

Discharge of Superior Collicular Neurons During Saccades Made to Moving Targets

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SUMMARY AND CONCLUSIONS

1. The discharge of neurons in the deeper layers of the monkey superior colliculus was recorded during saccades made to stationary and to smoothly moving visual targets.

2. All neurons that discharged for saccades made to stationary targets also discharged during saccades made to moving targets, but there was a systematic shift in the saccade vector yielding maximal activity (i.e., center of the movement field) of collicular neurons for the latter class of movements. The shift moved the center of the movement fields toward larger-amplitude pursuit saccades for target motion away from the fovea, in comparison with saccades made to stationary targets. However, the discharge at the center of the movement field for pursuit saccades was 14% lower when averaged over the sample of recorded cells.

3. The saccades made during pursuit tracking of moving visual stimuli have different dynamics than saccades made to stationary targets. At similar amplitudes pursuit saccades are slower, and their velocity profiles often show secondary velocity peaks or inflection points and have longer-duration decelerating phases.

4. The combined experimental observations of a change in saccade dynamics and the shift in movement fields in collicular neurons for pursuit saccades are compatible with the hypothesis that saccades made to moving targets are controlled by neural processing in two partially separate pathways. In this theory, one path is concerned with correction of a presaccadic retinal position error (a path that includes the colliculus) and another path is concerned with position extrapolations based on the velocity of the moving target (a path that does not include the colliculus).

INTRODUCTION

When primates track smoothly moving visual stimuli that appear in their surround, they follow the moving target with a combination of pursuit movements and saccades (Fuchs 1967; Robinson 1965). In particular, when a stationary target on which a monkey is initially fixating suddenly begins to move at constant velocity, the eyes initially accelerate smoothly in the direction of the target motion. This initial response is followed by a saccade that places the fovea close to the position of the moving target. Subsequently, additional saccades may be made to again position the fovea near the moving target. Such "catch-up" saccades made to smoothly moving targets will be called "pursuit saccades" throughout this paper, whereas saccades to stationary targets will be referred to as "fixed saccades."

Because monkey pursuit saccades land near the moving target even when target motion is randomized (Keller and Johnsen 1990), an interesting question arises concerning the nature of the neural mechanisms that produce this behavior

in the face of the well-documented delays that exist in the visual and oculomotor system. For example, information about retinal position error of the target 70–80 ms before a saccade does not affect the metrics of the subsequent movement (Becker and Jürgens 1979). Because the accuracy of pursuit saccades cannot be accounted for by the use of this delayed position error information alone, it has been hypothesized that the saccadic system also uses information about prior target motion to plan pursuit saccades (Keller and Johnsen 1990; Robinson 1973). Humans show similar patterns of alternating pursuit and saccadic movements when tracking smoothly moving visual targets, but their relative lack of saccadic accuracy for moving targets has raised questions about the use of predictive signals based on target velocity that seem to be required to explain the accuracy achieved by monkeys (Heywood and Churcher 1980; Ron et al. 1989).

The use of both retinal position and velocity error in planning pursuit saccades, at least in the monkey, leads to a further suggestion that the pathways generating pursuit saccades are partially segregated. According to this theory, one pathway is responsible for generating a saccadic error signal based on the retinal position error that existed at some point in time before saccade onset. This pathway would also be active for saccades to stationary targets, a situation in which the retinal error would not be changing before the saccade started. The other pathway originates with neural circuits that compute retinal error velocity but would contain additional neural structures involved in converting information about target motion into a corrective saccadic signal. These two streams of saccadic control signals would then have to be combined and coordinated to produce an accurate pursuit saccade that lands on the moving target.

In the present paper we examine the dynamics of pursuit saccades and the accompanying discharge of neurons in the deeper layers of the monkey superior colliculus (SC), a structure known to be involved in the generation of fixed saccades. We ask whether the discharge of these collicular neurons reflects the addition of the visual motion information when pursuit saccades are made, or whether they continue to code only the position error component for these saccades. If the collicular neurons incorporate visual motion information completely, their movement field tuning properties for pursuit saccades should be indistinguishable from those for fixed saccades. On the other hand, if the colliculus accounts only for the position error at some time before saccade onset, the movement field center of each neuron for pursuit sac-

cadences should be shifted compared with the tuning for fixed saccades, because of the additional target-velocity-related motor component added downstream from the SC.

We first present evidence that pursuit saccades are generated by partially separate pathways that contain different amounts of transmission and processing delays. The evidence is based on a close comparison of saccade dynamics in pursuit saccades and in fixed saccades. Then we present data that suggest that the SC is involved only in the position correction component of pursuit saccades. Some of the results described here have been presented previously in abstract form (Keller et al. 1996).

METHODS

Three adolescent male monkeys (2 *Macaca mulatta* and 1 *Macaca fascicularis*) were used in this study. All experimental protocols were approved by the Institutional Animal Care and Use Committee at the California Pacific Medical Center and complied with the guidelines of the Public Health Service policy on Humane Care and Use of Laboratory Animals. The monkeys were prepared for chronic recording of eye movements and single neurons by implantation of three devices under isoflurane gas anesthesia and aseptic surgical conditions. 1) A stainless steel recording chamber was placed stereotaxically on the skull, slanted posteriorly at an angle of 38° in the sagittal plane and aligned on the SC. 2) A head restraint consisting of two light stainless steel tubes was implanted transversely. The chamber and retraining tubes were secured to the bone with dental acrylic and small vanadium bone screws. 3) A coil of Teflon-coated stainless steel wire was implanted under the conjunctiva of one eye (Judge et al. 1980). Standard operating room and recovery procedures that have been described in detail elsewhere were followed (Keller and Edelman 1994). After complete recovery the animals were trained to climb voluntarily from their cages into a customized primate chair for daily experimental sessions.

Signals of horizontal and vertical eye position were obtained from the implanted search coil and external magnetic fields. Horizontal and vertical eye velocity was obtained by analog differentiation (with a cutoff frequency of 170 Hz) of the position signals. Data presented here are given as radial eye position and velocity, each computed by the Pythagorean sum of the component signals.

The animals were trained to execute behavioral paradigms for liquid rewards and were allowed to work to satiation during experimental recording sessions. Behavioral paradigms, visual displays, and storage of data were under the control of a real-time program running on a laboratory PC system. Horizontal and vertical eye position and velocity recordings were sampled at 1 kHz and stored on computer disk. Visual targets were back-projected on a translucent screen with an oscilloscope projector system (Crandall and Keller 1985).

We recorded from individual neurons in the deeper layers of the SC as the animals made saccades to stationary visual targets that appeared at eccentric positions on the screen. First, the optimal direction for each recorded cell for fixed saccades was determined from an on-line display of histograms of perisaccadic discharge for different target directions. After this direction had been determined, we had the monkey make saccades to stationary targets located at different amplitudes along this best direction. From these data we were able to plot the amplitude movement field (for the best direction) of each cell in subsequent off-line analysis. Next, for each cell, we had the monkey make pursuit eye movements in the best direction determined as just described. For pursuit trials the animal initially fixated a central spot that then suddenly stepped to an eccentric position and began to move at constant speed in the same direction as the preferred direction of the cell. For a

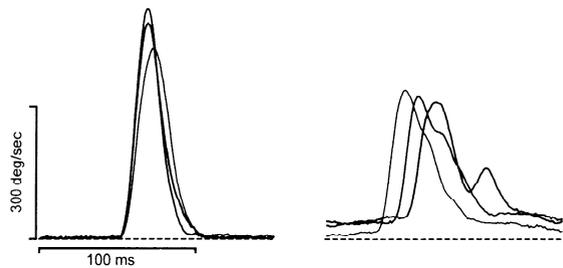


FIG. 1. *Left*: saccadic velocity profiles for 3 saccades made to stationary visual targets. *Right*: saccadic velocity profiles for 3 saccades made to visual targets moving at constant velocity. In all cases the saccades were of similar amplitude ($\sim 10^\circ$). The movements were all aligned on saccade onset, but pursuit saccades were then offset by increments of 10 ms so that the decelerating velocity phase of each individual movement could be seen more clearly. Dashed horizontal lines: zero velocity.

particular cell a narrow range of target speeds (typically 40–60°/s) was used and the initial step size (typically away from the fovea in the direction of target motion) was varied from 2 to 6° to produce saccades of the variable size needed to plot movement fields under pursuit conditions. If the cell had a small amplitude value for its movement field center, the target speed range was reduced (typically 20–40°/s). In some cases when activity for small saccades was desired, the target jumped in the null direction of the neuron before it smoothly moved across the fovea and into the preferred direction. However, in this case only saccades made in the direction of target motion were measured. Spline fits to the discharge data for the movement fields were computed with the Matlab Spline Toolbox (The Mathworks).

Single spikes in the amplified neural recording were discriminated with a standard electronic window discriminator based on both amplitude and time constraints, and the discriminated spikes were stored as counts in register with the analog eye data at each millisecond sample interval.

RESULTS

We recorded the saccadic eye movements made to stationary and moving targets and the discharge that accompanied these eye movements in the SC in the three monkeys. Figure 1 presents evidence that pursuit saccades have different dynamics than fixed saccades. Sample eye velocity profiles for fixed saccades are shown on the *left*, whereas sample velocity profiles for pursuit saccades are on the *right*. In all cases the amplitude of the saccades was $\sim 10^\circ$. The sample saccades were selected from the data for one animal and are typical of the many hundreds of each type examined in the three animals. Comparison of the two sets of examples illustrates that pursuit saccades were considerably slower than fixed saccades, an observation quantified by fitting linear regressions to the data relating peak saccadic velocity to saccadic amplitude (main sequence analysis). For all three animals the intercepts of the regression for pursuit saccades were significantly lower than those computed for fixed saccades (t -tests, $P < 0.01$), whereas the slopes of the regressions for the two types of saccades were not significantly different in two animals (t -tests, $P > 0.2$). In the remaining animal the slope of the regression was lower for pursuit saccades, but at a lower level of statistical significance ($P < 0.05$). The number of saccades of either type for any one animal ranged from 162 to 391 for the main sequence analysis. Only saccades up to 20° in amplitude were included in the analysis

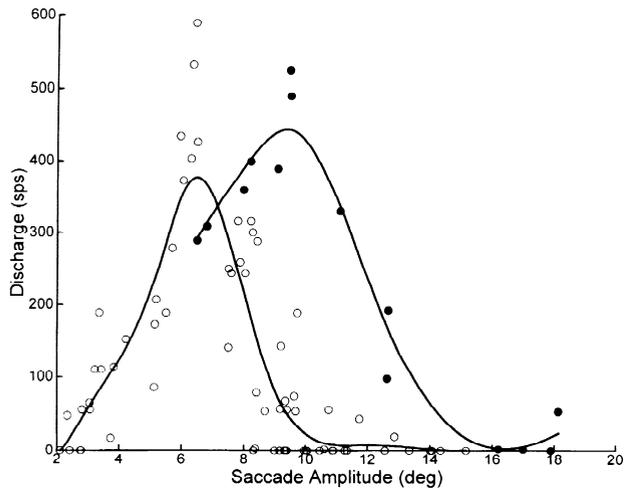


FIG. 2. Movement field plots for 1 typical neuron recorded in the deeper layers of the superior colliculus. All saccades were made in the preferred direction for the neuron and discharge was quantified as explained in the text. Target speed was $60^\circ/\text{s}$ and initial step size was varied from 2 to 6° . Open symbols: saccades made to stationary targets. Filled symbols: saccades made to moving targets. Smooth curves fit through data points of each type are cubic spline interpolations.

because saccades of this size were the largest pursuit saccades produced with our stimulus conditions. The relatively small amplitude range justified the use of a linear regression instead of an exponential fit for the main sequence analysis. These results show that pursuit saccades are slower than fixed saccades.

Figure 1 also illustrates that pursuit saccades have more variable and prolonged decelerating velocity phases in comparison with the very stereotyped, smooth decelerations for saccades to stationary targets. The examples for pursuit saccades shown on the *right* illustrate the range of the observed behavior: two clear peaks in the velocity profile, obvious inflection points on the decelerating phase, or a prolonged decelerating component. This varied behavior was measured as the skewness of the velocity profiles, defined as the duration of the acceleration phase (the time to the 1st velocity peak) divided by the total saccade duration (Van Opstal and Van Gisbergen 1987). Skewness values of 0.5 correspond to symmetric saccades, whereas skewness values greater or less than 0.5 imply that the acceleration or deceleration phase, respectively, of the velocity is longer. The mean values of skewness for fixed saccades were 0.5 ± 0.01 (SE), 0.48 ± 0.01 , and 0.46 ± 0.02 in the three monkeys. The mean values computed for pursuit saccades were 0.45 ± 0.01 , 0.4 ± 0.02 , and 0.34 ± 0.07 , respectively. The differences in mean skewness for the two types of saccades were significant (t -tests, $P < 0.05$) in all three animals. In summary, pursuit saccades have a longer decelerating phase than fixed saccades and often show prominent bumps on the declining phase of the velocity profiles that were not present for saccades to stationary targets.

Next we turn to the discharge of single neurons recorded in the SC. Neural responses for fixed and for pursuit saccades were recorded in separate blocks of trials as described in METHODS. Thirty neurons in the three monkeys were studied during both types of saccades. All cells had a burst of discharge that began ~ 20 ms before saccade onset and declined

rapidly during the movement for saccades made to the center of the cell's movement field. The cells were recorded at depths from 1.0 to 2.5 mm from the dorsal surface of the SC. Some also showed a sustained presaccadic discharge in a delayed saccade paradigm. Thus it is likely that the sample of cells included both burst (or discrete burst) neurons and buildup (or prelude burst) neurons (Glimcher and Sparks 1992; Munoz and Wurtz 1995). The discharge rate of each neuron was quantified as its mean rate over the 10-ms period just before saccade onset. Only the discharge for saccades in the best direction for each unit was studied as explained in METHODS.

An example of the amplitude movement fields that were obtained with this analysis is shown in Fig. 2 for one cell. The points shown by the open circles represent the discharge of the cell for fixed saccades of the amplitudes shown on the abscissa. The points shown by the filled circles represent the discharge in the same cell for pursuit saccades. Cubic smoothing splines (shown as the solid curves in Fig. 2) were fit through the data points to delineate the movement fields of the cell for each type of saccade. The cell shown in Fig. 2 discharged best for fixed saccades $\sim 6.5^\circ$ in amplitude and showed a lowered discharge for movements of both smaller and larger amplitudes. For pursuit saccades the cell showed the highest discharge for movements of $\sim 9.5^\circ$ in amplitude, a magnitude associated with very little discharge for fixed saccades.

The center of the movement fields and the corresponding discharge rate at the center of the fields for both types of saccades were determined from the cubic spline fits for all 30 SC neurons. The results of these measurements are shown in Fig. 3. The data for the locations of the movement field centers are shown in Fig. 3A. Each data point is for one cell plotted with the center of the cell's movement field determined for fixed saccades on the abscissa and the center of the movement field for pursuit saccades on the ordinate. The dashed line illustrates the locus of values that would

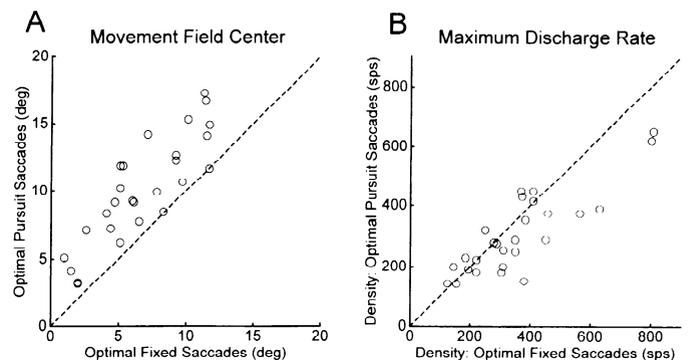


FIG. 3. A: summary figure showing the shift in movement field centers for superior colliculus neurons for pursuit saccades vs. fixed saccades. Each data point represents 1 neuron with the center of its movement field as determined for fixed saccades on the abscissa and the center of the movement field as determined for pursuit saccades on the ordinate. Dashed line: expected trend of the data if the movement field centers remained the same for both types of saccades. Data points above this line: shifts in movement field centers toward larger movements for pursuit saccades. B: discharge rate at the center of the movement field for collicular neurons for pursuit saccades vs. fixed saccades. Each data point represents 1 neuron. Dashed curve: expected trend of the data if discharge remains the same for the 2 types of saccades.

have been obtained if the movement field centers had remained the same for both types of saccades. Clearly, almost all cells lie above the dashed line, indicating that there was a shift in the movement field centers toward larger amplitudes in the direction of target motion for pursuit saccades. This means that cells showed the same discharge for a pursuit saccade that was larger than a fixed saccade, as if the pursuit saccade from the perspective of the colliculus had been planned as a smaller saccade. The discharge rates at the centers of the movement fields for the two types of movements are shown in Fig. 3B. Each symbol represents the measurements for one cell, with peak discharge for fixed saccades on the abscissa and that for pursuit saccades on the ordinate. The data indicate that cells always participated in each type of saccade, but the majority of cells showed a slightly lower discharge for pursuit saccades. The average discharge rate for fixed saccades was 324 spikes/s, whereas it was 277 spikes/s for pursuit saccades—a difference of ~14%.

DISCUSSION

Delays present in the visuoculomotor system prevent changes that occur in target position error after ~70–80 ms before the onset of a saccade from affecting saccade accuracy (Becker and Jürgens 1979). Nevertheless, saccades made to moving targets are still very accurate (Keller and Johnsen 1990). A simple explanation for this accuracy in pursuit saccades is that they are produced by a system that uses a past measure of the position error and combines this information with an additional correction based on extrapolation of the target velocity signal also measured at a prior epoch (Robinson 1973).

The experimental observation that the accuracy of saccades made to moving targets was compromised by lesions to the cortical middle temporal visual motion processing area, whereas saccades to stationary target were not affected by the lesions, showed that the position error processing portion of the system and the velocity error portion are partially separated in the brain (Newsome et al. 1985). The present study shows that this separation extends to the SC, which, in contrast to the cortical middle temporal area, seems to be involved exclusively in the position error portion. This assertion can be seen most clearly from examination of the shift in the movement field of the collicular cell illustrated in Fig. 2. The colliculus contains a motor map of the contralateral visual field. For any saccade a large population of cells are active with the most active region in the population defining the saccade vector. Thus the cell illustrated in this figure is located on the collicular map at about an eccentricity of 6.5°. Because the location of a particular cell on the map does not change, one can surmise that when it is most active a saccade of 6.5° is being coded by the population discharge of the SC. Yet for pursuit saccades the movement ends up as a 9.5° saccade. This observation is consistent with the hypothesis that the discharge of the SC called for a 6.5° movement and the additional increment in movement size was due to a target velocity correction that was combined with the collicular correction at some site downstream from the colliculus.

The experimental observation that pursuit saccades exhibit

a prolonged duration during the declining phase of the eye velocity profiles is also predicted if saccadic extension due to target velocity extrapolation is present and the parallel signal generating this extension has a slightly longer latency than the position correction path through the SC.

Although it has been shown that the SC receives a direct projection from the cortical middle temporal area in the monkey, this projection terminates exclusively in the superficial visual layers (Ungerleider et al. 1984) and not in the deeper layers, where the motor-related neurons for the present study were recorded. In light of these anatomic findings it is perhaps not surprising that saccade-related neurons in the SC do not reflect the target velocity extrapolation signals required for pursuit saccades.

A similar study during pursuit saccades has been conducted for neurons in the frontal eye fields (Shi et al. 1995). A difference in this study in comparison with our study in the colliculus was that directional tuning properties of frontal eye field neurons were compared for pursuit and fixed saccades. In contrast to neurons we recorded in the SC, some neurons in the frontal eye field appeared to contain both components of the control signal needed for accurate pursuit saccades. It is difficult to make more detailed comparisons between the discharge of frontal eye field neurons and SC neurons for the two types of saccades until further details on the discharge patterns of the former cells are reported.

A systematic shift of the movement fields in collicular saccade-related neurons for remembered targets in comparison to visually guided saccades has also been reported (Stanford and Sparks 1994). Although the experimental paradigm is very different from our visual motion case, the results are similar in that both produce a dissociation between saccade metrics and the activity on the collicular motor map.

This work was supported by National Institutes of Health Grants EY-06860 and 5 T32 GM-08155.

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Received 2 July 1996; accepted in final form 7 August 1996.

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