RESEARCH ARTICLE

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Pursuit and saccadic tracking exhibit a similar dependence on movement preparation time

Abstract Data from previous human and primate studies on saccadic and smooth pursuit eye movements suggest that there are shared internal inputs (for example, perception, attention, expectation, and memory) for the initiation of the two types of movements. Additional reports examining the effect of preparation time on movement responses have shown that when ample time is allowed subjects usually generate long-latency "reactive" responses. When the time allowed to prepare a movement is short, however, subjects respond with reduced latency and often anticipate the stimulus ("predictive" response). Based on these findings, we believe that the shared internal inputs at early stages of movement preparation may result in saccade and pursuit eye movements demonstrating the same dependence on preparation time despite acting through different neural pathways further downstream. Previously we demonstrated a behavioral "phase transition" when normal subjects tracked alternating targets with saccades. When preparation time was long (low-frequency pacing) subjects made reactive saccades (latency ∼180 ms). As preparation time monotonically decreased (pacing frequency increased), there was an abrupt transition to a predictive response (latency < 100 ms). In the present study we show that a similar transition exists in smooth pursuit tracking and that the point of transition between the two behaviors is the same for both systems. In other words, the same behavior (reactive versus predictive) is selected when pursuit and saccade tracking are tested under the same time constraints. This provides further evidence that the two types of movements are different motor outcomes of a common decision process.

Keywords Saccade · Pursuit · Prediction · Motor response · Preparation time

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Introduction

Recent work examining both saccadic and pursuit eye movements has led to the suggestion that the two are not completely independent oculomotor subsystems (Leigh and Zee 1999), but rather the different outcomes of a shared cascade of sensory-motor functions (for review see Krauzlis 2004, 2005). For example, the latencies of pursuit and saccade responses display the same dependence on gap duration during the "gap paradigm" (Krauzlis and Miles 1996a, b). In addition, there is evidence that the signals guiding pursuit target selection are the same as those involved in the preparation of saccades (Liston and Krauzlis 2003, 2005). These findings suggest that in addition to the overlap of visual and motor pathways (Missal et al. 2000; Yan et al. 2001; Missal and Keller 2002; Keller and Missal 2003) the two systems share processing at the level of response preparation.

Previous studies of repetitive saccadic eye movements in normal human subjects have demonstrated that either reactive or predictive tracking can be encouraged depending on the pacing frequency of alternating targets (Stark et al. 1962; Ross and Ross 1987; Zambarbieri et al. 1987; Shelhamer and Joiner 2003). When the movement preparation time (MPT) is large (for example, a 0.2 Hz target pacing frequency has a MPT of 2,500 ms) subjects make reactive eye movements. When this time is small (500 ms for 1.0 Hz target pacing) subjects anticipate the target jump and respond with a reduced latency. (This is true when the subject is simply instructed to "look at the targets" in each case, with no specific reference to timing performance.) In our earlier experiments

(Shelhamer and Joiner 2003) we showed that an abrupt "phase transition" from reactive to predictive behavior occurs when the target pacing frequency begins low (0.2 Hz) and monotonically increases to 1.0 Hz. (That is, the MPT begins high (2,500 ms) and monotonically decreases to 500 ms.) In addition, we demonstrated that there is hysteresis in this behavior as the MPT monotonically increases: subjects continue to predict the target jump at MPT (or target pacing frequencies) that initially promoted reactive eye movements.

There is evidence that smooth pursuit responses are also modified by MPT (Barnes and Asselman 1991a, b, 1992; Keating 1993; Kao and Morrow 1994; Lekwuwa and Barnes 1996; Morrow and Lamb 1996; Moschner et al. 1999; Barnes et al. 2002). When subjects tracked a constant velocity moving target presented at regular small intervals their smooth eye movements became progressively more predictive, in the sense that there was a buildup of eye velocity in the direction of target motion before actual target onset. In addition, when the interval between presentations was unexpectedly increased or the stimulus failed to appear, subjects timed their response based on the previous presentations, demonstrating an expectation of future target timing based on previous experience (Barnes and Asselman 1991a, b; Kao and Morrow 1994; Barnes et al. 2002). A recent study by Jarrett and Barnes (2005) has shown that smooth pursuit direction reversal becomes predictive when the time between direction reversals of a pursuit target is constant and small (420–840 ms). However, no study has examined smooth pursuit tracking as the interval before target reversal is systematically altered or to see if analogous manipulations of stimulus timing yield the same effects in both pursuit and saccades.

The present study examines both saccadic and smooth pursuit movements in normal human subjects as the MPT monotonically decreases and then increases. Based on the fact that the two types of eye movements have different latencies and kinematics we might expect their behaviors with respect to preparation time to be different, while the studies cited above suggest that these behaviors might be similar. Since pursuit is normally a steady-state response depending on continuous visual feedback, while saccades are generally open loop, our first task was to identify a common paradigm with which to test preparation time in the two systems. We did this by systematically manipulating the amount of time that subjects had to prepare before the next required saccade (target jump) or pursuit (target movement) response. By allowing the same amount of time to prepare for a response in the two eye-movement tasks, we could determine how manipulations to this time affect eye-movement initiation regardless of the type.

As previously demonstrated for saccades (Shelhamer and Joiner 2003), we find here that pursuit-tracking behavior undergoes a similar phase transition from reactive to predictive as MPT decreases. The critical MPT at which the transition is made is similar for both types of eye movements, despite the fact that other aspects of their timing are different. Furthermore, predictive tracking persists past the initial critical transition point as the MPT subsequently increases after having decreased, for both systems. These results (1) demonstrate that the amount of time allowed to prepare for the motor act influences both eye-movement types in a similar way, (2) show that once a predictive tracking strategy is adopted it is difficult to stop, and (3) support the theory that the initiation of both eye-movement types is influenced by the same factors.

Methods

General

The eye movements of seven subjects (A–G) were recorded while they performed two experiments. The first experiment was a saccade-tracking task and the second was a pursuit-tracking task. Only subject E had prior knowledge of the goals of the study. Informed consent, according to the local institutional review board, was obtained from each participant. Data were acquired on a PC-compatible Pentium 166-MHz computer running real-time experiment control software developed in-house. Horizontal movements of the eyes were recorded with a Series 1000 Binocular Infrared Recording System (Microguide), sampled at 1,000 Hz. The system was calibrated prior to data acquisition by having subjects fixate targets at known locations. Subjects were seated in a stationary chair, and the head was fixed with a chin rest. In each task, subjects were asked to follow the target and were given no explicit instructions as to timing or accuracy; they were told simply to "look at the target."

The goal of both experiments was to track a target as it repeatedly moved over a horizontal distance of 30° (±15° from midline). In all cases the target display was 1 m from the subject. In the first experiment subjects made saccades to two LED targets that alternated at one of several different frequencies. In the second experiment subjects smoothly tracked the target (a red laser back-projected onto a tangent screen) as it moved between the two extreme positions at 15°/s. As in previous studies (Kao and Morrow 1994; Morrow and Lamb 1996; Moschner et al. 1999) a back step of 2.5° was included in the second task before target movement. This was done in order to facilitate a pursuit response to the stimulus without an accompanying saccadic eye movement (Rashbass 1961; de Brouwer et al. 2002). Subjects were given breaks between the four experiments (pursuit, saccade, two control experiments described below) in each test session, and were encouraged to remain attentive throughout the session.

Control experiments

Prior to each main experiment, subjects performed a control experiment to determine the normal reactive
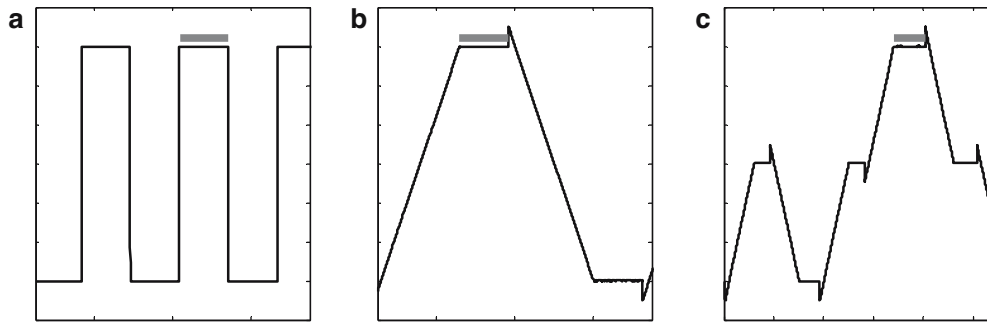
Fig. 1 Example of the target trajectory during the **a** Saccade experiment, **b** Pursuit experiment, and **c** Pursuit control experiment. The *gray bar* in each panel represents the MPT; the MPT duration is equal in **a** and **b**

latency of each eye movement. For saccades, subjects tracked the LED target as it jumped between ±15° with random timing (500–3,000 ms). For pursuit, the subject tracked the target as it moved smoothly at 15°/s between three horizontal positions (0, −15, and +15°) with random timing between movements (500–2,000 ms). When the target was at 0° the direction of target movement was random; the target could go to either −15 or +15° (see Fig. 1c). (These data were not however analyzed separately.) Twenty saccade and 20 pursuit movements were obtained from each subject in these control tasks.

Saccade experiment

The essential component of both experiments is that the target remained idle at the end points (±15°) for a specified (non-random) amount of time, between periodic target motions. In the saccade-tracking task the targets alternated at a given pacing frequency. In this case the target trajectory was step-like between the two positions (±15°) as shown in Fig. 1a. Target pacing followed the monotonically increasing sequence [0.2, 0.3, 0.5, 0.6, 0.7, 0.9, 1.0 Hz] and then monotonically decreased in the opposite order. Pacing at minor frequencies (0.25, 0.4, 0.55, 0.65, 0.8, 0.95 Hz) between the major pacing frequencies was included to allow for smooth transitions between pacing frequencies, allowing subjects more easily to establish steady-state tracking at each major frequency; these trials were excluded from analysis. The targets alternated continuously for 26 trials at each major frequency and 4 trials at each minor frequency (approximately 8 min total). The larger number of trials at each major frequency allowed us to examine steady-state behavior at these frequencies. The minor frequencies were not intended to provide transitions that were undetectable by the subject, but rather to make it easier for the subject to reach steady state at the subsequent major frequency. There was always a sufficient number of trials at each major frequency for the subject to attain steady state, from which the mean latency at that frequency was derived; this was not the case at the minor frequencies. [A "trial" is when the target moved from the idle position (±15°), such as a single target jump in Fig. 1a.]

In this task the MPT (or inter-stimulus interval) is half the period of the pacing frequency (e.g., 0.2 Hz pacing has a period of 5,000 ms and an MPT of 2,500 ms). Thus, the above monotonically increasing major frequency sequence has a monotonically decreasing MPT sequence: 2,500, 1,667, 1,000, 833, 714, 556, and 500 ms. An example of the MPT in this experiment is marked by the gray bar in Fig. 1a.

Smooth pursuit experiment

In the second task (pursuit tracking) the target remained idle at the end points (±15°) for a specified (non-random) amount of time, between periodic target movements. In this case the target position trajectory was trapezoidal between the two positions (±15°) as shown in Fig. 1b. The target remained idle for the following monotonically decreasing sequence of MPT: 1,250, 1,000, 833, 714, 556, and 500 ms. An example of the MPT in this experiment is marked by the gray bar in Fig. 1b. (The largest MPT for Subjects B and D was 1667 instead of 1,250 ms. This value was chosen in order for the pursuit experiment to contain the MPT at which these subjects made a phase transition during the saccade-tracking experiment.) The MPT then monotonically increased in the opposite order. Similarly to the first task, minor MPT (1,111, 909, 769, 625, 526 ms) were included between the major MPT. During a single continuous experiment (approximately 14 min), the target moved for 20 trials (step-ramps) at each major MPT separated by 4 trials at each minor MPT.

Data analysis

Analysis of eye-tracking data was done off-line. First, eye velocity and acceleration were calculated using a four-point digital differentiator based upon a least-squares derivative algorithm (Savitzky and Golay 1964). This is an efficient iterative method of fitting a third-order polynomial to each data point and the preceding and following two values, then finding the derivative of the fitted polynomial. It introduces less noise than conventional differentiators. To demonstrate that this processing did not affect the determination of pursuit onset time, on

sample traces we integrated the filtered velocity data, which reproduced eye position, and overlaid this on traces of raw position data; there was no apparent time shift between these two versions of the signal, demonstrating that the important low-frequency signal content, which embodies pursuit onset, is preserved.

For both eye-movement types, latency was determined by comparing the onset of the eye movement to the onset of the target in each trial. Saccade onset was determined using a velocity threshold ($\geq 60°/s$). Pursuit onset was found using a modified version of the method used in previous studies (Carl and Gellman 1987; Krauzlis and Miles 1996a, b; Moschner et al. 1999), as follows. First, the eye position in an interval from 80 ms before to 100 ms after target onset was examined to determine if a saccade had occurred (acceleration $\geq 300°/s^2$). A trial was excluded from analysis if a saccade occurred during this interval; between 8 and 20% of trials were rejected. The velocity data were then smoothed with a 50 ms moving-average filter. Next, the first time point within a 280 ms interval (80 ms before to 200 ms after target onset) at which the eye velocity exceeded 5°/s (33% of the target velocity) was found. A 60 ms interval around this time point (± 30 ms) was delineated and a linear regression was performed on the eye velocity within this interval. The x-intercept of the linear regression line—the intersection of the linear regression line with the zero-eye velocity line—marked the onset of pursuit.

An example of this analysis is shown in Fig. 2 for a reactive and a predictive pursuit response. To demonstrate the timing difference between the two behaviors, both responses (black traces) are shown with respect to the target (gray trace) in Fig. 2a. Predictive pursuit responses were often followed by a corrective saccade back to the target (indicated by the arrow); these saccades did not affect the determination of pursuit latency. Eye and target positions for each movement are shown in Fig. 2b and c (reactive and predictive respectively) between -80 and 300 ms with respect to target onset. Eye velocity (black trace) for each movement is shown in Fig. 2d and e and the time point were the eye velocity first exceeds 5°/s is marked by a gray square. The point where the linear regression line (diagonal gray line) and the zero-velocity line (horizontal gray line) intersect is marked by the dashed gray line. This intersection is defined to be the onset of the pursuit response which is labeled by the gray circles in Fig. 2a, b, and c. Using this method the latencies of the reactive and predictive responses were calculated to be 94 and 29 ms respectively, in this example.

Though the method described above can indicate if the eyes began to move prior to visual feedback (as in Fig. 2c, e), it is not immediately obvious if this is a legitimate "predictive" pursuit response. For example, the anticipatory pursuit responses found in previous studies (e.g., Kowler and Steinman 1979) were first identified as very slow (less than 1°/s) drift of the eyes in the direction of an expected target jump (a discrete target jump such as a saccade stimulus), before any actual target move-

ment. We found such movements also in our previous work (Shelhamer and Joiner 2003) on the transition between reactive and predictive saccade tracking, but these movements are of such low velocity that they do not impact the determination of saccade onset time. These slow anticipatory movements can, however, complicate the determination of pursuit onset time. Since they occur even in the presence of saccade stimuli, not solely pursuit stimuli, we did not consider them to represent a legitimate predictive pursuit response.

Barnes and colleagues (Barnes and Asselman 1991a, b; Lekwuwa and Barnes 1996; Barnes et al. 2002; Jarrett and Barnes 2002, 2005) investigated what we consider to be a more appropriate predictive response: a smooth pursuit-like movement that occurs before an expected smooth target movement (a pursuit stimulus), that scales its velocity according to the expected target velocity. These movements occur approximately 100 to 300 ms before target onset and are on the order of half the velocity of the target (Jarrett and Barnes 2002). Although it might seem natural to define pursuit onset as the time when eye velocity approximately matches target velocity (as shown in Fig. 2e, where there is a clear inflection in eye velocity at about 150 ms), our definition of onset time does not do so, but rather considers the preceding lower-velocity movement to be the predictive pursuit response. This is because, as pointed out above, this response has been found to scale with expected target velocity; it also occurs before visual feedback would modify its velocity and therefore is a true open-loop predictive response. Furthermore, it is about an order of magnitude larger than the anticipatory responses previously discussed.

We did not use the techniques of some previous studies (Carl and Gellman 1987; Krauzlis and Miles 1996a, b; Moschner et al. 1999) for determining the onset of pursuit because those methods are only adequate for reactive pursuit responses. Those methods calculate the onset of pursuit by determining when the eye velocity exceeds a threshold based on a period of fixation prior to the movement. In our experiment, in order to track correctly the moving target the eye must reverse direction at the end points ($\pm 15°$). Thus, the eye velocity must be zero at some point in the eye-movement trajectory. The major difference between the reactive and predictive pursuit responses is the time period over which the eye velocity remains near zero (compare the eye movement trajectories in Fig. 2a and the eye velocities in Fig. 2d, e). This type of method works poorly in determining the onset of the predictive pursuit responses we report here. After eye reversal, it is common in these cases for the eyes to never come to a complete stop and to drift in the expected direction of target movement (see Fig. 2a). Thus, in determining pursuit onset we identified the period where the velocity was not only greater than zero, but also greater than any anticipatory drift in the direction of the expected target movement (Kowler and Steinman 1979). Using this as a reference we were able to compute pursuit initiation time for both types of pursuit responses with
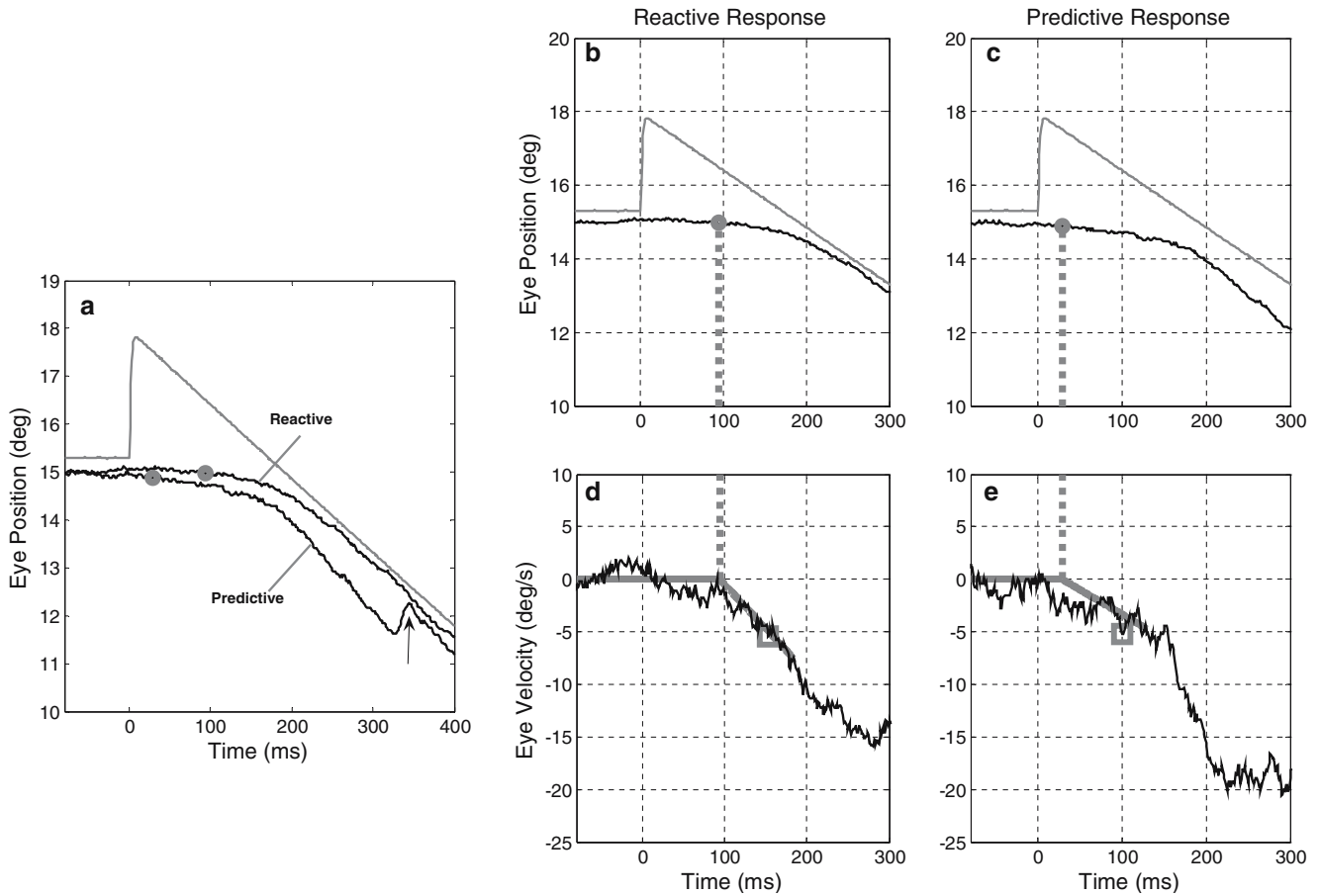
Fig. 2 Example of the calculation of pursuit initiation for subject D. **a** Eye (*black trace*) and target (*gray trace*) positions are shown for a reactive and predictive pursuit response (MPT of 1,667 and 500 ms, respectively). The latency of each movement is marked by the *gray circle*. The predictive movement is accompanied by a corrective saccade which is marked by the *black arrow*. **b** and **c** Eye and target position for the same reactive and predictive responses between −80 and 300 ms with respect to target onset. **d** and **e** The eye velocity (*black trace*) for the reactive and predictive movements. The first time point where the eye velocity exceeds 5°/s is marked by the *gray square*. The *vertical gray line* marks the point where the linear fit line (*diagonal gray line*) intersects the zero velocity line (*horizontal gray line*). This is the point of movement initiation which is labeled by the *gray circles* in panels **a**, **b** and **c**

the same method, which is essential for making comparisons between stimulus conditions.

Our method for determining pursuit initiation is further validated by examining pursuit responses from different conditions at a fixed time point. Five pursuit responses (black traces) for each of six different MPTs (from a decreasing-MPT series) for subject G are shown in the left column of Fig. 3. The small vertical black lines mark the points 0 and 100 ms after target movement begins in each trial. There is a systematic change in the timing of the pursuit response as MPT decreases; the slopes of the eye movement traces at the 100 ms point increase with decreasing MPT (top row to bottom row). This is also demonstrated in the respective velocity histograms (found at the same 0 and 100 ms points for all movements made at a given MPT) in the center and right columns. This analysis is similar to that used in some previous studies examining predictive pursuit (for example, see Barnes et al. 2002).

As shown in the histograms in the center column (0 ms after target movement), at the two smallest MPTs (556 and 500) the eye-velocity distribution is to the left of

the 0°/s line, marked by the gray vertical line. This indicates that at target onset the eye is moving with significant velocity in the direction of target movement and is a predictive pursuit response as defined in other reports (Barnes and Asselman 1991a, b, 1992; Lekwuwa and Barnes 1996; Barnes et al. 2002; Missal and Heinen 2004; Jarrett and Barnes 2005). This is not true for the three largest MPT (1,250–833), at which the eye-velocity distribution is close to the 0°/s line.

This pattern is similar to that found 100 ms after target onset (histograms in the right column). At the three largest MPT (1,250–833) the eye-velocity distribution remains close to the 0°/s line. This indicates that the majority of responses made at these MPT are reactive: there is little eye-movement response within 100 ms of target onset. At an MPT of 714 the velocity distribution (at 100 ms) becomes broad (between 0 and 5°/s) indicating that there is a mixture of predictive and reactive responses. This is also the MPT at which the transition between reactive and predictive tracking was found to occur for this subject (see Table 1). The velocity distributions are very close to 5°/s at
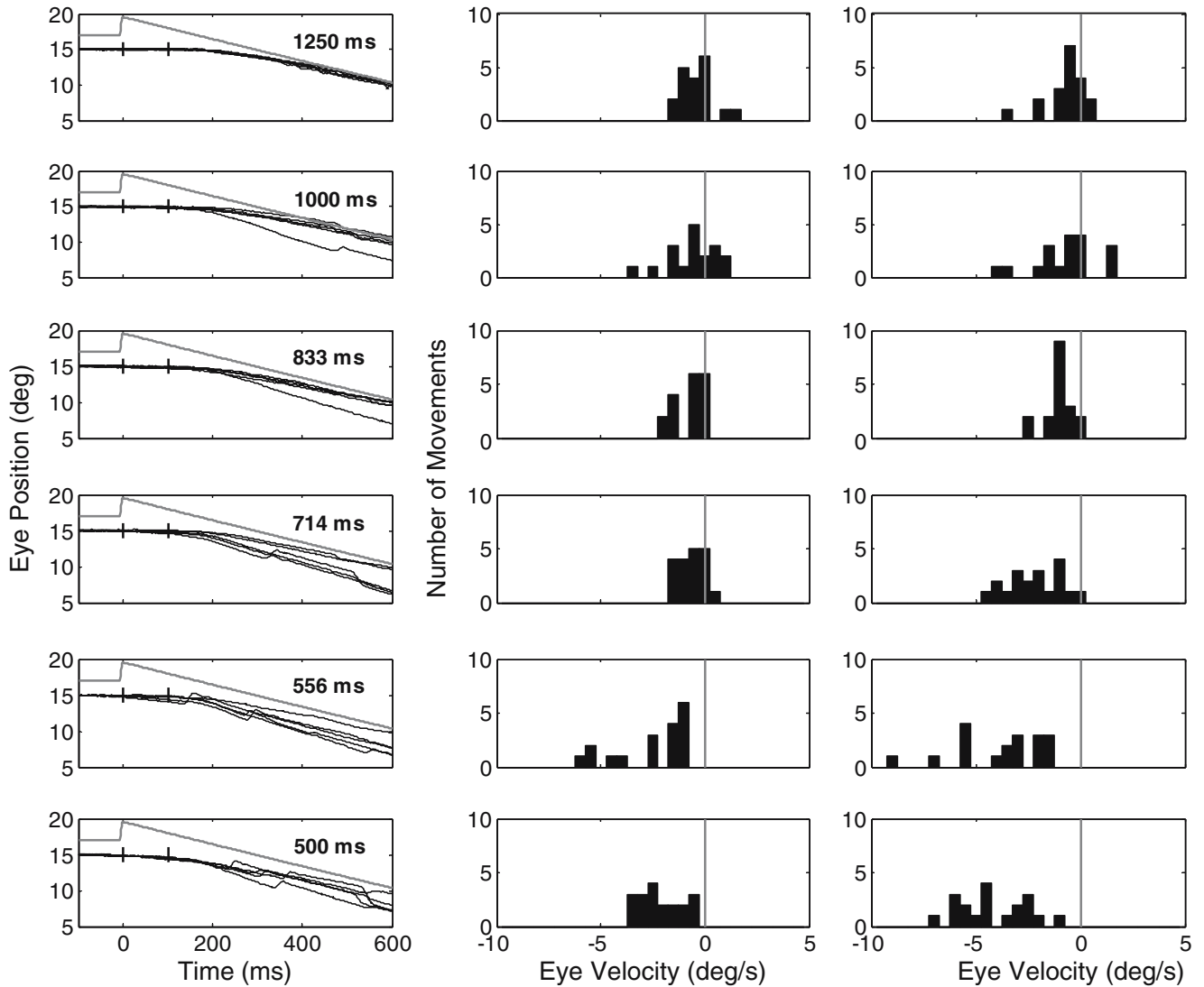
Fig. 3 Eye movement traces and corresponding eye velocity histograms for subject G during the smooth pursuit experiment. *Left column* Five sample eye movement traces (*black traces*) between −100 to 600 ms with respect to target (*gray trace*) onset for the six MPT. The *vertical black lines* mark 0 and 100 ms after target onset. Histograms (0.5°/s bins) of eye velocity at 0 and 100 ms after target onset for each MPT are presented in the center and right columns, respectively. The *vertical gray line* marks 0°/s

the smallest MPT (556 and 500 ms), again signifying that the majority of these responses are predictive. This also demonstrates that using 5°/s as a marker is reasonable for separating reactive and predictive pursuit responses, and again convincingly shows the timing difference between the two behaviors (note the distance of the eye trajectory from the target for the movements in each panel in the left column).

Though this method would give results that are qualitatively identical to what we find with our method (the presence of a phase transition is clear from the histograms), we did not use this latency-histogram method for pursuit analysis because it only indirectly gives information as to the timing of these movements. In order to compare results between pursuit and saccade responses in a quantitative manner we needed to quantify the pursuit latency, not just designate a response as predictive or not.

Table 1 Summary of MPT at which behavior changed from predictive to reactive (MPT increasing) and from reactive to predictive (MPT decreasing)

MPT transition points (ms)

Subjects	Saccade experiment		Pursuit experiment	
	Decreasing MPT	Increasing MPT	Decreasing MPT	Increasing MPT
A	833	1,000	774	917
B	917	1,334	917	1,334
C	635	833	774	917
D	635	1,334	556	1,334
E	714	917	635	917
F	833	1,000	917	1,000
G	1,000	1,000	714	1,000

Transition point calculation

The critical MPT at which the transition is made from one tracking behavior to the other was found by a statistical analysis that enabled us to decide between two representations of the latency data: an abrupt transition (represented by the solid black lines in the top panels of Figs. 6, 7, 8, 9) and a smooth transition (represented by the dashed black lines in the figures). Fitting of these functions was performed separately for each subject and for each direction of MPT change. The smooth-transition fit was determined by linear regression of the latency and MPT data. The abrupt-transition fit consists of two straight lines with zero slope—one across the mean latency of all reactive eye movements and one across the mean latency of all predictive eye movements. To delineate between reactive and predictive eye movements, the distributions of eye movements at a pure-reactive and a pure-predictive MPT were found (MPT of 2,500 ms and 500 ms), and the latency that equally divided these distributions was used as a threshold. This threshold was found separately for each subject for increasing and decreasing MPT. When a transition occurred within a single MPT (signified by latency histograms that are broad and often double-peaked as in Figs. 7 and 8), latencies were divided into reactive and predictive based on this threshold. Reactive eye movements for the transition fit were then defined as those in the pure-reactive range, plus those in the transition range (the MPT during which the transition occurred) with latencies greater than the threshold value. Similarly, predictive eye movements for the fitting were defined as those in the pure-predictive range, plus those in the transition range with latencies less than the threshold value. The mean-squared error was found for each of the two fitted functions (linear and abrupt), and these errors were compared with an F test (mean square error of the linear fit divided by the mean square error of the transition fit). All possible transition points (all tested MPTs and values midway between them) were tested and the transition point that gave the best abrupt-transition fit relative to the linear model was chosen as the critical MPT. When the transition occurred between two MPT (as in Figs. 6b, 7a) the critical MPT was chosen as the average of these two times. Using this method, the abrupt-transition fit was significantly better ($P < 0.05$) than the straight-line fit in all but 3 cases out of 28 (two pursuit-tracking and one saccade-tracking), though these subjects still demonstrated a phase transition qualitatively. (The two pursuit cases that failed to reach significance were from the subjects with the highest percentage of pursuit responses rejected due to premature saccades.)

Results

Typical examples of individual subject performance during the eye movement tasks will be shown in Figs. 3, 4, 5,

6, 7, with group results in Figs. 8 and 9. The saccade-tracking behavior for subject B at two different MPT is displayed in Fig. 4. For large MPT (top row, 2,500 ms), the subject made reactive eye movements (represented by the solid gray line) after the target jumped (represented by the solid black line). This can clearly be seen in the right column of the top row which displays the data within the area marked by the black dashed-lined box shown between −300 and 400 ms with respect to target onset. Saccade onset (marked by the black circle) occurred after the target jump, with a latency of 220 ms. This long-latency behavior was not promoted at small MPT (bottom row, 500 ms MPT), where instead the subject responded with a reduced latency to each target jump and often made a saccade before target movement. Again, an example of this behavior is seen in the area marked by the black dashed-lined box that is displayed in the right column of the bottom row. In this case, saccade onset occurred before the target jump, with a latency of −180 ms.

This dependence on MPT was also seen for pursuit eye movements. Figure 5 displays pursuit-tracking behavior for subject E at two different MPT. For large MPT (top row, 1,000 ms), the subject made reactive eye movements after the target had started to move. (The target and response traces are offset for clarity.) As before, this long-latency behavior is not promoted at small MPT (bottom row, 500 ms), where the subject responded with a reduced latency to target onset and often began to pursue the target before it moved. The difference in the timing of these responses is clearly seen in plots in the right column which are the data within the dashed-lined black boxes in the left column graphs. The larger plots display eye movement (black trace) and target position (gray trace) between −150 and 300 ms with respect to target onset. The smaller plots show eye velocity throughout the same period. In the top row pursuit onset (marked by the black circle) occurs after the target moves, with a latency of 115 ms. The eye-velocity plot for this movement shows how this time point was calculated (see Methods) and demonstrates that the eye velocity did not reach the threshold of 5°/s until well after the target onset. This was not the case for the predictive pursuit response. As seen in the right column, bottom row of Fig. 5, pursuit onset in this case occurred before target movement, with a latency of −40 ms. The analysis of eye velocity is the same as for the reactive example and shows that the velocity reaches 5°/s close to the time of target onset. In addition, these predictive pursuit movements were often accompanied by small corrective saccades (as seen in both Figs. 2 and 5 for the MPT of 500 ms), which further demonstrate that the subject was predicting target movement.

Latency data are shown in Fig. 6 for each MPT for one subject during the saccade-tracking task. In Fig. 6a the MPT was decreasing, in Fig. 6b the MPT was increasing. Refer first to Fig. 6a and the histograms beneath it. The individual latency values (gray circles) are plotted as a function of MPT in the top graph along
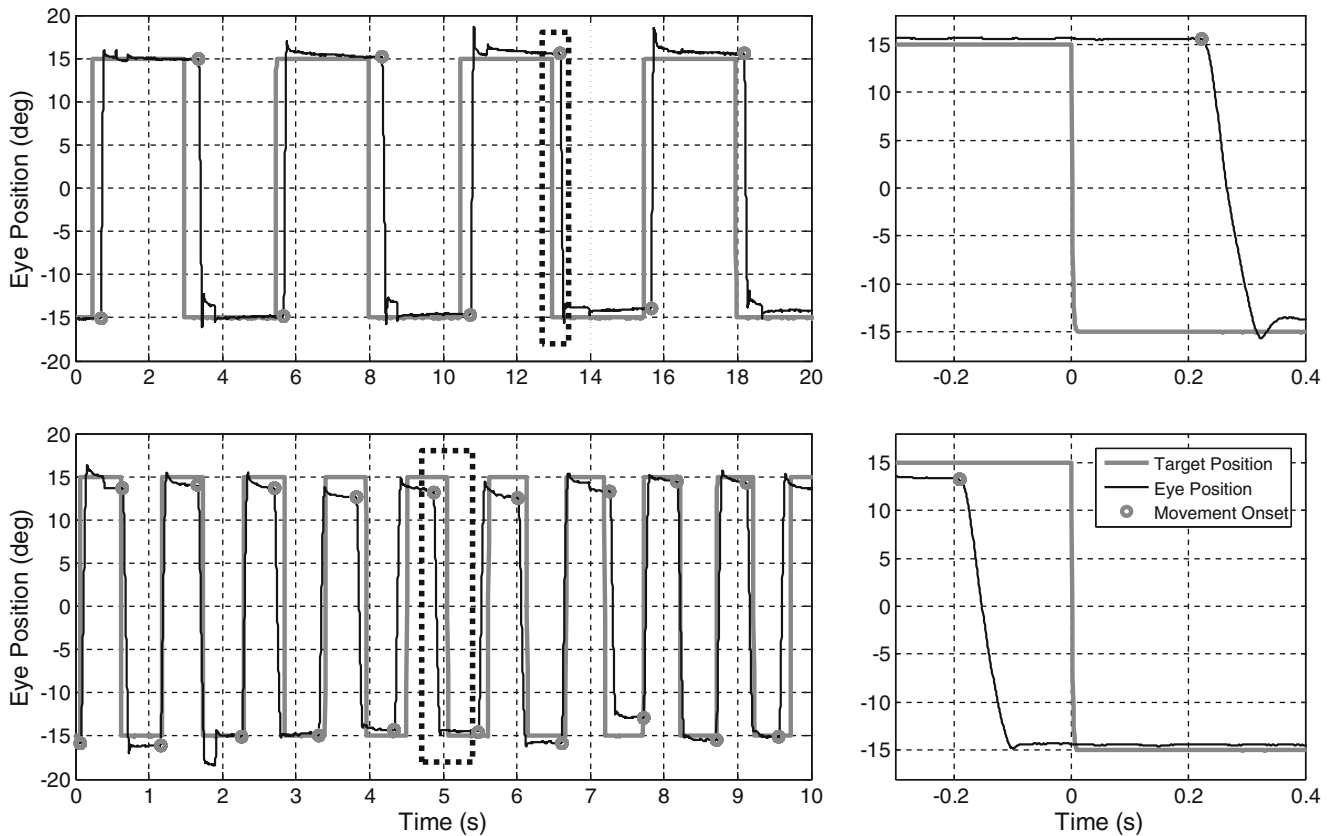
Fig. 4 *Left column* Examples of eye movement data from subject B showing saccade tracking in the different behavioral states: reactive tracking at an MPT of 2,500 ms (*top panel*), and predictive tracking at an MPT of 500 ms (*bottom panel*). LED target position is shown as a thick gray line and eye position as a *thick black line* in each plot. Saccade onset is marked by the *gray circle*. *Right column* Detailed plots of the sections marked by the *black dashed-lined box* in the left column plots. The plots are from −300 to 400 ms with respect to target onset

with mean latency (represented by the thick black ✖). Mean latency varies in a systematic manner with MPT. At the five largest times (2,500–714 ms), mean latency is almost constant at 140 ms, indicating that the subject is reacting to each target jump with a "normal" saccade latency. At the smallest MPT (556 and 500 ms) mean latency abruptly changes to −200 ms, signifying that the subject is making saccades in a predictive manner, in anticipation of each target jump. This change in tracking behavior is also present in the histograms of saccade latency presented below Fig. 6a. The gray line in each histogram marks the threshold (137 ms) between reactive and predictive responses for this subject (see Methods). As shown in the histograms, for large MPT (2,500–714 ms), eye movements are mostly reactive (latency is grouped to the right of the 137 ms marker). At the smallest MPT (556–500 ms), eye movements are mostly predictive (latency is grouped to the left of the 137 ms marker). For this subject the transition from reactive to predictive tracking occurs between 714 and 556 ms.

Latency data for subject C as MPT subsequently increased are shown in Fig. 6b. The subject predicts the target jump at the three smallest MPT (714–500 ms), with a mean latency of −175 ms. This is also seen in the histograms of eye-movement latency below Fig. 6b;

latency values at these three MPT are largely to the left of the 141 ms marker. At the MPT of 833 ms there is a transition from predictive to reactive tracking; the histogram at this MPT is broad and spans the threshold line, indicating that the subject is spontaneously switching between reactive and predictive responses. It is important to note that MPT at this transition point is greater than that at the previous transition (between 714 and 556 ms)—that from reactive to predictive as MPT decreased (Fig. 6a). (The method by which these transition points were statistically verified is in the Methods section.) After this transition, tracking behavior is steadily reactive at the three largest MPT (2,500–1,000 ms), with a mean latency of 180 ms. Similar to the MPT-decreasing case, this transition is also represented in the histograms by the shift of the latency distribution to the right of the 141 ms threshold.

Latency data during the pursuit-tracking task for subject C are shown in Fig. 7. The layout and interpretation are the same as for Fig. 6. As shown in Fig. 7a, at the three largest times (1,250–833 ms), mean latency is almost constant at 115 ms, indicating that the subject is reacting to the target movement rather than anticipating it. At the MPT of 833 ms the subject undergoes a transition between tracking states; the latency histogram at
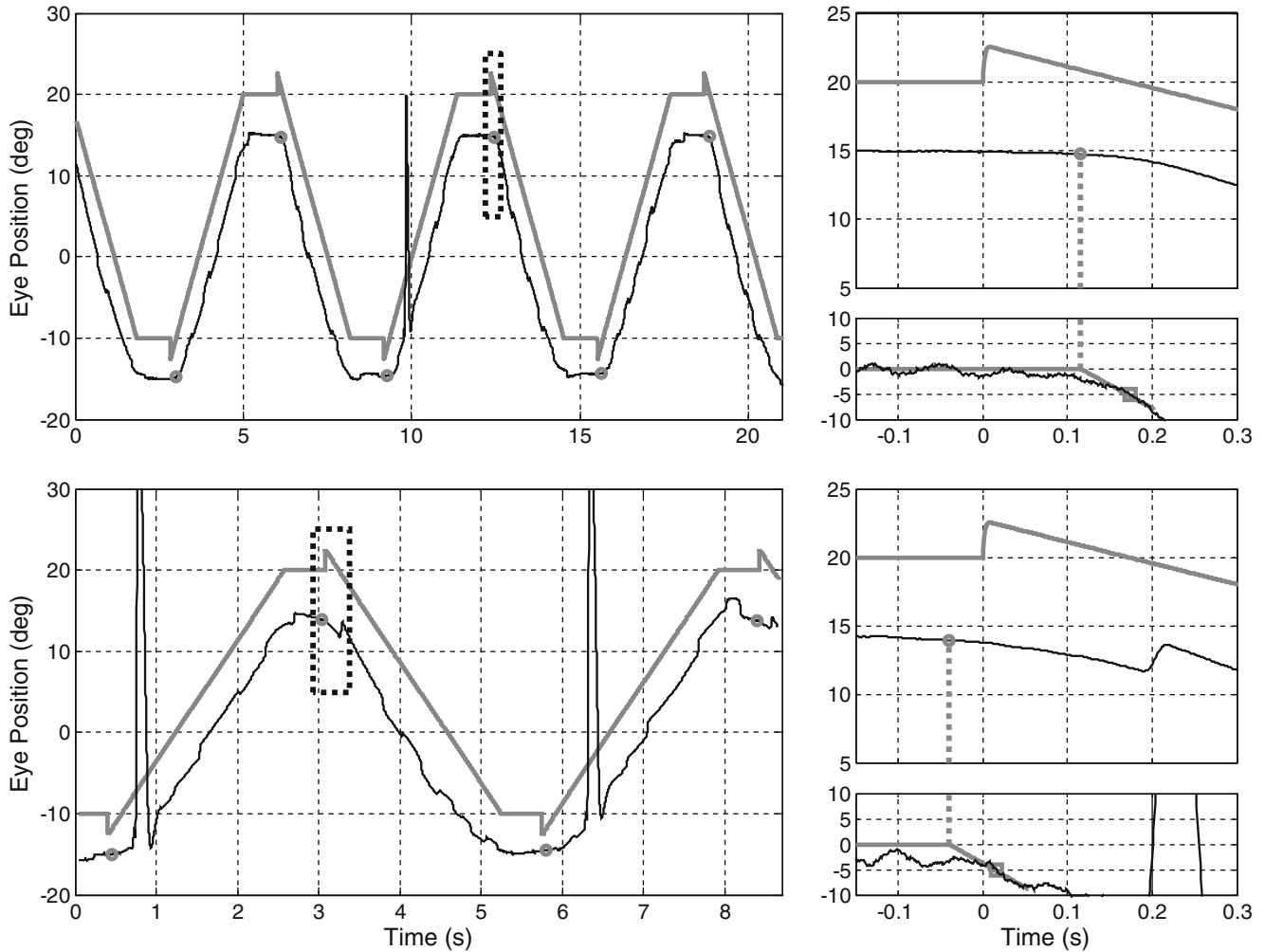
Fig. 5 *Left column* Examples of eye movement data from subject E showing pursuit tracking in the different behavioral states: reactive tracking at an MPT of 1,000 ms (*top panel*), and predictive tracking at an MPT of 500 ms (*bottom panel*). Target position is shown as a *thick gray line* and eye position as a *thick black line* in each plot. Pursuit on-set is marked by the *gray circle*. *Right column* Detailed plots of target and eye position (*large plots*) and eye velocity (*smaller plots*) for the sections marked by the *black dashed-lined box* in the left column graphs. The plots are from −150 to 300 ms with respect to target on-set. The analysis of the velocity traces is the same as that in Fig. 2

this MPT is broad and spans the threshold line. After this transition, tracking behavior is mostly predictive at the smallest MPT (500–714 ms), with a mean latency of 5 ms. This signifies that the subject is pursuing the target in a predictive manner, in anticipation of the target movement. This change in tracking behavior is also present in the histograms of pursuit latency presented below Fig. 7a. As shown in the histograms, for the large MPT (1,250 and 1,000 ms) eye movements are mostly reactive (latency is grouped to the right of the 60 ms marker). At the smallest MPT (500–714 ms) eye movement latency is grouped to the left of the 60 ms marker.

Latency data for subject C as MPT subsequently increased are shown in Fig. 7b. As shown in the top graph, the subject continues to anticipate the target movement at the four smallest MPT (500–833 ms) with a mean latency of −5 ms. This is also shown in the histo-grams of eye movement latency below Fig. 7b; latency values at these four MPT are largely to the left of the

45 ms marker. However, between the MPTs of 833 and 1,000 ms the subject undergoes a transition between the two tracking states. After this transition, tracking behav-ior is steadily reactive at the largest MPT (1,250 and 1,000 ms) with a mean latency of 105 ms. Similar to the MPT-decreasing case, this transition is also represented by the switch in the latency distribution to the right of the 45 ms threshold.

In all of these cases, the critical MPT, at which the phase transition was made from one tracking behavior to the other, was found by a statistical analysis (see Methods) designed to distinguish between two represen-tations of the latency data: an abrupt transition (repre-sented by the solid black lines in the top panels of Figs. 6 and 7) and a smooth transition (represented by the dashed black lines in the same figures). The critical MPT (transition points) for all subjects are displayed in Table 1 and plotted against each other (pursuit vs. sac-cade tracking) in Fig. 8. The data are separated into
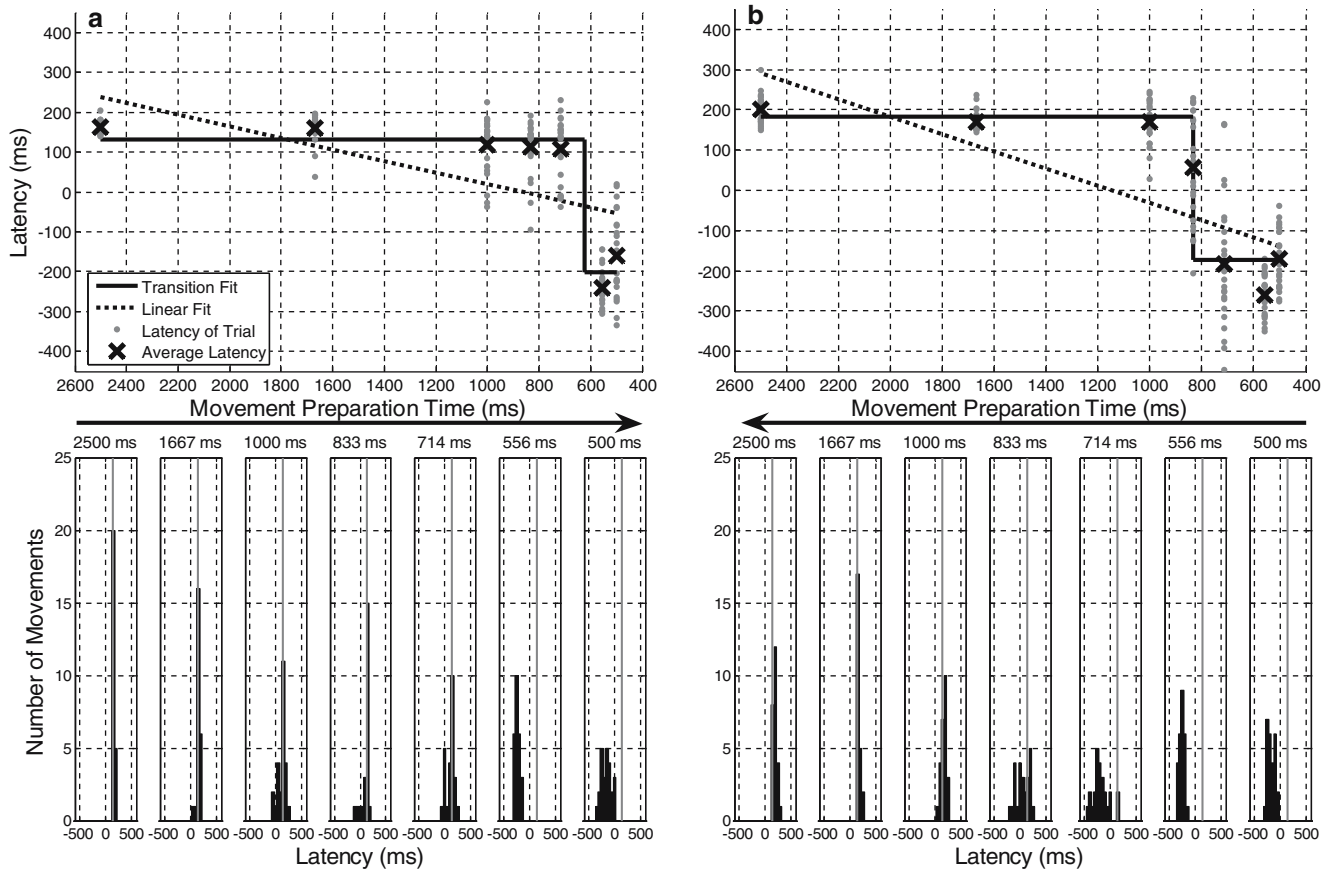
Fig. 6 Saccade latency as a function of MPT for subject C, for decreasing and increasing MPT (indicated by the direction of the *arrow*). **a** At each discrete MPT, the latency of each primary saccade is plotted as a single point; ✖ represents the mean latency at a given MPT. A *straight line* was fit to the latency data via linear regression (*dashed line*), which represents the hypothesis of a smooth change in latency with MPT. A "transition fit" was also made, in which data in the reactive range (2,500–714 ms) and in the predictive range (556 and 500 ms) were fit with separate *horizontal lines* through the two group means; this represents the hypothesis of an abrupt "phase transition" in latency as a function of MPT. Below this panel are histograms of saccade latency at each MPT. The *gray vertical lines* mark 137 ms. Latencies are tightly grouped and unimodal in the range 2,500–833 ms and in the range 556-500 ms. **b** Layout and interpretation as for **a**. The *gray vertical lines* plotted with the histograms mark 141 ms. Transition fit in this case is based on a transition at 833 ms, and the histogram at this MPT is broad indicating that both tracking behaviors are present simultaneously

decreasing MPT (circles) and increasing MPT (squares). As shown, the transition points for MPT decreasing are generally less than the transition points for the MPT-increasing case. This represents hysteresis: the initial transition point (reactive to predictive) is at a lower MPT than for the reverse transition (predictive to reactive). Except for subject G (saccade tracking), all subjects demonstrated hysteresis in both tracking tasks.

There is a strong correlation between the critical MPT (transition points) in the saccade and pursuit experiments. A linear regression line was fit to these data points (represented by the thick dashed black line in Fig. 8); the line has a slope of 0.86 (correlation coefficient of 0.81), confirming a positive linear relationship. This is the main result of the study and supports our hypothesis that the smooth pursuit and saccadic systems behave similarly in terms of MPT during repetitive tracking.

In addition to the above analyses we wished to determine if the two eye movements are related by their response to a randomly timed stimulus. These data (which

were obtained before each main experiment task; see Methods) for all subjects are displayed in Fig. 9. Saccade and pursuit responses (gray circles) were paired in decreasing order. That is, for a given subject, the largest saccade latency was plotted against the largest pursuit latency, then the next largest latency responses, and so forth. The thick black dashed line is the best-fit line to the data and has a slope of 1.22 (correlation coefficient of 0.83). As demonstrated in the graph, subjects who react faster to the randomly timed saccadic stimulus also tend to react faster to the randomly timed pursuit stimulus and vice versa. This result further suggests that the two movements behave similarly when the experimental conditions are equivalent.

Discussion

In this report we have demonstrated that saccadic and pursuit eye movements exhibit a similar dependence on
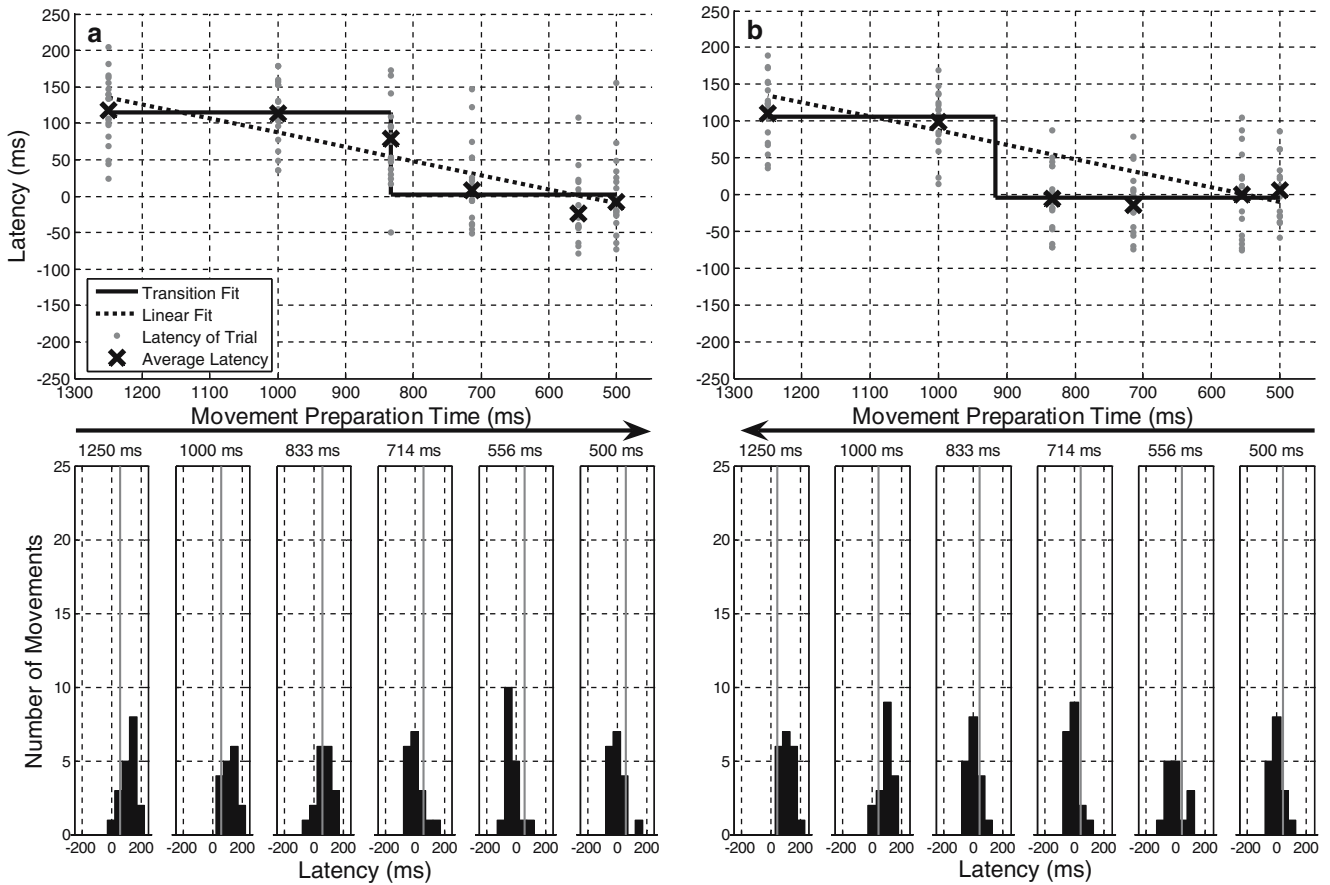
Fig. 7 Pursuit latency as a function of MPT for subject C, for decreasing and increasing MPT (indicated by the direction of the *arrow*). Layout and interpretation as for Fig. 6. **a** The *gray vertical line* plotted with the histograms marks 60 ms. Transition fit in this case is based on a transition at 833 ms. **b** Layout and interpretation as for **a**. The *gray vertical line* plotted with the histograms marks 45 ms. Transition fit in this case is based on a transition between 833 and 1,000 ms. Between these two MPT there is a transition from predictive responses to reactive as indicated by the histograms

the time allotted to prepare for a movement. When normal subjects tracked a constantly alternating target (saccade tracking) or a constant-velocity target (pursuit tracking) with large preparation times before target onset their responses typically were reactive. However, as this preparation time monotonically decreased, their eye movements abruptly became predictive at a critical MPT value. When the MPT was then monotonically increased, predictive behavior for both eye movement types persisted past the initial transition point (hysteresis). Furthermore, within each subject the critical MPT at which behavior switched modes were similar for the saccadic and pursuit tasks. These results were analogous to the saccade and pursuit responses to randomly timed stimuli; the latencies of these reactive movements tended to be correlated. That is, subjects with short-latency reactive saccade responses tended also to have short-latency reactive pursuit responses and vice versa.

Although our conclusions are based on relatively small samples (about 20 trials at each MPT), we are confident of their validity because they are internally consistent (pursuit and saccade latencies correspond) across subjects (Fig. 8), and are in accord with recent findings

on the overlap of saccade and pursuit pathways. Nevertheless, it is clear that experiments with larger data sets would be more convincing, especially in view of the natural variability of saccade and pursuit latencies.

Possible alternative interpretation

One might argue that the observed behavioral hysteresis is an artifact of the stimulus protocol and the analysis method—specifically, the fact that we include the first trials of every major MPT block in the analysis rather than discarding them. For example, during the MPT-decreasing case a subject may make predominantly reactive responses during the 833 ms block and then make a transition to predictive behavior when pacing switches to the subsequent 714 ms block. Then, during the MPT-increasing case, if this subject is making predictive saccades in the 714 ms block, these predictive saccades may continue into the first few saccades of the subsequent 833 ms block, with the response becoming reactive only in much later trials in this block. This could have the effect of making it appear as if predictive saccades are dominant in the 833 ms block, thereby incorrectly

Fig. 8 The critical MPT at which the behavioral transition occurs in the pursuit experiment versus the critical MPT for the saccade experiment for all subjects. The transition point for MPT decreasing (reactive response to predictive response) is represented by *circles*; for MPT increasing (predictive response to reactive response) by *squares*. This best fit line to the data has a slope of 0.86 (correlation coefficient of 0.81)
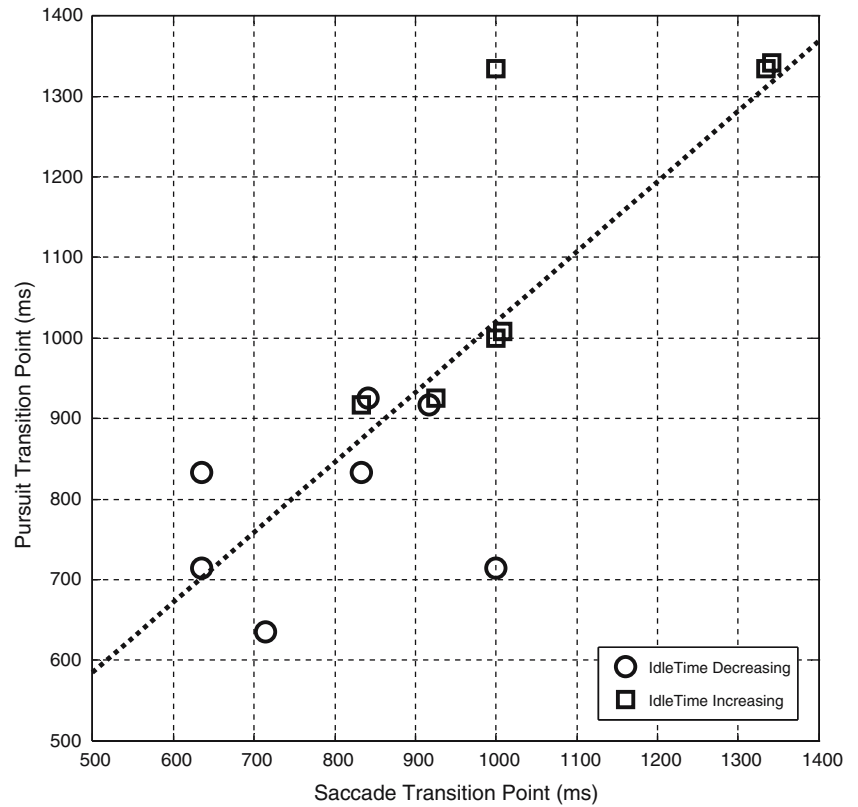
Fig. 9 Saccade latency to randomly timed alternating targets versus pursuit latency to a randomly timed moving stimulus. The *gray circles* represent paired pursuit and saccadic responses for all subjects; for a given subject the largest saccade and pursuit latencies are paired in decreasing order. The *thick black dashed line* is the best fit line to the data and has a slope of 1.22 (correlation coefficient of 0.83)
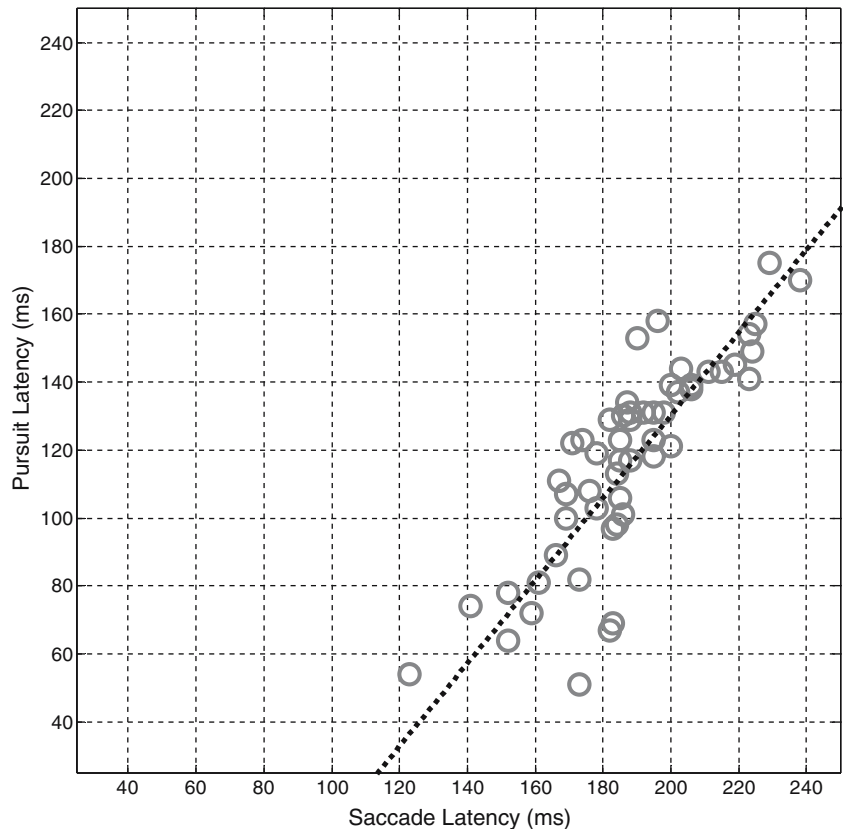
signifying hysteresis. This in fact is not an adequate explanation for our results. To verify this, we examined saccade and pursuit latency as a function of trial number within each MPT block. In no case was there a monotonic trend in latency within a block. There are blocks within which spontaneous transitions occur between

tracking modes, especially near the transition range, but there is no systematic difference between early and late trials in a single MPT block. One consequence of this can be seen in the broad latency distributions during pacing in the transition range, which are due to this mixture of tracking modes.

Relation to previous behavioral studies

The finding that saccadic and pursuit eye movements become predictive at similar MPT accords with recent evidence that there is significant overlap between the two oculomotor systems, and also with their similar performance in psychophysical experiments (for review see Krauzlis 2004, 2005). Specifically, the work of Krauzlis and Miles (1996b) has suggested that there is a single preparatory input that coordinates both types of movements based on a similar gap-duration-dependent change in eye movement latency. The reduction in latency for both eye movements during the "gap paradigm" demonstrates that expectation and preparation time affect the initiation of the two types of eye movements similarly. A more recent study that supports the above proposal (Erkelens 2005) examined the onset of pursuit and saccades when subjects switch from tracking one moving target to a second target moving in a different direction and speed. When the first target disappeared and second target appeared simultaneously the author reports that the latencies of the two movements were not correlated. That is, pursuit moved in the direction of the new target before the saccade was made to the new target. However, when the presentation of the two targets briefly overlapped the latencies of the two movements were significantly correlated; the change of pursuit in the direction of the new target and the saccade to the new target occurred at approximately the same time. The author argues that the overlap allows the engagement of attention to the new target resulting in the synchronous preparation of saccade and pursuit change. The results presented here agree with these findings and support that the same decision process governs the reaction times of both movements; the relative latency of saccadic and pursuit responses to randomly timed stimuli are correlated and the two eye movement types show a similar dependence on the time allotted to prepare for the movement within subjects. Furthermore, when this time decreases below a critical level predictive behavior is favored and remains preferred past this transition point.

The dependence of movement initiation on the time given for movement preparation has been inadvertently demonstrated in manual tasks such as serial response time (RT) learning (Willingham et al. 1997) and synchronized tapping (Miyake et al. 2004). In the first example, the task consisted of viewing a computer screen display of four possible stimulus locations and pressing the corresponding keyboard key. Between blocks of trials, the authors varied the delay between the subject's response and the time when the next stimulus appeared (response-to-stimulus interval, RSI) and measured the subject's RT. When RSI was decreased from 1,500 to 5,00 ms, subjects reduced their RT by approximately 100 ms. In addition, when the RSI was increased to 1,500 ms following training at 500 ms, subjects continued to perform the task at the faster RT. In the second example, subjects were required to tap in synchrony with an auditory stimulus as the investigators varied the inter-stimulus interval, ISI, between blocks of trials. Corresponding to our current results, subjects made reactive responses to the auditory stimulus at the longer ISIs and anticipated the stimulus at the shorter ISIs (ISIs of 3,600 and 600 ms, respectively). Interestingly, the authors also found that subjects exhibited mixed predictive and reactive behavior at the intermediate ISIs (1,500–2,400 ms). (This experiment was conducted in randomized blocks and not with a systematic decrease or increase in ISI. This may explain why the ISIs that promote reactive and mixed behaviors are larger than those reported in our experiments.) Consistent with our results, these experiments also show that the time allotted for motor preparation (the RSI and ISI) influences the timing of the motor act regardless of the movement type. Furthermore they also suggest that the shared internal inputs at early stages of movement preparation for saccade and pursuit movements might be relevant for other types of movements.

Behavioral transition and physiology

One question that our results raise is why and how the transition from reactive to predictive behavior occurs in the first place. A recent fMRI study comparing reactive and predictive saccades (Simo et al. 2005) has shown that the latter elicit greater activity in the basal ganglia (striatum and substantia nigra pars reticulata). The authors proposed that (1) the transition from reactive behavior to predictive might involve a shift in activity from neural systems supporting sensory guided behavior to ones supporting internally generated predictive behavior, and (2) the loops through the basal ganglia may be fundamental for the switching of behavioral control and for maintaining predictive behavior. Recent evidence that neurons within the basal ganglia (specifically the substantia nigra pars reticulata) are modulated during saccadic and smooth pursuit eye movements (Basso et al. 2005) suggests that signals arising from this region may be utilized by both movement types.

In addition to their role in predictive eye movement behavior (Bronstein and Kennard 1985; Crawford et al. 1989; Tian et al. 1991; Simo et al. 2005), the basal ganglia have also been demonstrated to play a part in the internal representation of time (Rao et al. 1997), a process modeled as an internal clock (Treisman 1963; Meck and Benson 2002). Such a model entails the transformation of some physical process into a perceptual psychological time, then encoding and storing this time information and comparing it to a reference according to some decision rule. We have evidence from other studies in our laboratory that predictive saccadic tracking of targets alternating at small MPT (500–1,000 ms) may be the

result of an internal clock: the movement timing at these MPT persists despite perturbations to the stimulus (abruptly increasing the MPT or extinguishing the targets altogether). Thus, the abrupt switch in timing behavior may reflect a switch to structures that establish this internal clock. The resulting neural signals could subsequently be utilized for the timing of both saccades and pursuit.

A predictive or anticipatory movement is the result of motor planning based on prior movements or sensory information (visual, auditory, etc.). Previous reports have suggested that the supplementary eye fields (SEF) could be involved in this process due to their role in the execution of internally generated eye movements. For example, Heinen and Liu (1997) showed an increase in SEF activity before predictive pursuit. In addition, microstimulation of the SEF before movement facilitates the initiation (increased velocity and decreased latency) of anticipatory smooth pursuit (Missal and Heinen 2004). Analogous results (increased and systematic patterns of SEF activity) have also been found in the planning of internally guided saccadic eye movement sequences (Grosbras et al. 2001; Isoda and Tanji 2002, 2003). The similarities between these reports and the predictive behavior presented here suggest that the SEF could also be involved in the transition between tracking behaviors.

Conclusion

We have shown that when the time given to prepare for a movement decreases, both saccadic and pursuit eye movements undergo a similar transition from reactive to predictive behavior at a similar MPT. This predictive behavior may be the result of these MPTs triggering an internal representation of the target timing (an internal clock). When this time is then increased predictive tracking persists past the initial transition point demonstrating hysteresis. Based on the examples cited above, multiple structures may drive the switch to an internal clock/predictive behavior (Matell and Meck 2004; Lustig et al. 2005; Meck 2005; Simo et al. 2005) and their continued activity may be the cause of the behavioral hysteresis. Furthermore, due to the involvement of these structures in both saccade and pursuit tracking, the transition point turns out to be similar when the two different movements are made under the same time constraints. These results support the hypothesis of a single preparatory input that coordinates both types of movements (Krauzlis and Miles 1996b) and further strengthens the neuropsychological and psychophysical evidence that both eye movements are the motor output of a common higher-order decision process.

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