

G. R. Barnes · S. F. Donelan

The remembered pursuit task: evidence for segregation of timing and velocity storage in predictive oculomotor control

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Abstract Regular, repeated presentation of identical constant-velocity target motion stimuli (ramps) appears to allow build up of an internal store, release of which can be used to generate anticipatory smooth pursuit prior to subsequent target onset. Here, we examine whether release of the anticipatory response can be controlled by timing cues unrelated to the motion stimulus itself. In experiment 1, the target moved in alternate directions and was exposed for 480 ms as it passed through centre; otherwise subjects were in darkness. Inter-stimulus interval (ISI) was either regular (3.6 s) or randomized (2.7–4.3 s). Presentations were given with or without audio cues that occurred at a constant cue time (CT) prior to target appearance. Even when ISI was randomized, cues could be used to generate anticipatory smooth pursuit. Eye velocity (V100) measured 100 ms after target onset (just prior to visual feedback influence) was greater with cues than without and decreased significantly as CT increased from 240–960 ms. In experiment 2, we assessed the effects of fixation between presentations and eccentricity of target starting position, using unidirectional ramps. The target was visible for 400 ms and started on, ended on or straddled the midline. Subjects held fixation on the midline until an audio cue signalled that preparation for ensuing target appearance could begin. There was no difference in V100 between starting positions or between presence/absence of fixation. In experiment 3, we compared the effects of using audio, visual or tactile cues. All types of cue evoked anticipatory smooth pursuit, but the response to the visual cue was significantly delayed compared with the others. However, V100 was not significantly different between cues. In all experiments, V100 was scaled in proportion to target velocity over the range 12.5–50°/s, showing that this was a truly predictive response. The results provide evidence that timing and velocity storage can be independently

controlled through different sensory channels and suggest that the two functions are probably carried out by separate neural mechanisms.

Key words Ocular pursuit · Eye movements · Timing · Prediction · Anticipation · Humans

Introduction

Over recent years, it has been shown that anticipatory smooth movements of the eye can be made prior to the appearance of a moving target if the subject has previously viewed the moving target (Becker and Fuchs 1985; Boman and Hotson 1988; Kowler and Steinman 1979a, 1979b) and that, under appropriate circumstances, these movements may be of high velocity (up to 30°/s) (Barnes and Asselman 1991, 1992; Barnes and Grealy 1992; Kao and Morrow 1994). This is in contrast to the normal situation, in which subjects are unable to initiate smooth eye movements of more than 4–5°/s in the absence of a moving target (Heywood and Churcher 1971; Barnes et al. 1987). To elicit such anticipatory responses in a repeatable manner, we have previously employed the technique of intermittently illuminating the moving target at regular intervals as it passes through the central position at constant velocity either in the same direction or in alternating directions (Barnes and Asselman 1991; Barnes and Grealy 1992; Ohashi and Barnes 1996). From all of these experiments, we have obtained the same important indication: that these anticipatory movements are truly predictive of the ensuing target velocity, since they are invariably scaled according to the velocity of the expected target presentation. Another common observation has been that the anticipatory velocity builds up progressively over the first 3–4 presentations of the moving target, suggesting that a store of velocity drive information is steadily being built up with repetition.

As a result of these findings, it was suggested that prediction in ocular pursuit operates through two separate mechanisms: the storage of velocity-coded informa-

G.R. Barnes (✉) · S.F. Donelan
MRC Human Movement and Balance Unit, Institute of Neurology,
23 Queen Sq., London WC1N 3BG, UK,
e-mail: g.barnes@ion.bpmf.ac.uk

tion and the subsequent release of such information on the basis of an estimate of the periodicity of the target motion stimulus (Barnes et al. 1987). This presupposes that there is some mechanism by which the oculomotor system is able to determine the periodicity of the stimulus waveform. Evidence of this behaviour was indeed found in two experiments (Barnes and Asselman 1991; Barnes and Grealy 1992), in which intermittent stimulus presentation was used and unexpected changes in inter-stimulus interval were introduced. When the target unexpectedly failed to appear, subjects went on producing a predictive movement, which reached a peak at a time that was highly correlated with the time predicted from the periodicity of the previous part of the stimulus. The timing of this predictive response varied across a wide range (1.28–3.85 s) after the previous response and was evidently not part of the transient decay of the previous response.

There is a lot of evidence in the literature for timing mechanisms related to motor processes of differing kinds (see O'Boyle 1997 for a recent review). Much of this research has examined simple motor tasks, such as finger tapping. These studies have shown that subjects can: (1) synchronize their activities with very small errors in timing (Michon 1967; Mates et al. 1994); and (2) continue to time such movements with good precision, even without the timing cue, as though an internal clock were pacing the activity (Wing and Kristofferson 1973). In general, good estimation of timing is obtained for short durations (<2 s), but precision of timing deteriorates for longer intervals (Mates et al. 1994).

The extent to which these timing mechanisms function in the generation of smooth eye movements is largely unknown. It is known that saccadic eye movements can be very adequately synchronized with a simple square-wave target-motion stimulus so as to generate anticipatory saccades (Bronstein and Kennard 1985; Waterston et al. 1996), particularly at frequencies in the range of 0.4–1.0 Hz. A recent study of the continuation paradigm for saccadic eye movements (Collins et al. 1998) has also shown that subjects can readily continue to make saccadic movements at different frequencies after termination of the timing cue, with a similar accuracy to that observed for finger tapping or other motor processes. The evidence given above suggests that a similar control of timing may well apply to the initiation of anticipatory smooth eye movement. However, it is difficult to demonstrate this in a continuous way because of the inability to sustain smooth pursuit beyond the first inappropriate predictive estimate that the subject makes when the target fails to appear (Barnes and Asselman 1991).

It might reasonably be argued that, if our hypothesis of separate timing and storage functions for anticipatory ocular pursuit is correct, then it should be possible to release the stored information at a time that is determined by a timing cue that comes from a source other than that of the motion stimulus itself. In the experiments described here, we have tested this hypothesis by present-

ing motion stimuli at irregular time intervals, but giving warning cues at prescribed times before each appearance of the target. We refer to this as a remembered pursuit task. The technique of using warning cues is not dissimilar to that used in a number of previous studies (Boman and Hotson 1988, 1992; Kowler and Steinman 1979b), but, in these, only low anticipatory velocities have been generated, which are difficult to relate to normal pursuit. There has also not always been a clear dissociation between the triggering effects of the timing cue and effects arising from changes in the conditions of fixation prior to target motion.

In the experiments presented here, we have examined high-velocity anticipatory smooth eye movements that can be more clearly related to normal pursuit. We have used the remembered pursuit task to investigate the effects of fixation between presentations, the starting position of the target motion, the type of warning cue used and the time between the cue and motion onset (cue time, CT). The results provide strong support for the hypothesis that timing and storage functions can be segregated. They also indicate that: (1) fixation between presentations does not modify the stored information; (2) the anticipatory response is similar whether the timing cue comes from auditory, tactile or visual sources; (3) timing cues are less effective when they occur earlier; and (4) anticipatory velocity is similar irrespective of target starting position and, thus, independent of the operating range of the eye in the orbit. A preliminary report of this work was presented earlier (Barnes and Donelan 1998).

Materials and methods

In experiments 1 and 2, subjects were seated in front of a circular screen (radius 1.5 m) with their head fixed by clamps to the side of the head and supported on a chin-rest. A visual target was presented on the screen and was made to move in the horizontal axis under the control of a motor-driven mirror. The target was composed of a circle with superimposed cross-hairs, subtending 50 min of arc at the eye. Eye movements were recorded by an infra-red limbus tracking technique (Skalar IRIS), were low-pass filtered at 80 Hz and sampled at intervals of 10 ms prior to storage on disc and off-line analysis. All stimulus combinations were presented in balanced, randomized combinations to avoid the effects of learning and fatigue. The experiments were conducted with local ethics-committee approval, and all subjects participated with informed consent. Subjects were drawn from a pool of 12 normals, six of whom were completely naive of oculomotor experiments.

In experiment 1, we examined the effect of two factors, timing cues and regularity of stimulus presentation on the ability to make anticipatory, smooth eye movements. The objective was to show whether timing cues from a sensory source other than the motion stimulus itself could be used to time the release of the stored anticipatory movement. The target moved with a brief constant velocity ramp, alternately to left and right (Fig. 1), the velocity taking values of ± 12.5 , 25, 37.5 or 50°/s in separate trials. The target was not continuously presented, but was briefly exposed, for 480 ms, under the control of an electromagnetic shutter in such a way that the motion path straddled the midline equidistantly. The subjects were instructed to follow the target as well as possible during the exposure period. There were no fixation cues present, the experiment being conducted in a darkened room. Because the movements alternated in direction, subjects were aware that the next

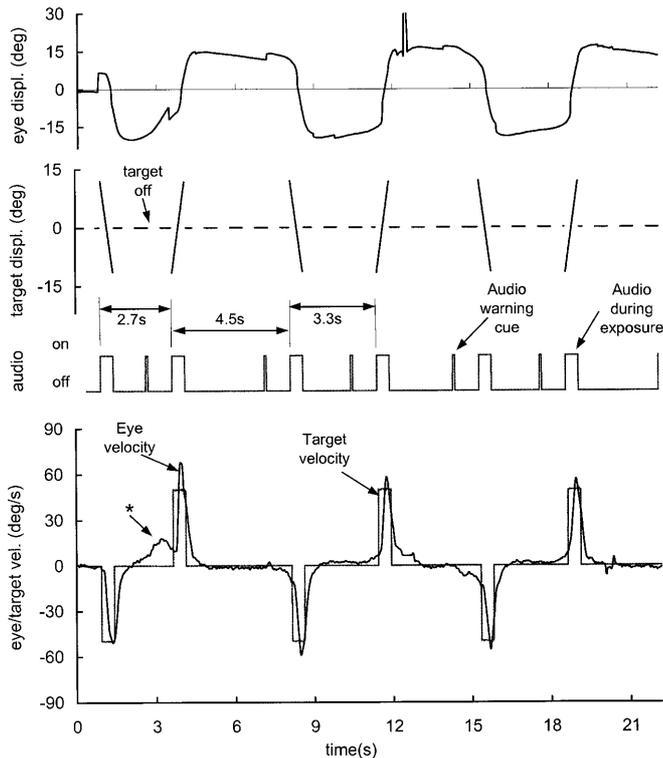


Fig. 1 An example of eye-displacement and velocity traces from a single subject during pursuit of intermittently presented, constant-velocity (50°/s) target motion stimuli (ramps), alternating in direction at randomized intervals of 2.7–4.5 s. The target was only presented for 480 ms during each ramp, but, between ramps, the subject was in darkness, as indicated by the *broken line* in the displacement trace. An audio warning cue was given 960 ms before target onset, as indicated, and an audio tone was also presented during each ramp. Eye-velocity traces have saccades removed. Pulses in target-velocity signal indicate both duration and magnitude of target velocity stimulus. * Example of initiation of inappropriately timed prediction

stimulus would begin where the previous one had finished. The interval between stimuli was either regular and predictable (PRD condition), with constant intervals (ISI) of 3.6 s, or irregular, with randomized intervals of 2.7, 3.3, 3.9 or 4.5 s (RND condition). For both regular and irregular presentations, there were five cue conditions. In four of these conditions, an audio warning (80 ms beep) was given prior to the appearance of the target. Cue times (CT) of 240, 480, 720 and 960 ms were examined in separate runs. In the fifth cue condition, no audio cue was given. Ten subjects were investigated.

In experiment 2, the primary objective was to show whether anticipatory eye movements could still be generated if the subject was required to fixate a stationary target between presentations and move to different starting locations in the periphery in order to follow the target effectively. We wanted to determine if fixation between presentations modified the stored information, resulting in a reduced anticipatory velocity. We also wanted to show that the generation of the smooth movement was not specifically associated with the eye starting from an eccentric position in the orbit. It is conceivable, for example, that it could result from the simple release of gaze holding, inducing a viscoelastic recoil from the extra-ocular muscles and orbital contents. The target executed sequences of 12 identical, unidirectional constant velocity ramps to the right (see Fig. 4B). Velocity varied from 12.5–50°/s in separate sequences. The target was exposed for 400 ms with a randomized interval of 2.25–3.75 s between presentations. An audio cue (80 ms beep) was given at a fixed time interval prior to target on-

set. Five stimulus conditions were examined, for each of which three warning cue times (CT) were used (300, 600 or 1200 ms), giving a total of 15 trials for each subject. To assess the effect of orbital starting position, target presentation was timed to start on the midline (M-R), straddle the midline (L-R) or end on the midline (L-M), the second of these corresponding to the condition in experiment 1. Two small, green LED targets (subtending 0.25°) placed on the midline, 3° above and below the moving target, served for fixation and were continuously present, as shown in Fig. 4A. These allowed fixation to be held at the midpoint without the interference that would result from the moving target passing over a single central fixation target. In conditions C1 (M-R), C2 (L-R) and C3 (L-M), subjects were required to hold fixation at the midpoint until an audio cue was given and then to initiate eye movements in preparation for the ensuing target appearance. To assess the effects of fixation cues, two further stimulus conditions were examined, in both of which the target movement straddled the centre (L-R). In C4, the subjects carried out the same task as in C2, but without the fixation cues present, so that this was equivalent to the conditions of experiment 1. In C5, fixation cues were present and the subject was instructed to hold fixation until the target passed through the centre (Fig. 4A). The objective was simply to assess how well the subjects could suppress the anticipatory movement. Six subjects participated.

In experiment 3, we attempted to determine whether other sensory cues (tactile and visual) could be used in the same way as the audio cue to initiate anticipatory movements. In order to eliminate any possible influence of the sound created by the opening and closing of the electromagnetic shutter used in experiments 1 and 2, we used a display that could be switched on and off silently. It consisted of a ring of 12 ultra-bright LEDs that were optically reduced to form a ring of dots subtending 1.2° on the screen. Motion of this target was controlled by reflection from a mirror galvanometer. The motion of the target was identical to that in the (L-R) condition of experiment 2, but the target was exposed for 480 ms and the randomised ISI was reduced to the range 1.8–3.0 s. Warning cues were all given 600 ms before target appearance. Five cue/timing conditions were investigated. In the first, an audio beep of 80 ms was given as before. In the second, a distinctive visual cue was given by illuminating only four of the 12 elements of the pursuit target for 80 ms whilst it was in a stationary phase at the centre of the screen. In the third, a tactile cue of 80 ms duration was administered to the middle finger by a solenoid-operated probe. In order to eliminate any effect of noise emanating from the tactile source, it was mechanically isolated from the subject's chair. Additionally, a white-noise source was played through a separate loudspeaker in this and all other stimulus conditions. In the fourth condition, there was no cue, but timing of the stimulus was still randomised (RND condition), whereas, in the final condition, no cue was given, but the stimuli appeared at regular intervals of 2.4 s (PRD condition). Nine subjects participated.

Data analysis

Eye movements were analysed by first identifying and removing the fast phase components of the response using a technique similar to that described previously (Barnes 1982), but based on a combination of acceleration and velocity threshold criteria. Linear interpolation was used to bridge the resulting gaps in the eye velocity signal. Fast phase movements were generally of small amplitude (<5°) and brief duration, making linear interpolation a simple and adequate method of waveform restoration. The following measures of eye movement were then derived from each response:

- A0: eye acceleration at time of target onset, derived from the slope of a linear regression on the sampled data from 100 ms before target onset to 80 ms after onset.
- V0: eye velocity at the time of target onset.
- V100: eye velocity 100 ms after target onset. This corresponds to the last time at which the response can be considered to have been uninfluenced by visual feedback and, thus, of internally generated origin.

- V_{pk} : the peak eye velocity of the response to each ramp.
- T_0 : the latency between target onset and the start of eye movement. This was calculated by identifying the point at which eye velocity reached a threshold equal to 10% of peak eye velocity for a particular response, carrying out a linear regression on the next 100 ms of the velocity data and, then, extrapolating back to obtain the point at which the regression line crossed through zero. This was usually a reliable way of identifying response onset for the anticipatory responses, for which eye velocity exhibited only a gradual increase with time, but each response was checked and corrected if necessary.

Statistical comparisons were carried out on these variables using SPSS software. Prior to performing repeated measures analysis of variance (ANOVAs), the data were tested for normality (Shapiro-Wilk test). The results showed that the data were normally distributed. The Mauchly test was applied to determine sphericity of the data and, when this was found to be significant, the Greenhouse-Geisser correction was applied to determine significance.

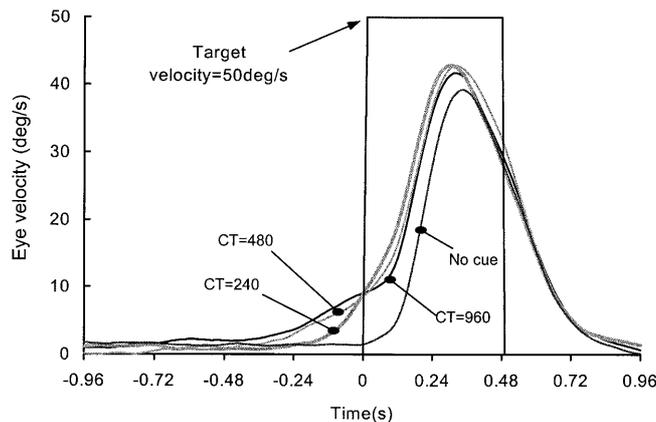
Results

Experiment 1. The effects of audio warning cues during regular and irregular presentations

All subjects were able to use the audio cues to time the release of an anticipatory, smooth eye movement at an appropriate time before target onset, even when the time between target presentations was not regular. Figure 1 shows an example of the response generated by a single subject to the RND condition in which the audio cue occurred 960 ms before target onset. From this it is apparent that the subjects were well able to synchronize the initiation of the anticipatory response with the target onset, despite the fact that the actual interval between motion stimuli varied in these examples from 2.7s-4.5 s. Initially, the subjects made a reactive response to the first presentation, as expected. They were then unable to assess the time interval between the audio cue and the target onset until the next presentation, but often initiated inappropriate attempts to generate anticipatory smooth movement, as indicated by the labelled example in Fig. 1. However, they were quickly able to determine an estimate of the elapsed time between the cue and the appearance of the target and use that stored timing information to control the release of the next anticipatory response.

Figure 2 shows selected examples of the smooth eye-velocity trajectories obtained when target velocity was 50°/s. They represent means across all ten subjects, but are representative of the effects observed in all subjects and the effects observed at other target velocities. All of the responses, except those for the RND/No cue condition, exhibited the characteristic pattern of anticipatory movement that has been described previously, in which the eye velocity builds up progressively prior to target onset. The majority (>95%) of the responses of all subjects showed this type of behaviour. There was no indication that the graded build-up seen in the average response resulted from averaging responses with widely differing timing characteristics. If the interval between the audio cue and the target onset was very long, as in

(A) RND conditions only.



(B) RND vs. PRD conditions

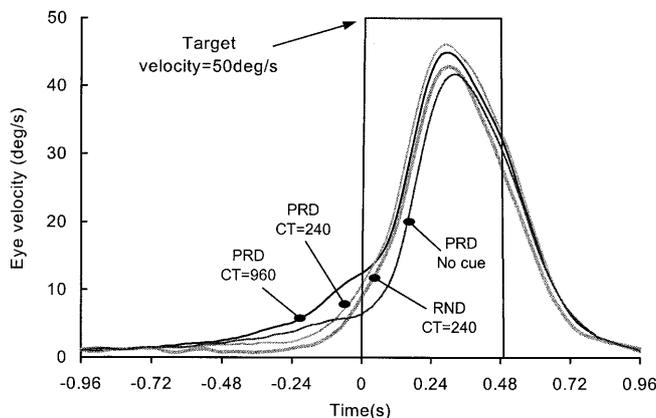


Fig. 2A, B Smooth eye-velocity trajectories in response to target velocity of 50°/s, averaged across ten subjects. time scale set to zero at target onset. In **A**, responses to randomized (*RND*) target presentation are compared for cue-timing (*CT*) conditions =240, 480, and 960 ms and “no cue”. In **B**, responses to predictable-target (*PRD*) and *RND* conditions are presented for *CT*=240 ms as well as *PRD* responses for *CT*=960 ms and “no cue”

the examples shown in Fig. 1, the anticipatory activity did not start until well after the audio cue, as is evident in Fig. 2A. The onset time and level of the anticipatory acceleration in the *RND* condition were very similar for all cue times, except the shortest (240 ms). However, even though the anticipatory eye movement started later for the 240-ms cue, eye velocity was very similar at target onset. When no audio cue was given in the *RND* mode, there was negligible eye acceleration before onset, but a small amount before visual feedback came in at 100 ms.

In the *PRD*/No cue condition, there was a sustained eye acceleration for over 500 ms before target onset, but the level attained at onset was less than when audio cues were given. When the audio cue was given in the *PRD* condition, subjects appeared to delay onset of anticipation until after the cue, so that the initial response was little different to that in the *RND* condition with cues.

Table 1 Mean values (with SEM in parentheses) obtained from ten subjects for variables measured in experiment 1 [the velocity at onset (V0), the velocity 100 ms after target onset (V100), peak velocity (Vpk) and anticipatory acceleration (A0)] for six of the ten

conditions tested. RND Randomized target presentation, PRD predictable target presentation. Cue conditions: CT=240 ms, CT=960 ms, No cue

	Target velocity (°/s)	RND CT=960	RND CT=240	RND No cue	PRD CT=960	PRD CT=240	PRD No cue
V0 (°/s)	12.5	3.79 (0.51)	2.97 (0.48)	1.66 (0.18)	3.61 (0.35)	5.32 (0.99)	2.60 (0.38)
	25	4.61 (0.80)	5.02 (0.51)	1.88 (0.40)	5.85 (0.58)	7.66 (1.04)	3.54 (0.44)
	37.5	6.10 (1.04)	5.74 (0.68)	2.56 (0.46)	8.57 (1.45)	8.74 (1.05)	4.56 (0.44)
	50	7.61 (1.70)	7.76 (0.59)	1.73 (0.28)	11.18 (0.92)	9.84 (1.09)	6.41 (1.24)
V100 (°/s)	12.5	5.15 (0.42)	5.40 (0.55)	2.93 (0.53)	5.68 (0.35)	7.35 (0.66)	3.63 (0.41)
	25	6.74 (1.24)	8.31 (0.92)	3.87 (1.17)	8.79 (0.84)	11.72 (0.47)	6.58 (0.73)
	37.5	9.43 (1.20)	11.36 (1.22)	4.97 (1.19)	14.22 (2.14)	14.23 (0.77)	8.47 (1.12)
	50	10.70 (1.85)	14.73 (1.70)	4.73 (1.48)	16.16 (1.31)	18.41 (1.24)	12.36 (2.76)
Vpk (°/s)	12.5	14.48 (0.56)	14.76 (0.59)	16.16 (0.59)	15.49 (1.03)	15.86 (0.67)	17.15 (1.16)
	25	23.84 (0.51)	22.46 (0.64)	26.23 (1.88)	26.16 (1.29)	26.69 (1.28)	28.43 (1.12)
	37.5	32.71 (1.58)	32.47 (1.73)	33.54 (2.09)	34.67 (2.12)	34.94 (1.29)	35.41 (1.31)
	50	39.80 (2.89)	41.98 (2.39)	39.97 (3.04)	44.51 (1.95)	45.47 (1.91)	42.73 (1.65)
A0 (°/s ²)	12.5	6.24 (0.96)	17.82 (1.87)	5.29 (2.55)	12.02 (1.65)	19.36 (2.04)	3.57 (1.51)
	25	15.28 (2.79)	26.39 (3.31)	8.27 (4.66)	19.52 (2.33)	36.69 (3.65)	12.22 (2.17)
	37.5	20.42 (3.28)	38.05 (5.44)	9.71 (2.88)	35.52 (5.72)	44.07 (3.58)	17.85 (3.35)
	50	22.92 (5.37)	51.58 (7.55)	11.36 (4.82)	33.64 (5.83)	56.81 (5.52)	27.44 (9.67)

Comparison of the responses to cue times of 240 ms (Fig. 2B) shows that they have a similar temporal characteristic, although velocity was slightly greater in the PRD mode.

In order to assess the magnitude of the effects for the different stimulus conditions, we have compared four measures; the anticipatory acceleration (A0), the velocity at onset (V0), the velocity 100 ms after target onset (V100) and peak velocity (Vpk). Repeated-measures analysis of variance was carried out to assess the effects of the three major factors tested: (1) predictability of the motion stimulus, (2) audio timing cue condition and (3) target velocity.

All measures of eye velocity and acceleration for the PRD conditions were significantly greater than those for the RND conditions (Table 1) ($F=297.4$, $df=1$, $P=0.001$ for V0; $F=40.26$, $df=1$, $P<0.001$ for V100; $F=399.4$, $df=1$, $P=0.014$ for Vpk; $F=23.638$, $df=1$, $P=0.001$ for A0). Comparison of the four conditions in which audio cues were used (i.e. excluding “no cue” conditions) indicated a significant reduction in V100 ($F=10.72$, $df=3$, $P=0.001$) with increasing cue times (CT), although the magnitude of the decline was not great (mean of 16% across all velocities between CT=240 and CT=960 ms). Separate analysis of the PRD and RND conditions revealed that, in the PRD condition alone, the decline in V100 with CT did not actually reach significance ($F=3.740$; $df=3$; $P=0.055$). So, although the anticipatory eye movement started earlier for earlier cues, the velocity attained 100 ms after onset was quite similar. There was no significant effect of cue time on V0 ($F=0.316$, $df=3$, $P=0.814$) or Vpk ($F=1.139$, $df=3$, $P=0.339$). When the “no cue” condition was included in the analysis, a priori simple contrasts revealed that V100 attained significantly higher levels when cues were given for both the RND and PRD conditions than for the “no cue” con-

dition ($F=8.608$, $df=1$; $P=0.017$ for CT=960 ms vs. “no cue”; Fig. 3). Note that V100 for the RND condition with no cue was not zero (Table 1 and Fig. 2). This was probably because the direction of motion was always predictable and subjects tended to initiate a slow drift movement in the expected direction prior to target onset, even though timing was randomized.

Analysis also revealed a highly significant linear increase in both V0 ($F=42.05$, $df=3$, $P<0.001$) and V100 ($F=50.72$, $df=3$, $P<0.001$) with increasing target velocity. Figure 3B demonstrates this effect for CT=240 ms and indicates how the effects of PRD versus RND and “cue” versus “no cue” affected the values of V100 at all levels of target velocity.

Although values of anticipatory velocity (V0 and V100) were similar around the time of target onset, they had quite different levels of anticipatory acceleration (A0) to build up to that level. Analysis of variance for conditions with cues showed that anticipatory acceleration decreased significantly as cue time increased ($F=29.52$, $df=3$, $P<0.001$) for both regular and randomized presentations (Table 1). A0 also increased significantly with target velocity ($F=32.22$, $df=3$, $P<0.001$). The values of acceleration attained for the PRD condition without cues in this anticipatory phase are comparable to those reported by Kao and Morrow (1994).

Experiment 2. The effects of target starting position and fixation cues

Examples of the eye movements generated in experiment 2 are shown in Fig. 4B for the C2 (L-R) condition. After each ramp presentation, the eye was returned to the central fixation area. On hearing the audio cue, the subject prepared for the onset of the target by moving the eye

Fig. 3 **A** Mean eye velocity 100 ms after target onset (V100) as a function of cue-timing (CT) condition (=240, 480, 720, and 960 ms and “no cue”). **B** V100 as a function of target velocity for the predictable target-presentation (PRD) and randomized target-presentation (RND) conditions with either “no cue” or CT=240 ms. Mean of ten subjects ± 1 SEM

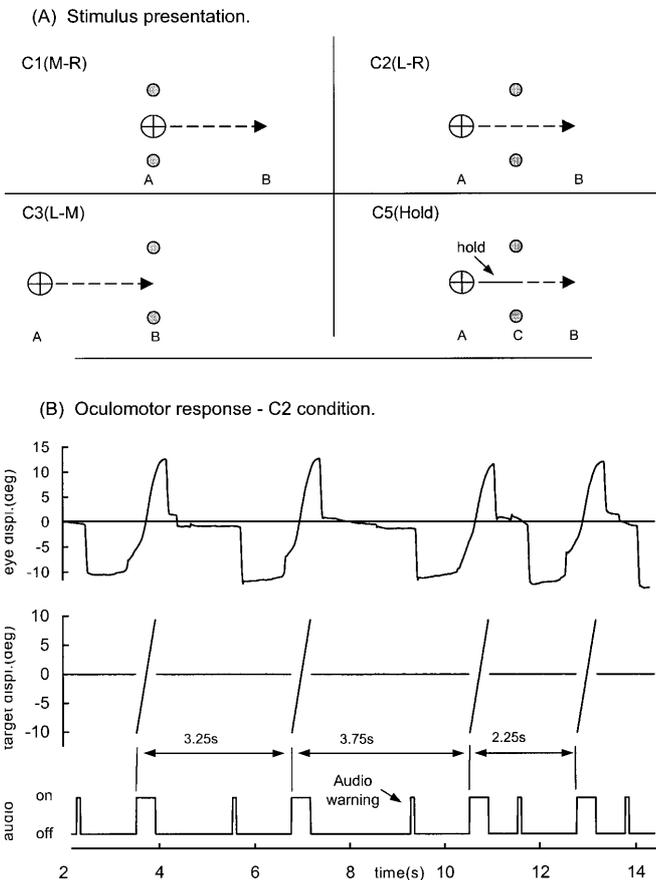
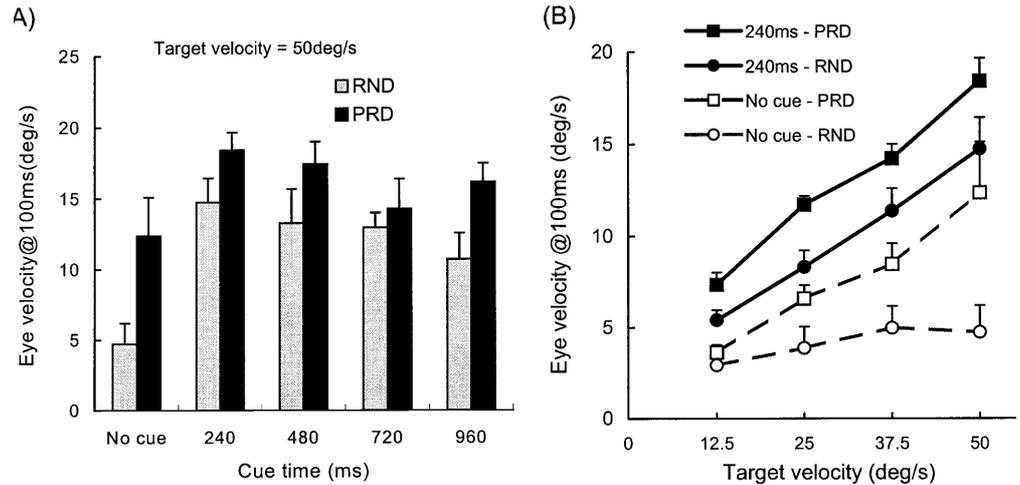


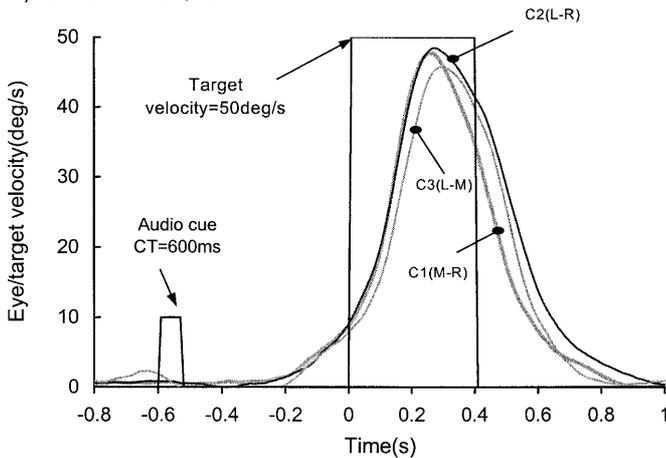
Fig. 4 **A** Stimulus presentation conditions for experiment 2. In all conditions shown, two fixation cues (filled circles) were presented continuously. The pursuit target (circle with crosshairs) was only visible as it moved from A to B and was presented so as to start at (C1), straddle (C2 and C5) or end on (C3) the vertical midline joining the fixation cues. In C5, subjects attempted to hold fixation until the target crossed the midline at C. In C4 (not shown), target presentation was as for C2, but there were no fixation cues. **B** An example of eye displacement from a single subject in response to randomized appearance of unidirectional ramp-motion stimuli of 400 ms duration at intervals of 2.25–3.75 s. An audio warning cue was given 1.2 s before target appearance, as indicated, and an audio tone was given during each ramp. Subjects returned gaze to centre between ramps using fixation cues, but could prepare their next response when a warning cue was heard

away from the fixation area to a point close to where the target was expected to appear, although the subjects were often not aware of making this move. Similar effects were observed for the M-R and L-M conditions, except that the starting position of the eye was appropriately adjusted. Subjects then initiated smooth eye movement prior to target onset (Fig. 4B). This occurred even though the time between successive presentations was varied over a range of 2.25–3.75 s. On occasion, smooth movements were initiated with a positive positional error and saccades were then seen in the opposite direction to the smooth movement, forming a nystagmus as the eye was realigned with the target after it became visible (c.f. Becker and Fuchs 1985).

The averaged velocity profiles generated in the C1, C2, C3 and C4 conditions were very similar as indicated in Fig. 5, but in the C5 condition, in which subjects held fixation until the target passed through the midline, the response was clearly delayed. (Note that all responses are slightly higher for this group of subjects than for the different group of experiment 1). The principal measures used for comparison were V0, V100 and Vpk. Factors in the analysis of variance were cue time, start condition and target velocity.

Initial analysis was carried out for the three different start conditions C1 (L-M), C2 (L-R) and C3 (M-R). There were significant linear increases in both V0 ($F=19.62$, $df=3$, $P=0.006$) and V100 ($F=35.63$, $df=3$, $P=0.002$) with increasing target velocity. Since there were no significant interactions, values of V100 are presented in Fig. 6 as the average across all velocities and cue times. Analysis indicated that starting position had no significant effect on V0 ($F=0.658$, $df=2$, $P=0.539$) or V100 ($F=1.723$, $df=2$, $P=0.241$) (Fig. 6). As in experiment 1, there was no significant change in V0 ($F=0.862$, $df=2$, $P=0.45$) with increasing cue time over the range tested (300–1200 ms), but there was a significant change in V100 ($F=10.41$, $df=2$, $P=0.007$), which was optimal for CT=600 ms and declined by 26% for CT=1200 ms. Mean V100 values for target velocity 50°/s were 18.05°/s, 21.55°/s and 14.79°/s for CT=300, 600 and 1200 ms, respectively, in the C2 condition. Although the

A) Conditions C1, C2 & C3



B) Conditions C2, C4 & C5

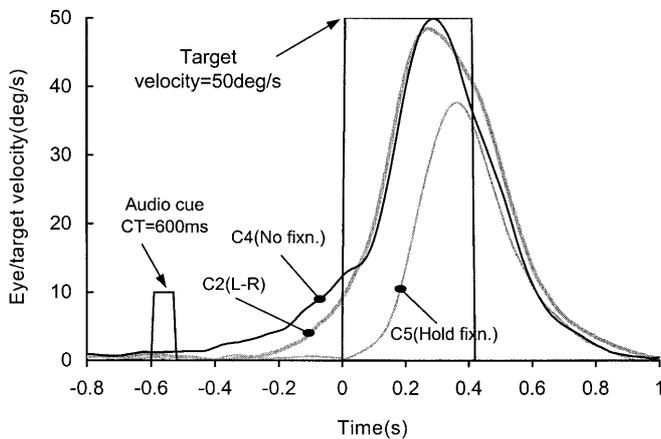


Fig. 5A, B Smooth eye-velocity trajectories in response to a target velocity of $50^\circ/s$, averaged across six subjects. **A** Responses to different starting points: C1 (M-R), C2 (L-R) and C3 (L-M) (see Fig. 4). **B** Responses to different fixation conditions: C2 (L-R), C4 (no fixation) and C5 (hold fixation). Time scale set to zero at target onset, irrespective of start condition

velocity trajectory for the C3 (L-M) condition was slightly attenuated (Fig. 5A), analysis of peak eye velocity (V_{pk}) indicated no significant difference between starting conditions ($F=1.571$, $df=2$, $p=0.255$).

In a second analysis of variance, conditions C2 and C4 were compared to determine the effect of the presence/absence of the fixation cues. Although the initial part of the anticipatory movement appeared to start earlier in the C4 (no fixation) condition (Fig. 5B), analysis revealed no significant difference in V_0 ($F=0.168$, $df=1$, $P=0.685$), V_{100} ($F=1.233$, $df=1$, $P=0.317$) or V_{pk} ($F=0.533$, $df=1$, $P=0.472$) between the C2 and C4 conditions. Mean values of V_{100} for C4 are illustrated in Fig. 6. It appeared that the subjects were easily able to unlatch fixation in the C2 condition and prepare for the ensuing target onset and that, once the anticipatory eye movement had been initiated, the small, vertically displaced fixation cues could largely be ignored.

Eye velocity @100ms vs. presentation condition

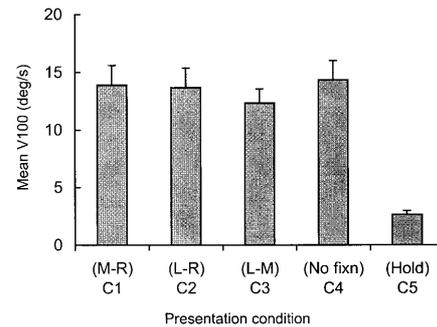


Fig. 6 Mean eye velocity ($+1$ SEM) 100 ms after target onset (V_{100}); averages across all four target velocities in six subjects as a function of target presentation conditions (C1–C5, see Fig. 4). In C5, the subjects held fixation until the target passed the midline

In the C5 condition, subjects were generally able to hold fixation until the target passed the midline as instructed, so there was little response before 100 ms and V_{100} was consequently very low (Fig. 5B). Comparison of the C5 and C2 conditions by analysis of variance indicated that V_{100} ($F=20.37$, $df=1$, $P=0.006$) and V_{pk} ($F=53.71$, $df=1$, $P=0.001$) were significantly less in the C5 condition than in the comparable C2 condition (Fig. 6). These results thus demonstrate that subjects can volitionally inhibit the release of the stored information when required to do so. However, note that mean V_{100} was not zero in the C5 condition because there was frequently a low-velocity drift present that some subjects found difficult to suppress.

Experiment 3. The effects of cue type

All three types of warning cue (auditory, visual and tactile) could be used to initiate anticipatory smooth eye movements, but there were significant differences in the timing of the response. As indicated by the averaged velocity profiles in Fig. 7, there was little difference between responses to the audio and tactile cues, but the response to the visual cue was considerably delayed. The response to the predictable (PRD) condition (not shown in Fig. 7) without audio cues was also quite similar to the audio and tactile conditions, whereas the RND condition resulted in the usual delayed onset of eye acceleration. To test for differences, we carried out analysis of variance to compare time of onset (T_0), V_0 , V_{100} (Fig. 8) and V_{pk} for each stimulus condition, with target velocity and cue type as factors. Responses to the RND condition were excluded from this analysis.

As before, there was a significant increase in V_0 ($F=13.88$, $df=3$, $P=0.002$) and V_{100} ($F=17.875$, $df=3$, $P=0.002$) with target velocity, but there were no significant interactions, and, thus, values of V_0 and V_{100} presented in Fig. 8 have been averaged across all velocities. Analysis indicated that V_{100} was not significantly different between cue types ($F=0.686$, $df=3$, $P=0.570$),

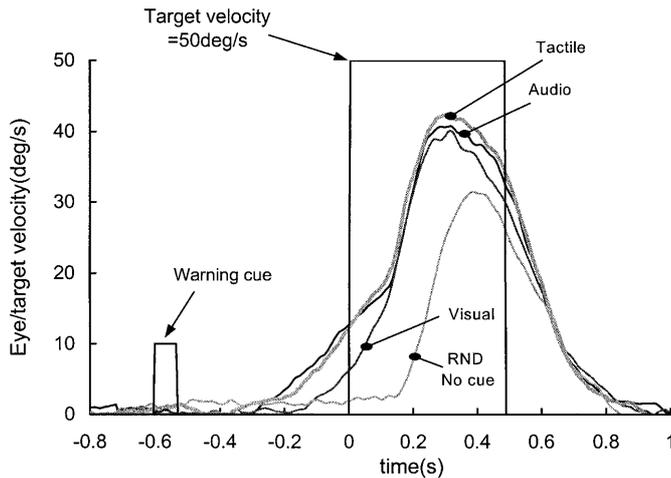


Fig. 7 Smooth eye-velocity trajectories in response to a target velocity of 50°/s, averaged across nine subjects. In all conditions illustrated, presentation was randomized, but different types of warning cue (*audio*, *visual* or *tactile*) were given 600 ms prior to target onset. These responses are compared with the conditions in which no cue was given. The predictable-target-presentation (*PRD*)/"no-cue" condition had a very similar profile to the randomized-target-presentation (*RND*) responses with tactile or audio warning cues

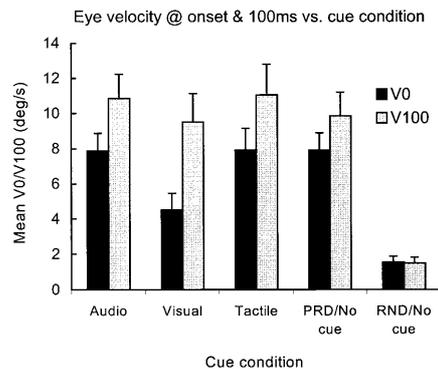


Fig. 8 Mean eye velocity (+1 SEM) at target onset (*V0*) and 100 ms after onset (*V100*), averaged across all four target velocities in nine subjects for each cue condition (see Fig. 7)

whereas *V0* showed a significant effect of cue type ($F=3.355$, $df=4$, $P=0.036$). A priori simple contrasts, using the auditory cue as the reference, indicated that there was no significant difference in *V0* between the auditory, tactile and predictable (*PRD*) motion conditions, but that *V0* was significantly reduced in the visual cue condition ($F=14.9$, $df=1$, $P=0.005$) (Fig. 8). Similar effects were found for the onset latency T_0 , which was significantly less anticipatory ($F=12.04$, $df=1$, $P=0.008$) in the visual condition [mean $T_0=-124.4$ ms (SEM= ± 59.9 ms) at 50°/s] than in the auditory condition [mean $T_0=-310$ ms (SEM= ± 43.0) at 50°/s]. There were no significant differences in V_{pk} attained for any of these four cue conditions ($F=0.465$, $df=3$, $P=0.709$). All subjects were equally able to use all types of cue, but, as in all of the experiments described here, there was a considerable variation between the subjects in the level of response produced.

Discussion

Segregation of timing and storage functions

Smooth anticipatory eye movements cannot normally be generated at will (Heywood and Churcher 1971; Barnes et al. 1987; Kao and Morrow 1994), certainly in the presence of fixation cues. In previous experiments, it has been shown that the ability to generate anticipatory movements of a velocity sufficient for use in normal predictive pursuit tasks appears to depend on storage of velocity-coded information derived from prior exposure to the moving target (Barnes and Asselman 1991; Barnes et al. 1997). On the basis of these and other experiments (Barnes et al. 1987), it was postulated that, during predictive pursuit tasks, the release of the stored information at an appropriate time is controlled by a periodicity estimator that derives timing information from the target motion stimulus itself.

The results of the experiments described here now provide strong evidence that the timing of the release of the stored information can be carried out through separate mechanisms, using different forms of sensory information to those used to accomplish the storage process. The results of experiment 1 demonstrate this for the simplest type of stimulus, in which target movements alternate in direction with no fixation or other distraction between presentations and where it is possible for the subject to imagine the underlying trajectory of a continuous oscillatory motion. Experiment 2 demonstrates that fixation between presentations does not destroy the stored information and that starting position has no significant effect on the response within the range tested (up to 20° eccentricity). Absence of fixation cues leads to a slightly earlier onset and higher level of anticipatory velocity before target onset. Experiment 3 shows that at least three different types of sensory timing cue may be used to time the release of the stored information and that there appears to be no significant difference in the magnitude of the anticipatory eye velocity (*V100*) generated, whether the timing cue is derived from auditory, visual or tactile stimuli. The timing cue serves to reinforce the expectancy of target appearance, without which it would not be possible to generate the smooth movement at all (Barnes et al. 1997). In all cases, an essential feature is that the anticipatory eye velocity, as indicated by the velocity 100 ms after target onset (*V100*), was scaled according to the ensuing target velocity and was, thus, predictive of it.

These experiments are not the first to show how subjects can use elapsed time cues to initiate smooth movements. Many of the early experiments in which anticipatory smooth movements were demonstrated used techniques in which there was a fixed time between a cue signalling the beginning of the trial and the onset of target movement (Kowler and Steinman 1979a, 1979b, 1981; Kowler 1989; Becker and Fuchs 1985). Using this technique with an interval of 1000 ms before target movement, Boman and Hotson (1988) also investigated

the effect of extinguishing the target for 0, 400 or 800 ms before target motion began. When no gap was left between fixation and the ramp stimulus, the anticipatory eye velocity was very small ($<1^\circ/s$), even for the highest target velocity used ($10^\circ/s$). Higher levels (up to $3^\circ/s$) were generated when a gap of 400 or 800 ms was left before the start of ramp motion. In these experiments, it is likely that the extinction of the target acted as the primary trigger to initiate the anticipatory movement, rather than the audio warning cue itself. In all of these previous experiments, the same target has been used for the fixation and pursuit parts of the stimulus. Here, our objective was to clearly define the effects of removing fixation prior to target onset by using a separate fixation cue. Using this technique, we were then able to investigate the effect of varying the duration of the time between the warning cue and the onset of target motion, the subjects being instructed to use the warning cue to switch attention from the stationary targets to the expected moving target.

Differences in eye velocity induced by different timing cues

When longer cue times were used, eye velocity built up more slowly and often reached a plateau before target onset (Fig. 2B; PRD/CT=960 ms), as observed previously by Boman and Hotson (1988) when they left a long (800 ms) gap between target extinction and onset of the ramp. When the velocity at 100 ms was compared, there were changes as CT increased, but these were only significant for the RND conditions. For cue times of 240–720 ms, there was little difference in V100, suggesting that the goal of the movement was to achieve the same velocity around the time when visual feedback would become available, irrespective of the time of actual initiation of anticipation. This effect was also observed in experiment 3, where onset time was significantly later for the visual cue than for the audio and tactile cues, but V100 values were similar.

It is of interest that there were significant changes in V100 with CT in the RND conditions, but not in the PRD conditions. However, in the RND condition, subjects must depend on the warning cues alone to time response initiation, and the evidence thus indicates that the cues become less effective when they occur earlier. In PRD/no-cue conditions, the timing cue was presumably provided by the previous target presentation, so that the inter-stimulus interval (ISI) became the effective cue time. Observations from a previous experiment (Wells and Barnes 1998) are in accord with this. It was shown that anticipatory eye movement decayed significantly as ISI was increased from 1.8 s to 7.2 s if no warning cues were given in a PRD/no-cue condition. If audio warning cues were given, starting 600 ms before stimulus appearance, anticipatory eye movement decayed less rapidly. Results from our experiment 1 are also compatible with this. The shortest warning cue (CT=240 ms) in the RND condition gave a larger response than the motion-derived

cue in the PRD/no-cue condition, for which the ISI of 3.6 s lay in the middle of the critical range over which Wells and Barnes found the greatest decay in V100. As CT increased to 960 ms in the RND condition, V100 decreased to a level comparable to that for the PRD/no-cue response. The finding that warning cues gave higher levels of V100 in the PRD condition than in the RND condition is more difficult to explain. It suggests that the combination of regular motion-stimulus presentation plus regular warning cues gives an even better indication of timing, which leads to a further enhancement of performance. Taken altogether, these results demonstrate that there is a complex interaction between the fidelity of timing cues and the release of stored velocity information.

Relevance to timing in other motor processes

The ability to initiate anticipatory smooth pursuit at an appropriate time clearly relies on the assessment of elapsed time between warning cue and target onset. However, there is a wealth of evidence from other studies on timing showing that humans are very good at such tasks, at least over restricted time intervals (Michon 1967). Indeed, this ability to synchronize motor activities to external timing cues underlies the ability to do such things as playing a musical instrument and singing in unison. The main findings from previous experiments are that the critical duration for relatively precise reproduction of timing is in the range up to 2 s (Peters 1989; Mates et al. 1994) and that timing variability increases in proportion to inter-stimulus interval up to this level (Peters 1989; Collins et al. 1998). Beyond this duration, the timing of events becomes increasingly unreliable (Mates et al. 1994) and subjects tend to make a mixture of reactive and anticipatory responses. The effect of different elapsed time intervals in our experiments is in accord with these findings, in that the ability to reproduce the anticipatory response deteriorates when the cue time (CT) approaches and exceeds 1 s in the RND condition. The differences that we have observed in the use of visual, auditory or tactile cues are also similar to those found previously for other motor processes. For example, there is evidence from the work of O'Boyle (1997) on synchronized finger tapping that visual cues take longer to process than either audio or tactile cues. Altogether, the evidence points to a common process for all types of motor activity, eye movements being no exception (Bronstein and Kennard 1985; Collins et al. 1998).

There are also many similarities in the anticipatory responses elicited here and the responses to classical conditioning of skeletomotor responses (Yeo and Hesslow 1998). We used a *conditioned stimulus* (the warning signal) to elicit a motor response in advance of the *unconditioned stimulus* (the onset of target motion) that would normally generate the eye movement. Clearly, there is one major difference in that we are concerned with voluntary initiation of the response, rather than building up a reflex

response. However, it should be noted that, in previous experiments, anticipatory responses were generated without volitional involvement during passive stimulation (Barnes and Asselman 1991; Ohashi and Barnes 1996). However, the limitations in timing of the conditioning signal prior to the unconditioned response are very similar to those for the warning signal used here (Flaherty 1985). This may point to a common role for the cerebellum in ocular pursuit and conditioning. It is known that the cerebellum is essential for the production of smooth eye movements (Westheimer and Blair 1973; Zee et al. 1981) and forms a vital role in such behaviour as eye-blink conditioning. The cerebellum has also been implicated in the timing of motor processes (Keele and Ivry 1990). It is quite feasible that the cerebellum may play a vital role in facilitating the continuation of the anticipatory response, if this necessitates the matching of the internally generated predictive estimate against the visual feedback signal at the specific time when current feedback is first likely to become available (i.e. after a delay of 100 ms).

Effect of fixation cues

The results of experiment 2 show that there is no effect of fixation between presentations on the anticipatory response, provided the subject actively removes fixation. Our results with fixation show comparable velocities at target onset to those of Boman and Hotson (1992) for our lowest-velocity stimuli (12.5°/s), but also demonstrate that anticipatory velocity can be much higher for higher target velocities. These higher velocities are comparable to those attained when no fixation was required between presentations.

A number of recent studies have examined the effect on smooth-pursuit reaction times of gaps in target presentation between fixation offset and onset of target motion (Merrison and Carpenter 1995; Krauzlis and Miles 1996). The findings suggest that the reaction time to pursuit onset can be reduced if a gap of approximately 200 ms is left between fixation cue offset and target motion onset. The shortest "gap" that we have used here was 240 ms, but this elicits reaction times that are anticipatory (i.e. negative) rather than simply reduced. The major difference lies in the non-randomised velocity and duration used in our experiments. Even if the timing is randomized, knowledge of direction allows some preemptive movement to be made prior to target onset. Only when direction, velocity and timing interval are randomized does there tend to be a complete absence of anticipatory movement.

Conclusions: the remembered pursuit task

One principle objective of carrying out the experiments described here was to develop a versatile task that could be used to show how information about timing and target speed can be stored and subsequently used to make an-

ticipatory movements. The demonstration that this process can take place even when there is fixation between presentations is important because it allows initial eye position and velocity to be carefully controlled. As a consequence, it is possible to clearly segregate the dynamic after-effects of any preceding eye movement from the anticipatory activity. This remembered pursuit task can form a powerful tool for studying short-term predictive control of smooth pursuit movements. In a recent experiment (Barnes and Barnes 1999), we have used the technique to show that, when target motion during each presentation is more complex (a single cycle sinusoid), phase errors can be minimised within the second presentation of the stimulus, even though the sinusoidal motion is not continuous. In analogy with the remembered saccade task, we feel that this process has potential for revealing the functional characteristics of not only ocular pursuit, but also other visuomotor tracking processes, and we have already used it to investigate anticipatory movements of the hand and eye during oculo-manual pursuit (Marsden et al. 1998).

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