Published in final edited form as:

Exp Brain Res. 2011 May ; 211(1): 27–36. doi:10.1007/s00221-011-2638-7.

Spatial and temporal aspects of cognitive influences on smooth pursuit

Sara A. Winges and John F. Soechting

Department of Neuroscience, University of Minnesota, 6-145 Jackson Hall, 321 Church Street SE, Minneapolis, MN 55455, USA

Abstract

It is well known that prediction is used to overcome processing delays within the motor system and ocular control is no exception. Motion extrapolation is one mechanism that can be used to overcome the visual processing delay. Expectations based on previous experience or cognitive cues are also capable of overcoming this delay. The present experiment was designed to examine how smooth pursuit is altered by cognitive information about the time and/or direction of an upcoming change in target direction. Subjects visually tracked a cursor as it moved at a constant velocity on a computer screen. The target initially moved from left to right and then abruptly reversed horizontal direction and traveled along one of seven possible oblique paths. In half of the trials, a cue was present throughout the trial to signal the position (as well as the time), and/or the direction of the upcoming change. Whenever a position cue (which will be referred to as a timing cue throughout the paper) was present, there were clear anticipatory adjustments to the horizontal velocity component of smooth pursuit. In the presence of a timing cue, a directional cue also led to anticipatory adjustments in the vertical velocity, and hence the direction of smooth pursuit. However, without the timing cue, a directional cue alone produced no anticipation. Thus, in this task, a cognitive spatial cue about the new direction could not be used unless it was made explicit in the time domain.

Keywords

Anticipation; Visual motion; Eye tracking; Smooth pursuit

Introduction

Smooth pursuit eye movements occur in response to retinal image motion with a latency of ~100 ms after unexpected ramps in target position (Carl and Gellman 1987; Robinson 1965). However, it is well known that prediction can be used to overcome processing delays within the ocular control system. One mechanism that can be used to overcome this visual processing delay is motion extrapolation. For example, when target motion is predictable, such as a periodic target path like a sine wave, the delay due to visual processing can be reduced or eliminated (Barnes et al. 2000; Collewijn and Tamminga 1984; Kettner et al. 1996; Soechting et al. 2010; Westheimer 1954). When subjects track a target that is occluded along its trajectory but is expected to reappear, eye velocity initially decreases and then rebounds to a magnitude that is graded with the predicted target velocity at reappearance (Bennett and Barnes 2003, 2004). Target motion can also be extrapolated along a curve during an occlusion resulting in pursuit along an invisible curved trajectory

(Mrotek and Soechting 2007). Thus, information about past motion can be utilized to maintain smooth pursuit with minimal delay after target occlusion.

Expectations of target movement based on prior experience can also reduce the delay due to visual processing. For example, predictable changes in target position result in smooth anticipatory eye movements prior to the onset of target movement (Kao and Morrow 1994; Kowler and Steinman 1979a, b). When the timing or the direction of motion is unpredictable, subjects nevertheless can exhibit anticipatory smooth eye movements by guessing the motion parameters of the upcoming trial (Kowler and Steinman 1981). Kowler (1989) showed that when target direction was unpredictable, anticipatory smooth pursuit eye movements reflected the target direction from the previous trial (see also Soechting et al. 2005).

Cognitive expectations about the speed or direction of upcoming target motion provided by auditory, verbal or visual cues also generate anticipatory smooth eye movements overriding the effects from previous trials (Kowler 1989). For example, Jarrett and Barnes (2001, 2002) showed that velocity and horizontal direction cues provided at a fixed time prior to motion onset could be used concurrently to produce anticipatory smooth pursuit eye movements scaled with velocity in the appropriate direction (right or left). Therefore, expectations based on target movement in previous trials as well as cognitive cues can be used to produce anticipatory eye movements and thus reduce the delay due to visual processing.

The present experiment was designed to further examine how predictive information in the form of cognitive cues about changes in target direction can alter smooth pursuit. Cognitive cues provided information about the time and/or the direction of the change in target motion. Subjects tracked a target that initially moved horizontally to the right then abruptly changed direction and followed one of seven possible oblique trajectories back toward the left. Cognitive cues were provided by a barrier that indicated the location (and therefore the time) and/or the direction of the subsequent motion. Timing cues always resulted in anticipatory changes in the horizontal velocity component, but cues indicating both the location and direction of the change in target motion were necessary to produce an anticipatory change in the vertical velocity component, and hence the direction of smooth pursuit. However, the direction cue alone produced no anticipation.

Methods

A total of seven right-handed subjects participated in the study (three men, four women, 21–35 year, 1.57–1.80 m in height). Each of the three experiments had six subjects (five subjects completed all three experiments). The three experiments were conducted several months apart. One subject completed only the first experiment but was not available for the other two; therefore, new subjects were recruited. Subjects had no history of sensory, perceptual, or motor disorders, and all had normal or corrected-to-normal vision. The experimental protocol was approved by the University of Minnesota's Institutional Review Board, and all subjects gave informed consent prior to each experimental session.

A computer monitor (Mitsubishi Diamond Scan 20 M) with a resolution of 640×480 pixels (34.8×26.0 cm; $41^\circ \text{va} \times 33^\circ \text{va}$) and a 60-Hz refresh rate was used to display a visual target. Eye movements were recorded binocularly at a sampling rate of 250 Hz with head mounted infrared cameras (SMI Eye Link). The positions of infrared markers on the corners of the monitor were also recorded by a camera on the head mount to correct for any head movement that occurred. However, the head was stabilized by means of a chin rest that was 40 cm from the monitor. The system was calibrated prior to data collection and after any

change in the position of the head mounted camera. Prior to every trial, a drift correction was performed. Gaze was determined by averaging the two eye position signals.

Participants tracked a target that always abruptly changed direction once during the trial. On half of the trials cues were presented that indicated the location and/or the amount by which the target would change direction. The target was a cyan circle with a radius of 4 pixels (0.3° of visual angle) that moved across the monitor at a constant rate of 240 pixels/s (18.2° /s). The target first moved from left to right across the monitor then abruptly changed direction and moved from right to left until the end of the trial. When the target changed direction (target corner), it either continued on a straight path from right to left (0° inclination) or changed its inclination by ± 30 , 45, or 60° . Ten randomly presented trials were completed for each of the seven target inclinations for two conditions per experiment (the uncued control condition and one of the three experimental conditions). The total data set was $10 \text{ trials} \times 7 \text{ target inclinations} \times 2 \text{ conditions} \times 6 \text{ subjects}$ for a total of 840 trials per experiment.

Figure 1 depicts the uncued (control) and the cued conditions for each experiment. The target cursor is shown in its starting position at the left edge of the screen with the arrow indicating the initial direction of travel. The target redirection zone, which was never visible to the subject, is indicated by the gray area and denotes the range in the x -dimension where the cursor could change direction. This range was from 400 to 500 pixels from the left edge ($21.75\text{--}27.2 \text{ cm}$; 7.7° va) and was large enough that subjects could not predict when the target would change direction if a “timing” cue was not given. During the un-cued control trials, the cursor was the only visible item on the screen. On cued trials, throughout the trial, the timing and/or direction of the target change was cued by a red line or dot as shown in the other three boxes in Fig. 1. The dimension of the red line was 10.9 cm high by 0.16 cm wide (15.2° va $\times$ 0.2° va) which was large enough for the subjects to discriminate its orientation.

Prior to each trial, a fixation cursor appeared in the middle of the screen for drift correction. Then the target cursor appeared stationary on the left portion of the screen along with any additional cue for that trial. After the subject had fixated on the stationary target cursor, there was a variable delay (200–1,000 ms) and then the trial began. For experiment 1, the cue was a bar into which the target collided and changed direction in a stereotypical billiards fashion (angle of reflection is equal to the angle of incidence), thus providing both timing and direction cues of the change in target motion. For experiment 2, only a timing cue was given by presenting a red circle, which was slightly larger than the target, where the target would change direction. For experiment 3, to remove the timing portion of the cue, a directional cue similar to that used in experiment 1 was present on the far right of the screen (centered at (550, 240) pixels; $(17.4, 0)^\circ$ va from center), so the target abruptly changed direction well before it reached the bar.

The x and y gaze position data were filtered (double-sided exponential filter with 4 ms time constant) and differentiated to get the velocity in the x - and y -dimensions. Saccades were identified and removed by interpolating the velocity traces using a cubic spline leaving only smooth pursuit data to be analyzed (Engel et al. 1999). The mean $\pm$ SD incidence of saccades in 4 ms time bins relative to the target corner was calculated across subjects for each inclination and condition. The desaccaded data were truncated at $\pm 500 \text{ ms}$ around the point at which the target changed direction (target corner, time = 0) allowing trials to be aligned and averaged for subsequent analysis. Speed and direction were then computed from the x - and y -velocities. The mean smooth pursuit speed and velocities for each target inclination in each condition were computed for each subject. ANOVA with Bonferroni correction for multiple comparisons was used to test differences between conditions and the amplitude of target inclinations.

Results

All subjects tracked a target that moved in a straight line across a computer screen at a constant speed, abruptly changed direction, and continued on a new trajectory. Prior to the start and throughout the trial no cue, a timing cue, and/or a directional cue was present. Figure 2 shows the average path of smooth pursuit across subjects for each target inclination and condition in each of the three experiments. The path of smooth pursuit was similar regardless of target inclination and condition up to about 2° prior to the target corner (vertical line). In all three experiments, when no cues were given (solid lines) on average ($\pm$ SD), the smooth pursuit path overshoot the target corner by $1.93 \pm 0.37^\circ$, $1.75 \pm 0.40^\circ$, and $1.89 \pm 0.36^\circ$, respectively for experiments 1, 2, and 3. When a directional and timing cue was present, there was a significant reduction in the overshoot ($0.34 \pm 0.18^\circ$, $P < 0.001$; Fig. 2a). This was also true when only a timing cue was present ($0.35 \pm 0.21^\circ$, $P < 0.001$; Fig. 2b). However, the presentation of a directional cue alone did not significantly reduce the overshoot (1.92 ± 0.41 , $P = 0.938$; Fig. 2c). Therefore, providing a timing cue resulted in smooth pursuit paths that appeared to change direction very near the target corner with minimal overshoot (Fig. 2a, b).

To further examine the effects of timing and directional cues on smooth pursuit eye movements, we analyzed the horizontal (x) and vertical (y) velocity components. The average profile of the horizontal velocity component across subjects for each direction and condition is shown in Fig. 3. In the uncued condition (solid lines), the horizontal velocity decayed gradually prior to the target direction change. Since the target always changed direction within a 100 pixel window (see Fig. 1), as the target moved further toward the right edge of the screen, subjects tended to slow down in anticipation of the direction change. This tendency was confirmed with a regression analysis of the horizontal eye velocity at the target corner against the location of the target corner on that trial (thin lines, Fig. 4). In the uncued conditions, this slope was always negative ($P < 0.001$), with slopes that ranged from -0.11 to $-0.23^\circ/\text{s/pixel}$.

Furthermore, in the uncued conditions, following this gradual decay in horizontal velocity, the horizontal velocity steeply decreased at a latency of 100 ms after the target changed direction (Fig. 3, dashed vertical lines). The average ($\pm$ SD) slope of the horizontal velocity within a 100 ms window after the start of this steep decrease was $138 \pm 16^\circ/\text{s}^2$ for the uncued conditions (across directions and experiments). When only a directional cue was present, the result was similar to the uncued conditions. The gradual decline in horizontal pursuit velocity had a slope of $-0.12^\circ/\text{s/pixel}$ (heavy dot-dashed line in Fig. 4) with respect to the location at which the target changed direction, and the latency of the abrupt decrease was the same as was its slope ($137 \pm 17^\circ/\text{s}^2$).

When timing cues were present, horizontal velocity declined appreciably, but this decline depended little on the location of the change in target direction (experiment 1: slope $-0.02^\circ/\text{s/pixel}$, $P = 0.018$; experiment 2: slope $-0.01^\circ/\text{s/pixel}$, $P = 0.44$). Instead, this decline was linked to the predicted time of the change in target direction, pursuit velocity being close to 0 at that time (time = 0), and smaller by $5.77^\circ/\text{s}$ (61%, time and direction) and $4.37^\circ/\text{s}$ (49%, time only) than in the uncued conditions (ANOVA, both $P < 0.001$). The opposite was true when only a directional cue was present (horizontal velocity being $1.96^\circ/\text{s}$ (22%) faster, $P = 0.002$). In the presence of a timing cue, there was no abrupt change in horizontal velocity and the slope of pursuit velocity during the period 100–200 ms after target change was also smaller, with average slopes being $\sim 44\%$ less steep than in the uncued conditions ($-77 \pm 18^\circ/\text{s}^2$ and $-77 \pm 19^\circ/\text{s}^2$; Fig. 3a, b dashed lines). ANOVA confirmed that when a timing cue was present, the slope of the horizontal velocity (from 100 to 200 ms) was not as steep as in the uncued condition (both $P < 0.001$), but this slope did not differ when only a directional

cue was present ($P = 0.778$). ANOVA also revealed that when only a directional cue was present, the horizontal velocity tended to be slightly larger ($1.18 \pm 0.42^\circ/\text{s}$) for the cued condition than it was for the uncued condition, although this difference was small and occurred prior to the reaction time (-376 – 120 ms, $P < 0.05$; Fig. 3c).

At time = 0, the target reversed direction; thus, the horizontal velocity should cross from positive to negative around this point if subjects are able to accurately anticipate the time of the target direction change. To further quantify the effects of cognitive cues, we determined the duration and rate of the smooth pursuit reversal to the new x -velocity for the new target trajectory. The start of the reversal was defined as the time point where x -velocity became negative and the end was the point when the x -velocity reached 95% of its peak after the start of the reversal. When timing cues were present, the mean ($\pm$ SD) start time of the reversal was 34 ± 80 ms but without timing cues the mean reversal in the horizontal velocity was 136 ± 72 ms for the direction-only cued condition and 120 ± 79 ms for the uncued control condition. The duration of the reversal period was longer and the rate of the change was slower with a timing cue (all $P < 0.001$) but not with a direction-only cue ($P = 0.077$, $P = 0.345$, respectively). These differences in the temporal profile of the x -velocity component reflect an anticipation of the target direction change due to the presentation of the timing cue.

The effects of the directional cue on the smooth pursuit eye movements may be more clearly evident in the vertical velocity component since perfect tracking would yield a vertical velocity equal to zero prior to the direction change and a graded response thereafter. Figure 5 shows the average vertical velocity profiles for each experiment. When no cues were present (solid traces), the vertical velocity stayed close to $0^\circ/\text{s}$ until ~ 125 ms after the target changed direction and then increased or decreased rapidly. For the uncued conditions, the average ($\pm$ SD) absolute value of the slope of the vertical velocity profile 100 ms after this rapid change across directions (except 0°) and experiments was $73 \pm 15^\circ/\text{s}^2$. With either a timing-only or direction-only cue, the latency of the change was similar and the slope of the increase in vertical velocity was similar to that of the uncued conditions ($64 \pm 8^\circ/\text{s}^2$, $67 \pm 13^\circ/\text{s}^2$; Fig. 5b, c, respectively). However, when the timing and directional cues were presented together (Fig. 5a), the vertical velocity began to change near the time target direction changed. This earlier increase in vertical velocity just after the target changed direction had a slope (from 25 to 125 ms) of $23 \pm 10^\circ/\text{s}^2$, $P < 0.001$. However, in the 100 ms interval after the normal reaction time (i.e. from 125 to 225 ms), the slope was smaller ($56 \pm 10^\circ/\text{s}^2$) than it was in the uncued condition. Thus, in conjunction with an earlier increase in the slope, the later slope was more shallow. ANOVA confirmed that the slope 125–225 ms in the presence of direction and timing cues was smaller than in the uncued condition ($P = 0.009$). However, when either timing or directional cues were presented alone, the slopes were similar ($P = 0.197$, $P = 0.132$, respectively).

When both timing and directional cues were present, the rise in vertical velocity (start by 10% of the peak) began 66 ms (46%) earlier, but the duration of the rise (time from start to 90% of peak) was 25% longer than in the uncued condition (ANOVA, all $P < 0.001$). There were no differences in the vertical velocity component when either timing or directional cues were presented alone compared with the uncued condition.

The latency at which the positive and negative directions could be distinguished from one another also provided an estimate of the start of the smooth pursuit direction change relative to the target direction change. ANOVA revealed that the latency at which positive and negative target inclinations could be differentiated statistically ($P < 0.05$) by vertical velocity ranged from 144 to 164 ms after the target changed direction for the uncued conditions. The latency was 152 ms when either timing or directional cues were presented

alone which was within the range of the uncued conditions. However, when both directional and timing cues were presented, the latency was -12 ms; thus, the vertical velocity was already changing just prior to the change in target direction. Consequently, in the experiment where direction cues were accompanied by timing cues, pursuit direction started to change even before the target changed direction. Importantly, direction-only cues caused no anticipation.

These effects can also be observed in Fig. 6, which is a plot of average smooth pursuit direction across subjects for experiment 1. When no cues were present, the smooth pursuit direction remained near zero until approximately 100 ms after the target direction change and then gradually changed to match the new target trajectory. However, when both timing and directional cues were present, the smooth pursuit direction began to change at around 50 ms prior to the target direction change. The effects of timing and directional cues were also consistent with the differences observed in the paths of smooth pursuit for each experiment. When both directional and timing cues were present, smooth pursuit changed direction to match the new target trajectory very close to the place where the target changed direction (Fig. 2). Although presentation of the timing cue alone allowed for anticipation of the reversal of horizontal target motion, as reflected in the horizontal eye velocity, there was a delay in the change to the new direction as reflected in the vertical eye velocity component. A directional cue alone did not provide enough information to produce a change in either velocity component and appeared to be insufficient for producing an anticipatory change in smooth pursuit.

The speed of the smooth pursuit eye movements should also have been affected by the presence of timing and/or directional cues. Regardless of condition, the speed of smooth pursuit was close to that of the target at around $19^\circ/\text{s}$ 500 ms prior to the target direction change. Smooth pursuit speed then declined to a minimum at some point after the target direction change and then rose steeply back to the speed of the target. It is clear in Fig. 7, which shows the average smooth pursuit speed relative to the target corner, that the temporal profile of smooth pursuit speed was affected when a timing cue was present with or without a directional cue (a, b) but not when a directional cue was presented alone (c). This anticipation of the target direction provided by the timing cue was reflected as an earlier and larger decrease in smooth pursuit speed compared with a later more gradual change when the timing cue was absent (uncued conditions and direction-only cue). Statistical analysis of the time and magnitude of the minimum smooth pursuit speed confirmed these differences. When a timing cue was present, minimum smooth pursuit speeds were achieved 69–86 ms earlier (35 and 44 vs. 121 and 113 ms, respectively; both $P < 0.001$) and were 23–33% slower (1.48 and 1.23 vs. 1.91 and $1.83^\circ/\text{s}$; $P = 0.05$ and 0.002 , respectively). When only a directional cue was present, the magnitude of the minimum smooth pursuit speed and the time at which the minimum speed occurred did not differ across conditions (1.75 vs. $2.10^\circ/\text{s}$, $P = 0.200$ and 118 and 127 ms, $P = 0.265$, respectively).

If a tracked target abruptly makes a change in direction, a saccade can be utilized to allow the eyes to quickly catch up to the target and then continue tracking with smooth pursuit. These saccades typically occur around 200 ms after the target direction change (Engel et al. 1999; Leigh and Zee 1991). If the saccadic system also makes use of cognitive cues about future target direction to anticipate the change in target direction, one might expect saccades to be generated earlier than the typical 200 ms latency relative to the target direction change. The experimental results did not support this hypothesis. Figure 8 shows the mean ($\pm$ SD) probability of a saccade occurring within each 4 ms time bin across all directions and subjects for the cued and uncued conditions for each experiment. For each experiment, regardless of condition, the probability of a saccade was highest in the interval 236–260 ms after the target changed direction (time = 0). When both direction and timing cues were

given, saccade probability was higher in the uncued condition than in the cued condition in the intervals from 48–128 ms and 204–224 ms after the target direction change ($P < 0.05$; Fig. 8a). This was also true at 44–140 ms when only a timing cue was present ($P < 0.05$; Fig. 8b). In the earlier interval (< 200 ms), the higher probability of saccades in the uncued condition reflects catch-up saccades in the horizontal direction that become more likely because speed gradually declines (Fig. 7). In the later interval (> 200 ms), smaller saccade probability in the cued condition is consistent with better anticipation of target motion via smooth pursuit. No differences were found in saccade probability when only a directional cue was present (Fig. 8c). Therefore, saccades were reactive to (rather than predictive of) the target direction change regardless of the presence of cognitive cues.

Effect of amplitude of target inclinations

Smooth pursuit of the target was not consistently affected by the amplitude of the target inclinations. For the smooth pursuit speed and velocity components, it is clear from the plots that there is little difference in the temporal profiles across the target inclinations within each condition. The statistical analyses confirm this observation. Table 1 summarizes the main effects of amplitude of target inclination from the ANOVA for minimum speed and measures of each velocity component. Positive and negative target inclinations were combined for statistical analysis to give four possible target amplitude changes for comparisons. These results indicate that the amplitude of a change in target direction generally does not affect the components of smooth pursuit investigated here. There were no significant interactions between condition and amplitude for any of the speed or velocity variables (all $P > 0.05$).

Discussion

The focus of this study was the effect of cognitive cues on anticipatory smooth pursuit. We wanted to determine the efficacy of location (timing) and/or directional cognitive cues for anticipatory smooth pursuit eye movements with respect to an abrupt change in the direction of target motion. In our experiments, we used a position cue, but since the target was constantly in view and moving at a constant speed, the *time* of the direction change could be estimated from the time to contact at any instant based upon the speed and distance from the target to the barrier. As the target moves closer to the cue, the estimate of time to contact should become more accurate. This differs somewhat from tracking and predicting target motion through an occlusion where target motion is extrapolated based on velocity and acceleration prior to the occlusion which can result in appreciable errors in time to contact estimates (Zago et al. 2009).

Consistent with previous studies, we found that smooth pursuit speed tended to decrease in anticipation of the target direction change even in the absence of specific cues (Engel and Soechting 2003; Soechting et al. 2005). We found that the decrease in smooth pursuit speed was more dramatic and began earlier when the location (and hence the timing) of the target direction change was known (Fig. 7a, b). Additionally, anticipatory adjustments to smooth pursuit eye movements were observable in the horizontal velocity component when timing cues were present. However, both timing and directional cues were necessary for anticipatory adjustments to be evident in the vertical velocity component, directional cues by themselves being insufficient. When both timing and directional cues were present, a change in the direction of smooth pursuit began around 50 ms prior to the change in target motion (Fig. 6), thus reflecting anticipation of the change in target motion. Our results demonstrated that cuing the future direction of the target motion alone was not enough to provide anticipation (Figs. 3c, 5c).

Although one might expect that cuing the direction alone should provide enough information to expedite the change in smooth pursuit direction, this was not the case. Interestingly, Badler et al. (2010) also found that the predictability of the target motion direction was not enough to reduce the latency of smooth pursuit compared with their control condition when causality was lacking. In their experiment, in the causal condition, the target motion was initiated predictably by the impact of a launcher. When their target movement direction was completely predictable, the latency of smooth pursuit was shorter for causal directions, but tended to be longer than the control trials for non-causal targets. They suggested that more processing time was needed to “counteract the effect of causal interference” (Badler et al. 2010). Thus, the cognitive expectation related to causal motion initiation of the target allowed for the anticipatory use of directional cues. Likewise, for targets that moved along a curved street, Ladda et al. (2007) found predictive changes in the eye velocity component associated with the direction of the curve when the curved path (street cue) was visible. By providing the actual path along which the target would travel, their cue gave both timing and direction information about future target motion, similar to the cued condition in our first experiment.

Kowler and Steinman (1979a, b) demonstrated that knowledge of future target direction resulted in anticipatory eye movements in a one-dimensional task (e.g. motion to the left or the right), but the timing need not be predictable for these movements to occur. Thus, contrary to our study, the future target direction alone was able to elicit anticipatory eye movements. One explanation for this difference is that our task included a larger range of target directions (seven compared with two). However, the previous study did report that the expectation of when the target movement would be initiated influenced the latency and acceleration of the anticipatory eye movements (Kowler and Steinman 1979b). Thus, the timing of the direction change was utilized for the production of anticipatory eye movements when it was available.

The nature of our timing cue may have been a factor in its relative importance for the production of anticipatory smooth pursuit eye movements. Spatial cues such as time-to-impact are essential for prediction in everyday life for both interceptive and evasive actions (for review, see Zago et al. 2009). Previous studies that have included cognitive cues for the timing of direction changes have used auditory or visual cues that warn of the change in target motion after a specified time interval (e.g. Kowler and Steinman 1979a, b; Burke and Barnes 2008). In our study, the timing of the direction change was represented by an impending collision of the cursor with either a red circle (timing cue-only condition) or a bar (timing and directional cue condition; see Fig. 1). Thus, our timing cue was a spatial cue that essentially provided a time-to-contact signal, similar to familiar situations that subjects have previously experienced.

Acknowledgments

This work was supported by a United States Public Health Service Grant NS-15018. We thank Dr. Martha Flanders for helpful comments on this work.

References

- Badler J, Lefevre P, Missal M. Causality attribution biases oculomotor responses. *J Neurosci.* 2010; 30:10517–10525. [PubMed: 20685994]
- Barnes GR, Barnes DM, Chakraborti SR. Ocular pursuit responses to repeated, single-cycle sinusoids reveal behavior compatible with predictive pursuit. *J Neurophysiol.* 2000; 84:2340–2355. [PubMed: 11067977]
- Bennett SJ, Barnes GR. Human ocular pursuit during the transient disappearance of a visual target. *J Neurophysiol.* 2003; 90:2504–2520. [PubMed: 14534275]

- Bennett SJ, Barnes GR. Predictive smooth ocular pursuit during the transient disappearance of a visual target. *J Neurophysiol.* 2004; 92:578–590. [PubMed: 14960562]
- Burke MR, Barnes GR. Anticipatory eye movements evoked after active following versus passive observation of a predictable motion stimulus. *Brain Res.* 2008; 1245:74–81. [PubMed: 18930718]
- Carl JR, Gellman RS. Human smooth pursuit: stimulus-dependent responses. *J Neurophysiol.* 1987; 57:1446–1463. [PubMed: 3585475]
- Collewijn H, Tamminga EP. Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds. *J Physiol.* 1984; 351:217–250. [PubMed: 6747865]
- Engel KC, Soechting JF. Interactions between ocular motor and manual responses during two-dimensional tracking. *Prog Brain Res.* 2003; 142:141–153. [PubMed: 12693259]
- Engel KC, Anderson JH, Soechting JF. Oculomotor tracking in two dimensions. *J Neurophysiol.* 1999; 81:1597–1602. [PubMed: 10200195]
- Jarrett CB, Barnes G. Volitional selection of direction in the generation of anticipatory ocular smooth pursuit in humans. *Neurosci Lett.* 2001; 312:25–28. [PubMed: 11578837]
- Jarrett CB, Barnes G. Volitional scaling of anticipatory ocular pursuit velocity using precues. *Brain Res Cogn Brain Res.* 2002; 14:383–388. [PubMed: 12421661]
- Kao GW, Morrow MJ. The relationship of anticipatory smooth eye movement to smooth pursuit initiation. *Vision Res.* 1994; 34:3027–3036. [PubMed: 7975338]
- Kettner RE, Leung HC, Peterson BW. Predictive smooth pursuit of complex two-dimensional trajectories in monkey: component interactions. *Exp Brain Res.* 1996; 108:221–235. [PubMed: 8815031]
- Kowler E. Cognitive expectations, not habits, control anticipatory smooth oculomotor pursuit. *Vision Res.* 1989; 29:1049–1057. [PubMed: 2617852]
- Kowler E, Steinman RM. The effect of expectations on slow oculomotor control. I. Periodic target steps. *Vision Res.* 1979a; 19:619–632. [PubMed: 547472]
- Kowler E, Steinman RM. The effect of expectations on slow oculomotor control. II. Single target displacements. *Vision Res.* 1979b; 19:633–646. [PubMed: 547473]
- Kowler E, Steinman RM. The effect of expectations on slow oculomotor control-III. Guessing unpredictable target displacements. *Vision Res.* 1981; 21:191–203. [PubMed: 7269296]
- Ladda J, Eggert T, Glasauer S, Straube A. Velocity scaling of cue-induced smooth pursuit acceleration obeys constraints of natural motion. *Exp Brain Res.* 2007; 182:343–356. [PubMed: 17562031]
- Leigh, R.; Zee, D. The neurology of eye movements. F.A. Davis Company; Philadelphia: 1991.
- Mrotek LA, Soechting JF. Predicting curvilinear target motion through an occlusion. *Exp Brain Res.* 2007; 178:99–114. [PubMed: 17053910]
- Robinson DA. The mechanics of human smooth pursuit eye movement. *J Physiol.* 1965; 180:569–591. [PubMed: 5846794]
- Soechting JF, Mrotek LA, Flanders M. Smooth pursuit tracking of an abrupt change in target direction: vector superposition of discrete responses. *Exp Brain Res.* 2005; 160:245–258. [PubMed: 15322786]
- Soechting JF, Rao HM, Juveli JZ. Incorporating prediction in models for two-dimensional smooth pursuit. *PLoS ONE.* 2010; 5(9):e12574. [PubMed: 20838450]
- Westheimer G. Eye movement responses to a horizontally moving visual stimulus. *AMA Arch Ophthalmol.* 1954; 52:932–941. [PubMed: 13217540]
- Zago M, McIntyre J, Senot P, Lacquaniti F. Visuo-motor coordination and internal models for object interception. *Exp Brain Res.* 2009; 192:571–604. [PubMed: 19139857]

Fig. 1. Experimental conditions. Depiction of the control trials used in the experiments (*upper left*) and each of the experimental conditions (*gray box*). *Circular cyan target cursor* initially moved in the direction of the arrow. The *gray area* represents target redirection zone in which the target changed direction. The *solid angled line* is an example of a directional and timing cue for experiment 1. The same was used for a directional cue only in experiment 3, but note that it was past the area where the target changed direction eliminating the timing cue. A *larger red circular cursor* was presented for experiment 2 to indicate where but not how the target changed direction

Fig. 2. Path of smooth pursuit. Each panel presents the average path of smooth pursuit computed across subjects for each inclination for the uncued (*solid lines*) and cued (*dashed lines*) conditions for each experiment. Position is given as degrees of visual angle in the *x* and *y*-directions

Fig. 3. Horizontal velocity component. *Panels a–c* The average horizontal velocity (x -dimension) computed across subjects for each inclination for the control (uncued, *solid lines*) and cued conditions (*dashed lines*) for experiments 1–3, respectively

Fig. 4.

Horizontal velocity trends within the target redirection zone. Regression lines depicting the horizontal velocity relative to the target corner position (*gray area* in Fig. 1) in the *x*-dimension for the uncued (*thin lines*) and cued (*thick lines*) conditions for each experiment across subjects are shown. All slopes are significant at $P < 0.02$ except for experiment 2, cued condition ($P = 0.440$)

Fig. 5. Vertical velocity component. Panels present the average vertical velocity computed across subjects for each inclination of target motion for the control and cued conditions (*solid and dashed lines*, respectively) for each of three experiments with different cues

Fig. 6. Smooth pursuit direction for experiment 1. The mean smooth pursuit direction was computed across subjects for each inclination for the control (*upper panel*) and cued conditions (*lower panel*). The smooth pursuit direction is shown from 200 ms before to 500 ms after the target direction change (*vertical line*, time = 0)

Fig. 7. Smooth pursuit speed. Panels present the average smooth pursuit speed computed across subjects for each inclination for the control and cued conditions (*solid and dashed lines*, respectively) for each of three experiments with different cues

Fig. 8.

Saccade probability. The probability of producing a saccade within 4 ms time bins is shown for each condition and each experiment (**a–c**). The saccade probability for one subject is shown for each experiment in the left column. The saccade probability computed across subjects is shown in the right column; the mean is shown with *solid lines*, while *dashed lines* outline the shaded $\pm$ SD range for each condition. *Vertical gray lines* indicate bins where there was a significant difference across conditions ($P < 0.05$). Mean probability of 0.7 = 42/60 (average # of catch-up saccades within a 4 ms bin/# trials for condition average)

Table 1

ANOVA with Bonferroni post hoc results for target inclination

	Experiment #1 Direction and timing cue	Experiment #2 Timing cue only	Experiment #3 Directional cue only
<i>Minimum eye speed</i>			
Magnitude	60>0 ($P<0.020$)	N.S. ($P = 0.473$)	N.S. ($P = 0.130$)
Time	N.S. ($P = 0.898$)	N.S. ($P = 0.942$)	N.S. ($P = 0.629$)
<i>Velocity</i>			
x-Component			
Rise time	N.S. ($P = 0.192$)	N.S. ($P = 0.503$)	N.S. ($P = 0.418$)
Rise rate	0>30, 45, 60 ($P<0.001$)	0>45, 60 ($P = 0.002$)	0>30, 45, 60; 30>60 ($P<0.001$)
y-Component			
Rise start	N.S. ($P = 0.873$)	N.S. ($P = 0.500$)	N.S. ($P = 0.620$)
Rise time	60>30, 45 ($P>0.001$)	60>30 ($P = 0.016$)	N.S. ($P = 0.052$)
Rise rate	N.S. ($P = 0.658$)	N.S. ($P = 0.125$)	N.S. ($P = 0.113$)