PURSUIT OF INTERMITTENTLY ILLUMINATED MOVING TARGETS IN THE HUMAN

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SUMMARY

1. Experiments have been conducted in order to establish the changes in oculomotor activity which take place when the human subject attempts to pursue an intermittently illuminated moving target.

2. In an initial experiment, target motion in the horizontal plane was composed of one or two sinusoids at frequencies between 0·11 and 0·2 Hz. The target was illuminated for varying durations (10–320 ms) at intervals between 40 and 960 ms. As pulse interval was increased or pulse duration was decreased there was a progressive increase in eye velocity gain for the smooth component of eye movement. Some smooth eye movement was generated even when the pulse interval was as large as 960 ms.

3. In a second experiment target motion consisted of a triangular waveform in which target presentation was timed to occur at regular intervals throughout each cycle. Overlaying and averaging the response from several cycles revealed a regular pattern of pulsatile activity associated with each target presentation. This response, which was particularly evident when the pulse interval was greater than 1 s, consisted of an initial build-up of smooth eye velocity followed by an exponential decay with a time constant of 0·5–2 s. When the pulse interval was less than 1 s there was a summation of the transient responses so that eye movement appeared quite smooth when pulse interval was reduced to 320 ms.

4. The pulsatile nature of the response was accentuated when the target was made to execute a staircase–ramp waveform in which the target was illuminated only during the ramp component. The elimination of position change between ramps and the ability to achieve higher target velocity led to clear evidence of the summation of transient oculomotor responses.

5. The summated effects, however, were not simply attributable to the addition of responses to individual target presentations as indicated by the timing of each response. The eye velocity pulse was frequently initiated 200–300 ms prior to target appearance, and well before the time (100 ms) at which visual feedback would be expected to become effective.

6. The effect of target step displacement alone was investigated by examination of the smooth eye movement initiated by varying numbers of steps in the waveform. This showed that the basic step response had a peak velocity of no more than

8–10 deg/s in most individuals. However, the rapid repetition of step displacements led to the apparent accumulation of eye velocity so that peak eye velocity built up to a mean of 40 deg/s for a series of eight steps separated by 40 ms intervals.

7. The results suggest that the ability to pursue intermittently illuminated targets is primarily dependent on the temporal decay characteristics of the oculomotor system, which allows smooth pursuit to be maintained by the summation of transient responses. However, the effects are attributable, not to the accumulation of transient responses generated directly by the visual stimulus, but to the summation of predictive velocity estimates, which may precede target presentation in their initiation.

INTRODUCTION

Human smooth pursuit is a complex process which involves more than the simple feedback of retinal velocity error information to control the eye as originally proposed by Rashbass (1961). Two features which emphasize this are the ability to produce predictive eye movements and the continued pursuit of a target when it has disappeared from view. An example of the latter type of response was provided by Morgan & Turnbull (1978), who showed that the tachistoscopic illumination of a moving target could still evoke a high proportion of smooth eye movement for pulse intervals as high as 300 ms. Pursuit eye movements, although still reasonably accurate in overall displacement, became progressively more saccadic in nature with increasing pulse interval because the slow-phase velocity was no longer able to match target velocity so well. Unfortunately, the precise nature of slow-phase eye velocity control was not investigated by these authors.

It is well established that when the human subject pursues a moving target which suddenly disappears from view, smooth eye movements may continue in the absence of any visual stimulus (von Noorden & Mackensen, 1962; Eckmiller & Mackeben, 1978; Mitrani & Dimitrov, 1978; Becker & Fuchs, 1985; Barnes & Asselman, 1991). However such eye movements tend to be of reduced velocity and to decay over a period of 0·5–2 s. These findings suggest that during tachistoscopic presentation of moving targets the smooth eye movements induced may result from the temporal summation of the transient response to each target presentation. Some evidence for this type of temporal summation was obtained in a previous experiment (Barnes & Asselman, 1991), in which the response to repeated stimulation in alternate directions was examined. One of the notable features of these responses was that each pulse of eye velocity became more predictive with repeated stimulation over the first three to four presentations. One objective of the experiments described here was to determine whether a similar effect could be demonstrated during successive presentations of an intermittently illuminated target moving with a more complex motion. If so, then it might be expected that the smooth eye movements would show a pulsatile modulation in velocity associated with the frequency of target presentations. There also should be a predictable decline in average slow-phase eye velocity gain with increasing pulse interval. Previous experiments by Barnes, Donnelly & Eason (1987) had demonstrated that when the interval between successive step displacements of a target in a staircase pattern waveform was

sufficiently long (> 240 ms) eye velocity did exhibit a pulsatile form in which each step initiated a sudden increase in eye velocity followed by a steady decay.

A secondary objective was to determine the relationship between the response to step displacements of the target and continuous target velocity. In the experiments carried out by Morgan & Turnbull (1978) the target was illuminated for a very brief period (200 μs). Under such experimental conditions the slow-phase component of eye movement must be driven by the change in target position rather than by its instantaneous velocity during the presentation period. A number of experiments have shown that step changes of target position can evoke such smooth eye movements (Pola & Wyatt, 1980; de Bie & van den Brink, 1984), although they rarely have a velocity of more than 4–5 deg/s. Moreover, such eye movements are frequently predictive in nature, being initiated before a step change in target position (Kowler & Steinman, 1979; Barnes *et al.* 1987). We wanted to know whether such eye movements exhibited a similar transient decay pattern to that of the eye movements induced by continuous target motion (Barnes & Asselman, 1991) and whether a cumulative effect would allow smooth eye velocity to reach higher levels than those recorded previously.

In the experiments described here we have sought to verify the validity of these ideas by systematically varying both the interval between target presentations and the duration of target exposure and carrying out a detailed examination of the oculomotor response to a number of target motion stimuli. The results of the experiments have revealed that, in large part, the effects may be explained by the transient persistence of the smooth eye movement in the absence of a visual stimulus, although the timing relationships indicate that prediction plays a very important part in the initiation of each transient response.

METHODS

Subjects were seated with head fixed at the centre of a screen of 2 m radius onto which a moving visual target was projected by a mirror galvanometer. The illumination of the moving target was controlled by an electro-mechanical shutter which could produce pulse durations down to 8 ms. The target comprised a circle of radius 25 min of arc with fine cross-hairs superimposed on it. Its luminance was sufficiently low (approximately 2 cd.m²) to eliminate the after-images which would otherwise persist after brief presentation. The experiments were conducted in an otherwise completely darkened room. The motion of the target was controlled by a computer-generated waveform which took various forms as described later. Eye movements were transduced by an infra-red limbus tracking technique with a resolution of 5–10 min of arc (SKALAR IRIS). The eye movement recorders were rigidly coupled to the head by a dental bite and helmet assembly.

Four types of experiment were carried out with local Ethics Committee approval, in which various combinations of stimuli were used. In all of the experiments each subject experienced each of the stimulus conditions in a balanced randomized order.

Experiment I. In the first experiment we investigated the effect of varying the pulse duration and interpulse interval during pursuit of a tachistoscopically illuminated target moving with two types of waveform. Initially, the waveform was a sinusoid of peak velocity 16 deg/s at a frequency of 0·2 Hz. Pulse interval was held constant at 640 ms whilst pulse duration was varied from 20 to 640 ms, the target being continuously illuminated for the longest pulse duration. Then pulse duration was held constant at 10 ms whilst pulse interval was varied from 10–960 ms. These stimulus conditions were repeated using a pseudo-random target motion composed of two sinusoids at frequencies of 0·11 and 0·19 Hz, each with a peak velocity of 8 deg/s. Eight normal subjects, three of whom required refractive correction, participated in this experiment.

Experiment II. In the second experiment the stimulus was a triangular waveform of frequency 0·125 or 0·195 Hz with a peak velocity of ± 10 or 14 deg/s respectively. The target was illuminated for 10, 80 or 160 ms at intervals of 320–4000 ms. It was evident from the results of experiment I and from the subjective impressions reported by the subjects that there was no instantaneous velocity information contained within the briefest presentation (10 ms), which therefore acted as a step displacement stimulus. In contrast, the 80 and 160 ms target exposures represented a combination of a step displacement and a velocity pulse. Six subjects took part in this experiment.

Experiment III. In the third experiment we attempted to eliminate the position change component of the stimulus by constructing the staircase–ramp waveform shown in Fig. 7, in which constant-velocity segments (henceforth referred to as the ramp components) were separated by zero-velocity phases. The target was exposed only during the ramp components of the waveform, which had a duration of 160 ms and a velocity of 32 deg/s. The basic frequency of the waveform was either 0·125 or 0·195 Hz and the interval between ramp components was varied from 320–4000 ms, so that there were one, two, four or eight ramps in each direction per half-cycle. Eight subjects participated in this experiment.

Experiment IV. In the final experiment, an attempt was made to remove the continuous constant-velocity components of the stimulus and to examine the nature of responses to successive individual step displacement stimuli. The target motion was a staircase–ramp waveform of frequency 0·25 Hz with ramp duration of 320 ms and ramp velocity of 32 or 64 deg/s. The interval between ramps was 2000 ms, so that there was only one ramp per half-cycle. The target was illuminated for brief periods (8 ms) during the ramp component of this waveform at interpulse intervals of 40, 80, 160 or 320 ms, so that there were nine, five, three or two presentations for each ramp (see Fig. 11). In this experiment each of the four subjects experienced each condition twice.

Eye movements were analysed using an interactive computer graphics technique described previously (Barnes, 1982). Eye displacement gain and phase were derived by correlation of the overall eye displacement signal (including fast phases) with target displacement using least-squares error regression procedures. After removal of the fast-phase components of the eye movements the slow-phase eye velocity was similarly correlated with target velocity to give eye velocity gain and phase. Many of the eye movements evoked in these experiments exhibited pulsatile activity which might be confused with fast-phase eye movements. However, the time course of such responses was considerably longer than that of fast phases and peak velocities were generally much lower. Nevertheless, great care was taken to ensure that only the fast-phase components were removed from the eye velocity traces. Cycle-by-cycle averages of slow-phase eye velocity were obtained by overlaying and averaging successive cycles of the response during periodic stimulation. Various other measures of eye velocity were also derived for particular experimental conditions as indicated in the Results section.

<div align="center">RESULTS</div>

Experiment I: pursuit of sinusoidal and pseudo-random target motion

When the subjects pursued the tachistoscopically illuminated moving target a consistent change in the pursuit response was observed in all subjects. In the first part of the experiment, in which the pulse interval was held constant at 640 ms during either sinusoidal or pseudo-random target motion, eye movements appeared relatively smooth for longer duration exposures (160–320 ms) but exhibited progressively increasing frequency of saccadic activity as pulse duration was decreased below 120 ms (Fig. 1).

Overall eye displacement matched target displacement very well for all values of pulse duration, the average values of eye displacement gain being 0·92 for the sinusoidal response and 0·94 for the pseudo-random response. Differentiation of the eye displacement signal and removal of the fast-phase components of the response revealed a progressive decline in the velocity of smooth eye movement as the pulse duration was decreased from 320 to 20 ms. In response to the sinusoidal stimulus eye velocity gain declined significantly ($P < 0.001$ by ANOVA) from a mean of 0·94 to 0·59. When the mixed-frequency stimulus was used the results were very similar, the

gain of both components decreasing significantly ($P < 0.01$ by ANOVA) with decreasing pulse duration from a maximum of 0.91 for continuous presentation down to 0.50 for a pulse duration of 20 ms (Fig. 2). However, there was no further decrease in eye velocity gain as pulse duration was reduced to 10 ms and at this pulse duration
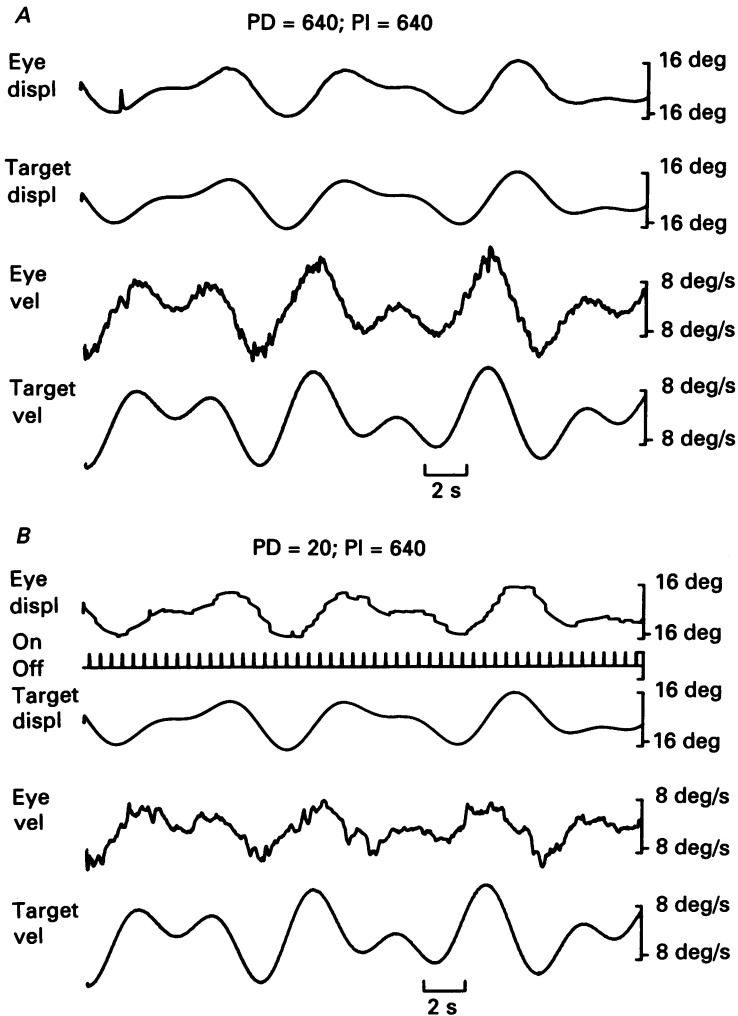

Fig. 1. Examples of the eye movements evoked during pursuit of a target moving with a pseudo-random waveform composed of two sinusoids of frequency 0.11 and 0.19 Hz and peak velocity 8 deg/s. In *A* the target was illuminated continuously whereas in *B* it was exposed for a pulse duration (PD) of 20 ms at an interpulse interval (PI) of 640 ms as indicated in the second trace. Fast-phase components have been removed from the eye velocity trace.

none of the subjects were able to observe any apparent motion of the target within its brief exposure period. There was an interesting difference in the phase of eye velocity between the single and dual sinusoidal stimuli. Phase in response to the

single sinusoid varied over a relatively small range with pulse duration, whereas in the responses to two mixed frequencies the lower frequency exhibited increasing phase lead and the higher frequency an increasing phase lag with decrease of pulse duration. (Fig. 2).
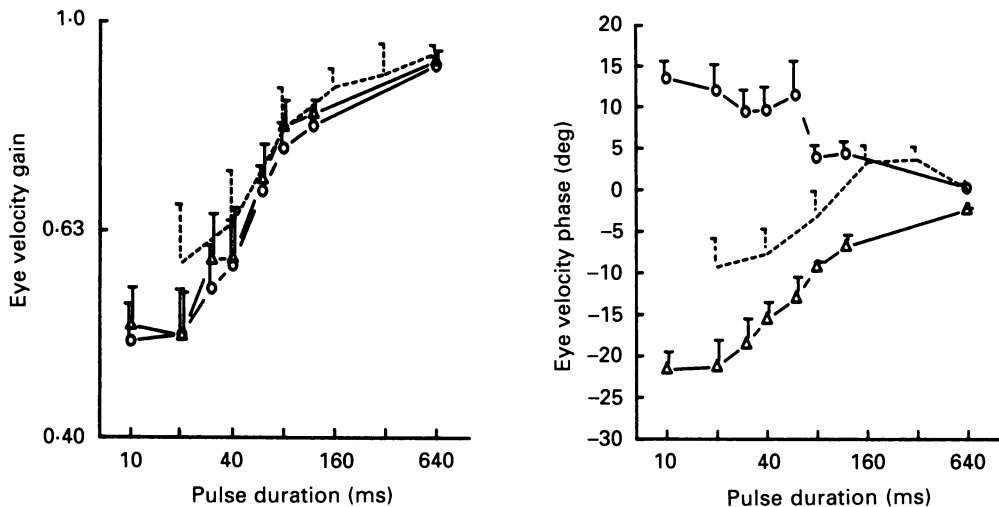

Fig. 2. The gain and phase of slow-phase velocity during pursuit of an intermittently illuminated target. Dashed lines represent responses to a single sinusoid of frequency 0·2 Hz; continuous lines represent responses for each of the two frequency components (○, 0·11 Hz; △, 0·19 Hz) of the mixed-frequency target motion shown in Fig. 1. The target was illuminated for durations of 10–640 ms at an interpulse interval of 640 ms, the largest value of pulse duration representing continuous illumination. Mean of eight subjects +1 s.e.m.

In the second part of the experiment, in which the pulse duration was held constant at 10 ms, there was also a progressive and significant decrease ($P < 0.01$ by ANOVA) in eye velocity gain with increasing pulse interval even though overall eye displacement again matched target displacement very closely (mean gain = 0·99 for both sinusoidal and mixed frequency). The changes in eye velocity gain were also similar for both the single sinusoidal stimulus and the mixed-frequency response, mean gain in the latter condition decreasing from 0·95 for an interpulse interval of 10 ms (i.e. continuous target presentation) to 0·25 for an interpulse interval of 960 ms (Fig. 3). However, as with the variation of pulse duration, the eye velocity phase for the two frequency components in the mixed-frequency stimulus exhibited a divergent change with increase of interpulse interval (Fig. 3), whereas the phase of the sinusoidal response lay midway between.

Visual inspection of the eye velocity responses to the longer pulse intervals (640 and 960 ms) revealed some pulsatile activity in the response (Fig. 1B), although this was sometimes difficult to distinguish because of a lack of resolution in the recording technique. For this reason it was decided to investigate the pulsatile nature of the response under more controlled circumstances in which an average of several presentations could be obtained.
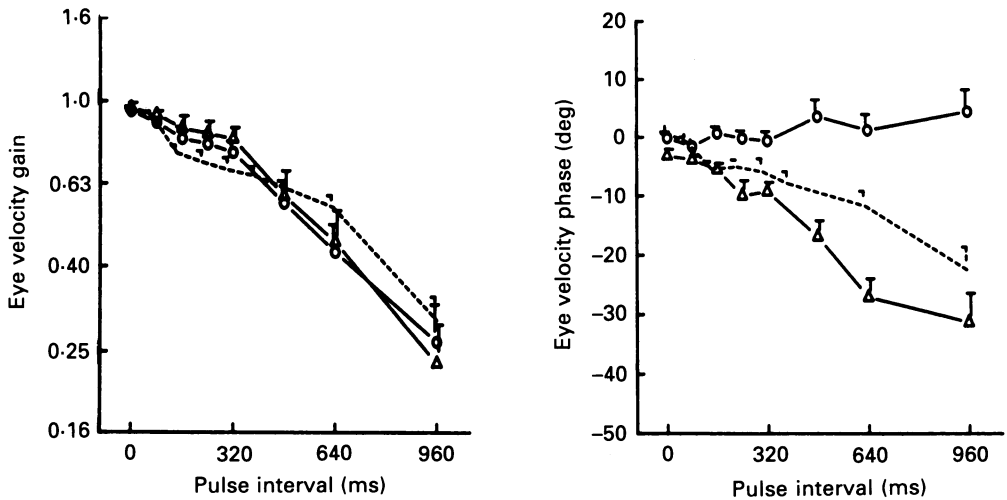
Fig. 3. The gain and phase of slow-phase eye velocity during pursuit of an intermittently illuminated target. Dashed lines represent responses to a single sinusoid of frequency 0·2 Hz; continuous lines represent responses for each of the two frequency components (○, 0·11 Hz; △, 0·19 Hz) of the mixed-frequency target motion shown in Fig. 1. The target was illuminated for a duration of 10 ms at interpulse intervals of 0–960 ms, the lowest value of interpulse interval representing continuous illumination. Mean of eight subjects +1 S.E.M.
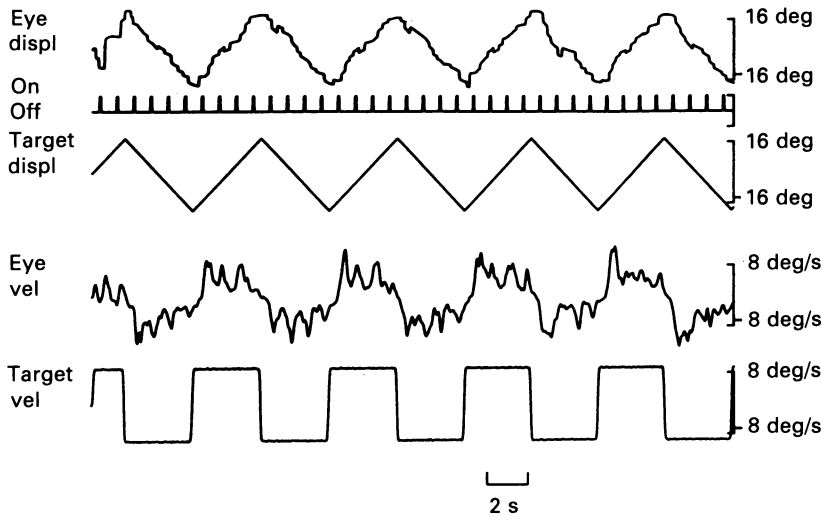

Fig. 4. An example of the oculomotor response evoked during pursuit of a triangular waveform target motion of frequency 0·125 Hz and peak velocity 10 deg/s. The target was exposed for 80 ms at intervals of 1000 ms, so that there were exactly four pulses per half-cycle. Note the pulsatile nature of the slow-phase eye velocity which remains even after removal of the fast-phase components.

Experiment II: pursuit of triangular waveform stimuli

A typical response to the tachistoscopic illumination of the target during triangular waveform stimulation is shown in Fig. 4, in which pulse duration was

80 ms. Peak eye displacement matched target displacement reasonably well for pulse intervals less than 2000 ms with average eye displacement gains greater than 0·95, although there was considerable deviation from the target trajectory, as might be expected when the target could not be seen continuously. After removal of the fast-
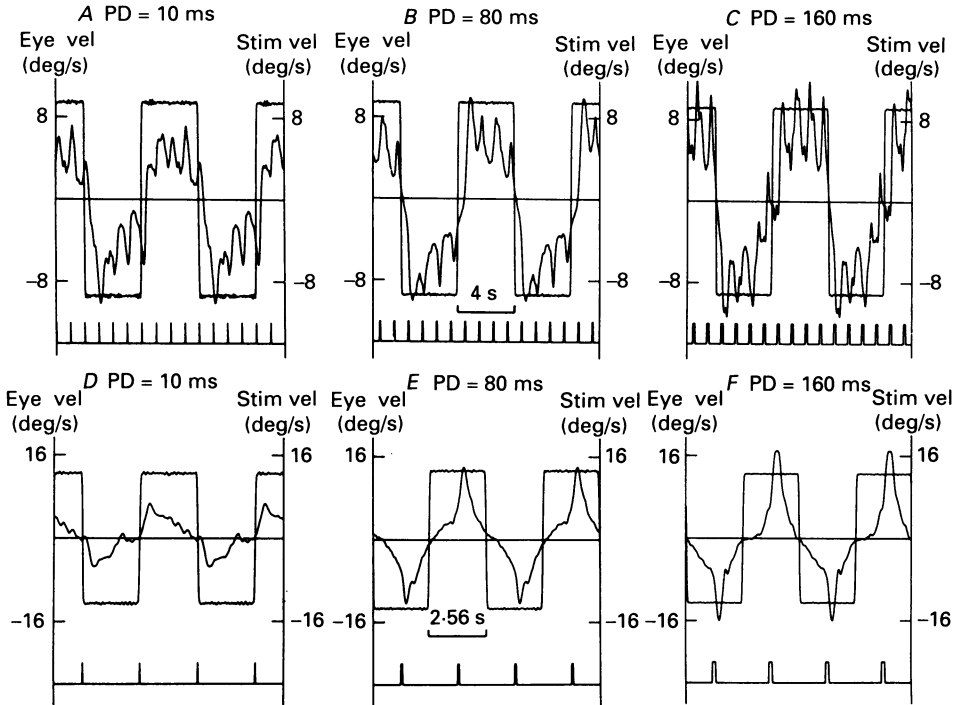

Fig. 5. Cycle-by-cycle averages of slow-phase eye velocity obtained by overlaying eight cycles of the steady-state response obtained from a single subject during pursuit of targets intermittently illuminated for a duration of either 10, 80 or 160 ms. In A–C the target was presented at interpulse intervals of 1000 ms. In D–F interpulse interval was 2560 ms and the target was exposed as it passed through centre when pulse duration was 80 and 160 ms and at the extreme positions when pulse duration was 10 ms.

phase components of eye movement, the eye velocity trace could be seen to exhibit regular pulsatile activity as indicated in Fig. 4.

A similar pattern of activity was observed for exposure times of 10 and 160 ms, a feature that became evident by comparison of the cycle-by-cycle averages of slow-phase eye velocity (Fig. 5). Each target presentation resulted in a sudden increase in eye velocity that reached a peak and then decayed towards its original level. The time constants associated with this decay were estimated using an iterative exponential regression analysis for conditions in which the pulse interval was greater than 1000 ms. There appeared to be two stages in the decay process: an initial rapid fall in velocity with a time constant of approximately 0·5 s, followed by a slower decay with a time constant of 1–2·5 s. When the stimulus was formed by the briefest (10 ms) pulse duration at the extremes of its trajectory, the eye velocity appeared to

consist almost solely of the more slowly decaying component (Fig. 5D). However, there was considerable variability in this particular response, even within subjects, and it was difficult to quantify the effects satisfactorily. Although the traces shown in Fig. 5A–D exhibited a regular beating with each target presentation in this
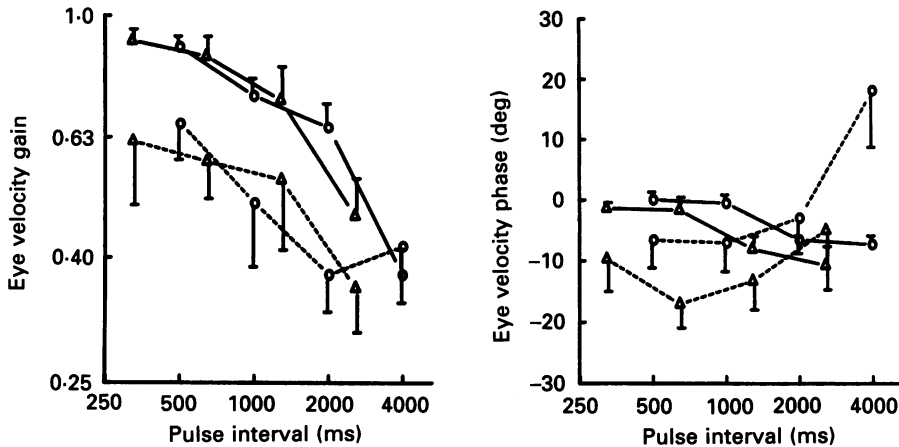

Fig. 6. The gain of slow-phase eye velocity evoked during pursuit of an intermittently illuminated target moving with a triangular waveform of frequency 0·125 Hz (○) or 0·195 Hz (△). Pulse duration was either 10 ms (dashed lines) or 160 ms (continuous lines). Mean of six subjects ±1 S.E.M.

particular subject, other subjects showed more irregular activity. The more irregular response typically occurred in subjects who tended to overestimate the required velocity of eye motion.

Another feature which could be observed in the averaged responses was the cumulative effect of repeated transient stimuli on the nature of the eye velocity profile. When the pulse interval was greatest (2560 and 4000 ms), the isolated response to a single pulse in each direction was obtained. As pulse interval was decreased to 320 ms there was an evident overlay of these single responses, resulting in a build-up of eye velocity within each half-cycle and a decrease in the depth of modulation about mean eye velocity. As a result, overall eye velocity gain increased with decreasing interpulse interval or increasing pulse duration (Fig. 6) in a similar manner to that shown in experiment I (Figs 2 and 3).

Experiment III: pursuit of staircase–ramp stimuli

The velocity of the target motion which could be generated by the stimulus used in experiment II was necessarily rather low because of limitations in the measurable amplitude of eye displacement. Moreover, the effects of repeated uni-directional velocity pulses could not be isolated because of the contribution of the step displacement between velocity pulses, which, as will be shown later, makes a significant contribution to the response. For these reasons the staircase–ramp waveform shown in Fig. 7 was developed. The target was illuminated only during the

constant-velocity portion of the waveform and the subject remained in darkness during the stationary phases. Subjects found no difficulty in generating a potent eye movement response to this stimulus (Fig. 7). The cycle-by-cycle average of slow-phase eye velocity (Fig. 8) exhibited very clearly the pulsatile nature of the response,
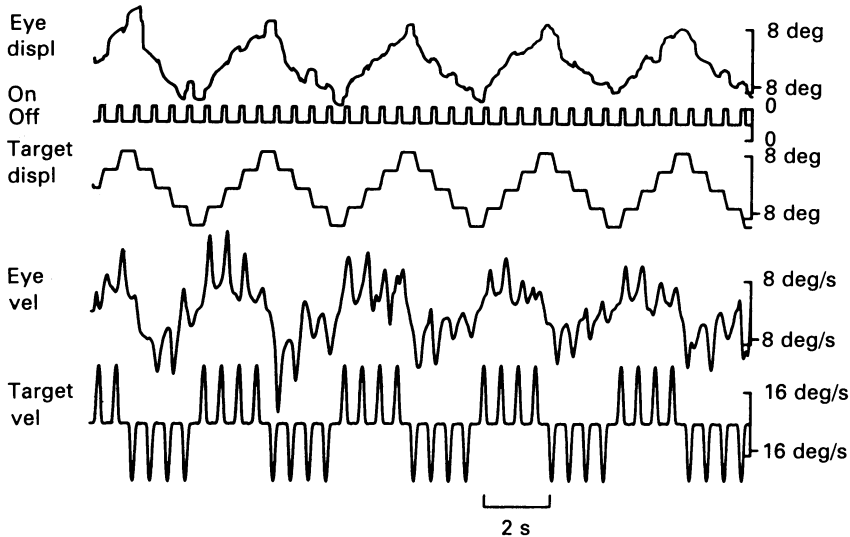

Fig. 7. An example of the eye movements evoked in response to the staircase–ramp target motion waveform. The target was illuminated for 160 ms only during the period of the ramp component, which had a velocity of 32 deg/s. Note from the eye displacement trace that the pulsatile modulation of the smooth-component eye velocity was frequently observed in the absence of any concomitant fast-phase activity.

particularly for the longer interpulse intervals (1–4 s). When the pulse interval was decreased below 500 ms (Fig. 8A and B) the transient responses to each pulse of target velocity showed the effects of summation so that the peak-to-peak amplitude between pulses was reduced whereas overall eye velocity throughout each half-cycle was increased.

One of the more interesting features of the transient decay pattern was that eye velocity frequently exhibited the characteristics of an adaptive response, that is, a reversal of eye velocity following the exponential decay. Some subjects showed this effect to a greater extent than others, but Fig. 8D shows a typical example of an isolated transient response. This appears to indicate that the dynamic characteristics of the links between the visual stimulus and the eye muscles exhibits some sensitivity to rate of change as well as a short time constant element giving rise to the exponential decay, features which have been noted previously (Barnes & Asselman, 1991).

The staircase–ramp stimulus induced a deeper modulation of eye velocity with each target presentation than obtained in experiment II. This feature allowed the timing of the pulsatile response to be examined in detail by calculating the reaction time between the onset of target illumination and the peak of the velocity pulse. In

order to gain some indication of the time at which each velocity pulse was initiated the troughs in the waveform were also determined. Both peak and trough responses were found by examination of zero cross-over points in the eye acceleration waveform indicated in Fig. 9. The results (Fig. 10, lower trace) show clearly that the
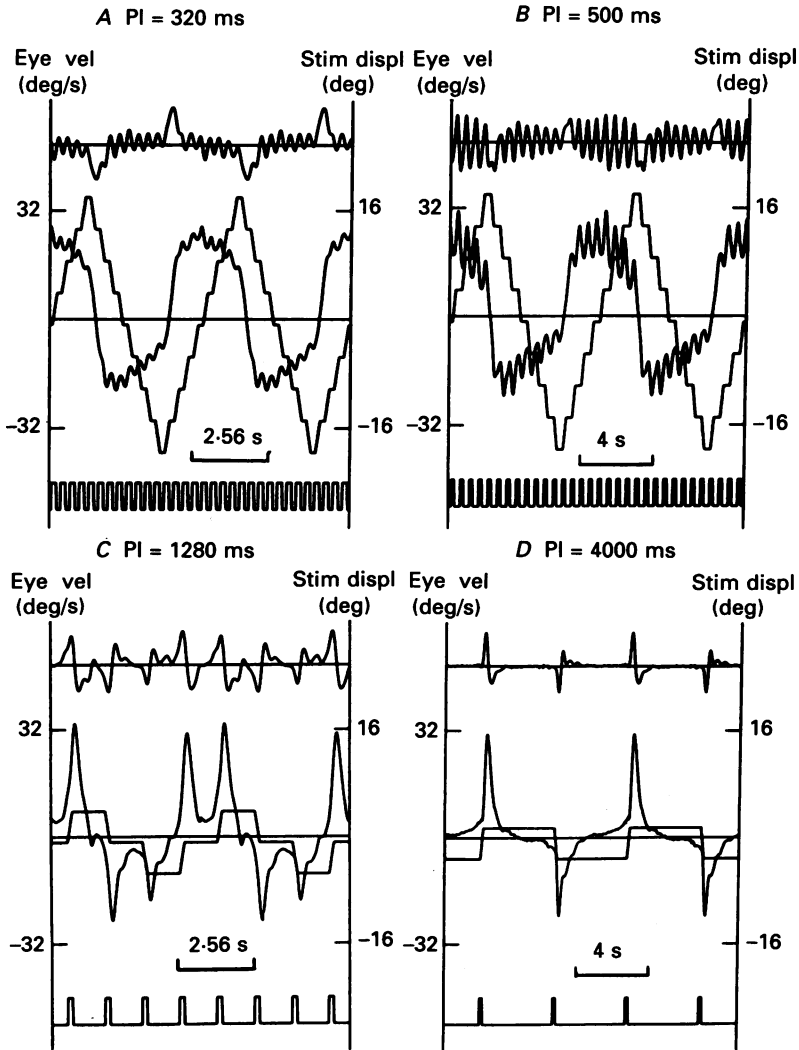

Fig. 8. Cycle-by-cycle averages in one subject of the response to the staircase–ramp waveform illustrated in Fig. 7, for varying interpulse intervals (PI) between 320 and 4000 ms. Uppermost traces in each example represent eye acceleration derived from the averaged eye velocity trace.

pulsatile activity was initiated well before target appearance if pulse interval was more than 500 ms and that this negative reaction time increased significantly with increasing pulse interval. The reason for this change in reaction time with pulse interval lies in the interaction between the transient decay and the initiation of the

next predictive pulse which occurs when the interpulse interval is less than approximately 1000 ms, as we have shown previously (Barnes & Asselman, 1991). Measurement of the time when the trough of the response occurs merely indicates the time at which the summation of two successive responses results in zero eye velocity, a time which is later than the actual initiation of the predictive pulse.
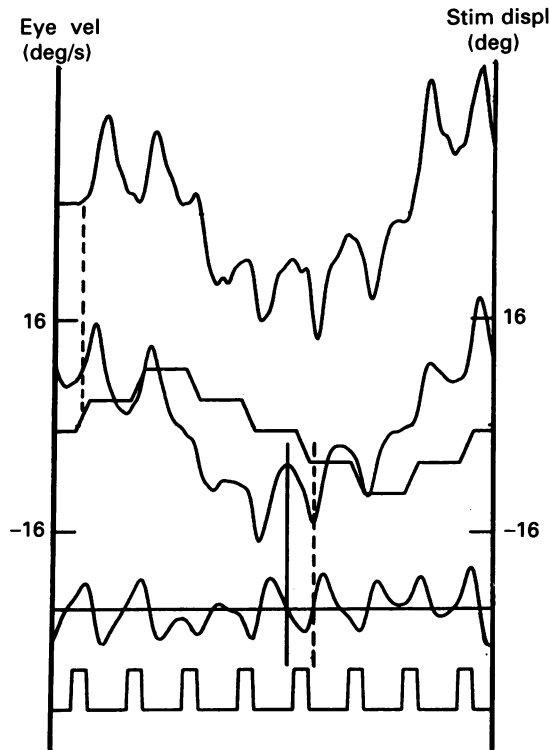

Fig. 9. An illustration of the timing changes which occur in the response to the staircase–ramp waveform. Bottom trace, pulses indicating time of target exposure. First (top) trace, eye velocity during the first cycle of the stimulus. Vertical dashed line indicates initiation of the first response in relation to target presentation. 2nd and 3rd traces, cycle-by-cycle averages of slow-phase eye velocity and target displacement, obtained by overlaying eight cycles of the steady-state response. The continuous vertical line indicates the method of defining the initiation of the predictive pulse in relation to the onset of target exposure, through the identification of zero cross-overs in the eye acceleration trajectory (4th trace). The dashed vertical line indicates the timing of the peak response in relation to target onset.

The reaction time between target onset and attainment of peak velocity increased only slightly with increasing pulse interval. The mean time to peak velocity varied from 260 to 320 ms (Fig. 10, upper trace), values which are similar to those obtained in previous experiments (Barnes & Asselman, 1991).

Another feature demonstrated in Fig. 9 is the manner in which the response became more predictive with repeated stimulation. During the first cycle of stimulation (upper trace in Fig. 9) the first two responses were initiated after the

onset of target illumination but with repeated exposures became progressively more phase-advanced with respect to target exposure. This feature was demonstrated previously for direction-changing stimuli (Barnes & Asselman, 1991).

Experiment IV: cumulative effects of step displacements

In further experiments we sought to study the effect of sequential step displacements of the stimulus by illuminating the target for only 8 ms at varying
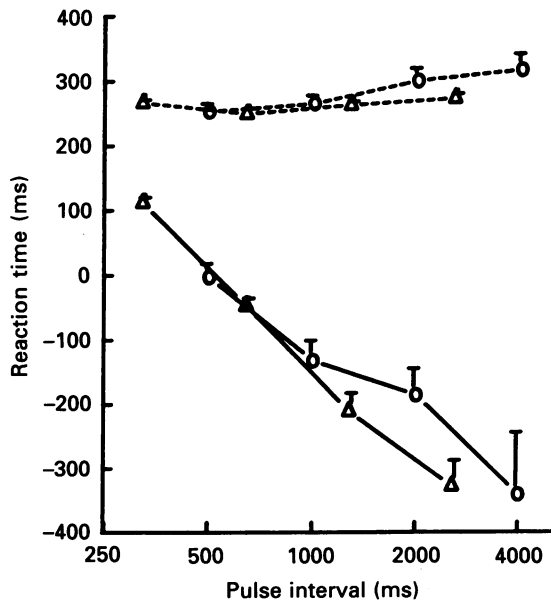

Fig. 10. The reaction time between onset of target exposure and either the initiation of the predictive velocity pulse obtained from the measurements indicated in Fig. 9 (continuous lines) or the attainment of peak eye velocity (dashed lines). Mean of eight subjects +1 s.e.m. ◯, 0·125 Hz; △, 0·195 Hz.

pulse intervals during the constant-velocity phase of the waveform. In the most extreme example the target appeared twice during this phase, once at the beginning and once at the end of the target movement (interpulse interval = 320 ms). In other examples interpulse interval was reduced to 160, 80 or 40 ms (i.e. three, five or nine pulses per ramp). The results are shown in Fig. 11 as the cycle-by-cycle average for a typical subject. It is clear from this that a steady increase in peak velocity was obtained during each ramp as the number of pulses was increased, despite the fact that effective velocity of the target remained constant during this phase. The response to two pulses exhibited a peak velocity of 8–16 deg/s (Fig. 11*D*) which is somewhat higher than the velocity levels obtained previously in response to step displacements of the target. However, the transient decay from peak velocity was similar for all values of interpulse interval having a time constant of approximately 0·5–1 s. These results strongly suggest that the response to successive step displacements also has an accumulative effect with the peak velocity induced by each

step displacement building upon the transient decay of the previous one to form a cumulative eye velocity profile. To obtain a clearer indication of this effect Fig. 12*B* shows a measure of the average peak eye velocity obtained during the first four half-cycles of the target waveform. There was a significant ($P < 0.001$) trend of increasing
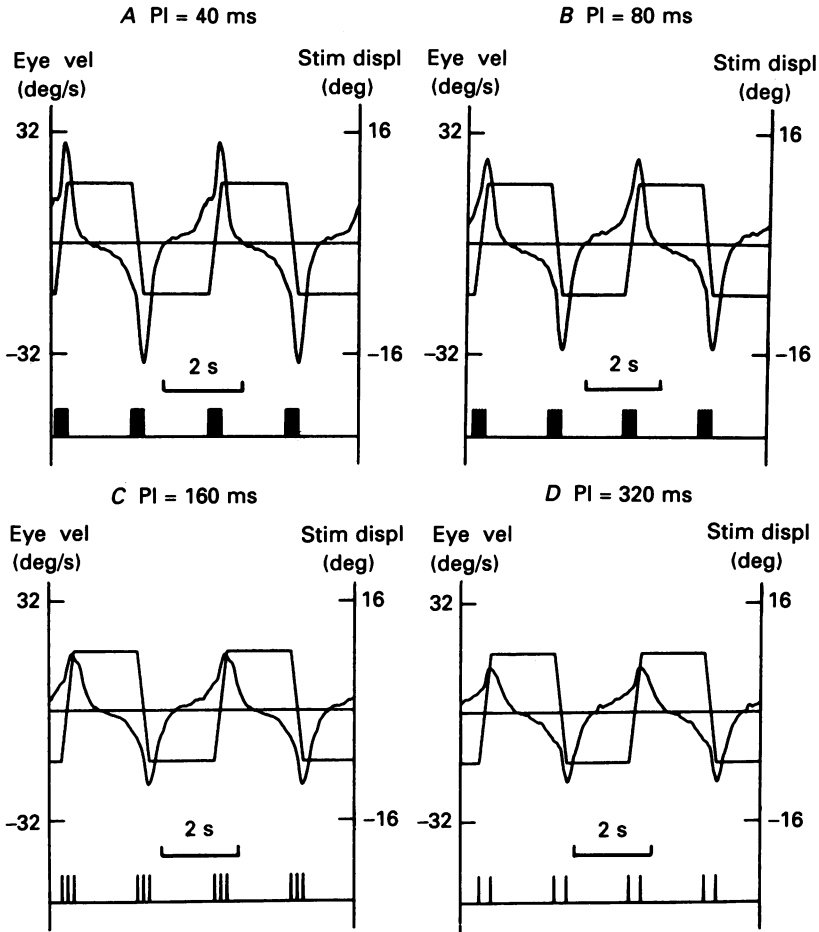

Fig. 11. Cycle-by-cycle averages of the response to successive step displacements of the target. The target moved at a constant velocity of 64 deg/s across the central visual field for a total ramp duration of 320 ms, but was illuminated for only 8 ms at intervals (PI) of 40, 80, 160 or 320 ms, so that there were nine, five, three or two target exposures in each direction of motion as indicated by pulses in the lower traces.

velocity with decreasing pulse interval, or in other words, with increasing number of steps per ramp, for each of the ramp velocity stimuli (32 and 64 deg/s). Moreover, velocities induced by the higher ramp velocity were, on average 1·62 times as great as those evoked by the lower velocity stimulus.

In addition, it was observed that peak eye velocity for each pulse duration increased to reach an asymptotic level between the first and fourth ramp stimuli (Fig. 12*B*), although this increase did not show the uniformity demonstrated in

previous experiments (Barnes & Asselman, 1991). Associated with the increase in peak velocity there were simultaneous changes in the timing of the response. The time between target onset and the initiation of the predictive response was measured from the point at which there was a sudden increase in eye velocity. This point was
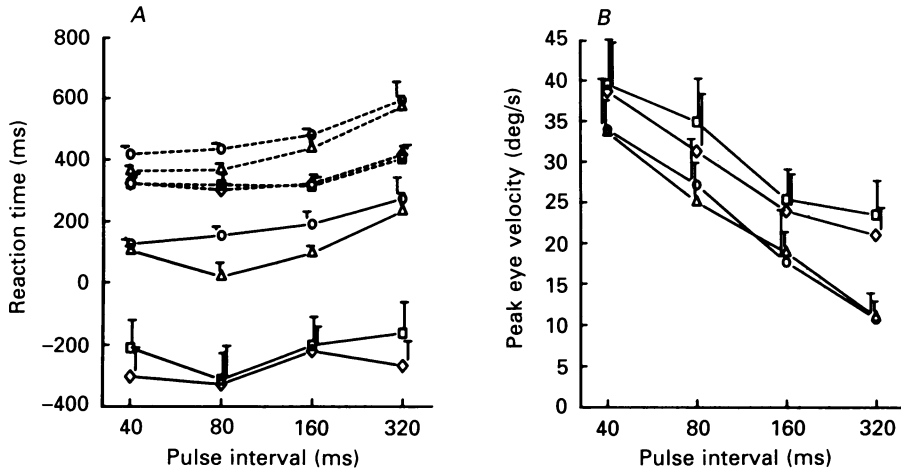

Fig. 12. *A*, changes in the reaction time from the onset of target presentation to either the initiation of the predictive response (continuous lines) or the attainment of peak eye velocity (dashed lines) during the first four presentations of the ramp target motion stimulus as a function of interpulse interval during each ramp component (□, 1st; △, 2nd; ▢, 3rd; ◇, 4th). *B*, changes in the magnitude of peak eye velocity during the first four ramp stimuli (symbols as in *A*). Mean of eight values from four subjects ±1 s.e.m. Ramp target velocity was 64 deg/s in these examples.

sometimes difficult to define, as is evident in Fig. 11. However, it was quite clear that whereas the first response was initiated well after the onset of the ramp motion, subsequent ramp responses became progressively more phase-advanced with respect to each ramp stimulus (Fig. 12*A*). Measurement of the reaction time between target onset and peak velocity was more reliably defined and this also showed a progressive decrease in reaction time over the first four presentations (Fig. 12*A*) in a similar manner to the responses to continuously illuminated ramp stimuli demonstrated previously (Barnes & Asselman, 1991).

DISCUSSION

The cumulative effect of repeated transient stimulation

The results of the experiments presented here demonstrate that when the 'smooth' eye movements induced during pursuit of a briefly illuminated moving target are examined in detail they can be seen to be composed of two phases: a transient increase in eye velocity associated with each appearance of the target, followed by an exponential decay of eye velocity during the ensuing period of darkness. The peak velocity of the eye induced by each target presentation increased in a monotonic manner with increasing pulse duration between 40 and 320 ms. These findings are compatible with the results of a number of previous experiments. Early experiments

by von Noorden & Mackensen (1962) established that the oculomotor response decays over a period of 1–2 s when the visual stimulus is suddenly removed and this was subsequently confirmed by other experimenters (Mitrani & Dimitrov, 1978; Whittaker & Eaholtz, 1982; Barnes *et al.* 1987). When Becker & Fuchs (1985) examined the eye velocity in more detail in this condition, they observed that the magnitude of eye velocity was dependent on exposure time up to 400 ms and decay occurred in a two-stage process over a period of 3–4 s. It is probable that the more rapid decay, with time constant of 0·5–1 s, represents the transient decay process of the visuomotor pathways whereas the slower decay represents a limited capability to produce sustained eye movements by volitional effort in the absence of visual information. The latter response does not normally exceed a velocity of 5 deg/s in most subjects.

In other experiments it has been shown that tachistoscopic presentation of a head-fixed fixation target has similar effects on the suppression of vestibular nystagmus induced by both active (Barnes, 1988) and passive head movement (Barnes & Edge, 1983) and on the eye movements induced by an optokinetic stimulus (Barnes & Crombie, 1985). In all of these experiments the degree of suppression increased with decrease of the interpulse interval over a similar range to that shown in Fig. 3 for the pursuit responses.

When a series of brief target presentations are made at regular intervals eye velocity may build up to higher levels through the temporal summation of the transient components of the response to each target presentation when the interpulse interval is less than 1000 ms. When the interpulse interval was more than approximately 300 ms the eye velocity trajectory could normally be seen to consist of pulses of activity synchronized with target illumination (Fig. 8), but for shorter intervals eye velocity appeared relatively smooth. The effects of this temporal summation process were evident in the changes in eye velocity gain obtained when either the pulse interval or pulse duration were modified (Figs 2 and 3). It is of particular interest that the differences in phase associated with these changes in gain for the two frequency components of the stimulus were consistent with those observed previously during pursuit of pseudo-random target motion stimuli (Barnes *et al.* 1987; Barnes & Ruddock, 1989), in which the breakdown in gain was caused by a rather different process.

The evidence for prediction in the pursuit response

Although the results demonstrate a clear cumulative effect of the transient responses the effect is not as straightforward as might appear, because each eye velocity pulse is actually predictive of the ensuing target appearance (Fig. 9). These predictive velocity pulses appear to be very similar to those recorded previously when using a simpler stimulus in which target motion was constantly unidirectional or changed direction in alternate presentations (Barnes & Asselman, 1991). Over the first three to four presentations the peak eye velocity progressively increased whilst simultaneously becoming more phase-advanced with respect to target presentation. In the steady state the predictive pulse was initiated well before each target appearance and reached a peak some 200–240 ms after target onset. The predictive velocity pulse was found to have a very stereotyped temporal characteristic, the peak velocity of which increased with pulse duration. When the repetition rate of

target exposure was increased a simple temporal overlay of successive predictive pulses could be demonstrated. On the basis of these findings it was hypothesized that the predictive velocity estimate was derived by sampling of the efference copy of eye velocity and that this sample was stored internally and subsequently launched under the control of a periodicity estimator. In this way the inherent delays in the visuomotor feedback pathways could be overcome by timing the peak eye velocity to occur simultaneously with the time of target exposure.

The results of our present experiments show that the same predictive process takes place continuously when the target motion stimulus is a more complex periodic waveform composed of both unidirectional and direction-changing components. As indicated in Fig. 9, the velocity pulses were more phase-advanced in the average response than they were in the first cycle of presentation (top trace). In the third presentation, when target motion changed direction, there was evidence of the initiation of a predictive pulse in the wrong direction that was subsequently corrected after a latency of approximately 100 ms. After the first cycle of stimulation there was little evidence of such inappropriate predictions indicating that the subject had quickly learned the pattern of reversals in relation to the number of unidirectional stimuli. The same features of the response were evident when there were differing numbers of unidirectional stimuli in each half-cycle as evidenced by the fact that the predictive pulses were initiated prior to target onset for all pulse intervals above 500 ms (Fig. 10). In subsequent (unpublished) experiments we have been able to show that much more complicated patterns of activity can be learned, although the time to do so naturally increases with the complexity of the task. It is evident therefore that whilst the basic entrainment mechanism that is responsible for estimating the periodicity of target presentations can operate in a fairly automatic manner (even during passive stimulation of the oculomotor system, for example) the mechanism for controlling the initiation of predictive estimates can operate in a more complex manner under volitional control.

It is difficult to imagine that this complex behaviour in the timing of the response revealed by intermittent target exposure is not directly related to the normal mechanism of prediction in the pursuit reflex. To prove that this mechanism is actually the one that is normally used would be difficult, but it is possible to demonstrate that the basic mechanisms revealed in these experiments could give rise to the types of response normally observed. As we have noted in our previous publication (Barnes & Asselman, 1991) it seems probable that the normal mode of operation of the pursuit reflex is one in which predictive estimates of eye velocity based on previous eye velocity are made and subsequently checked against the current visual stimulus. In the experiments described here the timing of the release of predictive estimates is usually, but not always, governed by the timing of target exposure. As we demonstrated previously (Barnes & Asselman, 1991), through the development of a model of the predictive mechanisms, it is quite possible that in the normal pursuit of a continuously illuminated target this process is controlled by a regular sampling mechanism with a sampling interval of approximately 250–300 ms. Such a system would give rise to small amplitude oscillations in eye velocity similar to those shown in Fig. 8A at a frequency of 3–4 Hz, a feature often observed experimentally (Robinson, Gordon & Gordon, 1986).

The evidence suggests that this system may operate in two ways. First, there is a

basic mechanism which takes continuous samples of the efference copy of eye velocity and constructs an estimate of the required eye velocity on the basis of current and previous samples. Such a system would almost certainly operate during the pseudo-random stimuli used in experiment I and the model derived on this basis can be shown to simulate the responses to continuous target exposure when all frequencies are below approximately 0·4 Hz (Barnes & Asselman, 1991). Secondly, there is a more complex system which is able to memorize more regular patterns of activity in terms of the timing of direction changes and the velocity of the eye in the previous cycle of stimulation. This system is able to simulate the response to periodic stimuli, even at higher frequencies of target motion (0·4–2 Hz).

Responses to step displacement of the target

Evidence from the experiments of Morgan & Turnbull (1978) suggests that the smooth eye movement response evoked by intermittent target illumination is not dependent upon the sensing of the instantaneous velocity during the period of target presentation, since smooth eye movements were observed in response to very brief durations of target exposure (200 μs). Similarly, in the vestibulo-ocular reflex suppression experiments mentioned above (Barnes & Edge, 1983) pulse duration was found to have no effect on the degree of suppression over a range from 20 μs to 1 ms. From the results of the experiments described here it would appear that the limit beyond which an increase in the duration of exposure leads to an increase in eye velocity is approximately 20–30 ms since the gain of the pursuit responses did not decrease further for pulse durations less than 20 ms (Fig. 2) and the perception of instantaneous target motion was lost at this exposure duration. Shorter pulse durations resulted in a baseline peak velocity of approximately 8–10 deg/s. The results of a number of previous experiments have indicated that retinal position error may form a sufficient stimulus to elicit smooth eye movements, although, for the most part, this has been thought of as a response to small (< 4 deg) step displacements (Pola & Wyatt, 1980; de Bie & van den Brink, 1984; Carl & Gellman, 1987; Barnes *et al.* 1987). In contrast, target displacement was as large as 20 deg in the experiments described here. As noted previously (Barnes & Edge, 1983), it is probable that image displacement on the retina actually forms the basis of the velocity-sensing mechanisms (Grusser & Grusser-Cornehls, 1973) through the sequential stimulation of spatially separated receptors feeding a single retinal ganglion cell. Thus velocity may be regarded as the rate of change of image position of the retina, a step displacement being equivalent to an impulsive velocity drive. It is evident from previous experiments (Barnes & Asselman, 1991) that the effective stimulus in such conditions is the change of target position rather than the absolute position of the target image with respect to the fovea.

The major objective of experiment IV was to show that stimulation of the visual system with repeated step displacements of the target has a cumulative effect on the induced eye velocity similar to that demonstrated for target velocity pulses in experiment III. The response to a single isolated target step is of low velocity and very variable and for this reason it is very difficult to assess the cumulative effects directly in the same manner as for velocity pulses, that is by examining the pulsatile nature of the response for interpulse intervals above 500 ms. However, the indirect evidence from experiment IV suggests that the cumulative process must be very

similar. If it is assumed that the subject can initiate a pulse with a peak velocity of only 4 deg/s to a single step displacement of the target and the time constant of oculomotor decay is approximately 1 s, then after a period of say 100 ms, the pulse will have decayed by only 10%, i.e. to 3·6 deg/s. The launch of subsequent pulses with the same time interval would allow eye velocity to build up to a maximum of approximately 40 deg/s within a period of 1 s even though no instantaneous velocity information was presented to the subject within the exposure period. This maximum velocity would be reduced as the interpulse interval was increased. In addition to this direct summation process it is evident that the eye velocity generated in this manner can be stored in the same way as for target velocity pulses (Barnes & Asselman, 1991), since peak eye velocity builds up over the first three to four presentations (Fig. 12). If, as suggested earlier, the system actually stores an efference copy of the eye velocity drive signal, it is of no consequence whether the original stimulus was a step displacement or a velocity pulse.

The pursuit of intermittently illuminated stationary targets

The conditions that prevail during intermittent illuminations of a moving target are clearly similar to those in which the subject attempts to pursue a row of stationary targets which are intermittently illuminated in sequence (Heywood, 1973; Young, 1977; Behrens & Grusser, 1979). It has been suggested that these conditions represent an example of the ability to 'pursue what we perceive' (Young, 1977), but the more mechanistic argument outlined in the previous paragraph might provide an equally good explanation. An important aspect of the performance of the predictive mechanism that we demonstrated previously (Barnes & Asselman, 1991), is that in order for the process to continue to produce smooth eye movements there should be no gross conflict when the predictive eye velocity estimate is checked against the current visual input. It is probable that if the target is exposed for less than approximately 30 ms, no retinal velocity error will be registered, so that it should make no difference whether the target is in motion or not. Thus, although the step displacement of the target provides only a limited drive to the oculomotor system, it also provides little resistance to the induced eye movements once they have been initiated. The process of pursuing the stationary targets would clearly be assisted by allowing the subject initially to pursue a real target so as to charge up the predictive velocity store.

On the other hand, if the target is exposed for more than 30 ms the relative motion of the target image across the retina will excite the visual velocity feedback mechanisms to interact with the predictive velocity estimate. If the target is in motion the velocity error will tend to act synergistically with the response to the step displacement and thus increase eye velocity in the manner shown in experiment I. In contrast, if the target is stationary, the image motion will act in an antagonistic manner and thus slow the eye movement. We have previously shown that there is, in fact, a graded decrease in eye velocity as the duration of exposure of a stationary display is increased from 10 to 320 ms (Barnes *et al.* 1987); the smooth eye movement is not suddenly switched off when the phi phenomenon of apparent motion perception is lost as suggested by Young (1977) and, as we have shown here, some smooth eye movement is present even when the motion is clearly discontinuous at pulse intervals as high as 1 s or more.

The same general argument may also be used to explain the smooth pursuit of after-images. Most subjects are able to initiate low-velocity (4–6 deg/s) smooth movements voluntarily but the response cannot be sustained in the absence of visual feedback, presumably because the predictive estimate of eye velocity is not confirmed by appropriate visual feedback. However, if the image is stabilized on the retina, there is never any retinal velocity error and the eye velocity estimate will be reinforced, allowing smooth eye movement to continue at any velocity (Heywood & Churcher, 1971; Kommerell & Taumer, 1972). It is possible that the transient persistence of the visual image, the duration of which is determined by the temporal characteristics of the visual system (Kelly, 1961), may play some part in the response to intermittent target illumination. Even the briefest stroboscopic illumination of the target forms a transiently stabilized retinal image, which may last for as long as 200–300 ms and could thus aid the process of sustaining the predictive response.

In conclusion, the evidence from our experiments indicates that the control of slow-phase eye velocity during ocular pursuit appears to be highly dependent on the nature of the retinal error information available to the subject, whether in the form of instantaneous velocity error or as changes in image position. This evidence is quite contrary to the view expressed by some authors (Steinbach, 1969; Young, 1977), that smooth pursuit is not dependent on the 'scraps of sensory information' available to the subject.

REFERENCES

BARNES, G. R. (1982). A procedure for the analysis of nystagmus and other eye movements. *Aviation Space and Environmental Medicine* **53**, 676–682.

BARNES, G. R. (1988). Head–eye co-ordination: visual and nonvisual mechanisms of vestibulo-ocular reflex slow-phase modification *Progress in Brain Research* **76**, 319–328.

BARNES, G. R. & ASSELMAN, P. T. (1991). The mechanism of prediction in human smooth pursuit eye movements. *Journal of Physiology* **439**, 439–461.

BARNES, G. R. & CROMBIE, J. W. (1985). The interaction of conflicting retinal motion stimuli in oculomotor control. *Experimental Brain Research* **59**, 548–558.

BARNES, G. R., DONNELLY, S. F. & EASON, E. D. (1987). Predictive velocity estimation in the pursuit reflex response to pseudo-random and step displacement stimuli in man. *Journal of Physiology* **389**, 111–136.

BARNES, G. R. & EDGE, A. (1983). The effect of strobe rate of head-fixed visual targets on suppression of vestibular nystagmus. *Experimental Brain Research* **50**, 228–236.

BARNES, G. R. & HILL, T. (1984). The influence of display characteristics on active pursuit and passively induced eye movements. *Experimental Brain Research* **56**, 438–447.

BARNES, G. R. & RUDDOCK, C. J. S. (1989). Factors affecting the predictability of pseudo-random motion stimuli in the pursuit reflex of man. *Journal of Physiology* **408**, 137–165.

BECKER, W. & FUCHS, A. F. (1985). Prediction in the oculomotor system: smooth pursuit during transient disappearance of a visual target. *Experimental Brain Research* **57**, 562–575.

BEHRENS, F. & GRUSSER, O. J. (1979). Smooth pursuit eye movements and optokinetic nystagmus elicited by intermittently illuminated stationary patterns. *Experimental Brain Research* **37**, 317–336.

CARL, J. R. & GELLMAN, R. S. (1987). Human smooth pursuit: stimulus-dependent responses. *Journal of Neurophysiology* **57**, 1446–1463.

DE BIE, J. & VAN DEN BRINK, G. (1984). Small stimulus movements are necessary for the study of fixational eye movements. In *Theoretical and Applied Aspects of Eye Movement Research*, ed. GALE, A. G. & JOHNSON, F., pp. 63–70. Elsevier, North-Holland, Amsterdam.

ECKMILLER, R. & MACKEBEN, M. (1978). Pursuit eye movements and their neural control in the monkey. *Pflügers Archiv* **377**, 15–23.

GRUSSER, O. J. & GRUSSER-CORNEHLS, U. (1973). Neuronal mechanisms of visual motion

perception and some psychophysical and behavioural correlations. In *Handbook of Sensory Physiology: Central Visual Information (A)*, ed. JUNG, R., pp. 333–429. Springer, Heidelberg.

HEYWOOD, S. (1973). Pursuing stationary dots: smooth eye movements and apparent movements. *Perception* **2**, 181–195.

HEYWOOD, S. & CHURCHER, J. (1971). Eye movements and the afterimage. 1. Tracking the afterimage. *Vision Research* **11**, 1163–1168.

KELLY, D. H. (1961). Visual responses to the time-dependent stimuli. I. Amplitude sensitivity measurements. *Journal of the Optical Society of America* **51**, 422–429.

KOMMERELL, G. & TAUMER, R. (1972). Investigations of the eye tracking system through stabilized retinal images. In *Cerebral Control of Eye Movements and Motion Perception*, ed. DICHGANS, J. & BIZZI, E., pp. 288–297. Karger, Basel.

KOWLER, E. & STEINMAN, R. M. (1979). The effect of expectations on slow oculomotor control. I. Periodic target steps. *Vision Research* **19**, 619–632.

MITRANI, L. & DIMITROV, G. (1978). Pursuit eye movements of a disappearing moving target. *Vision Research* **18**, 537–539.

MORGAN, M. J. & TURNBULL, D. F. (1978). Smooth eye tracking and the perception of motion in the absence of real movement. *Vision Research* **18**, 1053–1059.

POLA, J. & WYATT, H. J. (1980). Target position and velocity: the stimuli for smooth pursuit eye movements. *Vision Research* **20**, 523–534.

RASHBASS, C. (1961). The relationship between saccadic and smooth tracking eye movements. *Journal of Physiology* **159**, 326–338.

ROBINSON, D. A., GORDON, J. L. & GORDON, S. E. (1986). A model of the smooth pursuit eye movement system. *Biological Cybernetics* **55**, 43–57.

STEINBACH, M. J. (1969). Eye tracking of self-moved targets; the role of efference. *Journal of Experimental Psychology* **82**, 366–376.

VON NOORDEN, G. K. & MACKENSEN, G. (1962). Pursuit movements of normal and amblyopic eyes. *American Journal of Ophthalmology* **53**, 325–336.

WHITTAKER, S. G. & EAHOLTZ, G. (1982). Learning patterns of eye motion for foveal pursuit. *Investigative Ophthalmology and Visual Science* **23**, 393–397.

YOUNG, L. R. (1977). Pursuit eye movement – what is being pursued? In *Control of Gaze by Brainstem Neurons*, ed. BAKER, R. & BERTHOZ, A., pp. 29–36. Elsevier, North-Holland, Amsterdam.