

## PREDICTIVE VELOCITY ESTIMATION IN THE PURSUIT REFLEX RESPONSE TO PSEUDO-RANDOM AND STEP DISPLACEMENT STIMULI IN MAN

BY G. R. BARNES, S. F. DONNELLY AND R. D. EASON

*From the Royal Air Force Institute of Aviation Medicine, Farnborough,  
Hants GU14 6SZ*

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### SUMMARY

1. Eye movements have been recorded in man in response to various forms of continuous and discontinuous target motions in the horizontal plane in an attempt to establish the mechanisms of prediction in the pursuit reflex.

2. In an initial experiment the target motion was composed of four sinusoids, each of peak velocity  $\pm 3.3$  deg/s. The three lowest frequencies (0.11, 0.24 and 0.37 Hz) remained constant whereas the highest frequency ( $F_4$ ) was varied from 0.39 to 2.08 Hz. When  $F_4$  was 0.39 Hz, all frequency components had a high level of eye velocity gain (mean 0.92) but as  $F_4$  was increased there was a significant ( $P < 0.001$ ) decline in gain for all three low frequencies which reached a minimum (mean 0.53) when  $F_4$  was 1.56 Hz. However, the gain for  $F_4$  always remained at a high level, comparable to that evoked by a discrete frequency sinusoid of the same frequency.

3. When the highest-frequency sinusoid was replaced by a square wave of identical amplitude a similar decline in gain for the low frequencies was observed. Eye velocity exhibited a quasi-sinusoidal modulation at the frequency of the square wave even though the rapid steps did not constitute a suitable stimulus to the visual velocity feed-back mechanisms.

4. When only two sinusoids were mixed to form the pursuit stimulus a similar break-down in gain of the lower-frequency component was observed which reached a minimum (mean gain 0.58) when  $F_2$  was between 1 and 2 Hz. This implies that the predictability of stimulus motion is dependent, not on the complexity of the stimulus, but on its highest-frequency component.

5. Presentation of square-wave target displacements alone confirmed that smooth eye movements could be evoked by such a stimulus. Eye velocity was at a maximum between 1.0 and 1.5 Hz and was predictive of ensuing target displacement. Responses to staircase step sequences of varying duration indicated that prediction was based on an assessment of the duration of the preceding sequence.

6. Tachistoscopic presentation of targets during low-frequency sinusoidal oscillation indicated that illumination of the target for very short periods (10–320 ms) as few as two times per cycle during minimum velocity phases enhanced the perception of continuous movement. A predictive eye movement was evoked with a high level of peak velocity which then decayed until the subsequent exposure of the target.

7. The findings indicate the presence of a predictive velocity estimation mechanism which is probably used to enhance retinal velocity error feed-back in normal pursuit. At low frequency ( $< 0.4$  Hz) it operates on a continuous basis using estimates of velocity from prior stimulation. When a high frequency ( $> 0.8$  Hz) component is present, an estimate of its periodicity is also derived and selectively enhances the eye velocity gain for that frequency.

#### INTRODUCTION

When the human subject is required to pursue a visual target with the eyes alone, the nature of the response evoked is dependent on the type of stimulus used. If the target moves with a constant unidirectional velocity (Westheimer, 1954; Rashbass, 1961; Robinson, 1965; Schalen, 1980), or with a regular periodic wave form (Fender & Nye, 1961; Dallos & Jones, 1963; Winterson & Steinman, 1978; Wyatt & Pola, 1983; Barnes & Hill, 1984), eye displacement matches target displacement very closely, although break-down is observed if the frequency of target oscillation exceeds 1 Hz. In contrast, when the target moves in a more unpredictable manner pursuit reflex performance becomes considerably impaired. A comparison of responses to sinusoidal and random stimuli was made by Stark, Vossius & Young (1962) and by Dallos & Jones (1963), who showed that the ratio of eye displacement to target displacement (i.e. eye displacement gain) was considerably less than unity for a Gaussian noise stimulus at all frequencies above 0.3 Hz. Equally important was the observation that the associated phase relationships exhibited considerably greater phase lag than for the sinusoidal responses at all frequencies above 0.2 Hz. It was this latter finding, in particular, together with the observation that there are considerable time delays (125 ms) within the visual feed-back pathways (Robinson, 1965), that led to the realization that some form of predictive mechanism must function during pursuit of sinusoidally oscillating targets. Although these clear distinctions between the oculomotor responses to sinusoidal and random stimuli had been noted it became apparent from the work of Michael & Jones (1966) and St-Cyr & Fender (1969) that the responses to random stimuli could be heavily modified by the band width and centre frequency of the stimulus and that the values of gain and phase lay on a continuum between those of the sinusoidal response and of the response to a stimulus having a full Gaussian noise spectrum.

Although eye displacement gain may be close to unity at frequencies up to 1 Hz, eye velocity rarely matches precisely the velocity of the target. As a consequence the smooth following components are interspersed with corrective saccadic components which realign the target image with respect to the fovea. In considering the measures of eye displacement discussed above the authors analysed the response of both components together, even though the two components are essentially independent. It is only in more recent experiments (Bahill, Iandolo & Troost, 1980; Collewijn & Tamminga, 1984; Yasui & Young, 1984; Barnes, Crombie & Edge, 1985) that the saccadic eye movements have been removed in order to examine the ratio of slow-phase eye velocity to target velocity (eye velocity gain). The rationale for analysing the eye movements in this way is that the velocity error between the eye and the target is one of the most important components of the visual feed-back pathways which minimize retinal image slip (Rashbass, 1961).

In the experiments described here we have examined both the displacement and velocity characteristics of the oculomotor response to a pseudo-random stimulus in an attempt to determine those features of the stimulus which render it unpredictable. It has been known since the work of Stark *et al.* (1962) that an effective pseudo-random stimulus can be generated by mixing together a number of harmonically unrelated sinusoidal wave forms. By making a systematic investigation of the effects of changing the highest-frequency component of such a four-frequency combination, we have been able to show that the break-down in pursuit is associated not with the band width of the stimulus, but with the frequency of the highest-frequency component. Moreover we have also been able to show that the same break-down in the pursuit response may be observed with a much less complex wave form composed of only two sinusoids, provided that the frequency of the higher-frequency component lies in a critical range above 0.8 Hz. The mechanism of these changes in eye velocity during pursuit appeared to be one in which the eye velocity of the highest-frequency component was enhanced at the expense of the low-frequency components. In the remaining experiments described here we have therefore sought to find the mechanism by which this enhancement takes place.

Although the early experiments of Rashbass (1961) appeared to indicate that retinal velocity error formed the most important feed-back element for the control of the pursuit response, there is evidence that other mechanisms may play an important role. In essence, three different types of process have been postulated on the basis of experimental observations. First, there is the capacity to memorize salient characteristics of the target movement in terms of its velocity and/or frequency and thereby reproduce the response in the absence of the original stimulus (von Noorden & Mackenson, 1962; Mitrani & Dimitrov, 1978; Eckmiller & Mackeben, 1978; Becker & Fuchs, 1985). Such eye movements may continue for a prolonged period if the target does not reappear (Muratore & Zee, 1979; Whittaker & Eaholtz, 1982). The second mechanism is one in which the continuous feed-back of retinal position error serves continually to realign the image of the moving target on the fovea. Such a mechanism is probably responsible for the low-velocity drifting movements of the eye which realign the image on the fovea (St-Cyr & Fender, 1969; de Bie & Van den Brink, 1984). Pola & Wyatt (1980) were able to show that, in open-loop mode, a square-wave displacement of a target about foveal centre could evoke a continuous oscillatory smooth movement of the eye which they interpreted as evidence of positional feed-back. However, examination of the phase relationships of the response indicates that this is more likely to be a manifestation of the third type of mechanism, which may be referred to as a central predictive mechanism based on expected target displacement. An example of such a response was first provided by Westheimer & Conover (1954) who showed that subjects could make smooth oscillatory eye movements between two stationary targets in the complete absence of a moving target. Subsequently Kowler & Steinman (1979*a, b*) showed that smooth eye movements could be made prior to the onset of a step target displacement, a stimulus which would normally be thought of as evoking only a saccadic eye movement.

In order to assess whether this central predictive mechanism could be responsible for the effects observed with pseudo-random stimuli a number of additional experiments have been carried out. In the first of these, the high-frequency sinusoidal component of the four-frequency stimulus was replaced by a square wave of equiv-

alent amplitude. It was found that such a periodic stimulus containing only target displacement information and thus not stimulating the visual velocity feed-back mechanisms could nevertheless induce a predictive response of the type described by Pola & Wyatt (1980) with a consequent break-down in the response of the low-frequency components. Further experiments have also been carried out in which the smooth eye movement responses to various forms of target step displacement have been examined and compared with responses observed in the absence of any visual stimulus. The results provide firm evidence of a predictive mechanism that is able to provide an estimate of target velocity and periodicity based on prior information about target displacement.

#### METHODS

The subject was seated with head clamped at the centre of a semicircular screen of radius 2 m. A small motor-driven mirror mounted above the subject's head was used to control the movement of a projected target across the screen in the horizontal plane. The target was a small white cross, the height of which subtended a visual angle of 14 min arc with a luminance of 10 cd/m<sup>2</sup>. No other visual cues were available to the subject who viewed the target binocularly in otherwise darkened surroundings. Eye movements were recorded by an infra-red limbus reflection technique with a resolution of 5–10 min arc. The infra-red emitters and sensors were rigidly mounted on the head using a helmet and dental bite assembly (Barnes, 1983). Six experimental conditions were assessed. In each, the subjects were instructed to follow the movement of the target to the best of their ability. Each recording session was kept deliberately brief (< 15 min) so that subjects were suitably aroused throughout each session. All stimulus conditions were presented to subjects in balanced, randomized designs, calibration of eye movements being carried out prior to each individual stimulus. Subjects were taken from a pool of nine male volunteers, all of whom were easily able to see the target when stationary without refractive correction.

(1) In the initial experiment (I) the target motion was composed of the sum of four sinusoidal wave forms ( $F_1$ – $F_4$ ), each with a peak velocity of 3.37 deg/s. The frequencies were all harmonically unrelated. The three lowest frequencies ( $F_1$ ,  $F_2$ ,  $F_3$ ) remained constant at 0.112, 0.240 and 0.368 Hz, but the highest frequency ( $F_4$ ) was varied, having values of 0.391, 0.781, 1.563 and 2.083 Hz in four separate stimulus presentations. As a control condition all subjects were asked to track the target when it moved sinusoidally (peak velocity  $\pm 6.7$  deg/s) at eight discrete frequencies, seven of which were identical to those used for the mixed-frequency stimuli. In a second part of the experiment the highest-frequency sinusoidal component was replaced by a square-wave displacement having a peak equivalent to that of the original sine wave. The amplitude thus decreased with increasing frequency, having values of  $\pm 1.37$ ,  $\pm 0.69$ ,  $\pm 0.34$  and  $\pm 0.26$  deg at 0.391, 0.781, 1.563 and 2.083 Hz respectively. Eight subjects took part in this experiment.

(2) In experiment II the stimulus was formed from a mixture of only two harmonically unrelated sinusoids each with a peak velocity of  $\pm 6.7$  deg/s. In order to assess the effect of the ratio of the two frequency components four separate values of the lower frequency ( $F_1$ ) were mixed with each of the four values of the higher frequency ( $F_2$ ) as follows:  $F_1 = 0.11, 0.22, 0.33$  and  $0.44$  Hz for  $F_2 = 0.415$  Hz and  $F_2 = 0.83$  Hz;  $F_1 = 0.22, 0.44, 0.66$  and  $0.88$  Hz for  $F_2 = 1.67$  Hz and  $F_2 = 3.33$  Hz. In addition, in order to investigate the effects of the velocity of the higher-frequency component (h.f.) its velocity was set at four ratios ( $V = 0, 0.25, 0.5$  and  $1.0$ ) of the velocity of the low-frequency component (l.f.). Four subjects took part in this experiment.

(3) In experiment III a similar mixture of two sinusoids of equal peak velocity ( $\pm 6.7$  deg/s) was used, but the lower frequency was maintained constant at either 0.22 or 0.44 Hz, whilst the higher frequency was varied over a range from 0.391 to 4.12 Hz in eight steps. In a second part of the experiment the higher-frequency sinusoidal component was replaced by a square wave of equivalent peak displacement. Four subjects took part in this experiment.

(4) In experiment IV the target movement consisted of periodic wave-forms containing regular step displacements. In the first part (IVa) the target was made to move with a square-wave displacement for which the frequency was varied from 0.5 to 1.67 Hz and target displacement was

varied from  $\pm 0.3$  to  $\pm 2.4$  deg. In the second part (IVb) a periodic step displacement stimulus was superimposed on a triangular wave form (frequency 0.19 Hz; peak velocity  $\pm 4.5$  deg/s) to form the target motion (Fig. 7). The step displacement stimulus was formed of eight steps in each direction (interstep interval 320 ms) with a magnitude and polarity which could be used to either increase or decrease the over-all target displacement by a 'displacement factor' (see legend to Fig. 7). The response was examined for wave forms having a displacement factor between 2 and  $-1$ . The response to a step wave form without the ramp components was also examined. Eight subjects took part in this experiment. In addition four subjects were presented with the step wave form alone but the target was tachistoscopically illuminated for periods of 10–320 ms by the operation of a shutter mechanism at the mid-point of the stationary phase. Step size was increased to 3.2 deg, giving an average rate of change of displacement of 10 deg/s.

(5) In experiment V we examined the response to staircase steps which varied in either step size or periodicity. In the first condition (experiment Va) each sequence of unidirectional steps (displacement 1.2 deg) was followed by a similar sequence in the opposite direction. The number of steps in consecutive sequences was varied at random (five, seven, nine or eleven steps). In the second condition (experiment Vb) the number of steps in consecutive sequences remained constant (eight steps), but the step size was varied at random across four levels (0.3, 0.6, 0.9 and 1.2 deg). Both of these types of staircase sequence were examined for step intervals of 160, 240, 320 and 400 ms. Eight subjects took part in this experiment.

(6) In the final experiment (VI) we investigated the extent to which subjects could make smooth eye movements in complete darkness or with a minimal visual stimulus. Four subjects who found it particularly difficult to evoke a continuous smooth eye movement with a velocity of greater than 2 deg/s in darkness were presented with a low-frequency (0.1–0.4 Hz) sinusoidal target movement in which the target was tachistoscopically presented two, four or eight times during each cycle. The period of exposure was varied from 10 to 320 ms as indicated in the Results section.

#### *Experimental control and data analysis*

The experiment was controlled and analysed by computer (Hewlett-Packard 9816S). The required wave forms were software generated and output to the mirror drive was via a digital-analogue converter with internal buffer memory. The response of the mirror driver and the evoked oculomotor signals from the limbus tracker were simultaneously sampled by an analogue-digital conversion system at a clock frequency (200 Hz) which was directly related to that of the output signal (400 Hz). This allowed analysis of the recorded wave forms to be simplified since the response could be directly correlated with the internally generated wave form at the predetermined frequency components. The oculomotor response was assessed in two ways; first, by correlation of the over-all eye displacement (including any saccadic components) with target displacement to obtain eye displacement gain ( $G_D$ ) and phase ( $\phi_D$ ); and secondly, by correlation of the slow-phase eye velocity with target velocity using an interactive computer graphics procedure (Barnes, 1982) to extract the saccadic components and thus obtain the eye velocity gain ( $G_V$ ) and phase ( $\phi_V$ ). The correlation was carried out using a least-squares error curve-fitting procedure. The responses to the target step displacement stimuli were analysed using the same basic technique to remove the fast-phase components of the response. Other details of the analysis for specific conditions are given in the Results section.

## RESULTS

### *Responses to mixed-frequency stimuli: general observations*

When subjects were presented with a target movement composed of four sinusoidal components with all frequencies below 0.39 Hz, there was no apparent difficulty in following the target, even though its movement was unpredictable. This subjective assessment was supported by the observation that the evoked eye movements were smooth with relatively few catch-up saccades. In contrast, when the highest frequency of the quartet of frequencies was increased through 0.78 to 1.56 Hz it became increasingly difficult to follow the target movement, an effect which was reflected in

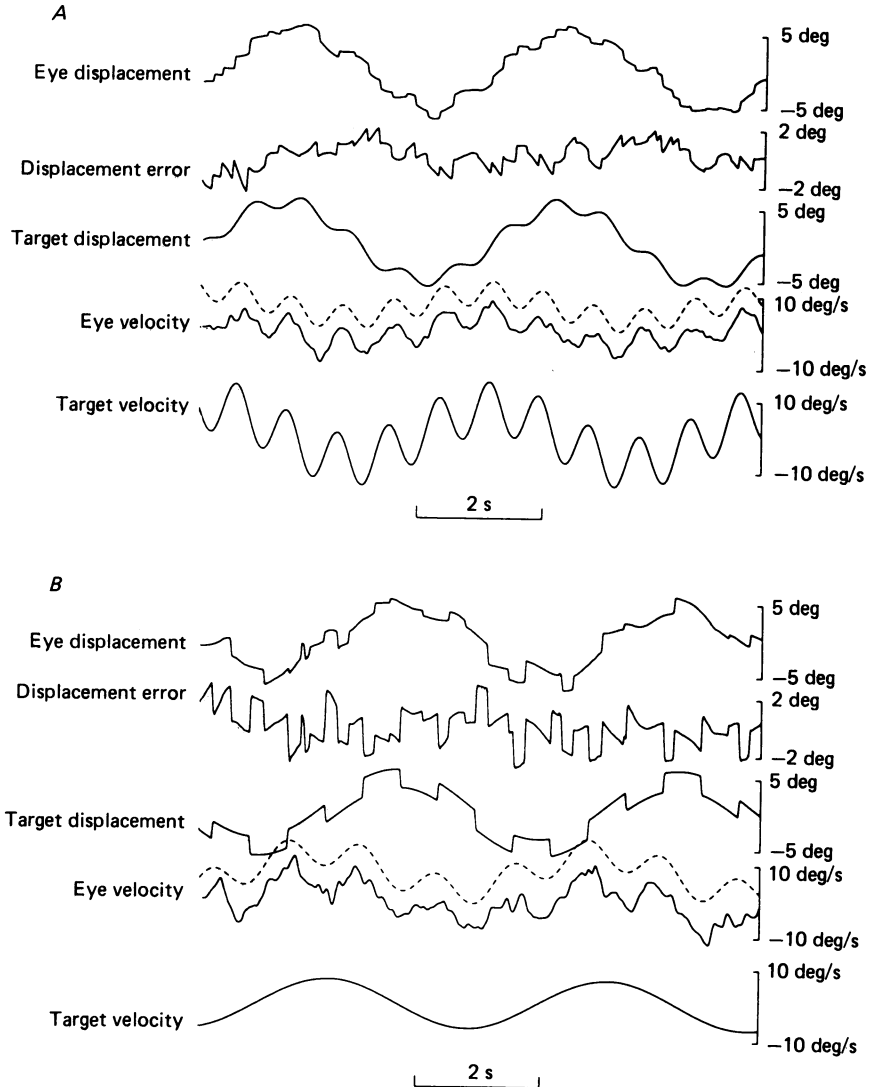


Fig. 1. The oculomotor response during pursuit of target displacements composed of two sinusoidal components at frequencies of  $F_1 = 0.22$  and  $F_2 = 1.25$  Hz (A) and one sinusoidal and one square-wave component at frequencies of  $F_1 = 0.22$  and  $F_2 = 0.83$  Hz (B). Interrupted line indicates best fit combination of two sinusoids of appropriate frequency through slow-phase eye velocity trace.

the reduced ability of the eye to match the velocity of the target movement with a consequent increase in the number of saccadic eye movements.

Exactly similar effects were observed when only two sinusoidal frequencies were mixed together. Subjects could follow smoothly a combination in which both frequencies were below 0.4 Hz, but when the higher frequency was increased pursuit was more difficult and eye movements tended to become broken with increased residual displacement error (Fig. 1A). When the high frequency increased beyond

3 Hz tracking became somewhat easier because the single target appeared as a stable dipole as a result of the temporal decay characteristics of the visual system.

When the high-frequency sine wave was replaced by a square wave of the same peak amplitude, pursuit was again very difficult and eye movements were broken even when the square wave was at its lowest frequency (0.39 Hz). This finding applied to mixtures of two or four frequency components. Examination of the eye velocity recordings after removal of the saccadic components (Fig. 1*B*) revealed that the velocity of the eye in response to such a stimulus exhibited a clear quasi-sinusoidal modulation at the frequency of the square-wave component (Fig. 1*B*). This feature of the oculomotor response was associated with an important subjective aspect of the response; namely, that the high-frequency component, whether it were a sine or square wave, was the most dominant component of such mixed-frequency combinations.

*Responses to a combination of four sinusoidal components (experiment 1a)*

*Eye displacement gain and phase.* For the two lowest-frequency combinations of sinusoids, that is when the highest frequency ( $F_4$ ) was either 0.39 or 0.78 Hz, the overall eye displacement, including the fast-phase components, closely matched the target displacement, with mean gains for the four frequencies between 0.95 and 1.05. However, as  $F_4$  was increased there was a considerable increase in mean gain at the highest frequency which reached a level of 1.47 at 1.56 Hz and 1.34 at 2.08 Hz, although the gain of the lower-frequency components (0.11 and 0.24 Hz) remained close to unity. The subject thus appeared to over-estimate the amplitude of over-all eye displacement for the highest-frequency component when  $F_4$  was above 0.78 Hz. This was in contrast to the response to individual discrete sinusoidal target movements, for which eye displacement was consistently less than unity at frequencies above 0.39 Hz (e.g.  $G_D = 0.76$  at 1.56 Hz;  $G_D = 0.61$  at 2.08 Hz).

*Eye velocity gain.* Whereas the composite eye displacement gain remained close to unity for the three low frequencies of each combination of four frequencies, the gain of slow-phase eye velocity showed significant changes as  $F_4$  was increased. When  $F_4$  was 0.39 Hz there was no significant difference between the eye velocity gains for the other three lower-frequency components of the stimulus (Fig. 2) and the mean level was high (0.90), despite the fact that the stimulus displacement was pseudo-random in nature. In fact, the eye velocity gain at each frequency was not significantly different from that obtained from the response to the individual sinusoidal components (Fig. 2*A*). As  $F_4$  was increased to 0.78 and 1.56 Hz the eye velocity gain for the low frequencies progressively decreased in a highly significant manner ( $P < 0.001$  by analysis of variance), and although the gain at 0.37 Hz tended to be lower than at 0.11 and 0.24 Hz there was still no significant difference between the gains at these three frequencies. In contrast, the gain of the highest-frequency component remained high. When  $F_4$  was 0.78 Hz there was no significant difference in gain at this frequency compared with the response to a discrete sinusoidal stimulus (Fig. 2*A*) even though the mean gain for the low frequencies ( $F_1$ ,  $F_2$  and  $F_3$ ) was reduced from 0.92 to 0.67. When  $F_4$  was 1.56 Hz there was a small but non-significant decrease in the gain of  $F_4$  compared with the single sinusoid of identical frequency but the mean gain of the three low frequencies was further reduced to 0.56. There was a larger and

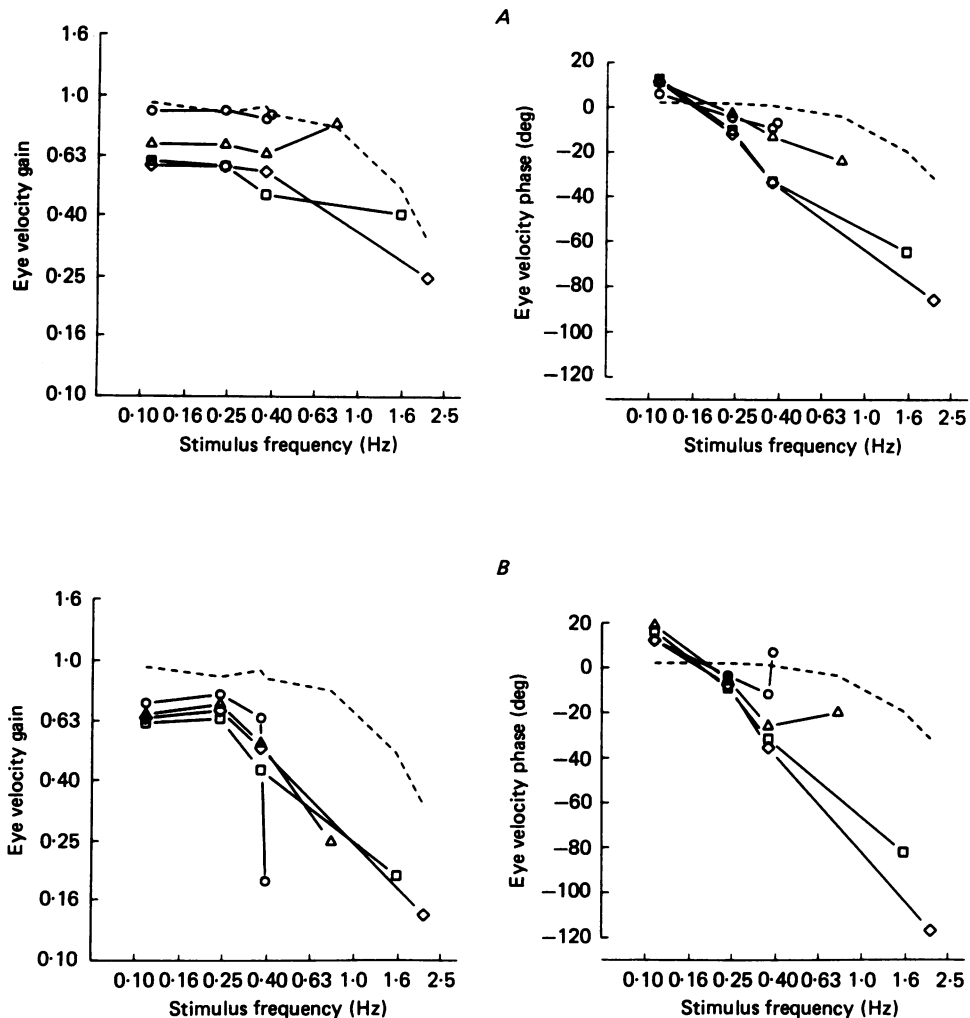


Fig. 2. Eye velocity gain and phase during pursuit of mixed-frequency pseudo-random target motion (experiment I). In *A* the stimulus consisted of four sinusoids, each with peak velocity of  $\pm 3.37$  deg/s. The three lowest frequencies remained constant (0.112, 0.240 and 0.368 Hz), whilst the highest frequency was varied having values of 0.391 ( $\circ$ ), 0.781 ( $\triangle$ ), 1.563 ( $\square$ ) and 2.083 ( $\diamond$ ) Hz. In *B* the highest-frequency sine wave was replaced by a square-wave displacement of equivalent peak amplitude. Interrupted line indicates gain and phase of responses to discrete frequency sinusoidal stimuli. Mean of eight subjects.

significant difference ( $P < 0.05$ ) between the gain of the single sinusoidal response and that of the highest frequency when  $F_4$  was 2.08 Hz but there was no further decrease in low-frequency gain.

*Eye velocity phase.* Although the gains of the low-frequency components ( $F_1$ ,  $F_2$  and  $F_3$ ) were not significantly different from each other at any given value of  $F_4$  the phase exhibited important modifications. Even when  $F_4$  was only 0.39 Hz there was a significant difference in phase from the individual sinusoidal responses (Fig. 2*A*),



with an increase in phase lead at 0.11 Hz but an increase in phase lag at all other frequencies. The phase thus appeared to rotate in a clockwise manner about a frequency in the region of 0.15 Hz and as  $F_4$  was increased this trend continued, although there was no significant change between  $F_4 = 1.56$  Hz and  $F_4 = 2.08$  Hz. The phase of the high-frequency component ( $F_4$ ) exhibited a highly significant increase ( $P < 0.001$  by analysis of variance) in phase lag compared with the individual sinusoidal responses despite the relatively small differences in gain (Fig. 2A).

*Responses to the combination of three sinusoids and one square-wave component (experiment Ib)*

*Eye velocity gain.* The replacement of the highest-frequency sinusoidal component by a square wave resulted in a quasi-sinusoidal modulation of eye velocity, the fundamental component of which was measured by comparison with a sinusoidal component having the same displacement amplitude as the square wave. The gain of  $F_4$  was always low and considerably less than the corresponding gain for the single sinusoidal stimulus (Fig. 2B). The peak level of gain (0.25) was observed at 0.78 Hz. The effect of the square-wave component was to reduce the gain of the three low-frequency components in the same manner as the high-frequency sinusoidal components (Fig. 2B). However, the reduction in gain was present not only for the higher values of  $F_4$  but even when  $F_4$  was only 0.39 Hz. In fact, the gain of the three low frequencies was always significantly less ( $P < 0.001$  by analysis of variance) than that of the responses to corresponding pure sinusoids. There was a small but significant ( $P < 0.05$ ) decrease in gain of the three low-frequency sinusoidal components with increase of  $F_4$  from 0.39 to 1.56 Hz and the gain at 0.37 Hz was significantly less ( $P < 0.05$ ) than that at 0.11 and 0.24 Hz. Analysis of variance of the eye velocity gains for the three lowest frequencies indicated that there was no significant difference between those obtained when  $F_4$  was either a square wave or a sine wave of frequency 1.56 Hz.

*Eye velocity phase.* The phase for the three low-frequency sinusoidal components exhibited a clockwise rotation with respect to the single sinusoidal responses (Fig. 2B) similar to that observed for the combination of four sinusoids. The phase angles for the three highest values of  $F_4$  were not significantly different from each other, nor were they significantly different from the corresponding values for the two highest-frequency values of  $F_4$  as a sinusoid. The phase of the square-wave component showed similar characteristics to those of the high-frequency component for the four sine waves but with a mean phase advance of 6.7 deg at 0.39 Hz (Fig. 2B).

*Responses to combinations of two sinusoids; effect of the velocity of the high-frequency component (experiment II)*

When only two sinusoids were combined to form the target movement the oculomotor response for both the higher (h.f.)- and lower (l.f.)-frequency components was found to be dependent not only on the frequency of h.f. but also on the velocity ratio ( $V$ ) between h.f. and l.f. The main findings may be summarized as follows.

(a) When both frequencies were below 0.42 Hz there was no significant change in any of the measures of eye displacement or eye velocity for either frequency as the velocity of h.f. was increased. In particular, eye velocity gain for l.f. did not decrease significantly with increase of the velocity of h.f. (Fig. 3A).

(b) When  $F_2$  was equal to or greater than 0.83 Hz there were progressive changes in eye displacement and eye velocity as the velocity of h.f. was increased and these changes were similar to those observed in the responses to a combination of four sinusoids. For example, eye displacement gain ( $G_D$ ) for the low frequency ( $F_1$ ) remained close to unity whereas that for  $F_2$  was frequently greater than one, but decreased significantly with the velocity of  $F_2$ . Thus when  $F_2$  was 1.67 Hz the mean value of  $G_D$  for h.f. had values of 1.63, 1.22 and 0.92 for  $V = 0.25, 0.5$  and 1.0 respectively. Most importantly, eye velocity gain for l.f. exhibited a significant ( $P < 0.001$ ) decrease with increasing velocity of h.f. (Fig. 3A), reaching a minimum value of 0.62 when  $F_2$  was 1.67 Hz and  $V$  was equal to 1.0. This decrease in eye velocity gain was comparable to that observed for the four-frequency combination. Eye velocity gain for h.f., which exhibited some modification with the frequency of l.f., was also significantly reduced by an increase in its own velocity at values of  $F_2$  above 1.67 Hz (Fig. 3B). This latter finding is compatible with previous observations concerning the effects of the velocity of the stimulus on the gain of the pursuit response (Lisberger, Evinger & Fuchs, 1981; Collewyn & Tamminga, 1984).

*Frequency characteristics of the interaction between two sine-wave stimuli (experiment IIIa)*

The results of experiment IIIa exhibited similar features of eye displacement and eye velocity to those for the combination of four sinusoidal components. The main findings may be summarized as follows.

(a) Eye velocity gain for l.f. exhibited a highly significant ( $P < 0.001$ ) change with the frequency of h.f. At the lowest frequency (0.39 Hz) the gain of l.f. was high (mean 0.86, Fig. 4) but decreased progressively as the frequency of h.f. increased, to reach a minimum of 0.57 at  $F_2 = 1.25$  Hz when  $F_1$  was 0.22 Hz and 0.54 at  $F_2 = 2.08$  Hz when  $F_1$  was 0.44 Hz. At higher frequencies gain showed a trend of returning to the levels observed for lower frequencies.

(b) Eye velocity phase for l.f. exhibited considerable variability amongst subjects but, as indicated in Fig. 4, there was a trend for the phase advance at low frequencies to change to phase lag at higher frequencies.

(c) Eye velocity gain and phase for h.f. showed, as in experiment I, a decrease of gain and an increase of phase lag with increasing frequency. The phase lag at the higher frequencies was considerably greater than that observed for the single sinusoidal responses at comparable frequencies (Fig. 3) but was comparable to that for the high-frequency components of the four sinusoidal stimuli.

*Responses to a combination of one sinusoid and one square-wave component (experiment IIIb)*

When a high-frequency square-wave component was combined with a low-frequency sinusoid there was no dramatic break-down in pursuit as there was when the square wave was added to the three low-frequency sinusoids in experiment I. Eye velocity gain for l.f. was not significantly modified by the frequency of h.f. and gain was only slightly depressed for  $F_1 = 0.22$  Hz (mean 0.80), although there was a greater reduction when  $F_1$  was 0.44 Hz (mean 0.73). However, the effect was obviously subject dependent. Two of the four subjects had a much greater reduction in gain

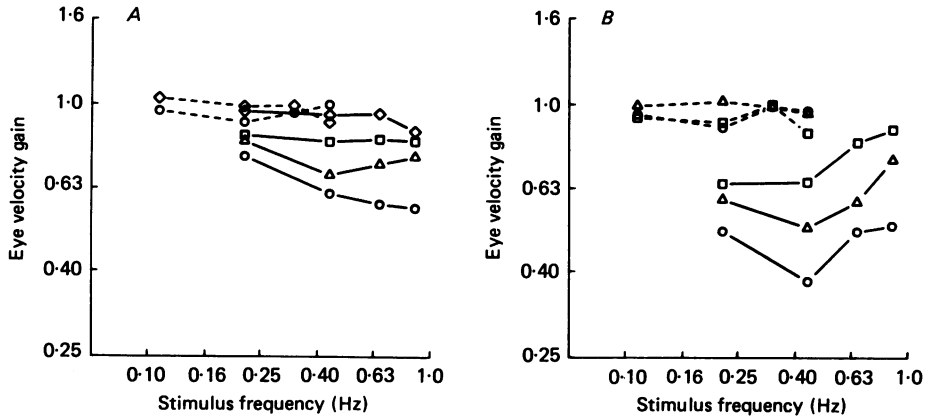


Fig. 3. Eye velocity gain during pursuit of a target motion composed of two sinusoids. Results shown are for two of the four values of the higher frequency ( $F_2$ ) tested in experiment II (0.42 Hz (interrupted lines) and 1.67 Hz (continuous lines)). Gains for the low-frequency component ( $F_1$ ) are shown in A, those for  $F_2$  in B. Both are plotted as a function of the frequency of  $F_1$ . The peak velocity of  $F_1$  was  $\pm 6.7$  deg/s, whereas that of  $F_2$  varied as a ratio ( $V$ ) of that for  $F_1$ . Mean of four subjects. Values of  $V$  shown by symbols:  $\circ$ , 1.0;  $\triangle$ , 0.5;  $\square$ , 0.25; and  $\diamond$ , 0.

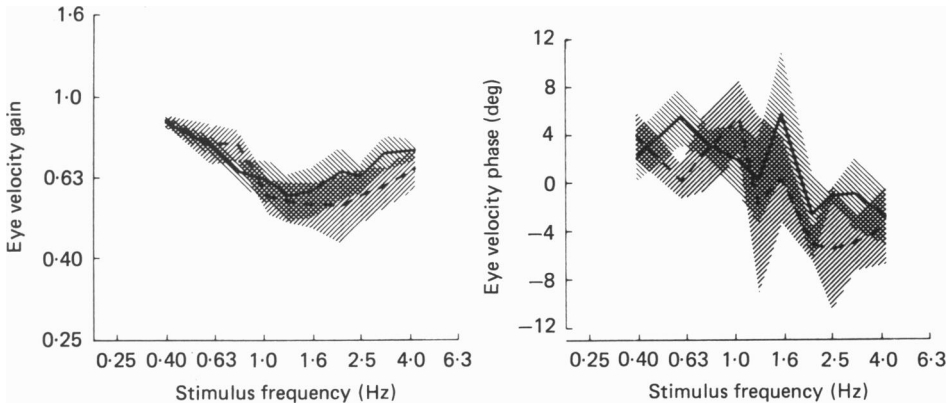


Fig. 4. Eye velocity gain and phase during pursuit of a target motion composed of two sinusoids (experiment III a). The results shown are for the lower-frequency component ( $F_1$ ) which had a frequency of 0.22 Hz (continuous line) or 0.44 Hz (interrupted line). Gain and phase are plotted as a function of the frequency of the higher-frequency component ( $F_2$ , which was varied in eight steps between 0.39 and 4.12 Hz. Mean of four subjects  $\pm 1$  s.e. of mean.

(means of 0.70 and 0.64 at 0.22 and 0.44 Hz respectively) whereas the remaining two showed little change in gain (means of 0.91 and 0.83 at 0.22 and 0.44 Hz). These differences could not be directly attributed to differences in the eye velocity response to the square-wave component, the gain and phase of which exhibited a trend with frequency (Fig. 5) similar to that for the combination of three sinusoids and one square wave (Fig. 2). Eye velocity gain for the square-wave component (Fig. 5)

reached a maximum of 0.2 between 0.78 and 1.04 Hz and there was no significant difference between the two levels of  $F_1$  (0.22 and 0.44 Hz). Perhaps the most important finding was that there was a consistent phase advance for h.f. in all but one subject at the two lowest frequencies (0.39 and 0.6 Hz), and a progressive increase in phase lag at higher frequencies (Fig. 5).

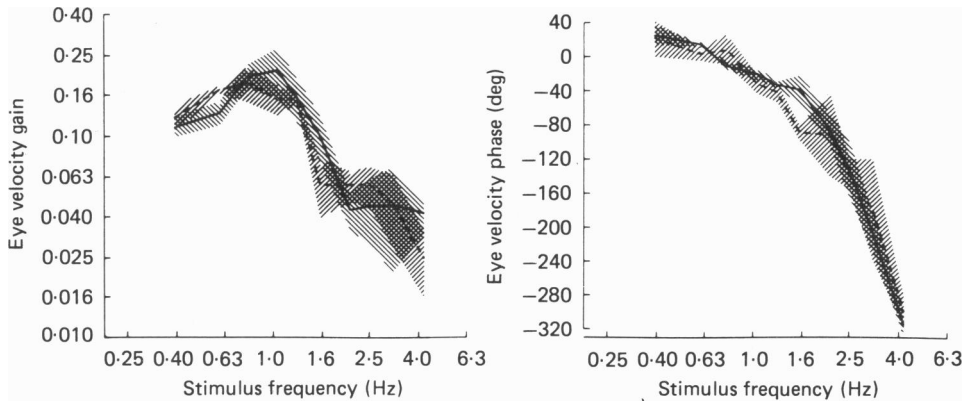


Fig. 5. Eye velocity gain and phase during pursuit of a target motion composed of one lower-frequency sine wave ( $F_1$ ) and one higher-frequency ( $F_2$ ) square wave (experiment III b). The results shown are for the square-wave component ( $F_2$ ), for which the frequency was varied from 0.39 to 4.12 Hz. The frequency of  $F_1$  was maintained at 0.22 Hz (continuous line) or 0.44 Hz (interrupted line). Mean of four subjects  $\pm 1$  s.e. of mean.

#### *Responses to target step displacements: general observations*

It was notable that all subjects tested could generate some smooth eye movement in response to the step displacement stimuli used in these experiments without any prior training, although there was considerable variation between subjects in the peak levels of velocity attained. Moreover, no specific instructions were required other than: 'Follow the target movement as well as possible'. The exception to this was the square-wave target movement for which it was necessary to instruct the subjects to imagine that they were making smooth eye movements between the two extreme displacements. This instruction often led to the type of response shown in Fig. 6, in which the subject initially responded with saccades only, but after only one or two cycles the eye velocity began to build up. In all stimulus conditions the interval between steps was sufficiently great ( $> 160$  ms) that there was little sense of a continuous target movement; it could always be perceived as discontinuous with periods of stationarity between steps. Moreover the steps were sufficiently rapid for there to be no perceived image blur during the step transitions.

#### *Responses to square-wave and multi-step periodic stimuli (experiment IV a)*

The oculomotor response to the square-wave target displacement at the lowest frequency tested (0.5 Hz, Fig. 6) was very similar to that reported previously by Kowler & Steinman (1979a, b). The most notable feature of the response was that the smooth eye movement was clearly anticipatory, being initiated well before the onset

of target displacement. At higher frequencies a modulated eye movement was induced with relatively few saccades so that over-all eye displacement was much smaller than target displacement. This type of quasi-sinusoidal eye velocity was very similar to that observed previously when the high-frequency square-wave stimulus was combined with the sinusoidal components (Fig. 1 *B*).

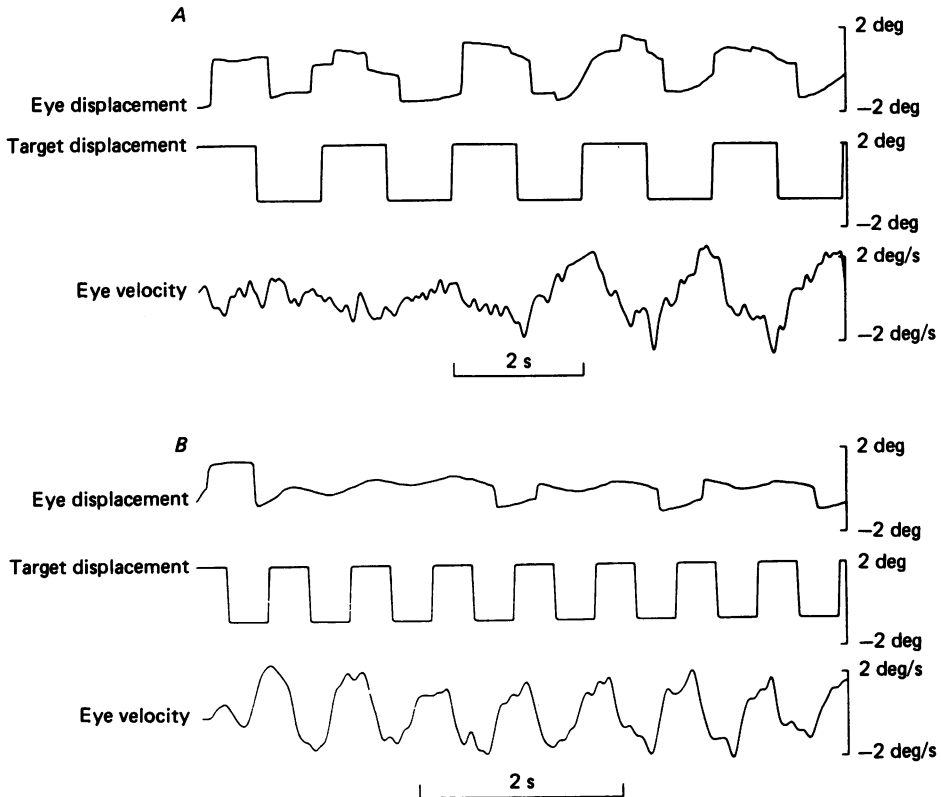


Fig. 6. Typical oculomotor responses to square-wave target displacements at two stimulus frequencies, 0.5 (*A*) and 1.25 (*B*) Hz (experiment IV *a*).

The responses were analysed by extracting the fast-phase components of eye velocity and then averaging eye velocity over at least five cycles of the square-wave stimulus. The results were very similar to those obtained when the square-wave stimulus was added to the sinusoidal components (Fig. 5) indicating that maximum eye velocity was attained around 1.25 Hz and phase advance was observed up to 0.83 Hz. Velocity tended to increase with increasing step size but there was very little increase in velocity for step sizes greater than  $\pm 0.6$  deg. Some subjects produced mean eye velocities as high as 3 or 4 deg/s in response to this stimulus.

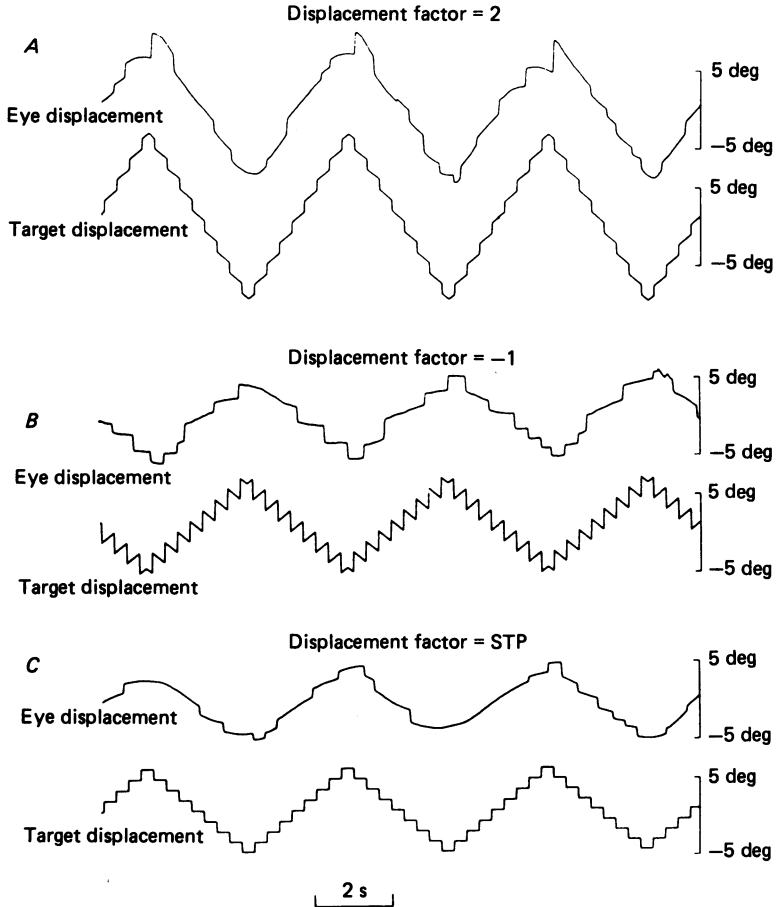


Fig. 7. *A* and *B*, the oculomotor response to a wave form composed of a basic triangular wave form (frequency 0.19 Hz; peak velocity  $\pm 4.5$  deg/s) overlaid with displacement steps of the type shown in *C*. The interstep interval was 320 ms. The 'displacement factor' represents the ratio between over-all peak target displacement and the displacement of the underlying triangular wave form (experiment IV *b*). STP represents stimulus composed of step displacements of amplitude equivalent to basic triangular wave form.

#### *Responses to the triangular wave form with displacement steps (experiment IV *b*)*

When ramp and step components were added so that the over-all target displacement was twice that of the underlying triangular wave, the eye tracked the target with a velocity which was, on average, some 20% greater than the velocity of the ramp component (Fig. 7*A*). Conversely, when the over-all eye displacement was equal in amplitude, but opposite in direction, to the triangular wave, eye velocity was reduced to near zero or actually became reversed in direction with respect to the ramp component (Fig. 7*B*). As indicated in Fig. 7 a number of resetting saccadic eye movements were present, but these did not correspond in number with those of the stimulus. Eye velocity was not constant throughout each half-cycle, but exhibited a pattern of modulation in synchrony with each step displacement (Fig. 8*A*). In

addition, eye velocity frequently peaked at the point of turn round and declined during the remaining half-cycle of the stimulus (Fig. 8*A*). Between the two extremes of target displacement there was a significant ( $P < 0.001$ ) trend for the average eye velocity during each half-cycle to increase as the displacement factor increased from  $-1$  to  $+2$  (Fig. 8*B*). The magnitude of the mean velocity induced by the dis-

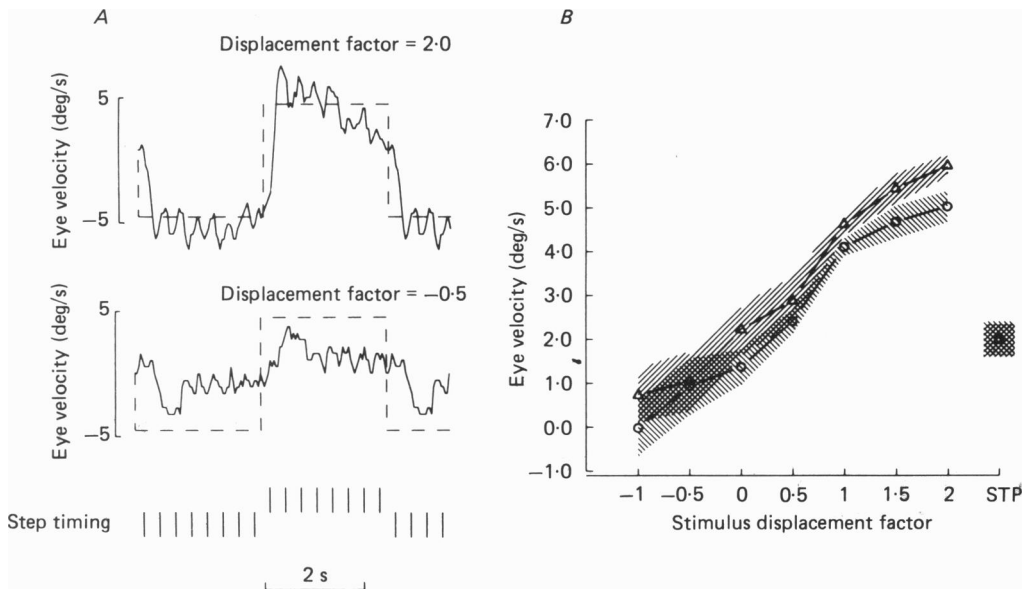


Fig. 8. *A*, mean eye velocity trajectories averaged over four cycles of the stimulus wave form for one subject in response to wave forms of the type shown in Fig. 7 (displacement factors = 2.0 and  $-0.5$ ). *B*, the variation in mean eye velocity as a function of stimulus displacement factor (○, right to left; △, left to right). STP represents the response to step displacements of the type shown in Fig. 7 *C*. Mean of eight subjects  $\pm 1$  s.e. of mean (experiment IV *b*).

placement steps alone was 1.64 deg/s whereas that evoked by the triangular wave form alone was 4.29 deg/s. When the step displacements alone were presented with tachistoscopic illumination during the stationary phases there was a significant ( $P < 0.001$ ) trend of increasing eye velocity as the duration of presentation was decreased. Mean eye velocity for the four subjects tested had values of 6.9, 7.0, 5.8, 5.6, 4.7 and 3.7 deg/s for strobe durations of 10, 20, 40, 80, 160 and 320 ms respectively.

#### *Responses to step sequences of randomized duration (experiment Va)*

The ability of subjects to produce smooth eye movements in response to target steps was not restricted to regular periodic stimuli but could also be induced by staircase sequences in which the duration of consecutive sequences was varied in a randomized manner (Fig. 9). In these sequences the velocity (or rather, displacement per unit time) was held constant and the direction of movement changed predictably at the end of each sequence. The average eye velocity remained remarkably constant but the onset and duration of the response was clearly modified by the expected

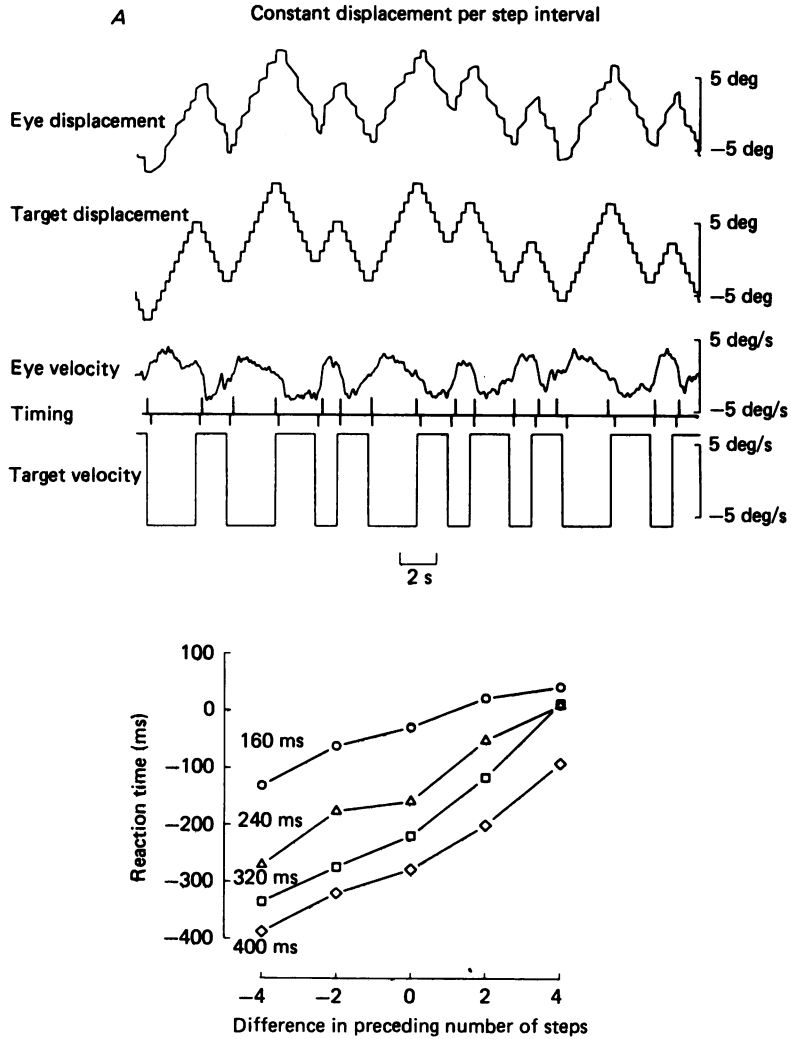


Fig. 9. *A*, the oculomotor response to a staircase sequence of step target displacements in which the number of steps was varied in consecutive sequences (experiment *Va*). Step amplitude = 1.2 deg. Interstep interval = 160 ms. Timing trace indicates the time ( $t_2$ ) at which eye velocity crossed zero (mark above line) and the time ( $t_1$ ) at which the first step of the sequence was initiated (mark below line). In *B* the derived reaction time ( $t_1 - t_2$ ) has been plotted as a function of the difference in number of steps between the two preceding sequences (see text). Mean of eight subjects.

duration of the sequence. In order to measure this effect a reaction time was derived by calculating the difference in time between the onset of the first step in the reversed direction and the time at which eye velocity crossed through zero. This measure of the timing of the oculomotor response was chosen as being the most consistently measurable but it does provide a rather conservative estimate of reaction time since, as indicated in Fig. 9, the eye velocity showed clear signs of changing direction well before the zero cross-over point in many examples. Reaction time defined in this



manner showed a significant ( $P < 0.001$  by analysis of variance) correlation with the 'expected' duration of the current sequence as defined by the difference between the number of steps in the current sequence and the number of steps in the preceding sequence. Thus, if the preceding sequence had eleven steps and the current one had only seven steps (difference = +4) there was a delay in onset of the reversal of eye

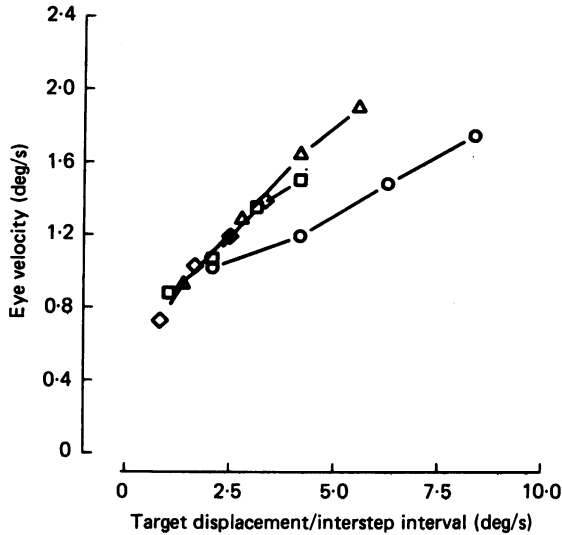


Fig. 10. Mean eye velocity in response to staircase step sequences of varying amplitude plotted as a function of the rate of change of target displacement (= target step displacement/interstep interval) (experiment Vb). Interstep intervals were: ○, 160; △, 240; □, 320; and ◇, 400 ms. Mean of eight subjects.

velocity. On average, the reversal of eye velocity occurred well before the onset of the first step of the next sequence and this negative reaction time was significantly greater ( $P < 0.001$ ) for steps of increased duration (Fig. 9B). The response was thus predictive of the ensuing sequence.

#### *Responses to step sequences of randomized velocity (experiment Vb)*

When the staircase sequences were of constant period (eight steps) but variable step size, subjects were able to modify the velocity of the eye from one sequence to the next even though the rate of change of displacement was varied at random. There was some evidence that the initial velocity of the eye immediately following reversal was related to the velocity of the preceding sequence but this could not be verified statistically because of the variability of eye velocity. Average eye velocity for step intervals between 240 and 400 ms exhibited a remarkably linear relationship with the rate of change of target displacement (Fig. 10). The velocities obtained for step intervals of 160 ms were somewhat less than those for the longer intervals, forming a separate population of responses (Fig. 10).

TABLE 1. Various measures of eye velocity evoked by the tachistoscopic presentation of a target oscillating sinusoidally at a frequency ( $F$ ) between 0.1 and 0.8 Hz

(A) Four or eight strobes per cycle					
$F$ (Hz) ...	0.1	0.125	0.2		
p.i. (s) ...	1.25	1.0	1.25		
$V_T$ (deg/s) ...	10	10	10	$V_M$ (deg/s)	$\phi$ (deg)
	p.d. (ms)				
	80	7.3	7.1	7.0	1.1
	40	5.7	6.0	4.0	2.6
	20	4.8	3.4	3.2	6.2
	10	4.4	2.5	2.8	-0.1
(B) Two strobes per cycle					
$F$ (Hz) ...	0.125	0.4	0.8		
p.i. (s) ...	4	2.5	1.25		
$V_T$ (deg/s) ...	10	16	32	$V_M$ (deg/s)	$V_P$ (deg/s)
	p.d. (ms)	p.d. (ms)	p.d. (ms)		
	320	7.4	4.9	19.3	18.8
	160	6.9	4.1	19.0	17.4
	80	5.7	3.5	10.9	16.2
	40	6.8	4.8	7.3	10.1

$V_P$ , mean peak eye velocity.  $V_M$ , mean eye velocity with respect to target velocity.  $V_T$ , peak target velocity. p.i., pulse interval. In *A* there were four or eight pulses per cycle and pulse duration (p.d.) was varied from 10 to 80 ms. In *B* pulses of duration 10-320 ms were presented at time of peak displacement. Mean of four subjects.

*Responses evoked in total darkness and in response to tachistoscopic target presentation (experiment VI)*

All subjects could produce smooth oscillatory or constant-velocity eye movements in darkness with a velocity of at least  $\pm 2$  deg/s, although most could not produce purely smooth responses without saccades (cf. Heywood & Churcher, 1971). In fact the responses were remarkably similar in form to those evoked by the step target displacements (Figs. 6, 7 and 9). Three of the eight subjects tested, however, could produce very smooth oscillatory eye movements with a peak velocity of between  $\pm 10$  and  $\pm 30$  deg/s at frequencies between 0.5 and 1.5 Hz. The instructions which seemed to elicit this response most readily were to pay attention to any residual transient visual effects which could be observed or to imagine movement of a finger oscillating in the dark after it had ceased to move in reality.

Four subjects who found it particularly difficult to evoke smooth eye movements in darkness were selected for further experiments in which the visual target was illuminated tachistoscopically whilst it traversed the screen with a low-frequency (0.1–0.4 Hz) sinusoidal oscillation (Fig. 11). In most instances the interpulse interval was at least 1 s, a strobe rate at which the visual velocity drive mechanisms have been shown to have negligible effect (Barnes & Edge, 1983; Barnes & Crombie, 1985). When the duration of the target presentation was very brief (< 10 ms) subjects were able to raise the average eye velocity very slightly above that found in the dark (Table 1) in response to a  $\pm 10$  deg/s velocity stimulus. However, a significant ( $P < 0.001$ ) increase in average velocity was obtained when the duration of target presentation was increased from 10 to 80 ms (Table 1) even though as few as four target presentations were made per cycle at a frequency of 0.2 Hz with an interval of 1.25 s. The increase in duration of presentation greatly enhanced the perception of continuous motion in these subjects. Even so, considerable concentration was required in order to achieve such smooth eye movements and several cycles of stimulation were frequently required for eye velocity to build up to its maximum level. Eye velocity frequently exhibited a clear pulsatile modulation in synchrony with target presentation (Fig. 11*B*) similar to that for the periodic step displacements (Fig. 8*A*).

In order to test whether the velocity information contained within the brief pulses was responsible for the eye velocity estimation the pulses were reduced to two per cycle and were presented at the time of peak target displacement and thus at minimum target velocity. A typical response to such a stimulus is shown in Fig. 11*A* in which the frequency of oscillation was 0.2 Hz, the peak velocity was 16 deg/s and the interpulse interval was 2.5 s. Average eye velocity for each half-cycle of the 0.2 Hz stimulus increased with the pulse duration, reaching a mean of 9.3 deg/s for a pulse duration of 320 ms, even though the instantaneous target velocity did not exceed  $\pm 3.2$  deg/s during the presentation of the target. However, the peak eye velocity attained just after the target pulse reached much higher levels of between 10 and 23 deg/s and decayed throughout the remaining half-cycle (Fig. 11*A*). Similar effects were observed for the other frequencies tested as indicated in Table 1. It was thus evident that initial eye velocity could be much greater than the instantaneous target velocity during the period of presentation and was probably based on target-

displacement information. The subjects who took part in these experiments were unable to sustain the velocity throughout the half-cycle, and no amount of training appeared able to change this. In contrast, subjects who could perform smooth eye movements in the dark were easily able to use even the briefest target presentations to produce a sustained velocity during each half-cycle.

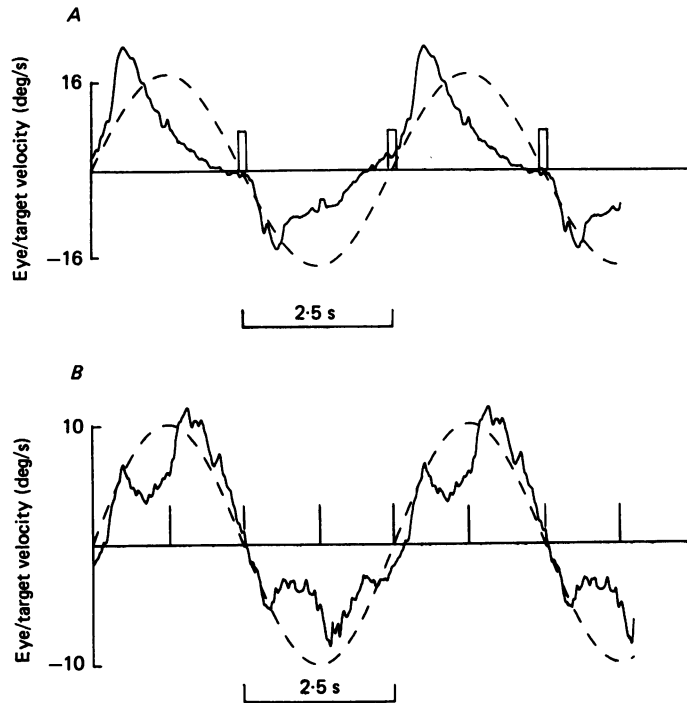


Fig. 11. Eye velocity trajectories (continuous line traces) evoked by tachistoscopic presentation of a target oscillating sinusoidally (interrupted line) at a frequency of 0.2 Hz (experiment VI). Trajectories were obtained by averaging four cycles of the response from one subject. In *A* the target was presented twice per cycle for a pulse duration of 160 ms around the time of zero target velocity as indicated by pulses on abscissa. In *B* four pulses of duration 20 ms were presented during each cycle at the times of zero and peak velocity.

#### DISCUSSION

##### *Criteria for defining a non-predictive pursuit response*

The findings of these experiments indicate that the most important factor affecting the predictability of a pursuit stimulus is the frequency of the highest-frequency component of the stimulus. If this highest frequency is in the range of approximately 0.8–3 Hz this represents a necessary and sufficient condition for non-predictability. In this context it is right that an attempt should be made to define what constitutes a non-predictive response. There have been many experiments in which the responses to pseudo-random pursuit stimuli have been compared with responses to single sinusoids. Only in the more recent of these (Bahill *et al.* 1980; Collewijn &

Tamminga, 1984; Yasui & Young, 1984) have measures for gain and phase of both total eye displacement (or composite eye movement) and slow-phase eye velocity (or cumulative smooth eye movement) been obtained. The results of these experiments allow three particular aspects of the response to pseudo-random and sinusoidal stimuli to be demonstrated: (a) the gain of eye *displacement* for the pseudo-random stimuli is greater than for sinusoids of discrete frequency over a critical range between approximately 1 and 3 Hz and gains in excess of unity are often observed; (b) in contrast, eye *velocity* gain for the pseudo-random stimuli is depressed with respect to the response to individual sinusoids, particularly at frequencies below approximately 1 Hz; (c) eye velocity phase in response to sinusoidal stimuli exhibits a small ( $< 5$  deg) lead at low frequencies ( $< 0.5$  Hz), and negligible phase error up to 1 or 2 Hz whereas pseudo-random stimuli induce considerable phase lead at low frequency (up to 84 deg at 0.046 Hz, Yasui & Young (1984)) combined with an increasing phase lag at frequencies beyond 0.5 Hz.

#### *The predictability of pseudo-random stimuli*

If the above criteria are compared with the responses to a mixture of either four (Fig. 2) or two (Figs. 3 and 4) sinusoidal stimuli it can be seen that they are satisfied with one notable exception; that is, that the eye velocity gain is not significantly depressed when the highest frequency is below approximately 0.4 Hz. Although Collewijn & Tamminga (1984) previously observed a reduction in eye velocity gain in response to a mixture of four sinusoids, this was probably attributable to the higher frequency range used (i.e. 0.15, 0.34, 0.52 and 0.58 Hz).

Factors other than the frequency of the highest-frequency component appear to play a minor role in determining the predictability of the stimulus. The complexity of the stimulus (i.e. the number of harmonically unrelated frequencies mixed together) seems of little importance, since a mixture of two sine waves is quite sufficient to render the target motion unpredictable provided that the higher frequency is in the range of 1–2 Hz (Fig. 4). Similarly, the ratio of stimulus frequencies appears to play a secondary role in determining the predictive nature of the response. It is evident from the results of Fig. 4 that the effect of the high-frequency component of the stimulus (h.f.) on the response to the low-frequency component (l.f.) is slightly different for the two values of  $F_1$  tested (0.22 and 0.44 Hz), so that there is clearly some interaction between frequencies. Nevertheless, it is the frequency of h.f. which is the determinant of predictability, not the ratio of frequencies. This is supported by other findings. First, the responses to two sinusoidal frequency stimuli (Fig. 3A) exhibited no significant decrease in gain when both frequencies were below 0.42 Hz, despite the fact that the lower frequency of the pair varied over a range of 4:1. When the higher-frequency component was greater (e.g.  $F_2 = 1.67$  Hz, Fig. 3A) there were changes in the gain of l.f., but these were mostly consistent with the trend of decreasing gain with increasing frequency. A comparison of velocity gains for specific frequency ratios (e.g.  $G_v = 0.96$  for 0.11 + 0.42 Hz;  $G_v = 0.77$  for 0.22 + 0.83 Hz;  $G_v = 0.61$  for 0.44 + 1.67 Hz in Fig. 3A) indicates that the gain of the low-frequency component can have several different levels for an identical frequency ratio.

*Evidence for a dual mode of oculomotor control in pursuit*

The responses to the combination of four sinusoidal stimuli (Fig. 2A) indicate that as the frequency of the highest-frequency component was increased beyond 0.78 Hz there was a decline in gain of all three low-frequency components. There was, however, no significant difference in gain between the three low frequencies, which suffered an equal decline. On the other hand, the gain of the high-frequency component remained high; not necessarily as high as the low-frequency components, but nearly as high as the gain elicited by discrete-frequency sinusoids. This implies that the subject has put all the effort of active pursuit into the highest-frequency component alone, whereas the gains of the lower frequencies fall to a common base level. When the highest-frequency sinusoid was replaced by a square wave of identical frequency a similar decrease in gain of the three low frequencies was observed. But with this type of stimulus, the effort of active pursuit was concentrated on the square-wave component, resulting in a quasi-sinusoidal modulation of eye velocity. This pattern of eye movement was also observed when subjects attempted to track the square-wave target displacement by itself (Fig. 6), even though the rapid step displacements of the target did not form a suitable stimulus for the retinal velocity feed-back mechanisms. This indicates that there must be at least two separate visually driven mechanisms which may be used in generating the smooth eye movements of the pursuit reflex response. One is the classical retinal velocity feed-back mechanism, which will henceforth be referred to as continuous velocity error feed-back. The other is what will be termed a velocity estimation mechanism, the evidence for which will now be considered.

*Characteristics of the velocity estimation mechanism*

The responses to square-wave target displacements (Fig. 6) were similar to those observed previously by Kowler & Steinman (1979a), but indicate that the maximum velocity is attained in a range of frequencies between 0.5 and 1.5 Hz (Fig. 5), with a rapid fall off in gain at higher frequencies. A particularly important feature of the response was that it was frequently predictive in nature, a characteristic which could not be fulfilled by a conventional continuous positional feed-back mechanism of the type described by de Bie & van den Brink (1984). In order for the response to be predictive in this manner it is a necessary prerequisite that some estimate of the periodicity of the stimulus be made so that the response may be reversed in direction prior to the estimated time of target reversal. The responses to the staircase sequences of variable duration (Fig. 9) demonstrate that this estimate of periodicity is probably derived from the duration of the period between the two most recent reversals in direction of the stimulus. It is equally apparent that when the response is predictive some prior estimate of the required velocity drive to the oculomotor system must be made. It seems likely that this estimate is based on previous changes in displacement of the target. The responses to the staircase steps indicate that the human subject is able to use this mechanism to make sustained low-velocity smooth eye movements over prolonged periods (Fig. 7) with a velocity proportional to the rate of change of target displacement (Fig. 10). Such a response could well form the means by which

the eye velocity induced by continuous velocity error feed-back is enhanced to achieve higher levels of gain during pursuit.

The velocity of eye movement induced by the step sequences was low and its usefulness in pursuit of target velocities greater than 5–10 deg/s might be thought of little value. But the results of experiment VI (Fig. 11) and of previous experiments in which stabilized target images have been used (Kommerell & Taumer, 1972; Pola & Wyatt, 1980), demonstrate that much higher velocities of smooth eye movement may be generated when continuous velocity error feed-back is eliminated or substantially reduced. It is likely that the low velocities elicited by the step displacement stimuli resulted from interaction between the velocity estimation mechanism and continuous velocity error feed-back. In the responses to the staircase step sequences the retinal velocity error feed-back works to counteract the drive from the velocity estimation mechanism as the eye moves across the stationary target during the periods between steps. When the inhibitory effects of retinal velocity error feed-back were reduced by decreasing the duration of the stationary phases (experiment IV *b*) there was a progressive increase in eye velocity, which then reached levels comparable to those obtained previously during tachistoscopic target presentation (Behrens & Grusser, 1979). The responses to the stimuli in which a triangular wave form was overlaid with staircase steps (Fig. 8) also demonstrate this interaction since the eye velocity induced by the ramp component of the stimulus was significantly modified by the direction and amplitude of the step components (Fig. 7). These findings provide strong support for the concept that the central velocity estimation mechanism and continuous velocity error feed-back are essentially separate mechanisms which can interact with each other.

It was a characteristic feature of the responses to the step sequences and of those to the tachistoscopically presented moving targets (Fig. 11) that the initial eye velocity exhibited a high peak level when the target changed direction which was then followed by a slow decay of eye velocity. Such a feature was previously noted by Becker & Fuchs (1985) when subjects anticipated the constant-velocity movement of a visual target. This implies that in the absence of continuous velocity feed-back the central velocity estimation mechanism is able to initiate a smooth eye movement with an approximately correct velocity, but is unable to sustain the oculomotor drive without further visual reinforcement. If the adequacy of this estimate is confirmed by the subsequent appearance of further target error information a continuous series of corrected estimates will be produced. Between each predictive pulse the response decays, giving rise to the oscillatory form observed so markedly in the response to the ramp-step combination (Fig. 8*A*) and the tachistoscopically illuminated targets (Fig. 11*B*).

The ability to produce high-velocity estimates was greatly improved when brief exposure of the target revealed its instantaneous velocity, although the induced eye velocity was substantially greater than the instantaneous velocity error. It is probable that the reinforcement of the perception which accompanied this type of stimulus is closely associated with the ability to produce such a response (Steinbach, 1976; Morgan & Turnbull, 1978; Wyatt & Pola, 1979). Indeed, the dichotomy in the oculomotor control mechanisms described here may have a parallel in the perception

of the apparent motion of tachistoscopically presented targets. Braddick (1974) has made a distinction between what are termed 'short-range' effects, in which small displacements ( $< 0.25$  deg) are perceived as being in continuous motion even in the presence of a highly structured background, and 'long-range' effects in which larger displacements may be perceived as in continuous motion only against a blank field. It is possible that 'short-range' perception is a manifestation of activity in the continuous velocity error feed-back, whereas the 'long-range' effects rely on, or may even form the basis for, the velocity estimation mechanism.

*The role of the velocity estimation mechanism in the response to pseudo-random stimuli*

The evidence from the experiments described here points to a central mechanism for velocity estimation that functions in two ways. When all frequencies of a pseudo-random stimulus are below 0.4 Hz the mechanism may be used for continual estimation of eye velocity in such a manner as to enhance the eye movement induced by continuous retinal velocity error feed-back. Thus, all frequency components of the response would have a high level of gain as observed in Fig. 1. In this role it would not be necessary for the periodicity of the wave form to be estimated because at such low frequencies prediction would not be required to overcome the time delays inherent in the feed-back pathways. In contrast, when any component of the stimulus has a frequency greater than about 0.8 Hz, the velocity estimation mechanism probably ceases to function in this manner because of delays within the central process of estimation. In these circumstances, if the stimulus were a single, discrete-frequency sinusoid the velocity estimation mechanism could be used to make an estimate of the periodicity of the wave form and generate a response which could be added to the continuous velocity error feed-back in order to enhance the gain. This could be accomplished by the generation of bursts of oculomotor velocity drive of opposite polarity at regular intervals. It would result in the type of response shown in Fig. 11A, except that at frequencies above about 0.5 Hz it would become more quasi-sinusoidal in form. It is of particular interest that the response to the square-wave stimuli was optimal at frequencies between 0.5 and 1.5 Hz (Fig. 5) which is precisely the range in which the single sinusoidal response shows gain enhancement compared with a pseudo-random response. Moreover, the considerable phase advance induced by the square-wave stimulus at frequencies up to 0.6 Hz (Fig. 5B) could contribute to the decrease in phase lag observed for pursuit of discrete sinusoids.

Finally, in the response to a mixed-frequency stimulus, in which the highest frequency is greater than 0.8 Hz, it is merely necessary to postulate that the velocity estimation mechanism can only produce a periodic response at one of the mixture of frequencies and thus, that it is this frequency which has an enhanced gain. The remaining frequency components must then rely predominantly on continuous velocity feed-back and as a consequence the gains of these components would all decrease to the same base level in the manner noted earlier (Figs. 2 and 4). It is notable that the minimum gain attained by the low-frequency components in all of the mixed-frequency experiments (I, II and III) was very similar (between 0.5 and 0.6). This level is comparable to that found previously in the response to passive stimulation of the oculomotor system (Barnes & Hill, 1984; Barnes & Crombie, 1985;



Pola & Wyatt, 1985), an experimental condition in which the velocity estimation mechanism is unlikely to participate. It is not altogether clear why subjects tend to enhance the highest-frequency component of the mixed-frequency stimulus although it does accord with the subjective reports that the highest frequency is most dominant. Although the gain of this component was enhanced the phase lag was still significantly greater than for the discrete sinusoid of identical frequency (Fig. 2), which suggests that velocity estimation may be involved without prediction in these particular conditions. However, the phase changes are not easily interpreted and clearly require further investigation.

## REFERENCES

- BAHILL, A. T., IANDOLO, M. J. & TROOST, B. T. (1980). Smooth pursuit eye movements in response to unpredictable target waveforms. *Vision Research* **20**, 923-931.
- 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. (1983). The effects of retinal target location on suppression of the vestibulo-ocular reflex. *Experimental Brain Research* **49**, 257-268.
- 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., CROMBIE, J. & EDGE, A. (1985). The effects of ethanol on visual-vestibular interaction during active and passive head movements. *Aviation, Space and Environmental Medicine* **56**, 695-701.
- 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.
- 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.
- BRADDICK, O. (1974). A short-range process in apparent motion. *Vision Research* **14**, 519-527.
- COLLEWIJN, H. & TAMMINGA, E. P. (1984). Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds. *Journal of Physiology* **351**, 217-250.
- DALLOS, P. J. & JONES, R. W. (1963). Learning behaviour of the eye fixation control system. *IEEE Transactions on Automatic Control* **AC-8**, 218-227.
- 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. Netherlands: North-Holland-Elsevier.
- ECKMILLER, R. & MACKEBEN, M. (1978). Pursuit eye movements and their neural control in the monkey. *Plügers Archiv* **377**, 15-23.
- FENDER, D. H. & NYE, P. W. (1961). An investigation of the mechanisms of eye movement control. *Kybernetik* **1**, 288-297.
- HEYWOOD, S. & CHURCHER, J. (1971). Eye movements and the after image 1. Tracking the after image. *Vision Research* **11**, 1163-1168.
- KOMMERELL, G. & TAUMER, R. (1972). Investigations of the eye tracking system through stabilised retinal images. In *Cerebral Control of Eye Movements and Motion Perception*, ed. DICHGANS, J. & BIZZI, E., pp. 288-297. Basel, Karger.
- KOWLER, E. & STEINMAN, R. M. (1979a). The effect of expectations on slow oculomotor control - I. Periodic target steps. *Vision Research* **19**, 619-632.
- KOWLER, E. & STEINMAN, R. M. (1979b). The effect of expectations on slow oculomotor control - II. Single target displacements. *Vision Research* **19**, 633-646.

- LISBERGER, S. G., EVINGER, C., JOHANSON, G. W. & FUCHS, A. F. (1981). Relationship between eye acceleration and retinal image velocity during foveal smooth pursuit in man and monkey. *Journal of Neurophysiology* **46**, 229–249.
- MICHAEL, J. A. & JONES, G. M. (1966). Dependence of visual tracking capability upon stimulus predictability. *Vision Research* **6**, 707–716.
- 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.
- MURATORE, R. & ZEE, D. S. (1979). Pursuit after-nystagmus. *Vision Research* **19**, 1057–1059.
- POLA, J. & WYATT, H. J. (1980). Target position and velocity: The stimuli for smooth pursuit eye movements. *Vision Research* **20**, 523–534.
- POLA, J. & WYATT, H. J. (1985). Active and passive smooth eye movements: effects of stimulus size and location. *Vision Research* **25**, 1063–1076.
- RASHBASS, C. (1961). The relationship between saccadic and smooth tracking eye movements. *Journal of Physiology* **151**, 338–362.
- ROBINSON, D. A. (1965). The mechanisms of human smooth pursuit eye movement. *Journal of Physiology* **180**, 569–591.
- SCHALEN, L. (1980). Quantification of tracking eye movements in normal subjects. *Acta otolaryngologica* **90**, 404–413.
- ST-CYR, G. J. & FENDER, D. H. (1969). Non-linearities of the human oculomotor system: gain. *Vision Research* **9**, 1235–1246.
- STARK, L., VOSSIUS, G. & YOUNG, L. R. (1962). Predictive control of eye tracking movements. IRE Transactions on Human Factors in Electronics **HFE-3**, 52–56.
- STEINBACH, M. J. (1976). Pursuing the perceptual rather than the retinal stimulus. *Vision Research* **16**, 1371–1376.
- VON NOORDEN, G. & MACKENSON, G. (1962). Pursuit movements of normal and amblyopic eyes. *American Journal of Ophthalmology* **53**, 325–336.
- WESTHEIMER, G. (1954). Eye movement responses to a horizontally moving visual stimulus. *Archives of Ophthalmology* **52**, 932–941.
- WESTHEIMER, G. & CONOVER, D. W. (1954). Smooth eye movements in the absence of a moving visual stimulus. *Journal of Experimental Psychology* **47**, 283–284.
- WHITTAKER, S. G. & EAHOLTZ, G. (1982). Learning patterns of eye motion for foveal pursuit. *Investigative Ophthalmology and Visual Science* **23**, 393–397.
- WINTERSON, B. J. & STEINMAN, R. M. (1978). The effect of luminance on human smooth pursuit of perifoveal and foveal targets. *Vision Research* **18**, 1165–1172.
- WYATT, H. J. & POLA, J. (1979). The role of perceived motion in smooth pursuit eye movements. *Vision Research* **19**, 613–618.
- WYATT, H. J. & POLA, J. (1983). Smooth pursuit eye movements under open-loop and closed-loop conditions. *Vision Research* **23**, 1121–1131.
- YASUI, S. & YOUNG, L. R. (1984). On the predictive control of foveal eye tracking and slow phases of optokinetic and vestibular nystagmus. *Journal of Physiology* **347**, 17–33.