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## Ocular pursuit of predicted motion trajectories

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**Abstract** The initiation and maintenance of slow eye movements (SEMs) usually depend on the perception of a moving stimulus. However, the endogenous representation of predictable target motion can be sufficient to initiate and maintain brief episodes of SEM even when the stimulus is not present. In this note, we show that expectancies generated by predictable stimulus motion trajectories can also produce smooth deceleration, reversal of direction, and subsequent acceleration in these movements, and explore the limits of the predictive component of the SEM control system quantitatively.

**Keywords** Oculomotor · Eye movements · Predictive control · Tracking · Smooth pursuit

### Ocular pursuit of predicted motion trajectories

Unlike saccades or smooth manual tracking movements, slow eye movements (SEM)<sup>1</sup> normally require the perception of a moving stimulus. This stimulus dependence is central to many models of the SEM system which propose that the system is driven by a retinal error signal that is minimized via negative feedback (e.g., Young and Stark 1963; Young 1971; Bahill and McDonald 1983; Robinson et al. 1986). However, this error signal is only one of several information sources available to the SEM system that can be used to generate an estimate of target position and velocity. There have been accounts of

<sup>1</sup> We tend to agree with Leonard Matin (Matin 1986), who contends that the terms “pursuit” and “tracking” eye movements are sometimes misleading with respect to what is actually being studied. We adopted his usage of “slow eye movements,” which in our study encompasses smooth eye movements made to pursue a visible stimulus, as well as those following a predicted stimulus motion trajectory.

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kinesthetic inputs driving SEM (e.g., Steinbach 1976; Mather and Lackner 1981), suggesting that retinal error signal is not a necessary condition of SEM. There is also evidence that purely endogenous influences can initiate SEM. For example, smooth pursuit of linear target motion continues briefly if the target disappears, albeit with an exponential decay in velocity (Becker and Fuchs 1985). In addition, Kowler and colleagues have shown that SEM can be initiated by the expectancy that a visible, stationary target is *about* to move (Kowler 1989; Kowler et al. 1984; Kowler and Steinman 1979a, 1979b). This is interesting partly because the initiation of SEM is presumably more difficult than the maintenance of an ongoing movement. It is also noteworthy since the initiation of slow pursuit while fixating a stationary target produces the very kind of error signal that the slow pursuit control system is normally working to minimize.

Moreover, there have been reports that some subjects can be trained to make SEMs in the absence of a moving target (Heywood and Churcher 1971); however, the direction, velocity, and flexibility of those movements were very limited. Finally, Whittaker and Eaholtz (1982) found that subjects could actually reverse the direction of their SEMs under “open loop” conditions – that is, in the absence of a visible target. However, their report was largely qualitative. In the present note we extend Whittaker and Eaholtz’s work by exploring such “open loop” reversals of direction quantitatively, with parametric manipulations of both stimulus velocity and the amount of stimulus support.

### Materials and methods

#### Subjects

Four subjects participated after indicating their informed consent by reading and signing subject consent forms. Two were completely naive with respect to the purpose of the study and had never participated in an oculomotor experiment. All subjects had normal or corrected-to-normal vision, and no neurological deficits that could affect their vision or eye movements. The study was

reviewed and approved by the Dartmouth College Committee for the Protection of Human Subjects.

### Apparatus

A dual Purkinje image eye tracker (Fourward Technologies, Generation 5) was used to monitor the eye movements. The system has a resolution of approximately 2 arcmin. The eye records were digitized at 250 Hz with 12 bit resolution. The stimulus consisted of a bright spot on an X-Y CRT monitor with a fast-decay phosphor (P-15). The stimulus spot subtended 2 arcmin and had a luminance of 20 cd·m<sup>-2</sup>, which appeared on a dark background with a luminance of <1 cd·m<sup>-2</sup>. The output of a function generator applied to horizontal input of the X-Y monitor controlled movement of the stimulus. Stimulus presentation and data recording were performed by an IBM PC. The eye records were stored on disk and analyzed offline.

### Procedure and experimental design

All subjects were instructed to track the motion of the target, and to attempt to continue following along the imagined stimulus path during the blanking intervals. Prior to formal data collection, some practice in visual pursuit was provided, but no practice on the experimental task (i.e., blanking trials) was given to any of the subjects. Both the order of trials within a block and the order of the blocks were randomized for each observer. Subjects viewed the display with both eyes at a distance of 1 m. Head movements were minimized using a dental bite bar.

We used a discrete trial procedure, and each trial began with a stationary point centered on the CRT screen. Subjects fixated this point until it began to move along a horizontal trajectory. The stimulus moved back and forth sinusoidally along a 20° path (simple harmonic motion reaching a maximum eccentricity of ±10°). The initial motion was always to the right, and each trial consisted of five complete cycles of motion. The target remained visible for the first three motion cycles, but on the fourth and fifth cycles the target disappeared at eccentricities of 2°, 4°, 6° or 8° from the center of the path. The (now extinguished) target would continue along the same sinusoidal motion trajectory, reverse direction at 10°, only to reappear at the same eccentricity on its return path. Thus, the actual reversals in the direction of motion were not visible, and the goal of the experiment was to study the quality of pursuit during the critical intervals. We will refer to these periods of stimulus disappearance as “blanking intervals” in the ensuing discussion. Trials were run in blocks of eight, and each blanking interval was tested twice during each block of eight trials.

The frequency of this predictable harmonic motion varied across trial blocks, and was 0.125, 0.25, 0.5 or 1.0 Hz. Given the amplitude of 20°, these frequencies produced mean target velocities of 5°, 10°, 20° or 40° s<sup>-1</sup>, respectively. The actual duration of the blanking intervals depended on both the blanking eccentricity and the frequency of the sinusoidal motion. The intervals were shortest at 1 Hz, ranging from 206 to 436 ms. The longest intervals occurred at 0.125 Hz, where the blanking duration ranged from 1574 to 3268 ms. The digitized motions of the right eye were saved to disk starting with the third cycle of each trial. Thus, the data from each trial consisted of one control cycle during which the target was continuously visible, and two critical cycles in which the target disappeared during the various blanking intervals. The entire dataset comprises 128 trials (a total of 512 blanking intervals). The data from 12 trials were not usable due to experimenter error or apparatus malfunction.

### Data analysis

The data acquisition program stored the position of the right eye, the position of the stimulus, and the target offset and onset times. Saccades were removed offline to isolate the SEM component in

each record. The saccades were detected using a sliding velocity criterion (from 20.8° s<sup>-1</sup> at 0.125 Hz up to 66.67° s<sup>-1</sup> at 1.0 Hz). Statistical analyses were performed using SPSS package for Windows 9.0 (SPSS Inc. 1989–1998).

## Results

When the saccades were removed, it was apparent that residual SEMs were present for all observers in every condition. This was the case despite the fact that with the longest blanking intervals the pursuit target was only visible for 20% of its path. Figure 1A shows an example of a raw eye record and the same record with the saccades removed. Table 1 provides a summary of means for the measures we report in the present note.

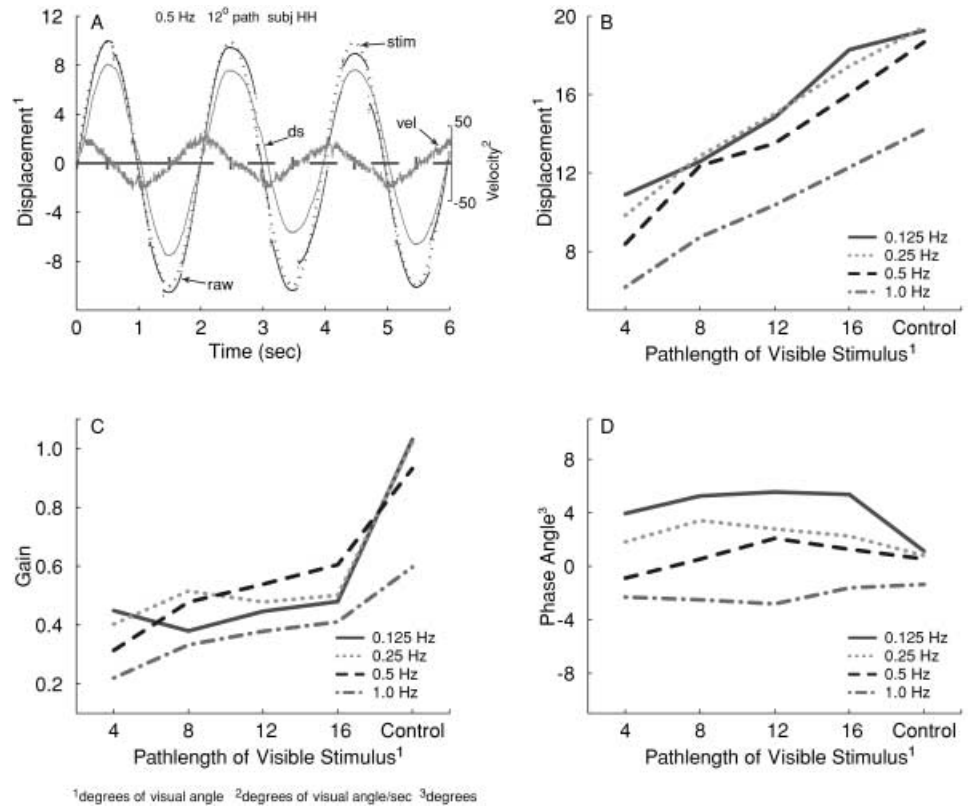
### Amplitude of total eye motion

We define total eye motion (TEM) as SEM plus saccades. First, we compared the peak-to-peak amplitude of TEM during blanking cycles with the amplitude observed during the control cycles. The overall amplitude of TEM increased in direct proportion to the length of the visible stimulus path (linear contrast  $t_4=4.6$ ,  $P<0.001$ ). During the control cycles, the measured amplitude of TEM averaged 97% of the angular displacement of the pursuit target, although the amplitude at the 1-Hz (highest) motion frequency was reduced to 92%. The amplitude of TEM decreased with decreasing visible stimulus pathlength, but the rate of this decrease did not differ reliably for the tested motion frequencies. The average amplitudes of TEM with 16°, 12°, 8° and 4° of stimulus visibility were 90%, 84%, 79% and 66%, respectively.

### Amplitude of SEM

To determine the contribution of SEM to TEM, we also performed the analysis describe above after the saccades had been removed. The results of this analysis are shown in Fig. 1B. Across all conditions, the SEM amplitude was significantly smaller ( $P<0.001$ ) than the TEM amplitude. Like the TEM amplitudes, SEM amplitudes decreased in direct proportion to the visible stimulus pathlength ( $P<0.001$ ). The SEM component accounted for 97% of the TEM amplitude in the control cycles of the 0.125-Hz, 0.25-Hz and 0.5-Hz conditions, but fell to 71% at 1.0 Hz (mean velocity at 1.0 Hz = 400 s<sup>-1</sup>). Bonferroni post hoc tests indicated that the SEM amplitude was significantly reduced at 1.0 Hz, but did not differ significantly for the other frequencies. A comparison of regression slopes indicated that the reduction of eye movement amplitude produced by decreased visible stimulus pathlength was similar for all stimulus frequencies, as well as for the mean TEM and SEM slopes.

**Fig. 1** **A** A sample eye record: *stim* stimulus trace, *raw* eye position trace with saccades present, *ds* desaccaded eye trace (scale for these three traces given by *left ordinate*), *vel* desaccaded eye velocity trace (scale given by *right ordinate*); *the horizontal line* indicates when the stimulus was present; *the short vertical bars* mark the location of the theoretical stimulus peak. **B** Slow eye movement amplitude, **C** gain, and **D** phase angle, all plotted as a function of visible stimulus pathlength for all frequencies



**Table 1** Stimulus velocity-to-match, gain, amplitude, and phase shift means

	Velocity <sup>a</sup>				Gain					Amplitude					Phase <sup>b</sup>	
	4°	8°	12°	16°	4°	8°	12°	16°	20°	4°	8°	12°	16°	20°	4°-16°	20°
0.125 Hz	8.2	7.5	6.5	4.7	0.41	0.41	0.43	0.5	1.00	10.9	12.6	14.8	18.3	19.3	5.2	1.2
0.25 Hz	15.5	14	12.1	8.2	0.40	0.52	0.49	0.48	1.01	9.8	12.9	15.0	17.5	19.5	2.6	0.8
0.5 Hz	29.6	26.4	21.2	14.7	0.31	0.48	0.52	0.63	0.93	8.4	12.4	13.5	16.0	18.7	0.8	0.8
1 Hz	54.6	46.6	36.1	19.9	0.20	0.33	0.40	0.46	0.59	6.2	8.7	10.4	12.3	14.2	-2.4	-1.4

<sup>a</sup> Degrees of visual angle <sup>b</sup> Degrees

## Gain

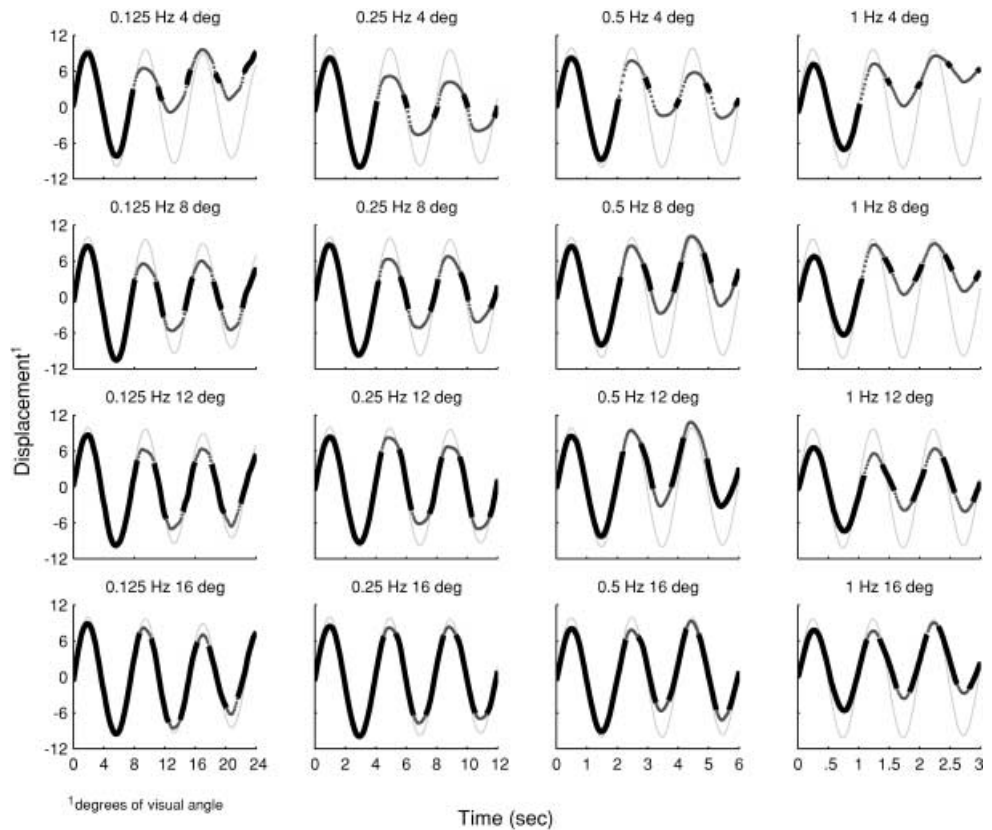
We computed the gain (eye velocity/target velocity) of SEM for the final 100 ms of each blanking interval, as well as the corresponding interval in the control sweeps. Since gain at the end of the blanking interval is measured *after* the eye has reversed direction, gain in the blanking sweeps can be regarded as a measure of the SEM system's ability to reaccelerate after the turnaround and match stimulus velocity using only what must be an endogenous representation of predictable target motion. The overall mean gains for the control sweeps were higher than those in the blanking sweeps (0.89 vs 0.43). A repeated-measures MANOVA revealed that this difference was significant ( $F_{1,3}=133.88$ ,  $P<0.001$ ). Overall, gain decreased significantly with the reduction in visible stimulus pathlength (linear contrast  $F_{1,3}=13.35$ ,  $P=0.035$ ). However, separate linear contrasts revealed this effect was driven by the 0.5- and 1.0-Hz frequencies

( $F_{1,3}=153.07$ ,  $P=0.001$ ); it was not found in the 0.25/0.125-Hz conditions ( $F_{1,3}=0.46$ ,  $P=0.54$ ). This dichotomy is readily apparent in Fig. 1C.

We think that this decline in gain as visible stimulus pathlength decreased in the higher frequency conditions is due to the fact that observers were hard-pressed to match the stimulus velocity when that velocity approached or exceeded  $\sim 30^\circ$ . In these cases, the endogenous predictive pursuit signal may have been insufficient for the eye to match the stimulus velocity.<sup>2</sup> In fact, some of this decrease in gain occurred in the control cycles: Whereas in the control cycles of the 0.125- and 0.25-Hz conditions the gain was close to unity, it decreased to 0.93 in the 0.5-Hz condition, and to 0.59 in the 1.0-Hz

<sup>2</sup> Note that the gain measurements were obtained from the last 100 ms of each blanking interval. Thus, for the longer blanking intervals, the eye velocity was measured closer to the center of the stimulus path, where the stimulus velocity was greatest. Please see Table 1 for stimulus velocity information.

**Fig. 2** Mean slow eye movement (SEM) traces and stimulus traces for all stimulus frequencies and visible stimulus pathlengths. The panels are arranged by frequency (0.125–1.0 Hz) *left to right*, and by visible stimulus pathlength (4°–16°) *top to bottom*. The *thin gray lines* are the mean stimulus traces, and the *black segmented lines* are the mean SEM traces. The *thick solid segments* in the SEM traces indicate when the stimulus was present; the *thin dotted sections* indicate when it was absent. Note the much smaller peak-to-peak amplitude in cycles 2–3 with the shorter visible stimulus path (4°, 8°) in the slower frequencies, and generalized amplitude compression and loss of eye velocity in the 1.0-Hz condition



condition. Reverse Helmert contrasts showed that these differences are statistically significant. Stimulus velocity was not a factor in the lower frequency conditions; gain in those conditions stayed relatively flat at around 0.4, even when the visible stimulus pathlength was only 20% of the total path, and the blanking period duration exceeded 2 s.

### Phase shift

The timing of the reversals in SEM for predicted sinusoidal trajectories provides another measure of the quality of pursuit under open loop conditions. We thus computed the phase shift of the reversals in SEM relative to the reversal of the pursuit target (whether it was visible or not). In the control sweeps, the eye led the stimulus by 101, 34, and 12 ms in the 0.125-, 0.25-, and 0.5-Hz conditions, respectively, and lagged it by 14 ms in the 1-Hz condition. To compare phase shift across the conditions, we transformed the data into degrees of phase angle. In this notation, the phase shift for the aforementioned conditions was 1.2°, 0.8°, 0.8°, and –1.36°. This ordering of stimulus frequency was preserved at every blanking interval, resulting in a significant effect of stimulus frequency on phase ( $P < 0.0001$ ). Nevertheless, in all conditions the phase shift remained quite close to zero, never exceeding  $\pm 6$  degrees. Thus, despite the changes in SEM gain and/or amplitude, the eye remained relatively well phase-locked to the implied stimulus path. A similar lack

of significant phase shift has been observed by Deno et al. (1995) in monkeys tracking single sinusoids, as well as in humans (Hallett 1986). The phase results are shown in Fig. 1D.

### Discussion

Our results confirm that active reversals of SEM can be made without the perception of a moving visual stimulus (Whittaker and Eaholtz 1982). Thus, this “predictive pursuit” observed in reversals must be driven by a signal derived from an endogenous representation of predictable target motion. Barnes and colleagues (Barnes and Donelan 1999; Barnes et al. 1997) suggested that information about the velocity of a predictably moving stimulus can be stored (presumably in short-term memory), and later utilized to generate predictive pursuit movements. These investigators also argue that observers need not pursue the target to construct an internal representation of its motion: viewing a moving target while fixating another, stationary target is sufficient for the storage of the velocity and timing information. Our findings are in agreement with these ideas, as well as with earlier work demonstrating the role of expectations in initiation and maintenance of SEM (e.g., Kowler and Steinman 1979a, 1979b; Kowler et al. 1984; Kowler 1989; Becker and Fuchs 1985).

Our manipulation of stimulus parameters revealed that the amount of stimulus support and stimulus velocity

ty influence both gain and SEM amplitude of “predictive pursuit” – a reduction in stimulus support and an increase in stimulus velocity were generally associated with reductions in amplitude and gain. However, the endogenous “predictor” signal is generally sufficient to maintain gains in the vicinity of 0.4. Figure 2 provides perhaps the best overview of our findings by showing the average SEM traces in all experimental conditions. It is evident from the figure that SEMs can be maintained for well over 2 s without stimulus support, and that the eyes can smoothly decelerate to change direction and accelerate with surprisingly little phase shift. Overall, we find the quality of endogenously driven SEMs much more impressive than their shortcomings. Further research is needed to understand how the endogenous signal combines with sensory signals to enable predictive SEM, as well as how it facilitates the pursuit of visible stimuli.

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## References

- Bahill AT, McDonald JD (1983) Model emulates human smooth pursuit system producing zero-latency target tracking. *Biol Cybern* 48:213–222
- Barnes GR, Donelan SF (1999) The remembered pursuit task: evidence for segregation of timing and velocity storage in predictive oculomotor control. *Exp Brain Res* 129:57–67
- Barnes G, Grealy M, Collins S (1997) Volitional control of anticipatory ocular smooth pursuit after viewing, but not pursuing, a moving target: evidence for a re-afferent velocity store. *Exp Brain Res* 116:445–455
- Becker W, Fuchs AF (1985) Prediction in the oculomotor system: smooth pursuit during transient disappearance of a visual target. *Exp Brain Res* 57:562–575
- Deno DC, Crandall WF, Sherman K, Keller EL (1995) Characterization of prediction in the primate visual smooth pursuit system. *Biosystems* 34:107–128
- Hallett PE (1986) Eye movements. In: Boff KR, Kauffman L, Thomas JP (eds) *Handbook of perception and human performance*, vol I, John Wiley & Sons, New York, pp 10.53–10.54
- Heywood R, Churcher J (1971) Eye movements and the afterimage. I. Tracking the afterimage. *Vision Res* 11:1163–1168
- Kowler E (1989) Cognitive expectations, not habits, control anticipatory smooth oculomotor pursuit. *Vision Res* 29:1049–1057
- Kowler E, Steinman RM (1979a) The effect of expectations on slow oculomotor control. I. Periodic target steps. *Vision Res* 19:619–632
- Kowler E, Steinman RM (1979b) The effect of expectations on slow oculomotor control. II. Single target displacements. *Vision Res* 19:633–646
- Kowler E, Martins AJ, Pavel AM (1984) The effect of expectations on slow oculomotor control – IV. Anticipatory smooth eye movements depend on prior target motions. *Vision Res* 24:197–210
- Mather JA, Lackner JR (1981) The influence of efferent, proprioceptive, and timing factors on the accuracy of eye-hand tracking. *Exp Brain Res* 43:406–412
- Matin L (1986) Visual localization and eye movements. In: Boff KR, Kauffman L, Thomas JP (eds) *Handbook of perception and human performance*, vol I, John Wiley & Sons, New York, pp 20.34–20.41
- Robinson DA, Gordon JL, Gordon SE (1986) A model of the smooth pursuit eye movement system. *Biol Cybern* 55:43–57
- Steinbach MJ (1976) Pursuing the perceptual rather than the retinal stimulus. *Vision Res* 16:1371–1376
- Whittaker SG, Eaholtz G (1982) Learning patterns of eye motion for foveal pursuit. *Invest Ophthalmol Vis Sci* 23:393–397
- Young LR (1971) Pursuit eye tracking movements. In: Bach-y-Rita P, Collins CC, Hyde JE (eds) *Control of eye movements*. Academic Press, New York, pp 429–443
- Young LR, Stark L (1963) Variable feedback experiments testing a sampled data model for eye tracking movements. *IEEE Trans Hum Factors Electronics HFE* 4:28–51