Ocular Pursuit Responses to Repeated, Single-Cycle Sinusoids Reveal Behavior Compatible With Predictive Pursuit

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The link between anticipatory smooth eye movements and prediction in sinusoidal pursuit was investigated by presentation of series of identical, single-cycle, sinusoidal target motion stimuli. Stimuli occurred at randomized intervals (1.2–2.8 s) but were preceded by an audio warning cue 480 ms before each presentation. Cycle period (T) varied from 0.64 to 2.56 s and target displacement from 4 to 20° in separate series. For T ≤ 1.28 s, responses to the first stimulus of each series exhibited a time delay across the whole cycle (mean = 121 ms for T = 0.8 s). But, in the second and subsequent (steady-state) presentations, anticipatory movements, proportional to target velocity, were made and time delay was significantly reduced (mean = 43 ms for T = 0.8 s). Steady-state time delays were comparable to those evoked during continuous sinusoidal pursuit and less than pursuit reaction time. Even when subjects did not follow the target in the first presentation, they responded to the second presentation with reduced time delay. Throughout the experiments, three types of catch trial (A–C) were introduced. In A, the target failed to appear as expected after the warning cue. Anticipatory smooth movements were initiated, reaching a peak velocity proportional to prior target velocity around 200 ms after expected target onset. In B, the target stopped midway through the cycle. Even if the target remained on and was stationary, the eye movement continued to be driven away from the stationary target with a velocity similar to that of prior responses, reaching a peak velocity that was again proportional to expected target velocity after ≥205 ms. In C, the amplitude of the single sinusoid was unexpectedly increased or decreased. When it decreased, eye velocity throughout the first half-cycle of the response was close to that executed in response to prior stimuli of higher velocity and did not return to an appropriate level for 382–549 ms. Conversely, when amplitude increased, eye velocity remained inappropriately low for the first half-cycle. Results of A and C indicate that subjects are able to use velocity information stored from prior presentations to initiate an oculomotor drive that predominates over visual feedback for the first half-cycle. Results of B indicate that the second part of the cycle is also preprogrammed because it continued despite efforts to suppress it by fixation. The results suggest that initial retinal velocity error information can be sampled, stored, and subsequently replayed as a bi-directional anticipatory pattern of movement that reduces temporal delay and could account for predictive control during sinusoidal pursuit.

INTRODUCTION

Two types of target motion stimuli have most often been used to examine oculomotor pursuit: constant velocity ramps and sinusoidal stimuli. The latter indicate the presence of predictive mechanisms in pursuit, since phase errors are less than those to be expected on the basis of time delays in visual feedback (Dallos and Jones 1963). When ramp stimuli are presented in the normal manner with randomized timing and direction, there is little evidence of predictive behavior, and the fastest onset of smooth eye movement occurs after a latency that is normally ≥100 ms (Carl and Gellman 1987). But repeated presentation of ramp stimuli with predictable timing, direction, and velocity does elicit anticipatory smooth pursuit several hundred milliseconds before target motion onset (Barnes and Asselman 1991; Becker and Fuchs 1985; Kao and Morrow 1994). A major feature of these anticipatory eye movements is that they allow the eye to attain target velocity ≥50 ms in advance of the normal reactive response to visual feedback, thus compensating in large part for the time delays in visual processing (Kowler and Steinman 1979; Oshahi and Barnes 1996). It is highly likely that this mechanism for reducing the effects of feedback delay plays some part in the minimization of phase errors during sinusoidal pursuit, but the precise means by which this is accomplished has not been demonstrated experimentally.

A number of experiments have shown that the mechanism for generating anticipatory movements involves the short-term storage of a velocity-coded premotor drive and its subsequent release under the control of a timing mechanism (Barnes and Asselman 1991; Barnes et al. 1987, 1997). In the experiments presented here, we have tried to find evidence for this ability to store and reproduce information about motion of a sinusoidally oscillating target.

To accomplish this, we have used what we have termed the remembered pursuit task (Barnes and Donelan 1999). In this, the subject is presented with a moving stimulus for a brief period preceded by a warning cue. The presentation of the cue/stimulus pair is repeated a number of times with a constant time period between cue and stimulus presentation. The time between cue/stimulus pairs, however, is randomized so that the subjects have to rely on the timing information provided by the warning cue. The motion stimulus itself remains the same in
each presentation, and in previous experiments, this stimulus has been a simple, constant velocity ramp. Although the response to the first presentation is normally reactive, the subject quickly builds up a pattern of anticipatory movements that can reach quite high velocity (~10°/s for a 50°/s target motion) before target onset.

A feature of the anticipatory responses to ramp stimuli is that they tend to have a very characteristic velocity profile in which eye velocity builds up rather slowly (Kao and Morrow 1994). This contrasts therefore with the response to a randomly appearing ramp stimulus, which generates a more abrupt response (Carl and Gellman 1987; Ohashi and Barnes 1996; Robinson 1965; Tychsen and Lisberger 1986). In recent experiments, it has been shown that very little modification of this anticipatory profile can be achieved even when the demand is to maintain a high level of acuity of the moving target when it is presented at different phases of the target trajectory (Wells and Barnes 1999). This appears to be a basic limitation of using a ramp stimulus; it is impossible for the slowly increasing anticipatory eye velocity trajectory to match the abrupt increase in target velocity and the response has to be a compromise.

In the experiments to be described here, the target motion was more complex than that used previously, consisting of a single cycle of a sinusoidal waveform. The aim was to determine whether subjects could modify the response to successive presentations of this single-cycle transient stimulus so as to reduce the phase lag of the response to the same degree that is observed during a continuous sinusoidal stimulus. To encompass a range of conditions in which large changes in gain and phase would be expected, we examined sinusoidal stimuli with periodicities ranging from 2.56 down to 0.64 s. In particular, we sought evidence for the role of anticipatory smooth eye movements in any changes. Taking into account the limitations in the ability of anticipatory movements to match abrupt changes in target velocity, the sinusoidal stimulus was constrained to start at zero velocity. This created a bell-shaped target displacement profile in which the target started at center, moved to the right, and returned to center. By using this stimulus waveform, we expected that the slow build up of the anticipatory movement would more closely match the target velocity profile at the beginning of each presentation and thus facilitate any phase changes.

Our objective was not only to demonstrate the characteristics of the initial anticipatory movement but also to determine what contribution this nonvisual component might make throughout the later parts of the response. To accomplish this, three types of catch trials, similar to those devised previously (Barnes and Asselman 1991), were incorporated into the experiments. In two of these, we examined what happens to the anticipatory movement if the target appears as expected but has a different velocity to that anticipated. These trials revealed that in some circumstances, the preprogrammed anticipatory response is sufficiently powerful to overcome the effects of visual feedback for the whole of the first half-cycle. In a third catch trial, we looked for evidence of response continuation in the second half-cycle when the target unexpectedly stops or disappears. The aim was to reveal evidence of prediction midway through these repeated discontinuous sinu-

oids, similar to that demonstrated by van den Berg (1988) in response to continuous sinusoidal stimuli. A brief report of some of this work was published earlier (Barnes and Barnes 1999).

**METHODS**

Subjects were seated at the center of a circular screen (radius, 1.5 m) with the head supported on a chin rest and fixed by clamps to the side of the head. A visual target was presented on the screen and was made to move in the horizontal axis under the control of a motor-driven mirror. The target was composed of a circle with superimposed cross hairs, subtending 50 min of arc at the eye. Eye movements were recorded by an infrared limbus tracking technique (Skalar IRIS), were sampled at intervals of 5 ms and low-pass filtered at 80 Hz (4-pole Bessel) prior to storage on disk and off-line analysis. All stimuli were presented in balanced, randomized combinations to avoid the effects of learning and fatigue. The experiments were conducted with local ethics committee approval and all subjects participated with informed consent. Six normal subjects participated, three of whom were completely naive of oculomotor experiments.

A total of four separate experiments were carried out, but the target motion stimulus and general procedure were common to all. Each trial consisted of four to six consecutive series. Within each series there were five to eight presentations of identical target motion stimuli. The target motion had a trajectory that started at center, moved to the right and returned to center (Fig. 1). The target was only visible (i.e., presented) while executing this trajectory. Each presentation was generally preceded by an audio cue (80-ms duration, 500-Hz tone) 480 ms before target onset. The interval between the end of one presentation and the beginning of the next was randomized in the range 1.2–2.8 s. The velocity profile of each stimulus was a single-cycle, sinusoid starting with zero velocity. Within each series peak displacement (Dpk) was constant but had values ranging from 4 to 20° in different series. The period of the sinusoidal motion also remained the same throughout each series, but stimuli with four different periods (T) from 0.64 to 2.56 s were examined. An audio tone (500 Hz) was also given throughout the duration of the target presentation (Fig. 1). Each trial was preceded by a calibration of the eye movement recorder. Two small targets placed on the midline, 3° above and below the moving target, served for fixation and were continuously present (see Fig. 1, inset). Using two targets rather than a single central one easily allowed the subject to hold fixation at the midpoint without causing local interference (as a single central fixation target would) when the eye moved across center. Subjects were required to hold fixation on the midline until an audio cue was given, and they were then free to initiate eye movements in preparation for the ensuing target appearance. The subjects were not given, nor did they require, any practice sessions except in experiment 3 (see following text). The stimulus conditions were deliberately interchanged and randomized to avoid long-term learning effects. Details of the four experiments were as follows.

In experiment 1 peak displacement (Dpk) had values of 4, 8, 12, 16, or 20° presented in randomized order in five consecutive series. The period of the velocity sinusoid remained the same throughout each trial, but four periods were examined in separate trials: 2.56, 1.28, 0.8, and 0.64 s. At the end of each series, a catch trial was introduced. For this catch trial, the audio warning cue was given as normal, but the target failed to appear as expected (see example in Fig. 1). Audio cues were not given before the first presentation of each series and a gap of 5–10 s was left between series. Responses to continuous sinusoidal stimulation were also recorded for a peak-peak displacement of 20° at each of the stimulus periods used for intermittent stimulation. To be compatible with the intermittent stimuli, target displacement was offset 10° to the right and started from center with zero velocity.

In experiment 2, four peak displacements of 5, 10, 15, and 20° were
each presented at each of the four stimulus periods (0.64, 0.80, 1.28, and 2.56 s), giving a total of 16 conditions. These 16 stimulus conditions were presented in randomized order so that within any one trial successive series contained stimuli with a different period and peak displacement. In addition, no audio cue was given before the first presentation of each series, so that, before the first appearance of the target, the subject was unaware of the amplitude, velocity, and total duration of the movement. There was also a randomized gap of 5–10 s between each series. The aim of all these measures was to ensure that subjects would make a reactive response to the first presentation of each series. At the end of each series, one catch trial was introduced in which target motion stopped half way through the trajectory (i.e., at the point of peak displacement). This catch trial (B) took two forms. The target either disappeared completely (OFF condition) or it remained on, but stationary, at peak displacement (ON condition). All sixteen target motion conditions were presented in both the ON and OFF conditions to each subject in separate sessions, giving a total of 32 series for each subject.

In experiment 3, conditions were identical to those of experiment 2 except for two features. First, subjects were instructed to hold fixation during the first presentation of each series and then to make a response to all further presentations. Second, the audio cue was presented throughout the whole of each series so that subjects were able to assess when to initiate the response to the second presentation. Subjects were given one practice trial with this experiment as the procedure was otherwise quite difficult to follow by instruction alone.

In experiment 4, the period of the sinusoid remained the same throughout each trial; two periods were examined, 1.28 and 0.80 s, in separate trials. Six series, each containing a randomized number of presentations (6, 7, or 8), were given in each trial. Warning cues were given before each target appearance. Peak displacement alternated between 8 and 20° in successive series, but subjects were unable to predict when the peak displacement would change. This unexpected change of displacement between series thus formed catch trial C.

**Data analysis**

Eye movements were analyzed by first identifying and removing the fast phase components of the response using a technique similar to that described previously (Barnes 1982) but based on a combination of acceleration and velocity threshold criteria. A linear interpolation routine was used to bridge the gaps produced by removal of saccades from the eye velocity trajectory. Fast phase movements were generally of small amplitude (5°) and brief duration, making linear interpolation a simple and adequate method of waveform restoration (e.g., see Fig. 1). Where measured variables are referred to as steady-state (SS) values, these have been derived by averaging velocity trajectories for the third and subsequent presentations of the repeated sinusoidal stimuli within each series, each component trajectory being time-locked to target onset. This yielded one SS trajectory per subject per series.

The following specific measures of eye movement were derived from each response.

V50, V100, V200. Eye velocity 50, 100, or 200 ms after target onset (V50, V100, and V200, respectively). The values at 100 ms will be examined because they correspond to the last time at which the response would normally be considered uninfluenced by visual feed-
back on the basis of most estimates of pursuit reaction time (e.g., Carl and Gellman 1987; Rashbass 1961; Tychsen and Lisberger 1986). However, since there are some reports of reaction times as short as 60–70 ms (Kao and Morrow 1994; Merrison and Carpenter 1994), we have also considered V50 values to establish velocity scaling of the anticipatory responses. The reason for examining V200 will emerge from subsequent discussion of results. For the catch trials, V100 and V200 were measured in relation to the time at which the target was expected to appear (480 ms after audio cue—A) or stopped (B).

\( V_{95} \).  The peak eye velocity of a response measured at various times—for example, to the first \( (V_{pk1}) \) or second \( (V_{pk2}) \) half-cycles of the repeated single cycle sinusoidal stimulus. Peaks were first estimated using a maximum value criterion. A cubic regression was then fitted to data from 100 ms before to 100 ms after the estimate, and the peak of the best-fit function was identified. This eliminated spurious results from occasional transient increases in signal noise.

\( T_{pk1} \).  The latency between peak target velocity and the attainment of peak eye velocity at various times—for example, for the first \( (T_{pk1}) \) or second \( (T_{pk2}) \) half-cycle, respectively, of the repeated single sinusoid. Measurement of these variables gives an approximate indication of the overall temporal shift in the response with repetition.

\( T_{cross} \).  The latency between peak target displacement (0 velocity) and the time at which eye velocity crossed through zero. \( T_{cross} \) was first estimated from the eye velocity trace, then a linear regression was fitted to points 100 ms either side of this, and a more precise value was calculated. This minimized occurrence of spurious values arising from noise in the eye velocity signal.

\( T \).  Overall latency between the stimulus (target velocity) and the response (eye velocity) derived by carrying out a cross-correlation between stimulus and response and then identifying the delay \( (T) \) at which the peak correlation was obtained. This gave an overall measure of temporal shift, irrespective of whether the period of the response is comparable to the period of the stimulus.

Gain and phase of eye velocity for the repeated sinusoids were assessed only for the SS conditions to carry out a direct comparison with gain and phase for the continuous sinusoidal stimulus of experiment 1. They were obtained by least-squares fitting of the velocity response profile with sine and cosine components of the appropriate periodicity (Barnes 1982).

\( T_{95} \).  The time at which the response in a catch trial was found to fall outside the 95% confidence interval associated with the SS response for the appropriate stimulus. This was derived in a two-stage process. First, the variance associated with the SS response at each sampling interval was used to derive the appropriate \( t \)-statistic and give an approximate indication for \( T_{95} \). A quadratic regression was then carried out on data points from 100 ms before until 100 ms after this initial estimate of \( T_{95} \). The estimate of \( T_{95} \) was then refined using the 95% confidence interval associated with the regression.

Statistical comparisons were carried out on these variables using SPSS software. Prior to performing repeated measures ANOVA, the data were tested for normality (Shapiro-Wilk test). The results showed that the data were normally distributed in all cases. The Mauchly test was applied to determine sphericity of the data and when this was found to be significant, the Greenhouse-Geisser correction was applied to determine significance. All interactions between main factors that are not mentioned in the text were nonsignificant.

**RESULTS**

**General response features—experiments 1 and 2**

A typical response to the repeated presentation of single sinusoids from experiment 1 is shown in Fig. 1. From this it is evident that the subject was able to obey the instruction to hold the eye at center between presentations, and as a result this largely eliminated drifting movements of the eye between presentations. The response to each target presentation thus started from near-zero velocity and was uncontaminated by the decay of the previous response. Even though the period of the stimulus in this example shown in Fig. 1 was relatively short \( (T = 1.28 \text{ s}) \)—equivalent to a pursuit frequency of 0.78 Hz, there was a considerable change in the velocity profile of the response between the first and second presentations. Subjects reported that although the target appeared blurred in the first presentation, by the third presentation they could see it with high acuity throughout the trajectory. They found the task easy and natural to carry out, hence there was no need to train the subjects for the task. The effects of repetition varied with the period of the stimulus as revealed by examination of the averaged velocity profiles for the first series shown in Fig. 2. For the shorter stimulus periods \([0.8 \text{ s} \text{ (Fig. 2B)} \) and \( 0.64 \text{ s} \), the response to the first presentation lagged well behind the stimulus throughout the whole period. But in response to the second presentation, an anticipatory movement was made prior to target onset and the phase shift was considerably reduced throughout the whole of that presentation. In fact, there was little improvement on this response in subsequent presentations, so that this second response differed little from the average of the subsequent (SS) responses (Fig. 2B). In contrast, in the response to the longest period stimulus \( (2.56 \text{ s}) \), the eye velocity during the first half-cycle of the first presentation did not match target velocity at all, but in the second half-cycle, it was evident that prediction began to take over and the velocity error was much reduced (Fig. 2A). Then during the second presentation, subjects initiated an anticipatory smooth movement prior to target onset and the phase error was reduced to almost zero throughout the whole period. (Note that the SS response for \( T = 2.56 \text{ s} \) has been omitted from Fig. 2A because it was so similar to the 2nd response.) For all stimulus periods, when the target unexpectedly failed to appear at the end of each series, there was normally some inappropriate smooth eye movement generated (the predictive velocity estimate—PVE, Figs. 1B and 2, C and D), which, for short stimulus periods, lasted for almost one half-cycle.

To analyze these results, we first discuss how these changes in the response can be measured through the assessment of changes with repetition, then consider the compatibility of the intermittent responses with conventional continuous sinusoidal responses and finally examine the effects revealed by the catch trials.

**Changes in initial eye velocity with stimulus repetition** (experiment 1)

To assess the changes taking place in the eye velocity with stimulus repetition, we first consider values of V100 and V200 over the first two presentations and the SS derived from the third presentation onward (Fig. 3). Note that we simply use the velocity at these times to monitor the change and make no assumption at this stage about whether they are wholly anticipatory or influenced by visual feedback. Analysis of variance was carried out with stimulus period \( (T = 2.56, 1.28, 0.8, \text{ and } 0.64 \text{ s}) \), target displacement \( (D_{pk} = 4, 8, 12, 16, \text{ and } 20^\circ) \) and stimulus repetition \( (1st, 2nd, \text{ and } SS \text{ responses}) \) as factors.
Repeated a priori contrasts showed that V100 for the first presentation in each series was significantly less than that in the second presentation ($F_{1,5} = 73.97; P < 0.001$), but there was no significant difference between the second and SS presentations ($F_{1,5} = 0.23; P = 0.65$). In fact, V100 in the first presentation of each series was very small, as expected, since this was intended to be a reactive response in the absence of a warning cue. ANOVA on the velocity 200 ms after target onset (V200—Fig. 3B) showed that, even at this later stage, when visual feedback should have had an influence on behavior, V200 for the first presentation in each series was significantly less than that in the second presentation ($F_{1,5} = 127.72; P < 0.001$), with no significant difference between the second and SS presentations ($F_{1,5} = 3.87; P = 0.106$).

ANOVA on V100 for the second and SS responses alone revealed a significant linear increase in V100 with target displacement ($F_{4,20} = 18.30; P < 0.001$). To be sure that this scaling of the anticipatory response was also present at a time when there was definitely no influence of visual feedback, a similar analysis was also carried out on SS V50 values. Even at this early stage of the anticipatory response, ANOVA revealed a significant linear increase ($F_{4,20} = 8.633; P < 0.001$) in V50 with increasing target displacement (Fig. 4A). The V50 values were thus also scaled in proportion to target velocity for...
a given period, amounting to 19.2% of peak eye velocity (Vpk₁) for the two shortest period stimuli (Fig. 4B). (Note that for a given Dpk, peak target velocity increased as T decreased—see legend to Fig. 4.)

Inspection of the results shown in Fig. 3 reveals that the difference in average eye velocity between the SS and first response is actually greater at 200 ms than at 100 ms. To define the time at which the peak in this difference occurred, we calculated the difference between the trajectory of the first response and that of the SS response. The objective was to identify the last time after target onset at which the effects due to the predictive internal drive could be shown to be greater than the effects of retinal error drive. The peak in this difference was found to occur at a mean time [Tpk(SS²₁st), Fig. 10B] of 199.7 ± 16.8 ms (mean ± SE) after target onset. The mean difference in eye velocity at this time [Vpk(SS²₁st)] increased significantly (F₄,20 = 40.894; P < 0.001) in a linear manner with target velocity, reaching a maximum of 36.6°/s for Dpk = 20° and T = 0.64 s.

These results indicate that, although the shortest latency for visual feedback may be as little as 60 ms, in practice, the reactive (1st) response is negligible after 100 ms, whereas the anticipatory response that is built up, even in the second repetition, is much greater and is appropriately scaled to be predictive of target velocity. Moreover, the centrally generated anticipatory response continues to outweigh the effects of visual feedback for 200 ms after target onset.

**Changes in latency with stimulus repetition (experiment 2)**

The randomization of both the period and peak displacement of stimuli in successive series plus the absence of an initial warning cue in experiment 2 ensured that the first response of each series was as reactive as possible in both the outward and return phases of the target movement. Nevertheless, for the longest period stimulus (T = 2.56 s), even within the first presentation, the timing of the eye movement response in the return phase (2nd half-cycle, Fig. 2A) indicated that this was not a reactive response, and thus the results for T = 2.56 s have been omitted from the following analysis. We have used two means to estimate the change in response timing.

First, we consider the average time delay (t) derived from the cross-correlation analysis (see Data analysis). Figure 5 shows the result of this analysis for the first, second, and SS velocity trajectories. Analysis of variance revealed a significant (F₂,22 = 206.79; P < 0.001) reduction in t across the first, second, and SS presentations. As is evident in Fig. 5A, most of the decrease occurred between the first and second presentations. The mean difference between values of t for the first and SS presentations was 51.9, 78.0, and 89.3 ms for T = 1.28, 0.8, and 0.64 s, respectively.

A second way of assessing the change in timing of the response is to examine the latency (Tpk) between the time at which peak target velocity occurs and the attainment of peak eye velocity in the first and second half-cycles of the response (Fig. 5B, T = 0.8 s only). For stimulus periods of ≤1.28 s, the
time of peak eye velocity in the first half-cycle (Tpk₁) decreased significantly with repetition. Repeated contrasts indicated that Tpk₁ occurred significantly later ($F_{1,11} = 70.66; P < 0.001$) in the first presentation than in the second with a much smaller difference between the second and SS presentations ($F_{1,11} = 25.27; P < 0.001$). The mean difference in Tpk₁ between the first presentation and the SS was 79.6, 69.1, and 92.0 ms for periods $T = 1.28, 0.80$, and 0.64 s, respectively. The latency of the second (negative) peak in eye velocity (Tpk₂) also exhibited a significant decrease between the first and second presentations ($F_{1,11} = 38.68; P < 0.001$) but not between the second and SS presentations ($F_{1,11} = 0.10; P = 0.754$). The mean difference in Tpk₂ between the first presentation and the SS was 17.4, 31.6, and 56.0 ms for periods $T = 1.28, 0.80$, and 0.64 s, respectively. Tpk₂ was always slightly less than Tpk₁, even for the SS conditions, and, as might be expected, the values of $\tau$ derived by the cross-correlation technique generally fell between the values of Tpk₁ and Tpk₂ (Fig. 5). The time at which eye velocity crossed through zero (Tcross, Fig. 5B) also exhibited a significant decrease with repetition ($F_{2,22} = 14.01; P < 0.001$). Differences in Tcross between the first and SS presentations were 29.3, 85.4, and 93.5 ms for $T = 1.28, 0.80$, and 0.64 s (Fig. 5B). The fact that the SS value for Tcross was less than either Tpk₁ or Tpk₂ (Fig. 5B) is a reflection of the asymmetry of the velocity profile.

**Effects of viewing but not pursuing the moving target (experiment 3)**

When the subjects were required to maintain fixation during the first presentation of the target in each series, they were able to make an anticipatory movement to the second presentation, even though this was then the first response that they made in that series (Fig. 6). All subjects managed to suppress eye movement on the majority of occasions during the first presentation (overall mean peak velocity was $2.3°/s$), although sometimes it was difficult to eliminate an initial reflexive response as observed, for example, in Fig. 6C. Note that this performance was achieved even though the frequency, and amplitude of target movement were

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**Fig. 6.** Examples of the oculomotor response at the start of 3 successive series in 1 trial of experiment 3 in which stimulus period ($T$) was 1.28, 0.80, and 2.56 s. The target was not visible during broken-line segments of the target displacement trace. Axes for eye and target shown on left and right, respectively. The subject attempted to hold fixation at the midline for the 1s presentation of each series, but actively pursued the target in subsequent presentations.
varied unpredictably, as exemplified in the three consecutive series shown in Fig. 6, so that the subjects had to make a rapid assessment of both timing and amplitude of movement within the first presentation. It was undoubtedly important in this respect that the warning cue time remained constant throughout all trials and this was reinforced by giving the warning cue even during the first presentation.

**CHANGES IN INITIAL EYE VELOCITY WITH REPETITION.** V100 in the first presentation (Fig. 7A) was negligible (overall mean 0.02 ± 0.62°/s), but during the second presentation could reach high levels [e.g., maximum V100 was 19.53 ± 4.72°/s (mean ± SE) for the T = 0.64 s, Dpk = 15° stimulus]. Analysis of variance was carried out with stimulus period (n = 4), target velocity (n = 4), and order of repetition (n = 3; 2nd, 3rd, and SS presentations) as factors. For both V100 and V200, repeated contrasts confirmed that there was no significant difference between the second and third or third and SS presentations (P > 0.296 in all contrasts). As in experiments 1 and 2, there was a significant increase in V100 with target velocity (F3,18 = 31.77; P < 0.001).

**CHANGES IN TIMING WITH REPETITION.** ANOVA on the overall delay (τ) revealed that there was a significant effect of repetition (F2,12 = 16.35; P < 0.001), but the change in timing was quite small compared with that observed in experiment 2. Thus the mean difference between the second and SS presentations was 5.4, 14.4, and 17.1 ms for periods T = 1.28, 0.80, and 0.64 s, respectively (cf. Figs. 5A and 7B). Analysis of the delays in the peak responses however showed no significant difference in Tpk1 or Tpk2 between responses to the second, third, and SS presentations.

**Compatibility with continuous sinusoidal pursuit (experiment 1)**

To relate the responses to the intermittent stimuli with responses to continuous sinusoidal stimulation, gain and phase of the SS eye velocity were calculated for each stimulus period and velocity (Fig. 8). For a period of 2.56 s (=0.39 Hz), the prediction in the intermittent response was so effective that phase error was reduced on average to a value of only −1.41° (Fig. 8B), and mean gain across all target velocities was 1.01 (Fig. 8A). Even for the shortest period (T = 0.64 s), the phase lag in the SS was only 26.3°, equivalent to a delay of 46.7 ms. Both gain and phase for the Dpk = 20° condition were comparable to the values obtained in response to continuous sinusoidal stimuli with a peak-peak amplitude of 20° as shown in Fig. 8. For example, the mean phase lag of 25.4° for continuous stimulation at 1.56 Hz (T = 0.64 s) was similar to that for intermittent stimulation. Also, as in previous studies of continuous sinusoidal pursuit (Barnes 1993; Lisberger et al. 1981), there was a progressive decrease in gain with increasing target peak displacement in the responses to intermittent presentation (Fig. 8A).

Although the individual responses to each intermittent presentation might not appear to be very similar to the responses to continuous sinusoidal stimuli, concatenation of successive responses showed that the resultant response waveform bore a

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**FIG. 7.** A: V100 in the 1st and 2nd target presentations compared with the SS as a function of T in experiment 3. Subjects attempted to suppress eye movement in the 1st presentation, hence V100 was low. B: overall time delay derived from cross-correlation (τ) for the 2nd and 3rd presentations compared with SS as a function of stimulus periods from 1.28 to 0.64 s. Mean across all stimulus amplitudes (Dpk) in 6 subjects, ±1 SE.

**FIG. 8.** Gain (A) and phase (B) as a function of frequency for SS eye velocity responses to repeated single-cycle sinusoids of varying peak displacement (Dpk = 4, 12, and 20°; 8 and 16° omitted for clarity). See note in Fig. 2 concerning the relationship of peak target velocity to Dpk and T. Cont. sine = gain and phase obtained during continuous sinusoidal stimulation (Cont. sine) = peak-peak displacement 20°. Mean of 6 subjects, ±1 SE.
close resemblance to the continuous response (Fig. 9). Note that neither the continuous sinusoidal response nor the reconstructed intermittent response exhibits a regular sinusoidal velocity profile; there are continuous fluctuations in the velocity waveform of both. To achieve the result shown in Fig. 9, the velocity profile; there are continuous fluctuations in the velocity waveform of both. To achieve the result shown in Fig. 9, the continuous sinusoidal waveform. As a result, the anticipatory response component that was present in the 500-ms zone before each presentation (indicated by examples in Fig. 9) merged with, and tended to balance out, the decay of the response in the 500-ms zone after the previous presentation (also indicated in Fig. 9), giving a smooth transition between peaks.

**Catch trial A (experiment 1): responses to nonappearance of expected target**

When the target failed to appear as expected, an anticipatory eye movement was normally initiated (Fig. 1) that reached a peak velocity ($V_{pkPVE}$) well after the expected time of target onset, before decaying to zero (Fig. 2). Because this response was elicited in the complete absence of visual feedback, it provides a valuable means of comparing the centrally driven anticipatory eye movement with the SS response, where visual feedback is present. First, ANOVA revealed no significant difference in $V_{100}$ between the SS and PVE responses ($F_{1,5} = 2.82; \, P = 0.154$), but there was a significant linear increase in $V_{100}$ with peak target displacement ($D_{pk}$) ($F_{4,20} = 17.21; \, P < 0.001$). The PVE actually continued well beyond the 100-ms mark before attaining peak velocity. We measured the magnitude of this peak velocity ($V_{pkPVE}$) and the time at which it occurred ($T_{pkPVE}$). Analysis of variance revealed that $V_{pkPVE}$ increased significantly ($F_{4,20} = 12.77; \, P < 0.001$) with the value of $D_{pk}$ in the previous part of the series (Fig. 10A). The time at which peak velocity was attained ($T_{pkPVE}$, Fig. 10B) was significantly modified by the stimulus period ($F_{3,15} = 15.60; \, P < 0.001$). It was greatest for the longest stimulus period ($T = 2.56$ s), with a mean of 284.5 ms but declined to a minimum of 198.5 ms for $T = 640$ ms (Fig. 10B). The minimum time to attain peak in any subject was 125 ms.

Although the PVE appeared very similar to the SS response in the early part of its trajectory (Fig. 2, C and D), a difference frequently emerged prior to attaining peak velocity. We therefore calculated the time ($T_{95PVE}$) at which the eye velocity first deviated from the 95% confidence interval associated with the SS trajectory. $T_{95PVE}$ changed in a similar way to $T_{pkPVE}$ with the period of the stimulus, as is evident in the two examples of Fig. 2, C and D. $T_{95PVE}$ was 43.8 ms for $T = 2.56$ s, and the minimum value in any subject was 110 ms.

After attaining its peak, eye velocity decayed in an approximately exponential manner (Fig. 2). The time constant of this decay ($T_c$) changed significantly ($F_{3,15} = 20.99; \, P < 0.001$) with the period of the stimulus, as is evident in the two examples of Fig. 2, C and D. Mean $T_c$ (±SE) had values of 0.52 (±0.13), 0.23 (±0.04), 0.15 (±0.05), and 0.11 (±0.03) s for periods of 2.56, 1.28, 0.80, and 0.64 s, respectively.
In summary, these findings from catch trial A show that the early part of the SS response, up to a mean of $\pm 147$ ms after target onset, was indistinguishable from the response to the PVE, which is known to be generated in the complete absence of visual feedback.

**Catch trial B: responses to unexpected target stop/disappearance at peak displacement (experiment 2)**

When the target stopped unexpectedly midway through the sinusoidal trajectory the subjects always continued to make some part of the return movement to center (Fig. 11). There was little difference in the eye velocity whether the target remained on (and stationary) or went off, but there were major differences in the eye displacement. In the on condition, subjects attempted to hold the eye at its eccentric position, but the ongoing smooth movement kept driving the eye toward center, often resulting in a vigorous nystagmus (Fig. 11B). In the off condition, smooth eye movement generally continued to drive the eye toward center until the time at which the movement was expected to end, when a volitional saccade was made toward center (Fig. 11A).

ANOVA was carried out on eye velocity measured 100 ms after the target stopped ($V_{100\ stop}$). This revealed that $V_{100\ stop}$ was not significantly different from $V_{100}$ for the SS conditions of the previous part of the series ($F_{1,11} = 1.11; P = 0.314$). The maximum eye velocity ($V_{pk\ stop}$; Fig. 12A) attained very high levels (up to a mean of 50.8°/s) in these catch trials. It also increased significantly ($F_{3,15} = 37.20; P < 0.001$) with $D_{pk}$ (Fig. 12A) and was not significantly different in the on or off conditions. The time at which peak eye velocity was attained ($T_{pk\ stop}$) changed significantly with stimulus period (Fig. 12B). Mean $T_{pk\ stop}$ had a maximum of 293.5 ms for $T = 2.56$ s and declined to 204.7 ms for $T = 0.64$ ms. The time at which the eye velocity first deviated outside the SS 95% confidence interval ($T_{95\ stop}$) had an overall mean of 197.6 ms (Fig. 12B). Note that the timing of $T_{pk\ stop}$ and $T_{95\ stop}$ is very similar to the corresponding timing of the PVE in catch trial A ($T_{pk\ PVE}, T_{95\ PVE}$; Fig. 10). For the shortest stimulus period ($T = 0.64$ s) 25% of responses showed no significant difference from SS throughout the remaining half-cycle of the response (i.e., $T_{95\ stop} > 0.32$ s).

**Catch trial C: response to unexpected changes in target velocity (experiment 4)**

In experiment 4, the SS response observed after the first two presentations of each series exhibited the same characteristics as in experiments 1 and 2. But at the transition between series, when the target velocity unexpectedly changed, there were considerable differences in the eye velocity compared with the remainder of the series, as shown for series 3 and 4 in Fig. 13. These examples are from a single subject but all subjects exhibited very similar behavior. In series 3, where the target velocity increased from 32 to 80°/s, the response to the first presentation had a velocity trajectory throughout the first half-cycle that was almost indistinguishable from that for the average (SS) velocity of the previous series. Peak velocity in this first response had a mean of 31.4°/s, but subsequently increased to a peak of $\sim 50°/s$ in the SS for that series. Conversely, in series 4, where the peak target velocity decreased from 80 to 32°/s, the response to the first half-cycle of the first

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**FIG. 11.** Examples of eye displacement (top traces) and desaccaded eye velocity (bottom traces) in catch trial B compared with the preceding SS. Target motion stopped at peak displacement and either went off (A) or remained on but stationary (B). Ordinate scale for SS on right of top figures.
presentation had a velocity (mean peak = 47.2°/s) that was well in excess of target velocity and very similar to the SS velocity profile for series 3. As a consequence of the over- or underestimation of velocity, eye displacement was also more irregular. In series 3 and 5, there were corrective saccades after an average of 223.4 ± 10.6 ms to catch up with the target and secondary saccades after a further 127.0 ± 20.4 ms. In series 2, 4, and 6, corrective backward saccades occurred later after an average of 317.9 ± 27.0 ms with further corrections after 220.8 ± 33.9 ms. These saccades brought eye position closer to the average displacement trajectory for that series. To test the significance of the changes from one series to the next, we compared V100, Vpk1 and Tpk1 by ANOVA.

INITIAL EYE VELOCITY. When ANOVA was carried out with series order, stimulus period and order of presentation within series as factors there were strong interactions between series and presentation order because of the large changes at the beginning of each series. Two separate analyses were therefore carried out, one for series 2, 4, and 6 (low-velocity stimuli) and another for series 3 and 5 (high-velocity stimuli) (N.B. series 1 was excluded because it contained the initial transient response). In series 2, 4, and 6, repeated contrasts revealed that there was a significant decrease \( F_{1,5} = 18.56; P = 0.008 \) in V100 (Fig. 14; 80 –32°/s) between the first response in each series and the second, but no change thereafter \( (P > 0.914) \). Similarly, in series 3 and 5 repeated contrasts showed a significant increase \( F_{1,5} = 33.17; P = 0.002 \) in V100 (Fig. 14; 32–80°/s) between the first and second responses, but no change thereafter \( (P > 0.078) \). Further analysis was then carried out by grouping the second, third, and fourth presentations of each series with the first presentation of the next series, using data from all series. Interactions between series...
and re-grouped presentation order were then nonsignificant. Simple contrasts, using the first response of the new series as the reference, showed that there was no significant difference in V100 among the second, third, or fourth presentations of the previous series and the first presentation of each new series \( [e.g., F_{1,5} = 0.62; P = 0.468 \text{ for 4th (prior) vs. 1st (new)}] \). For the shorter period stimulus \( (T = 0.8 \text{ s}) \), there was also no significant difference in V200 between the first response in each new series and the second to fourth presentations of the previous series \( [e.g., F_{1,5} = 2.18; P = 0.20 \text{ for 4th (prior) vs. 1st (new)}] \).

**PEAK EYE VELOCITY.** For both stimulus periods \((1.28 \text{ and } 0.8 \text{ s})\), there was a significant effect of order of presentation on Vpk1 (Fig. 14B). Repeated contrasts showed that when target velocity unexpectedly decreased, Vpk1 was significantly greater in the first presentation than the second \( (F_{1,5} = 57.72; P = 0.001) \) but did not change thereafter. Similarly, when target velocity increased, Vpk1 was significantly less in the first presentation than the second \( (F_{1,5} = 70.70; P < 0.001) \) and did not change in the subsequent presentations. However, the peak velocity attained in the first presentation of each series was generally different to the second, third, and fourth presentations of the previous series (Fig. 14). When target velocity decreased, Vpk1 was slightly attenuated (by 25% for \( T = 1.28 \text{ s} \) and 10% for \( T = 0.8 \text{ s} \)) compared with the previous series and when target velocity increased Vpk1 was somewhat higher (by 50% for \( T = 1.28 \text{ s} \) and 8% for \( T = 0.8 \text{ s} \)) than in the previous series. So, although the eye velocity 100 ms after target onset (V100) and peak velocity (Vpk1) occurring over the 1st through 4th target presentations within each series for the \( T = 0.8 \text{ s} \) stimulus, High- to low-velocity transitions \((80–32°/s)\) are averages of series 3 and 5, low- to high-velocity transitions \((32–80°/s)\) are averages of series 2 and 4. Mean of 6 subjects, \( +1 \text{ SE} \).

**DISCUSSION**

Implications of observed changes in response timing with stimulus repetition

The experimental results demonstrate that the repeated presentation of a single-cycle sinusoid leads to a temporal shift in the whole response that is evident even within the second presentation period. This is shown to greatest effect by the responses to the shorter duration stimuli. For example when \( T = 0.8 \text{ s} \) the whole of the first response was delayed on average by 121 ms with respect to the stimulus (Fig. 5). This initial latency falls well within the range \((100–130 \text{ ms})\) that has been found most often for the initiation of smooth pursuit (Carl and Gellman 1987; Rashbass 1961; Robinson 1965; Tychsen and Lisberger 1986). But in the SS response this delay had been reduced to only 43 ms. These changes occurred despite the fact that the eye was held fixed between presentations and the timing of presentations was randomized. Such changes cannot be explained as the behavior of a conventional linear feedback system, which would generate identical responses to randomly appearing transient stimuli of this kind. Moreover, the responses from experiment 3 (Fig. 6) show that the major adjustment of the timing and magnitude of the response occurred even when no eye movement was made during the initial presentation. We have previously shown that it is possible to do this for simple ramp stimuli (Barnes et al. 1997), but this new evidence suggests that the timing and velocity of a complete sinusoidal movement can be assessed on the basis of the sensory information alone.

Two factors suggest that the mechanisms responsible for generating the changes in timing with stimulus repetition could also be responsible for prediction during continuous sinusoidal stimulation. First, the timing of the SS responses to repeated single sinusoids, when represented as a phase shift with respect
to the stimulus, is very similar to that observed at equivalent frequencies in the continuous sinusoidal response (Fig. 8).
Second, although the individual responses to each single sinusoid tend to have a rather different velocity profile to the stimulus waveform, the concatenation of the successive responses gives a continuous waveform that is not dissimilar to the response to continuous sinusoidal stimulation (Fig. 9).

What is the origin of these changes in timing and what conclusions can be drawn about the role of visual feedback in the SS response? Is it possible, for example, that in the SS the response beyond the initial anticipatory movement could be explained by the behavior of a simple retinal error feedback system. Three arguments may be used to counter this. First, the SS delays of 40 ms for $T = 1.28$ s and 45 ms for $T = 0.80$ s are less than the assumed absolute minimum of 60 ms (Kao and Morrow 1994; Merrison and Carpenter 1994), and for $T = 2.56$ s, the mean delay was only 10 ms (as derived from the phase of $-1.41^\circ$ shown in Fig. 8). Second, it would have to be assumed that there was no other source within the feedback loop that would give rise to additional time delay. But the decay of eye velocity that takes place in the catch trials when the target disappears suggests the presence of a low-pass filter with a time constant of $\geq 0.11$ s as noted by others (Pola and Wyatt 1997; Robinson et al. 1986). Such a filter would add delay to the feedback loop at higher frequencies. Third, if, in the SS, the response was controlled wholly by visual feedback, it would be expected that when the target unexpectedly disappeared, as in catch trial $B$, the response would start to decay immediately after the latent period of 60 ms was exceeded. The continuation of the response for up to 200 ms after target offset indicates that this part of the response must, in fact, arise from another, internally driven, nonvisual source.

**The role of nonvisual, anticipatory mechanisms in the first half-cycle of the response**

The simplest interpretation of these findings is that information about the target motion is sampled and stored within the first presentation and then replayed in the second and subsequent presentations as suggested previously (Barnes and Asselmann 1991). The major question concerns what form this stored information takes and how it is related to the initial anticipatory movement.

It is a characteristic of anticipatory smooth movements that velocity increases rather slowly over several hundred ms (Becker and Fuchs 1985; Boman and Hotson 1988), approximating a constant acceleration (Kao and Morrow 1994). Previous experiments have shown that the velocity profile of the anticipatory response is very similar irrespective of factors such as the interval between presentations (Barnes and Asselmann 1991) and the duration for which the target is exposed (Barnes and Grealy 1992). Altogether these and other results suggest that the anticipatory velocity profile has a rather specific dynamic characteristic and that the anticipatory movements are initiated in a ballistic manner with preprogrammed scaling appropriate to the expected target velocity.

So how much contribution does the anticipatory movement make to the whole response? An important point to make first is that attempts to measure the effect of the anticipatory response need not be confined to examining the response prior to the effects of visual feedback. This is merely a convenient and safe way of defining the minimum time at which this may be measured. For this purpose, examination of V50 values (Fig. 4A) confirms the velocity scaling of the anticipatory response at a time that is less than the shortest latency observed experimentally (60 ms). But it is evident from the catch trials that a latency of 100 ms is a more realistic time limit for the first effects of visual feedback, since the shortest latency at which there was a significant difference between the predicted velocity in a catch trial and the prior SS, had a mean of 147 ms ($T_{95,\text{PVE}}$, Fig. 10B) and a minimum, in any subject, of 110 ms. Without the results from the catch trials, it would be difficult to determine what happens to the anticipatory movement after the effects of visual feedback start to take effect. However, results from the catch trials indicate that the effects of the preprogrammed movement can be observed for $\geq 200$ ms after target onset and, in some instances, for much longer.

First, in catch trial $A$, when the target failed to appear as expected, an anticipatory eye movement was generated that continued for nearly 200 ms after the time at which the target would have appeared, before attaining its peak velocity (Fig. 10B). This response was generated in the complete absence of any visual stimulus and must, therefore have been of central origin. The fact that the peak velocity ($V_{pk,\text{PVE}}$) was scaled in proportion to target velocity indicates that, at this time, the movement was predictively related to the expected target velocity. The velocity attained at this time could be very high (e.g., mean $V_{pk,\text{PVE}} = 40.9^\circ/\text{s}$ for $D_{pk} = 20^\circ$, $T = 0.64$ s, Fig. 10A), accounting for an average of 80% of the peak velocity attained in the SS response for the two shortest period stimuli (e.g., mean $V_{pk,\text{SS}} = 49.4^\circ/\text{s}$ for $D_{pk} = 20^\circ$, $T = 0.64$ s; Fig. 4B). Although the peak response was attained after $\sim 200$ ms, it then took some time to decay. The fact that the response took longer to decay for the longer period stimuli probably indicates that there was still some underlying central drive that had been preprogrammed to run for a period related to the half-period of that stimulus but that was progressively attenuated by visual feedback.

The prolonged effect of the anticipatory movement could also be observed in the difference between the first reactive response in each series and the SS response. Inspection of this difference also indicated that it took $\sim 200$ ms before the effects due to visual feedback outweighed the effects due to the predictive internal drive [$T_{pk}(\text{SS} - \text{1st})$, Fig. 10B].

The results of catch trial $C$ (experiment 4) indicate that the effects of the anticipatory movement can continue largely unmodified well beyond 200 ms. The inappropriate response that occurred at the beginning of each new series, when there was an unexpected change in target velocity, persisted for $\geq 100$ ms as evidenced by the similarity of V100 values to those of the previous series (Fig. 14). After this time, presumably, retinal error feedback started to modify eye velocity and $V_{pk,\text{PVE}}$ was thus attenuated (by 25% for $T = 1.28$ s; by 10% for $T = 0.8$ s) or amplified (by 50% for $T = 1.28$ s; by 8% for $T = 0.8$ s) as appropriate. But, it took an average of between 382 and 549 ms for the eye velocity to return to the level that was appropriate for the target velocity of the new series. In fact, for the shorter period stimulus ($T = 0.8$ s), a large percentage (53%) of responses did not fall within the 95% confidence interval of the appropriate SS velocity trajectory until well after the end of the first half-cycle. It is evident from the eye displacement responses shown in Fig. 13 that the subjects were...
well aware of the error and did try to correct this with saccadic eye movements. The control of the smooth movement appeared to be beyond cognitive control in the sense that the subject could not simply switch off this oculomotor drive signal but could only modify it more gradually through the attenuating effects of visual feedback. In this respect, the observed effects were similar to those seen when subjects attempt to suppress an ongoing vestibuloocular reflex response.

It is concluded from the foregoing evidence that the centrally generated response that starts off as the anticipatory movement actually develops into a velocity profile that, for ~400 ms after target onset at least, is very similar in form to the response that was generated in the previous presentation. In other words, although the SS response after target onset is reproduced in the presence of visual feedback, that visual feedback probably plays little part in the SS response and cannot quickly correct a major discrepancy between the centrally generated eye movement and actual target velocity. These general conclusions are also supported by evidence from a previous experiment in which the target was unexpectedly stabilized on the fovea in the blank interval between intermittent target presentations (Barnes et al. 1995). After stabilization, subjects continued to produce an eye velocity trajectory similar to that before stabilization even though there was now no retinal velocity error signal or target motion stimulus. Moreover they could repeat this response many times, as though they were simply reproducing preprogrammed output from an internal store.

Evidence for central drive mechanisms in the second half-cycle of the response

The latencies in the second half-cycle of the sinusoid in the SS conditions (Tcross and Tpk2, Fig. 5B) were also too short to be attributed to visual feedback, indicating that the return movement must also have been largely preprogrammed. The results of catch trial B provide evidence in support of this because the eye reversed direction and continued to move with the same velocity as it would have done in the SS for ~190 ms before there was any significant deviation (Fig. 12B). It reached a peak (VpkSTOP) that was scaled in proportion to expected target velocity (Fig. 12A) and comparable in magnitude to the peak velocity of the PVE in catch trial A (Fig. 10A). The time to reach peak velocity (TpksSTOP, Fig. 12B), at ~200 ms or more, was also similar to that of the PVE (TpkPVE, Fig. 10B). This indicates that the internal drive must have been stronger than the suppressive effect of visual feedback for at least this period. Note that for the shorter stimulus periods (T = 0.8 and 0.64 s), the eye had not even reached peak displacement at the time the target stopped because of the phase error in the SS. Yet still the eye reversed its direction and continued with the same velocity for 200 ms after target offset, bringing the eye back toward center. In fact, for the shortest stimulus period (T = 0.64 s), the second half of the response was completed without any significant difference from the SS trajectory in 25% of the trials. The fact that this occurred even in the presence of the stationary target (ON condition) indicates the strength of this internal drive. The values of TpksSTOP and VpkSTOP are comparable to those obtained by van den Berg (1988) in response to an unexpected target stop at the zero velocity crossover of a continuous multi-cycle sinusoidal stimulus. The findings also accord with the observation that eye movements continue in the expected direction when unexpected direction changes are introduced (Keating 1991; Lisberger et al. 1981) as well as the brief continuation that occurs when the target disappears (Whittaker and Eaholtz 1982).

One explanation for the behavior in the second half-cycle could be that a second anticipatory response, a mirror image of the initial anticipatory movement, is initiated prior to the expected change of target reversal and brings the eye back toward center. But, another possibility is that a different predictive process starts to take over after the anticipatory eye movement of the first half-cycle is complete. Evidence for this will now be considered with reference to modeling studies.

Modeling the mechanism of rapid prediction in pursuit

Models of predictive behavior in pursuit may be divided broadly into two basic categories: self-adaptive, error minimizing mechanisms (Bailh and MacDonald 1983; Deno et al. 1995; Kettner et al. 1997; van den Berg 1988) and systems that rely on storage of past activity (Barnes and Asselman 1991; Dallos and Jones 1963). Self-adaptive mechanisms generally allow estimation of eye velocity in the near future on the basis of samples taken from the recent past. Typically this might involve the summation of a number of delayed internal signals with different weighting factors that are determined adaptively by a continual process of minimizing error in the response. Kettner et al. (1997) presented an elegant model of this type based on the architecture of the cerebellum. Although this model is able to simulate responses to complex trajectories, it takes many iterations to establish a SS and is unable to account for anticipatory smooth pursuit movements. It is unlikely therefore that this model could explain the ability to generate and modify predictive activity as rapidly as observed in the experiments reported here, although it could account for the long-term adaptation of pursuit responses (Carl and Gellman 1986). Pavel (1990) has shown that a simpler scheme, based on a few (10) delays with sampling intervals of 200 ms can minimize phase error for a 1-Hz sinusoidal stimulus within one cycle. This could possibly account for the predictive behavior in the second half-cycle of the response to the single sinusoids but would also be unable to explain the anticipatory response in the first half-cycle.

An alternative approach is to suggest that prediction may be accomplished through short-term storage of waveform characteristics. Previously we have argued that prediction in pursuit can be modeled in a very simple way by assuming that two independent processes are involved: the temporary storage of premotor drive information and the assessment of periodicity or timing (Barnes and Asselman 1991; Barnes and Wells 1999; Barnes et al. 1995). The model consists of two pathways. One relays basic retinal velocity error feedback; the other is an internal positive feedback loop that samples premotor drive and subsequently replays it as an anticipatory movement under the control of a periodicity estimator. This model is similar to the (nonpredictive) efference copy models suggested by other authors (Lisberger and Fuchs 1978; Robinson et al. 1986; Yasui and Young 1975) with the important difference that the stored information can be replayed at a later time determined by the periodicity estimator. When pursuing a regular periodic target motion, periodicity is assumed to be derived from the stimulus itself, but timing information could be provided from...
an independent source such as the audio cue used in the experiments described here.

In simulations that we have presented so far (Barnes 1994; Barnes and Wells 1999), it has been assumed that the periodicity estimator sets a finite delay within the re-afferent feedback pathway that is related to the half-period of the stimulus. This has been shown to provide a good simulation for the response to continuous sinusoidal stimuli. It is equivalent to assuming that the store is like a first in-first out (FIFO) buffer, so that it is effectively the whole of the premotor drive over the last half-period that is being stored. Using the same model, it is possible to simulate the response to repeated single sinusoids. The model mimics the significant reduction of phase error that occurs between the first and second presentations and results in the release of the predictive velocity estimate (PVE) when the target unexpectedly fails to appear. However, it is unlikely that the degree of detail in the stored information that is inherent in the use of a delay line in this model is necessary. As we have shown before (Barnes and Asselman 1991), it is only necessary to represent the previous half-cycle of the waveform by a few stored samples (say 1–4) to simulate the response to frequencies >0.5 Hz, and these few samples might then be held in a true short-term store. In the context of the present experiment, the response to single sinusoids of period ≤1.25 s could easily be represented by two samples of opposite polarity, one for each half-cycle. Sequential release of this stored information would result in generation of two temporally separated and oppositely directed anticipatory movements. Boman and Hotson (1992) have provided experimental evidence that supports this idea. They showed that when a sequence composed of two ramp stimuli is repeatedly presented, the anticipatory response to the second ramp merges with the decay of the response to the first ramp to produce a smooth transition between the two. They also showed that summation of individual anticipatory responses to ramps in opposite directions simulated the predictive response to a triangular waveform stimulus.

Evidence for the neural substrate of our model has been reviewed previously (Barnes et al. 1995). It points to involvement of the frontal eye fields (FEFs) in the production of smooth eye movements through connections with the pons and cerebellum (Stein and Glickstein 1992). FEF receives input from visual motion processing areas (Komatsu and Wurtz 1988; Newsome et al. 1988), and other pursuit-related areas in parietal cortex (Tusa and Zee 1989) and lesions of the FEF are known to impair both predictive and visually guided components of smooth pursuit (Keating 1991, 1993). Most importantly, microstimulation of FEF can evoke smooth eye movements with a slow build up of velocity similar to that of anticipatory smooth pursuit and a velocity level that is dependent on the level of stimulation (Gottlieb et al. 1993). Heinen and Liu (1997) have shown that the supplementary eye field (SEF) in the dorsomedial frontal cortex appears to be involved in determining the time at which to release anticipatory smooth eye movements in response to predictable stimuli. SEF may thus serve as the periodicity estimator of our model, perhaps controlling the release of anticipatory activity through FEF. A possible site for the short-term storage of the anticipatory information is prefrontal cortex (PFC), which has been implicated in other delayed-response tasks (Goldman-Rakic 1991).

Conclusions

Repeated presentation of transient single-cycle sinusoidal stimuli leads to significant changes in timing of the smooth eye movement response through development of anticipatory movements that form the predominant part of the first half-cycle of the SS response. Evidence suggests that the anticipatory movements arise from short-term storage of reaффerent information derived from prior stimulation and its subsequent release under the control of a separate timing mechanism. Timing of responses in the SS is consistent with that of the response to continuous sinusoidal target motion, and concatenation of successive anticipatory responses indicates that prediction in sinusoidal pursuit could be accomplished by continuous initiation of appropriately timed anticipatory movements. There remains the possibility that self-adaptive predictive mechanisms may also exist and take over from initial anticipatory components, but the evidence suggests that such mechanisms may be more important in the longer-term adaptation of pursuit mechanisms rather than being involved in short-term prediction.

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PREDICTION IN OCULAR PURSUIT


