

Neural Correlates of Target Choice for Pursuit and Saccades in the Primate Superior Colliculus

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Summary

We have examined the role of the superior colliculus (SC) in choosing targets for pursuit and saccades by comparing neuronal activity at sites representing the possible choices. After recording during a two-alternative forced-choice paradigm, we measured the difference in activity of the populations representing the two choices by computing receiver operating characteristic (ROC) curves on a millisecond timescale. A signal indicating the correct choice emerged from noise over time, forming a tradeoff between speed and accuracy. The observed performance corresponded to particular points along the predicted speed-accuracy curves—pursuit emphasizing speed and saccades emphasizing accuracy. These results show that activity from the same set of neurons in the superior colliculus can predict target choices for both pursuit and saccades.

Introduction

Choosing where to look involves two different types of eye movements—pursuit and saccades. Saccades are brief high-velocity movements that quickly orient the eyes toward visual targets (Sparks and Mays, 1990), whereas pursuit is a continuous slow movement that smoothly rotates the eyes to maintain alignment with moving targets (Keller and Heinen, 1991; Lisberger et al., 1987; Krauzlis and Stone, 1999). The neural basis of saccade selection has been the focus of extensive research (Schall and Thompson, 1999), but we are only beginning to understand the neural mechanisms underlying pursuit selection (Ferrera and Lisberger, 1997; Krauzlis et al., 1999; Recanzone and Wurtz, 2000; Tanaka and Lisberger, 2001). Because pursuit and saccades typically follow the same visual target, they appear to be guided either by the same decision process or by different but coordinated decision processes (Krauzlis and Stone, 1999). However, two observations indicate that selection by the two movement systems is not strictly yoked. First, pursuit latencies historically have been reported as substantially shorter than saccade latencies (Leigh and Zee, 1999), suggesting that target choices are made more quickly for pursuit than for saccades. Second, pursuit and saccades do not always give the same answer. For example, when presented with “target” and “distractor” stimuli moving in opposite directions, human subjects sometimes incorrectly begin pursuit in the direction of the distractor, before reversing their pursuit direction and then making their first (cor-

rect) saccade to the target stimulus (Krauzlis et al., 1999). Thus, although pursuit and saccades are usually coordinated, the linkage between the two movement systems is not absolute, and little is known about the possible underlying neural mechanisms.

We have examined this issue by testing how neuronal activity in the primate superior colliculus (SC) might be read out to choose targets for the two types of eye movements. The intermediate layers of the SC form a retinotopic map for the control of eye and head movements (Sparks, 1999; Wurtz and Albano, 1980). In most of the SC, “buildup” and “prelude burst” neurons in these intermediate layers modulate their firing rates during the preparation and execution of saccades (Glimcher and Sparks, 1992; Munoz and Wurtz, 1995). Numerous previous studies have examined how these SC neurons are involved in the process of choosing targets for saccadic eye movements (Basso and Wurtz, 1997, 1998; Glimcher and Sparks, 1992; Horwitz and Newsome, 1999, 2001a, 2001b; Kustov and Robinson, 1996). In the rostral portion of the SC map, corresponding to the representation of the central visual field, many neurons also modulate their firing rates during pursuit eye movements (Krauzlis et al., 1997, 2000). Although the SC is not usually considered part of the pathways for pursuit eye movements, altering activity in the rostral SC by microstimulation or chemical microinjection modifies the metrics of pursuit (Basso et al., 2000), consistent with the idea that activity in the SC involves a signal used by pursuit as well as by saccades. We now report that buildup neurons in the rostral SC exhibit higher activity for target than for distractor stimuli for both pursuit and saccades. Moreover, by performing a Monte Carlo analysis of the population activity, we show that the time course of this preference can predict the timing of target choices for pursuit and saccades.

Results

We trained monkeys to track one of two differently colored stimuli based upon a color cue provided earlier on each trial. On pursuit trials (Figure 1A), two moving stimuli appeared in opposite visual hemifields at an initial eccentricity of 3°–4° and moved horizontally toward the center of the display at 15°/s. We chose our recording sites so that one of the two stimuli fell within the response field (RF) of the neuron under study (Figures 1A and 1B) and adjusted the horizontal starting positions to eliminate the need for any corrective saccades. For pursuit, we restricted our analysis to trials that were free of saccades for at least 100 ms before and 500 ms after the appearance of the moving stimuli (as illustrated by the sample trace of eye velocity in Figure 1C). On saccade trials (Figure 1B), the two stationary stimuli appeared at similar locations as on pursuit trials, but remained stationary. By randomly switching the color of the cue and the locations of the two stimuli, either the cued target or the noncued distractor appeared within the RF on interleaved trials.

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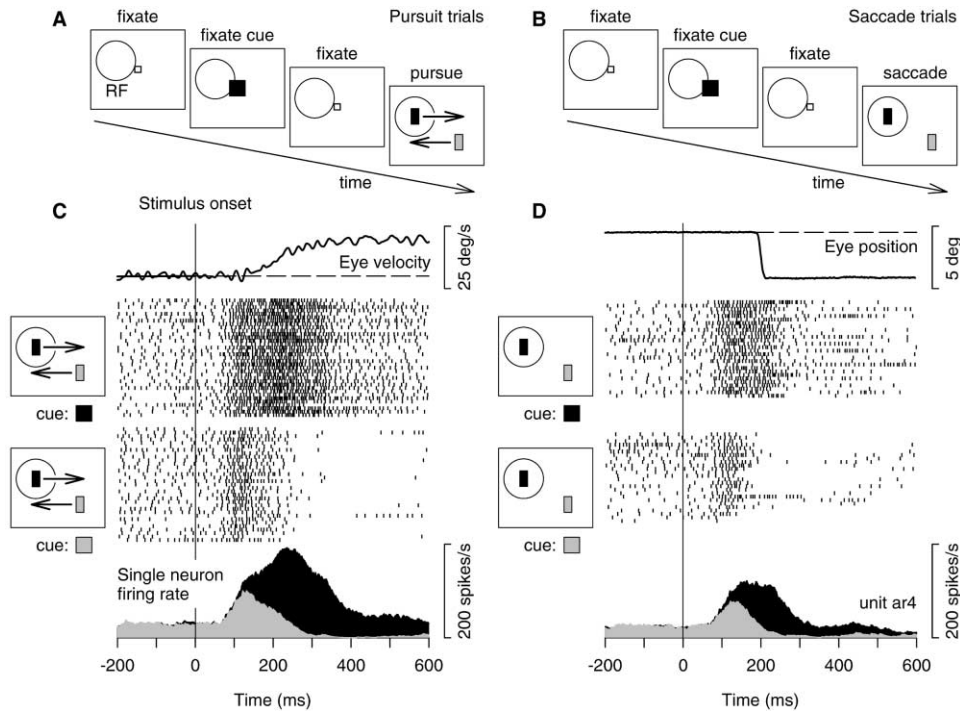


Figure 1. Activity of a Neuron in the Rostral SC during Selection of Pursuit and Saccadic Eye Movements

(A) Schematic depiction of the display sequence on pursuit trials. The monkey fixated the small central square and larger square cue before tracking the matching target stimulus when the fixation square was extinguished. Target and distractor stimuli moved at 15°/s in directions indicated by arrows. Actual color of target and distractor stimuli was red and green.

(B) Same as (A), except for saccade trials. Stimuli appeared at similar locations but did not move.

(C) Activity of one neuron during pursuit trials. From top, the stack of records shows eye position from one trial, raster display of neuron responses from trials during which the target stimulus appeared within the response field, raster display from trials with the distractor in the response field, and the average firing rates for target (black) and distractor (gray) trials, shown as a spike density function. All records are aligned with respect to target and distractor appearance, defined as 0 ms.

(D) Activity of same neuron as in (C), but from interleaved saccade trials. We attribute the slightly lower activity during saccades than during pursuit to the fact that the target location was slightly beyond the exact center of the neuron's response field; hence, on pursuit trials, the target moved through the center of the response field and elicited higher activity.

Buildup neurons in the rostral SC exhibited a preference for target over distractor stimuli, for both pursuit (Figure 1C) and saccades (Figure 1D). Initially (75–150 ms after stimulus onset), neurons exhibited changes in activity that did not depend on the identity of the stimulus in the RF, as indicated by the early superposition of the spike density functions from target (black) and distractor (gray) trials. Later (150–250 ms), neurons showed elevated activity if the stimulus in the RF was a target and depressed activity if the stimulus in the RF was a distractor. We observed this delayed selectivity for target stimuli across our sample of buildup neurons recorded in the rostral SC ($n = 83$). Activity later in the trial (200–250 ms) tended to be significantly higher for target than for distractor stimuli; we found a significant difference (Wilcoxon rank sum test, $p < 0.05$) during this interval for most neurons during pursuit (66%, 55/83) and saccades (82%, 68/83). In contrast, activity during the initial period (100–150 ms) generally did not show a difference; only a minority of neurons showed a significant difference during this interval (5/83 and 7/83 for pursuit and saccades, respectively).

To evaluate the temporal relationship between the neural events and the behavioral response, we aligned

the neuronal activity on the initiation of the monkey's eye movements. For example, Figure 2 shows the same data for the neuron illustrated in Figure 1, but temporally realigned with respect to the onset of pursuit (Figure 2A) and saccades (Figure 2B). As indicated by the separation of the spike density functions prior to movement onset, the elevated activity for target stimuli preceded the initiation of both pursuit and saccades. We found similar differences in activity prior to movement onset in many, but not all of our neurons. Activity in the 50 ms interval immediately preceding movement onset was significantly higher for target than for distractor stimuli (Wilcoxon rank sum test, $p < 0.05$) for 36% of the neurons on pursuit trials (30/83) and 66% of the neurons (55/83) on saccade trials.

Is this selective activity large enough and does it occur soon enough to guide the launching of both pursuit and saccade eye movements? To address this question, we adopted the perspective of a hypothetical monitor that read the activity of our SC neurons. Because movement choices must be made on each trial, this monitor could not accumulate information from a single neuron over many trials, as is typically assumed in analyses of neuronal data (e.g., Figures 1 and 2). However, it could pool

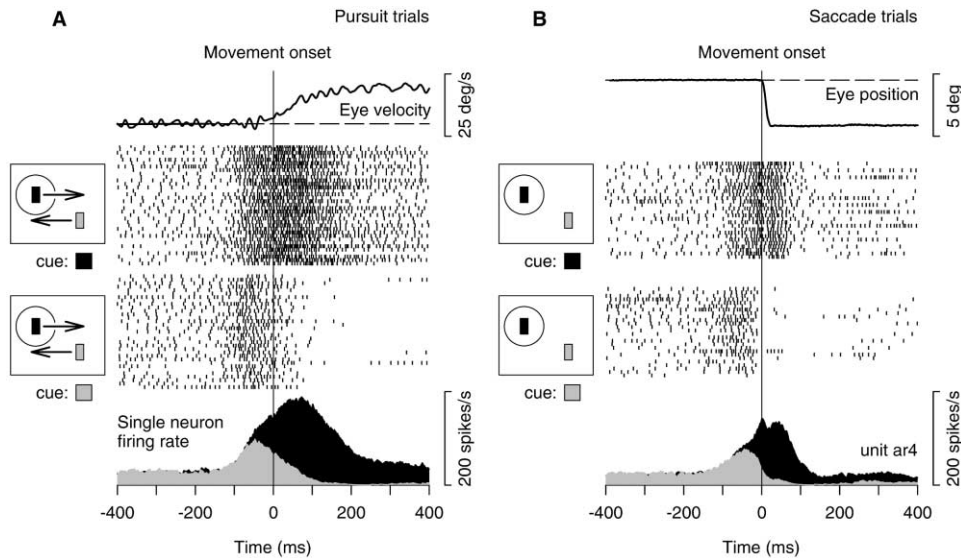


Figure 2. Activity of a Neuron in the Rostral SC during Selection of Pursuit and Saccadic Eye Movements, Aligned with Respect to Movement Onset

Data are from the same neuron as in Figure 1 but are temporally realigned with respect to the onset of the pursuit (A) or saccadic (B) eye movement. Other conventions are the same as in Figure 1.

information from many SC neurons, and it is known that information about eye movements is represented in the SC by activity distributed across a large population of neurons (Lee et al., 1988). We therefore estimated the population activity we might have observed if we had been able to study each of the neurons in our sample at the same time on single trials.

For this Monte Carlo analysis, we compared the activity of “neurons” representing the target location to the activity of “antineurons” (Britten et al., 1992) representing the alternative, distractor location (Figure 3A). The populations of neurons and antineurons were constructed by randomly selecting one spike train from the set of data recorded from each of our neurons. Spike trains from trials in which a target stimulus was located in the RF contributed to the population of neurons; spike trains from distractor trials contributed to the population of antineurons (Figure 3B). The histograms in Figure 3C show the average firing rates for the population of neurons (black) and antineurons (gray) obtained after one random sampling of spike trains from pursuit trials. These records reconstruct the activity we might have observed if we had recorded from buildup neurons in both SC simultaneously during a single pursuit trial. The preference for target over distractor stimuli is less dramatic for the population average than for the sample neuron (Figures 1 and 2), because these averages include activity from every neuron, even those with poor selectivity. The reconstructed activity is therefore based on the conservative assumption that the downstream monitor does not know which neurons are selective for the target, but only knows the locations represented by the neurons.

We then tested whether this reconstructed population activity could predict the monkey’s target choices. We constructed receiver operating characteristic (ROC) curves at each time point based upon the two distribu-

tions of firing rates (Figure 3C) and measured the area under each ROC curve for each millisecond during the course of the reconstructed trial (Figure 3D). The ROC area fluctuated around a value of 0.5 (solid line in Figure 3D) in the interval prior to the presentation of the two visual stimuli (–100 to 0 ms), as might be expected because the baseline firing rates of the neurons and antineurons were essentially identical. However, the ROC area remained near 0.5 even after the firing rates increased (50 to 150 ms), because the firing rates for the two populations initially increased in a similar manner. The ROC area increased only after the firing rates reached their peaks, because the activity of the antineurons decreased faster than the activity of the neurons, perhaps as the result of a competitive interaction or a delayed inhibitory input.

To test whether the ROC area from the reconstructed population firing rates could predict the monkey’s pursuit and saccade choices, we tested two simple decision rules. The first rule was time-based—we assumed that the choice involved waiting until a particular time and that the selection of the target was determined by the value of ROC area at that time point. For example, in the sample trial shown in Figure 3D, choices made before 100 ms would fluctuate between the two stimuli, but choices made after 150 ms would all be in favor of the target stimulus. The second rule was criterion based—here we assumed that the choice involved waiting for a criterion difference in activity between the two populations. With this rule, the timing of the movement would be predicted by when the ROC area deviated from chance (0.5) by some criterion amount, and the sign of this deviation would predict the target of the movement. For example, in the sample trial (Figure 3D) the ROC area reached the upper criterion (dotted line) at approximately 150 ms after stimulus onset, predicting a correct choice in favor of the target stimulus.

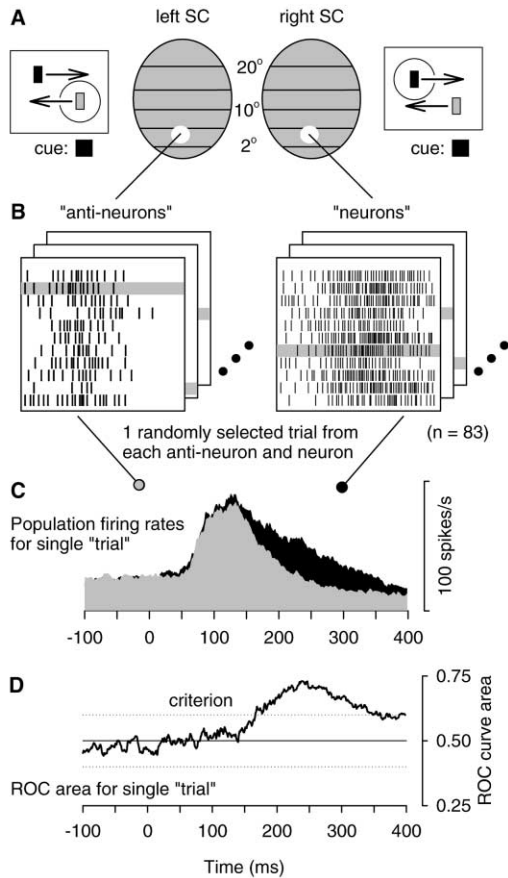


Figure 3. Prediction of Pursuit and Saccade Choices on Simulated Trials

(A) The predicted choices were based upon comparing the population activity at the two SC sites representing the target and distractor stimuli. In this example taken from pursuit trials, the target stimulus (black) appears in the left visual field and is represented by neurons in the right SC, whereas the distractor stimulus (gray) is represented by antineurons in the left SC.

(B) Spike trains from each neuron are depicted on separate sheets. We randomly selected one spike train (highlighted in gray) from each neuron ($n = 83$) when the target was in the RF (neurons) and when the distractor was in the RF (antineurons) to obtain matched pairs of neuronal activity in the two populations.

(C) Average firing rates for the population of neurons (black) and antineurons (gray) for a single simulated trial.

(D) The area under the ROC curve is shown as a function of time based on the distributions of neuron and antineuron firing rates. Solid horizontal line indicates an ROC area of 0.5, corresponding to chance performance. Dotted horizontal lines indicate a decision criterion of 0.6 (0.4) in favor of the target (distractor).

To compare the predictions of these decision rules to the observed behavior, we used a bootstrap method to generate many reconstructed trials and many predicted choices. The traces in Figure 4 show the results from 1000 pursuit trials (Figures 4A and 4C) and 1000 saccade trials (Figures 4B and 4D). The top traces in each panel show the average ROC areas as a function of time (thin lines indicate 1 SD), and the lower traces show the time-dependent performance predicted (% correct) by applying the time-based decision rule to the ROC areas from each of the 1000 reconstructed

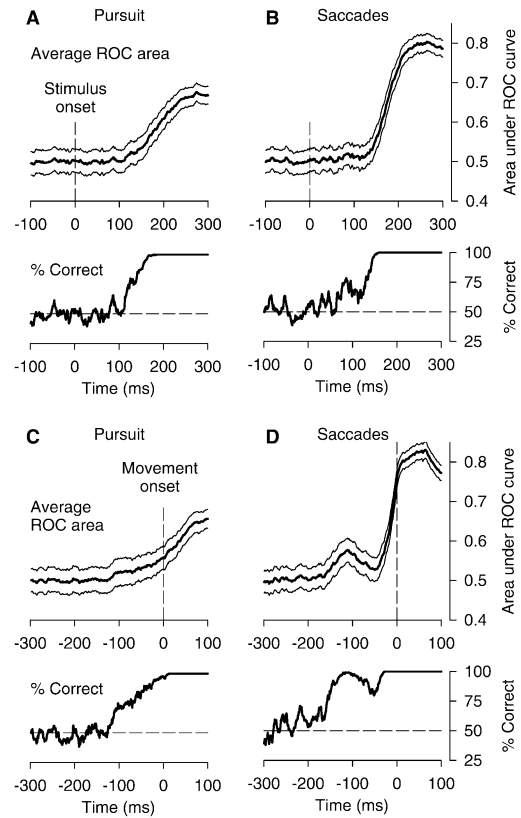


Figure 4. Summary of Simulated Trials and Predicted Choices Based on the Time-Based Decision Rule

(A) Upper trace shows the average ROC area from 1000 simulated pursuit trials plotted as a function of time; thinner lines indicate 1 SD. Lower trace shows the percentage of correct trials as a function of time predicted by the time-based decision rule. Vertical dashed line indicates time of stimulus onset, defined as time zero.

(B) Same as (A), except for saccade trials.

(C and D) Same as (A) and (B), except that the spike trains for these simulations were aligned with respect to movement onset for pursuit (C) and saccades (D) rather than stimulus onset. Vertical dashed line indicates time of movement onset, defined as time zero.

trials. When the neuronal activity was aligned with respect to stimulus onset (Figure 4A and 4B), the predicted choices were mostly near chance (50% correct) for decisions made within 100 ms of stimulus onset, but improved sharply after 125 ms and achieved near-perfect performance at approximately 150 ms after stimulus onset for both pursuit and saccades. When the neuronal activity was aligned with respect to movement onset (Figures 4C and 4D), the predicted performance improved from chance more than 100 ms before movement onset; predicted performance was perfect at saccade onset (100% correct) and almost perfect at the time of pursuit onset (97% correct).

To test the criterion-based rule, we applied a range of criteria to the ROC areas from the reconstructed pursuit and saccade trials. Because this decision rule involves waiting for a criterion change in ROC area after the appearance of the target and distractor stimuli, we applied it only to the neuronal data aligned with respect to stimulus onset. As might be expected, the choice of criterion had a large effect on the accuracy (% correct),

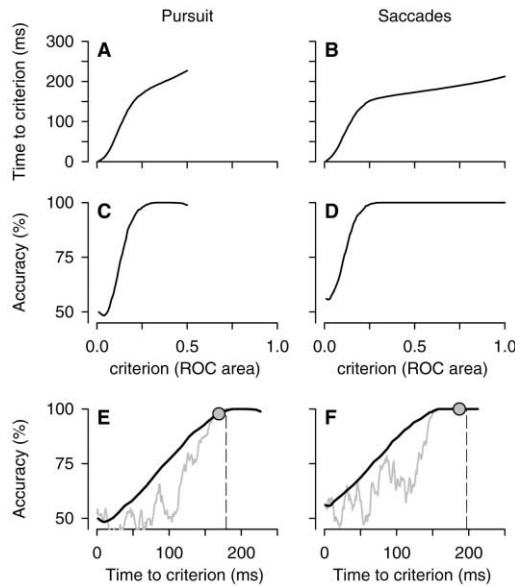


Figure 5. Predicted Tradeoffs between Speed and Accuracy

(A and B) The average time at which the criterion is first exceeded is plotted as a function of criterion, applying the criterion-based rule to the same 1000 simulated pursuit and saccade trials analyzed in Figure 4.

(C and D) Accuracy (percent correct decisions) is plotted as a function of criterion.

(E and F) Predicted speed-accuracy tradeoffs for pursuit and saccades, obtained by plotting accuracy from (C and D) against time to criterion from (A and B). The gray circles indicate locations along the speed-accuracy curves corresponding to 169 ms for pursuit (10 ms before the observed latency of 179 ms) and 187 ms for saccades (10 ms before the observed latency of 197 ms). The gray traces reproduce the predictions obtained from the time-based rule shown previously in Figures 4A and 4B.

as well as on the timing of the predicted choices. The plots in Figures 5A–5D summarize how predicted timing (Figures 5A and 5B) and accuracy (Figures 5C and 5D) varied as a function of criterion. Plotting these timing and accuracy results against each other shows the predicted speed-accuracy tradeoffs that would be expected if the choices were made by applying a criterion-based rule to the activity of these neurons (black lines in Figures 5E and 5F). For lower criteria (close to 0.5), pursuit and saccade choices were largely determined by chance fluctuations in ROC area, resulting in quick choices (<50 ms) but low accuracy (~50% correct). For higher criteria, the outcome was less affected by noise, resulting in higher accuracy but later choice times. Comparison of the results from the criterion-based rule to those from the time-based rule (gray traces in Figures 5E and 5F) shows that the criterion-based rule generally predicted higher accuracy and produced a more consistent relationship between speed and accuracy.

Our pursuit and saccade data were obtained from correctly performed trials (accuracy ~100%) and had latencies of 179 and 197 ms, respectively (dashed vertical lines in Figures 5E and 5F). These latencies were significantly different from each other (ANOVA $F(1,9769) = 725.56$, $p < 0.001$). Applying the criterion-based rule, we could match the timing of these choices by using deci-

sion criteria of 0.57 for pursuit and 0.69 for saccades. Taking into account the ~10 ms transmission delay between activity in the SC and the onset of eye movements (Miyashita and Hikosaka, 1996), these criteria predicted average latencies of 179 and 196 ms for pursuit and saccades, respectively. These values were statistically indistinguishable from the observed latencies (ANOVA $F(1,6493) = 0.48$, $p = 0.49$, pursuit; $F(1,5274) = 0.05$, $p = 0.83$, saccades). Our analysis of neuronal activity aligned with respect to movement onset (Figures 4C and 4D) allowed us to cross-validate this difference in decision criteria between pursuit and saccades. The average ROC area 10 ms before movement onset had a value of 0.55 for pursuit and 0.68 for saccades, indicating that the decision criteria for pursuit and saccades were not simply values arbitrarily chosen to match the observed latencies, but were measures of the difference in activity between the two population of SC neurons just prior to the onset of the two movements.

The criteria that matched the observed latencies corresponded to different points along the predicted speed-accuracy curves for pursuit and saccades. The placement of the criterion for pursuit at the shoulder of the speed-accuracy curve (gray circle in Figure 5E, 97.8% correct) suggests that the pursuit choices were triggered just as the speed-accuracy tradeoff approached perfect performance. In contrast, the placement of the criterion for saccades along the plateau of the curve (Figure 5F, 100% correct) suggests that saccade choices involved a somewhat more conservative strategy. Our analysis of neuronal activity aligned with respect to movement onset (Figures 4C and 4D) predicted the same difference between the two movements. Applying the time-based rule, the predicted percent correct 10 ms before movement onset was 95.7% for pursuit and 100% for saccades. Consistent with these predictions, we found that pursuit occasionally made early and short-lived mistakes. The traces in Figure 6 show examples of pursuit movements from a single recording session. On most trials, pursuit eye velocity increased smoothly from zero toward target velocity (gray traces). However, on a small minority of trials, pursuit eye velocity started in the wrong direction (arrows) before reversing and increasing toward target velocity (black traces). Across our entire data set ($n = 5198$ pursuit trials), we estimate that this type of initial pursuit error occurred on 212, or 4%, of the trials (see Experimental Procedures). As with all of our pursuit data, these changes in eye velocity occurred in the absence of any corrective saccades, as illustrated by the traces of eye velocity from individual trials (Figure 6A). However, because the eye accelerated more rapidly on error trials than on correct trials (compare the slopes of the gray and black traces of average velocity in Figure 6B), eye speed reached target speed at about the same time on both types of trials. The occurrence of these brief errors therefore did not substantially impede the ability of the pursuit system to quickly match eye speed to target speed.

Discussion

We have shown that buildup neurons in the rostral SC exhibit a preference for stimuli that will be the target of

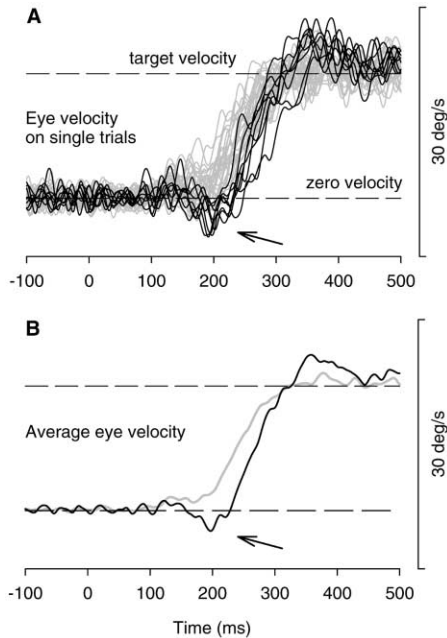


Figure 6. Initial Errors during Pursuit Eye Movements
(A) Traces show the eye velocity recorded on individual pursuit trials during a single experimental session. Black traces indicate trials on which eye velocity transiently increased in the wrong direction (arrow). Gray traces indicate trials without these transient errors. The upper dashed line indicates target velocity; the lower dashed line indicates zero velocity (fixation).
(B) The two traces show the average eye velocity from the same error (black) and nonerror trials (gray) shown in (A).

pursuit as well as saccades (Glimcher and Sparks, 1992). Historically, the SC has not been considered as part of the pathways for pursuit, but recent recording, microstimulation, and pharmacological studies have demonstrated that the rostral SC plays some role in pursuit (Basso et al., 2000; Krauzlis et al., 1997, 2000), in addition to its well-established role in the preparation of saccades. Our data and simulations demonstrate one possible function for this neuronal activity—the coordination of target choice between the two eye movement systems. We found that activity related to the selection of the target emerged over the course of the 150–200 ms required to prepare the two eye movements, providing a possible neural correlate of the tradeoff between movement speed and accuracy. These changes in activity likely reflect the integration of inputs from the bevy of cortical and subcortical regions that project to the SC and that are known to be involved in the perceptual discrimination of visual stimuli and the formation of eye movement decisions (Ferrera and Lisberger, 1997; Gottlieb et al., 1998; Hanes et al., 1998; Kim and Shadlen, 1999; Platt and Glimcher, 1997; Recanzone and Wurtz, 2000; Recanzone et al., 1997; Schall and Hanes, 1993; Schall et al., 1995). The dynamics of the changes probably also depend on the competitive interactions that take place directly within the circuitry of the SC (Munoz and Istvan, 1998).

We were able to predict the monkey's pursuit and saccade decisions by applying a simple decision rule

to the population activity. These predictions involved criteria at different locations along the speed-accuracy tradeoff, suggesting that the activity of these neurons was read out in different ways for the two types of eye movements. This result could explain why pursuit and saccades appear to be coordinated but not strictly yoked—the two responses might be correlated because of their use of common pools of neurons, but also decorrelated because of their use of different decision criteria. In particular, the lower decision criterion for pursuit provides a possible explanation for the observation that pursuit latencies are typically shorter than saccade latencies (Leigh and Zee, 1999).

As an alternative explanation, it might be argued that moving stimuli are inherently more salient than stationary stimuli. The shorter latency for pursuit might therefore be due to the higher activity associated with moving stimuli, rather than to the use of a lower criterion. Some of the neurons we studied did, in fact, exhibit higher activity for target stimuli during pursuit than during saccades (e.g., Figure 1). However, across the population, the preference for target stimuli during pursuit was smaller than that observed during saccades. Consequently, if the neurons we studied contribute to the pursuit choice, differences in their responses to moving and stationary stimuli cannot explain the shorter latency of pursuit.

Our predictions assumed the same 10 ms motor delay for both pursuit and saccades. If the actual motor delays were longer or shorter, the decision criteria would need to be lower or higher in order to match the observed latencies. It is also possible that pursuit and saccades involve different motor delays, in contrast to our simplifying assumption of the same delay for both movements. For example, if the execution of saccades involved a 46 ms motor delay, a criterion of 0.57—the same low criterion as used for pursuit—would match the observed latencies and almost match the observed percentage of correct trials (predicted accuracy, 99%). Although a 46 ms motor delay is much longer than the latency of eye movement effects typically evoked by electrical stimulation of the SC (Gandhi and Keller, 1999; Miyashita and Hikosaka, 1996; Robinson, 1972), it is similar to the latencies associated with near-threshold stimulation (Glimcher and Sparks, 1993; Robinson, 1972). We therefore cannot rule out the possibility that the longer latencies for saccades are due, at least in part, to longer motor processing times following target selection.

Our results suggest that saccade choices emphasize accuracy, whereas pursuit choices place a somewhat greater emphasis on speed. Consistent with this inference, our pursuit trials included a small number of errors, whereas all of the saccade trials were performed correctly. We necessarily restricted our analysis to trials on which the monkey followed the target stimulus without any corrective saccades, because the interpretation of pursuit-related activity in the SC becomes problematic if pursuit is interrupted by saccades. Despite this methodological constraint, we found that pursuit sometimes initially followed the wrong stimulus before reversing direction (Figure 6), as would be expected if its choice were based on a lower criterion than that applied by the saccadic system. Taking these brief errors into account, the observed accuracy of pursuit (96%) was very similar

to that predicted by applying a decision rule to the population activity (criterion based, 97.8%; time based, 95.7%). Thus, although the generation of pursuit depends on information in brain regions other than the SC—in particular, pursuit typically requires visual motion signals provided by extrastriate cortical areas (Dürsteler and Wurtz, 1988; Newsome et al., 1985)—our results show that activity in the SC is sufficient to account for the target choices made by the pursuit system during our experiment.

The slightly different speed-accuracy tradeoffs for pursuit and saccades suggested by our data might be related to the different consequences of errors by the two systems. Errors by the saccadic system carry a high cost. Every saccade interrupts visual processing, both by distorting perception of visual space and by suppressing sensitivity to visual motion (Ross et al., 2001). If the saccade lands at the wrong location, the newly relocated image of the target will remain in the peripheral visual field where acuity is low, or worse yet, will have been moved even further into the periphery. Programming a second saccade to correct this error takes additional time, and vision will again be disrupted during the corrective saccade. In contrast, errors by the pursuit system carry a lower cost. Unlike saccades, pursuit does not appear to interrupt visual processing, and the pursuit system can continuously and quickly correct its mistakes, sometimes without any time penalty (e.g., Figure 6). A more conservative decision criterion for saccades than for pursuit might therefore reflect an adaptive strategy driven by the higher cost of making errant saccades.

Admittedly, the decision model we used here is a simplification, because it assumes that the brain applies a fixed criterion that varies negligibly compared to the noise associated with the neuronal populations. In fact, decision criteria likely vary systematically across tasks and over time (Ditterich et al., 2001, Soc. Neurosci., abstract; Grice, 1968; Link and Heath, 1975; Nazir and Jacobs, 1991), as might be expected of a system that takes factors such as temporal expediency into account, as well as the level and type of evidence. It is also unclear how much these relatively automatic choices about eye movements have in common with the more deliberative process of self-conscious human decision making (Schall, 2001). Nonetheless, this framework for interpreting the tradeoff between speed and accuracy could be applicable to other neural systems, because choosing between alternatives in a timely and coordinated manner is a general problem confronted by perception and cognition, as well as by the motor system.

Experimental Procedures

Behavioral and neuronal data were obtained from two rhesus monkeys (*Macaca mulatta*). All experimental protocols were approved by the Institute Animal Care and Use Committee and complied with Public Health Service Policy on the humane care and use of laboratory animals. The monkeys were prepared and studied for single-neuron and eye movement recording using standard techniques that have been described previously (Krauzlis et al., 2000). The neurons we studied were located in the intermediate layers of the superior colliculus (1.0–3.5 mm below the surface), and electrode tracks were guided by structural MRI images. In addition to mapping of the response fields using visually guided saccades, we also tested neurons using the fixation blink paradigm (Munoz and Wurtz, 1993),

in which a fixated target is briefly extinguished. We selected neurons ($n = 83$; 22 and 61 for the two monkeys, respectively) that had the same functional properties as those described previously for “rostral buildup neurons” (Krauzlis et al., 2000). All of the neurons exhibited an increase in activity during the execution or preparation of small ($\sim 3^\circ$ – 5°) contraversive saccades; all neurons had movement fields with centers within the central $\sim 5^\circ$ of the visual field. Some of these neurons ($n = 26$) also met the criteria for fixation cells (Munoz and Wurtz, 1993)—they maintained a firing rate of at least 10 spikes/s during stimulus blinks imposed during fixation. As described previously (Krauzlis et al., 2000), neurons active during fixation and small saccades appear to compose a single functional class that encodes foveal and parafoveal position errors, and we refer to them jointly as rostral buildup neurons.

Monkeys performed the pursuit and saccade tracking tasks illustrated at the top of Figure 1 on pseudo-randomly interleaved trials. After a randomized period of fixation (200–400 ms), monkeys were briefly (600 ms) shown a color cue (a red or green square) at the center of the screen. After a second fixation period (900–1600 ms), monkeys were shown a pair of stimuli (one red and one green bar, 0.2° wide and 0.4° high) and were rewarded for tracking the stimulus that matched the color of the cue. The red and green stimuli were isoluminant (17 cd/m^2). The initial stimulus locations were displaced horizontally by approximately 3° to eliminate the need for corrective saccades on pursuit trials (Rashbass, 1961). A small vertical offset (0.3°) was also added so that the two stimuli did not occlude each other as they passed through the center of the display. The sign of the vertical offset was determined by whether the response field was predominantly above or below the horizontal meridian. Any pursuit trials containing saccades in a 600 ms interval beginning 100 ms before the onset of target motion were excluded from analysis. Using a combination of velocity and acceleration criteria, we were able to detect saccades with amplitudes as small as 0.2° (Krauzlis and Miles, 1998).

Measurements of population activity, discriminability, and application of the decision rule were performed using Matlab. For each simulated trial ($n = 1000$ each for pursuit and saccades), population firing rates for target and distractor trials were determined by randomly selecting one spike train (with replacement) from the data set from each neuron. To convert the discrete spike events into a continuous record of firing rate, we replaced each spike in the train with a replica of a postsynaptic potential (1 ms rising time constant, 20 ms decaying time constant) (Hanes et al., 1998). We compared the target and distractor distributions of firing rates by constructing ROC curves at each millisecond of the trial, using now standard techniques borrowed from signal detection theory (Britten et al., 1992; Thompson et al., 1996). For the time-based decision rule, at each millisecond we calculate “accuracy” as the percentage of the 1000 simulated trials for which the ROC area exceeded a value of 0.5. For the criterion-based rule, we determined the first point in time (after the onset of the target and distractor stimuli) at which the ROC area exceeded the criterion for at least 10 ms. We referred to this point in time as the “time to criterion” for that simulated trial. Accuracy was calculated as the percentage of trials in which ROC area was greater than 0.5 (i.e., in favor of the target stimulus) at the times to criterion across the set of 1000 simulated trials. This criterion-based rule is related to the family of diffusion models (also known as random walk or accumulator models) used to study reaction times in a variety of tasks (Link and Heath, 1975; Ratcliff et al., 1999; Schwarz, 1993), and to examine the relationship between neuronal activity and decision making (Gold and Shadlen, 2001; Kim and Shadlen, 1999). The criterion-based rule is also related to the family of race models (Logan et al., 1984; Osman et al., 1986; Grice, 1968), which likewise have been examined in numerous behavioral studies (Hanes and Carpenter, 1999; Hanes and Schall, 1995; Mordkoff and Egeth, 1993), and also used to examine the saccade-related activity of neurons in the frontal eye fields (Hanes et al., 1998; Hanes and Schall, 1996). For the purposes of our study, the diffusion model was more appropriate, because it uses increments and decrement in activity to predict correct and incorrect decisions, and could therefore be directly applied to our measurements.

To identify pursuit trials with initial errors, we measured eye velocity in two intervals: (1) a 200 ms baseline interval beginning 200 ms before the onset of the target and distractor stimuli, and (2) a 50

ms pursuit-initiation interval beginning 175 ms after the onset of the stimuli. A trial was defined as containing an initial error if the eye velocity during the pursuit-initiation interval was significantly different from that during the baseline interval (Wilcoxon rank sum test, $p < 0.05$), and if the sign of the difference was in favor of the distractor direction rather than the target direction.

Acknowledgments

We thank T.D. Albright, B.R. Beutter, F. Crick, J.D. Schall, C.F. Stevens, and L.S. Stone for their comments on a previous draft of this paper, and C. Cramer for administrative assistance. This work was supported by NIH grant EY12212 and a McKnight Scholar Award to R.J.K.

Received: April 16, 2002

Revised: May 13, 2002

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