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Dissociation of pursuit target selection from saccade execution

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ABSTRACT

Pursuit and saccades almost always select the same target. Is this the results of a common selection process or does smooth pursuit obligatorily follow the stimulus targeted by saccades? To address this question, we used microstimulation of the primate superior colliculus (SC) to redirect the eyes from a selected pursuit target to a distracter moving in the opposite direction. During each trial, monkeys pursued a horizontally moving array of colored target stimuli. In half of the trials, this target array was accompanied by a distracter array moving horizontally in the opposite direction, offset by the vertical amplitude of the stimulation-evoked saccade. We stimulated the SC during maintained pursuit on half of the trials, and measured pursuit eye velocity during the 50-ms interval immediately following the stimulation-evoked saccade to the distracter array. Saccades evoked by SC stimulation did not alter pursuit target selection. Pursuit velocity on average changed by less than 10% of that expected if the monkey had completely switched targets. Moreover, the same changes in velocity occurred when there was no distracter, indicating that even these small changes in pursuit velocity were a direct effect of the evoked saccade, not partial selection of the distracter. These results show that motor execution of saccades is not sufficient to select a pursuit target, and support the idea that the coordination of pursuit and saccades is accomplished by a shared target selection process.

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1. Introduction

Primates use two types of voluntary eye movements when exploring their visual environment – saccades and smooth pursuit. Saccades use spatial information about the selected visual object to align gaze direction with the target, thereby placing the image of the object on or near the fovea (Schall & Thompson, 1999; Sparks & Mays, 1990). Smooth pursuit uses visual motion signals to match eye velocity to the velocity of the selected visual object, thereby minimizing the blur that would otherwise be created by the motion of the object's image across the retina (Krauzlis, 2004; Lisberger, 2010). Perhaps the most distinctive feature of voluntary eye movements is the ability to be selective in what is tracked, and since the two components of voluntary eye movements are almost always in agreement, there appear to be central mechanisms that coordinate the process of target selection between them.

At least part of this coordination is related to the mechanisms of visual spatial attention. Several lines of evidence illustrate a tight linkage between the control of voluntary eye movements and the allocation of spatial attention. For example, performance on discrimination tasks is best at the location of the saccade target even

before the onset of the movement, indicating that the preparation of saccades involves resources shared with spatial attention (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995); conversely, directing attention away from the saccade target reduces the accuracy and increases the latency of saccades (Deubel & Schneider, 1996; Kowler et al., 1995). Similarly, perceptual performance during smooth pursuit is best for the tracked stimulus (Khurana & Kowler, 1987; Lovejoy, Fowler, & Krauzlis, 2009), and directing attention to non-tracked stimuli reduces the accuracy of pursuit tracking (Kerzel, Souto, & Ziegler, 2008; Khurana & Kowler, 1987).

Although it is generally accepted that both saccades and smooth pursuit are linked to spatial attention, the specific mechanism that establishes this coordination remains an unsettled issue. Some evidence suggests that target selection for smooth pursuit is dependent on the selection processes associated with saccades. When pursuit begins to follow a moving stimulus presented alone, eye velocity is markedly increased in the immediate wake of targeting saccades; this post-saccadic enhancement of pursuit suggests that the generation of saccades regulates the strength of visual motion signals for pursuit (Lisberger, 1998). When two moving stimuli are presented, pursuit tends to follow the average of the two motions, but this changes when a targeting saccade is made to one of the two stimuli – the post-saccadic pursuit eye velocity is strongly weighted in favor of the stimulus targeted by the saccade (Gardner

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& Lisberger, 2001, 2002; Schoppik & Lisberger, 2006). These findings provide support for the conclusion that saccade motor commands play a causal role both in enhancing visual-motor transmission for pursuit and in selecting the target for pursuit (Gardner & Lisberger, 2001, 2002; Lisberger, 1998). This viewpoint predicts that the state of pursuit selection should be changed by saccades that redirect tracking to an alternate stimulus – pursuit eye velocity should match the speed of the stimulus acquired by the saccade.

An alternate hypothesis is that pursuit and saccades are alternate outcomes from a shared process of target selection. The introduction of a temporal gap between fixation point offset and the appearance of a visual target decreases the latencies of both pursuit (Knox, 1996; Krauzlis & Miles, 1996a; Merrison & Carpenter, 1995) and saccades (Fischer & Boch, 1983; Fischer & Weber, 1993; Krauzlis & Miles, 1996a; Saslow, 1967), suggesting that there are common inputs for triggering the two types of movements. The presence of distracter stimuli has similar effects on the latencies of pursuit and saccades (Ferrera & Lisberger, 1995; Knox & Bekkour, 2002; Krauzlis, Zivotofsky, & Miles, 1999; Walker et al., 1997), supporting the idea that target selection for both movements depends on the allocation of spatial attention. When pursuit and saccade selection are directly compared on a trial-by-trial basis, the pursuit choice always matches the saccade choice by the time of saccade onset (Liston & Krauzlis, 2003), and the speed-accuracy curves for pursuit and saccades suggest that they are guided by a common decision process but use different response thresholds (Liston & Krauzlis, 2005). These findings support the conclusion that pursuit and saccades are different outcomes from a shared cascade of sensory-motor functions, rather than one movement regulating the signals that drive the other (Krauzlis, 2004). This viewpoint predicts that the state of pursuit selection should not necessarily be changed by saccades that redirect tracking to an alternate stimulus – pursuit velocity should change only if a new target is selected.

In this study, we have explicitly tested how the execution of saccades affects the selection of targets for smooth pursuit. We used electrical microstimulation of the intermediate layers of the superior colliculus (SC), a structure well known for its role in the motor control of saccades (Gandhi & Katnani, 2011; Wurtz & Albano, 1980), to artificially evoke saccades during maintained smooth pursuit of a selected visual stimulus. The stimuli were arranged so that the evoked saccade redirected gaze from the target stimulus to an alternate, distracter stimulus that moved in the opposite direction. We found that smooth pursuit eye velocity was little changed by the evoked saccade, and continued to follow the motion of the originally selected target stimulus, even though the saccade placed the distracter stimulus at the center of gaze. These results demonstrate that motor execution of saccades is not sufficient to change the state of pursuit selection, and are consistent with the idea that selection is accomplished by an earlier stage of sensory-motor processing that is shared by pursuit and saccadic eye movements.

2. Materials and methods

2.1. Animal preparation

We collected data from two adult (A and W) male rhesus monkeys (*Macaca mulatta*). All experimental protocols for the monkeys 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 for physiological study of the SC using standard surgical techniques that have been described in detail previously (Krauzlis, 2003).

2.2. Data acquisition

Our experiments were controlled by a computer using the Tempo software package (Reflective Computing), and a second computer running the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) in Matlab (MathWorks) acted as a server device for presenting the visual stimuli. Stimuli were presented with a video monitor (75 Hz, ~ 20 pixels/°, $\sim 44^\circ$ horizontal by $\sim 33^\circ$ vertical) at a viewing distance of 41 cm. Eye movements were recorded using scleral search coils (Judge, Richmond, & Chu, 1980) and the electromagnetic induction technique (Fuchs & Robinson, 1966) using standard phase detector circuits (Riverbend Instruments). The coil output voltages were low-pass filtered (six pole Bessel filter; -3 dB at 180 Hz) and calibrated with respect to eye position by having the animal fixate small spot stimuli at known eccentricities. All data and events related to the onset of stimuli were stored on disk during the experiment (1 kHz sampling rate) for offline analysis.

2.3. Behavioral tasks

Each behavioral task began with the presentation of a small white crosshair (33 cd/m²) against a uniform gray background (19 cd/m²). Once the monkey fixated this stimulus, an experimental trial initiated (Fig. 1). After a 500-ms delay, the fixation stimulus was briefly (500 ms) replaced by a color cue. The cue was a colored square (red or green, 33 cd/m²) presented for 500 ms that indicated the color of the target array that should be tracked later in the trial. The cue was replaced by the fixation crosshair and then, after a variable delay (500–1000 ms), the fixation point was extinguished and the choice stimuli were displayed. At this point, the trial branched into one of two possible conditions.

The first condition was “target plus distracter”, and comprised 50% of the trials (Fig. 1, top). In this condition, monkeys were presented with two horizontal rows of moving stimuli. Each row consisted of 0.3° squares, spaced 0.6° apart, and moving in opposite directions, either rightward or leftward, at 13 deg/s. The task of the monkey was to smoothly follow the row of stimuli that matched the color of the cue. The two rows were vertically offset from each other by a distance that was matched to the vertical amplitude of the saccade evoked by microstimulation at that particular site in the SC; the vertical amplitudes ranged from $\sim 0.5^\circ$ to $\sim 12^\circ$ (details presented in Fig. 7). Different combinations of the stimuli (i.e., color and direction of motion of the target array) were presented with equal probability. The monkeys were required to keep their eyes directed within a 2° vertical position window cen-

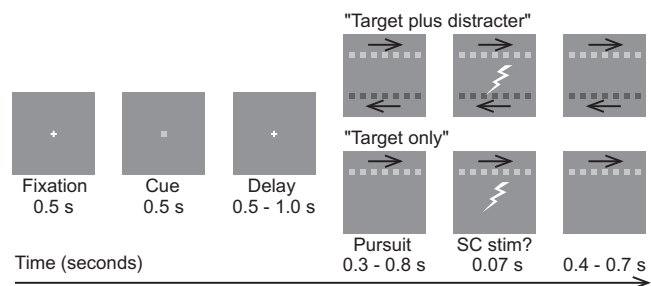


Fig. 1. Schematic of the pursuit task and timing of trial events. Each box depicts the monitor display during a particular epoch in the task for “Target plus distracter” (top) and “Target only” (bottom) trials. The monkey was required to smoothly pursue the moving squares whose color matched the cue. On randomly selected trials (50% probability) in both conditions, microstimulation was applied to the SC midway through the trial, evoking a fixed-vector saccade. The vertical eccentricity of the rows of moving colored squares was tailored during each experiment, based on the vertical amplitude of the saccade evoked at the SC site, so that SC microstimulation shifted gaze to the distracter row (target-plus-distracter trials) or to a blank region of the display (target-only trials).

tered on the target array, and were given a grace period of 300 ms from stimulus onset to enter this window. If the monkey failed to enter the window on time, or subsequently exited this window, the trial was aborted and the monkey was given a timeout. If the monkey successfully remained in the window that matched the target stimulus, he was given a juice reward at the end of the trial. On half of the target-plus-distracter trials, electrical microstimulation of the SC (500 Hz, 10–30 μ A) was applied for 70 ms at a randomized time starting 300–800 ms after the onset of the moving stimuli. At the onset of stimulation, the requirement to remain within a 2° vertical position window centered on the target array was suspended for 300 ms, but was then reapplied for at least 100 ms at the end of each trial.

The second condition was “target only”, and comprised the other 50% of the trials (Fig. 1, bottom). This condition was identical in timing and organization to the target-plus-distracter condition, except that only the target row of moving stimuli was presented. Once again, SC microstimulation was applied on half of these trials, although now the consequence of the evoked saccade was for gaze to land on a blank region of the screen, rather than onto the distracter stimulus. This condition was randomly interleaved with the target-plus-distracter condition, and served as a control for changes in pursuit eye velocity caused by factors other than the presence of the moving distracter.

During a single experiment, we typically collected a total of 200–400 behavioral trials, divided evenly between target-plus-distracter, target-only, stimulation, and no-stimulation conditions, resulting in about 50–100 trials per condition. The different trial conditions were pseudo-randomly interleaved using a shuffled list.

2.4. Recording and stimulating procedures

Prior to conducting the behavioral tasks described above, we identified our site in the SC by the presence of single-units whose activity was modulated during saccades and by documenting the effects of microstimulation. Single-neuron recordings and microstimulation were performed in the intermediate and deep layers of the SC (1–3.5 mm below the SC surface), and electrode tracks were guided by structural MRI. For microstimulation, biphasic currents (10–30 μ A, 500 Hz) were applied through tungsten microelectrodes (Frederick Haer) with impedances between 0.1 and 3.5 M Ω measured at 1 kHz, using a Grass S11 stimulator and PSIU6 isolation units (Astro-Med, Inc.). To determine the characteristic saccade vector associated with each SC site, we applied microstimulation for 70 ms – the same duration as in the main behavioral experiment. These parameters (10–30 μ A, 500 Hz, 70-ms pulse train) evoked single saccades, and we analyzed the evoked saccades from approximately 20 trials to determine the vertical and horizontal amplitude of the fixed-vector saccade evoked during each session (Fig. 2). The vertical distance of the distracter was then set to a fixed value equal to the vertical amplitude of the evoked saccade.

2.5. Data analysis

Our data analysis focused on the values of smooth eye velocity that immediately followed the saccade evoked by SC microstimulation. Because pursuit was always directed horizontally, post-saccadic eye velocity was defined as the average horizontal eye velocity in the 50-ms interval immediately after the stimulation-evoked saccade. As in previous studies (e.g., Gardner & Lisberger, 2002), we analyzed the first 50 ms of post-saccadic eye velocity in order to avoid including effects of post-saccadic image motion; using this interval also makes our results more directly comparable to those from previous studies. We detected saccades using

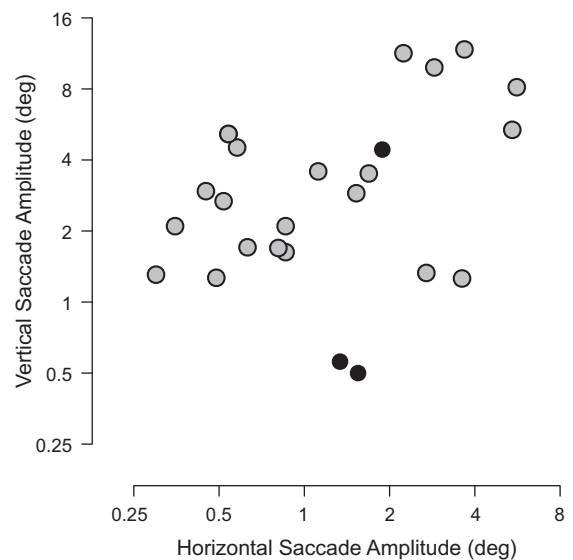


Fig. 2. Saccades evoked by SC microstimulation. Each symbol indicates the average vertical and horizontal amplitude of the fixed-vector saccade evoked during one experimental session ($n = 26$ experiments). For convenience, upward (gray) and downward (black) saccade amplitudes are plotted together; the horizontal component was always directed toward the side contralateral to the site of microstimulation. Most of the microstimulation sites were located in the medial half of the SC, resulting in more saccades with upward than downward directions, and the vertical amplitudes tended to be larger than the horizontal amplitudes.

velocity and acceleration thresholds (Krauzlis & Miles, 1996b). Because velocity was non-zero during smooth pursuit, the velocity threshold was applied relative to the average eye velocity to avoid erroneously flagging periods of smooth tracking with nonzero velocity as saccades (de Brouwer et al., 2002). All detected saccades were visually verified. For the no-stimulation trials, which did not contain stimulation-evoked saccades, we used the saccade measurements from the stimulation trials to define a list of post-saccadic intervals. These post-saccadic intervals were then randomly assigned to the no-stimulation trials to provide a set of yoked control measurements from the no-stimulation trials.

For statistical tests, we used Wilcoxon rank-sum tests to assess the significance of differences in post-saccadic eye velocity measurements between stimulation and no-stimulation trials, and between target-plus-distracter and target-only trials, using commercially available software (Matlab, Mathworks).

3. Results

In 26 experiments in 2 monkeys (11 in monkey A, and 15 in monkey W), we found no evidence that stimulation-evoked saccades that shifted gaze from one moving stimulus to another had any effect on the selection of targets for pursuit. We first describe sample results from one experimental session to illustrate the nature of the effects we observed, before presenting a summary of the measurements obtained across all experiments.

3.1. Sample results of stimulation-evoked saccades during smooth pursuit

Saccades evoked by SC microstimulation did little to change the velocity of smooth pursuit, even when the saccades landed gaze on a stimulus moving in the opposite direction. As shown by the sample data from individual trials in one experimental session, the steady-state pursuit response of the subject (monkey W) closely followed the motion of the target stimulus, as shown by the trajectory of eye position overlying the location of the target array in the

lower half of the display (Fig. 3A), and the match between eye velocity and the speed of the target (Fig. 3B). When microstimulation was applied in the SC during target-plus-distracter trials, gaze was shifted to the distracter array and remained there for about 100 ms (Fig. 3C) before returning to the target array with a corrective saccade. Nonetheless, throughout this period, eye velocity was similar to target speed (Fig. 3D). In addition, the small differences between post-saccadic eye velocity and target speed on target-plus-distracter trials (Fig. 3D) were also found when the evoked saccade redirected the eye to a blank portion of the display on target-only trials (Fig. 3F). Thus, even after the eye was redirected to the oppositely moving distracter array, pursuit eye velocity remained a value close to the originally selected target.

The stability of post-saccadic eye velocity during steady-state pursuit was especially evident when all the trials from this experimental session were averaged together and aligned on the end of the saccade. When the target row moved in the same direction as the saccade evoked by SC microstimulation (Fig. 4A), the traces of post-saccadic eye velocity from target-plus-distracter (black) and target-only (gray) trials were superimposed, and mostly overlaid the trace from no-stimulation trials (dashed). The post-saccadic horizontal eye velocities (measured in the 50-ms analysis window) on target-plus-distracter and target-only trials were not significantly different from each other (Wilcoxon rank-sum, $U = 3438$, $p = 0.12$, two-tailed), although there were idiosyncratic effects compared to the no-stimulation trials (Wilcoxon rank-sum, $U = 1379$, $p < 0.01$ and $U = 1659$, $p = 0.22$, respectively). Similarly, when the target row moved in the direction opposite the evoked

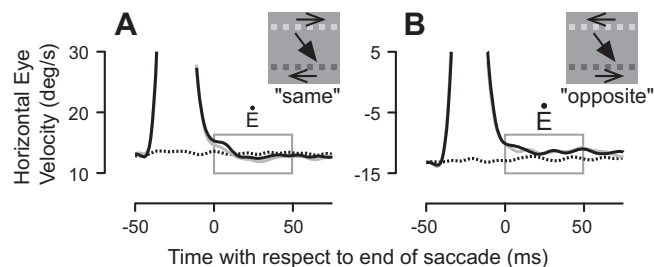


Fig. 4. Average eye velocity traces from the same experimental session illustrated in Fig. 3 aligned on the end of the saccade. (A) The superimposed traces compare the average horizontal eye velocity from different trial types when the target row moved in the same direction as the saccade evoked by SC microstimulation. (B) Average horizontal eye velocity when the target row moved in the opposite direction as the saccade evoked by SC microstimulation. Data are aligned on the end of the stimulation-evoked saccade, which appears as the large upward deflection in the target-plus-distracter (black) and target-only (gray) traces. The dashed trace shows average horizontal eye velocity from the no-stimulation trials.

saccade (Fig. 4B), the traces of post-saccadic eye velocity again superimposed, although they were both offset, and at slightly lower speeds, compared to the trace from the no-stimulation trials. In this case, the post-saccadic horizontal eye velocities on target-plus-distracter and target-only trials were again not significantly different from each other (Wilcoxon rank-sum, $U = 3880$, $p = 0.27$), and both were significantly lower than the post-saccadic velocities on the no-stimulation trials (Wilcoxon rank-sum,

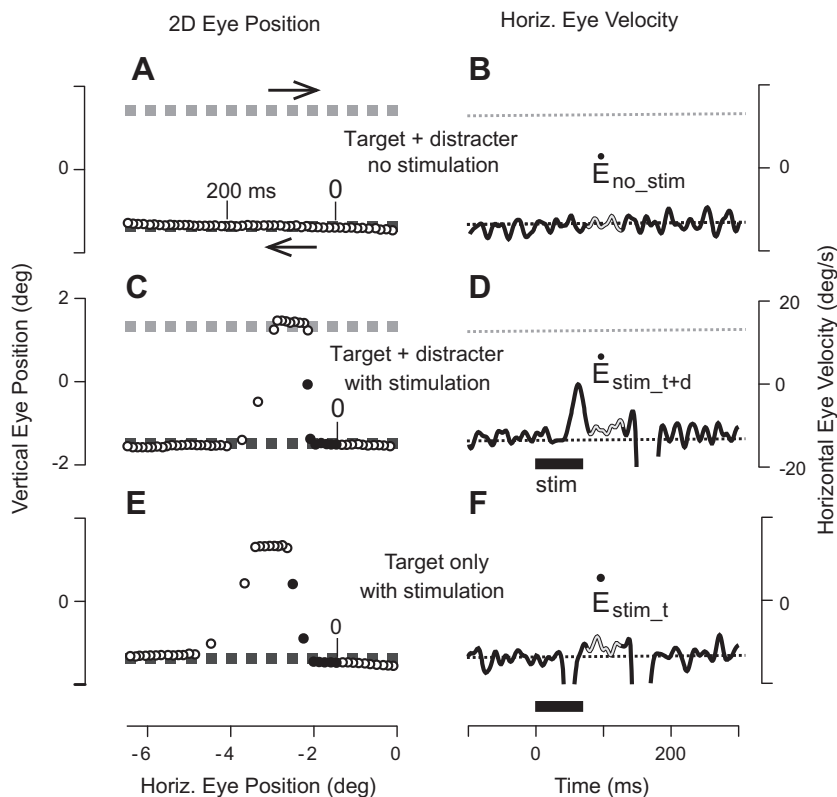


Fig. 3. Examples of eye movements from individual trials during one experimental session. (A) Eye position trajectory from a target-plus-distracter trial with no SC microstimulation. Each circle shows the instantaneous eye position at a particular time during the trial plotted in Cartesian coordinates; successive symbols show eye position at 10-ms intervals. Subject was smoothly pursuing the lower row of squares, which were moving leftward on this trial as indicated by the arrow; hence, time progresses from right to left in this plot. (B) Horizontal eye velocity trace from the same target-plus-distracter trial shown in (A), plotted as a function of time. The black dashed line indicates the target velocity of -13 deg/s; the segment highlighted in gray indicates the 50-ms interval used for the data analysis. (C) Eye position trajectory from a target-plus-distracter trial including SC microstimulation. The microstimulation was applied starting at time zero and lasted for 70 ms, as indicated by the black circles. (D) Horizontal eye velocity trace from the same trial shown in (C). The black bar indicates the time when microstimulation was applied. (E) Eye position trajectory from a target-only trial including SC microstimulation. The evoked saccade shifted gaze upward, but in this case eye position landed on a blank portion of the display. (F) Horizontal eye velocity trace from the same trial shown in (E).

$U = 769$, $p < 0.001$ and $U = 979$, $p < 0.001$, respectively). In both cases, the post-saccadic horizontal eye velocities were not significantly altered by the presence or absence of the oppositely moving distracter stimulus.

3.2. Summary of effects of stimulation-evoked saccades on pursuit target selection

Similar effects were found across the full set of 26 experimental sessions. We first compared the post-saccadic velocities on trials with and without SC microstimulation (Fig. 5). When the target row moved in the same direction as the evoked saccade, post-saccadic eye velocity was similar on stimulation and no-stimulation trials, as indicated by the cluster of data points located along the line of unity slope in Fig. 5A and C. When the target row moved in the direction opposite the evoked saccade, post-saccadic eye velocity tended to be lower on stimulation trials, compared to no-stimulation trials, as shown by the data points lying below the unity slope line in Fig. 5B and D. The gray symbols in the figure indicate data sets from individual sessions showing a significant difference between stimulation and no stimulation trials (Wilcoxon rank-sum test, $p < 0.05$); white symbols indicate lack of significance.

These changes in post-saccadic eye velocity are small compared to what would be expected if the saccade had switched the state of pursuit selection in favor of the distracter stimulus. When the target row moved in the same direction as the evoked saccade, the average post-saccadic eye velocity across the 26 experiments (Fig. 5A) was 12.52 deg/s, compared to 12.86 deg/s with no stimulation; the difference in eye velocity between these conditions was not significant (Wilcoxon signed-rank test, $z = -0.8$, $p = 0.42$). If the evoked saccade had switched pursuit selection to the distracter row, post-saccadic eye velocity would be expected to be 12.86 deg/s in the opposite direction, based on pursuit eye velocity

with no stimulation-evoked saccades. Thus the evoked saccade changed pursuit velocity by only $\sim 1\%$ (0.34 deg/s divided by 2×12.86 deg/s) of the amount expected if it had switched the state of pursuit target selection. When the target row moved in the opposite direction as the evoked saccade, the effects were slightly larger and significant – the average post-saccadic eye velocity (Fig. 5B) was 10.34 deg/s, compared to 12.94 deg/s with no stimulation (Wilcoxon signed-rank test, $z = -4.38$, $p < 0.001$), corresponding to a change of $\sim 10\%$ of the amount expected if the evoked saccade switched the state of pursuit target selection. For comparison, in previous work showing that the state of pursuit selection was changed by stimulation-evoked saccades, the state of pursuit choice in the 2-alternative task changed from slightly above chance before the saccade (50–60%) to heavily biased in favor of the saccade target (80–90%), within 50 ms following the end of the saccade (Fig. 5 of Gardner and Lisberger (2002)).

Moreover, we found the same pattern of results for the target-only trials (Fig. 5C and D). When the target row moved in the same direction, the average post-saccadic eye velocity (Fig. 5C) was 12.38 deg/s, compared to 12.86 deg/s with no stimulation (not significantly different, Wilcoxon signed-rank test, $z = -1.1048$, $p = 0.27$), corresponding to a change of $\sim 2\%$ of the total amount expected if the evoked saccade changed pursuit selection. Conversely, when the target row moved in the opposite direction, the average post-saccadic eye velocity (Fig. 5D) was 10.25 deg/s, compared to 12.94 deg/s with no stimulation (Wilcoxon signed-rank test, $z = -4.38$, $p < 0.001$), corresponding to a change of $\sim 10\%$ of the total amount expected. These changes are the same magnitude as those found in the presence of the distracter row (Fig. 5A and B), indicating that even the small changes in post-saccadic eye velocity did not depend on the presence of the moving distracter stimulus, but appeared to be a nonspecific consequence of the evoked saccade.

To underscore this point, we next directly compared the post-saccadic velocities on target-plus-distracter and target-only trials (Fig. 6). Regardless of whether the target row moved in the same (Fig. 6A) or opposite (Fig. 6B) direction, compared to the stimulation-evoked saccade, the post-saccadic eye velocities were largely unaffected by the presence or absence of the oppositely moving distracter, as indicated by how the data points all lie along the line of unity slope. For the large majority of measurements (24/26 for “same”, 23/26 for “opposite”), there were no significant differences between post-saccadic eye velocities measured on trials with and without the distracter stimulus (Wilcoxon rank-sum test; white symbols, $p > 0.05$; gray symbols, $p < 0.05$). These findings illustrate

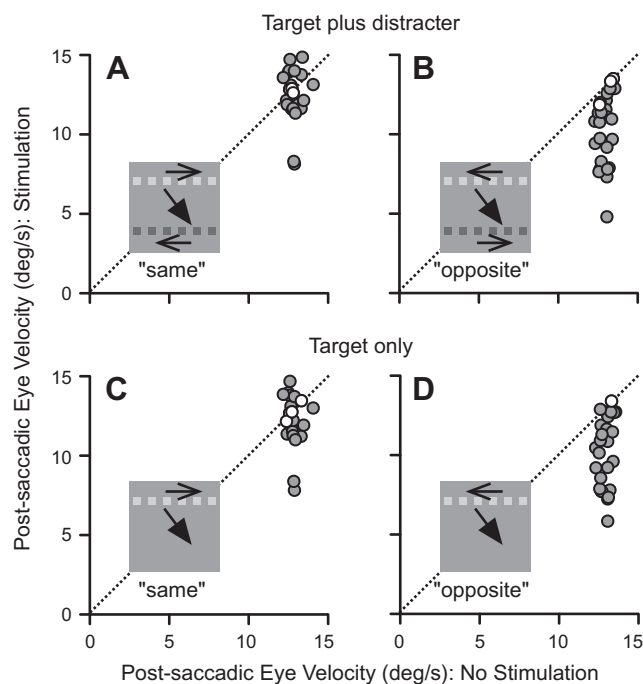


Fig. 5. Summary of the post-saccadic eye velocity measured from different trial types during 26 experimental sessions. In each plot, the average post-saccadic eye velocity on trials with SC microstimulation is plotted against average post-saccadic eye velocity on trials without SC microstimulation. The presence (A and B) or absence (C and D) of the oppositely moving distracter stimulus had little effect on post-saccadic eye velocity.

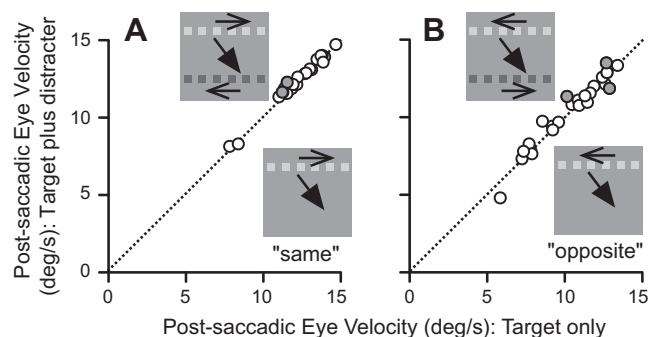


Fig. 6. Direct comparison of post-saccadic eye velocity in the presence or absence of the oppositely moving distracter stimulus. Results are shown separately for cases when the evoked saccade had a horizontal component the same (A) or the opposite (B) as the direction of pursuit. In both plots, post-saccadic eye velocity measured from target-plus-distracter trials is plotted against post-saccadic eye velocity measured from target-only trials. Each symbol shows results from 1 experimental session.

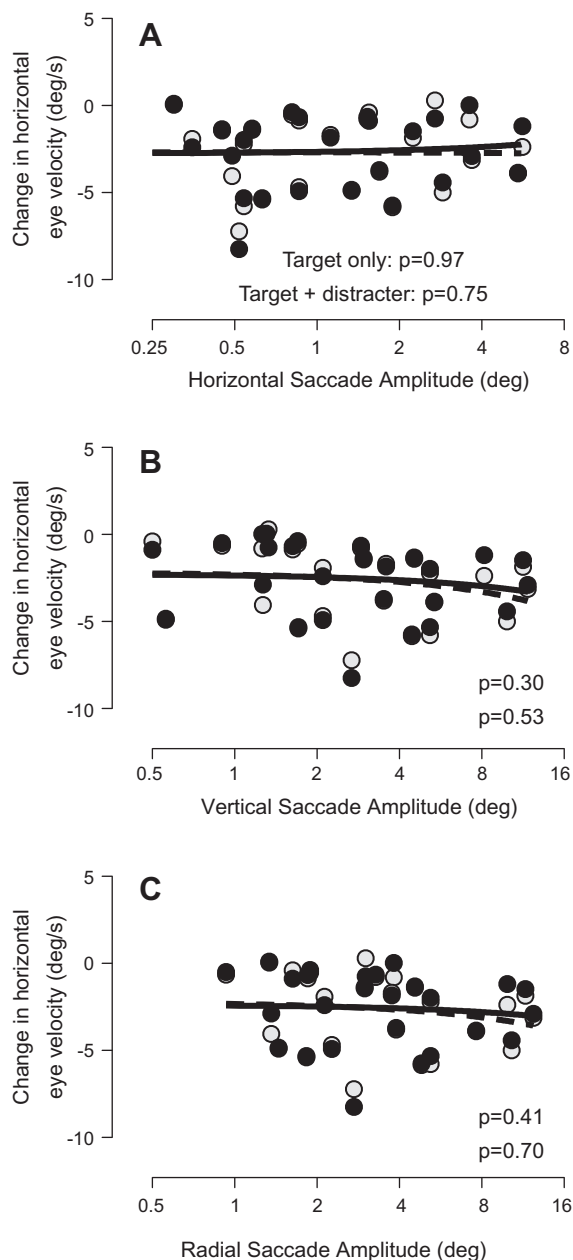


Fig. 7. Changes in post-saccadic eye velocity did not depend on the amplitude of the saccade evoked by SC microstimulation. Each symbol plots the change in post-saccadic horizontal eye velocity, compared to time-matched no-stimulation data, as a function of the horizontal amplitude of the evoked saccade (A), the vertical amplitude (B), or the radial amplitude (C). Results from target-only (gray) and target-plus-distracter (black) trials are shown separately, and form pairs of 26 data points at particular values along the x-axes, based on the saccade evoked by microstimulation during each session. Lines show best-fit linear models for target-only (dashed) and target-plus-distracter (solid) data sets.

that simply bringing gaze to another moving stimulus with a saccadic eye movement was not sufficient to change the value of steady-state pursuit eye velocity.

3.3. Dependence on amplitude of the stimulation-evoked saccade

In the preceding results, there was variability in the amplitudes of the saccades evoked by SC microstimulation, and it is possible that our results could have been influenced by this property of the evoked saccades. For example, larger saccades might have been

more effective in changing pursuit eye velocity, since these involved a larger spatial separation between the target and distracter stimuli. To assess this possibility, we considered how the changes in post-saccadic eye velocity were related to saccade amplitude.

We found no systematic relationship between the change in pursuit eye velocity and the amplitude of the saccade evoked by SC microstimulation, regardless of whether we considered the horizontal (Fig. 7A), vertical (Fig. 7B), or radial (Fig. 7C) amplitude of the evoked saccades. The data points form the target-plus-distracter (black) and target-only (gray) trials form closely spaced or overlapping pairs of data points that form a horizontally elongated cloud, with no tendency to increase or decrease as a function of saccade amplitude. Linear regression analysis indicated that the slopes of the best-fit linear models were not significantly different from zero for any of the data sets (A: target-only, $p = 0.97$, target-plus-distracter, $p = 0.75$; B: target-only, $p = 0.30$, target-plus-distracter, $p = 0.53$; C: target-only, $p = 0.41$; target-plus-distracter, $p = 0.70$). Thus, there was no evidence that the absence of changes in post-saccadic eye velocity was due to the amplitudes of saccades evoked by SC microstimulation in our experiments.

4. Discussion

We have found that motor execution of saccades during ongoing tracking is not sufficient to select the target for smooth pursuit, and in fact does little to perturb the state of pursuit target selection. By applying microstimulation in the intermediate and deep layers of the SC, a structure closely related to the final motor pathways for saccades (Gandhi & Katnani, 2011; Wurtz & Albano, 1980), we were able to artificially shift gaze away from the selected target stimulus and place an alternate distracter stimulus, moving in the opposite direction, at the center of the fovea. Despite this imposed foveation of the distracter, post-saccadic pursuit velocity changed by only 1–10% of the value expected if the monkey had switched to the new moving stimulus. In addition, the same changes in velocity occurred even when there was no moving stimulus present at the endpoint of the evoked saccade. A direct comparison of post-saccadic pursuit eye velocities with and without the distracter stimulus showed no significant difference in all except a few experiments (Fig. 6), demonstrating that even these small changes in post-saccadic eye velocity did not depend on the presence of the moving distracter stimulus, but instead appear to be a nonspecific consequence of the evoked saccade.

These results are inconsistent with the viewpoint that saccade motor commands play a causal role in target selection for smooth pursuit (Gardner & Lisberger, 2001, 2002). If pursuit target selection depended on saccade motor plans, we would have expected to find that pursuit eye velocity matched the speed of the distracter stimulus acquired by the microstimulation-evoked saccade; instead, it was essentially unchanged. Together with previous behavioral studies showing that smooth pursuit can selectively follow the motion of a target stimulus in the presence of a distracter stimulus (Ferrera & Lisberger, 1995; Krauzlis, Zivotofsky, & Miles, 1999), even in the absence of saccades, these results indicate that the motor execution of saccades is neither necessary nor sufficient to accomplish pursuit target selection.

Instead, these results support the viewpoint that pursuit and saccades are alternate outcomes from a shared process of target selection (Krauzlis, 2004). If pursuit target selection were determined by an earlier stage of sensory-motor processing shared with saccades, we would not expect the state of pursuit selection to be changed by the interjection of a saccade that mimics the expression of a new choice but without actually changing the underlying state of selection.

Our findings are consistent with the previous conclusion, based on tracking under more natural circumstances, that voluntary pursuit and saccade responses are guided by common decision signal that is read out in different ways when implementing the two types of movements – specifically, pursuit uses a lower response threshold than saccades. This difference in response threshold is demonstrated, in part, by the correlation between the differences in latency between pursuit and saccades on each trial and the absolute latencies of saccades (Liston & Krauzlis, 2005); this correlation is expected if two different thresholds were applied to the same decision signal. A consequence of this difference in response threshold is that the initial pursuit response tends to be less selective, and the occurrence of saccades, triggered by their more stringent criterion, provides a temporal landmark for a more advanced state of target selection. Post-saccadic pursuit velocity also reflects this more advanced state of target selection, and establishes a correlation between the occurrence of the saccade and pursuit selection. However, as our current results illustrate, this is only a correlation – the occurrence of the saccade does not necessarily play a causal role in regulating the state of pursuit selection.

How can our current results be reconciled with previous studies showing that stimulation-evoked saccades do change the state of pursuit selection? In particular, Gardner and Lisberger (2002) showed evidence that when microstimulation of either the frontal eye field (FEF) or the SC evoked saccades to a moving target, the same target was chosen for smooth pursuit. The difference is unlikely to be related to parameters of microstimulation, because both studies used essentially identical parameters (10–30 μ A, 500 Hz, 70-ms pulse train), and the range of evoked saccade amplitudes were similar. Likewise, the post-saccadic eye velocity intervals used for data analysis were identical. However, the behavioral paradigms were very different. Gardner and Lisberger (2002) used a vector-averaging free-choice task in which microstimulation was applied as the animals considered which of two moving stimuli to follow, and the stimulation occurred just before saccades would naturally occur to one or the other moving stimuli. In contrast, we used a match-to-sample task in which microstimulation was applied after the animals had already selected the moving target and would never normally make a saccade to the distracter stimulus. This difference in the state of target selection at the time of microstimulation could explain the difference in results – microstimulation applied as the target was being selected could bias target selection for both saccades and pursuit, whereas microstimulation applied after target choice might evoke a saccade without changing the state of selection.

Is it plausible that SC microstimulation could bias target selection for saccades and pursuit, as well as evoke a saccadic eye movement? Indeed, several studies provide evidence that in addition to contributing to the motor control of saccades, activity in the intermediate layers of the SC also contributes to earlier stages of sensory-motor processing related to target selection. Microstimulation of the SC biases pursuit and saccadic eye movements to select the stimulus at the corresponding location in the visual field (Carello & Krauzlis, 2004; Dorris, Pare, & Munoz, 1997) and reversible chemical inactivation of the SC biases pursuit and saccades to select stimuli outside the affected portion of the visual field (McPeck & Keller, 2004; Nummela & Krauzlis, 2010). Moreover, SC inactivation not only affects the winner-take-all selection of targets for pursuit and saccades, it also biases the weighted integration of visual motion signals in vector-averaging tasks like that used in Gardner and Lisberger (2002) (Nummela & Krauzlis, 2011). In addition to its role in target selection, activity in the intermediate SC is also causally involved in the control of visual spatial attention during perceptual judgments (Cavanaugh & Wurtz, 2004; Lovejoy & Krauzlis, 2010; Müller, Philastides, & Newsome, 2005). Thus, when microstimulation is applied to the

SC, it is very plausible that it causes parallel changes in the state of target selection as well as eliciting saccades.

These considerations provide an explanation for why previous work found changes in pursuit target selection after microstimulation-evoked saccades – the microstimulation had effects on the process of target selection shared by pursuit and saccades as well as a possible direct motor effect on saccades. If so, then why did we not find effects on target selection in the current experiments? The ability to perturb target selection or saccade motor control using SC microstimulation depends on the behavioral context, and in our case, the situation was tilted in favor of effects on saccade motor execution and against effects on target selection – the microstimulation was applied during ongoing pursuit of an already-selected visual stimulus. Regardless of the actual reason, the logic of the situation favors our interpretation. Given that SC activity is causally involved in both target selection and saccade control, if one observes a correlation between target selection and saccades, it is difficult to eliminate the possibility that both effects unfolded in parallel, rather than one causing the other. However, in our case we evoked saccades but found no changes in pursuit target selection; this dissociation makes it possible for us to conclude that saccade execution does not play a causal role in determining pursuit target selection.

In summary, our results show that the motor execution of saccades is not sufficient to select a pursuit target, and support the idea that the coordination of pursuit and saccades is accomplished by a shared process of target selection. One key unresolved issue is the extent to which this process of target selection for eye movements is synonymous with the mechanisms of spatial attention, or whether there are additional control mechanisms for selecting the goal of orienting movements that operate independently of those which regulate the content of visual perception.

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References

- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10(4), 433–436.
- Carello, C. D., & Krauzlis, R. J. (2004). Manipulating intent: Evidence for a causal role of the superior colliculus in target selection. *Neuron*, 43(4), 575–583.
- Cavanaugh, J., & Wurtz, R. H. (2004). Subcortical modulation of attention counters change blindness. *Journal of Neuroscience*, 24(50), 11236–11243.
- de Brouwer, S., Missal, M., Barnes, G., & Lefevre, P. (2002). Quantitative analysis of catch-up saccades during sustained pursuit. *Journal of Neurophysiology*, 87(4), 1772–1780.
- Deubel, H., & Schneider, W. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, 36(12), 1827–1837.
- Dorris, M., Pare, M., & Munoz, D. (1997). Neuronal activity in monkey superior colliculus related to the initiation of saccadic eye movements. *The Journal of Neuroscience*, 17(21), 8566–8579.
- Ferrera, V., & Lisberger, S. (1995). Attention and target selection for smooth pursuit eye movements. *Journal of Neuroscience*, 15(11), 7472–7484.
- Fischer, B., & Boch, R. (1983). Saccadic eye movements after extremely short reaction times in the monkey. *Brain Research*, 260, 21–26.
- Fischer, B., & Weber, H. (1993). Express saccades and visual attention. *Behavioral and Brain Sciences*, 16, 553–610.
- Fuchs, A. F., & Robinson, D. A. (1966). A method for measuring horizontal and vertical eye movement chronically in the monkey. *Journal of Applied Physiology*, 21(3), 1068–1070.
- Gandhi, N. J., & Katnani, H. A. (2011). Motor functions of the superior colliculus. *Annual Review of Neuroscience*, 34, 205–231.
- Gardner, J. L., & Lisberger, S. G. (2001). Linked target selection for saccadic and smooth pursuit eye movements. *Journal of Neuroscience*, 21(6), 2075–2084.

- Gardner, J. L., & Lisberger, S. G. (2002). Serial linkage of target selection for orienting and tracking eye movements. *Nature Neuroscience*, 5(9), 892–899.
- Hoffman, J., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception & Psychophysics*, 57(6), 787–795.
- Judge, S. J., Richmond, B. J., & Chu, F. C. (1980). Implantation of magnetic search coils for measurement of eye position: An improved method. *Vision Research*, 20(6), 535–538.
- Kerzel, D., Souto, D., & Ziegler, N. E. (2008). Effects of attention shifts to stationary objects during steady-state smooth pursuit eye movements. *Vision Research*, 48(7), 958–969.
- Khurana, B., & Kowler, E. (1987). Shared attentional control of smooth eye movement and perception. *Vision Research*, 27(9), 1603–1618.
- Knox, P. (1996). The effect of the gap paradigm on the latency of human smooth pursuit of eye movement. *NeuroReport*, 7(18), 3027–3030.
- Knox, P. C., & Bekkour, T. (2002). Non-target influences on the initiation of smooth pursuit. *Progress in Brain Research*, 140, 211–224.
- Kowler, E., Anderson, E., Doshier, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, 35(13), 1897–1916.
- Krauzlis, R. J. (2003). Neuronal activity in the rostral superior colliculus related to the initiation of pursuit and saccadic eye movements. *Journal of Neuroscience*, 23(10), 4333–4344.
- Krauzlis, R. J. (2004). Recasting the smooth pursuit eye movement system. *Journal of Neurophysiology*, 91(2), 591–603.
- Krauzlis, R. J., & Miles, F. A. (1996a). Decreases in the latency of smooth pursuit and saccadic eye movements produced by the “gap paradigm” in the monkey. *Vision Research*, 36(13), 1973–1985.
- Krauzlis, R. J., & Miles, F. A. (1996b). Release of fixation for pursuit and saccades in humans: Evidence for shared inputs acting on different neural substrates. *Journal of Neurophysiology*, 76(5), 2822–2833.
- Krauzlis, R. J., Zivotofsky, A. Z., & Miles, F. A. (1999). Target selection for pursuit and saccadic eye movements in humans. *Journal of Cognitive Neuroscience*, 11(6), 641–649.
- Lisberger, S. G. (1998). Postsaccadic enhancement of initiation of smooth pursuit eye movements in monkeys. *Journal of Neurophysiology*, 79(4), 1918–1930.
- Lisberger, S. G. (2010). Visual guidance of smooth-pursuit eye movements: Sensation, action, and what happens in between. *Neuron*, 66(4), 477–491.
- Liston, D., & Krauzlis, R. J. (2003). Shared response preparation for pursuit and saccadic eye movements. *Journal of Neuroscience*, 23(36), 11305–11314.
- Liston, D., & Krauzlis, R. J. (2005). Shared decision signal explains performance and timing of pursuit and saccadic eye movements. *Journal of Vision*, 5(9), 678–689.
- Lovejoy, L. P., Fowler, G. A., & Krauzlis, R. J. (2009). Spatial allocation of attention during smooth pursuit eye movements. *Vision Research*, 49(10), 1275–1285.
- Lovejoy, L. P., & Krauzlis, R. J. (2010). Inactivation of primate superior colliculus impairs covert selection of signals for perceptual judgments. *Nature Neuroscience*, 13(2), 261–266.
- McPeck, R. M., & Keller, E. L. (2004). Deficits in saccade target selection after inactivation of superior colliculus. *Nature Neuroscience*, 7(7), 757–763.
- Merrison, A., & Carpenter, R. (1995). “Express” smooth pursuit. *Vision Research*, 35(10), 1459–1462.
- Müller, J. R., Philiastides, M. G., & Newsome, W. T. (2005). Microstimulation of the superior colliculus focuses attention without moving the eyes. *Proceedings of the National Academy of Sciences of the United States of America*, 102(3), 524–529.
- Nummela, S. U., & Krauzlis, R. J. (2010). Inactivation of primate superior colliculus biases target choice for smooth pursuit, saccades, and button press responses. *Journal of Neurophysiology*, 104(3), 1538–1548.
- Nummela, S. U., & Krauzlis, R. J. (2011). Superior colliculus inactivation alters the weighted integration of visual stimuli. *Journal of Neuroscience*, 31(22), 8059–8066.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Saslow, M. G. (1967). Latency for saccadic eye movement. *The Journal of the Optical Society of America*, 57(8), 1030–1033.
- Schall, J. D., & Thompson, K. G. (1999). Neural selection and control of visually guided eye movements. *Annual Review of Neuroscience*, 22, 241–259.
- Schoppik, D., & Lisberger, S. G. (2006). Saccades exert spatial control of motion processing for smooth pursuit eye movements. *Journal of Neuroscience*, 26(29), 7607–7618.
- Sparks, D. L., & Mays, L. E. (1990). Signal transformations required for the generation of saccadic eye movements. *Annual Review of Neuroscience*, 13, 309–336.
- Walker, R., Deubel, H., Schneider, W., & Findlay, J. (1997). Effect of remote distractors on saccade programming: Evidence for an extended fixation zone. *Journal of Neurophysiology*, 78(2), 1108–1119.
- Wurtz, R. H., & Albano, J. E. (1980). Visual-motor function of the primate superior colliculus. *Annual Review of Neuroscience*, 3, 189–226.