Predictive Smooth Ocular Pursuit During the Transient Disappearance of a Visual Target

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Bennett, Simon J. and Graham R. Barnes. Predictive smooth ocular pursuit during the transient disappearance of a visual target. J Neurophysiol 92: 578–590, 2004. First published February 11, 2004; 10.1152/jn.01188.2003. When a moving target disappears and there is a complete absence of visual feedback signals, eye velocity decays rapidly but often recovers to previous levels if there is an expectation the target will reappear further along its trajectory. Given that eye velocity cannot be maintained under such circumstances, the anticipatory recovery may function to minimize the developing velocity error. When there is a change in target velocity during a transient, any recovery should ideally be scaled and hence predictive of the expected target velocity at reappearance. This study confirmed that subjects did not maintain eye velocity close to target velocity for the duration of the inter-stimulus interval (ISI). The majority of subjects exhibited an initial reduction in eye velocity followed by a scaled recovery prior to target reappearance. Eye velocity during the ISI was, therefore, predictive of the expected change in target velocity. These behavioral data were simulated using a model in which gain applied to the visuomotor drive is reduced after the loss of visual feedback and then modulated depending on subject’s expectation regarding the target’s future trajectory.

INTRODUCTION

To overcome the delay in processing visual feedback and pursue a moving target without significant retinal position and velocity error, it is necessary to predict the moving target’s future trajectory. For a target moving with a predictable trajectory (e.g., constant velocity or sinusoidal motion), smooth pursuit with gain close to unity can rapidly be achieved (Leigh and Zee 1991 Lisberger and Fuchs 1978). In fact, even when target motion is irregular (Dallos and Jones 1963; Kowler and Steinman 1979), subjects exhibit reasonable tracking, revealing the primacy of prediction in the control of the ocular response (for a review of cognitive influences on smooth pursuit, see Kowler 1990). When pursuing a continuously visible moving target, future eye motion could be predicted using a corollary discharge mechanism in which the input is an efference copy of the ongoing eye movement (Krauzlis and Lisberger 1994; Krauzlis and Miles 1996; Leigh and Zee 1991; Robinson et al. 1986). Feedback of visual motion signals, such as image velocity and acceleration (Krauzlis and Lisberger, 1994), would then correct for any difference between target and eye motion, resulting in the continual update of the efference copy (Lisberger et al. 1981). This type of model, however, does not provide a satisfactory account for anticipatory smooth pursuit eye movements that occur in the absence of an efference copy (Barnes et al. 1997) or the influence of expectancy regarding the upcoming target velocity (Jarrett and Barnes 2001; Kao and Morrow 1994; Boman and Hotson 1992). Consequently, it has been recognized that the extra-retinal input is a more complex arrangement reflecting velocity-coded information (Barnes and Asselman 1991; Churchland et al. 2003), which is influenced by cognitive factors such as perception, expectation, and attention (Beutter and Stone 1998; Madelain and Krauzlis 2003b; Pola and Wyatt 1997; Tanaka and Lisberger 2000).

Extra-retinal input continues to drive smooth pursuit at a reduced gain when visual feedback is removed, such as when the image of a moving target is stabilized on the retina (Morris and Lisberger 1987; Pola and Wyatt 1997). Similar to pursuit initiation, the continuation of smooth pursuit in the absence of a visual target is under volitional control and can be mediated by the subject’s intention. For example, when there is a complete loss of a visual feedback signal after target disappearance, smooth pursuit continues at a reduced gain only if subjects expect the target will reappear (Becker and Fuchs 1985) or if they direct attention to “pushing” the imagined target (Pola and Wyatt 1997). If subjects do not attempt to maintain pursuit of the non-visible moving target, eye velocity decays to zero in roughly an exponential manner (Mitranu and Dimitrov 1978) after the termination of the extra-retinal input to the visuomotor drive (Barnes and Asselman 1991).

Recent attempts to model the reduced velocity smooth pursuit that is exhibited during the transient disappearance of a moving target (Bennett and Barnes 2003; Churchland et al. 2003; Madelain and Krauzlis 2003a) typically include a variable gain signal acting on the visuomotor drive (see Krauzlis and Lisberger, 1994), which is reduced after the loss of visual feedback. By altering the value assigned to the variable gain signal between trials (i.e., increasing the rate at which gain was reinstated from zero to one), Madelain and Krauzlis (2003a) simulated their finding of an increase in pursuit velocity gain from 0.59 to 0.89 after 8–10 daily sessions of training with auditory reinforcement. The authors therefore concluded that in addition to accounting for long-range adaptation to changes in the relationship between visual input and motor output...
(Optican et al. 1985), modifying an internal gain parameter could explain transient adaptation to changes in visual input after extended training (see also Churchland and Lisberger 2002). Similar to Becker and Fuchs (1985), the authors also found that when target velocity remained unchanged between trials, and hence was highly predictable, eye velocity was higher compared to randomized velocity trials. Presumably, then, predictability regarding target velocity influenced eye velocity during the transient by modifying the time at which gain was reinstated and/or the magnitude of slope of the variable gain signal.

Bennett and Barnes (2003) also proposed that modifying gain applied to the visuomotor drive after target offset could simulate the eye-velocity trajectory in response to transient target disappearance. Unlike previous models in which the visuomotor drive is passed through a leaky integrator (Krauzlis and Lisberger 1994, Madelain and Krauzlis 2003a), making it necessary to increase gain higher than unity to reinitiate eye velocity back to the original level, they proposed that a local memory structure preserved the visuomotor drive after the loss of visual feedback. This arrangement enabled eye velocity to be simulated with an increasing profile up to target reappearance by reinstating gain to unity (for other behavioral data, see Becker and Fuchs 1985; Churchland et al. 2003). It was also noted that the inclusion of a local memory structure and variable gain signal could simulate a predictive, anticipatory response prior to the onset of target motion in a single-velocity ramp (see Jarrett and Barnes 2002) and a change in target velocity during a double-velocity ramp (Barnes and Asselman 1991; Boman and Hotson 1992). However, because only multiple, constant-velocity ramps were examined (Becker and Fuchs 1985; Bennett and Barnes 2003), it was not possible to determine whether the increase in eye velocity during the transient was simply a non-predictive recovery to the level prior to the loss of visual feedback.

Work using double-ramp stimuli in which the target is continually visible has demonstrated that the eye-velocity trajectory around the time of an expected direction change is predictive of target velocity associated with the upcoming ramp (Boman and Hotson 1992). Furthermore, in experiment 3, when an ISI (200–2,000 ms) was inserted between ramps of the same velocity, there was some evidence of anticipatory eye velocity during the transient. However, because the target remained stationary during the transient and target velocity was the same in the first and second ramps, it was not possible to determine if the eye velocity during the transient was predictive of the second ramp. Although there was some evidence of anticipatory eye velocity during the transient, this was more similar to the slow build-up in velocity that is exhibited prior to target onset in successive single ramps. To date, only Barnes and Schmid (2002) have examined quantitatively the eye-velocity trajectory in response to double-ramp stimuli separated by an ISI in which the target continues to move at the same or a changed velocity. However, because only a single, brief ISI (200 ms) was used, the interaction between the decaying eye velocity and the anticipatory increase could not be clearly identified and had to be inferred by correlation.

The present study was designed to examine subjects’ ability to extrapolate pursuit over a transient period of non-visible target motion and, more specifically, to determine if they exhibit scaled (i.e., predictive) eye velocity prior to target reappearance. Our results show that the recovery in eye velocity after the loss of visual feedback was scaled and hence predictive of the upcoming target velocity. We show that such behavior can be simulated using an extension of our previous model in which the visuomotor drive is preserved after the loss of visual feedback. We propose that predictive changes of eye velocity are the result of scaled modifications of an internal gain signal.

**METHODS**

**Subjects**

Eight subjects participated [mean age: 34 ± 9.6 (SD) yr], all of whom had some previous experience of oculomotor experiments. Subjects had normal or corrected-to-normal vision, were healthy, and had no relevant medical or psychiatric history. The experiment was conducted according to a protocol approved by University of Manchester Institute of Science and Technology local ethics committee in conformity with the tenets of the Declaration of Helsinki. Subjects participated with informed consent.

**Apparatus**

The experiment was conducted in a purpose-built dark room. Subjects were seated centrally, in front of a flat white screen (1.5 × 1.5 m) at a viewing distance of 1.7 m. The head was supported on an adjustable chin-rest and fixed by clamps to the sides. The visual target consisted of a ring of 12 light-emitting diodes (LEDs) that were optically reduced to form a ring of dots subtending 1.2° on the screen. When projected on the screen, the LEDs had a luminance of 0.5 cd/m². Subjects reported no difficulty seeing the target. The multiple-dot stimulus was sufficient to drive smooth pursuit (Bennett and Barnes 2003; Heinen and Watamaniuk 1998).

The horizontal motion of the target was controlled by reflection from a mirror galvanometer. Toggling the illumination of the LED’s controlled target visibility. The images of both eyes were recorded at intervals of 5 ms using an infrared pupil-tracking system (Chronos, Skalar Medical BV) and stored to disc for later off-line analysis. During static fixation, the noise within eye-position data was approximately ± 0.1° (Clarke et al. 2002). Prior to each trial a calibration was performed in which subjects pursued a sinusoidal horizontal oscillation at a frequency of 0.4 Hz with amplitude of ±20°. At the end of the calibration, the target remained stationary at the center position for 2,500 ms, during which subjects maintained fixation. Eye position was recorded with a resolution of ¬5–10 min arc. A calibration was deemed successful when the linearity between the eye and target signal was >99%

**Procedures**

Subjects performed four experimental trials and two control trials, each consisting of 24 presentations. Trials were received in randomized combinations to minimize any sequence effects. An example of representative experimental and control presentations and the corresponding eye displacement and velocity are shown in Fig. 1. The start of a presentation was signaled by an auditory warming cue of 80-ms duration. Simultaneously, a target was illuminated and remained stationary at a position of ¬20° to the left of the screen center for 800 ms. In experimental trials, the target was extinguished for a 400-ms gap period and reappeared, moving horizontally to the right with a constant velocity of 12 or 24°/s for 400 ms. The predictable gap period

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1 It may be undesirable to increase gain beyond unity because this could introduce instability (Dallos and Jones 1963) although this can be overcome by increasing the damping within the system (Robinson et al. 1986).
FIG. 1. Representative examples of eye displacement (thin black line) and velocity (thick black line) from a single presentation for subject 4 pursuing a 24°/s target (medium gray line). In the experimental presentation (A) the target was presented for 400 ms in ramps 1 and 2 with an inter-stimulus interval (ISI) of 800 ms. In the Ctrl I presentation (B), the target was presented for 1,600 ms. In the Ctrl II presentation (C), the target was presented for 400 ms and then continued to move while not visible for a further 1,200 ms. The target is visible when the shutter (broken gray line) is high. The auditory signal is not depicted but occurred 800 ms before the onset of ramp 1. Saccades have been removed from the velocity trace.
was included to facilitate prediction of target motion onset. The target was then extinguished for a 400- or 800-ms inter-stimulus interval (ISI). During the first 12 presentations, the mirror turned at the same rate throughout the ISI, and hence the non-visible target continued to move with a constant velocity. In the next 12 presentations, the mirror turned at either a decreased or increased rate, corresponding to a constant target velocity of 12 or 24°/s. The duration of the ISI was the same in the first and second block of 12 presentations within an experimental trial. At the end of the ISI, the target was re-illuminated and reappeared for 400 ms, moving with the same velocity as that during the ISI (Fig. 1A). The target was then extinguished for 1,800 or 1,400 ms before the start of the next presentation. The duration of this final part of the presentation was balanced with the duration of the ISI such that each presentation lasted 4,200 ms. Subjects were instructed to pursue the target during both the visible (ramps 1 and 2) and non-visible (ISI) portions of the trajectory. Subjects performed one trial for each combination of ISI (400, 800) and target velocity (12, 24°/s).

In control trials, subjects received two different types of target presentation. In the first 12 presentations (Ctrl I), the target was extinguished for a 400-ms gap period and reappeared, moving horizontally to the right with a constant velocity of 12 or 24°/s for 1600 ms (Fig. 1B). The target was then extinguished for 1,400 ms before the start of the next presentation. Subjects were instructed to return towards the start position when the moving target was extinguished. In the next 12 presentations (Ctrl II), the target was also extinguished for a 400-ms gap period and reappeared, moving horizontally to the right with a constant velocity of 12 or 24°/s for 400 ms (Fig. 1C). The same target velocity was delivered in the first and second block of 12 presentations within a control trial. The target was then extinguished for 1,200 ms before a second auditory warning cue of 80-ms duration signaled the end of the target motion. During this time, the mirror continued to turn at the same rate, and hence the target continued to move, although not visible, with a constant velocity. Subjects were instructed that although the target would not reappear, they should continue to pursue the target until the non-visible portion of the trajectory and return to the start position only after hearing the second auditory warning cue. There was a 1,400-ms interval before the start of the next presentation. The visible and non-visible portions of the trajectory in control trials were balanced such that the overall duration was 4,200 ms. The inclusion of the two control trials enabled us to determine if the eye velocity in experimental trials was a response to the loss of visual feedback during the transient or simply reflected the normal pursuit response when the target remained visible (Ctrl I) or was not expected to reappear (Ctrl II).

**Data analysis**

Eye velocity and acceleration were derived from eye position using a two-point central difference algorithm. Eye movements were then analyzed by first identifying and removing saccades from the response using a technique similar to that described previously (Bennett and Barnes, 2003). Saccades were first identified as points in the acceleration trace exceeding a threshold of 1,000°/s². When the threshold criteria were exceeded, the complete saccade trajectory was identified by finding the peak and trough of acceleration. On the rare occasions when the use of the acceleration threshold failed to identify a saccade, a second pass was made in which a velocity threshold (30°/s) was applied. Data points equivalent to 25 ms at the beginning and end of the identified saccade trajectory were then excluded to ensure that no saccadic element remained when applying subsequent interpolation. Using these criteria saccades of ≥0.3° were reliably detected. A linear interpolation routine was used to bridge the gaps produced by removal of saccades from the eye-velocity trajectory. Saccades occurring during eye movements were only filtered at 25 Hz with a low-pass, zero phase filter. To provide a measure of eye velocity that was reflective of a steady-state response uninfluenced by initial uncertainty, eye-velocity data were averaged separately for each subject from presentations 3–6, 9–12, 15–18, and 21–24. Presentations 3–6 and 15–18 were representative of an early block, and 9–12 and 21–24 were representative of a late block.

Eye velocity at onset and 100 ms after onset of ramp 1 (V₀₁ and V₁₀₀₁, respectively) and ramp 2, (V₀₂ and V₁₀₀₂, respectively) was derived for each subject from their averaged response to the block of four presentations for each combination of the independent variables. These values were examined because they correspond to a time at which the response is considered to be uninfluenced by visual feedback, and therefore represent smooth pursuit driven by extra-retinal inputs alone. To provide an indication of the magnitude of the visually driven response to ramp 1, the peak eye velocity (Vₚk) was extracted. To examine the effect of expectation on the eye-velocity trajectory between target offset and reappearance (during the ISI), eye velocity at the beginning of the ISI (Vₑₛᵢ), minimum eye velocity (Vₘᵢₙᵢ), and the time of minimum velocity (Tᵥₘᵢₙᵢ) were also determined.

To establish if there was any effect of the independent variables on smooth pursuit in the experimental trials, the intra-individual means for each dependent variable were submitted to separate two velocity (12, 24°/s) × two block (early, late) × two ISI (400, 800 ms) × two presentation type (constant target velocity, changing target velocity) analysis of variance (ANOVA) with repeated measures on all factors. Main and interaction effects were further analyzed using Tukey’s HSD post hoc procedure. The critical alpha level was set at P < 0.05. Where previous analysis revealed no effect of a particular independent variable(s), the factor(s) was collapsed in subsequent ANOVA. Data from control trials were not included in the primary analysis because there were unequal levels of independent variable. However, where it was deemed appropriate and relevant, further ANOVA on the collapsed experimental data and control data were conducted.

**RESULTS**

**Pursuit prior to and following target appearance**

The predictable gap period and velocity of the first ramp facilitated the generation of anticipatory smooth pursuit prior to target appearance at ramp 1 (V₀₁ and V₁₀₀₁). There was some between-subject variation, but still, for the majority of presentations [e.g., 185 of the 192 measures derived from 2 target velocities, 6 trials (4 experimental, 2 control), 2 blocks, 8 subjects] subjects exhibited eye velocity >2°/s as the moving target first became visible (V₀₁). Anticipatory smooth pursuit was still evident 100 ms later, V₁₀₀₁ being >2°/s for all presentations. As expected, V₁₀₀₁ was almost always higher than V₀₁ (185 of the 192 comparisons) and was significantly different from zero for each level of independent variable (t-test, P < 0.001). ANOVA on the experimental trial data indicated that there was no difference between the first and second block of presentations and no systematic effect of ISI and presentation type for both V₀₁ and V₁₀₀₁. However, anticipatory smooth pursuit was scaled to the expected target velocity in the first ramp. Figure 2 shows that V₀₁ and V₁₀₀₁ were significantly higher when pursuing the 24°/s compared to 12°/s target during the first ramp. The group means ±SE for V₀₁ and V₁₀₀₁ collapsed across block, ISI, and presentation type were 4.6 ± 0.7 and 5.9 ± 1.1°/s for the 12°/s stimulus, and 7.9 ± 1.0 and 10.7 ± 1.3°/s for the 24°/s targets, respectively. Not surprisingly, eye velocity continued to be scaled to target velocity when visual feedback became available. This was confirmed by ANOVA, which showed that the peak ve-
Pursuit at and during transient target disappearance

The significant difference in eye velocity when pursuing the 12 and 24°/s targets was still evident as the target disappeared at the start of the ISI ($V_{\text{off}} = 10.5 \pm 0.5$ and $21.2 \pm 0.9$°/s, respectively). ANOVA indicated that there was no difference in $V_{\text{off}}$ across each level of block, ISI, and presentation type. Therefore eye velocity at the moment of target disappearance was scaled to target velocity during the first ramp and was not influenced by the subjects’ expectation regarding the possible change in target velocity in the ISI and second ramp (Fig. 3).

A comparison of $V_{\text{pk}}$ to $V_{\text{off}}$ (collapsed across block, ISI, and presentation type) indicated that there was a significant difference between these measures for both target velocities (Fig. 3). Although this difference was small, it was evident for all 128 comparisons (2 target velocities, 2 blocks, 2 ISI, 2 presentation types, 8 subjects). Therefore as has been shown previously (Boman and Hotson 1988), subjects reached a peak in eye velocity prior to the time corresponding to the start of the ISI, followed by a significant anticipatory slowing down.

After target disappearance in experimental presentations, subjects continued pursuit during the ISI using a combination of saccadic and smooth movement (Fig. 1A). Generally, eye velocity decayed after target offset until it reached a global minimum ($V_{\text{min}}$). Depending on the expectation regarding the target velocity during the ISI and second ramp, there was then a predictive recovery in eye velocity that occurred prior to target reappearance. Observation of the individual subject data revealed evidence of prediction in seven of the eight subjects. Figure 4 shows subject 6’s average response, which was representative of the majority (5 subjects). In the other three subjects, there was a mixed, idiosyncratic response. In presentations where target velocity remained unchanged, subjects 2 and 7 did not appear to exhibit a sizeable decay but rather maintained eye velocity reasonably well throughout the ISI (Fig. 5). However, in presentations where target velocity was changed, these subjects exhibited evidence of a predictive response, scaling up or down eye velocity accordingly. Subject 8 alone did not exhibit a clear anticipatory response regardless of the target velocity in the ISI and second ramp (Fig. 6). Eye velocity was reasonably well maintained when pursuing the 12°/s target and was not obviously influenced by target velocity during the ISI and second ramp. However, eye velocity underwent significant decay when pursuing the 24°/s target and only recovered to previous levels when visual feedback became available.

ANOVA on $V_{\text{min}}$ indicated that there was a significant effect of presentation type for both the 12 and 24°/s targets. In presentations where target velocity increased during the ISI and second ramp (i.e., 12–24°/s), $V_{\text{min}}$ was significantly higher compared to presentations where target velocity remained unchanged (Fig. 7). Observation of the individual subject mean data indicated that 31 of the 32 comparisons (2 blocks, 2 ISI, 8 subjects) were consistent with this trend. A similar, but reverse trend was evident when pursuing the 24°/s target during the first ramp; $V_{\text{min}}$ was significantly higher in experimental presentations where the target velocity remained unchanged compared to where it was reduced. Observation of the individual subject mean data indicated that 30 of the 32 comparisons (2 blocks, 2 ISI, 8 subjects) were consistent with this trend. A further comparison between the experimental and control presentations confirmed the influence of expectation on the resulting $V_{\text{min}}$ (see Fig. 4). When the expectation was that the target would not reappear (Ctrl II), eye velocity continually decayed, $V_{\text{min}}$ generally occurred toward the end of ISI and was significantly lower compared to experimental presentations, and the control presentation in which the target remained visible (Ctrl I). In the Ctrl I condition, eye velocity was significantly higher than in experimental presentations where the target velocity remained unchanged during the ISI and second ramp.

Because of the subjectivity in determining $TV_{\text{min}}$ in the three subjects who did not exhibit a clear decay followed by an increase prior to target reappearance in the unchanging condition, we excluded their data from the analysis of $TV_{\text{min}}$. ANOVA on the remaining group data ($n = 5$) revealed that there was an influence of expectation on the time that minimum velocity occurred. When there was no change in velocity during the ISI, $TV_{\text{min}}$ occurred at the same time across the different levels of target velocity, ISI and block. Figure 8 shows that there was some individual subject variation but no systematic effect of the independent variables. The group
means, collapsed across block, for these particular comparisons were 275 ± 1100 ms (12–12, 800 ISI), 321 ± 320 ms (12–24, 400 ISI), and 363 ± 440 ms (24–24, 800 ISI). However, when subjects expected the velocity to decrease from 24 to 12°/s, TVmin occurred at a significantly later time during the 800-ms ISI (see Figs. 5 and 8). The group means, collapsed across block, for the presentations where target velocity changed during the ISI were 233 ± 23 ms (12–24, 400 ISI), 333 ± 28 ms (12–24, 800 ISI), 332 ± 65 ms (24–12, 400 ISI), and 602 ± 46 ms (24–12, 800 ISI).

Pursuit at and after target reappearance

The influence of expectation regarding the change in target velocity during the ISI was particularly apparent at the moment of target reappearance. V02 was significantly lower in presentations where subjects expected a decrease in target velocity from 24 to 12°/s, TVmin occurred at a significantly later time during the 800-ms ISI (see Figs. 5 and 8). The group means, collapsed across block, for the presentations where target velocity changed during the ISI were 233 ± 23 ms (12–24, 400 ISI), 333 ± 28 ms (12–24, 800 ISI), 332 ± 65 ms (24–12, 400 ISI), and 602 ± 46 ms (24–12, 800 ISI).

Pursuit at and after target reappearance

The influence of expectation regarding the change in target velocity during the ISI was particularly apparent at the moment of target reappearance. V02 was significantly lower in presentations where subjects expected a decrease in target velocity from 24 to 12°/s compared to those where target velocity remained unchanged at 24°/s. This was evident in all of the 32 possible comparisons (2 block, 2 ISI, 8 subjects) between the individual subject means, resulting in group means (collapsed across block and ISI) of 11.0 ± 0.8°/s when it decreased and 18.3 ± 1.9°/s when it was unchanged. The reverse trend, which was also significant, was apparent when subjects expected an increase in target velocity from 12 to 24°/s. Observation of the individual subject means indicated that 30 of the 32 possible comparisons (2 block, 2 ISI, 8 subjects) were in the predicted direction, resulting in a group mean (collapsed across block and ISI) of 14.2 ± 1.6°/s when target velocity increased and 10.2 ± 0.9°/s when it was unchanged. At 100 ms after target reappearance (V1002), the effects of prediction were more consistent with all comparisons of the individual subject data being in the hypothesized direction (Fig. 9). The group mean V1002 (collapsed across block and ISI) was significantly lower in presentations where target velocity decreased from 24 to 12°/s (10.1 ± 0.8°/s) compared to when target velocity remained unchanged at 24°/s (18.5 ± 1.9°/s). Conversely, V1002 was significantly higher in presentations where target velocity increased from 12 to 24°/s target (16.5 ± 1.9°/s) compared to when target velocity was 12°/s throughout the presentation (10.9 ± 0.9°/s).

Because there was an influence of expectation on both the eye velocity during the ISI (TVmin) and at target reappearance (V1002), it was necessary to determine if the difference between these measures was also in accord with the expected target velocity. We therefore collapsed the individual-subject mean TVmin and V1002 over block (early, late) and ISI (400, 800 ms) and submitted the resulting data to a two variable (TVmin and V1002) × two velocity (12, 24°/s) × two presentation type (constant target velocity, changing target velocity) ANOVA with repeated measures on all factors. When target velocity was unchanged, the difference between TVmin and V1002 was significant when pursuing both the 12 or 24°/s target. The

**FIG. 4.** Representative examples of smooth eye velocity from subject 6, averaged across block, pursuing a 12°/s target (top) and 24°/s target (bottom) during the 1st ramp as a function of ISI (400, 800 ms) and presentation type (target velocity unchanged in A and C; target velocity changed in B and D). Gray lines represent 400 ISI, black lines represent 800 ISI. Average eye velocity from control presentations (Ctrl I = thin black line, Ctrl II = thin gray line) is included for comparison.
group mean difference was $2.4 \pm 0.7^\circ/\text{s}$ for the $12^\circ/\text{s}$ target and $2.4 \pm 1.0^\circ/\text{s}$ for the $24^\circ/\text{s}$ target. Observation of the individual subject data for these presentations revealed a positive difference between $V_{\text{min}}$ and $V_{100,2}$ in 29 and 28 of the 32 possible comparisons (2 block, 2 ISI, 8 subjects) for the $12$ and $24^\circ/\text{s}$ target, respectively. In presentations where the target velocity increased during the ISI from $12$ to $24^\circ/\text{s}$, the difference between $V_{\text{min}}$ and $V_{100,2}$ was also significant. There was a positive difference between $V_{\text{min}}$ and $V_{100,2}$ in 30 of the 32 possible comparisons (2 block, 2 ISI, 8 subjects), resulting in a group mean of $6.9 \pm 1.6^\circ/\text{s}$. Notably, this difference between $V_{\text{min}}$ and $V_{100,2}$ was significantly greater than when target velocity remained unchanged ($12$ to $12^\circ/\text{s}$), indicating that the anticipatory response was appropriately scaled. Finally, in presentations where the target velocity decreased during the ISI, the difference between $V_{\text{min}}$ and $V_{100,2}$ ($-0.7 \pm 0.6^\circ/\text{s}$) was not significant. Subjects did not simply release a default, non-predictive recovery that was scaled to the higher $24^\circ/\text{s}$ target velocity pursued during the first ramp.

**DISCUSSION**

When a moving target suddenly disappears, eye velocity decays rapidly (Barnes et al. 2000; Mitrani and Dimitrov 1978) but can be sustained with a reduced gain if subjects exert volitional effort to maintain pursuit (Becker and Fuchs 1985; Pola and Wyatt 1997). Therefore depending on the duration that the moving target is nonvisible, it follows that there will be a velocity error at the moment of target reappearance. Made- lain and Krauzlis (2003a) demonstrated that eye velocity during a transient disappearance increases after extensive training with an auditory reinforcing cue, thus reducing the developing velocity error. However, recent work (Bennett and Barnes 2003; Churchland et al. 2003) indicates that untrained subjects exhibit a reduction in eye velocity upon target disappearance, which is often followed by an anticipatory increase prior to target reappearance (see also Becker and Fuchs, 1985). Although this is a satisfactory solution when the target velocity remains the same during the ISI, an anticipatory increase that brings eye velocity back to its previous level would not be sufficient when velocity changes. In such cases, it would be necessary for the anticipatory increase to be predictive of the upcoming velocity.

The results of the present study confirm that subjects do indeed exhibit an anticipatory recovery in eye velocity toward the expected target velocity. There was no evidence of a significant decay in eye velocity in control presentations where the target remained visible. Neither was there evidence of a significant, sustained recovery in eye velocity in control presentations where there was no expectation that the target would reappear (Barnes and Asselman 1991, 1992; Becker and Fuchs 1985; Pola and Wyatt 1997). The implication is that the eye-
velocity trajectory during experimental presentations does not simply reflect the oscillatory dynamics of sustained pursuit in the presence or absence of visual feedback. Notably, it was also found that the anticipatory response was modified depending on the expected target velocity during the ISI and at reappearance. Subjects did not simply generate an anticipatory increase in eye velocity, resulting in a recovery to the previous level before the loss of visual feedback. The anticipatory response was predictive, increasing or decreasing in accord with the expected target velocity.

As we found before (Bennett and Barnes 2003), the majority of subjects exhibited a change in eye velocity at a comparatively similar time \( TV_{\text{min}} = 351 \pm 14 \) (SE) ms] over the two ISIs. This corresponds well with our previous findings \( TV_{\text{min}} = 359 \pm 8 \) ms). As a consequence, the increase in eye velocity often occurred early in the 800-ms ISI, resulting in the eye velocity occasionally reaching a peak and then decelerating up to and beyond the moment of target reappearance until visual feedback became available. We previously suggested that such a response, although anticipatory, was not appropriate to the duration of the ISI. We noted this observation is not consistent with the finding that anticipatory smooth pursuit can be initiated with fairly precise timing to repeated presentations of predictable stimuli (Barnes and Donelan, 1999; Kao and Morrow 1994) and speculated that the apparent lack of predictive timing could have been due to receiving limited repeated presentations \((n = 6)\) or a compression effect based on experience of the ISIs \((420, 660, 900 \) ms). Our current finding that block did not influence the time of minimum eye velocity indicates that the former of these two explanations is unlikely.

An alternative position also discussed previously is that, unlike the initiation of anticipatory smooth pursuit from a stationary location, the timing of the recovery in eye velocity during the ISI is not actually predictive of the target’s reappearance. Rather the change in eye velocity at a fixed time after target offset could have been triggered because it took a certain amount of time to register and respond to the loss of visual feedback (with the caveat that this is dependent on the expectancy that the target will reappear). There is strategic benefit to be had if the system responds in this way. Because both position and velocity error will accumulate after target offset unless eye velocity is increased, it is advantageous to start reducing these effects as soon as possible rather than allowing them to reach a level that becomes more problematic to eradicate. One potential drawback of this approach, which we observed in the longer ISIs, is that eye velocity was not maintained after the initial recovery if there was no confirmation from visual feedback. Therefore eye velocity decays after the initial recovery and may be decelerating as the target reappears. It remains to be verified if subsequent attempts to recover eye velocity and hence reduce the developing error, are exhibited in longer ISIs where there is sufficient time for more than one recovery.

FIG. 6. Representative examples of smooth eye velocity from subject 8, averaged across block, pursuing a 12°/s target (top) and 24°/s target (bottom) during the 1st ramp, as a function of ISI (400, 800 ms) and presentation type (target velocity unchanged in A and C; target velocity changed in B and D). Gray lines represent 400 ISI, black lines represent 800 ISI. Average eye velocity from control presentations (Ctrl I = thin black line, Ctrl II = thin gray line) is included for comparison.
Model of ocular pursuit enabling predictive extrapolation of a nonvisible moving target

The results of the present study confirm previous suggestions that cognitive factors such as expectation play a primary role in ocular pursuit (Jarrett and Barnes 2002; Kowler 1990; cf. Churchland et al. 2003). The question remains how such cognitive factors influence the underlying control mechanisms. In this section, we present a theoretical model (Fig. 10) that incorporates these cognitive factors, while maintaining the actual dynamics of smooth ocular pursuit. It is an extension of a model presented previously (Bennett and Barnes 2003) and is based on the general principle that ocular pursuit is modified by variable gain signal that adjusts the behavioral response according to ongoing changes in both retinal and extra-retinal input (Barnes and Wells 1999; Becker and Fuchs 1985; Churchland and Lisberger 2002; Churchland et al. 2003; Madelain and Krauzlis 2003a; Optican et al. 1985). Unlike our previous model, the extra-retinal feedback system is composed of two loops that produce either a direct or indirect pursuit response (see Barnes and Asselman, 1991). This refinement provides a means by which a purely reactive response can be made by the direct loop, while at the same time allowing velocity-based information to be accumulated in the indirect loop for subsequent predictive control (see following text). The visuomotor drive signal ($vmd$) inputs to the efference copy loop, which reaches its maximum level over the initial 200 ms of the response. Simultaneously $vmd$ also inputs to the indirect loop, which is arranged to allow the temporary creation of a short-term store (MEM) that represents velocity-coded information. MEM is represented as a local feedback loop containing an integrator that sums the error within the local feedback loop until the error is zero (NB. This is simplified for unidirectional movement). The output of this loop thus reaches a level equivalent to the visuomotor drive ($vmd$) and can even be “charged” independently of eye motion as long as there is retinal input (see Barnes et al. 1997). In effect, it acts as a sample and hold mechanism. Using this arrangement, gain $\beta$ applied to the extra-retinal output need not be unity to maintain the store. Therefore if there is a temporary modification in $\beta$, the stored level of the predictive loop will remain the same, acting as a retained reference. A further feature is that the short-term store may be temporarily charged according to the highest target velocity recently experienced. Therefore rather than storing several levels of velocity coded information, a predictive response could be generated by grading gain $\beta$. Note, however, that this would still require the storage of information related to prior responses to the different target velocities so that gain could be modified accordingly. Findings using either single-ramp (Jarrett and Barnes, 2002) or multiple-ramp stimuli (Barnes and Schmid, 2002) indicate that prior exposure enables at least four levels of velocity-coded information to be stored. At present, however, it is not clear whether

![Figure 7](image1.png)

**FIG. 7.** Group mean $V_{off}$ and $V_{min}$ (collapsed across block) as a function of target velocity, presentation type, and ISI. Error bars indicate SE. $V_{off} 12 =$ velocity at target offset having pursued a $12^\circ$/s target during the 1st ramp; $V_{min} 12 =$ minimum velocity during the ISI having pursued a $12^\circ$/s target during the first ramp; $V_{off} 24 =$ velocity at target offset having pursued a $24^\circ$/s target during the 1st ramp; $V_{min} 24 =$ minimum velocity during the ISI having pursued a $24^\circ$/s target during the 1st ramp.

![Figure 8](image2.png)

**FIG. 8.** Individual subject mean $TV_{min}$ (collapsed across block) as a function of target velocity, presentation type, and ISI. Bold line indicates group mean. Error bars indicate SE.
the storage capacity is similar to that for other visual items in working memory (Irwin, 1991; Lachter and Hayhoe, 1995; Luck and Vogel, 1997). The decision to switch between direct and indirect modes is dependent on the strength of the subject’s expectation regarding the timing and velocity characteristics of the upcoming presentation. On the first attempts to pursue a stimulus of unknown characteristics (e.g., a double velocity ramp), subjects generate an initially reactive response, while at the same time charging the short-term store of the indirect loop to the highest target velocity and deriving appropriate gain levels. Then, having pursued one or two presentations of an identical stimulus, subjects produce a predictive response, driven by the output of the short-term store contained within the indirect loop and initiated prior to target onset to form an anticipatory response.

Using this model, the response observed when the target disappears and then reappears moving with the same velocity can be simulated by temporarily reducing gain $\beta$ applied within the extra-retinal feedback loop. The signal to initially reduce gain comes from a conflict detector (CD), responding to the loss of visual feedback. If $\beta$ is reduced from its normal value (1) to zero for a short period, eye velocity will decay to a minimum but then recover towards target velocity as in the majority of our responses. If $\beta$ goes to zero for sufficient time, however, eye velocity will decay exponentially to zero as is the case when there is no expectation regarding target reappearance and subjects do not attempt to maintain pursuit (Mitrani and Dimitrov, 1978). Alternatively, by reducing $\beta$ to an intermediate value (0.3), rather than to zero, eye velocity can be maintained at reduced level over the entire ISI (Ctrl II condition, Fig. 4), regardless of the duration (Becker and Fuchs, 1985; Pola and Wyatt, 1997). If subjects then expect the target to reappear, the reinstatement of gain to its normal value will generate an anticipatory increase in eye velocity (Fig. 11, A and C). Modifying gain in this way can also simulate the response observed when the target disappears and then reappears moving with an increased or decreased velocity. Assuming that the normal value of $\beta$ (1) permits the continuous pursuit of a $24/\text{s}$ target during the first ramp, a reduction to an intermediate value (0.3) followed by an increase to 0.5 will enable eye velocity to be maintained at reduced level over the remainder of the ISI, as appropriate for the lower target velocity ($12/\text{s}$) (Fig. 11D). Alternatively, by setting gain to a reduced level (0.5) at the start of the presentation, then decreasing it briefly to 0.3 after target extinction before reinstating it to unity during the ISI, it is possible to generate a predictive increase in eye velocity (i.e., $12–24/\text{s}$) in anticipation of target reappearance (Fig. 11B).

Gain modification in accord with expected target velocity also influences $V_{\text{min}}$. Eye velocity reaches a lower minimum and accelerates at a lower rate when pursuing a $12/\text{s}$ target.
throughout the presentation compared to when the target velocity increases in the ISI and second ramp to 24°/s (see Fig. 11, A and B). The opposite effect is observed when the target velocity is reduced in the ISI and second ramp. Eye velocity assumes a higher minimum and accelerates at a higher rate when pursuing a 24°/s target throughout the presentation compared to when the target velocity decreases in the ISI and second ramp to 12°/s, respectively. C and D: the response when target velocity remains unchanged at 24°/s or decreases from 24 to 12°/s, respectively. Ramp 1 = 400 ms, ISI = 400 ms (A and B) or 800 ms (C and D), ramp 2 = 400 ms. Solid gray line represents output from MEM. The target is visible when the shutter (broken gray line) is high. NB. Because β is influenced by expectation, attention and experience of prior stimulus characteristics, there will be individual subject variation in the reduced magnitude of β and the time of reinstatement.

In addition to producing behaviorally realistic simulations of the results of the present study, this model is compatible with other findings. For example, it is possible to produce eye-velocity profiles that are qualitatively similar to those reported by Madelain and Krauzlis (2003a) after training with auditory reinforcement by modifying the intermediate value of gain assumed between trials. Training would then involve learning to modify the magnitude of gain rather than changing the rate (i.e., slope) at which gain is ramped from zero back to unity. Eye velocity might also be maintained as a moving target disappears behind a physical occluder (Churchland et al. 2003) if the conflict detector did not register a sudden and complete loss of visual feedback and therefore did not terminate the extra-retinal input. Finally, once MEM has been charged, cue-evoked responses (Tanaka and Lisberger, 2000) and smooth anticipatory pursuit (Barnes and Donelan, 1999; Kowler and Steinman, 1979) could be generated by switching gain from zero during fixation to some intermediate level prior to target onset (Krauzlis and Miles, 1996) as shown in the simulations (Fig. 11).

Of course, it should be acknowledged that our model is not alone in being able to simulate changes in eye velocity, but it

FIG. 11. Simulation of eye velocity by modifying gain β. β is reduced from its initial level (0.5 or 1) to 0.3 and then reinstated at 200 ms after target offset. A and B: the response when target velocity remains unchanged at 12°/s or increases from 12 to 24°/s, respectively. C and D: the response when target velocity remains unchanged at 24°/s or decreases from 24 to 12°/s, respectively. Ramp 1 = 400 ms, ISI = 400 ms (A and B) or 800 ms (C and D), ramp 2 = 400 ms. Solid gray line represents output from MEM. The target is visible when the shutter (broken gray line) is high. NB. Because β is influenced by expectation, attention and experience of prior stimulus characteristics, there will be individual subject variation in the reduced magnitude of β and the time of reinstatement.
does present a simple scheme that can simulate scaled smooth pursuit in anticipation of target motion onset and target reappearance after a period of transient nonvisible motion. Other models, such as that of Madelain and Krauzlis (2003a), require unity gain positive feedback to maintain eye-velocity information and, therefore, simulate a significant recovery after target offset by temporarily increasing gain beyond unity. In this case, precise control of the magnitude and timing of the increase in gain would be required so that eye velocity was predictive of target velocity. We also acknowledge that our model of smooth oculomotor pursuit does not account for the saccadic response that occurs during the transient (see Bennett and Barnes, 2003). Certainly, when there is retinal slip and/or retinal position error, these oculomotor subsystems act in synergy to achieve a common goal (de Brouwer et al. 2001, 2002). Further work is required to determine what triggers a saccade during a transient when there is no visual feedback and whether the saccade amplitude is also predictive of future target trajectory. Despite this limitation of our model, however, it is important to recognize that although saccades to the predicted target position may minimize the developing position error, eye velocity at target reappearance still must be predictive of target velocity in order to reduce retinal slip.

**Neural substrate**

As described in the preceding text, the storage of velocity-coded information plays a key role in predictive smooth pursuit. Although the neural substrate for the short-term storage of this information remains unclear, it is worthwhile considering how our model, which includes both a direct and indirect loop, may be realized. Currently, it is known that velocity-coded information is processed in areas MT (middle temporal cortex) and MST (medial superior temporal cortex) in the monkey (V5/V5A in humans) and that MST exhibits some features compatible with short-term memory. For example, Bisley et al. (2004) have recently shown evidence that MT may retain velocity-coded information for subsequent comparison in a motion discrimination task (see alsoPasternak and Zakas, 2003), a finding also supported by evidence that lesions in V5/V5A of humans give deficits in retaining motion information (Greenlee et al. 1995). Furthermore, sustained activity in MST has been found during the transient disappearance of a pursuit target and has been suggested to represent the release of stored information (Komatsu and Wurtz, 1989). The frontal eye field (FEF), which communicates directly with MST, has also been shown to exhibit similar activity (Tanaka and Fukushima, 1998). However, FEF has also been implicated in the generation of predictive pursuit (Gottlieb et al. 1993) and in the regulation of gain for pursuit (Tanaka and Lisberger, 2001). Finally, prefrontal cortex (PFC), an area that communicates with FEF, has been associated for some time with working memory (Levy and Goldman-Rakic, 2000) and cognitive control (Passingham, 1993). Therefore one interpretation of our model might be that MT/MST forms the basis of the efference copy loop (see Newsome et al. 1988), whereas PFC and FEF may participate in the indirect loop, being responsible for the sampling and temporary storage of velocity-coded information and the regulation of gain, which to some extent is under cognitive control.

**Summary**

Although subjects’ extrapolated smooth pursuit over a period of nonvisible target motion, they did not maintain eye velocity close to target velocity, particularly when pursuing the 24°/s target. In response to the change in eye velocity, most subjects released a scaled recovery in eye velocity prior to the onset of the second ramp. The recovery was therefore predictive of the expected change in target velocity and was not simply a non-predictive recovery to the level prior to the loss of visual feedback. We provide a model in which these effects are explained by the modification of gain within an extra-retinal feedback system containing a short-term store that maintains the visuomotor drive.

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