

Timing and velocity randomization similarly affect anticipatory pursuit

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Smooth pursuit eye movements are guided largely by retinal-image motion. To compensate for neural conduction delays, the brain employs a predictive mechanism to generate anticipatory pursuit that precedes target motion (E. Kowler, 1990). A critical question for interpreting neural signals recorded during pursuit concerns how this mechanism is interfaced with sensorimotor processing. It has been shown that the predictor is not simply turned-off during randomization because anticipatory eye velocity remains when target velocity is randomized (E. Kowler & S. McKee, 1987; G. W. Kao & M. J. Morrow, 1994). This study was completed to compare pursuit behavior during randomized motion-onset timing with that occurring during direction or speed randomization. We found that anticipatory eye velocity persisted despite motion-onset randomization, and that anticipation onset time was between that observed in the different constant-timing conditions. This centering strategy was similar to the bias of eye velocity magnitude away from extremes observed when direction or speed was randomized. Such a strategy is comparable to least-squares error minimization, and could be used to facilitate acquisition of a target when it begins to move. Centering was in some observers accounted for by a shift of eye velocity toward that generated in the preceding trial. The results make unlikely a model in which the predictor is disengaged by randomizing stimulus timing, and suggest that predictive signals always interact with those used in sensorimotor processing during smooth pursuit.

Keywords: smooth pursuit, visual motion, prediction, anticipation, timing, human

Introduction

Smooth pursuit is used to follow moving objects. While normally guided by image motion on the retina, a predictive mechanism also modulates pursuit when object motion is repetitive. Factors that affect prediction of continuous motion by the pursuit system have been studied extensively (Dodge, Travis, & Fox, 1930; Westheimer, 1954; Stark, Vossius, & Young, 1962; Dallos & Jones, 1963; Bahill & McDonald, 1983; Barnes & Hill, 1984). However, in most contemporary work, targets move in multiple, discrete trials. The pursuit initiation (open-loop) response in discrete trials has been analyzed to determine visual motion inputs for pursuit (Keller & Khan, 1986; Lisberger, Morris, & Tychsen, 1987; Heinen & Watanianuk, 1998). This approach assumes that pursuit is a closed-loop control system, and that pursuit dynamics and the related neural signals during this time reflect image motion when the eyes are stationary (Robinson, Gordon, & Gordon, 1986; Krauzlis & Lisberger, 1989). When target motion is predictable, additional signals are used by the pursuit system because anticipatory eye movements and changes in the magnitude of eye velocity occur during the open-loop period (Kao & Morrow, 1994).

An important question for interpreting neural activity during smooth pursuit concerns how the predictor interfaces with sensorimotor structures. A simple scheme is that the neural substrate for the predictor is independent from the sensorimotor substrate, and the two are connected by a switch that disables the predictor when motion is unpredictable (Dallos & Jones, 1963). Under the assumption that the predictor can be turned off, target direction, speed, and the timing of motion onset are usually randomized in the laboratory. However, randomizing direction or speed does not necessarily abolish anticipatory eye velocity at either low target speeds (Kowler & Steinman, 1979b; Kowler & McKee, 1987) or at higher ones comparable to those used to study pursuit physiology (Kao & Morrow, 1994). Furthermore, randomization changes eye velocity during the open-loop period in a similar fashion as it does anticipatory pursuit (Kowler & McKee, 1987; Kao & Morrow, 1994). These results imply that a predictive signal may always supplement the visual signal at pursuit initiation.

One way to disengage the predictor might be to randomize stimulus timing. While anticipatory eye movements can occur before saccades to static targets presented at unpredictable times (Kowler & Steinman, 1979b), it is known that timing information is used by the pursuit system to predict continuous periodic motion (Barnes & Asselman,

1992) and to generate anticipatory eye velocity during discrete target motions as well (Barnes & Asselman, 1991, 1992). A prominent model of prediction uses a periodicity estimator that learns the timing of repetitive target motion, and releases a velocity pulse stored by the pursuit system based on previous trials (Barnes & Asselman, 1991). Although there is evidence that a cue can be used to release the velocity (Barnes & Donelan, 1999), periodic motion is necessary for this model to predict timing and generate anticipatory pursuit, and could also be necessary for the pursuit system to anticipate in the absence of a cue. There is also physiological evidence supporting a timing mechanism in predictive pursuit. Some neurons in the supplementary eye field, a structure involved in smooth pursuit control (Heinen, 1995; Petit, Clark, Ingeholm, & Haxby, 1997; Berman et al., 1999; Petit & Haxby, 1999; O'Driscoll et al., 2000) are most active at times preceding predictable stimulus motion when timing is the only cue available to modulate their response (Heinen & Liu, 1997).

This study was completed to determine how randomized-target motion-onset timing affects smooth pursuit, and to compare the strategy used by the pursuit system in this condition with that used during randomization of target direction or speed. Randomizing motion onset did not eliminate anticipatory eye velocity, and biased the timing of both anticipatory pursuit onset and the start of the open-loop period to less extreme values than those observed for constant motion-onset times. This behavior was at least partially accounted for by a bias in pursuit timing toward that appropriate for the target in the previous trial. The behavior of the pursuit system when direction or speed was randomized followed similar rules as onset timing did during randomization.

Methods

General

Four subjects participated in the experiments. Two (SH and WT) were experienced in smooth pursuit experiments and two (AB and ML) were naive. All had visual acuity that was corrected to normal by optics, and all had normal ocular motility. Eye position was recorded monocularly with a Generation-V Purkinje eyetracker while the other eye was patched. Eye velocity was obtained by analog differentiation of eye position, and both signals were sampled at 500 Hz and saved to disk for off-line analysis. Eye acceleration was computed by digital differentiation. Subjects' heads were stabilized with a bite bar. Overall system noise was determined to be less than 1 arcmin while recording from an artificial eye. The target was a 0.2-deg spot presented on a dimly lit background and generated by an HP vector scope (Model 1345a). Before each session, eye position was calibrated to the output of the eyetracker by having the observer fixate the target at the center and at each of four ec-

centric positions while the experimenter adjusted offsets and gains. All participants gave informed consent, and ethical permission for the procedures was obtained through the California Pacific Medical Center Institutional Review Board.

Paradigms

The basic task, to fixate a spot target and pursue it when it moved, had three variations. When fixation duration was manipulated, after a period of either 500 ms or 1000 ms, the target moved rightward at 20 deg/s. When target direction was manipulated, the target moved either leftward or rightward at 20 deg/s. When target speed was manipulated, the target moved rightward at 5, 10, or 20 deg/s. In both the direction and speed experiments, fixation duration was 1000 ms. To achieve a greater target excursion for the duration and speed experiments, the fixation position was offset 7 deg left, and the target moved in the opposite direction for 15 deg. For the direction experiments, target motion began in the center on every trial, so subjects could not use initial target position to cue them about the direction of upcoming motion, and the target moved only 10 deg. In all experiments, trial parameters were randomized so that the probability of a given condition occurring was the same for every trial, and each condition occurred a minimum of 25 times within a trial block. In addition, separate control blocks were run in which all parameters were held constant.

Eye movement analysis

Saccades were removed from the eye velocity traces using an algorithm that detected saccade onset by determining when eye acceleration first exceeded and then fell below a threshold (2000 deg/s²). The end of the saccade was determined by finding when the absolute value of eye deceleration exceeded and fell below the threshold again. The saccade epoch was excised from the velocity record and replaced with a line connecting the point preceding the saccade to the point following it in a fashion similar to algorithms used in the past (e.g., Keller & Khan, 1986; Krauzlis & Lisberger, 1994; Watamaniuk & Heinen, 1999). After the saccades were removed, eye velocity signals were filtered digitally using a non-causal Butterworth filter (2 pole, cutoff = 50 Hz). MATLAB software (The MathWorks Inc.) was used for data analysis.

To obtain eye velocity during the open-loop period, it was necessary to know when the visually guided eye movement began. This point is easy to detect by visual inspection because there is a sharp deflection when the eye begins to accelerate rapidly as a result of the visual signal. This is a method we have used before to detect the onset of visually guided pursuit in the presence of anticipatory eye velocity (Heinen & Watamaniuk, 1998; Watamaniuk & Heinen, 1999), and we used it here for the direction and speed ex-

periments. However, it proved more difficult to assess the onset of anticipatory pursuit by visual inspection because eye acceleration is small at that time. Because anticipatory velocity records have a stereotypical shape, rising at a fairly constant rate between baseline and the sharp acceleration of visual pursuit onset (see Figure 4), we were able to use a linear regression method to detect anticipatory pursuit onset, as has been done in previous work (Kao & Morrow, 1994). In our routine, the operator selects two points on the velocity record that define the approximately linear region of the anticipatory movement. The program then plots a regression line through the record and marks anticipatory pursuit onset as the time that the line intersects zero. For the time experiments, the latency of “visually guided” pursuit also was determined using the regression method to compare directly the results with anticipation onset. This method and visual inspection produce virtually identical results in our laboratory.

The magnitude of anticipatory pursuit was determined by averaging eye velocity over the 20-ms interval centered at target motion onset. The initial velocity of visually guided pursuit was measured during the open-loop period. This interval has been studied in the past to assess visual-motion inputs to the pursuit system under the assumption that the response measured here is due to retinal-image slip before eye movement onset (e.g., Lisberger & Westbrook, 1985; Keller & Kahn, 1986; Tychsen & Lisberger, 1986; Heinen & Watamaniuk, 1998). In the current experiment, average eye velocity was computed over the interval 40-140 ms after the eyes began to move in response to the visual target because the second epoch of the open-loop period is more sensitive to target velocity than the first (Lisberger & Westbrook, 1985; Tychsen & Lisberger, 1986).

For the randomized-direction experiments, we characterized open-loop and anticipatory eye velocity using the

absolute value of the 20-ms time average for each trial. This was necessary because anticipatory velocity occurred to both the left and right, which together would average close to zero (see Figure 4). To distinguish anticipatory velocity from trial-to-trial noise, eye velocity was also measured midway during the fixation period (20-ms average centered at 500 ms) as a control.

Results

In each experiment, we compared smooth pursuit eye movements recorded when all parameters were held constant with those obtained when a single parameter (fixation duration, direction, or speed) was randomized.

Fixation-duration randomization

In the primary experiment, target motion-onset timing was manipulated. Fixation duration was either held constant or randomized while target speed and direction were held constant (20 deg/s rightward). Short (500 ms) and long (1000 ms) fixation durations were used. Figure 1 shows average eye velocity traces recorded during this experiment for subject WT. When fixation duration was short, anticipatory eye velocity began earlier in the constant than in the random condition (Figure 1A). The earlier onset time likely contributed to a greater anticipatory eye velocity that was observed for the constant condition with short fixation durations. When fixation duration was long, anticipatory eye velocity began earlier in the random condition (Figure 1B). Higher anticipatory eye velocity now accompanied the random trials, likely because the eye movement began earlier.

Anticipatory pursuit onset times are summarized for all observers in Figure 2A. When fixation duration was constant at 500 ms, anticipatory pursuit began 463 ms after the

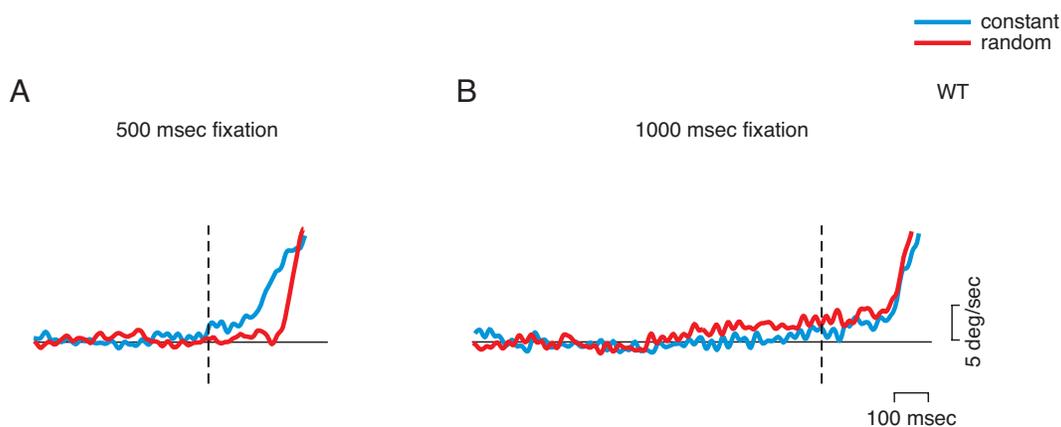


Figure 1. Mean eye velocity traces from the timing experiment for observer WT. Target direction was rightward; target speed was 20 deg/s. A. 500-ms fixation-duration trials. The blue trace is an average of trials from a constant-duration block and the red trace is from a randomized-duration block. Dashed vertical lines indicate when the target began to move. B. 1000-ms fixation duration. Details as in A. Note that for the 500-ms fixation trials, randomization reduced eye velocity and delayed movement onset and for the 1000-ms fixation trials increased eye velocity and shortened movement onset time. Note also that for the 500-ms fixation trials, the rapid acceleration characteristic of visual pursuit initiation was delayed by randomization.

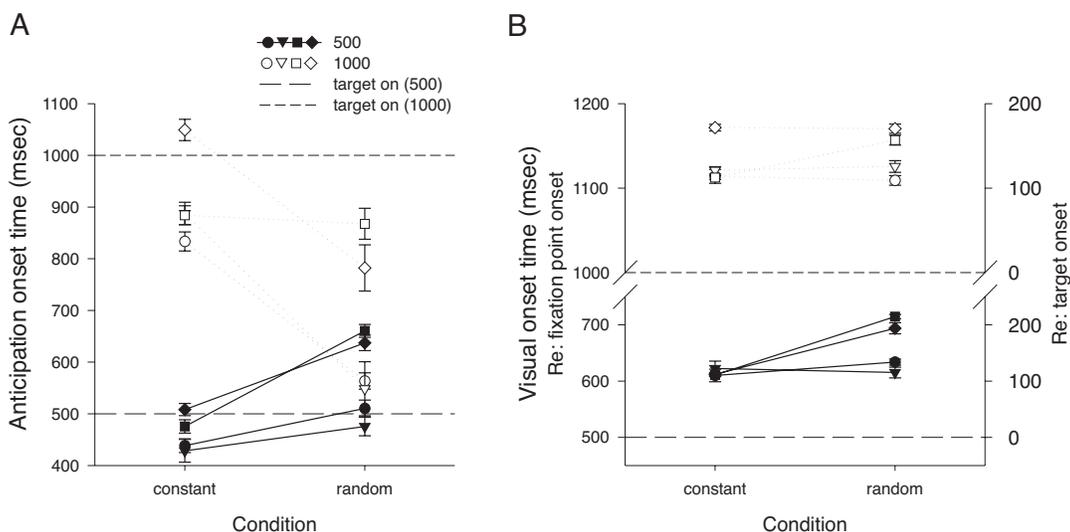


Figure 2. Summary of the timing results. A. Anticipatory pursuit onset. For 500-ms fixation trials (filled symbols), randomization delayed movement onset, and for 1000-ms fixation trials (open symbols), movement onset was shortened. For clarity, the ordinate with respect to target onset is not shown. B. Visual pursuit onset. Randomization produced a delay in movement onset for the 500-ms trials, but did not change it for the 1000-ms trials. Latencies less than 80 ms were considered anticipatory and excluded from the dataset. Subject legend: ●○ AB, ▼▽ ML, ■□ SH, and ◆◇ WT.

fixation point appeared (average of subjects). For the 1000-ms duration fixation period, pursuit began at 914 ms. Relative to the constant conditions, when fixation duration was randomized, pursuit occurred later in trials with a 500-ms fixation period (571 ms). This difference was found to be significant based on a two-way ANOVA (factor 1 = subject, factor 2 = condition; effect of condition $p < .001$). In many trials the anticipatory response disappeared altogether, so the onset time was that of the visually guided movement. Pursuit began earlier for 1000-ms fixation trials (690 ms) ($p < .001$). We also measured the onset time of the rapid acceleration typical of open-loop pursuit initiation (Tychsen & Lisberger, 1986) (Figure 2B). Again, the data are plotted relative to the onset of the fixation interval, but now the axes with respect to target motion onset are also shown. For short fixation durations, randomization delayed open-loop onset ($p < .001$), in some cases yielding latencies longer than those normally observed for humans (100-130 ms) (Tychsen & Lisberger, 1986). Open-loop pursuit latency was on average 114 ms relative to target motion onset for the constant-fixation interval and 164 ms for the randomized interval in this condition. For long fixation durations, there was no consistent effect across subjects, with average latencies of 130 and 140 ms for constant- and randomized-trial blocks, respectively.

Trial history

Previous work demonstrated that the direction of target displacements in preceding trials can bias the direction of anticipatory eye movements (Kowler, Martins, & Pavel, 1984). Our data provide evidence that pursuit onset time is biased in a similar fashion toward that appropriate for the

fixation duration in the previous trial (Figure 3). Here, data from blocks where fixation duration was randomized are displayed in a “tree” fashion similar to that used in the target displacement study (Kowler et al., 1984). Figure 3 shows a tree diagram of anticipatory pursuit onset as a function of preceding trials for one observer (SH). Displayed as separate trees are pursuit onset times for long (top) and short (bottom) duration trials. Note that on average, the eyes began to move earlier in trials that were preceded by a short fixation period, and later in trials that were preceded by a long one. Furthermore, two preceding short trials or two preceding long trials biased the response even more. To determine the significance of the tree data, we tested whether the fixation duration of the immediately preceding trial affected eye velocity for each observer using two-way ANOVA (factor 1 = duration in current trial, factor 2 = duration in previous trial; test effect of factor 2). The history effect was significant for three out of four observers (Table 1).

The magnitude of anticipatory and open-loop eye velocity was also affected by randomization. For short fixation durations, less anticipatory eye velocity was seen for random fixation durations than for constant ones (ANOVA, factor 1 = subject, factor 2 = condition; effect of condition, $p < .001$), and for long fixation durations, randomization produced more ($p < .05$). Randomization decreased open-loop eye velocity for short durations ($p < .001$) and increased it for long ones ($p < .05$). Two observers showed a significant effect of preceding fixation duration on the magnitude of anticipatory and open-loop eye velocity (Table 1).

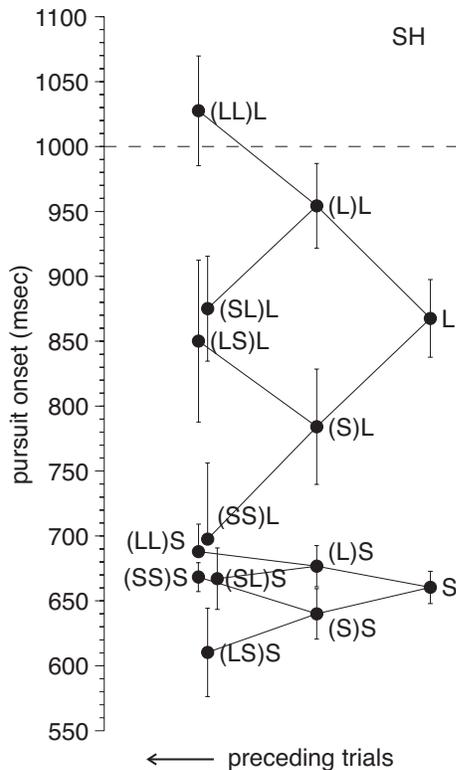


Figure 3. The effect of previous trials when fixation duration was randomized. Mean pursuit onset times for one observer (SH) as a function of fixation interval in preceding trials, in tree graph format. The parent nodes (right) represent mean pursuit onset in all trials that had a 500-ms fixation period (short period: S) or all trials that had a 1000-ms fixation period (long period: L). The next nodes (center) show onset time grouped by fixation duration in the first preceding trial. Labels show the duration of the preceding trial in parentheses, followed by the duration for the current trial represented by that node. To the left, pursuit onset is further grouped by fixation duration in the two preceding trials. For example, the node labeled (LS)S shows mean pursuit onset for all trials that had a 500-ms fixation interval, preceded by another 500-ms trial, preceded by a 1000-ms trial. Error bars represent standard error of the mean. Some data points are offset horizontally for clarity. Note that in most cases a longer fixation period in the previous trial biased pursuit onset toward a later time, and a shorter fixation period in the previous trial biased it earlier. The dashed line shows the end of the fixation interval (target onset) for 1000-ms trials.

We found that anticipatory eye velocity was not abolished when motion timing was randomized, and that the onset of pursuit was biased toward a time between when it would normally begin for the short and long fixation durations. Given this, we wished to know if the pursuit system behaved in a similar fashion when target direction or speed was randomized. Anticipatory eye velocity has been shown to persist following randomization of target direction (Kowler & Steinman, 1979b). However, this result was ob-

		Subject			
		AB	ML	SH	WT
Time (onset)		<0.01*	0.01*	<0.01*	0.26
Time (velocity)	ant	<0.01*	0.57	<0.01*	0.13
	ol	<0.01*	0.20	0.02*	0.14
Direction	ant	<0.01*	0.98	0.23	0.08
	ol	0.42	0.76	0.38	<0.01*
Speed	ant	0.06	<0.01*	0.27	0.16
	ol	<0.01*	<0.01*	0.29	0.51

Table 1. Effect of previous trial conditions on pursuit. A two-way ANOVA was used to test whether the condition of the immediately preceding trial (fixation duration, target direction, or target speed) affected the current trial for the trials in the randomized blocks. Lower *p* values correspond to a more pronounced effect. Asterisks indicate significance at the 0.05 level. ant = anticipatory, ol = open-loop.

tained for saccades made to randomized target steps, not moving stimuli that are generally used to study the pursuit system. Target speed has previously been randomized using motion stimuli. However, in one study (Kowler & McKee, 1987), the speeds used were very small (0.5-4.7 deg/s), limiting the ability to generalize the effect to contemporary studies of pursuit that use much higher speeds and to our fixation duration results. In the other study (Kao & Morrow, 1994), higher speeds were used, but speed and direction were randomized within the same block of trials. For these reasons, we felt it necessary to perform separate direction and speed randomization experiments to compare pursuit behavior under these conditions to the results we obtained when fixation duration was randomized.

Direction randomization

In this experiment, we randomized target direction. Holding all parameters constant (speed = 20 deg/s; direction = rightward; fixation duration = 1000 ms) produced anticipatory eye velocity (Figure 4A). When target direction was randomized, anticipatory eye velocity remained, but was considerably reduced (Figure 4B). In addition, the mean velocity variance of the randomized trials exceeded the mean variance during fixation 50-100 ms before target onset in this subject (Figure 4C). Note that during open-loop pursuit, eye velocity was greater when target direction was held constant. This is surprising given that pursuit during the open-loop period is theorized to be due solely to retinal slip before the target moves. If true, eye velocity during the open-loop period should be lower when anticipa-

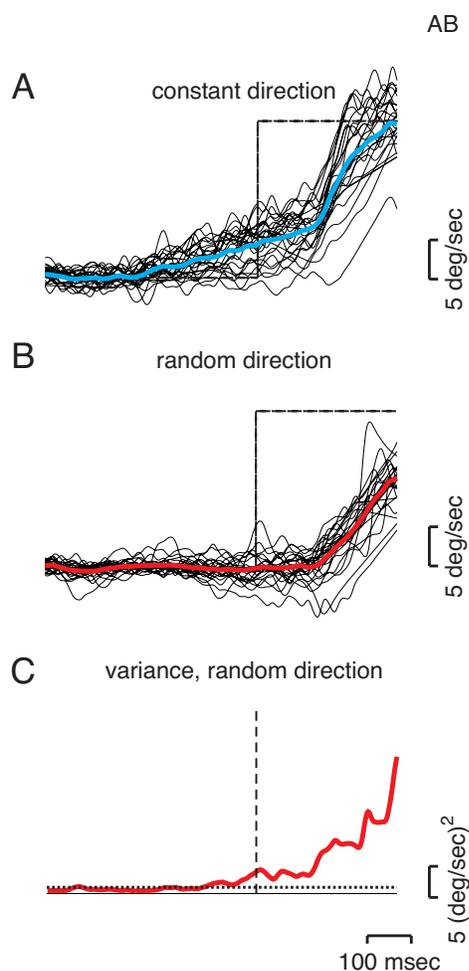


Figure 4. Anticipatory eye velocity traces from the direction experiment for naive subject AB. Traces are shown for both the constant-(A) and the random-direction condition (B); for clarity, not all trials are shown. The target moved rightward at 20 deg/s. Thin lines are individual eye velocity traces, the thick line is mean eye velocity, and the dashed line is target velocity. Note that higher anticipatory eye velocity occurred when target direction was constant than when it was random, and that open-loop eye velocity in the constant condition was also higher. Note also that in several trials in the random condition, the observer anticipated incorrectly that the target would move leftward, contributing to the overall lower rightward eye velocity observed. C. Variance of the random-direction trials plotted in B. The dotted horizontal line is the mean variance measured 250-650 ms into the fixation interval.

tory eye velocity in the direction of target motion is present, because appropriate anticipatory eye velocity would reduce the amount of slip in that direction.

The magnitude of anticipatory and open-loop eye velocity in the random and constant conditions for all subjects is summarized in Figure 5. Overall, randomizing the direction in which the target moved reduced anticipatory pursuit. This was confirmed using ANOVA (factor 1 = sub-

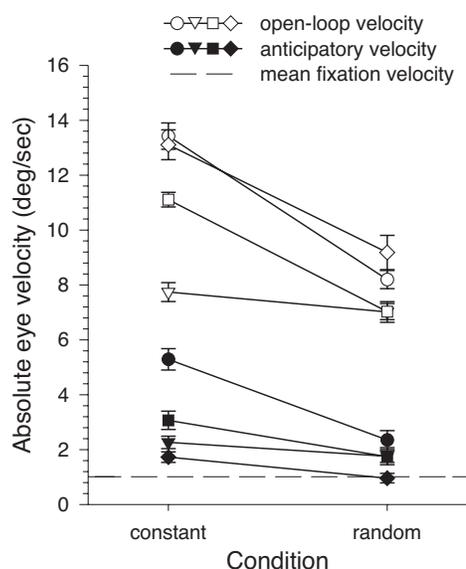


Figure 5. Summary of results from the direction experiment. Filled symbols show the absolute value of anticipatory eye velocity for 20 deg/s rightward target motion in the constant and random conditions. Eye velocity was measured in a 20-ms bin centered at the time the target began to move. Open symbols show eye velocity late in the open-loop period (averaged 40-140 ms after pursuit onset) in constant and random conditions from the same blocks of trials. The dashed line shows the absolute value of eye velocity measured in the middle of the fixation period in the random condition. Note that randomizing target direction reduced anticipatory eye velocity but did not eliminate it and decreased eye velocity during open-loop pursuit. Error bars are standard error of the mean. Subject legend: ●○ AB, ▼▽ ML, ■□ SH, ◆◇ WT.

ject, factor 2 = condition), which yielded a significant effect of condition ($p < .001$). When considered individually, three out of four subjects were significant (Bonferroni t test, $p < .0125$ for all except ML). However, anticipatory pursuit was not eliminated by randomization. When the magnitudes of eye velocity in the random conditions were compared to those measured during fixation, the effect of condition was still significant (ANOVA, $p < .001$). This also held for three out of four subjects (Bonferroni t test, $p < .0125$ for all except WT). Randomization also reduced open-loop velocity overall (ANOVA, $p < .001$). This is consistent with the results of direction randomization reported in the past (Kowler & Steinman, 1979b; Kao & Morrow, 1994).

Saccades commonly occur during pursuit initiation. By convention, saccades were excised from the eye velocity records, and the records were interpolated over the duration of the removed saccade. A potential problem arises from using this method because pursuit eye velocity following saccades can be enhanced (Lisberger, 1998). Specifically, if randomization systematically moved more saccades into or out of the open-loop period, eye velocity could be

increased or decreased, respectively, independently of a direct effect of randomization on pursuit eye velocity. When we compared the latencies of the first saccade after target motion onset in the constant and random conditions, no effect of stimulus randomization was found (ANOVA, effect of condition, $p = .87$).

Speed randomization

In this experiment, observers pursued one of three target speeds (5, 10, and 20 deg/s) that were either randomized or held constant in a block. In all trials, the target moved rightward and fixation duration was 1000 ms.

The first aspect of the data examined was how well eye velocity segregated for the different target speeds. When speed was held constant, greater anticipatory eye velocity occurred with high target speeds than with low ones. Again, this was confirmed using two-way ANOVA (factor 1 = subject, factor 2 = speed; test effect of speed, $p < .001$). As expected, this difference was eliminated by randomization (effect of speed, $p = .56$), but anticipatory velocity was still greater than zero (factor 2 = velocity in random block vs. velocity during fixation; effect of condition, $p < .001$) (Figure 6A). During open-loop pursuit (Figure 6B), eye velocities for different target speeds were significantly different for both the constant- and randomized-target conditions (effect of speed, $p < .001$ for both). Randomization did not eliminate this difference because in the later portion of the open-loop period, target speed information is available to the pursuit system (Tychsen & Lisberger, 1986). Note, however, that eye velocity more closely matched target velocity when target velocity was predictable.

Note that in Figures 6A and 6B, eye velocity tended to converge toward an intermediate value when target speed was randomized. To quantify this we compared the low- and high-speed data for the constant and random conditions. That is, we grouped the data according to speed and performed the ANOVA with factor 1 = subject and factor 2 = condition. If a bias toward intermediate eye velocity was occurring, eye velocity for fast targets should be higher in the constant than in the random condition, and conversely, lower for slow targets. This was true for both the anticipatory and open-loop periods (effect of condition, $p < .001$ for all). These results are consistent with studies of target speed randomization in the past (Kowler & McKee, 1987; Kao & Morrow, 1994).

Pursuit direction and speed were for some observers influenced by the conditions in previous trials, as was the case in the fixation-duration experiments. As before, a two-way ANOVA was used (factor 1 = direction or speed of current trial, factor 2 = direction or speed of previous trial; test effect of previous trial on pursuit velocity). Subjects AB and WT showed a significant direction bias and subjects AB and ML a significant speed bias (Table 1).

Discussion

In summary, randomizing fixation duration produced anticipatory pursuit onset times that were later for short durations and earlier for long ones, and open-loop latencies in some subjects followed the same trend. Randomization also produced lower anticipatory eye velocity for short durations and higher for long relative to the constant condi-

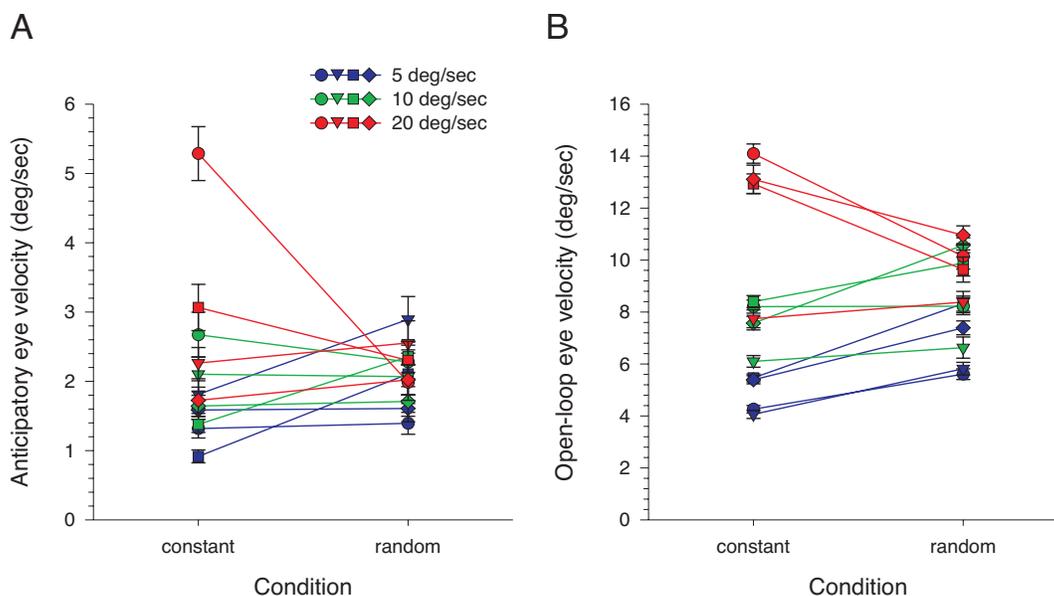


Figure 6. Summary of speed randomization results. A. Anticipatory pursuit when target speed was either held constant at 5, 10, or 20 deg/s or randomized. B. Open-loop eye velocity from constant- and random-speed conditions from the same experiment. Note that randomization causes both anticipatory and open-loop eye velocity to move away from the extreme values observed in the constant-speed trials. Subject legend: \circ AB, ∇ ML, \square SH, \diamond WT.

tion. Randomizing target direction reduced anticipatory pursuit and also reduced the magnitude of open-loop pursuit. Randomizing target speed reduced anticipatory and open-loop eye velocity for high target speeds, but increased it for low ones. The net overall effect of randomization was to modify pursuit amplitude or onset timing toward less extreme values than those observed when parameters were held constant.

Stimulus parameters are randomized in the laboratory in an attempt to eliminate prediction and enable the study of sensorimotor processing. Conversely, to activate predictive regions in the brain, target motion is rendered predictable by holding stimulus parameters constant (Heinen & Liu, 1997; Schmid, Rees, Frith, & Barnes, 2001). Much work has been done to determine sensorimotor processing underlying nonpredictable or “reflexive” smooth pursuit eye movement generation (Wurtz, Komatsu, Yamasaki, & Dursteler, 1990; Keller & Heinen, 1991). However, the pursuit system predicts target motion to reduce delays inherent in the sensorimotor stream (Kowler, 1990). Predictive signals must somehow interface with those used to generate the pursuit reflex. There are several simple models of how predictive and visuomotor processing could be interfaced. One is that separate neural substrates underlie both processes, and when target motion is unpredictable, the predictor is “switched off” and its effect on pursuit eliminated (Dallos & Jones, 1963). Various other properties of the visual stimulus are thought to similarly disengage the predictor (reviewed in Kowler & Steinman, 1979a; Kowler, 1990). The other is that anticipation is modulated by a gain control mechanism, and the more predictable the target motion, the higher the gain.

Under the switching hypothesis, the pursuit system would rely on visuomotor processing to follow an object and no anticipation would occur. However, anticipatory pursuit perseveres when either target direction (Kowler & Steinman, 1979b) or speed (Kowler & McKee, 1987) is randomized at low target speeds (0.4 - 5.3 deg/s) and at higher ones (Kao & Morrow, 1994). Therefore, because anticipatory pursuit occurs during randomization, the predictor is not just switched off. There is also evidence against the gain theory. When target speed is randomized, anticipatory and open-loop eye velocity during pursuit of the lower target speeds can be higher than when those low target speeds are held constant in a block of trials (Kao & Morrow, 1994).

Our results with randomizing stimulus timing provide additional evidence that neither a switch nor a gain control mechanism operates solely during randomization. It has been known for some time that stimulus timing is used by the pursuit system to predict target motion. This was first suggested by work demonstrating that observers predict stimuli moving with a sinusoidal velocity profile (Dodge et al., 1930; Westheimer, 1954; Stark et al., 1962; Dallos & Jones, 1963; Bahill & McDonald, 1983; Barnes & Hill, 1984). However, timing cues are not necessary to predict

sinusoidal stimuli because there is a gradual decrease in speed that precedes target reversal, which could be sensed by the pursuit system and used instead of timing (Deno, Crandall, Sherman, & Keller, 1995). A convincing experiment demonstrated that the pursuit system uses stimulus timing because predictive pursuit still occurs when targets change direction instantaneously (Barnes & Asselman, 1991). Because timing cues are used to predict changes in target direction, prediction might not occur without them. We found that this was not the case, as making motion-onset timing unpredictable did not eliminate anticipatory eye velocity. In our study, randomization produced higher anticipatory and open-loop eye velocity for long fixation durations than when timing was predictable.

Previous investigators demonstrated that anticipatory eye movements occur before saccades to static targets that are presented at unpredictable times (Kowler & Steinman, 1979b). Our results show that anticipatory eye velocity is generated by the smooth pursuit system before stimuli with unpredictable movement onset timing and reveal the strategy that governs this behavior. The pattern of eye movements resulting from randomization was the same for all observers: When fixation duration was short, the eyes began to move at a later time than in the constant condition; when fixation duration was long, anticipatory pursuit began earlier. This centering strategy was also observed when either direction or speed was randomized. For direction, centering was manifest as lower eye velocity relative to when target direction was predictable (i.e., the “center” of two motions of equal magnitude and opposite direction is zero). For speed, higher eye velocity was seen for lower speeds and lower velocity for higher speeds relative to the speed-constant condition, again evidence for centering.

One factor that contributed to the centering phenomenon was the tendency for observers to bias their response toward that appropriate for target motion on the preceding trial. Specifically, in the time experiments, eye movement onset of some observers was biased toward the fixation duration of the previous trial. The influence of prior trials was also apparent in both the direction and speed experiments, but to a much lesser extent. This “history effect” has been documented before for anticipatory pursuit in response to target steps (Kowler et al., 1984), for saccades (Dorris, Pare, & Munoz, 2000), and for canceling pursuit and saccades (Kornlyo, Dill, Saenz, & Krauzlis, 2004), and has been modeled as a two-state Markov process (Kowler et al., 1984). For direction and speed, the history effect might be due to sensory priming or motor learning as a result of a low-level memory in either the motor or sensory system.

Sensory priming could result from sensitization of neurons in the direct visuomotor pursuit pathway, possibly in the middle temporal and medial superior temporal (MT/MST) complex, which has been shown to be involved in remembering recently viewed motions (Bisley & Pasternak, 2000). During successive pursuit trials, the population

response could be biased toward the vector specified by the sensitized neurons, and as a result bias the pursuit response. An analogous priming in the visual system occurs following repeated presentations of static targets in search tasks (Maljkovic & Nakayama, 1994), which can bias saccades (McPeck, Maljkovic, & Nakayama, 1999). For motor learning, an analogous sensitization of neurons might be expected in a structure in the motor limb of the pursuit pathway, possibly in the vermis of the cerebellum, which is thought to be involved in smooth pursuit adaptation (Takagi, Zee, & Tamargo, 2000).

There is also physiological evidence that suggests how the history effect for timing occurs. The activity of a population of neurons in the supplementary eye field builds up during the fixation period with peak activity that occurs around the time that a target moves (Heinen & Liu, 1997). In this study, fixation duration was changed, and the peak activity of the neurons shifted in time in the appropriate direction to signal a new target onset time. The pursuit system could read the time at which the buildup activity crosses a threshold and use it to generate anticipatory pursuit at an appropriate time. The history effect would occur if the peak activity shifted slightly toward the time of target motion on a given trial, and on the subsequent trial, the threshold was reached at the time of the biased peak activity. For time, as well as direction and speed, the history effect might contribute to the centering phenomenon by gradually shifting eye movements to the center of the extreme values observed in constant conditions.

Alternatively, or as a contributing factor, cognitive expectations might cause centering. The pursuit system could deduce the set of parameters of a given experiment and choose a response in the center of that which it generates in the constant condition for each parameter value. It has been shown that cognitive expectations can bias pursuit when observers are cued about the direction of upcoming target motion (Kowler, 1989; Krauzlis & Adler, 2001). In a study more similar to the current one, eye velocity during pursuit of a test target in a block of higher speed targets was higher if that target was the slowest, compared to when the same target was the fastest in a block of lower speed targets (Kowler & McKee, 1987). The authors reasoned that observers biased their response to the target based on a cognitive expectation about the speed it would move when they had deduced whether the block was composed of high or low speeds. While a reasonable explanation, this result could alternatively be due to target history, which would bias pursuit of the test target toward the target speeds in each block. The results of our study do not distinguish between these alternatives, although there was one exception: In the direction experiment, open-loop eye velocity for subject WT showed a reversed history effect (i.e., preceding target motion in one direction biased eye velocity in the opposite direction, as if that subject was expecting the target to move in the opposite direction on the next trial).

Whether accomplished by low-level learning or cognitive factors, we think that centering may have adaptive value for the oculomotor system. Centering is reminiscent of a least-squares optimization in the sense that it minimizes the error between the extremes at target motion onset. This error minimization might be done because when only a range of possible object velocities is known, a bias toward any particular extreme might leave the oculomotor system too far away from the object if it moved at a velocity near the other extreme. A centering strategy would prevent this from occurring.

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