The Influence of Briefly Presented Randomized Target Motion on the Extraretinal Component of Ocular Pursuit

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Barnes GR, Collins CJ. The influence of briefly presented randomized target motion on the extraretinal component of ocular pursuit. J Neurophysiol 99: 831–842, 2008. First published December 5, 2007; doi:10.1152/jn.01033.2007. We assessed the ability to extract velocity information from brief exposure of a moving target and sought evidence that this information could be used to modulate the extraretinal component of ocular pursuit. A step-ramp target motion was initially visible for a brief randomized period of 50, 100, 150, or 200 ms, but then extinguished for a randomized period of 400 or 600 ms before reappearing and continuing along its trajectory. Target speed (5–20°/s), direction (left/right), and intertrial interval (2.7–3.7 s) were also randomized. Smooth eye movements were initiated after about 130 ms and comprised an initial visually dependent component, which reached a peak velocity that increased with target velocity and initial exposure duration, followed by a sustained secondary component that actually increased throughout extinction for 50- and 100-ms initial exposures. End-extinction eye velocity, reflecting extraretinal drive, increased with initial exposure from 50 to 100 ms but remained similar for longer exposures; it was significantly scaled to target velocity for 150- and 200-ms exposures. The results suggest that extraretinal drive is based on a sample of target velocity, mostly acquired during the first 150 ms, that is stored and forms a goal for generating appropriately scaled eye movements during absence of visual input. End-extinction eye velocity was significantly higher when target reapparance was expected than when it was not, confirming the importance of expectation in generating sustained smooth movement. However, end-extinction eye displacement remained similar irrespective of expectation, suggesting that the ability to use sampled velocity information to predict future target displacement operates independently of the control of smooth eye movement.

INTRODUCTION

It has long been recognized that ocular smooth pursuit relies on both retinal and extraretinal inputs. Retinal input comes from direct feedback of visual motion signals and has an inherent visuomotor delay of 80–100 ms (Carl and Gellman 1987). Extraretinal inputs reflect several real or hypothetical influences, including efference copy (“eye velocity memory”), remembered target motion ("target velocity memory"), volition, attention, and expectation. During sustained pursuit of a continuously visible target, retinal and extraretinal signals work together to maintain a stable response with high gain despite the delays in the basic visual feedback control.

Several influential models of the pursuit system assume that extraretinal inputs reflect an efference copy of ongoing eye movement (Krauzlis and Lisberger 1994; Krauzlis and Miles 1996; Robinson et al. 1986). Models such as these, in which there is a continuous positive feedback, adequately simulate the pursuit response to constant velocity targets and can account for features such as the typically seen initial overshoot of target velocity by eye velocity and its subsequent oscillation at 3–4 Hz with a velocity gain of about 0.9–0.95 (Fuchs 1967; Robinson et al. 1986). They fail to account, however, for the considerable influence that cognitive and voluntary factors can exert over the pursuit response under certain conditions.

Volition, expectation, and attention are all critical when smooth pursuit is continued in the absence of any visual input (e.g., if a moving target is extinguished or disappears behind an occluder) since the response then relies solely on extraretinal signals. In these circumstances smooth pursuit continues, albeit at reduced gain, only if subjects have a high expectation that the target will reappear (Becker and Fuchs 1985; Bennett and Barnes 2003); otherwise, eye velocity quickly decays to zero (Mitrani and Dimitrov 1978; Pola and Wyatt 1997). Importantly, when smooth eye velocity declines, irrespective of whether there is expectation of reappearance, there is evidence that overall eye position can be maintained along a path that approximates the unseen target trajectory, through the interjection of saccades (Bennett and Barnes 2003, 2006; Orban de Xivry et al. 2006).

It has been suggested (Churchland et al. 2003) that when a target disappears very briefly behind an occluder, pursuit is maintained by the efference copy loop acting as a memory of the eye velocity immediately prior to target disappearance. Other evidence, however, suggests that target velocity information may be sampled and held in working memory (Bennett and Barnes 2004). By assuming that the sampled velocity acts as a goal for internal drive mechanisms it is then possible to account for the recovery of eye velocity toward target velocity often observed during target extinction. In addition, if it is assumed that the sampled velocity information can be continuously integrated to form an estimate of the future target trajectory, this may explain the ability to track the unseen target with combined smooth and saccadic movements. It would also provide an explanation of the ability to make estimates of the point of target reappearance after a period of occlusion (Barborica and Ferrara 2003).

If target velocity is sampled at the onset of pursuit and if that sample is acquired before eye velocity has had time to respond to the visual input, it is reasonable to expect that the internal drive would continue to cause eye velocity to increase toward its goal even if visual input is withdrawn. Moreover, it should be accompanied by evidence of the ability to forecast the future...
position of the target at the end of extinction through a combination of smooth and saccadic eye movements. The critical unknown factor here is the timescale over which sampling may be accomplished. Evidence suggests that 200 ms is certainly sufficient to fully extract target velocity information. During pursuit initiation, in which an initial saccade often occurs with a latency of around 200 ms, Lisberger (1998) showed that smooth velocity may fall well short of target velocity prior to the initial saccade, but can nevertheless closely match target velocity after the end of the saccade, implying that velocity information has effectively been extracted within 200 ms. This is supported by the recent findings of Bennett et al. (2007), who showed that 200 ms was sufficient to extract velocity information, but that longer exposure was required to extract acceleration. In addition, Osborne et al. (2004) recently showed that it takes about 100 ms for activity in the visual motion-sensitive area MT (middle temporal cortex) in the monkey to build up to 80% of its steady-state firing rate. Thus altogether, it seems likely that between 100 and 200 ms are required to effectively extract velocity information.

In the current experiment we have attempted to find evidence for target velocity sampling and to examine the timescale over which this might occur. To accomplish this we have presented fully randomized step-ramp stimuli in which the initial target motion is presented for brief periods of 50–200 ms, prior to a prolonged period (400 or 600 ms) of extinction.\(^1\) In addition, we have compared responses when there is expectation of target reappearance with those when there is no such expectation. Our hypothesis was that if velocity can indeed be sampled within the initial brief presentation and if there is expectation of reappearance, there should be evidence of eye velocity continuing to increase throughout extinction and attaining a level at the end of extinction that is scaled to target velocity. The results show that when subjects expect the target to reappear, there is clear evidence of increasing eye velocity during extinction for the shortest initial presentations (50 and 100 ms) and of the scaling of eye velocity at the end of the 600-ms extinction for initial exposures of 150 and 200 ms. Moreover, overall eye displacement at the end of extinction was also scaled to target velocity, with or without expectation of reappearance, and there was evidence of independent scaling of the saccadic component alone for initial exposures of 150 and 200 ms.

METHODS

Subjects

Six human subjects took part with voluntary consent. They had no known neurological or oculomotor problems and had normal or corrected-to-normal vision. Experiments were conducted in accordance with the Helsinki Declaration with the approval of the local ethics committee.

\(^1\) To clarify the definition of different experimental tasks in this experiment we have adopted terminology different from that used previously by our group. We define “extinction” as a condition in which the target disappears because it is extinguished; we previously referred to this as “occlusion” (Bennett and Barnes 2003; 2004; Collins and Barnes 2006), whereas Churchland et al. (2003) referred to it as a “blinking.” In common with Churchland et al. (2003), we now define “occlusion” as the disappearance of the target behind a real or virtual obstacle.

Apparatus

Subjects sat in a darkened room and were presented with a red target against a black background. The target was moved across a flat screen by a mirror galvanometer system. The target was formed by the projection of a ring of light-emitting diodes (inner diameter 0.5°) onto the screen (2.5 m wide × 1.5 m high), which was located 1.5 m from the subject’s head. The head was immobilized by side clamps and by a chin rest. Eye movements were recorded with a limbus tracking device (Skalar Iris) that was firmly attached to the head.

Procedure

A total of three different conditions were undertaken by each subject. In all runs the target moved as a step-ramp stimulus (Rashbass 1961), in which it initially stepped to the left or right and then moved with a velocity of 5, 10, 15, or 20°/s in the opposite direction. In the Mid-ramp Extinction (ME) task, the target was initially stationary for a randomized period of 500–1,000 ms, then stepped in the direction opposite to the subsequent ramp motion. Following the step, the target was visible for a brief period [presentation duration (PD)] of 50, 100, 150, or 200 ms. It was then extinguished for a period [extinction duration (ED)] of 400 or 600 ms before reappearing and continuing to move at the same speed for a further 400 or 200 ms, respectively. There was a randomized interval of 2.7–3.7 s between successive trials, PD, ED, target speed, direction, and step size were also all randomized, making the stimulus highly unpredictable. In particular, it was important that subjects should not be able to glean cues to the velocity of the ramp from the initial step size. It is known from previous experiments that a reliable way of reducing saccadic activity in the first 200 ms is to ensure that the magnitude of the step is such that it takes about 200 ms for the target to cross back through its starting position. Unfortunately, this results in a fixed relationship between step size and target velocity and the step could thus be used as a cue for velocity. To avoid this we used this criterion for half of the trials and randomized the relationship between the step size and target velocity in the other half. Random and nonrandom steps were intermingled during the presentation and subjects did not detect an association between step size and target velocity. Every combination of PD, ED, and target velocity was thus presented twice, once with the relationship between step size and ramp velocity fixed and once with it randomized. An additional 10% of trials were ME Catch trials, in which the target failed to reappear at the end of the extinction period as expected. These trials, in which velocity was either ±10 or ±20°/s and PD was either 150 or 200 ms, were intermingled with the regular trials.

In the Short Ramp task, the target was presented for the same brief initial durations as in the Mid-ramp Extinction task, but did not reappear after the extinction period. Subjects were made aware of this but were instructed to try to continue eye movement during the extinction period as if the target would reappear; thus this condition was identical to the catch trials of the Mid-ramp Extinction task, although subjects’ expectation of target motion differed. An additional 10% of trials were SR catch trials in which, contrary to expectation, the target did reappear. As in the ME Catch trials, velocity was either ±10 or ±20°/s and PD was either 150 or 200 ms.

In the Control task, the conditions were identical to those of the Mid-ramp Extinction task, except that the target remained visible throughout the whole of the ramp, for a period of 1,000 ms.

In total, subjects performed eight separate runs, each preceded by a calibration of eye movement. Each run lasted about 150 s and consisted of 44 trials. The first eight trials in each run were Controls, the remainder being composed of either 1) 32 Mid-ramp Extinction plus 4 ME catch trials or 2) 32 Short Ramp trials plus 4 SR catch trials. In total, 64 trials were presented to each subject in each of the three conditions, resulting in four repeats of each velocity and PD condition in the Mid-ramp Extinction and Short Ramp tasks.
Data analysis

Analogue eye and target displacement signals were low-pass filtered at 80 Hz prior to digitization at 200 Hz and storage on disc. Eye and target velocity were derived from the digitized data by the two-point central difference method and saccades were removed from the eye velocity signal using techniques described in detail elsewhere (Bennett and Barnes 2003). Saccade latencies were calculated in relation to target motion onset. Linear interpolation was used to fill the gaps left by the saccades removed (for justification of using this technique, see Collins and Barnes 2006) and the resultant data were then further filtered using a zero-phase autoregressive low-pass digital filter with a cutoff frequency of 30 Hz. The following variables were then examined in detail.

Vpk and Tpk. Responses to the Mid-ramp Extinction task were typified by an initial rapid rise to a low-gain peak, followed by a lower rate of rise. The initial peak velocity (Vpk) was calculated by examining eye acceleration for each response and determining the time (Tpk) at which acceleration passed through zero prior to the secondary, lower level of acceleration. Tpk values were calculated with respect to both target movement onset (TpkT) and eye movement onset (TpkE).

Latency. The latency of smooth eye movement initiation with respect to the start of target motion was calculated with a semiautomatic procedure. A linear regression was carried out from the time at which eye velocity reached 10% of Vpk until 100 ms thereafter and latency was calculated by extrapolation back to zero velocity. An interactive procedure allowed the appropriateness of the calculated value to be confirmed or corrected.

V450, V650. Smooth eye velocity measured 450 or 650 ms after target motion onset.

TED, SAD. Total eye displacement (TED; i.e., the combination of smooth and saccadic movements) was measured at the end of the target extinction period. The component of TED contributed by saccades [saccadic eye displacement (SAD)] was obtained by subtraction of the cumulative smooth eye displacement derived from integration of smooth eye displacement over the same period.

Statistical analyses were carried out using SPSS software. All data were tested for departures from normality using the Shapiro–Wilk test. The Mauchly test was used for sphericity within and between factors. If the assumption of sphericity was violated, a Greenhouse–Geisser correction was used to calculate adjusted P values. All comparisons were made using repeated-measures ANOVAs. Since there were no significant directional differences, results presented in the figures have been averaged across direction where appropriate.

RESULTS

General observations

In the Mid-ramp Extinction task subjects were able to gain a clear perception of the motion and direction of the target when the initial exposure period (PD) was ≥100 ms. When PD was only 50 ms it was more difficult to perceive the motion, although subjects only occasionally misdirected their response. From the examples shown in Fig. 1 it is evident that during extinction subjects continued to track the unseen target trajectory and eye velocity continued to increase in many examples, even though target velocity and direction were randomized. It is important to emphasize that the increasing velocity characteristic was present within the smooth component of the eye movement response. Indeed, in 21.7% of responses, similar to those in Fig. 1D, there was no saccadic eye movement until after the reappearance of the target. The majority of saccades occurred from 400 to 450 ms after motion onset. Overall, 72% of all responses to the Mid-ramp Extinction conditions were made without any saccades occurring before 400 ms after target onset, indicating that the step-ramp paradigm had been reasonably successful in maximizing the amount of smooth movement in the critical period concerned. Even when saccades were present during extinction (as in the example of Fig. 1A), smooth eye velocity continued to increase between the end of the saccade and the reappearance of the target.

For both ED = 400 ms and ED = 600 ms, comparison of responses to different PDs and target velocities revealed systematic changes in the eye velocity trajectory. Data averaged across subjects for ED = 600 ms are shown in Fig. 2. There was a latent period of >100 ms before eye motion was...
initiated; consequently, for PD = 50 ms and PD = 100 ms no eye movement response was elicited until after the target had been extinguished. There was then a short period in which eye velocity increased quite rapidly toward target velocity, reaching an initial peak (Vpk). We will refer to this as the initial phase. It was followed by a secondary phase, after the initial peak was reached, in which eye velocity varied depending on PD and target velocity. At the shortest PD (50 ms; Fig. 2A for ED = 600 ms), eye velocity exhibited a further, more slowly developing increase toward target velocity than observed in the initial part of the response, even though no visual stimulus was present. For PD = 100, 150, or 200 ms (Fig. 2B and C for ED = 600 ms) eye velocity decreased from its initial peak value and then either remained fairly constant or recovered toward target velocity in the manner previously reported by Bennett and Barnes (2003). For all responses there was a further rapid increase in eye velocity that started about 100 ms after target reappearance and was presumably associated with the onset of visual input. Since the duration of target reappearance was only 200 ms in the examples of Fig. 2, A–C, eye velocity did not necessarily reach target velocity during this period.

In the Short Ramp task, in which subjects were presented with the initial exposure of the target alone, without expectation of further reappearance within the same run, the smooth eye movement could not be sustained in the way it could when reappearance was expected; thus mean smooth eye velocity decayed toward zero after target extinction (Fig. 2D). When PD was 200 ms the decay was initially quite rapid, but then slowed to a lower rate of decay. In contrast, when PD was only 50 ms eye velocity exhibited a slower increase to about 7°/s, followed by a later decay to zero.

**Response latency**

There was no significant difference in the latency of pursuit onset in the Mid-ramp Extinction, Short Ramp, and Control tasks. There was also no significant difference in latency as a function of target velocity or PD, although there was a trend for longer latency when PD was only 50 ms. Mean latencies (±SD) were 151.4 (±53.8), 133.0 (±36.1), 137.7 (±29.3), and 147.2 (±24.5) ms for ED = 600 ms, respectively.

**Figure 2.** Smooth eye velocity averaged across all 6 subjects in the Mid-ramp Extinction (A–C) and Short Ramp (D) tasks. In A and B target velocity = 5°/s (orange), 10°/s (blue), 15°/s (green), or 20°/s (black); PD = 50 ms in A; PD = 200 ms in B. In C and D target velocity = 20°/s; PD = 50 ms (magenta), 100 ms (gray), 150 ms (red), or 200 ms (black). Also shown in C is the average smooth eye velocity in the Control response for target velocity = 20°/s (cyan trace). In C and D dotted lines denote 650 ms after target onset; note that for clarity, gray shading is omitted since target extinction occurred at a different time for each data series.
140.0 (±25.7) ms for PD = 50, 100, 150, and 200 ms, respectively. Mean latency in the control condition was 133.0 ms (±29.3), a typical value for a step-ramp task. There were very few anticipatory movements, confirming that the randomization had made the task very unpredictable.

**Peak velocity of initial phase (Vpk)**

There was no significant difference in the peak velocity (Vpk) of the initial phase between the Mid-ramp Extinction and Short Ramp tasks (Fig. 3). Vpk did increase significantly, however, with both target velocity \([F(3,15) = 81.57; P < 0.001] and PD \([F(3,15) = 93.89; P < 0.001]\), as evident in Fig. 3. There was also no significant difference between tasks in the time to peak \((Tpk_E)\) calculated with respect to eye movement onset. \(Tpk_E\) increased significantly with increasing PD \((F(3,15) = 15.23; P < 0.001)\) and there was a marginally significant increase with target velocity \((F(3,15) = 3.25; P = 0.047)\). Mean \(Tpk_E\) values (±SD) were 127.1 (±28.67), 129.9 (±25.92), 145.1 (±28.50), and 173.3 (±31.63) ms for PD = 50, 100, 150, and 200 ms, respectively. These results thus suggest that the initial part of the response was dependent on the duration of the initial visual stimulus, but not on the expectation of target reappearance. When calculated with respect to target motion onset, time to peak \((Tpk_T)\) had mean values (±SD) of 278.2 (±17.00), 269.60 (±11.52), 287.73 (±7.44), and 315.96 (±8.22) ms, for PD = 50, 100, 150, and 200 ms, respectively.

**Comparison of response in initial phase with control**

Although the initial phase of both the Mid-ramp Extinction and Short Ramp responses appeared similar to controls, detailed comparison revealed evidence of attenuation. To specifically compare the dynamic development of responses, each velocity response was first aligned with respect to its onset. Eye velocity profiles for all values of PD were compared with the Control condition at 20-ms intervals using separate ANOVAs for each value of PD, but with target velocity and direction as factors. For the Mid-ramp Extinction task (Fig. 4), the times relative to response onset at which eye velocity first became significantly less than the Control were as follows: 80 ms for PD = 50 ms, 100 ms for PD = 100 ms, 140 ms for PD = 150 ms, and 160 ms for PD = 200 ms. For PD = 200 ms, eye velocity at 160 ms was, on average, 16% less than the Controls. Initiation of the response in the absence of a visual stimulus thus resulted in a small, but significant, attenuation of the normal response evoked in the presence of the target. As expected, in all responses, including those in the control condition, eye velocity increased significantly with target velocity [e.g., \(F(3,15) = 58.33; P < 0.001\) at 160 ms after onset], but in all comparisons, there was no significant difference in eye velocity between the Mid-ramp Extinction and Short Ramp tasks.

The preceding comparison between tasks was also carried out for responses aligned with target motion onset using separate ANOVAs at 20-ms intervals, starting 80 ms after target onset. This indicated, again, no difference between Mid-ramp Extinction and Short Ramp responses. The times at which these responses first became significantly less than the control were: 160 ms for PD = 50 ms, 180 ms for PD = 100 ms, and 240 ms for PD = 150 and 200 ms. This measure is affected by changes in latency as well as response dynamics and the early difference for PD = 50 ms was probably associated with the longer response latency for this value of PD. For all values of PD, these times indicate that the difference first occurred well after target extinction, although for PD = 200 ms this critical time occurred only about 40 ms after extinction.

**Response during extinction**

In the Mid-ramp Extinction task, eye velocity during extinction changed with PD and ED. To assess these changes we first measured eye velocity 450 ms after target onset (V450). For the shortest PD (50 ms) and ED (400 ms) combination this represented the end of the extinction period for all other ED/PD combinations it occurred prior to the end of extinction. ANOVA indicated a significant increase in V450 with both increasing target velocity \((F(3,15) = 26.14; P < 0.001)\) and increasing PD \((F(3,15) = 21.67; P < 0.001)\). There was no significant difference, however, between V450 values for the 400- and 600-ms extinctions. To assess whether there was any evidence of an eye velocity increase beyond the peak velocity attained in the initial phase V450 was com-

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**FIG. 3.** Peak eye velocity (Vpk) in the initial phase for the Mid-ramp Extinction and Short Ramp tasks, for all presentation durations (PDs) and all target velocities. Mean of 6 subjects ± 1SE.
pared with Vpk. For both PD/H11005 50 ms and PD/H11005 100 ms, V450 was significantly greater than Vpk \(F(1,5) = 7.32; P = 0.043\). Note that Vpk occurred, on average, 273.9 ms after target onset for these values of PD (see TpkT values given earlier).

For ED/H11005 600 ms, a further examination of eye velocity was carried out 650 ms after target onset (V650: Fig. 5). Comparison of V650 with Vpk by ANOVA revealed a significant interaction with PD \(F(3,15) = 67.99; P < 0.001\). Separate analysis for each PD indicated a significant increase for PD/H11005 50 ms \(F(1,5) = 7.88; P = 0.038\), no significant difference for PD/H11005 100 \(F(1,5) = 2.96; P = 0.146\) and 150 ms \(F(1,5) = 0.84; P = 0.401\), and a significant decrease for PD/H11005 200 ms \(F(1,5) = 7.83; P = 0.038\). This quantifies the qualitative features observed in Fig. 2C, where the response changed from one that steadily increased during extinction (PD/H11005 50 ms) to one that decreased during extinction (PD/H11005 200 ms). In fact, whereas mean Vpk (averaged across velocity) increased by 68% from 7.17°/s at PD = 100 to 12.01°/s at PD = 200 ms, mean V650 increased by only 2% from 8.91 to 9.11°/s.

**Comparison of Short Ramp and Mid-ramp Extinction: effects of expectation**

**EYE VELOCITY AT END OF EXTINCTION.** It is clear that expectation makes a large difference to the response in the secondary phase, but how does that difference change with initial target exposure and velocity? To assess this, we examined eye velocity (\(V_{\text{END}}\)) at the time corresponding to the end of extinction in the ED = 600 ms condition of the Mid-ramp Extinction task, i.e., 650, 700, 750, and 800 ms after target onset for PD = 50, 100, 150, and 200 ms conditions, respectively. Specifically, we compared \(V_{\text{END}}\) for the ED = 600 ms condition of the Mid-ramp Extinction task with \(V_{\text{END}}\) for the Short Ramp task (Fig. 6). [Note that \(V_{\text{END}}\) in the Mid-ramp Extinction task (Fig. 6) was very similar to V650 (Fig. 5) since eye velocity tended to remain fairly constant after 650 ms (Fig. 2C).] ANOVA revealed that \(V_{\text{END}}\) in the Mid-ramp Extinction task was significantly greater than that in the Short Ramp task \(F(3,15) = 9.859; P = 0.035\); however, there was a significant interaction of Task and PD \(F(3,15) = 11.926; P = 0.001\). Separate analysis for the Short Ramp condition showed no significant difference...
across PDs, as evidenced by the similarity of data points and the relatively consistent mean $V_{\text{END}}$ values (Fig. 6), although there was a significant increase with target velocity $[F_{(3,15)} = 12.663; P = 0.001]$. Analysis of the Mid-ramp Extinction responses alone also showed a significant effect of target velocity $[F_{(3,15)} = 7.288; P = 0.003]$, but complex effects of PD. Simple contrasts showed that $V_{\text{END}}$ was significantly less in the PD = 50 ms condition than when PD was 100, 150, or 200 ms. This effect is evident in the plots of mean $V_{\text{END}}$ (averaged across target velocity) shown by broken lines in Fig. 6. These plots also make it evident that the velocity scaling for PD = 100 ms was clearly not as well developed as for the PD = 150 ms and PD = 200 ms conditions. Linear regression analysis was carried out with $V_{\text{END}}$ and target velocity as the dependent and independent variables, respectively, on the combined data of all subjects. As indicated by the regression results in Table 1, this indicated that there was no significant correlation with velocity for PD = 50 ms or PD = 100 ms, but a strongly significant correlation for the PD = 150 ms (slope = 0.42) and PD = 200 ms conditions (slope = 0.48).

It is also evident in Fig. 6 that the difference between $V_{\text{END}}$ values for the Mid-ramp Extinction and Short Ramp tasks increased as PD increased. This difference increased significantly with target velocity $[F_{(3,15)} = 5.87; P = 0.007]$ for the PD = 150 ms and PD = 200 ms conditions. In other words, the expectation-dependent component developed within the extinction interval was modulated by target velocity information extracted prior to extinction.

### Table 1. Regression statistics for fit of eye to target data

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Linear regression based on 48 values from six subjects (df = 47). Dependent variables are: $V_{\text{END}}$, eye velocity at end extinction; TED, total eye displacement at end extinction; SAD, saccadic eye displacement at end extinction. Tasks compared are: ME, Midramp Extinction; SR, Short Ramp.
ms eye displacement was greater for the higher than for the lower target velocity and, in the average response, was also greater for the PD = 150 ms than the PD = 50 ms condition. The total eye displacement (TED) at the time corresponding to the end of extinction in the Mid-ramp Extinction condition is shown for all values of PD and target velocity in Fig. 8A. In contrast to the $V_{END}$ values shown in Fig. 6, there was no significant difference between TED for the Mid-ramp Extinction and Short Ramp tasks, but there was a significant effect of target velocity [$F_{(3,15)} = 30.80; P < 0.001$] and PD [$F_{(3,15)} = 41.59; P < 0.001$]. Notably, TED was reasonably close to the expected target displacement at the end of extinction for PD = 150 and 200 ms, but was quite imprecise when PD was 50 or 100 ms (Fig. 8A). Regression analysis between TED and target velocity for the Mid-ramp Extinction task (see Table 1) indicated that there was a significant correlation with velocity at each level of PD, but, as for $V_{END}$, the slope of the relationship increased from low values of 0.15 and 0.168 for PD = 50 and 100 ms, respectively, to higher values of 0.364 for PD = 150 ms and 0.554 for PD = 200 ms.

Segregation of the smooth and saccadic components also allowed the contribution associated with saccadic eye displacement (SAD) at the end of extinction to be derived, as shown in Fig. 8B. In a similar manner to the $V_{END}$ values, regression analysis for each PD (Table 1) revealed that there was no significant effect of target velocity for PD = 50 and 100 ms, but highly significant relationships for PD = 150 and 200 ms, with slopes of 0.143 and 0.239, respectively. Note that, because cumulative smooth eye displacement is reduced in the Short Ramp condition in association with the lower values of $V_{END}$, the saccadic component has to increase to achieve the similarity of total eye displacement (TED, Fig. 8B).

**CATCH TRIALS.** As a further verification of the effects of expectation, occasional catch trials were included in the Mid-ramp Extinction task in which the expected target reappearance did not occur. The actual stimulus was thus identical to the Short Ramp task, but subjects’ expectation regarding target reappearance was different. In these ME catch trials the response generated was initially similar to that of the Short Ramp task (Fig. 9A). However, after attaining its initial peak, eye velocity in the catch trial was sustained, just as in the regular Mid-ramp Extinction trials, in contrast to the regular Short Ramp trials, in which eye velocity decayed to zero. ANOVA was used to compare $V_{650}$ in all three conditions (regular Mid-ramp Extinction trials, Mid-ramp Extinction catch trials, and regular Short Ramp trials). It revealed no significant difference between $V_{650}$ for the Mid-ramp Extinction regular and catch trials [$F_{(1,5)} = 2.87; P = 0.151$], whereas $V_{650}$ for the Short Ramp trials was significantly lower than that for the regular Mid-ramp Extinction task [$F_{(1,5)} = 10.47; P = 0.023$]. Furthermore, responses in the catch trials were scaled for expected target velocity, being 52% higher for the 20 than for the 10°/s target motion. Occasional SR catch trials were also included in the Short Ramp task, in which the target unexpectedly appeared after a 400-ms extinction. As expected, the response was very similar to the regular Short Ramp response until about 100 ms after target appearance, when a reactive response to target appearance occurred (Fig. 9B).

**DISCUSSION**

In these experiments we have investigated the ability of human subjects to capture target motion information during the brief initial presentation of a moving target and their ability to use that information to modulate smooth eye velocity during a
subsequent period of target extinction. All parameters of the stimulus [time of initiation, target speed, target direction, initial step size, initial presentation duration (PD), and extinction duration (ED)] were randomized, so that the likelihood of predicting the upcoming target stimulus was extremely low. Subjects thus had to rely on using motion information extracted during the brief initial exposure to predict future motion. The results indicate that the smooth eye movement response was dependent on two factors: the duration of initial exposure and the expectation of target reappearance after extinction. When subjects expected the target to reappear, smooth eye velocity exhibited a bipartite response. The first part appeared to be

![FIG. 8. Total eye displacement (TED, A) and the saccadic component of eye displacement (SAD, B) at the time corresponding to the end of extinction in the Mid-ramp Extinction and Short Ramp tasks, for all PDs and all target velocities. Broken lines denote target position at the end of extinction. Mean of 6 subjects ± 1SE.](image)

![FIG. 9. Smooth eye velocity averaged across all 6 subjects for Mid-ramp Extinction (ME), Short Ramp (SR), and Catch trials. PD = 150 ms; target velocity = 20°/s. A: extinction duration (ED) = 600 ms. Gray shading denotes the extinction period for regular ME trials. In the Regular SR and ME Catch trials the target was extinguished after 150 ms and did not reappear; this was expected in the Regular SR trials but was contrary to expectation in the ME Catch trials. B: ED = 400 ms. In the SR Catch trials the target reappeared at the end of the extinction period, contrary to expectation; gray shading therefore denotes the extinction period for both Regular ME and SR Catch trials. In the Regular SR trials the target was extinguished after 150 ms and did not reappear.](image)
associated with visual input, the second with the internal, extraretinal drive. When the initial presentation was very brief (50 ms), the visually driven response was much less than target velocity, although eye velocity nevertheless continued to increase toward target velocity in the complete absence of any visual stimulus for a period of up to 600 ms. As the duration of the initial exposure of the target was increased to 200 ms, the visual component became more dominant and the pattern of response changed, giving the more familiar dip in eye velocity after extinction (Becker and Fuchs 1985; Nagel et al. 2006) followed, in some examples, by a recovery toward target velocity (Bennett and Barnes 2003). In contrast, when experience indicated that the target would not reappear, as in the Short Ramp condition, the first, visually dependent part of the smooth eye movement response was generated, but the ability to sustain smooth eye movement was lost; eye velocity simply decayed to zero. It thus appears that development of the secondary component is dependent on the expectation that target motion will continue in the future.

Although the initial part of the response in both the Mid-ramp Extinction and Short Ramp conditions was modulated by initial exposure duration and target velocity and thus appeared dependent on visual input, the relationship was not straightforward. In the Short Ramp condition the stimulus is a foreshortened version of a conventional step-ramp stimulus typified by the Control task. In response to such a stimulus eye velocity starts to increase toward target velocity after a latency of about 130 ms. If the subject has no knowledge of the ramp duration, eye velocity starts to decay with a similar latency after target extinction (Mitranu and Dimitrov 1978; Pola and Wyatt 1997). The time constant of decay is normally around 100–200 ms. The origin of these discrepancies is unclear at present. It could simply result from the fact that, in contrast to the Control condition, the initial response was produced in darkness since for all except the PD = 200 ms condition most of the response was made after target extinction. However, the finding that the PD = 200 ms response first deviated from the Control only about 40 ms after target extinction argues against an influence of the change in visual input (minimum latency ~80 ms). It is thus possible that, despite randomization of initial exposure duration, there was some preprogrammed attenuation of the response similar to that observed at the termination of more prolonged ramp motion (Barnes et al. 2005; Krauzlis and Miles 1996).

Against this background of a response that normally decays to zero after the initial exposure has terminated, the response obtained in the Mid-ramp Extinction condition clearly shows evidence of an additional internal drive component that continues in the absence of visual input. The existence of an internal (or extraretinal) component of pursuit has long been acknowledged and it has been customary to represent the system as an internal efference copy feedback system (Churchland et al. 2003; Robinson et al. 1986). Traditionally, this has been represented as a continuous positive feedback mechanism that boosts the gain of the pursuit response while allowing stability to be maintained in the presence of finite visual processing delays. The response of such models to extinction of the target is to maintain eye velocity at the preextinction level until after the target reappears (Krauzlis and Miles 1996). Consequently, our current finding that eye velocity can continue to rise after extinction does not fit with this concept. The results are compatible, however, with a model produced previously by Bennett and Barnes (2004, 2006) to explain the recovery of eye velocity toward the end of extinction. This model also relies on internal positive feedback, but with the major difference that the internal feedback is a system that samples the visuomotor drive signal rather than relaying it continuously. Critically, we find support for the proposal, made earlier (Bennett and Barnes 2003), that output of the internal pathway is regulated by expectancy, which controls the gain of the internal feedback.

It should be noted that our findings appear different from those in a similar investigation carried out by Churchland et al. (2003) in monkeys. These authors found no evidence of increasing velocity during target extinction (or "blinking"), although they did report some increase when a physical occluder was used. However, the extinction interval they used was only 200 ms and, given the rather slow increase in velocity during extinction observed here (e.g., Fig. 2A), this may not be long enough to demonstrate the effect.

Although emphasis has been placed before on the demonstration of increasing velocity during extinction as a test for the validity of the conventional efference copy model (Bennett et al. 2007; Churchland et al. 2003), this tends to underplay the actual contribution of expectation. The response in the Short Ramp condition was the best the subjects could achieve when there was no expectation of reappearance and they were clearly able to maintain the positional control of the eye (Fig. 8A), but not the smooth eye velocity (Fig. 6). In fact, it had been expected that eye velocity would decay to zero within the 600-ms extinction interval on the basis of previous evidence (Pola and Wyatt 1997), but there was clearly still some ability to sustain a residual, more slowly decaying eye velocity. This effect may be related to previous demonstrations of an ability to volitionally generate low-level (<5°/s) smooth eye velocity in darkness (Barnes et al. 1987; Heywood and Churcher 1971), which may also contribute to the slow rise of eye velocity observed in response to the 5°/s target. Whatever its origin, the response in the Mid-ramp Extinction task, where there was expectation of reappearance, was evidently additional to this baseline level in the Short Ramp task. The true effect of expectation of reappearance is thus to be found in the difference between the responses to these two tasks, up until the end of the extinction period. As evident in Fig. 6, the velocity at the end of the extinction period, before there was any chance of visual influence, was much greater in the Mid-ramp Extinction condition than that in the Short Ramp condition. Moreover, the difference between \( V_{\text{END}} \) in these conditions increased significantly with target velocity, suggesting that initial target velocity information had been used to grade this expectation-dependent response.
Interestingly, when values of $V_{\text{END}}$ in the Mid-ramp Extinction condition were averaged across target velocity, they showed no difference for PD $\geq$100 ms, but a significant reduction for PD $\geq$ 50 ms. It thus seems that there is little increase in the mean internal drive level once PD is $>100$ ms. However, it is also evident that the scaling of $V_{\text{END}}$ with target velocity was not as good for PD = 100 ms as for PD = 150 and 200 ms, implying that longer exposure gives time for further refinement of velocity sensing. Moreover, a similar picture emerged when examining both overall eye displacement (TED) and the saccadic component of that displacement (SAD), which also increased markedly in sensitivity for the PD = 150 and 200 ms initial exposures. From this we conclude that, although the system can obtain a sample of eye velocity over a period as short as 50 ms, the ability to discriminate velocity is poor and effective scaling of eye velocity emerges only after an initial exposure of about 150 ms. In future experiments it would be useful to probe this effect with smaller time increments within this 200-ms window. Note that the time period over which velocity can be extracted is considerably shorter than that for sensing target acceleration, as demonstrated recently by Bennett et al. (2007). Once obtained, this estimate of target velocity can be used as a reference for the buildup of the extraretinal component. In the Mid-ramp Extinction condition, the increase in eye velocity toward this reference level during the secondary phase then develops relatively slowly in comparison with the visually dependent component in the initial phase.

The target-extinction paradigm has now been used in a large number of experiments (Becker and Fuchs 1985; Bennett and Barnes 2003, 2004, 2005, 2006; Churchland et al. 2003; Madelain and Krauzlis 2003; Nagel et al. 2006; von Noorden and Mackensen 1962) and one of the common features is that eye velocity normally decreases to a residual level about 100 ms after extinction if pursuit has reached a steady state. It has generally been argued that the residual velocity represents the magnitude of the internal drive component (Becker and Fuchs 1985; Nagel et al. 2006). However, this argument does not explain why the decline may be less with a physical occluder (Churchland et al. 2003) or when feedback of results is given (Madelain and Krauzlis 2003). It also does not explain why velocity may increase toward the end of extinction, as frequently observed (Becker and Fuchs 1985; Bennett and Barnes 2003). A possible explanation is that the extinction of the target itself causes a transient suppression of the smooth component of the response. Although this might be the result of a decrease in the magnitude (or gain) of the internal component (Bennett and Barnes 2003; Churchland et al. 2003), our current finding of attenuation of the initial phase of both the Mid-ramp Extinction and Short Ramp responses suggests that the visually dependent response may be similarly affected.

To summarize, we find evidence to support the hypothesis that target velocity information is sampled within a period of 100–150 ms after onset of a randomized target motion stimulus and that this sampled estimate is then used as a goal for internally generated eye movement to attain even after the target has been extinguished. The ability to generate the smooth component of this eye movement during target extinction is dependent on the expectation of target reappearance, thus supporting the idea that expectation modulates the output of internal (or extraretinal) pursuit mechanisms. However, total eye displacement remains similar irrespective of expectation, suggesting that the ability to use the sampled velocity information to predict future target displacement operates independently of the control of smooth eye movement. The maintenance of eye displacement is accomplished by the interjection of saccades, demonstrating the synergy between smooth and saccadic systems observed previously (Orban de Xivry et al. 2006).

REFERENCES


