Competition between Saccade Goals in the Superior Colliculus Produces Saccade Curvature

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ABSTRACT

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 which ended near the target but curved toward a distractor were accompanied by increased pre-saccadic activity of SC neurons coding the distractor site. This increased activity occurred ~30 ms before saccade onset and was abruptly quenched upon 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 vs. 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 sub-threshold 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 2000; Minken et al. 1993; Port and Wurtz 2000; Van Gisbergen et al. 1987), in contrast to the relatively straight trajectories seen when only a single saccade goal is present (Keller 1980; Van Gisbergen et al. 1985; King et al. 1986; Quaia et al. 2000; Viviani et al. 1977; Bahill and Stark 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
pre-saccadic 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
pre-saccadic 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 sub-threshold for evoking movements, but we found that
optimally configured pre-saccadic 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 below), 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 five 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 superior
colliculi. Neural activity was recorded using tungsten microelectrodes with impedances ranging from 0.8 - 2.5 M ohms at 1 kHz, advanced by a hydraulic microdrive. Action potentials were identified using a time-amplitude window discriminator. The computer data acquisition system registered 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 disc, with a luminance of 0.90 cd/m² or 0.92 cd/m², respectively. The size of the target was M-scaled in order 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 450-650 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 disc, 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 above, 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, upper). 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 which 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 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, lower). 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 pre-set
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 which 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 about 5% of stimulated responses (56 out 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 standard deviations 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 pre-saccadic 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 (Sparks 1978; Munoz and Wurtz 1995). In the summary analyses comparing 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 above 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 which 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 buildup 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. While 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 which 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. Since 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 which 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 which 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 verses 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. Since we found similar pre-saccadic 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 2 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 at least 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°. The left column in Fig. 2 shows the neuron’s activity for saccades made into the response field (Into field), while the right column shows its activity for saccades made out of the field to the target located in the same visual field (Ipsi location). All neural data is aligned on saccade onset (time 0). The upper row in each column shows the saccadic trajectories, divided into straight (left in each pair) and curved (right in each pair) saccades that accompanied the neural responses shown below. Overall, the discharge for saccades made to the Into field location was much larger than that for saccades made to the Ipsi location, as expected. When saccades were made into the field there was no noticeable difference in the discharge for curved vs. straight movements either before or during the saccade. In particular, the discharge during the 30-ms period just before saccade onset was not significantly different over the set of trials for curved vs. straight movements (P = 0.77).

In contrast, when saccades were made to the Ipsi location, there was a marked difference in the pre-saccadic discharge of the neuron between straight and curved saccades. For straight saccades, the cell’s pre-saccadic discharge began to decline about 50 ms before saccade onset and was near zero by movement onset. However, when saccades were curved toward the cell’s movement field, the activity increased sharply beginning about 30 ms before saccade onset before declining rapidly near saccade onset. The difference in discharge during the 30-ms pre-
saccadic interval for this cell was significant (P < 0.05). Much of the earlier pre-saccadic 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 at 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 to 30° in a range of different directions. In the plots shown on the left, the mean spike density over all the cells for straight saccades is shown with dashed lines and the mean for saccades curved toward the response field with solid lines. 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 (heavy trace) and straight trajectories (dashed trace) are almost identical for the pre-saccadic time period and during the saccade, for movements made to the \textit{Into field} location. In the 30-ms presaccadic time window designated in gray, there was no significant difference in activity for curved vs. 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. Fig. 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 pre-saccadic time window, and this difference is significant (*P* < 0.05). When saccades were made to the *Contra* target location (Fig. 3C), the pre-saccadic 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 curved saccades is spatially restricted, as expected if curvature results from competition between neighboring goals.

As described in the 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 endpoint 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 endpoints.

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 pre-saccadic 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 pre-saccadic 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 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 vs. 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 ($r^2 = .006$, Pearson product moment correlation), but there was a significant trend ($P = .04$) toward greater curvature with shorter latencies.

Is the amount of curvature related to pre-saccadic 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 variations in curvature for saccades to different parts of the visual field.
We computed each cell’s mean firing rate during the 30-ms pre-saccadic period for accurate, straight (see Methods) saccades made to the *Ipsi* and *Contra* locations. We took these values as the baseline pre-saccadic 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 pre-saccadic firing rate from the cell’s mean rate for straight saccades to the same locations. In order to pool across cells with different maximum firing rates, we normalized the change in pre-saccadic firing rate observed for each curved saccade by dividing it by the mean pre-saccadic 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 pre-saccadic activity at a distractor site – is correlated with greater curvature toward the distractor.

**PRE-SACCADIC 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. In order 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, lower), 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. 3B 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 fixed-vector saccade (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 sub-threshold 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 Fig. 6D for trials without stimulation. When the saccadic trajectories in Fig. 6C 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 endpoint of the FVS). Note that in this condition the site of the electrical stimulation was in the same colliculus (the right SC) as 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. Since 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.
The effect of deadtime

For each stimulation trial, we measured the time between the final stimulation pulse and the onset of the saccade, which we label “deadtime”. Figure 7 shows the effects of deadtime 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 sub-threshold stimulation paradigm are shown as solid lines. We sorted these trials according to deadtime and found that when deadtime is greater than about 20 ms (Fig. 7A), saccades show much less curvature than when deadtime is less than 20 ms (Fig. 7B). Indeed, when deadtime is long, the saccadic trajectories are not noticeably more curved than in trials in which no stimulation occurred (compare trajectories in Fig. 7A and 7C). 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.

Fig. 8 shows the relationship between corrected curvature (see Methods) and deadtime for the range of deadtimes 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 which 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 deadtime (plotted at the right edge of Fig. 8), while trials in which the stimulus train stopped before saccade onset are assigned positive deadtime values. Figure 8 shows that it was necessary for the stimulus train to continue to within approximately 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 approximately 20 ms of saccade onset.

The 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 deadtimes are considered, there is still considerable variability in the amount of curvature produced by stimulation (Fig. 7B and Fig 8, oblong cloud of points near zero deadtime). To explain this variance, we examined the relationship between the frequency of stimulation in the immediate pre-saccadic 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 pre-saccadic time window and calculating the final pre-saccadic 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 pre-saccadic stimulating frequencies. Controls with no stimulation are also shown for comparison.

Fig. 9C shows summary results for this site across all pre-saccadic frequencies. Corrected curvature is plotted against mean pre-saccadic stimulation rate for movements made to the Ipsi (left graph) or Contra (right graph) target location. At this particular site, no noticeable
curvature was produced by mean pre-saccadic stimulation frequencies of 150 Hz or lower, 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 +/- one standard deviation is plotted at the left edge of the graph. If we increased the maximum frequency beyond the range of 200 to 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 pre-saccadic stimulation frequency are shown in the left column of Fig. 10. 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 the right column of Fig. 10, we plot comparable results for neural activity recorded in the SC, pooled across neurons. In these plots, we grouped trials according to the pre-saccadic 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 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.

The 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 sub-threshold pre-saccadic 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 endpoint of the FVS (i.e., when the visual target was represented in the same colliculus as the stimulation site). Stimulation at sites coding 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; Van Gisbergen et al. 1987; Minken et al. 1993) 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 which 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 sub-threshold 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 which 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 (Robinson 1972; Schiller et al. 1979; Schiller and Sandell 1983; Sparks and Mays 1983; Edelman and Keller 1998). 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 buildup 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 D_\text{ipsi}) are almost silent by saccade initiation (Fig. 3B). In contrast, when saccades with curvature toward D_\text{ipsi} 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 pre-saccadic interval, leading to an initial deviation of the saccade trajectory toward D_\text{ipsi}.

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 D_{ipsi} 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 which 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 grey 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 mis-direction 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 grey 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), demonstrate 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 sub-threshold electrical stimulation, delivered during the latent 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 pre-saccadic 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 spatio-temporal 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 $D_{\text{ipsi}}$ and $D_{\text{contra}}$ 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 ($\text{Ipsi site}$). However, we did not observe such a clear difference between $\text{Ipsi}$ and $\text{Contra}$ activity for curved saccades in our recording experiments (e.g., Fig. 10). Thus, it is possible that this $\text{Ipsi/Contra}$ 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 versus curvature with sub-threshold stimulation*

While we used sub-threshold stimulation to alter the trajectory of saccades to a visual target, sub-threshold pre-saccadic 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 which 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 about 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 sub-threshold 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 which 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 non-target 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. Since 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 (Glimcher and Sparks 1992; Basso and Wurtz 1997, 1998; McPeek and Keller 2002a; Horwitz and Newsome 1999, 2001). 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 which 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; Port and Wurtz 2000; McPeek and Keller 2002b). 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 (Miyashita and Hikosaka 1996; Munoz and Wurtz 1993; Gandhi and Keller 1999), the medium levels of activity (~250 Hz) measured in the 30-ms pre-saccadic 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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FIGURE LEGENDS

Figure 1. Schematic representations of the visual search and stimulation paradigms. The drawings on the left show paradigm events versus time and those on the right show the spatial arrangement. In the search task the animal was required to fixate a central fixation point. After a random time interval, the fixation point was extinguished and the stimulus array, consisting of a target and 3 distractors, appeared. The animal was rewarded for making a saccade to the target, which was delineated by its odd color. The array was positioned so that one visual stimulus, either the target or a distractor, always appeared near the center of the response field (grey shaded region) of the SC neuron being recorded. The stimulus location which neighbors the response field (RF), and is in the same visual hemifield as the RF, is referred to as the Ipsi location. The neighboring location in the opposite hemifield is referred to as the Contra location. The Opposite location is diametrically opposed to the RF location, while the Into field location coincides with the cell’s RF. In the stimulation paradigm the fixed vector saccade (FVS), an invariant saccade determined primarily by the location of the stimulating electrode in the collicular motor map, was first measured (dashed arrow). After the FVS was determined a series of trials ensued in which the animal was required to fixate a central fixation point, and after a random interval, the fixation point was extinguished and a single visual target appeared at one of the neighboring locations (Ipsi or Contra) with respect to the endpoint of the FVS. The animal was rewarded for saccading to the location of this visual stimulus. On randomly interleaved trials pulsatile electrical stimulation was delivered through the microelectrode just before the visually evoked saccade began. Stimulation was terminated by saccade onset or after 125 ms, whichever occurred first.
Figure 2. Activity of a SC neuron during curved or straight saccades in the visual search task. Neural activity is represented by raster plots in which each tick mark signifies the occurrence of a discharge. In the raster plots the solid horizontal line separates the discharge for straight saccades (trials above the line shown in blue) and curved saccades (trials below the line shown in red). Activity over trials is plotted as average spike density with sigma = 3 ms (Richmond et al. 1987). All data is aligned on saccade onset. The gray bar in the density plots indicates the time interval that was used for quantitative analyses of the difference in discharge for straight and curved saccades. A: Saccades made into the response field of the neuron. The upper two plots show the saccadic trajectories that accompanied the individual trials shown below. The target location is shown by the open circle and distractor locations by filled circles. The gray regions show the approximate extent of the response field of the neuron when tested using single visual targets. In the pair of upper plots, the one on the left (blue) contains all the straight saccades (n = 14) and that on the right (red) all the curved saccades (n = 6) made when the target was located in the response field of the cell. B: Same format as in A except that saccades were made to a target located out of the response field of the neuron. In this case only saccades made to the target when it was located in the upper-left visual field are shown. Since this field location is in the same hemifield as the response field of the neuron, these sets are labeled the Ipsi location. Upper plot on the left shows 16 straight saccades (blue) and on the right (red) 7 curved saccades.

Figure 3. Comparisons of averaged population discharge for curved and straight saccades. In each temporal plot the dashed curve shows the normalized population mean spike density for straight saccades and the solid curve is the same for curved saccades. All responses are aligned
on saccade onset (time = 0). The gray bars indicate the time interval that was used for quantitative analyses of the difference in discharge for straight and curved saccades. The insets on the right are schematic representations of the target (open circles) and distractor (filled circles) locations. A: The target appeared in the 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.

Figure 4. Scatter plots compare, for each neuron, mean pre-saccadic discharge rates for straight saccades (abscissa) vs. curved saccades (ordinate). Discharge rates for each trial of a particular type were computed for the 30-ms time period just before saccade onset and results from all trials of that type were averaged to determine mean rate. If the rates for curved saccades were the same as straight saccades, the plotted symbols would fall along the diagonal lines. A: Result for saccades made to the target when it appeared in the RF of the neuron (inset on the right), comparing straight saccades with saccades curved in either direction. B: Result for saccades to the *Ipsi* location, comparing straight saccades with saccades curved toward the cell’s RF. C: Result for saccades to the *Contra* location, comparing straight saccades with saccades curved toward the cell’s RF.
Figure 5. Relationship between the curvature of saccades to the target and the level of neural discharge at adjacent distractor sites, pooled across neurons. The abscissa indicates the corrected curvature of saccades, with positive values denoting curvature toward the response field and negative values curvature away from the response field. The ordinate represents the difference in pre-saccadic activity from the mean level seen for straight saccades to the same location. The difference in neural activity is normalized according to the maximal discharge rate for each neuron (see text). Individual responses are binned according to their curvature. The horizontal error bars show the range of each bin and the vertical error bars show the standard error of the mean. The right side of the plot shows that increasing curvature toward the response field is accompanied by an increase in pre-saccadic SC discharge, presumably reflecting greater competition from the distractor goal, while the left side shows that curvature away from the response field is associated with a slight decrease in activity below the normal baseline level for straight saccades to the same locations.

Figure 6. Saccade curvature produced in visually evoked saccades by sub-threshold SC stimulation. A: Saccades evoked by conventional high-frequency stimulation at this site in the SC illustrate the site’s fixed vector saccade (FVS). B: Electrical stimulation at the same site with lower pulse frequency and lower current does not evoke any movement. The dot in the center of the spatial plot shows the position of the eyes as they remain at the fixation point. C: Spatial plot shows the saccades made to a single visual target (open circle) that appeared at a location either, left and down, or, up and right. An example movement vs. time is shown on the left. The vertical (upper trace) and horizontal (lower trace) components of one example curved saccade are shown and the stimulus train for that particular trial is plotted at the bottom. The trace in the
middle indicates the time of the appearance of the visual target. D: Control visually guided saccades made to the same two target locations without stimulation.

Figure 7. Plots in the left column show vertical and horizontal eye movement components vs. time for one example movement in each stimulation condition. Plots on the right are spatial plots of superimposed saccade trajectories. The particular movement used as an illustration on the left is shown in red in the panels on the right. A: Trial in which the stimulus train reached its maximum frequency and was terminated more than 20 ms before saccade onset. Arrow and vertical dashed lines show the time interval between the final stimulation pulse and the onset of the saccade. This interval was called **deadtime**, and was > 20 ms for the movements shown here. These saccades were not noticeably more curved than unstimulated controls shown in C. B: This saccade occurred before the stimulation train had reached its maximum frequency and deadtime was less than 20 ms (actually near zero in this case). Saccades with short deadtimes showed a range of curvatures depending on the frequency of stimulation immediately before saccade onset (see Figs. 9-10). C: Control saccades to the same target locations without stimulation.

Figure 8. The relationship between saccade curvature and deadtime, for all stimulation trials pooled across the 22 sites. Close approximation of the end of the stimulus train to the onset of the saccade is necessary for the stimulation to produce saccade curvature. Each data point represents the value of corrected curvature vs. deadtime in an individual trial. The open symbol at left shows the mean corrected curvature of unstimulated trials, with error bars indicating +/- one standard deviation.
Figure 9. The relationship between saccade curvature and pre-saccadic stimulation rate. Same site as in Fig. 6. The FVS is shown by the dashed arrows. A: In each individual trial with stimulation, the mean stimulation rate in the final 30-ms period before saccade onset was computed. In the example shown, the number of stimulus spikes that occurred in this interval was 7, so the mean final stimulation rate was 233 Hz. The vertical (upper trace) and horizontal (lower trace) components of the curved saccade associated with that particular stimulus in one trial are shown above. B: Each plot shows the trajectories of all the saccades made to the ipsilateral (left and down) and contralateral (right and up) target for a range of mean stimulation frequencies in the 30-ms pre-saccadic interval. The plot at the lower right shows the trajectories for trials without stimulation. Target locations are shown by the open circles. C: Plots show the relationship between corrected saccade curvature and mean stimulus frequency in the 30-ms pre-saccadic interval at this SC site for movements to the ipsilateral (left) and contralateral (right) target locations. Each symbol represents one movement, and the lines represent the mean curvature across stimulation rates. The open circles and vertical error bars at the left edge of the plots show the mean value and standard deviation of curvature obtained in trials in which no stimulation occurred.

Figure 10. Left panels show summary results across stimulation sites for saccade curvature as a function of stimulation frequency during the 30-ms pre-saccadic interval. For comparison, left panels show analogous results, pooled across neurons, from the recording experiments. The upper panels show results for the Ipsi target locations and the lower panels for the Contra target locations. Both sets of graphs plot mean corrected curvature, with error bars indicating the standard error of the mean. In both the stimulation and recording experiments, higher pre-
saccadic stimulation frequency or neural discharge is associated with greater curvature. There is also a tendency, particularly at higher rates, for greater curvature for saccades made to the *Ipsi* target than to the *Contra* target.

Figure 11. Activity in the superior colliculus (SC) for straight and curved saccade trajectories in a visual search paradigm. The schematic on the left shows a typical spatial arrangement of the stimuli in our paradigm superimposed on a map of the visual field. Eccentricity in the field is shown by circles at 2, 5, 10 and 20°. The odd colored stimulus or target (T) is shown by the green disk. The three distractors are shown by red disks. D_{ipsi} is the location of the distractor that neighbors T and is located in the same hemifield. D_{contra} is the neighboring distractor in the opposite visual field. D_{oppos} is the distractor located diametrically opposite T. The dashed curve shows the trajectory of a saccade that goes in a straight-line path between the fixation point and T. The solid curve shows a saccade that goes to T after first curving in a direction between D_{ipsi} and T. The schematics on the right illustrate the activity that occurs in the left SC in the immediate presaccadic interval, when the movement is straight (middle plot) or curved (right plot). The site T in the SC is the image of the target in SC space and D_{ipsi} is the image of the corresponding distractor. The intensity of the population activity in SC is shown with the color-coded intensity scale. The dashed line above shows the location of the midline with respect to the left SC. The grey shaded region indicates the region of the SC that would be expected to become active for the terminal trajectory of the curved saccade, if the SC codes final saccade trajectory.
Search Paradigm

- Fix Pt
- Target + Distr
- Eye Movt

Stimulation Paradigm

- Fix Pt
- Target
- Eye Movt
- Stim Pulses

Stimulation Paradigm:
- Fixed-Vector Saccade
- Ipsi location
- Contra location
A. Saccades Into Field

B. Saccades to Ipsi Location

Time from Saccade Onset (ms)
A. Saccades into Movement Field
- Curved
- Straight

B. Saccades to Ipsi Location

C. Saccades to Contra Location

D. Saccades to Opposite Location

Normalized Firing Rate

Time from Saccade Onset (ms)
Pre-saccadic Discharge for Curved Saccades (sp/s)

A

Saccades into Movement Field

n = 63

Pre-saccadic Discharge for Curved Saccades (sp/s)

B

Saccades to Ipsil Target

n = 60

Pre-saccadic Discharge for Straight Saccades (sp/s)

C

Saccades to Contra Target

n = 54
Normalized Activity Difference

Corrected Curvature

Away From RF

Corrected Curvature

Toward RF
A. Fixed-Vector Saccades
- 5 deg
- 100 ms
- Vert Eye
- Horiz Eye
- Stim Pulses
- 400 Hz, 20 uA

B. Sub-Threshold Stimulation
- 250 Hz, 12 uA

C. Sub-Threshold Accelerating Stimulation Before Visually-Guided Saccades
- 10-250 Hz, 12 uA

D. Visually-Guided Saccades Without Stimulation
- No electrical stimulation

Visual target (n=10)
A  Deadtime > 20 ms

B  Deadtime <= 20 ms

C  No Stimulation
Figure A: Pre-Saccadic Interval (30 ms) and 233 Hz Mean Stim Rate During Interval.

Figure B: Comparison of saccadic paths for different stimulation rates: 233 Hz, 200 Hz, 167 Hz, 116 Hz, 50 Hz, and No Stim.

Figure C: Graph showing corrected curvature toward FVS as a function of mean pre-saccadic stimulation rate (Hz) for ipsi and contra paths.
Ipsi Stimulation

Ipsi Recording

Contra Stimulation

Contra Recording

Corrected Curvature

Pre-Saccadic Stim Rate

Pre-Saccadic Firing Rate
Saccades curved toward $D_{\text{IPSI}}$