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Coordination of Smooth Pursuit and Saccade Target Selection in Monkeys

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Case GR, Ferrera VP. Coordination of smooth pursuit and saccade target selection in monkeys. *J Neurophysiol* 98: 2206–2214, 2007. First published August 22, 2007; doi:10.1152/jn.00021.2007. The coordination of saccadic and smooth pursuit eye movements in macaque monkeys was investigated using a target selection paradigm with two moving targets crossing at a center fixation point. A task in which monkeys selected a target based on its color was used to test the hypothesis that common neural signals underlie target selection for pursuit and saccades, as well as testing whether target selection signals are available to the saccade and pursuit systems simultaneously or sequentially. Several combinations of target color, speed, and direction were used. In all cases, smooth pursuit was highly selective for the rewarded target before any saccade occurred. On >80% of the trials, the saccade was directed toward the same target as both pre- and postsaccadic pursuit. The results favor a model in which a shared target selection signal is simultaneously available to both the saccade and pursuit systems, rather than a sequential model.

INTRODUCTION

To bring the image of small moving visual targets onto the fovea, primates use a combination of smooth pursuit and saccadic eye movements. Pursuit and saccades are generated by distinct yet overlapping neural systems (Krauzlis 2004, 2003). At issue is the mechanism by which these two systems are internally coordinated in the presence of multiple potential targets. An understanding of this problem may reveal strategies that the brain uses to coordinate multiple motor systems. Two different views have emerged regarding the manner in which target selection is coordinated for pursuit and saccades. Krauzlis and colleagues (Adler et al. 2002; Krauzlis 2003, 2004; Krauzlis and Dill 2002; Krauzlis et al. 1997; Liston and Krauzlis 2003, 2005; Madelain et al. 2005) have provided evidence that a common selection input, possibly related to spatial attention, simultaneously guides both pursuit and saccadic eye movements. Lisberger and colleagues (Gardner and Lisberger 2001, 2002; Schoppik and Lisberger 2006) have argued for a sequential relationship in which the target is first selected by the saccade system and the saccade decision is subsequently passed on to the pursuit system.

The relationship between cognitive signals driving pursuit and saccades can be investigated using oculomotor target selection paradigms. Subjects are given a choice between two or more targets and their eye movements are recorded to determine which target was chosen and when. An advantage presented by the oculomotor system is that the output, eye position, and velocity can be measured to a high degree of accuracy. This makes it possible to distinguish quantitatively between different modes of choice behavior, such as "vector averaging" or "winner-takes-all," as well as intermediate outcomes (Ferrera 2000; Lisberger and Ferrera 1997). The ability to quantify selectivity in the oculomotor system is important because target selection may not always be an all-or-none phenomenon, but may often manifest as a subtle bias toward one choice or another.

To understand how pursuit and saccades are coordinated, it is important to recognize that smooth pursuit is often the faster of the two systems, with latencies around 100 ms (in monkeys), compared with about 150 ms for saccades. Thus when presented with a moving target, a subject will typically initiate a smooth eye movement, make a corrective saccade if necessary, and then continue to track smoothly. A deeper understanding of the coordination between pursuit and saccade target selection can be obtained by deconstructing what happens before, during, and after the first saccade (deBrouwer et al. 2001, 2002a,b). In earlier work, we studied smooth pursuit and saccades evoked by two moving targets using a paradigm in which the target was endogenously selected (Ferrera 2000). Here we extend this two-target approach by varying the eccentricity of the targets over a wide range and by relaxing the behavioral constraints so that the monkey is required to fixate one target or the other only at the very end of a trial. If a shared input simultaneously drives pursuit and saccade target selection, then the saccade, as well as both pre- and postsaccadic pursuit, should all be directed toward the same target. If a serial mechanism links saccade and pursuit target selection, then one expects presaccadic pursuit to be relatively nonselective, whereas postsaccadic pursuit is driven by the same target as the saccade. The current results strongly favor the former scenario, albeit with some qualifications. Some of this work was first presented in abstract form (Case and Ferrera 2001).

METHODS

Experiments were conducted on three juvenile male rhesus monkeys (*Macaca mulatta*). Methods were approved by the Institutional Animal Care and Use Committees at Columbia University and the New York State Psychiatric Institute. Monkeys were trained to move voluntarily from their home cage to a primate chair. A method modified from Wurtz (1969) was used to train each monkey to attend a stationary target. Surgery was then performed under sterile conditions to implant a coil of wire on one eye (Judge et al. 1980) and to secure a post to the skull for head restraint (Miles and Eighmy 1980). For all subsequent training and experiments, the monkey's head was secured to the primate chair and a set of field coils was lowered over the chair so that a magnetic search coil could be used to monitor

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horizontal and vertical eye positions. The eye coil was calibrated by having the monkey fixate targets at different positions and the monkey was subsequently required to keep the direction of gaze within 2–3° of target position. Correct performance of the task was rewarded with drops of fruit juice or water.

Behavioral tasks

Monkeys were trained to track moving targets presented on a color CRT monitor. Trials were initiated when the monkey looked at a stationary central fixation light. After a short interval, one or two perifoveal moving targets appeared (Fig. 1, *A–C*). At this point in time, the monkey was allowed to move his eyes freely. After a variable delay, the central fixation light was turned off, which served as the "go" signal for the monkey to initiate tracking. The monkey was given a liquid reward provided that his gaze was within ±3° of the designated target at the end of the trial. There was a grace period of 400 ms, starting 100 ms before the "go" signal, during which the monkey was allowed to move his eyes freely.

On each trial, either one or two moving targets appeared. The targets were red or green and of equal luminance (15 cd/m^2). On two-target trials, the targets were always different colors. Both targets moved at the same speed: 10, 15, 20, or 30°/s. The target direction was 0, 90, 180, or 270°. On two-target trials, the directions were always orthogonal.

A complete block of 256 trials constituted 50% single-target and 50% two-target trials. For the two-target trials, the same color was rewarded for an entire experimental session (2,000–3,000 trials). The rewarded target color was varied between sessions. The single-target trials were 50% red and 50% green and, of course, the rewarded color was that of the target. Thus within each session, one color was rewarded on 75% of the trials whereas the other color was rewarded on 25% of the trials. Monkeys were given 100 trials at the beginning of each session to learn the reward contingencies before data were recorded.

There was a variable delay of either 200, 400, 600, or 800 ms between the onset of target motion and the "go" signal. The two targets always appeared simultaneously. The delay was selected at random for each trial. The initial location of the targets was chosen so that they would cross the center of the display at the same time the fixation target was extinguished. The targets would then continue for a variable amount of time until they reached an eccentricity of 10–30° and then disappeared. The monkey was rewarded if his eye position was within 3° of the rewarded target during the last 300 ms of the trial. This constraint was sufficient to ensure that monkeys would track one or both targets with their eye movements generally biased toward the rewarded target.

We also used an "unbiased" version of the task (Fig. 1, *D–F*) in which the two targets had the same color (yellow), luminance (15 cd/m^2), size, shape, and speed, and differed only in direction of motion. After the targets crossed in the center of the screen, one target, chosen at random, was extinguished. The monkey was rewarded for tracking the remaining target. The unbiased trials were otherwise the same as the biased red/green target trials.

Visual stimulation

Visual stimuli were generated by a CRS VSG2/3F video frame-buffer with an on-board microprocessor (TMS 34020; Texas Instruments). The output from the video board was displayed on a calibrated 37-in. (Mitsubishi) color monitor with a 60-Hz noninterlaced refresh rate. The monitor stood at a viewing distance of 20 in. so that the display area subtended roughly 50 × 40°. The spatial resolution of the display was 1,280 pixels by 1,024 lines, and the depth was 8 bits/pixel. Pursuit targets were small (1.0°) colored squares presented on a uniform gray background. The target luminance was 15.0 cd/m^2, whereas the background was 0 cd/m^2. The frame buffer was programmed to send out digital pulses (frame sync) for timing purposes at the beginning of each frame in which a stimulus first appeared or started to move. These pulses were sampled by the computer and stored along with the eye movement data.

Eye movement recording

Eye position was monitored using a monocular scleral search coil system (CNC Engineering). Separate horizontal and vertical eye position signals were fed through an analog differentiator (low-pass, −3 dB at 25 Hz) to yield horizontal and vertical eye velocity. The eye

Biased Red/Green Target Task
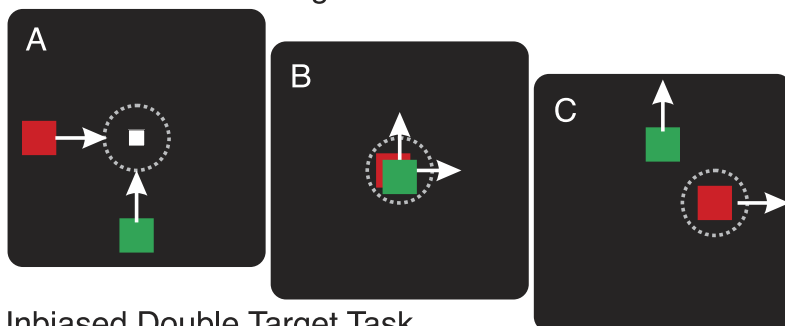
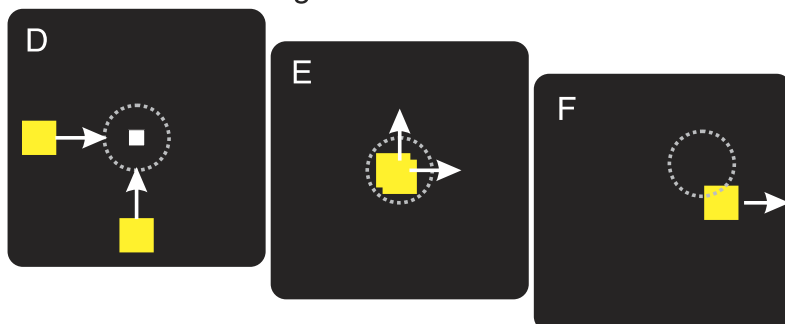

Unbiased Double Target Task

FIG. 1. Task paradigm. Shown are representations of the video display at 3 critical stages of the task. Red and green squares represent the targets and the arrows represent their respective motions. White square represents the fixation target and the dashed circle is the monkey's eye position. *A*: while the monkey fixates the center of the screen, the targets appear eccentrically and move toward the center. Fixation target is extinguished at this point and the monkey is free to look wherever he chooses. *B*: as the targets cross the center of the screen, the fixation target disappears. *C*: toward the end of the trial, the monkey's eye position must be within 3° of the rewarded target to receive reinforcement. *D–F*: unbiased task. Targets are identical in all respects except direction of motion. Task is the same as that in *A–C*, except that one target is extinguished after the targets crossed the center of the display.

position and eye velocity signals were then digitally sampled by computer with 12-bit resolution (0.025° for position, 0.092°/s for velocity) at 1 kHz/channel and stored on disk for further analysis. Eye acceleration was computed off-line by digital differentiation of eye velocity.

We used an automatic algorithm to detect saccades that occurred at any time during target motion. The algorithm used an acceleration criterion of 500°/s² to detect the beginning and end of each saccade. The performance of the algorithm was checked by visually inspecting the data for each trial. We took care that estimates of pre- and postsaccadic eye velocity were not contaminated by saccade onset and offset.

Data analysis

We analyzed eye position and velocity around the time of the first saccade after target motion onset to address the following issues: *1*) How selective are the pursuit and saccade systems? In other words, were eye movements driven primarily by one target or by both targets? *2*) Were saccades and pursuit aimed at the same target or did the two systems choose their targets independently?

The selectivity of pursuit was quantified by expressing the eye velocity evoked by two moving targets as a linear combination of the target velocities (Fig. 2*A*)

$$\mathbf{V}_E = w1 \cdot \mathbf{V}_{T1} + w2 \cdot \mathbf{V}_{T2} \qquad (1)$$

where $\mathbf{V}_E$ is a two-dimensional vector representing horizontal and vertical eye velocity and $\mathbf{V}_{T1}$ and $\mathbf{V}_{T2}$ represent the target velocities. The scalar weights, w1 and w2, can be used to distinguish between four possible idealized outcomes: *1*) vector summation: w1 = w2 = 1.0; *2*) vector averaging: w1 = w2 = 0.5; *3*) winner-take-all for T1: w1 = 1.0, w2 = 0.0; and *4*) winner-take-all for T2: w1 = 0.0, w2 = 1.0. In practice, the weight values generally fell somewhere between pure averaging and winner-take-all selection. However, weights can fall outside the range of [0 1] when eye position/velocity exceeds target position/velocity or has the opposite sign. This tends to happen only when target velocity is small or position is near zero. This analysis is similar to that used previously (Ferrera 2000; Lisberger and Ferrera 1997). One difference is that in previous work, the basis vectors were derived from eye velocity measured on single-target trials. Here, the basis vectors are the target velocities. We took this approach because the target velocities were constant within a trial, as opposed to eye velocity, which varies during the course of a trial. Target velocity therefore provided a more stable basis for each trial condition.

The pursuit target selection analysis was performed twice on every saccade-containing trial; first using presaccadic eye velocity (average eye velocity in a 5-ms window terminated with the beginning of the saccade) and, again, using postsaccadic eye velocity (5-ms window starting at the end of the saccade).

The selectivity of the saccade was based on a similar analysis using eye and target position rather than velocity. Eye position before and after the saccade was expressed as a weighted sum of target position (Fig. 2*B*). The difference in weights for the beginning and end of the saccade was computed as

$$\Delta W_i = w_{i_f} - w_{i_0} \qquad (2)$$

where ΔW_i is the change in eye position weight for the ith target, w_{i_0} is the initial weight, w_{i_f} is the final weight, and i = 1, 2. [Note: To calculate both initial and final weights, the target position at the end of the saccade was used. Several studies have shown that saccades to moving targets are driven by an estimate of target position at the end rather than the beginning of the saccade (Gellman and Carl 1991; Heywood and Churcher 1981; Keller and Steen Johnson 1990; Ron et al. 1989a,b).] If the saccade moves the eye closer to one target, then the change in position weight for that target will be positive. If the saccade moves the eye farther away from one target, then the weight will decrease. We assume that the target that has the larger change in position weight is the one that was selected by the saccade system. As with the pursuit target selection analysis, the change in position weight provides a graded estimate of the degree of target selectivity that the saccade exhibits, not simply an all-or-none measure.

RESULTS

We analyzed eye movements (position and velocity) evoked by two moving targets around the time of the first saccade to determine *1*) how selective was pursuit before and after the saccade? and *2*) was pursuit directed toward the same target as the saccade? Figure 3*A* shows two representative trials from one monkey (E). Both trials had the same stimuli: a rightward moving green target and an upward moving red target. In one trial, the rewarded target was green and for the other it was red. In both cases, there was an initial smooth eye movement that followed the vector average of the two target motions up until the time of the first saccade. The saccade and postsaccadic pursuit were both directed at the rewarded target. This is the pattern of behavior expected from the serial target selection hypothesis: initial averaging pursuit, followed by a targeting saccade, followed by pursuit of the saccade target.

Figure 3*B* shows two additional trials from the same monkey (E), with the same target motions, but with the green target being rewarded in both cases. For one trial, it is clear that pursuit was biased toward the rewarded target well before the
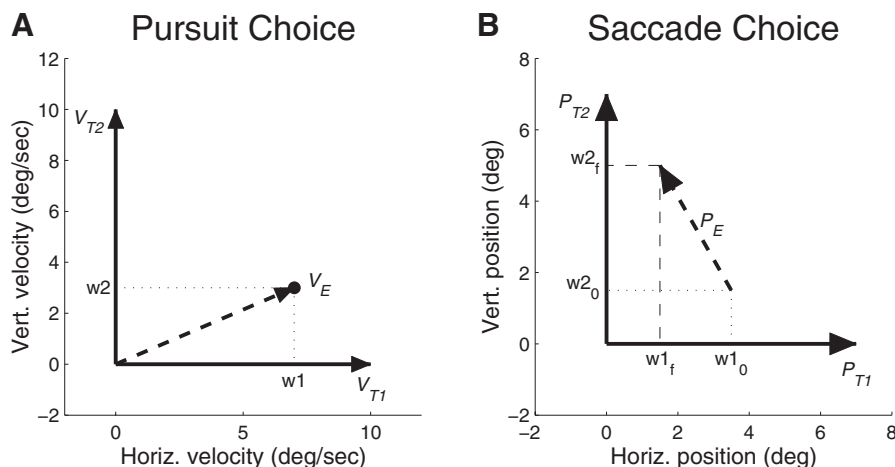

FIG. 2. Target selection analysis. *A*: pursuit choice was quantified by decomposing the eye velocity vector ($\mathbf{V}_E$) using the target velocity vectors ($\mathbf{V}_{T1}$, $\mathbf{V}_{T2}$) as a basis set. This results in a pair of weights (w1, w2) that express how strongly pursuit is driven by each target. *B*: saccade choice was quantified by calculating the target position weights at the start and end of the saccade. Change in weights indicates how strongly the saccade is influenced by each target. Arrow represents the saccade vector, whereas $\mathbf{P}_{T1}$ and $\mathbf{P}_{T2}$ represent the target positions. Weights are represented by the dotted and dashed lines.
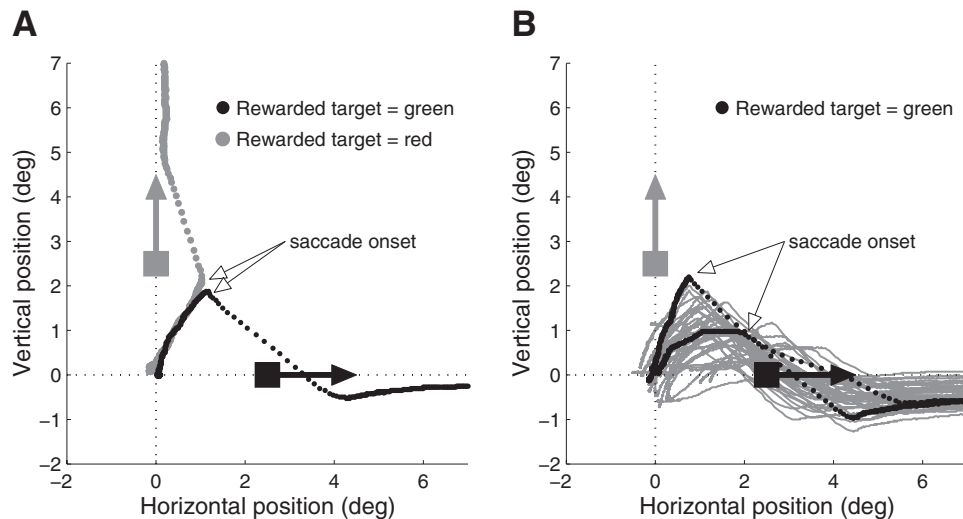
FIG. 3. Example trials. *A*: 2 trials are shown in which the target motions were the same, but the rewarded target was different. Large black square with attached arrow represents a rightward-moving green target. Large gray square represents an upward-moving red target. Gray and black points represent eye position sampled every 1 ms. *B*: 2 additional trials (filled and open black circles) with the same target motions as *A*. Rewarded target was green for both trials. Gray lines show eye position for all trials with the same target motion from a single session.

saccade. This pattern of results supports the hypothesis that the pursuit and saccade systems receive a common target selection signal and that this signal is available to the pursuit system at the same time as, if not before, the saccade system. The other trial is an example where the animal initially tracked the nonrewarded target and then switched to the other by making a targeting saccade. This behavior does not support either hypothesis, but demonstrates that the link between pursuit and saccades can be fairly flexible. Thus it is not a foregone conclusion that pursuit and saccades automatically choose the same target. These examples show that the task design allowed for behavioral outcomes that could potentially support either the shared or serial hypotheses, or neither hypothesis. To provide a sense of the range of outcomes, the gray lines in Fig. 3*B* show all trials from a single session with the same target motions.

Which pattern of results was more prevalent? We analyzed 13,841 trials from six sessions performed by three monkeys (two sessions per monkey; in one session the green target was rewarded and in the other the red target was rewarded). As an index of pursuit target selection, we measured how strongly pursuit was weighted toward either target (rewarded or nonre-

warded) using the analysis in Fig. 2*A*. Figure 4 shows pooled data for all three monkeys, both rewarded target colors, and all four target speeds, but only the condition in which the delay between target onset and the "go" signal was 800 ms (results were similar for the other delays). Figure 4*A* shows the results for pursuit just before the saccade. The target weights (*Eq. 1*) are plotted as a function of the time when the saccade occurred relative to target onset ("time of saccade"). The time of the "go" signal relative to target onset is indicated by the vertical dotted line in Fig. 4, *A–C*. Times before the targets crossed in the middle of the screen (and were therefore converging) are indicated to the left of this line; times after the targets crossed (diverging motion) are indicated to the right of this line. The behavioral constraints were loose enough to allow the monkey to initiate tracking before the "go" signal (in fact, there was no fixation requirement during the time interval 100 ms before to 300 ms after the "go" signal). Thus the delay between target onset and "go" signal resulted in saccade latencies that spanned a wide range and were generally much longer than normal saccade latencies for monkeys (~150 ms).

The separation between the weight distributions for rewarded and nonrewarded targets is an index of pursuit target
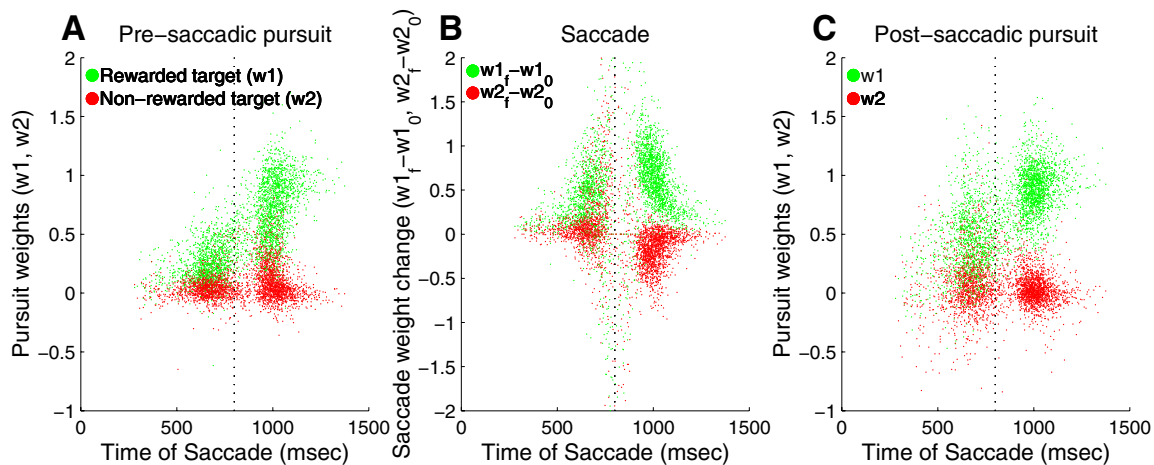

FIG. 4. Target selection around the time of the saccade. All trials (3 monkeys, 4 speeds, 2 rewarded target colors) with delay = 800 ms are shown. *A*: rewarded (green dots) and nonrewarded (red dots) target weights for presaccadic pursuit plotted as a function of time of saccade. Dotted vertical line is the time when targets crossed paths in the center of the display. *B*: change in target position weights for saccades plotted as a function of time of saccade. Same color convention as *A*. *C*: target weights for postsaccadic pursuit. Same conventions as *A*.

selectivity. The data in Fig. 4*A* suggest that presaccadic pursuit was highly selective and that the weight given to the rewarded target increased with increasing time of saccade. The same pattern of results was observed for all monkeys, target speeds, and delays.

For the saccade, target selection was quantified as the change in target position weights (Fig. 4*B*). The selected target was considered to be the one for which there was the greatest increase in position weight (ΔW). Distributions of ΔW for the rewarded and nonrewarded targets show little overlap except for saccades initiated around the time of target crossing. These saccades tend to be smaller than saccades initiated well before or well after the target crossing. They also tended to be more random, even though presaccadic pursuit around the time of target crossing was not random. This could be a clue to the neural organization underlying saccade and pursuit target selection because the parts of the superior colliculus and frontal eye field where pursuit neurons are found tend to be nearer to the representation of small saccades than that of large saccades. This issue will be addressed in the DISCUSSION.

The target weights for postsaccadic pursuit are shown in Fig. 4*C*. The results are generally quite similar to those for presaccadic pursuit, suggesting that both pre- and postsaccadic pursuit may be driven by the same signal. This will be addressed by examining *1*) the correlation between the weights on a trial-by-trial basis and *2*) the proportion of trials on which pre- and postsaccadic pursuits were biased toward the same target.

Target selectivity was quantified by using region of overlap condition (ROC) analysis to quantify the overlap of the weight distributions for the rewarded and nonrewarded target. ROC analysis (Green and Swets 1966) is an effective way to quantify the overlap of two distributions of arbitrary shape. The area under the ROC curve can vary from 0.5 (complete overlap) to 1.0 (no overlap). In this case, the weight distribution for the rewarded target was treated as the "signal," whereas that for the nonrewarded target was treated as the "noise." ROC area is plotted in Fig. 5 for all trials, sorted by delay. The analysis was repeated for different saccade times by grouping trials by time of saccade in 50-ms bins. Figure 5*A* shows that for presaccadic

pursuit, even though the magnitude of the rewarded target weight increased with time of saccade (Fig. 4*A*), selectivity was high for all delays and across saccade latencies.

For the saccade, the pattern of results was quite different. Saccade selectivity was highly variable (Fig. 5*B*). Saccades initiated around the time of target crossing (dotted vertical lines in Fig. 5*B*) were almost completely random. Saccade selectivity increased as the time of saccade became farther removed from the crossing time. Presaccadic pursuit showed no such dip in selectivity around the target crossing time. In fact, when saccades were initiated before the target crossing, presaccadic pursuit (Fig. 5*A*) tended to be more selective than postsaccadic pursuit (Fig. 5*C*), suggesting that in some cases the saccade may disrupt pursuit target selection rather than coordinating it.

These results raise the issue of how closely saccades and pursuit were coordinated on a trial-by-trial basis. Figure 6*A* shows the correlation between the weights for pre- and postsaccadic pursuit for all trials. The weights for the rewarded target were highly correlated, whereas those for the nonrewarded target tended to cluster around zero and were weakly correlated. Thus pre- and postsaccadic pursuit tended strongly to be driven by the same target.

Figure 6*B* plots the proportion of trials in which pre- or postsaccadic pursuit was biased in favor of the same target as the saccade. The data were separated by animal, rewarded target, target speed, and target direction to yield a total of 96 conditions. Averaged over all conditions, presaccadic pursuit selected the same target as the saccade on 81% of the trials. Postsaccadic pursuit was directed to the same target as the saccade on 86% of the trials. There were also some quantitative individual differences between the monkeys. For monkey E, postsaccadic pursuit was better coordinated with the saccade. For monkey A, presaccadic pursuit was better coordinated, whereas for monkey F both pre- and postsaccadic pursuit were strongly and equally coordinated with the saccade.

One concern is that the apparent coordination of pursuit and saccades might be driven by small "corrective" saccades. A true intention to switch targets might be associated with larger saccades. Thus one might expect small saccades to be better
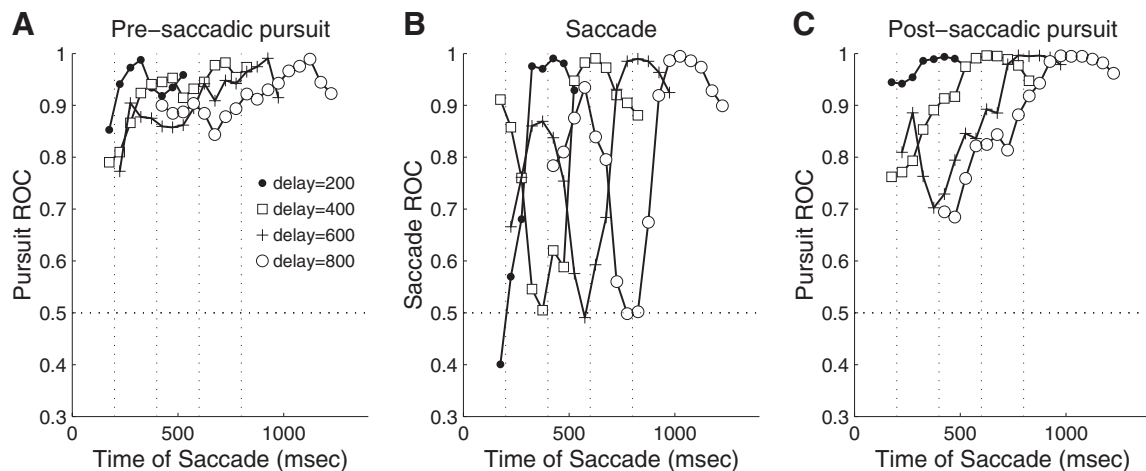

FIG. 5. Target selectivity estimated by region of overlap condition (ROC) analysis. *A*: area under ROC (comparison of weight distributions for rewarded and nonrewarded targets) for presaccadic pursuit as a function of time of saccade. All trials (3 monkeys, 4 speeds, 4 delays, 2 rewarded target colors) are shown sorted by delay. Dotted horizontal line is the ROC value (0.5) representing completely overlapping distributions. Dotted vertical lines represent the times when the targets crossed in the center of the screen. *B*: ROC values for the first saccade on each trial. Same conventions as *A*. *C*: ROC values for postsaccadic pursuit. Same conventions as *A*.
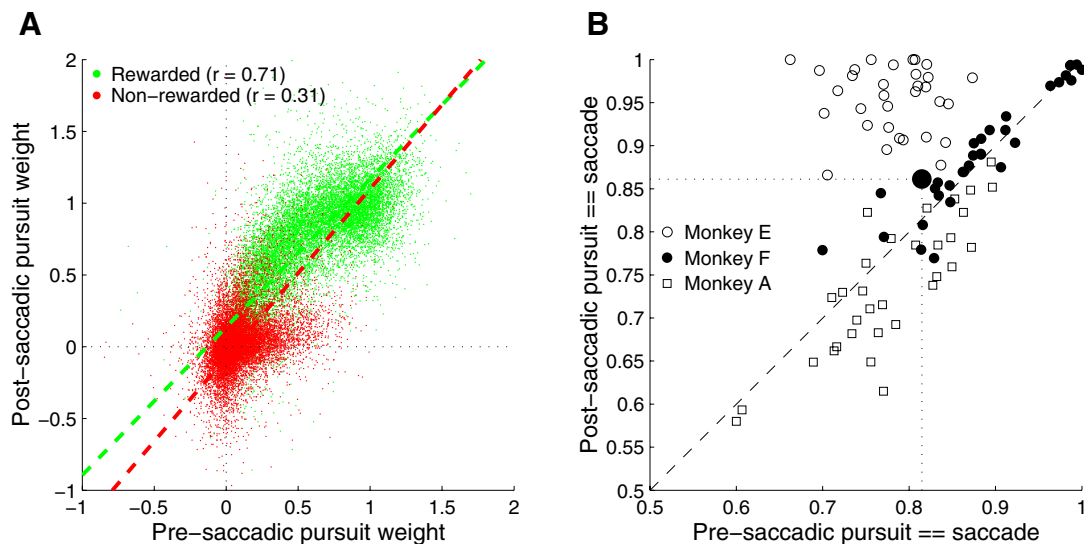
FIG. 6. Trial-by-trial comparison of pursuit and saccade selectivity. *A*: correlation between target selectivity (weights) for pre- and postsaccadic pursuit. Green dots are weights for the rewarded target, red for the nonrewarded target. Dashed lines are regression lines fit to the first principal component of the data. "*r*" is the standard correlation coefficient. *B*: proportion of trials in which pursuit and saccades selected the same target. Data are sorted by animal, rewarded target color, speed, and delay for a total of 96 points. Large black dot represents the grand mean for pre- and postsaccadic pursuit. Dashed line is x = y, representing equal coordination for pre- and postsaccadic pursuit.

coordinated with pursuit, especially presaccadic pursuit, than large saccades. We found that, overall, the typical saccade amplitude was $2.1 \pm 1.5°$ (mean $\pm$ SD). We therefore divided trials into those with saccades $<2.0°$ and those $>2.0°$. For small-saccade trials, presaccadic pursuit chose the same target as the saccade 81% of the time (6,790/8,433 trials), whereas postsaccade pursuit was coordinated with the saccade on 80% of trials (6,711/8,433). For large saccade trials, presaccadic pursuit was coordinated with the saccade 83% of the time (4,492/5,407 trials) and, as one might expect, postsaccadic pursuit followed the saccade target 98% of the time (5,273/5,407 trials). All effects were highly significant ($P < 10^{-50}$). Larger saccades were equally if not better coordinated with pursuit than small saccades; thus the effects reported here were not driven solely by "corrective" saccades.

It is possible that the coordination of saccades with both pre- and postsaccadic pursuit is due to two factors: *1*) a strong top-down bias to track the rewarded target and *2*) the possibility that the saccade is initiated long after the actual decision is made about which target to track. To address these issues, we performed an additional experiment in which we eliminated the bias and examined behavior for trials with the shortest saccade latencies.

In the "unbiased" experiment, the two targets always had the same color (yellow), size, shape, and speed, but moved in different directions. When the targets crossed the center of the screen, one target, chosen at random, was extinguished and the monkey was rewarded for tracking the other target. Otherwise, the unbiased trials were identical to the previously discussed red/green biased experiment.

The same three monkeys performed in the unbiased experiment. In all, there were 9,067 trials, of which we selected 2,125 (23%) in which the time of saccade was shorter than the delay between target onset and "go" signal (i.e., the saccade occurred before the targets crossed the center of the screen). Based on the experimental design, it is expected that both pursuit and saccades would be unselective and unbiased. ROC

analysis showed that, on average, eye movements made in this time interval were indeed not selective for either target. The ROC areas were 0.50 for presaccadic pursuit, 0.49 for the saccade, and 0.52 for postsaccadic pursuit, showing that the target weight distributions were completely overlapping. In other words, neither eye position nor velocity was systematically biased toward the rewarded target.

The same analysis was conducted for the biased red/green experiment. In this case, there were 4,398/13,841 (32%) trials in which the first saccade was initiated before the time of target crossing. The ROC areas were 0.84 for presaccadic pursuit, 0.71 for the saccade, and 0.83 for postsaccadic pursuit. These numbers are consistent with the analysis of Fig. 6, showing that there was a consistent bias for eye movements initiated before target crossing for the red/green target experiment.

For the unbiased experiment, even though there was no net bias revealed by ROC analysis, there was still trial-to-trial variability. Was this apparently random variability correlated between pursuit and saccades? To address this, we again asked whether pursuit and saccades chose the same target on an individual trial basis. We found that presaccadic pursuit was biased toward the same target as the saccade on 1,449/2,125 (68%; $P < 10^{-50}$) trials, whereas postsaccadic pursuit was biased toward the saccade target on 1,432/2,125 (67%; $P < 10^{-50}$) trials. Thus even though there was no apparent net bias, saccades and pursuit were moderately well coordinated trial by trial. The same analysis was performed for the "biased" experiment. In this case, presaccadic pursuit was biased toward the same target as the saccade on 3,094/4,398 (70%; %; $P < 10^{-50}$) trials, whereas the numbers for postsaccadic pursuit were 3,015/4,398 (69%; $P < 10^{-50}$). Interestingly, the unbiased experiment shows about the same trial-to-trial coordination as the biased experiment, suggesting that a certain degree of coordination is present even in the absence of an explicit top-down selection bias. Overall, the proportion of trials in which pursuit and saccades were biased toward the same target was in the range 67–70%. One might expect a proportion much

closer to 1.0 if the eye movements occurred after the completion of a winner-takes-all decision process.

It should be noted that saccades initiated before target crossing tended to be small. The average saccade amplitude for the unbiased experiment was $1.4 \pm 0.6°$ (mean $\pm$ SD) and $1.2 \pm 0.6°$ for the biased experiments. One might expect a high degree of endpoint variability in such small saccades. If this variability were purely random, then it might mask the saccade choice, which should weaken the apparent correspondence between pursuit and saccades. Thus the observation that saccades and pursuit chose the same target about 70% of the time is likely to underestimate the true degree of coordination between the two systems.

How far in advance of the saccade are pursuit choices predictive of saccade choices? We expanded two of the analyses described previously to estimate *1*) the selectivity of presaccadic pursuit and *2*) the coordination of presaccadic pursuit with the saccade, as a function of time before the saccade. Figure 7*A* shows the selectivity of presaccadic pursuit using an ROC analysis similar to that in Fig. 5. Here, we looked at pursuit eye velocity ≤300 ms before saccade onset. For each time point, we used only trials where pursuit was initiated ≥50 ms prior (e.g., the 250-ms time point includes trials where pursuit was initiated ≥300 ms before the saccade). Data were sorted by delay time, but collapsed across target speed and monkey. Pursuit was biased toward the rewarded target well before the saccade occurred. Presaccade pursuit predicts the saccade target 55–60% of the time as much as 350 ms before the saccade and becomes even more predictive around 100–150 ms before the saccade (Fig. 7*B*). There thus appears to be a time window of several hundred milliseconds during which the pursuit decision evolves and becomes more closely coordinated with the saccade decision. This evidence supports either a parallel selection mechanism or a sequential process in which the pursuit choice guides saccade target selection. It argues against a sequential process in which the saccade choice guides pursuit.

DISCUSSION

To track moving targets, primates use a combination of smooth pursuit and saccadic eye movements. Smooth pursuit

and saccades are controlled by distinct neural circuits, and the degree of overlap between these systems is a currently debated topic (see Krauzlis 2004, 2005). We investigated the coordination of these two systems by presenting monkeys with two moving targets and recording their eye movements. The task was designed to give the subjects a high degree of flexibility in their response; it was easily possible for the monkeys to track one target and then saccade to the other. Yet this behavior was seldom observed. Rather, the first saccade tended to be highly selective for the rewarded target, unless that saccade occurred near the time when the targets crossed in the middle of the screen, in which case it tended to be random. Smooth pursuit, both before and after the first saccade, tended to be driven toward the same target as the saccade. These results argue strongly in favor of a shared signal for pursuit and saccade target selection as proposed by Krauzlis and colleagues (Adler et al. 2002; Krauzlis 2003, 2004; Krauzlis and Dill 2002; Krauzlis et al. 1997; Liston and Krauzlis 2003, 2005; Madelain et al. 2005). They argue equally strongly against a serial selection mechanism in which the target choice is first made by the saccade system, which subsequently causes the pursuit system to shift from tracking the vector average of the target motions to tracking the motion of the saccade target exclusively (Gardner and Lisberger 2001, 2002; Schoppik and Lisberger 2006).

Some studies in humans (Garbutt and Lisberger 2006) have indicated that smooth pursuit can be highly selective before the first saccade. However, they have not indicated how pursuit selectivity relates to saccade target selection. We found that pursuit starts to become selective ≤300 ms before the saccade and that pursuit selectivity and the coordination of pursuit and saccade choice evolve with similar time courses. These results further argue for a parallel selection mechanism or, if anything, a serial process in which the pursuit choice precedes saccade selection. They provide further evidence against a scenario in which saccade selection precedes and guides the pursuit decision.

The current findings warrant some refinement of the shared target selection hypothesis. Small saccades made around the time of the targets' crossing tended to be directed randomly. Thus the saccade system appears to be nonselective when the
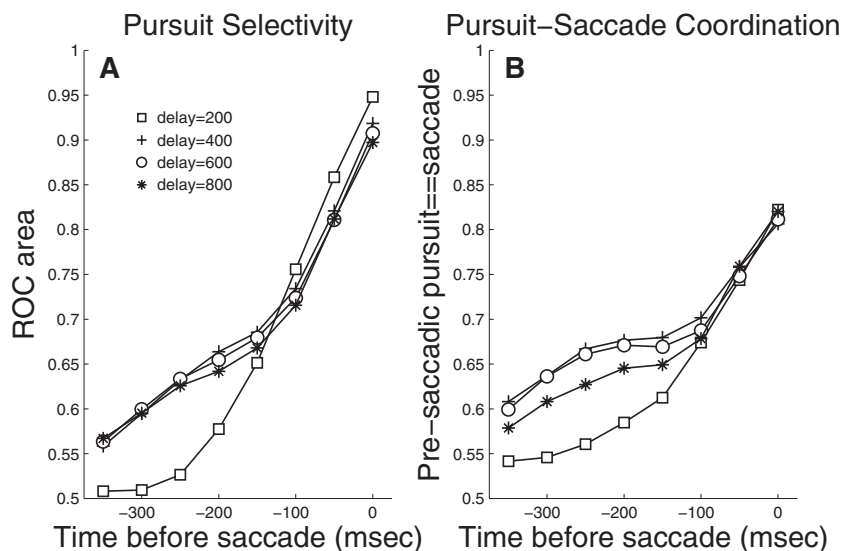

FIG. 7. Pursuit selectivity and pursuit-saccade coordination as a function of time before the saccade. *A*: pursuit selectivity measured as the ROC area, a measure of the separation between the rewarded and nonrewarded target weight distributions. "Delay" is the time between target motion onset and the "go" signal. *B*: proportion of trials for which presaccadic pursuit was biased toward the same target as the saccade. Bias was measured as the difference in the target weights (rewarded target weight − unrewarded target weight).

targets are in close proximity or are near to the center of gaze. This is in keeping with the observation of averaging saccade for targets that are close together (Ottes et al. 1984). At the same time, smooth pursuit was strongly selective, suggesting that small saccades may not be driven by the same target selection signal as pursuit. Also, the coordination of pursuit and saccade target selection was as strong or stronger for larger saccades ($>2.0°$) than that for small saccades, including "corrective" saccades (de Brouwer et al. 2002).

One might have expected otherwise based on the known functional organization of oculomotor centers such as the frontal eye field (FEF) and superior colliculus (SC). Both structures contain maps of saccade amplitude. In the FEF, small saccades are represented laterally whereas large saccades are represented medially (Bruce et al. 1985). The small saccade region of the FEF is adjacent to the frontal pursuit area (FPA), which contains neurons that respond continuously during smooth pursuit, whose discharge is correlated with eye velocity, and which causes smooth eye movements when stimulated electrically (Gottlieb et al. 1993, 1994; MacAvoy et al. 1991; Tanaka and Lisberger 2002). In the SC, small saccades are represented rostrally and large saccades caudally (Robinson 1972). The rostral colliculus also contains cells that respond during smooth pursuit and whose activation or inactivation alters pursuit (Basso et al. 2000; Krauzlis et al. 2000).

Given the close proximity in two different brain structures of neurons involved in smooth pursuit and small saccades, one might have expected these two behaviors to be more closely coordinated. Yet, it is almost as if target selection for small saccades is turned off under certain circumstances. It is possible that the target selection signal is sent separately to pursuit neurons and to large saccade neurons, while avoiding the small saccade neurons that lay between. This argues against a selection signal that originates with the large-saccade neurons and spreads to pursuit neurons, or vice versa. More likely is that both neuronal pools receive target selection inputs from a higher-order area, perhaps one involved in spatial attention (Adler et al. 2002).

Our results also suggest that the coordination of saccades and pursuit is not entirely driven by selection bias. This conclusion is supported by the results of an additional experiment in which it was impossible for the monkey to choose a target until the second half of the trial. ROC analysis confirmed the absence of bias. When we examined saccades initiated during the first half of each trial, we found that they skewed toward the same target as pursuit on about 67–68% of the trials. This is similar to the proportion of trials (69–70%) in which saccades and pursuit were coordinated in the biased red/green target experiment. These results suggest that saccades and pursuit are coordinated not only by top-down inputs, but also suggest the presence of lateral interactions between the neural structures that control pursuit and saccades.

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