, the presaccadic discharge for most cells for curved saccades was higher than that associated with straight saccades, and overall, the increase is significant (P < 0.05).

Figure 4C shows a similar plot for saccades made to the contra location. Again only saccades initially deviated in the direction of the RF were included, resulting in sufficient data to analyze 54 cells. Although most cells (41/54) showed a higher discharge when the initial movement was curved toward their RF, the overall difference for the population was not quite significant (P = 0.079). This lack of significance for the contra location may be due to limited statistical power because of the relatively small number of curved saccades observed for some of the cells.

We also compared the discharge of cells for curved and straight saccades made to the Opposite location. If curvature results from competition between neighboring saccade goals, then we would not expect to find any difference in discharge for curved versus straight saccades made to the opposite stimulus location. As predicted, we found no significant difference across our population of cells (P = 0.63; n = 62) for the opposite location.

IS THE AMOUNT OF SACCADE CURVATURE RELATED TO SACCADE LATENCY? We observed a great deal of trial-to-trial variability in the magnitude of saccade curvature produced even when data were considered for a single target position in one animal. One possible contributing factor could have been saccade latency. It has been reported that the latency of saccades in the color oddity search task is longer, on average, than the latency of saccades made to the appearance of single visual targets (McPeek and Keller 2001; Schiller et al. 1987). It is possible that the saccades made with the shortest latency in search, when the target direction had less time to be resolved, have the most curvature. We tested this idea by combining the data for all three monkeys included in the recording experiment and computing the correlation of the “corrected curvature” measure (see METHODS) with saccade latency. The correlation explained little of the variance (r² = 0.006, Pearson product moment correlation), but there was a significant trend (P = 0.04) toward greater curvature with shorter latencies.

IS THE AMOUNT OF CURVATURE RELATED TO PRESACCADE DISCHARGE RATE AT NEIGHBORING SITES? If saccade curvature is caused by competition between neurons coding the target...
and a distractor, it might be expected that a greater amount of curvature would be accompanied by more intense activity at the distractor site toward which the saccade is curved. We were unable to test this prediction on a neuron-by-neuron basis because of the limited number of saccades curved toward each cell’s RF for each neighboring target location. However, pooling the data across neurons allowed us to investigate the relationship between the amount of curvature and the change in firing rate of neurons coding distractor locations.

To collapse the data across cells, we used the corrected curvature measure to eliminate the influence of natural varia-
tions in curvature for saccades to different parts of the visual field. We computed each cell’s mean firing rate during the 30-ms presaccadic period for accurate, straight (see METHODS) saccades made to the ipsi and contra locations. We took these values as the baseline presaccadic firing rate of each cell for straight saccades made to the ipsi and contra locations. This allowed us to examine the extent to which deviations from the natural curvature of saccades made to these locations are correlated with changes in the presaccadic firing rate from the cell’s mean rate for straight saccades to the same locations. To pool across cells with different maximum firing rates, we normalized the change in presaccadic firing rate observed for each curved saccade by dividing it by the mean presaccadic discharge rate of the same cell for accurate, straight saccades made to the into field location. This normalization gave equal weight to each cell by preventing cells with a higher maximal discharge rate from dominating the analysis.

In Fig. 5, we plot normalized change in discharge rate against corrected curvature. The data were binned by corrected curvature value and the horizontal error bars show the width of each bin. The right side of the graph shows that as curvature toward the cells’ RFs increases, SC activity at the distractor site increases sharply over its baseline rate for straight saccades made to the same location. Interestingly, the left side of the graph shows a smaller tendency toward a decrease in activity for saccades curved away from the cells’ RFs. Overall, the data pooled across neurons supports the idea that more intense competition—manifested by greater presaccadic activity at a distractor site—is correlated with greater curvature toward the distractor.

Presaccadic electrical stimulation in the SC

CURVATURE PRODUCED BY SC STIMULATION. In the neural recording experiments, we found that curved movement trajectories in the search task are correlated with greater than normal discharge, occurring just before saccade onset, at a competing SC site that is not normally associated with the vector of the saccade to be executed. To establish whether this competing SC activity actually causes the observed saccade curvature, we used electrical microstimulation to experimentally induce competing SC activity similar to that observed in the search task.

After an initial fixation period, we presented a single eccentric visual target (Fig. 1, bottom), and the animal was rewarded for executing a saccade to the target. A previous study has shown that during the latent period of saccades, an extended region of the SC becomes active, centered on the site representing the location of the visual target (Anderson et al. 1998). In randomly selected trials, prior to saccade onset, we delivered a pulse train with an accelerating frequency profile at a site in the SC that was not normally active for saccades to the target. This stimulation train was terminated when the onset of a saccade was detected. The stimulus profile was tailored to resemble the neural activity recorded at competing, neighboring sites in the SC (see Fig. 3, B and C) for curved saccades in the search task: neural activity started before saccade onset and increased in frequency (but remained well below the level of activity seen at the site coding the saccade vector), before declining rapidly near saccade onset. We applied this stimulation paradigm at 22 separate sites in the SC of three monkeys.

Figure 6 illustrates the procedure with results obtained at an example site in the right SC. After the microelectrode was determined to be in the deeper layers of the SC (see METHODS), we ascertained the FVS for the site by delivering a high-frequency train of stimuli (400 Hz), which evoked a consistent saccade up and slightly to the left (Fig. 6A). The current threshold at this site was 20 μA, and a train duration of 70 ms produced the site-specific maximum amplitude saccade (Stanford et al. 1996). Stimulation with a lower frequency stimulus train (250 Hz) and a current of 12 μA was subthreshold for evoking any movement at this SC site (Fig. 6B). We then conducted a block of trials in which a single visual target appeared in one of two positions (Fig. 6C). The target positions were at the same amplitude as the FVS, but each was offset in direction by 90° from the FVS. Thus these visual stimuli were located at the ipsi and contra locations with respect to the
response field in the search task (see Fig. 1). In about one-half of the trials, selected at random, we delivered an accelerating pulse train after a short delay from the appearance of the target. Trials with and without stimulation were sorted into separate sets, and the results are shown in the spatial plots in Fig. 6C for stimulated trials and D for trials without stimulation. When the saccadic trajectories in Fig. 6, C and D, are compared, it is clear that saccades produced in stimulated trials often had much greater curvature than those in trials without stimulation. This effect was more pronounced in trials in which the visual target was presented at the ipsi location (in the same visual hemifield as the end point of the FVS). Note that in this condition the site of neural activity related to the visually guided saccade.

The electrical stimulation was always terminated 125 ms after its initiation [when the instantaneous pulse frequency reached 200 Hz (or 250 Hz for some sites)] or when the visually guided saccade began, whichever event occurred first. Because we were not able to predict exactly when the saccade would start, this paradigm led to a variety of different final stimulating frequencies (when the stimulation was terminated by saccade onset) as well as different termination times before saccade onset. We hypothesized that the wide variety of curvature values seen in our results (Fig. 6C) was related to these two stimulus variables. We test this idea in the following sections.

EFFECT OF DEAD TIME. For each stimulation trial, we measured the time between the final stimulus pulse and the onset of the saccade, which we label “dead time.” Figure 7 shows the effects of dead time on saccade curvature for a representative stimulation site in the right SC. The FVS evoked by high-frequency stimulation at this site is shown by the dashed arrow. Movements produced in our subthreshold stimulation paradigm are shown as solid lines. We sorted these trials according to dead time and found that when dead time is greater than ~20 ms (Fig. 7A), saccades show much less curvature than when dead time is <20 ms (Fig. 7B). Indeed, when dead time is long, the saccadic trajectories are not noticeably more curved than in trials in which no stimulation occurred (compare trajectories in Fig. 7, A and C). We conclude that the continuation of stimulation until close to the time of saccade onset is necessary for stimulation-driven activity in the SC to affect the trajectory of the upcoming saccade.

Figure 8 shows the relationship between corrected curvature (see METHODS) and dead time for the range of dead times produced in our paradigm. Data from all 22 stimulation sites are combined in this figure. The real-time controller that terminated the stimulation train near saccade onset employed a saccade detection algorithm that was able to detect the onset of saccades, on average, 4 ms after the actual time of saccade onset as determined by our off-line analysis method. Thus it was possible for one or two stimulus pulses to occur after the actual time of saccade onset in some trials. We assigned such trials negative values of dead time (plotted at the right edge of Fig. 8), whereas trials in which the stimulus train stopped before saccade onset are assigned positive dead-time values. Figure 8 shows that it was necessary for the stimulus train to continue to within ~20 ms of saccade onset to produce greater curvature than seen in control trials without stimulation. In trials in which the stimulation was terminated earlier relative to saccade onset (due to the stimulus frequency reaching its preset maximum value), curvature was similar to that observed in unstimulated trials. This result indicates that simply reaching a stimulation frequency of 200–250 Hz at a neighboring site in the SC is not sufficient to produce curvature. Rather it seems that stimulation must occur within ~20 ms of saccade onset.
EFFECT OF MEAN FINAL FREQUENCY. In the previous section, we established that saccade curvature in our paradigm depends on stimulation within a temporal window shortly before saccade onset. However, even when only trials with brief dead times are considered, there is still considerable variability in the amount of curvature produced by stimulation (Figs. 7B and 8, oblong cloud of points near 0 dead time). To explain this variance, we examined the relationship between the frequency of stimulation in the immediate presaccadic period and the amount of curvature in the subsequent saccade. In this analysis, we measured the mean frequency of the stimulation train in the 30-ms interval just before saccade onset (Fig. 9A), just as we did in the previously described single-unit analysis, by counting the number of stimulus pulses delivered during the presaccadic time window and calculating the final presaccadic stimulation frequency. In Fig. 9B, we show, for a typical site, the curvature produced in saccades to the ipsi and contra locations for five different mean presaccadic stimulating frequencies. Controls with no stimulation are also shown for comparison.

Figure 9C shows summary results for this site across all presaccadic frequencies. Corrected curvature is plotted against mean presaccadic stimulation rate for movements made to the ipsi (left) or contra (right) target location. At this particular site, no noticeable curvature was produced by mean presaccadic stimulation frequencies of \( \leq 150 \) Hz, but saccade curvature increased very rapidly as the mean frequency increased beyond this level. In addition, the values of curvature produced for saccades to the contra target were smaller than those for saccades to the ipsi target. For unstimulated controls, mean curvature \( \pm SD \) is plotted at the left edge of the graph. If we increased the maximum frequency beyond the range of 200–250 Hz or increased the stimulating current, we began to produce saccades that stopped in place and then resumed to land on the target or the endpoint of the FVS, depending on the stimulation levels. These interrupted saccades more closely resemble redirected saccades (Schlag and Schlag-Rey 1990) and were not studied.

Summary plots across all 22 stimulation sites relating corrected curvature toward the FVS and presaccadic stimulation frequency are shown in Fig. 10, left. In general, stimulation was more effective in producing curvature in saccades to ipsi target locations than to contra locations. For both target locations, increasing the stimulation frequency produced greater curvature in the direction of the FVS. In Fig. 10, right, we plot comparable results for neural activity recorded in the SC pooled across neurons. In these plots, we grouped trials according to the presaccadic discharge rate of the neuron in the trial. For each recorded discharge rate, we plotted the mean corrected curvature of saccades made in trials having that rate across all neurons. The pattern of results in the recording data is similar to that seen for stimulation in that it shows a consistent increase in curvature toward the cell’s movement field with increasing discharge rate. However, curvature in the stimulation data increases more steeply than in the recording data. We speculate that this difference is due to the fact that stimulation presumably causes a large proportion of cells near the stimulation site to fire consistently and in synchrony. Another apparent difference between the stimulation and recording data is that the greater curvature for the ipsi location over the contra location, which is seen at a variety of different stimulation

![Graph](http://jn.physiology.org/doi/10.1152/jn.00060.2003)
frequencies, is apparent in the recording data only at high discharge rates. Nonetheless, given the fact that the recording results are based on pooled data from many neurons, the correspondence between the stimulation and recording results is quite good, suggesting that our stimulation paradigm captures the essential features of competition between saccadic goals that leads to curved saccades.

EFFECT OF DIRECTIONAL DIFFERENCES IN THE FIXED VECTOR AND VISUALLY GUIDED SACCADE. At a majority of the stimulation sites, we used two visual target locations (both orthogonal to the direction of the FVS). This restricted selection raises the question of whether saccades made to other locations would be similarly affected by our stimulation train. At three sites, we examined the effect of subthreshold presaccadic stimulation when visual targets were presented at other angles with respect to the FVS. These other directions included 45° from the FVS, in the same direction as the FVS, and in the direction opposite the FVS. Similar curvatures to those produced for orthogonal directions were produced for target locations at 45°. The amount of curvature observed was greater for comparable stimulus parameters when the visual target was located ipsilateral to the end point of the FVS (i.e., when the visual target was represented in the same colliculus as the stimulation site). Visual targets in the same or directly opposite direction to the FVS did not produce curvature. We believe the mechanism that produces curved saccade trajectories is operable over a broad range of directions, but confirmation of this conjecture requires additional experimental verification.

DISCUSSION

Curved saccade trajectories and target/distractor competition

Curved saccades have been observed in a variety of tasks in which competing saccade targets are present, including double-step tasks (Findlay and Harris 1984; Minken et al. 1993; Van Gisbergen et al. 1987) and visual search tasks (McPeek and Keller 2001). It has been hypothesized that curved saccades are the result of competition between saccade goals in visuo-motor structures such as the SC (McPeek and Keller 2000, 2001; Port and Wurtz 2000, 2001). In the present study, we directly tested this hypothesis by recording the activity of SC neurons at distractor locations during a search task. We found that curvature of the movement trajectory toward a distractor was associated with increased activity at that distractor location. This
increased activity, which was absent for straight-trajectory saccades toward the target, occurred immediately before saccade onset and was abruptly curtailed as the movement began. Furthermore, a greater degree of elevated discharge at the distractor site was associated with greater curvature toward the distractor. This suggests that curvature results from an initial competition between two salient saccade goals that is resolved near the time of saccade onset. Due to delays between the time of SC discharge and its effect on eye movement production, this activity immediately preceding the saccade perturbs the initial part of the movement’s trajectory.

To establish whether this observed pattern of SC activity actually causes curvature, we used subthreshold electrical microstimulation to experimentally produce competing activity in the SC immediately before saccades to single visual targets. We tailored the stimulus pulse train to resemble the pattern of activity recorded from cells at distractor sites when curved saccades occurred. We found that our stimulation paradigm was highly effective in producing saccades that curved toward the location coded by the stimulation site, indicating that the pattern of SC activity recorded in the search task is causally related to saccade curvature. We did not test other patterns of stimulation to determine whether our particular pattern is uniquely effective in producing curved movements.

The results support our hypothesis that saccade curvature in search arises from competition between the target and a distractor goal that is resolved near the time of saccade onset. We speculate that as a result of this competition, the initial movement vector is directed between the target and the competing distractor, similar to what is seen with averaging movements that result from SC activity at two distinct loci (Edelman and Keller 1998; Robinson 1972; Schiller and Sandell 1983; Schiller et al. 1979; Sparks and Mays 1983). The difference between curved and averaging saccades seems to be that for curved saccades, the competition is quickly resolved near the time of saccade onset. As a result, the initial averaging movement is corrected in-flight and the movement ends near the target. This scenario is illustrated in Fig. 11. When straight saccades are made to the target (illustrated by the dashed trajectory in the visual field schematic on the left), a population of neurons centered at the image of the target in the SC (region T) is activated. For the population of neurons that we recorded (including both prelude and burst neurons), this target-related activity peaks just after saccade onset (Fig. 3A). Neurons located at the SC image of the ipsilateral flanking distractor (region Dipsi) are almost silent by saccade initiation (Fig. 3B). In contrast, when saccades with curvature toward Dipsi are made (the solid trajectory shown on the left in Fig. 11), the activity at the ipsilateral flanking distractor site is significantly higher in the immediate presaccadic interval, leading to an initial deviation of the saccade trajectory toward Dipsi.

Port and Wurtz (2000) have reported preliminary results in which they recorded simultaneously from two microelectrodes located at sites that would be roughly equivalent to T and Dipsi in the schematic shown in Fig. 11, during curved saccades produced in a double-step paradigm. Their curved saccades are initially directed toward one target but then curve away from that target and end near the other target. The initial curvature is accompanied by temporally overlapping activity at the two SC sites, with the site that codes the initial target peaking before the activity at the second site. If we assume that our ipsilateral distractor site corresponds to their initial target site, then our observation of presaccadic activity at this site followed by a peak of activity at the target site slightly after saccade onset is similar to their simultaneously-recorded temporal differences.

**Correction of the initial direction error in curved saccades**

We found that the SC population activity near T in the SC for curved saccades is virtually the same as that observed for straight movements. This suggests that SC discharge at site T does not reflect the perturbation in saccade trajectory that actually occurs. Near the end of the saccade, the movement vector is in an almost straight upward direction, and this...
terminal movement vector is not represented by the activity centered at either SC location, T or D_ipsi. This terminal portion of the movement could be explained by two alternative mechanisms. If the colliculus encodes movement trajectory, the final movement vector would be produced by the appearance of activity at the medial edges of both colliculi, which together code upward-directed movement vectors. The field shaded gray in Fig. 11 for curved saccades indicates this latter locus in the ipsilateral SC only. The mechanism responsible for this shift in the locus of SC activity could be similar to the remapping process described by Walker et al. (1995).

Alternatively, if the SC encodes the final goal of the movement but not its trajectory, one would expect the activity at T to remain as the activity at D_ipsi disappeared. Neural structures below the level of the SC (e.g., Quaia et al. 1999) would then be responsible for producing the final curvature to compensate for the initial misdirection of the saccade, allowing the eye to land near the goal (specified by T).

Port and Wurtz (2001) have produced preliminary evidence that collicular neurons recorded in areas that would be equivalent to the gray shaded field in Fig. 11 do not become active during the terminal phase of such curved saccades. These results favor the idea that the SC does not directly control saccade trajectory, at least in the latter portion of curved saccades. This interpretation is consistent with results from the colliding-saccade paradigm (Schlag-Rey et al. 1989) and is also compatible with a study of blink-perturbed saccades to a visual target (Goossens and Van Opstal 2000), which found that activity continues at the site in the SC corresponding to the original, retinotopically coded displacement vector even as the saccade trajectory initially veers away from the target and then curves back to end near it. However, the investigators in this latter experiment did not attempt to record at regions in the SC that could code the direction of the terminal trajectory vector.

**Electrical stimulation in the SC and curved saccade trajectories**

Although our recording study, as well as the results of Port and Wurtz (2000), demonstrates a neural correlate of curved saccades in the SC, such evidence alone cannot establish whether a given pattern of SC activity actually produces curvature. To verify that this SC activity is causally related to saccade curvature, we used subthreshold electrical stimulation, delivered during the late period of saccades to single visual targets, to mimic the competitive activity observed at distractor sites during curved saccades in the search task. The stimulation trains increased in frequency up to 200 or 250 Hz and terminated near the time of saccade onset. This frequency (200–250 Hz) was similar to the presaccadic activity level that we recorded from single neurons at ipsilateral distractor sites in the SC for the most highly curved saccades observed in search (compare results shown in Fig. 10).

The stimulation paradigm had an additional advantage: a problem with both the double-step task (Port and Wurtz 2000) and our search task is that highly curved saccades occur only infrequently. Thus it is difficult to obtain enough data from individual neurons to test for subtle changes in the spatiotemporal patterns of activity during these curved movements. Our stimulation experiments allowed us to overcome this limitation to some extent by using electrical stimulation in the SC to substitute for the activity that occurs at distractor sites for curved saccades in search. In this way, the timing, location, and intensity of the competing activity can be easily manipulated across repeated trials.

In the present experiments, we typically placed the stimulating electrode in the SC at sites that would be equivalent to D_ipsi and D_contra, as shown in Fig. 11. We found that stimulation produced consistently larger values of curvature when it occurred in the colliculus that was activated by the visual target (ipsi site). However, we did not observe such a clear difference between ipsi and contra activity for curved saccades in our recording experiments (e.g., Fig. 10). Thus it is possible that this ipsi/contra asymmetry is specific to the stimulation paradigm and would not be seen with visual distractors.

Even though we produced a greater proportion of curved saccades in the stimulation paradigm than we observed in search, there was still considerable variability in the amount of curvature, and some relatively straight saccades occurred in the stimulation paradigm (Fig. 6C). We found that the timing of the stimulus with respect to saccade initiation was critical in producing curvature: it was necessary for stimulation to continue until just before saccade onset. Indeed, we found that the mean stimulation frequency (in the stimulation experiments) or mean activity level (in the recording experiments) in the 30-ms period immediately before saccade initiation was well correlated with the curvature of the subsequent saccade.

**Directional averaging verses curvature with subthreshold stimulation**

While we used subthreshold stimulation to alter the trajectory of saccades to a visual target, subthreshold presaccadic stimulation has also been used to alter the endpoints of subsequent saccades (Glimcher and Sparks 1993). These authors used a delayed, memory saccade paradigm in which two visual targets appeared at separate locations. After the targets disappeared, the animals were cued as to which remembered visual stimulus was to be the target of a delayed saccade. The fixation point was subsequently extinguished, and the animals were rewarded for saccading to the cued location. A stimulating electrode was located in the SC at a site that was the collicular image of one of the visual targets. A low-frequency pulse train was delivered through the stimulating electrode during the delay period, which was several seconds in duration, after the potential targets were extinguished. Low-frequency stimulation biased the distribution of saccade end points but did not initiate saccades. At very low stimulus frequencies (10 Hz), the saccade ended at the location of the cued remembered target. As the stimulation frequency was increased, the end point of the subsequent saccade began to be biased more toward the location in the visual field coded by the stimulated site in the SC. No bias occurred if the termination of the stimulation occurred more than ~40 ms before saccade onset. Thus their experimental conditions produced clear averaging effects, and the resulting saccadic trajectories were straight.

There are several differences in experimental design that may have produced these results, which differ from ours. Our subthreshold presaccadic stimulations were delivered in a reaction-time paradigm in which the visual target remained visible. In our experiments, only one visual target appeared in a particular trial, and the stimulation in the SC played the role of...
the second visual target. We did not obtain averaging movements, but instead the saccade usually ended very close to the location of the visual target after its initial partial deviation toward the vector coded by the stimulated SC site.

Relationship to behavioral studies

Saccadic eye movements are associated with a mound of activity in the SC, centered on the site coding the movement vector (e.g., Anderson et al. 1998). Our results indicate that the presence of a second locus of SC activity shortly before movement onset results in saccades that curve in the direction coded by the second site. This supports the idea that the curvature of saccades toward salient distractors observed in several behavioral paradigms (Findlay and Harris 1984; McPeek and Keller 2001; Minken et al. 1993; Port and Wurtz 2000; Van Gisbergen et al. 1987) arises from temporally overlapping SC activity at two sites that correspond to the competing target and distractor goals.

Curved saccades have also been observed when there is a local decrease in SC activity. Quaia et al. (1998) found that when a portion of the SC is temporarily inactivated by a microinjection of muscimol, saccades tend to curve away from a location in space near (but not identical to) the location encoded by the injection site. This result could offer an explanation for the observation that in some behavioral paradigms, saccades curve away from previously attended areas of space or from irrelevant nontarget stimuli.

Specifically, when human subjects are instructed to focus attention on an eccentric stimulus without moving their eyes, subsequent saccades to a different region of space tend to curve away from the previously attended location (Sheliga et al. 1994, 1995). An explanation of this effect that is consistent with the physiological results is that focusing attention on a region of space without moving the eyes requires the active suppression of a saccade (Sheliga et al. 1994). This suppression temporarily depresses activity in a local region of oculomotor structures (such as the SC), corresponding to the location of the attended stimulus. If the suppression is present near the time of a subsequent saccade to a different location in the field, it could cause the saccade to curve away from the previously attended region, similar to the curvature seen by Quaia et al. (1998).

Curved saccades have also been observed in humans in a task that places an irrelevant distractor at a location flanking the expected saccade trajectory (Doyle and Walker 2001). In this paradigm, the saccade trajectory also curves away from the distractor. The most likely explanation for the difference in curvature seen in our study (toward the distractor) and in this study (away from the distractor) is that in our search paradigm, the distractors represent potential saccade goals that are in intense competition with the odd-colored target. In contrast, in the Doyle and Walker study, the distractor locations are never used as saccade goals. Because the irrelevant distractors in the Doyle and Walker study were placed at fixed positions for each block of trials, we speculate that the activity in motor maps at these sites may have been depressed near the time of saccade execution by top down influences to prevent reflexive saccades to the distractors. Similar to the situation with the Sheliga et al. experiments, this suppression would create a “hole” in the activity map and, based on the results of Quaia et al. (1998), would be expected to cause saccades to curve away from the distractor location (Doyle and Walker 2001; Tipper et al. 2001). In contrast, our salient distractor stimuli create activity at multiple sites that is not always suppressed by saccade onset, resulting in saccades curved toward the distractors.

Target selection and lack of strict winner-take-all behavior in the SC

Several recent studies have identified neural activity related to saccade target selection in the SC (Basso and Wurtz 1997, 1998; Glimcher and Sparks 1992; Horwitz and Newsome 1999, 2001; McPeek and Keller 2002a). In the present study, we find that competitive interactions between potential saccade goals can continue in SC neurons even up to the time of saccade execution. Thus it appears that activity in the SC provides a continuous readout of a saccade target selection process that presumably includes cortical regions such as the FEF and area LIP as well as the SC. This conclusion is also supported by the finding that during an initial saccade to one goal, SC activity at a second site can represent the salience of a subsequent saccade goal at a different location in the visual field (McPeek and Keller 2002b).

These results imply that the distributed network in the SC does not necessarily converge on a single saccade goal before movement onset and, hence, does not function as a strict winner-take-all circuit. Several other studies have also produced evidence supporting the idea that significant activity can exist at two or more sites in the SC even at the time of saccade initiation. (Edelman and Keller 1998; McPeek and Keller 2002b; Port and Wurtz 2000). In the present study, in addition to activity at the target site, considerable activity often remained at a distractor site near saccade onset. In view of the fact that a delay of 10–20 ms exists between modulations in SC activity and the accompanying alteration in eye movement (Gandhi and Keller 1999; Miyashita and Hikosaka 1996; Munoz and Wurtz 1993), the medium levels of activity (∼250 Hz) measured in the 30-ms presaccadic period at distractor sites indicate that no clear winner had emerged even during the initial part of the saccade when viewed from a neural time frame.

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