

Shared decision signal explains performance and timing of pursuit and saccadic eye movements

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Each voluntary eye movement provides physical evidence of a visuomotor choice about where and when to look. Primates choose visual targets with two types of voluntary eye movements, pursuit and saccades, although the exact mechanism underlying their coordination remains unknown. Are pursuit and saccades guided by the same decision signal? The present study compares pursuit and saccadic choices using techniques borrowed from psychophysics and models of response time. Human observers performed a luminance discrimination task and indicated their choices with eye movements. Because the stimuli moved horizontally and were offset vertically, subjects' tracking responses consisted of combinations of both pursuit and saccadic eye movements. For each of two signal strengths, we constructed speed–accuracy curves for pursuit and saccades. We found that speed–accuracy curves for pursuit and saccades have the same shape, but are time-shifted with respect to one another. We argue that this pattern occurs because pursuit and saccades share a decision signal, but utilize different response thresholds and are subject to different motor processing delays.

Keywords: pursuit, saccades, speed–accuracy tradeoff, choice behavior, response threshold

Introduction

Primates generate two types of voluntary eye movements: pursuit and saccades. Pursuit responds continuously to target motion signals (Dodge, 1903; Robinson, 1965; Krauzlis, 2004; Lisberger, Morris, & Tychsen, 1987), stabilizing the target's image on the retina, whereas saccades correct for the target's position, placing the target's image on or near the fovea (Dodge, 1903; Robinson, 1964; Schall & Thompson, 1999; Sparks & Mays, 1990). Between visual sensation and motor action, however, a complicated cascade of neural events transpires, a simplified functional description of which includes at least three components: a visual processing stage, a response selection stage (i.e., a putative decision stage), and a motor output mechanism.

Physiological as well as behavioral data support the idea that visual processing (i.e., retinal encoding through processing in striate and extrastriate cortex) is shared for pursuit and saccades. Both systems depend on signals from V1 (Zee et al., 1987) and are influenced by later visual processing areas (Komatsu & Wurtz, 1989; Newsome, Wurtz, Dursteler, & Mikami, 1985). Behaviorally, we found evidence for similar visual processing for pursuit and saccades on a visual discrimination task (Liston & Krauzlis, 2003). While fixating, human observers were briefly exposed to probe stimuli that were later masked by response stimuli, which elicited both pursuit and saccadic movements. The two systems exhibit similar visual thresholds, arguing for similar, if not shared, visual processing. Furthermore, pursuit and saccades also show similar re-

sponse biases, agreeing on 87–99% of trials, suggesting shared processing downstream of the visual stage.

Additional evidence supports the idea that pursuit and saccades share a common decision stage. First, subthreshold stimulation in the superior colliculus, a motor preparatory structure, biases both pursuit and saccadic responses (Carello & Krauzlis, 2004). Second, the offset of a fixated stimulus before the appearance of a target stimulus (i.e., gap paradigm) results in reduced latencies for pursuit (Knox, 1996; Krauzlis & Miles, 1996; Merrison & Carpenter, 1995) and saccades (Fischer & Boch, 1983; Fischer et al., 1993; Saslow, 1967). Both systems show a similar trend as the duration of the temporal gap increases, suggesting that common inputs trigger both types of movements (Krauzlis & Miles, 1996). Lastly, spatial cues affect response latency more than motion cues for both movements, suggesting that both systems share a spatial response selection mechanism (Adler, Bala, & Krauzlis, 2002).

Despite these similarities, there are well-known differences in the timing and choice properties of the two movements. Pursuit tends to occur at shorter latencies (~125 ms) than saccades (~200–250 ms) (Leigh & Zee, 1991; Robinson, 1965). Pursuit often initiates in one direction, only to later turn around (Krauzlis et al., 1999), whereas a saccade typically reflects a more final choice of the oculomotor system (Liston & Krauzlis, 2003).

How can two systems be guided by common input yet still display differences in timing and choices? **Figure 1** shows three possible mechanisms that might coordinate target selection for pursuit and saccades. First, pursuit and

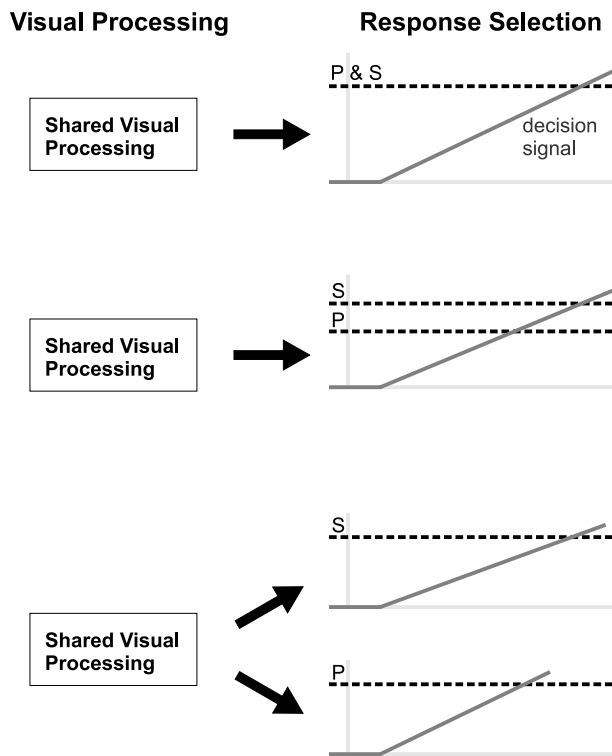


Figure 1. Possible mechanisms coordinating target selection for pursuit and saccades. The top panel illustrates a shared visual processing stage driving a shared decision signal to a common response threshold (P & S). The middle panel shows a shared visual processing stage driving a shared decision signal that crosses a lower response threshold for pursuit (P) than saccades (S). The bottom panel shows a shared visual processing stage driving two independent decision signals to different response thresholds.

saccades might share a common decision signal and a common response threshold (top panel). This mechanism predicts complete concordance between pursuit and saccade choices as well as correlation between their latencies. Second, both systems might share a decision signal, but pursuit might employ a lower response threshold than saccades (middle panel, Krauzlis & Dill, 2002). This mechanism would allow for disagreements between pursuit and saccades (given nonlinear decision signals), as the low-response threshold would give rise to faster responses and more errors, whereas a high response threshold produces slower responses and fewer errors (Green & Swets, 1988; Luce, 1986). Third, the two systems might utilize independent decision signals (bottom panel), which makes testable predictions about the level of agreement between pursuit and saccade decisions.

Additional timing differences between pursuit and saccadic movements might stem from different delays in their motor output pathways. For example, the programming of a motor command might involve a ballistic processing interval occurring between response selection and motor execution. Different ballistic processing intervals in

the pursuit and saccadic pathways could introduce an additional delay between pursuit onset and saccade onset (Kornylo, Dill, Saenz, & Krauzlis, 2003).

Speed–accuracy analysis provides a useful tool for investigating these types of issues, but has not yet been applied to pursuit and saccades. By measuring performance as a function of time, speed–accuracy analysis provides a tool for examining the dynamics of visuomotor processing. For example, speed–accuracy analysis has demonstrated that covert attention accelerates the rate of visual processing (Carrasco & McElree, 2001) and that processing across the visual field is nonuniform (Carrasco, Giordano, & McElree, 2004). Here, we use speed–accuracy analysis and response time modeling to compare visuomotor processing for pursuit and saccade choices. We report that pursuit and saccade speed–accuracy curves have the same shape, but also exhibit time shifts that can be attributed to differences in response thresholds and to a ballistic delay in saccadic pathways.

Materials and methods

Subjects

Three naïve adult human subjects participated in this experiment. Each subject participated in a total of 13 sessions, the first three of which were training sessions. The data used in this study were collected in the last 10 sessions, each consisting of 768 trials and lasting ~50 min.

Stimuli and paradigm

Our subjects were asked to perform a luminance discrimination task. The temporal sequence of the stimuli presented during a single experimental trial is illustrated in Figure 2. A trial began with the appearance of a central 0.5° fixation cross. We recorded the subjects' eye movements and confirmed that the subjects maintained fixation during this epoch. After a random 500- to 1000-ms interval, two elongated noise strips (12 pixels vertical \times 1024 pixels horizontal; 0.7° vertical \times 45° horizontal) were presented above and below the fixation cross ($\pm 2^\circ$), moving horizontally in opposite directions at 14.2 deg/s. Observers were asked to make an eye movement to and smoothly follow the brighter of the two strips. To elicit a range of latencies, the offset of the fixation cross was varied in time (+200, 0, –200 ms) relative to the onset of the noise strips.

The pixel luminance values in the “noise” strips were drawn from two distributions with different means (pixel size of .0583 deg/pixel vertical \times .0439 deg/pixel horizontal; distractor luminance, 33.4 cd/m²; target luminance, 33.6 or 33.8 cd/m²), but with the same standard deviation ($SD = 3.2$ cd/m²). The difference in means was adjusted to produce stimuli with discriminability of $d' = 0.05$ or 0.10

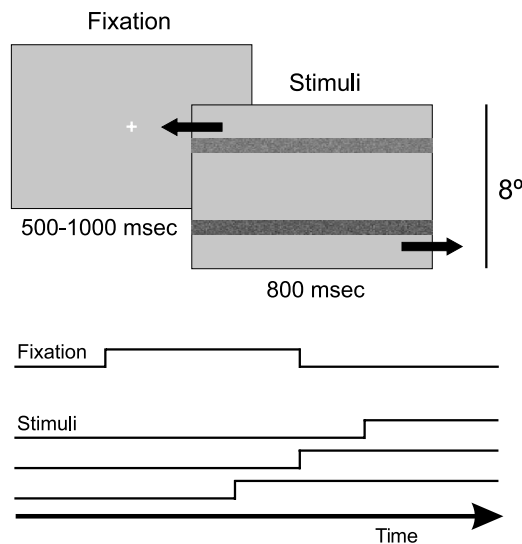


Figure 2. Schematic diagram of one trial. The sequence of screen images depicts a single trial. Each screen image represents the central portion (11.7° horizontal \times 8° vertical) of the video monitor. The large black arrows in the mask interval signify the opposed horizontal motion of the masks and did not appear on the monitor. The offset of the fixation cross was varied in time (+200, 0, -200 ms) relative to the onset of the noise strips. Observers were asked to maintain fixation until the fixation cross disappeared.

(Green & Swets, 1988). Because these d' (sensitivity) values represent a measurement of the distance between the luminance distributions and not performance values for an ideal observer on our task, we will refer to these as conditions of low and high signal, respectively. To ensure consistency in the distance between the luminance distributions, we tested each unique pair of noise strips, using only pairs whose measured d' value was within 1% of the value reported.

Software and hardware

Our stimuli were presented on a gamma-corrected video monitor (29.3° vertical \times 45° horizontal, positioned 41 cm from the subjects, 120 Hz, 1024 horizontal pixels \times 768 vertical pixels). Eye position was recorded with an infrared video-based eye tracker (RK-726; ISCAN, Burlington, MA) to a precision of $\sim 0.1^\circ$ and was sampled at 1 kHz.

The experiment was executed on a personal computer running the Tempo software package (Reflective Computing, St. Louis, MO). Tempo controlled the timing of the stimuli, acquired the data, and saved it to disk. An additional personal computer, equipped with a high-speed graphics card (Cambridge Research Systems VSG2/3, Kent, UK) and VisionWorks software (Vision Research Graphics, Durham, NH), acted as a server to present the visual stimuli under the control of the Tempo machine. The visual display computer returned trigger signals to the

Tempo machine as each stimulus was displayed, which allowed us to synchronize eye position data with the trigger signals at a resolution of 1 ms. All eye-movement data and signals related to onset of stimuli were stored on the hard disk of the Tempo machine during the experiment, and later transferred to a freeBSD (Berkeley Software Distribution) system for off-line analysis.

Oculometric measurements

Because our noise strips moved horizontally in opposed directions and were vertically offset, our subjects made both a pursuit response and a saccade response on each trial. For each trial, we made measurements of pursuit onset and pursuit acceleration by fitting a “hinge” model (Adler et al., 2002) to horizontal eye velocity. This algorithm identifies pursuit initiation by fitting a “hinge” consisting of a “baseline” interval immediately followed by a “response” interval to the eye velocity trace. The baseline and response intervals both were assigned durations of 100 ms, and we tested possible hinge placements ranging from ± 30 ms, in increments of 1 ms, from an initial subjective estimate of pursuit latency. For each of these hinge placements, the slope of the response interval was determined by linear regression, and we measured the mean squared error between the data and the model (baseline plus response intervals). The hinge placement that minimized the mean squared error was defined as the latency of pursuit, and the slope during the 100-ms response interval was recorded as pursuit acceleration.

We identified saccades by applying combined criteria to vertical velocity and acceleration signals (Krauzlis & Miles, 1996) from each trial. We measured saccade onset and offset and the vertical component of saccade amplitude. Latency was defined as the elapsed time between appearance of the noise strips and eye movement onset. The pursuit decision (rightward or leftward) was defined to be the sign of pursuit acceleration in the “open-loop” interval (the first 100 ms following pursuit onset). The initial saccade decision (upward or downward) was defined to be the sign of the vertical component of saccade amplitude. We assigned signal-detection outcomes according to the spatial properties of our two-alternative forced-choice task (hit: correct response to upper stimulus; miss: incorrect response to lower stimulus; correct reject: correct response to lower stimulus; false alarm: incorrect response to upper stimulus). We discarded trials containing eye blinks, saccades during the fixation interval, and anticipatory responses with latencies shorter than 100 ms (together 6% of total trials).

Each of the remaining usable trials consisted of an agreement or a disagreement between pursuit and saccades. On average, 93% of our trials contained agreements, although this varied by subject (subject N, 93% low signal, 94% high signal; subject C, 91%, 92%; subject D, 93%, 96%).

Speed–accuracy curves

We constructed speed–accuracy curves for each subject by measuring sensitivity as a function of response time. The following procedure was repeated for each type of eye movement and for both signal strengths for each experimental session. The latency distribution in question, containing both agreement and disagreement trials, was partitioned into nonoverlapping 25-ms bins centered on integer multiples of 25 ms. For each time bin with five or more observations, we made a measurement of d' , correcting for infinite sensitivity values using established methods (Macmillan & Creelman, 1991). To minimize noise in our sensitivity measurements, we defined the speed–accuracy curve for one session to be the mean of 1000 speed–accuracy curves bootstrapped using the data from that session (Efron & Tibshirani, 1994). We retained time bins that contained at least five sensitivity measurements (i.e., measurements from at least half of the 10 possible experimental sessions).

Time shift between curves

The above method allowed us to compare pursuit and saccade speed–accuracy curves with a resolution of 25 ms. To measure the time shift between the curves with finer resolution, we measured sensitivity every millisecond by moving our bin centers in 1-ms increments, then repeating our sensitivity measurements, iterating until we had filled in the 24-ms gaps between our original measurements. As this procedure includes each eye-movement response in more than one bin, the overlapping bins were not included in our analyses of variance (ANOVAs) testing whether pursuit and saccades speed–accuracy curves have the same shape.

To measure the “best time shift” between pursuit and saccades, we calculated the correlation between the two continuous speed–accuracy curves as a function of time shift. Leaving the speed–accuracy curve for saccades fixed, we shifted the pursuit curve forward in 1-ms increments, measuring correlation over the interval from 0 to 100 ms. We defined the “best time shift” as the shift that yielded maximal correlation between the pursuit and saccade curves. This procedure was repeated for both signal strengths.

Estimation of threshold ratio

Using techniques from response time modeling, we estimated the relative location of pursuit and saccade “response thresholds.” We define “response threshold” to be the threshold necessarily crossed by a response preparatory decision signal to trigger a behavioral response. The linear rise to threshold approach (e.g., Carpenter & Williams, 1995; Hanes & Schall, 1996; Reddi & Carpenter, 2000) commonly makes three assumptions about the

decision-making process: that decision signals increase linearly; that the starting value of the decision signal is fixed across conditions; and that the response threshold is fixed within a condition. Any and all variability in response timing, other than anticipatory responses, is attributed to normal variability in the rate of rise of the underlying decision process (Carpenter, 1981; Carpenter & Williams, 1995). A similar approach posits that decision signals rise stochastically (Ratcliff & Rouder, 2000), instead of at a constant rate. As long as the primary factor that determines response time is the mean rate of rise of an underlying decision signal, rather than noise in this signal, our estimation of threshold ratio remains valid. Because pursuit turnaround trials (trials on which pursuit initially follows one target, then switches to follow the other target) violate these assumptions, we did not include the 7% of trials that contained disagreements in this analysis.

Input and motor delays are components of response time (Ratcliff & Rouder, 2000; Stone, 1960) and are recognized to contribute to saccadic latency (Reddi & Carpenter, 2000); the linear rise to threshold approach has recently factored these delays into analyses of latency (see Carpenter, 2004). We have included visual input and motor delays into our analysis using values from the physiological literature. Reports of the visual delay between stimulus onset and visually evoked spikes in the SC vary somewhat, but are on the order of 50 ms (60–70 ms, Munoz & Wurtz, 1995; 40–90 ms, Schiller & Koerner, 1971; 60 ms, Sparks, 1978; 40–50 ms, Wurtz & Goldberg, 1972). A measurement of the ballistic delay between the trigger signal for saccades (cessation of omnipause neuron activity via membrane hyperpolarization; Sparks, 2002) and saccade onset is about 15 ms (10–12 ms, Everling, Pare, Dorris, & Munoz, 1998; 15 ms, Missal & Keller, 2002; 16 ms, Yoshida, Iwamoto, Chimoto, & Shimazu, 1999). Less is known about ballistic processing for pursuit, and a value has not been assumed in our analyses.

Each of these delays can be classified as either a shared or an unshared delay. The visual input delay is presumably common to both systems and has been labeled C in the analyses that follow. The ballistic motor delay for saccades is not shared by the pursuit system and has been labeled U, for unshared. If the pursuit system does indeed require a motor processing interval, then this delay would then be added to the shared visual delay and subtracted from the unshared ballistic motor delay for saccades. To assess the impact that a motor delay for pursuit would have on our estimates of threshold ratio, we tested a range of values for our shared delay (40–80 ms) and unshared delay (10–20 ms) and found only modest changes (<9%).

Reward schedule

A recent study showed that subjects adopt different response thresholds during conditions of accuracy and

urgency (Reddi & Carpenter, 2000). Because we wanted our subjects to employ a consistent response threshold, we employed a monetary reward schedule that incorporated both response time (i.e., the size of the reward decreased as latency increased) and accuracy (i.e., only correct trials were rewarded) on individual trials. This encouraged subjects to establish a consistent balance point between fast and accurate responses (Green & Swets, 1988). Additionally, to discourage response bias, we dispensed these incentives using a procedure that maintained a 1:1 reinforcement ratio between the two targets (McCarthy & Davidson, 1984). Our reinforcement schedule randomly assigned one of the two targets as “rewardable” with a probability of .5. A reward was dispensed when this target was correctly chosen, and the randomization proceeded anew, guaranteeing a nearly equal number of reinforcements for the two correct responses.

Results

Speed–accuracy curves

Pursuit and saccades do not obey the same tradeoff between speed and accuracy. Figure 3 shows pursuit and saccade speed–accuracy curves, plotted as solid gray and black lines, respectively, for the two signal strengths (columns) and the three experimental subjects (rows). Pursuit sensitivity increased with latency over the interval from 100 to 200 ms, reaching a peak between 200 and 300 ms. Saccadic sensitivity increased somewhat later, over latencies ranging from 150 to 275 ms. The curves rise more steeply in the high signal strength condition, although their timing is similar across our two stimulus conditions. At longer latencies, the sensitivities tend to drop, perhaps because these responses include more trials in which the subjects were uncertain. Although the curves in each pair had similar shapes, there was a significant difference between pursuit and saccade speed–accuracy curves in all conditions, for all subjects ($p < .05$, two-way ANOVA).

The similarity in shape between the speed–accuracy curves for pursuit and saccades suggests that they might be time-shifted versions of the same function. To test this, we moved the pursuit curve forward in 25-ms increments and repeated our two-way ANOVA. We found that by shifting the pursuit curve forward by either 25 or 50 ms, we were no longer able to resolve a statistical difference between the overlapping regions of any pair of pursuit and saccade speed–accuracy curves ($p > .05$, two-way ANOVA). Nonetheless, the pursuit and saccade data occupy different temporal regions of the same speed–accuracy curves. For instance, if subject N’s pursuit curve is time-shifted by 50 ms, the two curves do not completely overlap. The pursuit curve includes short-latency time points of low sensitivity, whereas the saccade curve includes long-latency time points of near-asymptotic sensitivity. Finally, the time shifts we

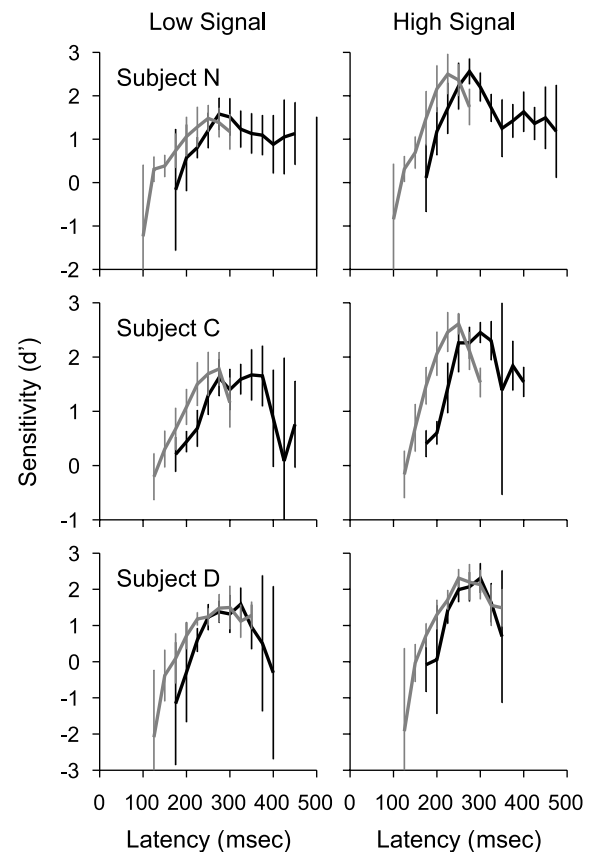


Figure 3. Speed–accuracy curves for pursuit and saccades. The solid lines in each set of axes represent pursuit (gray) and saccade (black) sensitivity plotted as a function of latency. Error bars represent the *SD* taken across experimental sessions. Each row of graphs shows data from one subject. The columns show data from the two stimulus conditions (low and high signal).

observed between the speed–accuracy curves for pursuit and saccades are related to a difference in their latencies. We compared the best time shift for each pair of speed–accuracy curves (see [Materials and methods](#)) to the median latency difference on those trials. As shown in [Figure 4](#), the best time shifts were significantly correlated with the differences in latency (Pearson’s R , $r = .72$, $p < .05$).

The time shift between pursuit and saccade speed–accuracy curves could be due to two factors: differences in response threshold (Krauzlis & Dill, 2002) or differences in downstream motor delays (Kornylko et al., 2003). As described in the next sections, our data provide evidence that both factors contribute to the time shift.

Different response thresholds for pursuit and saccades

We found that on 7% of our trials, the initial pursuit decision was different from the initial saccade decision.

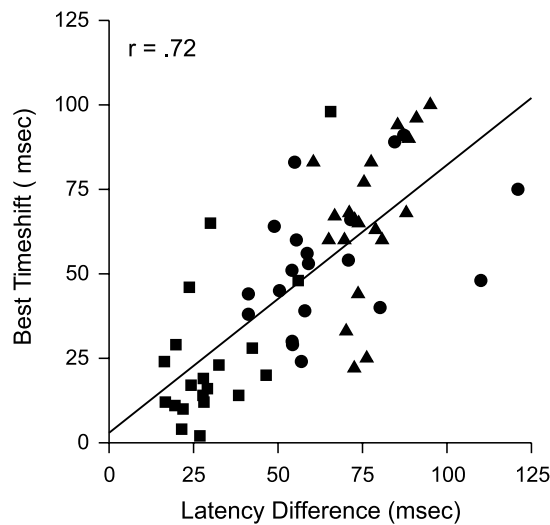


Figure 4. Relationship between latency difference and time shift. The set of axes shows the relationship between the median latency difference (saccade latency – pursuit latency) and the best time shift between pursuit and saccade speed accuracy curves. Each symbol represents a time shift measurement for one subject on one stimulus condition during an experimental session (circles: subject N; triangles: subject C; squares: subject D). The solid line is a regression on these data (slope = 0.8, intercept = 3 ms).

The fact that this happens at all provides strong evidence that pursuit and saccades employ different response thresholds. If both systems employed the same response threshold (Figure 1, top panel), the timing of their responses could differ, but disagreements could not occur because a shared response threshold would necessitate identical responses. These disagreements, however, could be because of different response selection mechanisms for pursuit and saccade choices (i.e., Figure 1, bottom panel).

To assess whether independent decision signals guide pursuit and saccade choices, we measured the fraction of trials on which pursuit and saccade choices agree. We compared the observed fraction of same decisions (Figure 5, filled circles) with the fraction expected from completely independent mechanisms (unfilled circles). The fractions associated with independent decision-making mechanisms were calculated from the equation: $F_{\text{independent}} = F_{\text{pursuit}} \times F_{\text{saccades}} + (1 - F_{\text{pursuit}})(1 - F_{\text{saccades}})$, in which F_{pursuit} and F_{saccades} are the fraction of correct pursuit and saccade trials for a given stimulus condition, respectively.

For each of our observers, the fraction of same decisions was always significantly greater than the fraction expected from independent mechanisms ($p < .05$, 2-way ANOVA). Thus, our data did not match the predictions based on independent response-selection mechanisms for pursuit and saccades.

Evidence for a difference in response thresholds is provided by a telltale correlation between the difference in latency between pursuit and saccade responses and the absolute latency of the saccade. If two fixed response

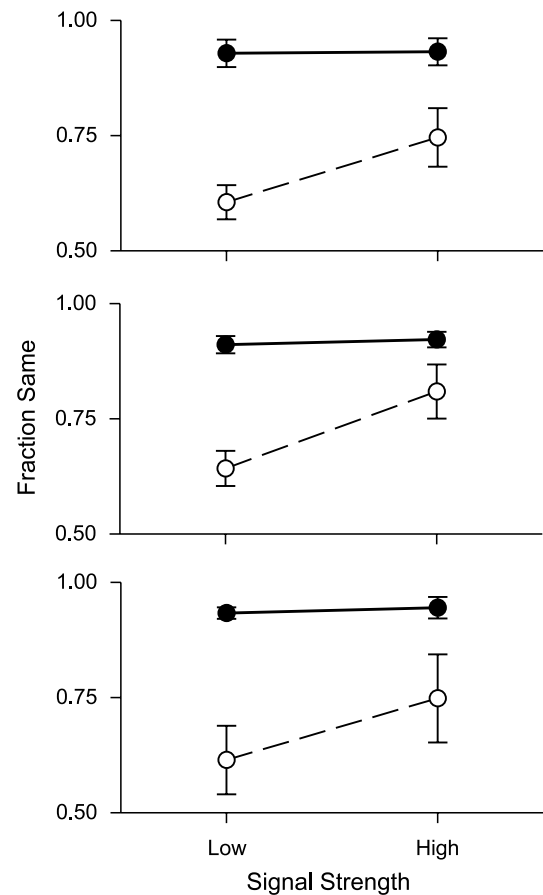


Figure 5. Analysis of sameness of pursuit and saccade decisions. The filled circles and solid lines in each graph show the fraction of trials on which initial pursuit and saccade decisions agreed, plotted as a function of signal strength. The unfilled circles and solid lines show the proportion of trials on which the two systems would be expected to agree if their decision-making mechanisms were independent. The observed fraction of “same” decisions was always significantly greater than the proportion predicted from independent mechanisms.

thresholds are applied to a single linear decision signal, as shown in the middle panel of Figure 1, then fast responses (i.e., a steep decision signal) will show small differences in latency between the two systems, whereas slow responses (i.e., a shallow decision signal) will show a greater latency difference. We tested for this correlation in each subject’s data, for each session. Consistent with the prediction, we found that as the absolute latency of saccades increased, the difference in latency between pursuit and saccades also increased. This correlation was significant for all subjects, for all sessions (Pearson’s R , $p < .05$).

Estimating threshold ratio

By assuming a simple decision mechanism, one can estimate the relative location of two response thresholds, as

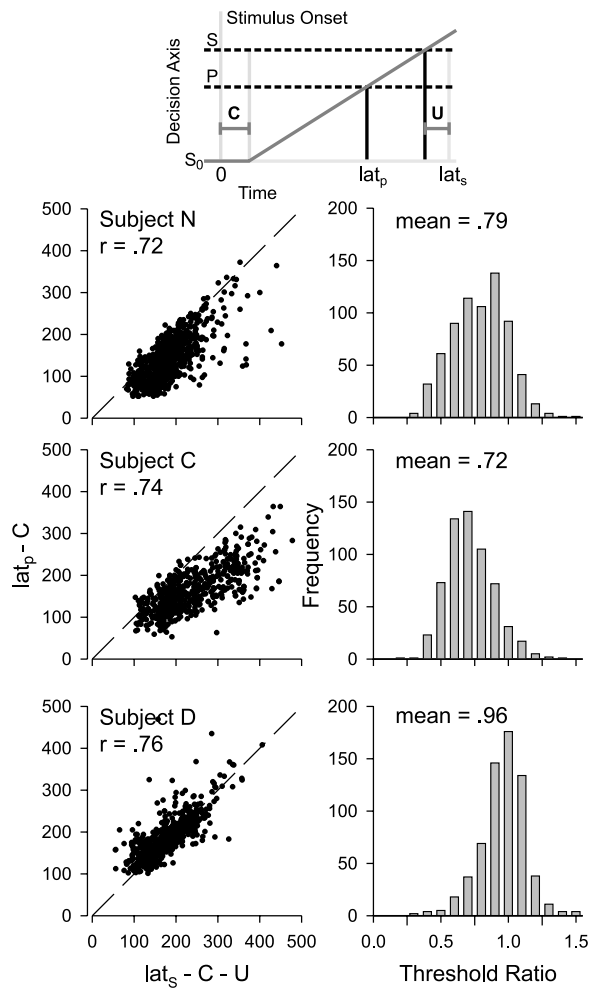


Figure 6. Estimation of threshold ratio. The top graph shows a linear decision signal that rises from an initial level (S_0) after a common visual delay (C) to cross two response thresholds (P and S). The y axis has been given a generic label. When threshold P is crossed, a pursuit response begins at lat_p . The saccadic system is subject to an additional unshared motor delay, delaying the saccadic response by U ms to begin at lat_s . The left column of graphs plots pursuit latency (minus the visual delay) as a function of saccade latency (minus the visual and motor delays) using data from the final experimental session. Each point represents the two latency measurements from one trial. The histograms at right show the distribution of threshold ratio estimates across these trials. Each row shows data from one subject.

the top plot in Figure 6 shows. The decision signal (plotted as a solid gray line) is subject to a common visual delay C , which is the input time delay (Stone, 1960) based on the latency of visual responses in eye movement-related brain structures (see Materials and methods). After this delay, the decision signal rises at a constant rate from an initial level S_0 (Carpenter & Williams, 1995; Reddi & Carpenter, 2000). The pursuit response begins at time lat_p , corresponding to the moment at which the decision signal

crosses the threshold P . The saccadic system is subject to an unshared motor delay U , based on the motor time delay (Stone, 1960) in the output pathways of the saccadic system (see Materials and methods), offsetting its response by U ms. If pursuit and saccades share a decision signal, then the ratio of the latencies is related to the ratio of the thresholds, once the internal delays C and U have been taken into account. Hence, we defined the quantity P/S to be the threshold ratio, according to the equation: $P/S = (lat_p - C) / (lat_s - C - U)$.

Support for a shared decision signal comes from the finding that pursuit and saccade latencies are correlated on a trial-by-trial basis. This allowed us to estimate the threshold ratio (P/S) by comparing the latencies of pursuit and saccades from single trials. In Figure 6, left column, we show a plot of pursuit latency (minus the common visual delay) as a function of saccade latency (minus the common visual and unshared motor delays) for data from the final experimental session. Each point in these plots represents one trial on which pursuit and saccade choices agreed. The Pearson's R values of these correlations range from .72 to .76, indicating a mostly linear decision signal. A perfectly linear decision signal would yield a correlation with an R value of 1.0. The right column of Figure 6 shows the distribution of threshold ratio estimates. We defined the threshold ratio as the mean of this distribution, and made individual measurements across sessions and signal strengths. The average threshold ratio was .81, indicating that the pursuit threshold was about 19% lower than the saccade threshold; the threshold ratio estimates also showed slight differences across subjects (averaged across all 10 sessions: subject N, .75; subject C, .75; subject D, .91).

The difference in thresholds between pursuit and saccades accounts for a portion of the time shift between their speed-accuracy curves. Figure 7 shows the relationship between threshold ratio and the best time shift between pursuit and saccade curves, based on individual measurements from each subject for each session and both signal strengths. Overall, there was a significant correlation between threshold ratio and the best time shift (Pearson's R , $r = -.67$, $p < .01$), indicating that the difference in threshold ratio can account for 45% of the variance in the time shifts between the speed-accuracy curves. Within subjects, this correlation was also significant (subjects N and D at $p < .05$, subject C at $p < .10$, Pearson's R). In absolute terms, the time shift attributable to the difference in threshold is simply the time shift minus the putative motor delay (15 ms), which, on average, was 34 ms (subject N, 39; subject C, 51; subject D, 11) or 64% of the total time shift (subject N, 72%; subject C, 77%; subject D, 42%).

The values we used for C and U (50 and 15 ms, respectively) were taken from the physiological literature and represent reasonable median values for the visual and motor delays. Increases in C decrease the value of threshold ratio estimates, and increases in U increase the value

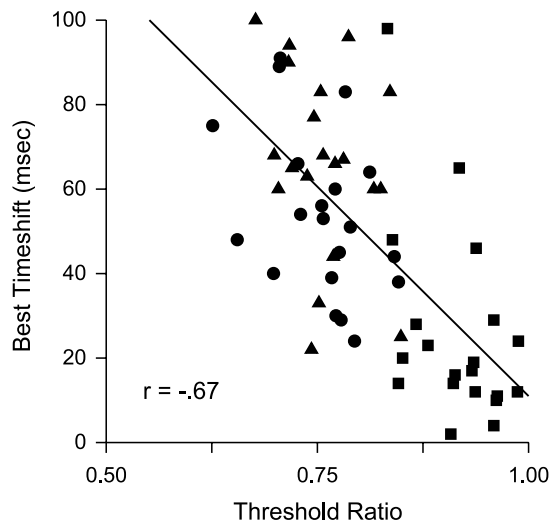


Figure 7. Predictions of threshold ratio. This graph shows the relationship between threshold ratio and time shifts between pursuit and saccade speed–accuracy curves. Each symbol represents the best time shift for one condition (low or high signal) for one subject (circles: subject N; triangles: subject C; squares: subject D) for one session plotted as a function of mean threshold ratio. The solid line represents a regression on these data, which has a value of 11 ms for a threshold ratio of 1.0 (with 95% confidence limits of 12 ms).

of the threshold ratio estimates. Table 1 summarizes how threshold ratio estimates change as C varies from 40 to 80 ms and U varies from 10 to 20 ms, showing that changes in these physiological delays have modest effects on our threshold ratio estimates. As C increases from 40 to 80 ms,

our threshold ratio estimates decrease by less than 9%. As U increased from 10 to 20 ms, these estimates increase by less than 9%. Changes in these delays shift the values of the two quantities ($lat_P - C$) and ($lat_S - C - U$), but not the relationship between them. Therefore, the correlation between pursuit latency and saccade latency remains unchanged as the values for C and U change, with an average r value of .69 across subjects (subject N, .66; subject C, .69; subject D, .71), which was always significant (Pearson's R , $p < .00001$).

Ballistic motor delay

Our data also support the idea that there is a ballistic motor delay for saccades, but this support is less direct than the evidence for different response thresholds. First, the regression relating best time shift to threshold ratio (Figure 7) has a residual value of 11 ms (± 12 ms) for a threshold ratio of 1.0, implying that pursuit choices would still occur 11 ms before saccade choices if both systems employed the same threshold value. This predicted temporal difference is consistent with the saccadic motor delay of 10–20 ms based on physiological data. Second, removing the unshared ballistic motor delay from our estimates of the threshold ratio yields a prediction inconsistent with the observed data. When the motor delay is omitted, the regression relating best time shift to threshold ratio has a value of -7 ms for a threshold ratio of 1.0. This predicts that saccade responses should occur before pursuit responses when the two systems employ similar thresholds. Contrary to this prediction, pursuit

		Subject N	Subject C	Subject D	All
C	U	P/S	P/S	P/S	P/S
40	10	.75 ± .05	.74 ± .03	.90 ± .04	.79 ± .08
	15	.77 ± .05	.76 ± .04	.92 ± .05	.81 ± .09
	20	.79 ± .06	.78 ± .04	.94 ± .05	.84 ± .09
50	10	.73 ± .05	.73 ± .04	.89 ± .05	.79 ± .09
	15	.75 ± .06	.75 ± .05	.91 ± .05	.81 ± .09
	20	.78 ± .06	.77 ± .05	.94 ± .05	.83 ± .10
60	10	.72 ± .05	.71 ± .04	.89 ± .05	.77 ± .09
	15	.74 ± .06	.73 ± .04	.91 ± .05	.80 ± .10
	20	.77 ± .06	.76 ± .06	.94 ± .06	.82 ± .10
70	10	.71 ± .06	.70 ± .05	.88 ± .05	.76 ± .10
	15	.73 ± .06	.72 ± .04	.91 ± .05	.79 ± .10
	20	.76 ± .06	.74 ± .05	.94 ± .06	.81 ± .11
80	10	.69 ± .06	.68 ± .04	.88 ± .05	.75 ± .10
	15	.72 ± .06	.70 ± .03	.91 ± .06	.77 ± .11
	20	.75 ± .07	.72 ± .04	.94 ± .06	.80 ± .11

Table 1. Estimates of threshold ratio using different visual and motor delays. The table lists the ratio of the thresholds for pursuit and saccades (P/S). Values are provided for each subject individually and also averaged across all subjects (± 1 SD), given a range of visual (V) and motor (M) delays. The correlation between pursuit latency and saccade latency remained unchanged across these delays (Pearson's R ; subject N: $r = .66$; subject C: $r = .69$; subject D: $r = .71$; all subjects: $r = .69$) and was always significant ($p < .00001$).

nearly always led saccades, even for subject D, with a very high (~ 9) threshold ratio.

Discussion

Our results demonstrate that pursuit and saccades exhibit nearly the same tradeoff between speed and accuracy, with saccadic responses delayed by 25–50 ms. This outcome provides an answer to the question raised in the **Introduction**: How can two systems be guided by common input yet still display differences in timing and choices? On the one hand, our results provide additional evidence that pursuit and saccade choices are determined by a common decision signal—in particular, the speed–accuracy curves for pursuit and saccade have the same shape. On the other hand, we also identified two specific differences between pursuit and saccades in how the putative decision signal is read out to determine the eye movement choices. First, the pursuit system employs a lower response threshold than saccades; this difference can account for approximately 60% of the time-shift as well as the occurrence of trials in which the two motor choices disagree. Second, the saccadic system is subject to an additional motor delay that is not present in the pathways for pursuit; this difference accounts for the remainder of the time-shift observed between the two responses.

Pursuit uses a lower response threshold than saccades

Our results show that pursuit uses a lower response threshold than saccades (**Figure 1**, middle panel). First, our current results and those of previous studies (Krauzlis et al., 1999; Liston & Krauzlis, 2003) have documented trials in which pursuit and saccades disagreed. If both systems applied the same response threshold to a common decision signal, the timing of their responses could differ, but disagreements could not occur. Moreover, the timing of the responses indicates that pursuit has the lower threshold. In all of the trials with disagreements (7% of the total), pursuit initially followed the motion of one stimulus before reversing to follow the same stimulus targeted by the saccade; the pursuit reversal always occurred before or during, but never after, the saccade. Furthermore, the fraction of agreement trials was greater than the fraction predicted from independent decision-making mechanisms for the two systems based upon shared visual processing. Our interpretation of these disagreement trials is that the decision signal underlying the eye movement choice crosses the pursuit threshold but then turns around before it reaches saccade threshold, later crossing both thresholds in favor of the other target. We previously documented the time course of pursuit reversals

in a task similar to our current one (Liston & Krauzlis, 2003). In that study, we showed that the initial disagreement between pursuit and saccades was resolved by at least 60 ms before the saccade, and the time course of this disagreement was explained by a time-varying spatial bias.

Second, we found a telltale correlation between the differences in latency between pursuit and saccades on each trial and the absolute latencies of the saccades. This correlation between relative and absolute latencies is what would be expected if two different response thresholds were applied to a single decision signal. For example, on trials with decision signals that rise more steeply, the absolute latencies of pursuit and saccades are shorter, and it also takes less time to travel the distance between the pursuit threshold and the saccade threshold. This finding therefore supports the idea of a common decision signal, as well as providing additional evidence that pursuit uses a lower response threshold than saccades.

Additional motor delay for saccades

The most direct evidence for a motor delay in the pathways for saccades comes from previous physiology experiments, rather than our own data. Omnipause neurons in the reticular formation, which act as the final gatekeepers for saccades by inhibiting saccade burst neurons, exhibit a pause in activity 10–20 ms before the onset of each saccade (Cohen & Henn, 1972; Evinger et al., 1982; Everling et al., 1998; Keller, 1974; Luschei & Fuchs, 1972). Similarly, the saccade-related burst of activity by neurons in the paramedian pontine reticular formation precedes saccade onset by 5–20 ms (Scudder, Fuchs, & Langer, 1988; Strassman, Highstein, & McCrea, 1986a, 1986b). Although saccades can be stopped by microstimulation of the omnipause neurons (Keller & Edelman, 1994), under normal conditions, it does not appear possible to stop a saccade once the saccade-related burst begins, indicating that the pathways for saccades include a ballistic interval of 5–20 ms.

The values of the saccade motor delay obtained from physiological experiments were corroborated by our behavioral data. We found that the time shift between the pursuit and saccade speed–accuracy curves decreased as a function of the threshold ratio (**Figure 7**) and that this relationship predicts that saccades would lag pursuit by 11 ms even if both systems employed the same decision threshold. Conversely, if the saccade motor delay is left out of these calculations, this function erroneously predicts that saccadic responses should lead pursuit responses by 7 ms, an outcome we did not observe even for subjects with threshold ratios near 1. Our results therefore provide indirect evidence that the pathways for saccades include an additional motor delay not present in the pathways for pursuit. A similar conclusion was drawn by a recent study comparing the canceling of pursuit and saccadic eye movements (Kornylo et al., 2003).

Pursuit versus optokinetic responses

Our study involved stimuli and methods that differ from those typically used to study pursuit. Rather than using small discrete targets, we used long horizontal strips. A few other studies have used extended moving stimuli for pursuit to reduce or eliminate catch-up saccades (Krauzlis & Adler, 2001; Madelain & Krauzlis, 2003; Watamaniuk & Heinen, 1999). The use of large stimuli raises the possibility that the evoked smooth eye movements were optokinetic responses, rather than smooth pursuit. However, stimulus size is not the most useful basis for identifying pursuit, because pursuit can also track large extrafoveal stimuli (Ilg & Their, 1999; Stone et al., 2000). Conversely, passive smooth eye movements can be elicited by small spot stimuli under passive or “stare” optokinetic nystagmus conditions (Wyatt & Pola, 1987). Instead, we think pursuit is better distinguished from the optokinetic response by the ability to selectively track one motion signal in the presence of alternative motion signals (Krauzlis, 2004). In the present study, because subjects actively selected one of two moving stimuli as the goal of their tracking response, we refer to the smooth eye movements as pursuit. Nonetheless, we cannot completely rule out the possibility that these pursuit responses included some contribution from the optokinetic system.

Relationship to physiology

Our estimates of the pursuit and saccade thresholds from behavioral data are consistent with physiological data about target selection. A recent study showed that buildup neurons in the superior colliculus exhibit selectivity for stimuli that will be the target of either pursuit or saccadic eye movements and that the time course of this selectivity can predict the timing of pursuit and saccades (Krauzlis & Dill, 2002). Using an analysis based on constructing receiver operating characteristic (ROC) curves (Britten, 1992), this study also found that the degree of selectivity evident before movement onset was lower for pursuit (ROC area: 0.57 or 0.55) than for saccades (ROC area: 0.69 or 0.68), leading to the suggestion that pursuit uses a decision criterion that is lower (81–83%) than that used to trigger saccades (Krauzlis & Dill, 2002). These values are similar to what we found in our behavioral experiments. Based on the latency differences between pursuit and saccades, we estimate that the response threshold for pursuit is 75–84% that of the threshold for saccades, depending on the values used for the visual and motor delays (subject N, 73–79%; subject C, 70–78%; subject D, 88–94%).

Our results highlight the important role played by the response threshold, although relatively little is known about the neural mechanisms involved in its regulation. Behavioral experiments have shown that higher order factors such as task instructions (Reddi & Carpenter, 2000) and spatial

probability cues (Carpenter & Williams, 1995) affect saccadic response times in a manner consistent with a change in response threshold. In our own data, our estimates of the response thresholds varied across experimental sessions and showed idiosyncratic differences across subjects. However, the response threshold might not always be determined by higher order processes. For example, whether pursuit is accompanied by catch-up saccades depends on position error and retinal slip (de Brouwer, Yuksel, Blohm, Missal, & Lefevre, 2002), suggesting that particular combinations of visual signals could raise or lower the response threshold for saccades. We speculate that the cerebellum, which is known to be important for the visual adaptation of saccade metrics (Optican & Robinson, 1980), might also be important for adjusting the response threshold for pursuit and saccades, perhaps by influencing the activity of a common inhibitory mechanism in the brainstem (Missal & Keller, 2002). Thus, from the viewpoint of our speed–accuracy analysis, adaptive control mechanisms may not just tune the metrics of the movement, but also define the conditions under which the movements should be launched.

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