SACCADE-RELATED ACTIVITY IN THE PRIMATE SUPERIOR COLLICULUS DEPENDS ON THE PRESENCE OF LOCAL LANDMARKS AT THE SACCADE ENDPOINT

Jay A. Edelman & Michael E. Goldberg

Laboratory of Sensorimotor Research, National Eye Institute
Bethesda, MD 20892

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Correspondence should be addressed to

Jay A. Edelman, Ph.D.
Dept. of Biology, The City College of New York
J526, Marshak Science Building
New York, NY 10031

e-mail: jedelman@ccny.cuny.edu
PH:(212) 650-8461 FAX: (212) 650-8585

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Key words: Superior colliculus, monkey, saccade, visually guided, memory-guided, single-unit, object

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ABSTRACT

Saccade-related discharge in the superior colliculus is greater for saccades made to a spot of light than for saccades in complete darkness. However, it is unclear whether this enhancement is due to the discontinuity of the spot or due to its being a new object of fixation. In these experiments we examined the saccade-related activity of intermediate-layer neurons in the primate superior colliculus during delayed saccades to the center or corner of a large, bright square, as well as for visual and memory-guided movements to small spots in isolation. The saccade-related discharge for movements made to a local visual landmark present at the time of the saccade, be it a corner of a square or a small spot, was higher than that for saccades made to the center of a square that contained no local visual landmarks within. Moreover, discharge for movements to the center of a square were very similar to that for saccades to blank, dark space. Saccade velocity was similarly dependent on the presence of such a landmark, though less dramatically. The end points of saccades directed toward a square’s corner were slightly displaced toward the center of the square. Across all neurons, discharge and velocity for saccades to the center of a square increased as the square size was decreased, but were never greater than those for saccades to a small spot of light. These results suggest that both saccade-related discharge in the superior colliculus and saccade metrics are enhanced for movements directed to parts of the visual scene with high contrast, while shifting fixation to a new object is not itself sufficient to elevate discharge and metrics above those of saccades to blank space.
INTRODUCTION

Movements are most often made to what is seen, suggesting an intimate link between visual and motor-related areas of the brain. This link is perhaps most evident for saccadic eye movements, which facilitate high-resolution primate vision by quickly moving the eye to image objects of interest on the fovea, the area of the retina with the greatest density of photoreceptors. Behavioral and neurophysiological evidence suggests that the processes involved in saccade generation depend on whether or not a saccade is visually guided. Saccades to a small spot of light are of higher speed and more precise than non-visually guided saccades (Edelman and Goldberg 2001; Gnadt et al. 1991; White et al. 1994). Neurons in the intermediate layers of the primate superior colliculus, long known to play an important role in saccadic generation (Sparks and Hartwich-Young 1989), have enhanced discharge for saccades to a spot of light relative to saccades to blank space. Strikingly, this elevated discharge is manifest not only in the visual response of these neurons at the time of target appearance, but in activity temporally coincident with the saccade itself (Edelman and Goldberg 2001; Everling et al. 1999; Mohler and Wurtz 1976; Sparks and Porter 1983).

What is it about small spots that caused this enhancement? Is it because the spot is a two-dimensional discontinuity in the properties of the visual field (which we'll refer to here as a local landmark)? Or is it because the spot is simply a new object of fixation? In these experiments we probed the dependence of discharge in the superior colliculus and behavioral properties of saccades for movements to different parts of a spatially extended visual object. Specifically, to assess whether discharge and metrics were elevated to a local landmark, even if it were part of a larger object, we elicited saccades to the vertex of a large square. To assess whether instead these saccade-related properties could be elevated simply by making a saccade to a new object that was not directed to a local landmark, we elicited saccades to the center of a large square. As most saccades in the real world are made to stable targets, we
used variants of delayed saccade tasks (Fischer and Boch 1981a; Hikosaka and Wurtz 1983) (Mays and Sparks 1980) rather than tasks involving saccades made immediately to suddenly appearing targets. Standard memory-guided and visually guided delayed saccade tasks were used to provide, respectively, a baseline and ceiling of activity and performance to which the other tasks could be compared. Finally, we attempted to determine how the size of an object influences collicular discharge and movement metrics for movements made to the center of the object.

MATERIALS AND METHODS

Animals and surgery

Neurons were recorded in the superior colliculi of three adult rhesus monkeys (Macaca mulatta). In preparation for these experiments, the monkeys were surgically implanted with a recording chamber above the superior colliculus, a head holder that could be coupled to an animal chair to restrain the head during recordings, and scleral search coils in each eye (Judge et al. 1980). The head holder and recording cylinder were embedded in an implant made of dental acrylic attached to the skull by titanium surgical-grade screws. General anesthesia was induced using Ketamine (10.0 mg/kg), valium (1.0 mg/kg), and glycopyrrolate (0.01 mg/kg), and maintained with isoflurane. For two of the monkeys, the recording chamber was implanted several months after the implant, head-holder device, and eye coils. After surgery, animals were given Banamine as analgesia as needed (2.0 mg/kg). The antibiotic Polyflex was administered every other day for the two weeks following surgery. Monkeys were allowed to recover for at least one week after surgery before their participation in these experiments. The animal's fluid intake, weight, and general health status were carefully monitored. All procedures were approved by the Animal Care and Use Committee of the National Eye Institute in compliance with the Public Health Service Guide for the Care and Use of Laboratory Animals.
Animal restraint, physiological methods, and neuron criteria

Monkeys were housed unrestrained either singly or in pairs in between recording sessions. During recording sessions the monkey sat comfortably in a primate chair. The monkeys' heads were restrained by attaching a metal post to the implanted head holder and coupling this to another post attached to the chair using a metal sleeve. Neural activity was monitored using tungsten microelectrodes (FHC) manipulated by an electronic microdrive system. Electrodes were positioned within the recording chamber by being placed in a 23 gauge stainless steel guide tube and inserted into a hole of a plastic grid fastened inside the cylinder (Crist et al. 1988).

We recorded from all neurons that we were able to isolate extracellularly in the superior colliculus that had substantial saccade-related discharge in a visually guided delayed saccade task. After isolating a single neuron, the approximate center of its movement field (the loci of endpoints of saccades accompanied by perisaccadic neural discharge) was estimated by monitoring neural activity while monkeys made 30-40 trials of visually guided delayed saccades to targets whose position was manipulated by a joystick in between trials.

Experimental control and data acquisition

Experiments were controlled and data were collected using the REX (Real Time Experimental) control language (Hays et al. 1982) running on a Hewlett-Packard HP Vectra 486/337 computer under the QNX operating system. Eye position was sampled and stored at 1000 Hz. A liquid crystal television projection system (Sharp), with a refresh rate of 60 Hz, and running the VEX graphics system (Gottlieb et al. 1998) was used to back-project visual stimuli onto a tangent screen located 57 cm away from the monkey. The luminance of red stimuli (see below) was 1.1 cd/m² and that of the white stimuli was 3.3 cd/m². The background was dimly lit at 0.3 cd/m².
Behavioral tasks

Single neurons were recorded while monkeys performed four tasks, all variants of a delayed saccade paradigm (Fischer and Boch 1981a; Hikosaka and Wurtz 1983). Each task began with the appearance of a small white square (0.5° width) at the center of the screen, which the monkey had to fixate within 500 ms, positioning its eye in a 2° x 2° "window" surrounding the target. In the Spot task, after 300 ms of fixation, a second small white square of 0.5 deg width appeared near the center of an isolated neuron's movement field (Fig. 1). The monkey was required to maintain central fixation for another 750-1000 ms after which the central fixation point disappeared. For a reward the monkey had to make a saccade that landed in a square window (dimensions described below) surrounding the target within 400ms of the fixation point's disappearance. A drop of water or juice was delivered after the eye had remained in the peripheral window for 200 ms. A similar task was referred to as the “Step” task in a recent study from this lab (Edelman and Goldberg, 2001).

The Nothing task was identical to the Spot task except that the peripheral spot appeared for only 250 ms, so that when the fixation point disappeared the monkey had to make a saccade to the remembered location of the small white square that had disappeared 500-750 ms earlier (Fig. 1). After the saccade, the peripheral target was turned back on for 300 ms at its original location to provide spatial feedback. A similar task was referred to as the “Memory” task in a recent study (Edelman and Goldberg, 2001).

The Vertex task was similar to the Nothing task except that in addition to the presence of the small white square, a large red square appeared 50 ms after the monkey fixated the central spot. Note that the large square appeared before the small white square appeared. This larger square remained on the screen for the rest of the trial. The square's sides were always horizontal/vertical and it was situated so that the small white square appeared at its corner nearest to the fixation point (Fig. 1). The width of the square was set to be approximately equal
to the radial eccentricity of the center of the movement field and was held constant while activity of an individual neuron was recorded. Unlike in the Nothing task, the original peripheral square was not turned back on after the saccade.

The Center task was identical to the Vertex task except that the square was situated so that the target appeared at its center (Fig. 1). Also, as in the Nothing task, the peripheral target was turned back on for 300 ms at its original location to after the saccade.

Note that in the Spot and Vertex tasks, a distinct, localized visual feature, or "local landmark" was present at the saccade goal. In contrast, in the Nothing and Center tasks, no such landmark was present at the saccade goal at the time of the saccade, though the Center task required a saccade to a new object. In the Spot task the local landmark was the still-present saccade target itself. In the Vertex task the local landmark was the corner of the square – the small spot appeared at the location of the corner, but had disappeared by the time that the monkey actually had to make the saccade (Fig. 1).

In all four tasks, saccades were required to land within a square region of space centered at the estimated center of the neuron’s movement field. The width of this window was set to 4° x 4°. This window was sometimes enlarged when the required saccade was more than 20° in radial amplitude. Since monkeys were well trained in the different tasks by the time neural recordings began, errors caused by saccades not landing in the reward window occurred vary rarely (<2% of trials). The size of the windows was not adjusted to require optimal accuracy, but merely to ensure that saccades were not grossly misdirected.

The four trial types were run intermixed in pseudorandom order. At least 15 trials were collected for each trial type for each collicular neuron recorded.

Data analysis

Selection of trials for comparison of neural discharge and saccade velocity
To help ensure that differences in neural activity or saccade velocity between different trial types was not due to systematic differences in vector between two types of saccades, we used a graphical user interface program written for MATLAB (MathWorks Inc.) to select a subset of the data for each neuron for each of the four tasks. For each neuron's neural data set, the chosen subset consisted of trials whose saccade endpoints were within a circular region whose diameter was at most 15% of the average saccade amplitude. The length of the vector difference between the average vectors of any two trial types for a given neuron's data set was at most 5% of the mean saccade amplitude. For some data sets we made the region of chosen saccades even smaller if an adequate amount of data was available (>= 8 trials for each trial type). We observed that we could tighten or loosen these criteria considerably in our data analysis with virtually no effect on the estimated discharge for a given task. Nevertheless, for analysis of saccade velocity, we accounted for any residual differences in saccade amplitude by normalizing for saccade amplitude (see below).

In contrast, for analyses of the effect of trial type on the amplitude and precision of saccade vector we examined all trials that were rewarded.

**Measures of neural discharge level and selectivity**

To assist both the graphical comparison and quantitative analysis of the visuomotor burst waveform, the raw spike data were convolved with a Gaussian of fixed standard deviation (5ms) to yield a spike density trace (Richmond and Optican 1987). This transform yielded a continuous measure of neural activity. The level of perisaccadic discharge was defined as the average of the spike density trace in a 20 msec window centered on saccade initiation.

In order to compare neural activity of two different tasks, we calculated a contrast index,

\[ \frac{Z_A - Z_B}{Z_A + Z_B}, \]
where $Z_A$ and $Z_B$ are the levels of perisaccadic discharge for a particular neuron in the two tasks being compared. Such an index can vary from 1 to -1. Thus, if a neuron discharged only in the Task A or Task B, its TDF would equal 1 or -1, respectively.

**Normalization of saccade velocity**

To examine how saccade velocity depends upon trial type, we accounted for differences in saccade amplitude by computing a *velocity index* for all saccades in our data set. To calculate this index we first calculated the dependence of peak velocity on saccade amplitude (or saccade "main-sequence", Bahill et al. 1975) using as a data set all Spot trials recorded in all sessions by regressing peak velocity against saccade amplitude to fit a rising exponential curve (Becker 1989):

$$V_{\text{max}} \times (1-\exp(-k \times A)),$$

where $A$ is saccade amplitude and $V_{\text{max}}$ and $k$ are parameters of the model calculated to provide the best fit of the curve to the data. After determining these parameters for each neuron’s data, the velocity index for each saccade with saccade amplitude, $a$, and peak velocity, $v$, was calculated:

$$velocity_{\text{index}} = \frac{v}{V_{\text{max}} \times (1-\exp(-k\times a))},$$

Thus, for example, saccades with peak velocities higher than that expected for its particular amplitude would have a velocity index greater than one.

**Analysis of covariance procedure**

One of our analyses assessed whether the difference of presaccadic discharge between the *Vertex* and *Center* tasks could be explained merely as a dependence on saccade velocity. An analysis of covariance (ANCOVA) procedure was used to help isolate the effect that trial type *per se* had on discharge. Such a procedure fits a model expressing a *dependent variable*
(in this case, the observed perisaccadic discharge), as a sum of an effect strictly dependent on an \textit{independent variable} (in this case, task – Vertex and Center), and an effect due to a \textit{covariate} (in this case, peak saccade velocity) (Snedecor and Cochran 1989). Use of the procedure for each neuron’s data set yielded $\beta$, the slope of the linear dependence of perisaccadic discharge on saccade velocity. This term can then be used to calculate, $\hat{D}$, an estimate of neural discharge for each task \textit{adjusted} for differences in saccade velocity among the two tasks, using the following formula (after Snedecor and Cochran 1989):

$$\hat{D} = D + \beta (V_i - \bar{V})$$

where $D_i$ is the actual mean perisaccadic discharge observed for a given task (i.e. the raw data), $V_i$ is the mean peak saccade velocity for a given task, and, $\bar{V}$, is the mean peak saccade velocity across both tasks.

\textit{Statistical tests}

Measures of neural discharge and saccade metrics in the four tasks were compared across the 44 neurons in our sample using a repeated measures one-factor ANOVA followed by a Bonferroni multiple comparison procedure (Glantz 1992).

\textbf{RESULTS}

\textit{Elevated saccade-related discharge for movements to a local landmark}

We recorded from 44 neurons in the intermediate layers of the superior colliculus, each of which had a presaccadic burst in one or more of the tasks that we used. Our sample had neurons with varying levels of delay-period activity and thus was composed of both “burst” and “buildup” neurons (Munoz and Wurtz 1995). Neurons generally discharged with a greater
intensity in the tasks in which a local landmark was still present at or near the saccade endpoint (Spot and Vertex) than when a local landmark was not present (Center and Nothing). Data from neurons whose saccade-related discharge is representative of our sample are shown in Fig. 2. Neurons were found that discharged at a high level only for movements to a local landmark (Spot and Vertex tasks, Fig. 2AB). Other neurons discharged at a high rate only when saccades were directed towards a single spot (Spot task, Fig. 2C). Still others had discharge that did not depend on task (Fig. 2D).

Across our sample of 44 neurons, activity was greatest when saccades were directed to a discrete spot (Spot), somewhat less strong when directed towards the corner of the square (Vertex), and weakest when saccades were directed to the center of a square (Center) or else were “pure” memory saccades directed to blank space (Nothing, Figs. 3A and 3B Table 1). Examining Figs. 3A and B more closely, there was very little evidence of a subset of neurons selective for saccades at which a landmark was not present at saccade endpoint. It was also found that activity in the Nothing and Center tasks was not only very similar, but strongly correlated across the sample of neurons (r = 0.91, p < 0.001).

Rather than finding distinct classes of neurons selective for the two tasks (Spot and Vertex) in which saccades were directed to local landmarks, or just for the Spot task, we found a continuum of selectivity for the 44 neurons. This was established by examining the relationship between a Spot task selectivity index and a Vertex task selectivity index (see Methods): the former comparing activity of the Spot task and the average activity in the Nothing and Center tasks and the latter comparing activity of the Vertex task and the average activity in the Nothing and Center tasks (Fig. 3C). No distinct clusters of neurons with respect to selectivity are evident in this plot.

Enhanced discharge for movements made to a local landmark when the landmark was the corner of the square (Vertex) was found for neurons regardless of their transient visual and delay-period activity. We calculated a contrast index to compare the level of perisaccadic
activity in the Vertex task with that in the Center task for each of the 44 neurons in our sample. We then estimated magnitude of the transient visual response of these neurons by calculating the mean firing rate in a 20 ms window centered on the peak of a neuron's response within the 100 ms after target appearance in the Spot task. We estimated the delay-period activity of a neuron (indicative of its "buildup" activity, Munoz and Wurtz, 1995) by calculating the mean of the firing rate occurring from 400 ms to 100 ms before saccade initiation in the Spot task. The level of a neuron's enhanced discharge in the Vertex task compared to that in the Center task (as measured by the contrast index) was not correlated with its transient visual response ($r = 0.0$, $p = 0.97$), nor its delay period activity ($r = 0.117$, $p = 0.45$).

Effect of local landmarks on saccade metrics and the relation between saccade metrics and neural activity

Saccade velocity was also enhanced for movements to a local landmark (Table 1). Similar to differences in saccade-related activity in the superior colliculus, saccades in the Spot task tended to have higher peak velocities than saccades directed to the corner of a square (Vertex), which in turn were faster than saccades not directed to a still-present landmark (Center and Nothing). However, these differences in velocity tended to be much smaller percentage-wise than those of saccade-related activity in the colliculus. Moreover, the elevated saccade-related discharge when saccades were made to the corner of a square (Vertex) compared with that for movements made to the center of a square (Center) was only partly attributable to differences in peak saccade velocity between the two tasks. Recalculating mean discharge after taking velocity into account using an analysis-of-covariance (ANCOVA) procedure (see METHODS) showed a difference only $\sim 30\%$ smaller than that found without the adjustment (adjusted means-- Vertex: 181 spk/s, Center: 154 spk/s, c.f. Table 1). Furthermore, 13/44 neurons had significantly greater discharge in the Vertex task independent of saccade velocity, while only 2/44 neurons had discharge greater in the Center task. Note that since we reduced
our sample of trials in our analyses to match saccade vectors more precisely across tasks, our findings of statistical significance for each neuron most likely provided a conservative view of underlying differences between the two tasks. In any case, these results suggest that although saccade velocity and superior colliculus discharge tend to correlate, the presence of a local landmark at the saccade endpoint has an effect on superior colliculus discharge independent of its effect on velocity.

Saccade vector also depended on task. Saccade endpoint variability was lowest when saccades were directed to single spot. Saccades tended to have greater amplitude in the Vertex task compared to the other tasks, often overshooting the desired goal (the vertex of the square closest to the fixation point, Fig 4, Table 1). Across the entire data set, saccades in the Nothing and Center tasks had approximately the same amplitude gain as those in the Spot task, though they were considerably more variable (Table 1).

Could the differences in saccade amplitude and variability among the tasks affect our estimations of saccade-related activity? It has been long known that saccade-related discharge in the superior colliculus decreases as movements land further away from the center of the movement field (Sparks and Hartwich-Young 1989). With respect to the present study, the slightly increased amplitude of saccades to the corner of a square (Vertex task) relative to the other tasks could result in a shift of the movement field, just as Stanford and Sparks (1994) showed that when memory-guided saccades have a systematic vector difference from visually guided saccades their movement field shifts with respect to that of visually guided saccades accordingly. For all neurons we examined the subset of Vertex trials used previously to compare neural activity and found no systematic relationship between the endpoint displacement towards the center of the square of each saccade and its accompanying level of movement-related activity. This suggests that any movement field shift could not be responsible for the task dependence of our results.
Dependence of saccade-related activity and saccade velocity on square size

Our finding that discharge for saccades to the center of a large square (Center task) is much less than discharge to a very small square (Spot task) raises the question of how much smaller the square needs to be for collicular discharge and metrics to be enhanced. We addressed this question by recording from 15 neurons in the Center task described previously while varying square size. Four sizes were used: squares of 100%, 50%, and 20% of the width of the “standard” size square (having a diameter equal to the approximate eccentricity of the center of the movement field), and a small square of 0.5 deg width (same size as in the Spot task).

The dependence of discharge on square size varied considerably across these 15 neurons. Discharge decreased monotonically as square size increased, although, as illustrated in Fig. 5A, this fall-off was not always gradual, nor did it always occur at a particular size change of the square. For the neuron whose activity is shown at the top of Fig. 5A, discharge remained high for the 20% square, but then decreased more gradually for the larger squares. In contrast, the bottom of Fig. 5A shows a neuron whose discharge dropped for the 20% square relative to the spot, and then fell to a minimum by the 50% square. Reflecting this cell-to-cell variability, across all neurons discharge increased gradually as the square became smaller (Fig. 5B). Saccade velocity depended on square size in a similar manner (Fig. 5B). We did not find any systematic dependence of saccade-related discharge and saccade velocity on the distance between saccade endpoint and the center of the square.

DISCUSSION

Our data indicate that neurons in the superior colliculus discharge more for saccades to the location of a distinct, highly localized visual landmark that was present at the time of the saccade, be it a distinct spot of light or the corner of a salient square, than for saccades made to
the center of a square or to blank space. This preference for saccades to a local landmark did not depend upon a neuron's transient visual or delay period activity. Activity in the two tasks in which saccades were not directed to a local landmark (Center and Nothing) was roughly equivalent and highly correlated. Peak velocity was also greater for movements to the location of a landmark, though differences in perisaccadic discharge were more dramatic and were accounted for only partially by differences in velocity. Saccades directed towards the corner of a square in the Vertex task tended to be displaced toward the center of the square. Saccades not made to a local landmark tended to have higher endpoint variability than saccades to a discrete spot. Finally, when saccades were directed toward the center of a square, both discharge and saccade velocity increased as the size of the square was decreased to resemble more closely a small spot.

Previous work has demonstrated that memory-guided saccades made in darkness to the location of a recently vanished stimulus are less accurate and slower than visually guided saccades to the same stimulus (Edelman and Goldberg 2001; Gnadt et al. 1991; White et al. 1994). The enhanced performance of saccades to small visual targets is not surprising, given that the primary purpose of the saccadic system is to facilitate high-acuity vision. In keeping with this higher performance, visually guided saccades have a larger perisaccadic burst than memory-guided saccades (Edelman and Goldberg 2001). In the present study, we found that collicular discharge and saccade velocity were elevated in the Vertex task, in which a local landmark was present at saccade endpoint, often close to those of saccades to a small spot. In contrast, when a saccade was not made to local landmark, even when the saccade was directed to a new object (Center task), neural activity was lower and saccade metrics were degraded.

It is doubtful that these differences in neural activity are due to factors other than the difference in visual features at saccade endpoint. Use of variants of a delayed saccade task rather than an immediate saccade task resulted in a saccade data set roughly equated for
vector. Furthermore, only subsets of data that contained movements with closely matched vectors were analyzed, so neural activity differences were unlikely to result from differences in vector. In any case, we found that we could strengthen or weaken our criteria for selecting the subset of saccades to be analyzed with little or no effect on the results. Stanford and Sparks (1994) demonstrated that movement fields for memory-guided saccades elicited in complete darkness are shifted with respect to those for visually guided saccades in a manner that corresponds with the systematic up-shift of memory-guided saccades relative to the target location (White et al. 1994), such that collicular activity as a whole better reflects target location than saccade vector. However, our recent work has shown that the movement fields of memory-guided saccades are not shifted when a low-luminance background and post-saccadic feedback of target location eliminated this systematic dysmetria (Edelman and Goldberg 2001). In the present study we again failed to observe a systematic dysmetria for saccades made to blank space (as well as for those to the center of a square), so it is unlikely that a shift in the movement field could explain the lower discharge for saccades not made to a local landmark. Saccades towards a corner of the square were on the average slightly increased in amplitude relative to the other tasks, but we found no evidence that, saccade-by-saccade within this small amplitude range, discharge depended on saccade amplitude. Given that the systematic increase in amplitude for these saccades was so small compared to the other saccades (~5%), this suggests the results for saccades in the Vertex task can also not be explained by a shift in movement field.

The procedure in the Nothing task used in this study to elicit saccades to blank space was the same as that in the Memory task used in a recent study from this lab (Edelman and Goldberg, 2001). However, on the average saccade-related activity in this study's Nothing task was somewhat higher than that observed in the Memory task of the previous study. While this discrepancy may simply have resulted from a slightly different sample of neurons being recorded in the two studies, it may also have resulted from the dim boundary at the edge of the
illuminated projection screen used in this study (the previous study used a laser/mirror galvanometer system in near darkness). Whatever small effect these “global landmarks” had on neural activity was likely to have resulted from a mechanism different from that due to the presence of local landmarks near the saccade endpoint, since discharge was the same in the Nothing task as it was in the Center task, though in the latter the boundary provided by the large square was much more distinct and much closer to the saccade endpoint.

As in the previous report on visual target dependence (Edelman and Goldberg, 2001), we found that differences in activity across the tasks were evident even after taking account of saccade velocity. This provides further evidence that although superior colliculus activity influences saccade velocity tremendously (Stanford and Sparks, 1996), there is a partial dissociation of saccade-related activity and velocity. This dissociation may result from activity of neurons in other saccade-related areas that are not feature-selective and that influence premotor saccade areas in the brainstem via a pathway that bypasses the superior colliculus, or else may suggest that some of the more feature-selective neurons that we recorded do not project or else project less strongly to such premotor areas. In either case, it appears that neural activity in the superior colliculus is a more sensitive indicator of the properties of the saccade target than the velocity at which that saccade is made.

One plausible explanation for the slight displacement towards the center of the square of the endpoint of saccades made in the Vertex task is that although the cue indicating the target location was at the corner of the square, the visual system spatially averaged the adjacent red square segments, providing a point image on the colliculus skewed slightly eccentrically. This is reminiscent of the effect of lidocaine lesions in the colliculus: saccades made to stimuli slightly more eccentric than the center of the lidocaine locus are hypermetric, as if they are created by an averaging network that did not include the smaller saccade region (Lee et al. 1988). Similarly, the adjacent borders of the square provide an averageable component that is not balanced by a less eccentric component. This logic predicts that a saccade made to the
furthest corner of the square would be relatively hypometric, and a saccade made to the sides or other vertices would also be slightly skewed toward the center of the square. Noise in this averaging process could produce the increased saccade endpoint variability that we observed in the Vertex task compared to the Spot task.

The dependence of saccade-related activity on features at or near saccade endpoint may result from visual stimuli at or near the saccade target goal evoking visual responses in the neurons of the intermediate superior colliculus (Sparks and Hartwich-Young 1989), lateral intraparietal area (LIP) and frontal eye field that project to the intermediate layers of the colliculus (Paré and Wurtz 1997; Sommer and Wurtz 2000). Furthermore, neurons in area V4 of the macaque have been shown to increase their activity around the time of saccades to visual targets in their receptive fields (Fischer and Boch 1981a, b; Moore 1999; Moore et al. 1998). The sustained components of these visual responses could potentiate the presaccadic burst of the collicular neurons that actually drive the saccade, provided either the object is small enough to be considered by the oculomotor system to be a distinct saccade target or else that the object's spatial discontinuities, such as an edge or corner, are close enough to the saccade goal. Given that visual or attentional crowding resulting from lateral interactions in visual or parietal cortex may hinder perceptual processing (Bouma 1970; He et al. 1996; Intriligator and Cavanagh 2001; Levi et al. 1985), it may also be necessary for a local landmark to be spatially separated from other landmarks.

Our results suggest that the ability of local landmarks to enhance discharge and performance for the saccadic system is not an all-or-nothing phenomenon. Discharge for saccades made to the corner of a square, while elevated compared to saccades not made to a local landmark, was less than that when saccades were made to a small spot. Moreover, when a saccade was directed to the center of square whose size was varied we found that collicular discharge and saccade velocity increased gradually as an inverse function of square size. The real world, unlike the laboratory, is essentially devoid of small points of light (the night sky a
notable exception). Nevertheless, our data demonstrate that the small spot, present at the time of movement, is indeed an "optimal" stimulus for a saccade, at least when the saccade is made after an instructed delay. We found that increasing target size never increased saccade-related activity and saccade performance over that for movements to a small spot. This size-dependent continuum of activity and performance complements a recent finding suggesting a temporal continuum of visual guidance, in that perisaccadic discharge in the superior colliculus, saccade velocity, and endpoint precision are inversely dependent on the time between target disappearance and saccade initiation (Edelman and Goldberg 2001). In that study neural activity and metrics in a memory-guided task identical to that used here were only slightly enhanced relative to anti-saccade trials, in which no target appeared in the movement field. This suggests that in the present experiments, although the memory of a stimulus that has recently appeared may have slightly enhanced saccade-related discharge and metrics, additional, much stronger enhancement was provided by the presence of a local landmark at the saccade endpoint.

Although a major purpose of vision is to segment the visual scene and analyze its component objects, the major purpose of saccadic eye movements is not simply to guide the eyes to new objects, but to direct the eyes to visual elements that require foveation for further scrutiny, a process that may itself facilitate visual scene segmentation. It is thus not surprising if only saccades made toward spatial discontinuities in the visual scene have enhanced metrics and are accompanied by greater activity in the superior colliculus. Such visible local landmarks may comprise a saccadic oculomotor "menu" from which a target is subsequently selected for movement in a complex scene. Indeed, in tasks in which subjects are allowed to freely scan a visual scene, saccades tend to land near elements with local contrast, such as edges (Mannan et al. 1997, 1996; Reinagel and Zador 1999). Enhanced discharge in the superior colliculus for saccades to local landmarks may reflect a neural mechanism underlying such behavior.
REFERENCES


Mannan SK, Ruddock KH, and Wooding DS. The relationship between the locations of spatial features and those of fixations made during visual examination of briefly presented images. *Spat Vis* 10: 165-188, 1996.


TABLE AND FIGURE LEGENDS

Table 1 – Mean values of perisaccadic discharge and saccade metrical values across sample of neurons (n=44). For perisaccadic discharge and each measure of saccade metrics, a repeated measures analysis of variance procedure was performed followed by paired t-tests (whose resulting p-values were adjusted by Bonferroni correction (Glantz 1992). Superscripts on each value indicate the rank of the task for the particular measure, from highest to lowest. For each measure, values are assigned to the same rank only if no one value is significantly different from all other values in that rank. For example, the paired t-tests showed that for perisaccadic discharge Spot > Vertex, Spot > Center, Spot > Nothing, Vertex > Center, and Vertex > Nothing, but did not show a difference between the Center and Nothing tasks.

Fig. 1. Temporal and spatial schematics for the four tasks used in the experiments are shown. In all four tasks monkeys first fixated a central point. In the Spot task, after 300 ms of fixation, a small white square appeared in the center of the neuron’s movement field (whose boundary is indicated by the dashed line). After an additional 750-1000 ms monkeys had to make a saccade to the spot. The Nothing task was identical except that the spot in the movement field appeared for only 250 ms. The Vertex task was identical to the Nothing task except that a large, red square appeared on the screen situated so that its corner was located at the same position as the briefly appearing spot. The Center task was identical to the Vertex task except that the large square was situated so that the small square appeared centered within it. See text for details.

Fig. 2. Visual and motor-related activity of four neurons in the four tasks. A) Four panels on the left show spike rasters superimposed over spike density traces for a single neuron. For each of the four tasks, discharge aligned with target onset is shown on the left underneath the
schematic of the task, with the vertical dashed line representing the time of target appearance and each horizontal raster trace showing the data for one trial. On the right side under the schematic discharge aligned with saccade onset is shown. The vertical dashed line represents time of saccade initiation. Panel on the far right shows spike density traces of saccade-related activity of the four tasks superimposed. B,C,D) Discharge of three additional neurons. Conventions identical to A), except that schematics of the four tasks are omitted. See text for details.

Fig. 3. Scatter plots of summary data for perisaccadic activity recorded during Spot, Nothing, Vertex, and Center tasks for all 44 neurons in our sample. A) Perisaccadic activity in the tasks in which a local landmark was present at saccade endpoint (Spot & Vertex) is compared with discharge recorded when no tag was present (Nothing & Center). Plots of Spot vs. Nothing activity are superimposed on plots of Vertex vs. Center activity. Each dot represents mean spike density in a 20ms wide temporal window centered on saccade initiation for a single neuron in the two tasks. Dashed line represents points at which discharge would be equal in the two tasks. B) Perisaccadic activity in the tasks in which a large square was present (Vertex & Center) is compared with discharge recorded when no large square was present (Spot & Nothing). Other conventions as in A. C) Neural selectivity for the Vertex task relative to an average of activity in the Nothing and Center tasks is plotted against analogous selectivity for the Spot task. Selectivity was quantified by a contrast index (see Methods). Diagonal dashed line represents the loci of points at which neurons have equal activity in the Spot and Vertex tasks. Vertical line represents neurons in which discharge in the Spot task is equal to the average activity in Center and Nothing tasks. Horizontal line represents neurons in which discharge in the Vertex task is equal to the average activity in Center and Nothing tasks.
Fig. 4. Distribution of endpoints of rewarded saccades made while recording activity from a single neuron. For the Spot task (top panel), an ‘x’ represents the central fixation point, and the intersection of the two dashed lines represents the location of the small cue spot. For the bottom three panels the fixation ‘x’ is omitted and spatial scale is identical to that of the top panel. Each round dot marks the endpoint of a single saccade. See text for details.

Fig. 5. A) Discharge for two neurons recorded in the Center task while varying square size. Relative sizes of squares are shown attached to relevant plot of discharge. B) Mean perisaccadic discharge and normalized velocity for saccades to the centers of red squares of four different sizes (large, medium, small, spot) made during the recording of 15 neurons. Data for saccades to a spot of white light (Spot task) and for saccades to blank space (Nothing task) for these 15 neurons are also shown.
<table>
<thead>
<tr>
<th></th>
<th>Perisaccadic discharge (spk/s)</th>
<th>Peak saccade velocity (norm.)</th>
<th>Saccade amplitude (norm.)</th>
<th>Endpoint variability (norm.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spot</td>
<td>226$^1$</td>
<td>1.00$^1$</td>
<td>0.95$^2$</td>
<td>0.041$^2$</td>
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<tr>
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<td>0.83$^4$</td>
<td>0.93$^2$</td>
<td>0.059$^1$</td>
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<tr>
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<td>0.93$^2$</td>
<td>1.00$^1$</td>
<td>0.058$^1$</td>
</tr>
<tr>
<td>Center</td>
<td>148$^3$</td>
<td>0.88$^3$</td>
<td>0.94$^2$</td>
<td>0.061$^1$</td>
</tr>
</tbody>
</table>
Edelman & Goldberg
Fig. 2

A

Target onset       Saccade onset
250 spk/s
50 ms

Vertex

Spot

Nothing

Center

B

Spot

Nothing

Vertex

Center

C

Spot

Nothing

Vertex

Center

D

Spot

Nothing

Vertex

Center

Spikes/s

0 50 100 150 200 250 300 350 400 450 500

msec relative to saccade onset

Spot

Vertex

Nothing

Center
Figure 4
Edelman & Goldberg

A. Spot

B. Nothing

C. Vertex

D. Center