

# Extraction of visual motion information for the control of eye and head movement during head-free pursuit

Rochelle Ackerley · Graham R. Barnes

Received: 12 November 2010 / Accepted: 17 January 2011 / Published online: 6 February 2011  
© Springer-Verlag 2011

**Abstract** We investigated how effectively briefly presented visual motion could be assimilated and used to track future target motion with head and eyes during target disappearance. Without vision, continuation of eye and head movement is controlled by internal (extra-retinal) mechanisms, but head movement stimulates compensatory vestibulo-ocular reflex (VOR) responses that must be countermanded for gaze to remain in the direction of target motion. We used target exposures of 50–200 ms at the start of randomised step-ramp stimuli, followed by >400 ms of target disappearance, to investigate the ability to sample target velocity and subsequently generate internally controlled responses. Subjects could appropriately grade gaze velocity to different target velocities without visual feedback, but responses were fully developed only when exposure was >100 ms. Gaze velocities were sustained or even increased during target disappearance, especially when there was expectation of target reappearance, but they were always less than for controls, where the target was continuously visible. Gaze velocity remained in the direction of target motion throughout target extinction, implying that compensatory (VOR) responses were suppressed by internal drive mechanisms. Regression analysis revealed that the underlying compensatory response remained active, but with gain slightly less than unity (0.85), resulting in head-free gaze responses that were very similar to, but slightly greater than, head-fixed. The sampled velocity information was also used to grade head velocity, but in contrast to gaze, head velocity was similar

whether the target was briefly or continuously presented, suggesting that head motion was controlled by internal mechanisms alone, without direct influence of visual feedback.

**Keywords** Expectation · Extra-retinal · Head movement · Prediction · Smooth pursuit · Vestibulo-ocular reflex

## Introduction

During ocular pursuit, both retinal and internal (extra-retinal) mechanisms aid in tracking. Pursuit is initially driven by direct visual feedback from retinal signals, but over time, internal drive mechanisms take over a large part of this response and sustain tracking even in the absence of the visual stimulus (Becker and Fuchs 1985; Bennett and Barnes 2003). Central processing of retinal slip results in a delay of ~80–100 ms (Carl and Gellman 1987; Krauzlis and Miles 1994), but internal predictive mechanisms can overcome this delay (Barnes and Asselman 1991; Barnes 2008). Internal drive mechanisms are widely thought to be mediated by positive feedback of an efference copy of eye velocity, which allows a memory of eye velocity to be retained (Robinson et al. 1986; Krauzlis and Lisberger 1994; Krauzlis and Miles 1996). However, cognitive factors such as expectation can have a substantial influence on this non-visual component (Kowler 1989; Barnes et al. 2002). If a moving target unexpectedly disappears, eye velocity rapidly decays to zero (Mitrani and Dimitrov 1978), but when there is an expectation of target reappearance and the subject attempts to track the target during extinction, smooth eye velocity can be sustained (Bennett and Barnes 2003, 2004; Collins and Barnes 2006; Barnes and Collins 2008b). In a recent experiment, Barnes and

R. Ackerley · G. R. Barnes (✉)  
Faculty of Life Sciences, University of Manchester,  
Moffat Building, Sackville Street, PO Box 88,  
Manchester M60 1QD, UK  
e-mail: g.r.barnes@manchester.ac.uk

Collins (2008b) exploited the effect of expectation to reveal the interaction between visual and internal mechanisms of pursuit. They showed that if the moving target is only presented for 100–150 ms and if the target is expected to reappear, smooth eye movements, scaled to target velocity, continue to increase in the absence of visual input. This suggests that internal drive is based on sampling and storing the initial visual input.

Although experiments with the head fixed provide insight about visual versus non-visual input to pursuit, it is more natural for the head and eyes to move together during pursuit, particularly when following fast targets (>20 deg/s). If head movement occurs in the absence of vision, the eyes are reflexively driven in the opposite direction by the vestibulo-ocular reflex (VOR) with near-equal velocity, thus stabilizing the eye in space. Early experiments by Lanman et al. (1978) suggested that the VOR was fully functional during head-free pursuit, since gaze movements remained similar irrespective of head movement and even continued virtually uninterrupted after unexpected braking of the head. If so, a question then arises about how this VOR response interacts with the visually and internally generated components of pursuit. Experiments have shown that, in humans, there is a close association between pursuit and VOR suppression (Barnes et al. 1978; Barnes 1993), but the manner in which the VOR might interact with the separate components of pursuit is unknown. This question is complex because cognitive influences, such as imagining a head-fixed target in the dark, can modify VOR gain (Barr et al. 1976), although the level of suppression is much less than achieved with a visual input (Barnes and Eason 1988). There is also evidence from recording in vestibular nuclei that vestibular efferent signals may be partially suppressed by non-visual mechanisms during active head movements (Roy and Cullen 2002, 2004; Cullen and Roy 2004).

The aim of the current experiments was to determine whether similar effects of brief presentation of the moving target and expectation of target reappearance would apply to the control of smooth gaze movements during head-free pursuit as previously observed during head-fixed pursuit (Barnes and Collins 2008b). Given that during the prolonged extinction of the target there could be no visual input to suppress any ongoing VOR response, we questioned whether the remaining extra-retinal component of pursuit would interact with the VOR or not. A second objective was to examine how the head movement was generated in head-free pursuit, particularly with respect to the varying duration of initial exposure and the changing expectation. Would head velocity, like gaze velocity, be dependent on exposure duration? The evidence suggests that the internal drive for pursuit is similar in head-fixed and head-free conditions and that it acts to counter the VOR (or a neck afferent-/efferent-derived substitute) in the

absence of visual input. In addition, the initial sampling of target velocity is used to scale the velocity of head movement, but with less influence of target exposure duration than for gaze control.

## Method

A total of seven consenting healthy subjects participated in the present study, which conformed to local ethical approval and was performed in accordance with the Declaration of Helsinki. Subjects were seated in a darkened room and instructed to follow a small round visual target with their eyes and head. The target was formed by projection of an LED onto a semi-circular screen (radius 1.5 m) via a mirror galvanometer; target motion was controlled by a computer program. The subjects head was placed directly below the mirror galvanometer at the centre of image rotation. The use of an LED target allowed rapid switching and precise timing of target visibility. Eye movements were recorded using an infra-red limbus tracking system (Skalar Iris) attached to a lightweight helmet. Rotational (yaw) head movements were transduced by a continuous turn potentiometer attached to the helmet. The helmet was coupled to an impression dental bite bar, which ensured that the eye movement recorders and the helmet were rigidly coupled to the subject's head.

Subjects were presented with a step-ramp visual stimulus; a stationary target stepped either left or right of centre (Rashbass 1961), then moved in the opposite direction at 10, 20, 30 or 40 deg/s, to encourage smooth pursuit eye movements, rather than an initial saccade. There were two main experimental conditions where, after a brief initial appearance, the moving target disappeared and then either regularly reappeared or not, thus creating two different expectations. In the mid-ramp extinction (MRE) condition, the target moved for an initial presentation duration (PD) of 50, 100, 150 or 200 ms, but was then extinguished for 400 or 600 ms (extinction duration, ED) during which time the unseen target continued on its trajectory. It subsequently reappeared and continued to move along the same trajectory for 400 ms (when ED = 400 ms) or 200 ms (when ED = 600 ms). Thus, in the MRE condition, subjects had an expectation that the target would move briefly, disappear, then reappear later. In the short-ramp extinction (SRE) condition, the target moved, disappeared and the subject had no expectation of the target reappearing. The experimental condition (MRE or SRE) remained the same for blocks of 32 trials, with four trials for each value of PD. The subject was informed of the condition for the block prior to the start of each block and had a brief rest period between condition blocks. There was a randomised interval of 1–3 s between successive trials. In both the MRE and

the SRE conditions, individual trials had randomised initial step size, presentation duration, movement direction, speed and extinction duration, making the target trajectory highly unpredictable. It is known that an initial backward step reduces initial saccadic activity if the target crosses back through its starting position in  $\sim 200$  ms. Unfortunately, this gives a fixed relationship between step size and target velocity so that the step could be used as a cue for velocity. To avoid this we used this standard criterion for half of the trials and randomised the step size within  $\pm 40\%$  in the other half. Random and non-random steps were intermingled during the presentation. Subsequent analysis showed no significant difference in gaze velocity for standard and randomised steps.

All subjects completed four MRE condition blocks and four SRE condition blocks that were presented in a balanced, randomised order. Each block of trials was preceded by a calibration of the eye movement recorders in which subjects were instructed to maintain the head stationary whilst following a sinusoidal target motion (0.4 Hz,  $\pm 20$  deg) with the eyes alone. Any inadvertent head movements were accounted for by also recording head rotation during the calibration. Prior to each block of MRE or SRE trials, eight Control trials were given in which the target was illuminated continuously throughout the step ramp. There was also a randomised period of 1–3 s between each trial.

During the experiment, subjects were instructed to pursue the target with their eyes and head when visible and to attempt to track the target along its expected trajectory during target extinction. The analogue eye and head displacement data were low-pass filtered at 80 Hz and stored offline after digitization at 200 Hz. The left eye and the head displacement signals were summated to give gaze displacement data after making adjustment for eccentricity of eye with respect to head rotational centre (Huebner et al. 1992b). Head and gaze displacement signals were then digitally differentiated to obtain corresponding velocity signals. Before the main analysis, saccadic movements and blinks were removed using an interactive graphics procedure [see (Bennett et al. 2004)]. Linear interpolation was used to fill the gaps after saccade removal, and the resultant smooth gaze velocity movements were filtered with a 30-Hz zero-phase digital low-pass filter. Head and target velocity information were derived by digital differentiation of head and target displacement data, respectively. In further analyses, responses were averaged over repeats of identical velocity trials and also over left and right going targets, as no significant directional disparity was found.

The displacement at the end of extinction was calculated for gaze, head and eye movements. Gaze and head velocity at the end of the extinction period and at other time points during target extinction were also calculated and compared

between different presentation durations and target velocities. Only the results from the 600-ms extinction period are presented in the current study, since this gave the longest period for internal drive to develop. Statistical comparisons of gaze and head velocities were made with repeated-measures ANOVA tests using SPSS software, with planned contrasts where relevant. Mauchly tests were used to test sphericity within and between factors; if sphericity was violated, a Greenhouse-Geisser correction was used to calculate the *P* value. The results from the present study were compared with similar data from a head-fixed paradigm (Barnes and Collins 2008b) to assess the effect of head movement on the tracking of an unseen target. A total of six subjects completed both the head-free and the head-fixed, in which target velocities were 5, 10, 15, 20 deg/s. Here, direct comparisons in gaze velocity were made with these subjects in the matched target velocities of 10 and 20 deg/s.

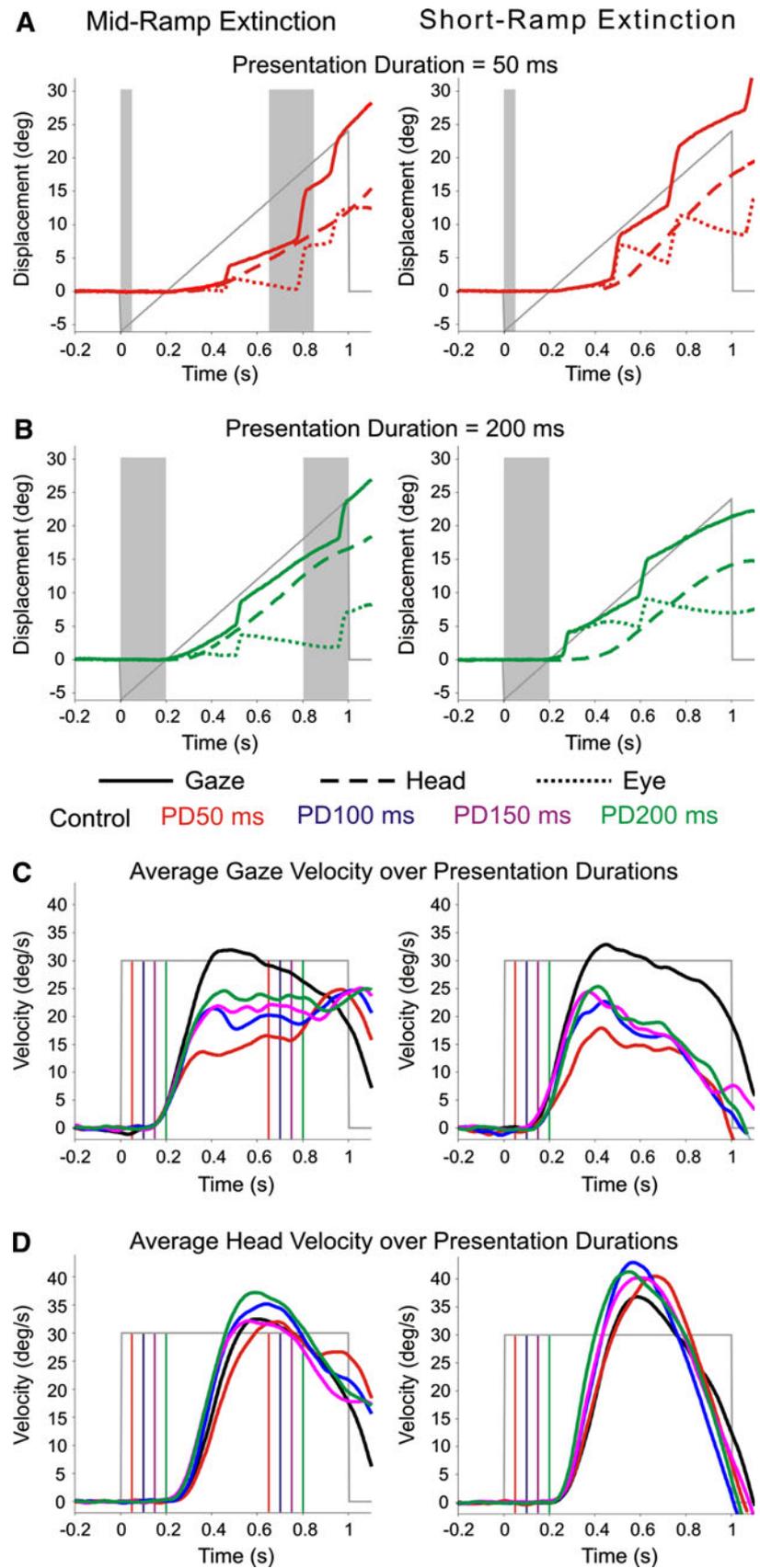
## Results

### General observations

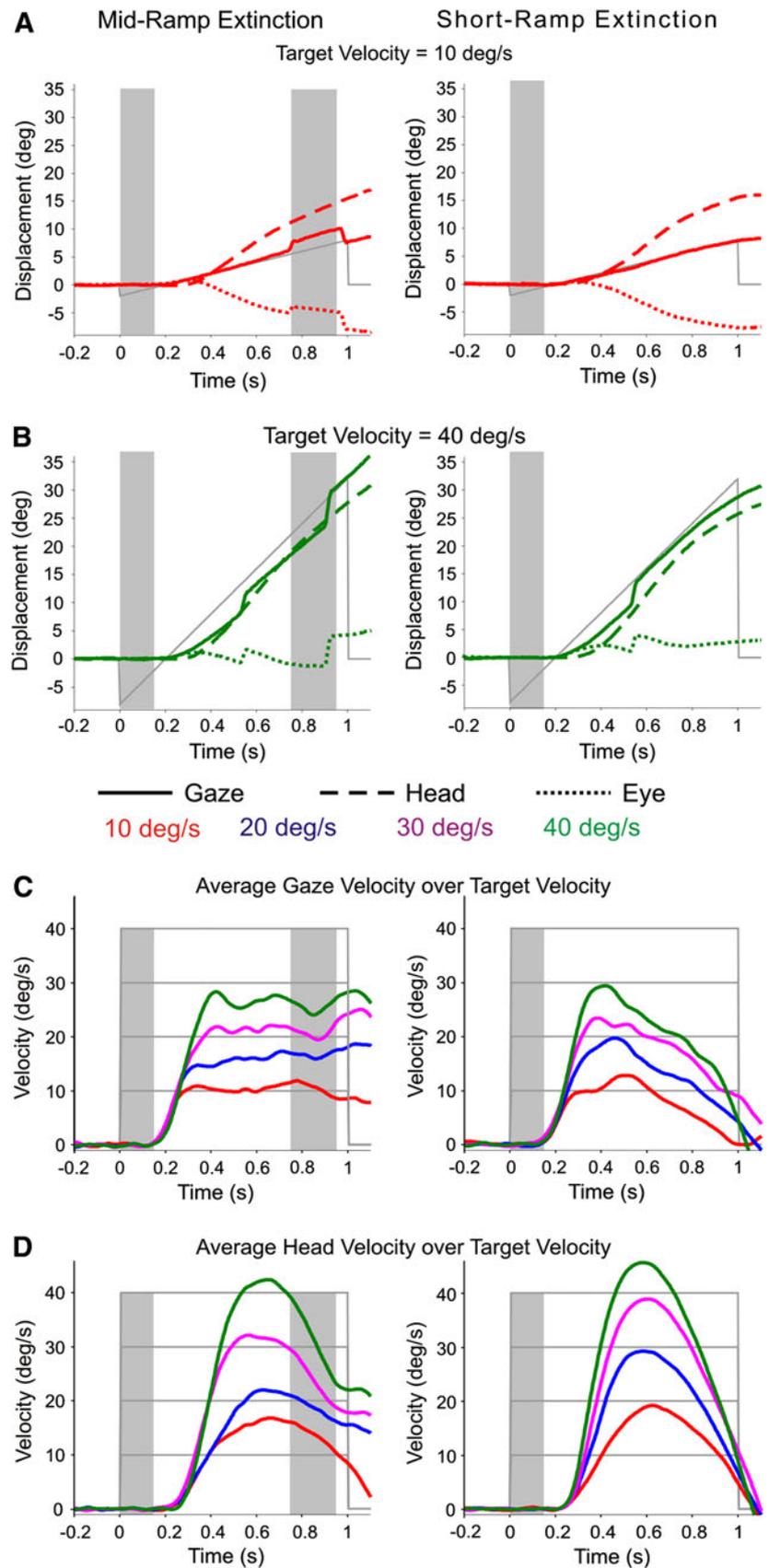
In the majority of trials, subjects were able to successfully determine the direction and speed of the target and initiate a pursuit response, even with only the briefest target presentation duration of 50 ms (Fig. 1a). The pursuit response was initiated after a latent period and exhibited the expected visually driven acceleration towards target velocity. Responses comprised both eye and rotational head movement to the MRE and SRE conditions. Eye displacement with respect to the head often exhibited nystagmus, presumably of vestibular origin, in which the smooth eye movement was in the opposite direction to the head (Fig. 1a, b). Virtually no anticipatory gaze movements were observed prior to target motion, as expected, given that target speed, direction and timing were randomised. Although the eyes and head worked in concert to produce the gaze response, gaze and head velocity had quite different trajectories and were differently affected by the initial presentation duration (compare mean gaze and head velocity traces in Fig. 1c, d). Following the initial visually driven component, subjects were able to sustain gaze responses that were scaled to target velocity (Fig. 2c) even though the response was frequently not initiated until the target had been extinguished.

Mean gaze velocity reached a higher proportion of target velocity during the extinction period as presentation duration (PD) increased; this was particularly true in the MRE condition where gaze velocity tended to reach a higher plateau throughout the ensuing blank period prior to target reappearance, with more than 100 ms of target motion

**Fig. 1** Differences in response to presentation duration. *Left* mid-ramp extinction responses; *right* short-ramp extinction responses. Examples of raw displacement responses for gaze (filled line), eye (dotted line) and head (dashed line) from subject 1 at **a**  $PD = 50$  ms and **b**  $PD = 200$  ms at 30 deg/s. Average velocities for **c** gaze and **d** head over all subjects for each presentation duration at 30 deg/s



**Fig. 2** Differences in response to target velocity. *Left* mid-ramp extinction responses; *right* short-ramp extinction responses. Examples of raw displacement responses for gaze (*filled line*), eye (*dotted line*) and head (*dashed line*) from subject 4 at **a** 10 deg/s and **b** 40 deg/s at  $PD = 150$  ms. Average velocities for **c** gaze and **d** head over all subjects for each velocity at  $PD = 150$  ms



information. However, even with only 50 ms initial presentation, gaze velocity frequently increased over the 600 ms period of extinction in the MRE condition (Fig. 1c). In the SRE condition, the response exhibited some decay after reaching an initial peak but was nevertheless scaled to target velocity and reached higher velocities for PD > 100 ms. Conversely, head velocity did not appear to be greatly influenced by initial presentation duration and generally reached a peak in the middle of the extinction period for both the MRE and the SRE conditions (Fig. 1d); however, mean head velocity was also scaled to target velocity (Fig. 2d). Generally, the speed of the smooth eye-in-head movement was less than head speed, so that gaze and head velocity were in the same direction.

### Gaze velocity

The MRE responses, which were associated with the expectation of target reappearance, followed similar trajectories of near-constant gaze velocity after the initial visually driven response to target motion (Fig. 2c, left). By contrast, in the SRE condition, gaze velocity slowly decreased after reaching peak velocity, then, approximately 750 ms after the onset of the trial, decreased more rapidly (Fig. 2c, right). However, for both MRE and SRE conditions, mean gaze velocity increased with increasing target velocity (Figs. 2c, 3a). Analysis of variance was conducted for end-extinction gaze velocity with target velocity, initial presentation duration and expectancy condition (MRE vs. SRE) as factors. This revealed a significant main effect of target velocity ( $F_{(3, 15)} = 12.97$ ,  $P < 0.01$ ); a repeated contrast showed significant increases in target velocity increases from 10 to 20 deg/s ( $F_{(1, 15)} = 18.71$ ,  $P < 0.01$ ) and 20–30 deg/s ( $F_{(1, 15)} = 7.43$ ,  $P < 0.05$ ). There was also a significant effect of initial target presentation duration ( $F_{(1, 15)} = 6.58$ ,  $P < 0.01$ ) on end-extinction gaze velocity, although contrasts showed a significant increase in the values from 50 to 100 ms only ( $F_{(1, 15)} = 15.28$ ,  $P < 0.01$ ). Differences between the MRE and the SRE conditions were also found; end-extinction gaze velocity was significantly greater in the MRE condition than in the SRE condition ( $F_{(1, 15)} = 6.65$ ,  $P < 0.05$ ).

Measuring at end-extinction gives only a snapshot of gaze control. To reveal more information about differing PD levels and to compare them with Control responses, gaze velocity was also examined at fixed times of 400, 500 and 600 ms after target onset when it was near its maximum. The Control condition was included with the different PD levels to form a single factor PD' in the analysis of variance. At 400, 500 and 600 ms there was a significant effect of PD' on gaze velocity ( $F_{(4, 24)} > 6.266$ ;  $P < 0.001$ ) and repeated contrasts showed that gaze

velocity was always less for PD = 50 ms than for PD = 100 ms ( $F_{(1, 6)} > 6.16$ ;  $P < 0.048$ ) and was less for PD = 200 ms than for the Control ( $F_{(1, 6)} < 23.381$ ;  $P < 0.003$ ). At 500 ms, gaze velocity for PD = 100 ms was also significantly less than for PD = 150 ms ( $F_{(1, 6)} = 50.673$ ;  $P < 0.001$ ). At each of these times, there was also a significant effect of target velocity ( $F_{(3, 18)} < 20.272$ ;  $P < 0.001$ ) but no significant difference between MRE and SRE responses. To put this into context, gaze velocity at 600 ms reached only 46% of Control for PD = 50 ms, 65% for 100 ms, 75% for 150 ms and 74% for 200 ms.

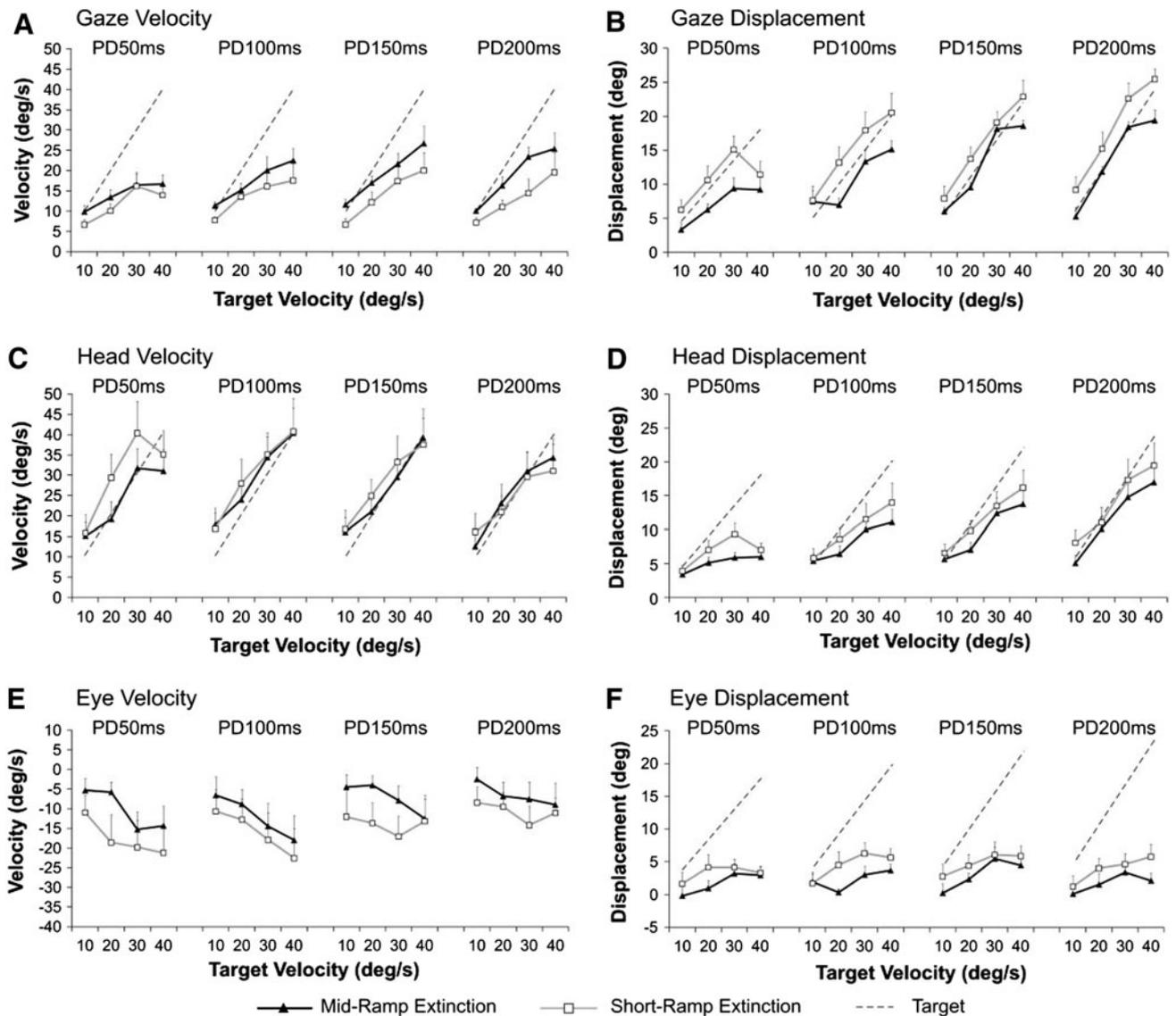
In general, these results confirm that (1) subjects were able to use the motion information available in the brief initial presentation to scale gaze velocity in proportion to target velocity, although gaze velocity generally fell short of target velocity (Fig. 1) except at 10 deg/s; (2) 50 ms of initial presentation was too brief to give reliable velocity information and 100–150 ms of motion information was needed to attain the maximum level of gaze velocity during extinction; and (3) the maintenance of gaze velocity by the internal drive during target extinction was influenced by cognitive expectation.

### Gaze displacement

Although gaze velocity during target extinction was often less than target velocity (Fig. 3a), gaze displacement was generally well matched to the unseen target displacement (Figs. 2a, b; 3b). Measurements taken at end-extinction in the MRE condition, and at the equivalent time in the SRE condition, showed that gaze displacement was very close to the required target displacement (Fig. 3b). ANOVA showed a significant main effect of target velocity on end-extinction gaze displacement ( $F_{(3, 15)} = 115.69$ ,  $P < 0.001$ ), i.e. gaze displacement was scaled to target velocity. There was also a significant main effect of expectation of target reappearance for the end-extinction gaze displacement ( $F_{(1, 15)} = 7.41$ ,  $P < 0.05$ ), the SRE end-extinction gaze displacement being higher than that for the MRE condition. Inspection of Fig. 3b reveals that for initial presentations of 100 ms or more, MRE gaze displacement was closer to target displacement (mean gain = 0.95), than in the SRE condition (mean gain = 1.30). The relative inaccuracy in the SRE condition was probably associated with the continual absence of any target position information beyond the initial presentation that would have reinforced the accuracy of estimates.

### Head velocity

The mean velocity of head rotation at end-extinction increased monotonically with target velocity, as indicated



**Fig. 3** Measures of gaze and head movement at end-extinction for mid-ramp (MRE) and equivalent time for short-ramp (MRE) as a function of target velocity for each presentation duration (PD). **a** and

**b** show gaze velocity and displacement; **c** and **d** show head velocity and displacement; and **e** and **f** indicate eye-in-head velocity and displacement, respectively. Error bars indicate +1SEM

in Fig. 3c. ANOVA confirmed that there was a significant effect of target velocity on end-extinction head velocity ( $F_{(3, 15)} = 18.45, P < 0.01$ , Fig. 3c), and a repeated contrast revealed significant differences for the increases in target velocity from 10 to 20 deg/s ( $F_{(1, 15)} = 14.51, P < 0.01$ ) and 20–30 deg/s ( $F_{(1, 15)} = 22.32, P < 0.01$ ). There was no effect of expectation (MRE vs. SRE) on end-extinction head velocity. There was, however, a significant effect of initial presentation duration on end-extinction head velocity ( $F_{(3, 15)} = 3.37, P < 0.05$ ), although in a repeated contrast, the only significant difference was between PD = 150 and PD = 200 ms ( $F_{(1, 15)} = 9.31, P < 0.05$ ).

As for gaze velocity, more information on the effects of PD was revealed by examining head velocity at fixed times (400, 500 and 600 ms) after target onset and including the Control responses with different PD values as a single factor (PD') in the ANOVA. At each of these within-extinction times, there was a significant effect of target velocity ( $F_{(3, 18)} > 19.889; P < 0.001$ ), but no significant difference between MRE and SRE conditions. At 400 and 500 ms, there was a significant effect of PD' ( $F_{(4, 24)} > 3.108; P < 0.034$ ), but not at 600 ms. Repeated contrasts revealed no significant differences between levels of PD' and, in fact, when the PD = 50 ms data were removed, there was no longer a main effect of PD'.

Underlying these findings was the fact that the differences in head velocity between levels of PD and the Control were small and considerably less than the corresponding differences in gaze velocity. At 600 ms, head velocity for combined MRE and SRE conditions reached 83% of Control velocity for PD = 50 ms and 102, 103 and 109% for PD = 100, 150, 200 ms, respectively. Thus, head velocity at 600 ms in the Control condition was slightly less than that for all other PD levels except PD = 50 ms, in marked contrast to the findings for gaze velocity at 600 ms.

#### Head displacement

Although clearly related to head velocity, the calculation of head displacement at the time corresponding to end-extinction provides a clear indication of the parsing of gaze between head and eye at this time (cf. Fig. 3b, d). ANOVA revealed that there was a significant main effect of target velocity on end-extinction head displacement ( $F_{(3, 15)} = 33.07$ ,  $P < 0.001$ ) and a repeated contrast showed that there was a significant increase for each increase in target velocity (10–20 deg/s:  $F_{(1, 15)} = 36.38$ ,  $P < 0.001$ ; 20–30 deg/s:  $F_{(1, 15)} = 27.77$ ,  $P < 0.01$ ; 30–40 deg/s:  $F_{(1, 15)} = 14.53$ ,  $P < 0.01$ ). It can also be seen that the effect of expecting the target to reappear influenced the head; there was a trend for increased displacement in the SRE condition compared with the MRE condition, similar to the gaze displacement, although for the head, this did not quite reach significance ( $F_{(1, 15)} = 4.95$ ,  $P = 0.068$ ). From inspection of Fig. 3b, d, it is evident that the head displacement forms a large proportion of total gaze displacement. During target extinction, the eye was often positively displaced in the orbit (see raw responses in Fig. 1a, b), showing that the gaze was leading the head.

#### Eye-in-head movement

The end-extinction values for eye-in-head velocity (Fig. 3e) were always negative, reflecting the activity of mechanisms compensatory for head movement. However, end-extinction eye displacement (Fig. 3f) was always positive and like head and gaze displacement, increased with increasing target velocity ( $F_{(3, 15)} = 11.93$ ,  $P < 0.001$ ). Increases were significant for target velocity increases from 10 to 20 deg/s ( $F_{(1, 15)} = 12.47$ ,  $P < 0.05$ ) and 20–30 deg/s ( $F_{(1, 15)} = 16.00$ ,  $P < 0.01$ ). There was a significant increase in the end-extinction eye displacement from the MRE to the SRE conditions ( $F_{(1, 15)} = 9.98$ ,  $P < 0.05$ ), as found with the expectancy of target reappearance in gaze displacement. Taken together with the head displacement data, these eye displacement results indicate how these two components of gaze both increased in proportion to target displacement.

#### Comparison of head-free and head-fixed responses

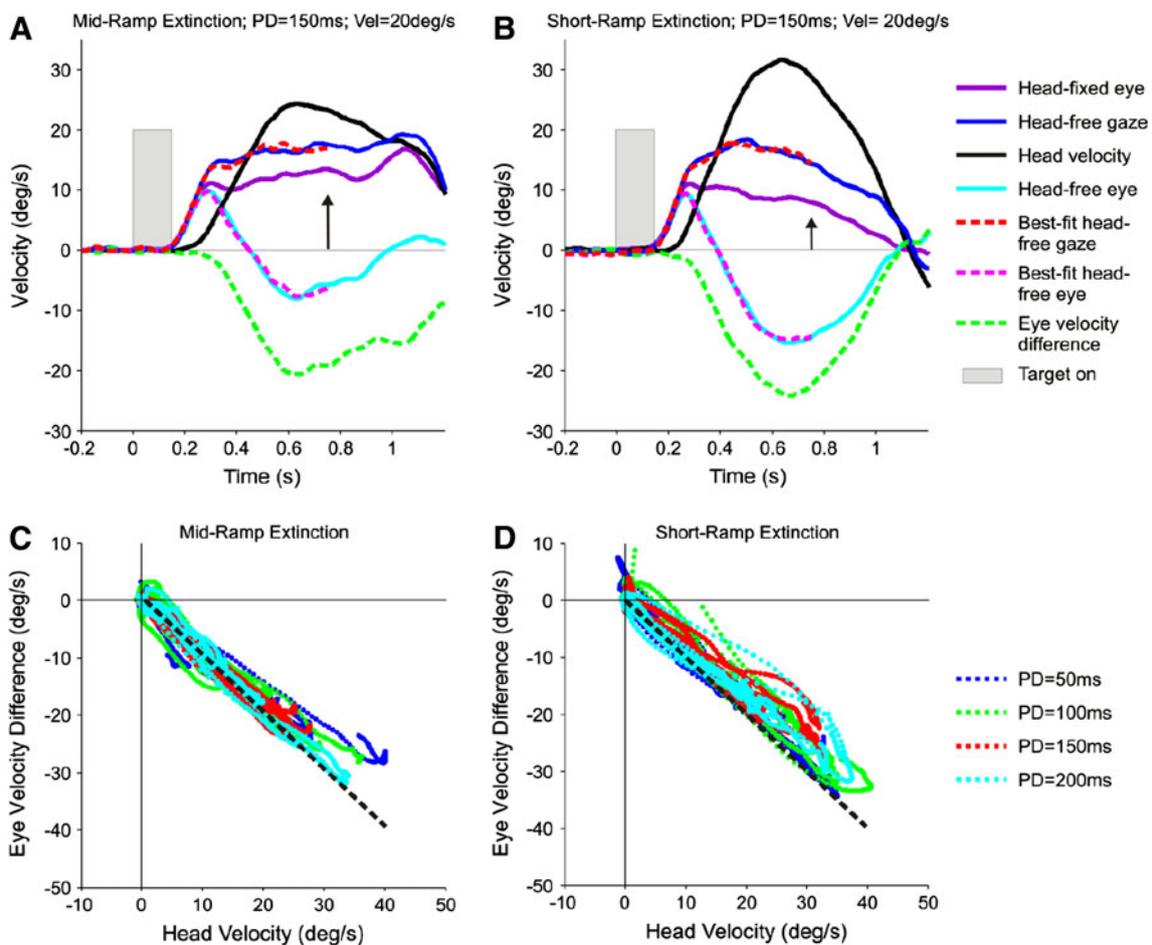
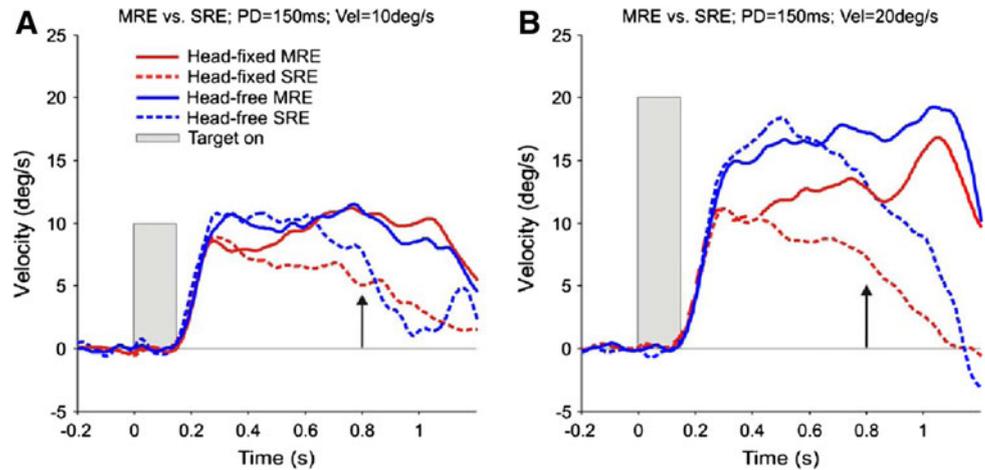
The head-free results from the present experiment were compared with the results from matched subjects in the head-fixed paradigm (from Barnes and Collins 2008b; head-fixed eye displacement and velocity now referred to as gaze displacement and velocity, respectively, for comparison). Responses made to target velocity levels of 10 and 20 deg/s for Controls and all presentation durations were compared. Figure 4a, b show gaze velocity trajectories for head-fixed and head-free responses in the MRE and SRE conditions at 10 and 20 deg/s, respectively. Three distinct trends are revealed in Fig. 4: (1) head-free responses for both MRE and SRE conditions had higher gaze velocity than head-fixed responses; (2) the differences between the head-fixed and the head-free SRE responses were larger than those for the MRE responses; (3) the increase in target velocity from 10 to 20 deg/s induced a proportional increase in gaze velocity in both the head-fixed and the head-free responses; and (4) the initial part of the gaze velocity response was very similar in head-fixed and head-free conditions, but with head free, gaze velocity continued for longer and reached a higher level that was sustained throughout extinction.

Since end-extinction occurred at different times after target onset for different values of PD, we measured gaze velocity 600 ms after onset to examine differences between PD values. ANOVA revealed significant effects of velocity in the MRE condition ( $F_{(1, 5)} = 20.05$ ;  $P = 0.007$ ) and PD ( $F_{(3, 15)} = 6.80$ ;  $P = 0.004$ ) and velocity ( $F_{(1, 5)} = 46.23$ ;  $P = 0.001$ ) in the SRE condition. A significant difference between head-fixed and head-free was found across both target velocities in the SRE condition ( $F_{(1, 5)} = 16.91$ ;  $P = 0.009$ ), but only at 20 deg/s in the MRE condition ( $F_{(1, 5)} = 6.94$ ;  $P = 0.046$ ).

#### The role of compensatory eye movements

In the head-free condition, head rotation would be expected to evoke a compensatory VOR response and consistent with this, eye-in-head position often moved in the opposite direction to the head (see examples in Fig. 2a, b). On average, eye-in-head velocity was of opposite polarity to head velocity towards the end of extinction, as shown in Fig. 5 (cyan trace). If it is assumed that the internal drive that gives rise to the sustained response in the head-fixed condition is identical in head-fixed and head-free conditions, the compensatory (VOR) response should be revealed by calculating an eye velocity difference signal, i.e. the difference between head-free eye-in-head velocity and head-fixed eye velocity. This approach is similar to that used by Lefevre et al. (1992) when investigating compensatory response characteristics during saccadic

**Fig. 4** Examples of velocity profiles for both head-free and head-fixed pursuit in the mid-ramp extinction (*MRE*) and short-ramp extinction (*SRE*) conditions. Responses are averaged across 6 subjects and 4 repeats/subject for  $PD = 150$  ms and target velocity 10 deg/s (a) and 20 deg/s (b). Black vertical arrow indicates end of extinction in *MRE* condition



**Fig. 5** a and b show averaged gaze, head and eye-in-head velocity trajectories in *MRE* and *SRE* conditions, respectively. Dashed magenta and red traces indicate best-fit predictions of head-free eye-in-head and gaze velocity, respectively. Green dashed trace indicates eye velocity difference between head-free and head-fixed eye-in-head responses. Black vertical arrow indicates end of extinction. Colour coding of traces is given in legend. Best-fit functions

obtained by regression analysis of head-free gaze velocity versus the combination of head velocity and head-fixed eye velocity. c and d show the eye velocity difference signal plotted point-by-point against head velocity for *MRE* and *SRE* conditions, respectively. Data from each  $PD$  condition plotted in separate colour as shown in legend. Dashed black line indicates the ideal compensatory gain of  $-1$

gaze shifts. As indicated in Fig. 5, the eye velocity difference signal (black dashed trace) clearly has a similar trajectory to head velocity, but is of opposite polarity. It normally appeared slightly delayed with respect to head velocity. Plotting the difference signal versus head velocity point-by-point over the first 650 ms (i.e. prior to target reappearance in any condition) revealed an apparently linear relationship in all subjects (Fig. 5c, d), with a clear overlay of responses to different PD values.

In deriving the eye velocity difference signal, it has been assumed that the non-compensatory part, which is composed of visually driven and extra-retinal components, is identical in head-fixed and head-free conditions, but given the response variability, it is more probable that although they share similar dynamic characteristics they may differ in magnitude. To establish the contribution of the compensatory and non-compensatory components, we therefore conducted a multiple regression analysis in which it was assumed that the head-free eye-in-head velocity was composed of two components, one related to the head-fixed eye velocity, the other to delayed head velocity. Because of the evident delay noted above, the analysis was carried out with delay increasing in 5-ms steps from 0 to 50 ms; the delay that accounted for the greatest percentage variance (i.e. largest  $R^2$  value) was selected as optimum. Analysis was carried out for individual subjects separately. Coefficients for the head velocity ( $K_v$ ) and head-fixed eye velocity ( $K_{fx}$ ) components and the optimum delay values for individual subjects are given in Table 1. Analysis of variance revealed no significant effect of PD on either  $K_v$  or  $K_{fx}$ . There was also no significant effect of expectation (MRE vs. SRE); hence, gain values in Table 1 have been averaged across this factor. The mean value of  $K_v$ , the compensatory component, was 0.85, whilst the mean value of  $K_{fx}$  was 0.99, very close to the ideal, expected value of unity. Both components contributed significantly ( $P < 10^{-8}$ ) to the relationship in all subjects and all conditions. To probe for possible head-velocity dependent changes in  $K_v$ , regression analyses were also conducted looking for quadratic terms related to head velocity. For this purpose, the data for all PD values (but not including the Control) were combined for each subject on the basis that any prevailing non-linearity should apply to all conditions with target extinction. This analysis yielded significant quadratic coefficients ( $K_{v2}$ ) in 5 of the 6 subjects, but these coefficients were positive in two individuals and negative in three. Analysis based on all 6 subjects gave the following coefficients ( $\pm 95\%$  confidence intervals):  $K_{fx} = 0.95 (\pm 0.060)$ ;  $K_v = -0.81 (\pm 0.037)$  and  $K_{v2} = -0.0024 (\pm 0.0002)$ , with an  $R^2$  value of 0.96. On this basis, therefore, average compensatory gain showed a slight increase from 0.82 at a head velocity of 5 deg/s to 0.92 at 50deg/s.

**Table 1** Coefficients ( $\pm 95\%$  confidence intervals) of the regression analysis linking head-free eye-in-head velocity to head velocity ( $K_v$ ) and head-fixed eye velocity ( $K_{fx}$ )

Subject	Delay (ms)	Head velocity coefficient ( $K_v$ )					Head-fixed eye coefficient ( $K_{fx}$ )				
		Control	PD50	PD100	PD150	PD200	Control	PD50	PD100	PD150	PD200
S1	10.0	-1.03 ( $\pm 0.027$ )	-0.76 ( $\pm 0.058$ )	-0.78 ( $\pm 0.028$ )	-0.81 ( $\pm 0.025$ )	-0.68 ( $\pm 0.034$ )	1.12 ( $\pm 0.029$ )	0.87 ( $\pm 0.059$ )	0.72 ( $\pm 0.063$ )	0.81 ( $\pm 0.043$ )	0.82 ( $\pm 0.040$ )
S2	14.7	-0.95 ( $\pm 0.067$ )	-0.84 ( $\pm 0.041$ )	-0.90 ( $\pm 0.056$ )	-0.93 ( $\pm 0.029$ )	-0.98 ( $\pm 0.059$ )	1.18 ( $\pm 0.048$ )	0.93 ( $\pm 0.049$ )	0.85 ( $\pm 0.052$ )	1.02 ( $\pm 0.071$ )	1.13 ( $\pm 0.065$ )
S3	14.4	-0.93 ( $\pm 0.025$ )	-0.71 ( $\pm 0.028$ )	-0.69 ( $\pm 0.042$ )	-0.90 ( $\pm 0.042$ )	-0.70 ( $\pm 0.031$ )	0.92 ( $\pm 0.036$ )	0.62 ( $\pm 0.064$ )	0.73 ( $\pm 0.078$ )	0.78 ( $\pm 0.057$ )	0.66 ( $\pm 0.049$ )
S4	5.9	-1.04 ( $\pm 0.018$ )	-0.81 ( $\pm 0.021$ )	-0.86 ( $\pm 0.027$ )	-0.77 ( $\pm 0.025$ )	-0.81 ( $\pm 0.023$ )	0.96 ( $\pm 0.042$ )	0.75 ( $\pm 0.046$ )	1.07 ( $\pm 0.068$ )	0.92 ( $\pm 0.061$ )	0.86 ( $\pm 0.049$ )
S5	19.1	-0.87 ( $\pm 0.024$ )	-0.99 ( $\pm 0.021$ )	-0.99 ( $\pm 0.034$ )	-0.97 ( $\pm 0.019$ )	-0.91 ( $\pm 0.020$ )	0.79 ( $\pm 0.047$ )	0.95 ( $\pm 0.042$ )	1.96 ( $\pm 0.063$ )	1.04 ( $\pm 0.072$ )	0.85 ( $\pm 0.065$ )
S6	23.1	-1.06 ( $\pm 0.019$ )	-0.88 ( $\pm 0.030$ )	-0.93 ( $\pm 0.018$ )	-0.89 ( $\pm 0.023$ )	-0.90 ( $\pm 0.016$ )	1.08 ( $\pm 0.044$ )	1.43 ( $\pm 0.050$ )	1.34 ( $\pm 0.076$ )	1.25 ( $\pm 0.066$ )	1.23 ( $\pm 0.045$ )
Mean	14.5	-0.98	-0.83	-0.86	-0.88	-0.83	1.01	0.92	1.11	0.97	0.92

Delays are averaged across all PD values

The coefficients derived from this regression analysis were then used to calculate the best-fit estimate of head-free eye-in-head velocity and gaze velocity. The average of these responses is plotted in Fig. 5 (red and magenta dashed traces), where it is evident that these best-fit functions match not only the oppositely directed eye movement in the later part of extinction, but also the differences between head-free and head-fixed gaze velocity in the early response that was dominated by visual input. If the compensatory response had had a gain of exactly  $-1$ , this difference would not be evident. The small difference in gaze velocity with head-free thus appears attributable to a compensatory gain that was slightly less than one, but which remained consistent across all target extinction conditions.

## Discussion

These experiments were designed to explore how visual and extra-retinal components of smooth pursuit develop and interact with the VOR in response to very brief exposure of a moving visual target when the head is free to rotate. In line with previous observations for head-fixed pursuit (Barnes and Collins 2008a, 2008b), the present experiment has demonstrated that during head-free pursuit, human subjects are able to extract and temporarily store motion information after brief presentation of randomised target motion and use it both to initiate a visually driven eye movement response and to sustain appropriately scaled gaze and head movements during prolonged target extinction. The results suggest that just 100–150 ms of retinal slip visual information is sufficient for adequate sampling and storage of the target velocity, enabling a high level of sustained gaze velocity (mean of 27 deg/s at 40 deg/s target velocity) for a duration of  $>400$  ms in the absence of visual feedback (Fig. 1c). The ability to sustain gaze velocity to an unseen target is a manifestation of internal drive (pursuit maintenance) mechanisms and is dependent on expectation of target reappearance; the reduced cognitive expectation in the SRE condition led to an earlier decline of both gaze velocity and head velocity than in the MRE condition.

As found previously for head-fixed responses (Barnes and Collins 2008a, 2008b), significant differences were observed in the effects of the various experimental factors (initial exposure (PD), cognitive expectation (MRE vs. SRE) and head motion) on smooth gaze velocity and overall gaze displacement. In general, overall gaze displacement was fairly close to target displacement at the end of extinction even though gaze velocity might be considerably less than target velocity throughout the extinction period. This was particularly true for the SRE condition

where gaze velocity was much less than target velocity at the end of extinction, but gaze displacement was actually slightly greater than target displacement (Fig. 3). As noted previously (Bennett and Barnes 2003, 2006; Collins and Barnes 2006; Orban de Xivry et al. 2006), the saccadic system appears to compensate, on average, for deficiencies of smooth movement, as if gaze position control has access to a reasonably accurate estimate of the continuing trajectory of the unseen target (Barborica and Ferrera 2003). Since subjects experienced only a brief presentation of target motion in MRE and SRE conditions, the implication is that this initial velocity sample can be continuously integrated to provide an internal representation of continuing target motion.

In the head-free pursuit condition, initial sampling of target velocity also governed the control of average head velocity. Like gaze velocity, mean head velocity was scaled to target velocity in the absence of visual feedback. Unlike gaze, though, head velocity appeared to be more independent of the visual input in the sense that head velocity in mid-extinction (at 600 ms after target onset) was similar for all PD values except the shortest (PD = 50 ms) and, more importantly, was also very similar in the Control condition in which there was continuous target presentation. In contrast, although gaze velocity at 600 ms was similar for PD = 100–200 ms, there was a large difference between PD = 200 ms and the Control condition. It appears, therefore, that any exposure of the target for 100 ms or more gives a reasonable estimate of target velocity that leads to a similar head velocity. Gaze velocity, on the other hand, is affected not only by this initial estimate but also by the duration for which the target is exposed. This lends support to the argument that gaze is dependent on both current visual input and stored information derived from the initial sampling of visual input, whereas the head is only dependent on the sampled and stored information and is not directly affected by current visual input.

The role of retinal and extra-retinal mechanisms in head-fixed pursuit is now fairly well understood (Barnes 2008). The initial response to a random stimulus is largely driven by visual input (Lisberger and Westbrook 1985; Carl and Gellman 1987; Lisberger et al. 1987), but extra-retinal mechanisms rapidly take over and generate a large part of the sustained response. Typically, if the target is extinguished during the sustained response, eye velocity initially decays with a time constant of  $\sim 100$ – $150$  ms to a plateau level that is thought to represent the extra-retinal component (Becker and Fuchs 1985). Barnes and Collins (2008a) have shown that the extra-retinal component is initiated  $\sim 50$  ms after the visual component and develops much more slowly than the visually driven response, taking  $\sim 500$  ms to reach the plateau level. The magnitude

attained by the initial visually driven part of the eye velocity response is dependent on the duration of initial target exposure (Barnes and Collins 2008b), and its termination is usually marked by an abrupt reduction in eye acceleration. Any continuation of smooth eye movement in the absence of visual input results from the combination of the decay of the visually driven response and the build-up of the extra-retinal component (Barnes and Collins 2008c). When PD = 50 ms, the visual component is very small, but eye velocity continues to increase during extinction to a higher level that is not much less than for PD = 200 ms, implying that a high proportion of velocity sampling is complete within 50 ms. This timescale for velocity assimilation is reasonably compatible with recent observations on the temporal development of motion integration for pursuit (Tavassoli and Ringach 2009) and saccades (Etchells et al. 2010) and the build-up of motion-dependent discharge in MT (middle temporal cortex) neurons of the monkey (Osborne et al. 2004).

During head-free pursuit, the control of gaze velocity is very similar to that of eye velocity during head-fixed pursuit. With head-free, though, the termination of the initial visually driven component of gaze velocity is less distinct because the initiation of head movement modifies the gaze response. In fact, comparison of pursuit with and without head rotation reveals that, in both MRE and SRE conditions, gaze velocity appears to continue for longer and reaches a higher plateau during extinction (see Figs. 4, 5). Detailed examination of head and eye movement during extinction indicated that the increase in gaze velocity with head free was specifically related in magnitude and timing to head movement and was thus most likely associated with the VOR and/or neck-related inputs that compensate for head movement. Regression analysis revealed that the observed increases in head-free conditions resulted from a compensatory gain that was slightly less than unity (Fig. 5). The consequence of this is shown in the simulations of gaze velocity derived from the regression analysis in Fig. 5. Because head movement was initiated ~50 ms later than eye movement, the small fraction of head movement (~15%) that was not compensated for was summated with the extra-retinal component of eye movement, prolonging it and allowing a higher gaze velocity to be achieved. The small difference in pursuit gain between head-fixed and head-free conditions accords with previous observations [see Barnes (1993)], in which performance has been assessed when both visual feedback and internal drive mechanisms are functioning. Note, though, that our current experiment gives a much clearer indication of the interaction between the VOR and the extra-retinal mechanisms because the interaction takes place in open loop conditions; in normal conditions, visual feedback would suppress much of the difference that is observed here.

The average gain level for the compensatory response (0.85) is comparable to the values typically recorded in humans during voluntary head rotation in darkness [see Barnes (1993)]. However, we cannot be certain that this represents a pure VOR response; cervico-ocular and/or corollary discharge mechanisms may also participate. The major issue of concern is whether the compensatory response is appropriate in these circumstances. It has been suggested that the VOR is not useful during head-free pursuit (Robinson 1982), since it drives the eye in the opposite direction to the goal. Robinson hypothesised that the VOR might be switched off during planned head movements in order to enhance gaze velocity. On the other hand, a VOR gain of unity allows pursuit to be the same irrespective of the level of head movement. The findings of Lanman et al. (1978) in monkeys provide some support for a near-unity compensatory gain, since there was little perturbation of gaze on head braking, but the detailed velocity analysis required to yield reliable quantitative information was not carried out. Huebner et al. (1992a) used a similar head-braking technique in humans in a combined pursuit and head motion task, but head rotation was passively induced by whole-body rotation on a turntable. These authors observed a transient reduction in gaze velocity compatible with a VOR gain of ~0.76, slightly lower than the values we observe, but this may reflect the frequent observation that VOR gain is slightly higher during active versus passive head movement [see Barnes (1993)]. There is stronger evidence that VOR gain is reduced during gaze shifts. Lefevre et al. (1992), for example, showed that gaze velocity is greater during head-free gaze shifts than in comparable head-fixed saccades. It could be argued that the level of gain that we find represents a useful compromise that allows head-free pursuit gain to be slightly increased over that in the head-fixed condition. This may help to overcome the velocity saturation problems that are potentially associated with high velocity pursuit (Meyer et al. 1985) and thus go some way to realising Robinson's original concept. As Roy and Cullen (2004) have reported, VOR gain in these circumstances may, in fact, decrease with increasing head velocity. By including quadratic terms in our regression analysis, we found some hint of this in some subjects but not in others. The VOR is a very labile reflex, and it is notoriously difficult to obtain a consistent measure of gain in darkness because it can be affected by factors such as arousal. Humans are certainly able to use non-visual mechanisms to suppress the VOR if, for example, they imagine the presence of a head-fixed target (Barr et al. 1976; Barnes and Eason 1988) in darkness. However, it seems unlikely that such mechanisms would be called upon in head-free pursuit where the objective is to follow the moving target, not to hold fixation on a head-fixed target.

In summary, the results from this head-free pursuit study support, but extend, those obtained previously during head-fixed pursuit. They show that 100–150 ms is sufficient time of target exposure for an estimate of target velocity to be obtained that can then be used to scale internally driven movements of the head and gaze. Notably, the estimate of head velocity for a 150 or 200 ms exposure is not distinguishable from the estimate that is used to drive head movement in the Control condition when the target is continuously visible, suggesting that vision has no direct input to head movement control. Finally, during head-free pursuit, the VOR appears to remain active, with gain slightly less than unity, but is countermanded by the extra-retinal gaze control command.

**Acknowledgments** This work was supported by a grant from the Medical Research Council, UK.

## References

- Barborica A, Ferrera VP (2003) Estimating invisible target speed from neuronal activity in monkey frontal eye field. *Nat Neurosci* 6:66–74
- Barnes GR (1993) Visual-Vestibular interaction in the control of head and eye movement: the role of visual feedback and predictive mechanisms. *Prog Neurobiol* 41:435–472
- Barnes GR (2008) Cognitive processes involved in smooth pursuit eye movements. *Brain Cogn* 68:309–326
- Barnes GR, Asselman PT (1991) The mechanism of prediction in human smooth pursuit eye movements. *J Physiol (Lond)* 439:439–461
- Barnes GR, Collins CJS (2008a) Evidence for a link between the extra-retinal component of random-onset pursuit and the anticipatory pursuit of predictable object motion. *J Neurophysiol* 100:1135–1146
- Barnes GR, Collins CJS (2008b) The influence of briefly presented randomised target motion on the extra-retinal component of ocular pursuit. *J Neurophysiol* 99:831–842
- Barnes GR, Collins CJS (2008c) Internally generated smooth eye movement: its dynamic characteristics and role in randomised and predictable pursuit. *Prog Brain Res* 171:441–449
- Barnes GR, Eason RD (1988) Effects of visual and non-visual mechanisms on the vestibulo-ocular reflex during pseudo-random head movements in man. *J Physiol (Lond)* 395:383–400
- Barnes GR, Benson AJ, Prior ARJ (1978) Visual-vestibular interaction in the control of eye movement. *Aviat Space Environ Med* 49:557–564
- Barnes GR, Schmid AM, Jarrett CB (2002) The role of expectancy and volition in smooth pursuit eye movements. *Prog Brain Res* 140:239–254
- Barr CC, Scultheis LW, Robinson DA (1976) Voluntary, non-visual control of the vestibulo-ocular reflex. *Acta Otolaryngol (Stockh)* 81:365–375
- Becker W, Fuchs AF (1985) Prediction in the oculomotor system: smooth pursuit during transient disappearance of a visual target. *Exp Brain Res* 57:562–575
- Bennett SJ, Barnes GR (2003) Human ocular pursuit during the transient disappearance of a moving target. *J Neurophysiol* 90:2504–2520
- Bennett SJ, Barnes GR (2004) Predictive smooth ocular pursuit during the transient disappearance of a visual target. *J Neurophysiol* 92:578–590
- Bennett SJ, Barnes GR (2006) Smooth ocular pursuit during the transient disappearance of an accelerating visual target: the role of reflexive and voluntary control. *Exp Brain Res* 175:1–10
- Bennett SJ, Barnes GR, Orban de Xivry JJ, Lefèvre P (2004) Ocular pursuit to a predictable velocity and/or position change during the occlusion of a moving target. *Soc Neurosci Abstr* 33:712–716
- Carl JR, Gellman RS (1987) Human smooth pursuit: stimulus-dependent responses. *J Neurophysiol* 57:1446–1463
- Collins CJS, Barnes GR (2006) The occluded onset pursuit paradigm: prolonging anticipatory smooth pursuit in the absence of visual feedback. *Exp Brain Res* 175:11–20
- Cullen KE, Roy JE (2004) Signal processing in the vestibular system during active versus passive head movements. *J Neurophysiol* 91:1919–1933. doi:10.1152/jn.00988.2003
- Etchells PJ, Benton CP, Ludwig CJ, Gilchrist ID (2010) The target velocity integration function for saccades. *J Vis* 10:7
- Huebner WP, Leigh RJ, Seidman SH, Thomas CW, Billian C, DiScenna AO, Dell’Osso LF (1992a) Experimental tests of a superposition hypothesis to explain the relationship between the vestibulo-ocular reflex and smooth pursuit during combined eye-head tracking in humans. *J Neurophysiol* 68:1775–1791
- Huebner WP, Leigh RJ, Thomas CW (1992b) An adjustment to eye movement measurements that compensated for the eccentric position of the eye relative to the center of the head. *J Vestib Res* 2:167–173
- Kowler E (1989) Cognitive expectations, not habits, control anticipatory smooth oculomotor pursuit. *Vis Res* 29:1049–1057
- Krauzlis RJ, Lisberger SG (1994) A model of visually-guided smooth pursuit eye movements based on behavioral observations. *J Comput Neurosci* 1:265–283
- Krauzlis RJ, Miles FA (1994) Similar changes in the latency of pursuit and saccadic eye movements observed with the “Gap Paradigm”. In: Delgado-Garcia JM (ed) *Information processing underlying gaze control*. Pergamon Press, Oxford, pp 269–277
- Krauzlis RJ, Miles FA (1996) Transitions between pursuit eye movements and fixation in the monkey: dependence on context. *J Neurophysiol* 76:1622–1638
- Lanman J, Bizzi E, Allum J (1978) The coordination of eye and head movement during smooth pursuit. *Brain Res* 153:39–53
- Lefevre P, Bottermanne I, Roucoux A (1992) Experimental study and modelling of vestibulo-ocular reflex modulation during large shifts of gaze in humans. *Exp Brain Res* 91:496–508
- Lisberger SG, Westbrook LE (1985) Properties of visual inputs that initiate horizontal smooth pursuit eye movements in monkeys. *J Neurosci* 6:1662–1673
- Lisberger SG, Morris EJ, Tychsen L (1987) Visual motion processing and sensory-motor integration for smooth pursuit eye movements. *Ann Rev Neurosci* 10:97–129
- Meyer CH, Lasker AG, Robinson DA (1985) The upper limit of human smooth pursuit velocity. *Vis Res* 25:561–563
- Mitrani L, Dimitrov G (1978) Pursuit eye movements of a disappearing moving target. *Vis Res* 18:537–539
- Orban de Xivry JJ, Bennett SJ, Lefevre PP, Barnes GR (2006) Evidence for synergy between saccades and smooth pursuit during transient target disappearance. *J Neurophysiol* 95:418–427
- Osborne LC, Bialek W, Lisberger SG (2004) Time course of information about motion direction in visual area mt of macaque monkeys. *J Neurosci* 24:3210–3222
- Rashbass C (1961) The relationship between saccadic and smooth tracking eye movements. *J Physiol (Lond)* 159:326–338
- Robinson DA (1982) A model of cancellation of the vestibulo-ocular reflex. In: Lennerstrand G, Zee DS, Keller EL (eds) *Functional basis of ocular motility disorders*. Pergamon Press, Oxford, pp 5–13

- Robinson DA, Gordon JL, Gordon SE (1986) A model of the smooth pursuit eye movement system. *Biol Cybern* 55:43–57
- Roy JE, Cullen KE (2002) Vestibuloocular reflex signal modulation during voluntary and passive head movements. *J Neurophysiol* 87:2337–2357
- Roy JE, Cullen KE (2004) Dissociating self-generated from passively applied head motion: neural mechanisms in the vestibular nuclei. *J Neurosci* 24:2102–2111. doi:[10.1523/JNEUROSCI.3988-03.2004](https://doi.org/10.1523/JNEUROSCI.3988-03.2004)
- Tavassoli A, Ringach DL (2009) Dynamics of Smooth Pursuit Maintenance. *J Neurophysiol* 102:110–118. doi:[10.1152/jn.91320.2008](https://doi.org/10.1152/jn.91320.2008)