# HUMAN SMOOTH AND SACCADIC EYE MOVEMENTS DURING VOLUNTARY PURSUIT OF DIFFERENT TARGET MOTIONS ON DIFFERENT BACKGROUNDS

BY HAN COLLEWIJN AND ERNST P. TAMMINGA*

*From the Department of Physiology I, Faculty of Medicine, Erasmus University Rotterdam, P.O. Box 1738, 3000 DR Rotterdam, The Netherlands*

SUMMARY

1. Horizontal and vertical eye movements of ten human subjects were recorded with a scleral induction-coil technique during voluntary pursuit of sinusoidal, triangular and pseudo-random target motions of different frequency, amplitude and dimensionality upon a dark, diffuse or structured background.

2. Data processing included separation of the composite eye movement into a cumulative smooth and saccadic displacement, computation of gain and phase of the composite and smooth eye movements with respect to the target movement and analysis of retinal position error.

3. Pursuit eye movements were never completely smooth. Smooth pursuit gain was always lower than 0·95 and saccades were used to supplement the smooth eye movements in pursuing the target with the proper amplitude.

4. The gain of composite eye movements was about unity for sinusoidal target motions and ramps; it exceeded unity for the highest frequency components in a pseudo-random motion.

5. The gain of the smooth eye movements decreased monotonously whenever target velocity increased. It was higher for single sine waves than for a pseudo-random motion, however, with pseudo-random motion it was relatively higher for the higher frequency components.

6. Phase lags were in general smaller for single sine waves than for pseudo-random motion, but for the latter a phase lead of the smooth component was consistently found for the lower frequency components.

7. During pursuit of a rhomboid trajectory, the eye movements showed directional errors which are interpreted as anticipatory behaviour.

8. The distribution of the retinal error was symmetrical around zero. Its standard deviation varied between about 0·2 and 1·3°; it was about proportional to target velocity and inversely proportional to smooth pursuit gain. It was limited by the insertion of saccades which were in general corrective.

9. The influence of a diffusely illuminated background was minimal. A structured background inhibited smooth pursuit in the horizontal direction by about 10% and in the vertical direction by about 20%. This deficit of smooth pursuit was fully

* Authors in alphabetical order.

compensated by the insertion of more saccades and had no consequences for the standard deviation of the retinal error. The type of structure of the background was only of marginal importance.

10. Horizontal pursuit was in general slightly smoother and more precise than vertical pursuit.

## INTRODUCTION

If a human observer wants to inspect a moving object in detail, he will make voluntary pursuit eye movements to keep the image of the object as close as possible to the retinal area of maximal visual acuity: the centre of the fovea. Voluntary pursuit is composed of continuous smooth pursuit and of saccades which are discrete and step-like. At one time, it was thought that after acquiring a target by a saccade a subject was able to track the target entirely smoothly with a velocity equal to the target velocity (Westheimer, 1954; Rashbass, 1961; Robinson, 1965). Later on it has become clear that smooth pursuit gain is as a rule smaller than unity (Puckett & Steinman, 1969; Murphy, Kowler & Steinman, 1975; Murphy, 1978). Therefore smooth pursuit is supplemented by saccades to maintain foveation (Dodge, Travis & Fox, 1930; Stark, Vossius & Young, 1962; Bornemann, Drischel & Niedergesäsz, 1964; Mackeben, Haegerstrom-Portnoy & Brown, 1980).

A precise study of the contribution of smooth and saccadic components requires sufficiently reliable recording and separation techniques. The performance of voluntary pursuit can be expressed in the distribution of position and velocity of the retinal image of the target as a function of time or in the amplitude ratio and phase shift between eye and target motion as a function of frequency. The latter approach has been followed in earlier system-analytical studies (Fender & Nye, 1961; Stark *et al.* 1962; Dallos & Jones, 1963; Michael & Jones, 1966; St-Cyr & Fender, 1966*a,b;* Stark, 1971). In several of these studies predictability has been identified as an important stimulus parameter influencing pursuit performance. However, a systematic distinction between smooth and saccadic pursuit has usually not been made in descriptive models of the pursuit system.

Another simplification in most laboratory studies of pursuit is the absence of a structured background. In daily life, moving targets are normally seen against a stationary background and pursuit of the target will induce a concomitant opposite motion on the peripheral retina. The effect of this conflicting stimulus on the over-all performance has been little investigated. Kowler, Murphy & Steinman (1978) found a non-significant interaction of a homogeneous light background with pursuit of a slowly moving target. Murphy *et al.* (1975) found a modest increase of drift in the direction of the movement of a background grating during fixation of a stationary target. On the other hand, Ter Braak (1957, 1962) and Hood (1975) noticed a facilitation of smooth pursuit of a central target in a direction opposite to the motion of the background. In contrast to the latter findings, Merrill & Stark (as reported by Stark, 1971) found acceleration of pursuit in the direction of the background movement and inhibition in the opposite direction.

Here we report a systematic study of voluntary pursuit in which its performance, distinguished in smooth and saccadic components, is evaluated in the frequency and

time domain as a function of the following stimulus variables: background, predictability, spectral composition, shape (sinusoidal *vs.* triangular), direction (horizontal *vs.* vertical), dimensionality (one- or two-dimensional) and amplitude.

Preliminary communications of parts of these results have been published (Tamminga & Collewijn, 1981; Collewijn, Conijn, Martins, Tamminga & Van Die, 1982).

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

*Subjects*

Ten subjects, ranging in age from 21 to 45 years, were used. Four subjects were experienced in oculomotor experiments; six were not. Five of the ten subjects served in all experiments and only their data will be described in detail (the other five subjects did not differ in any significant way). All had 20/20 visual acuity (normally or after correction), and no known ocular or oculomotor pathology.

*Recording*

Horizontal and vertical eye movements were measured with an induction coil mounted in a scleral annulus in an a.c. magnetic field as first described by Robinson (1963) and modified by Collewijn, Van der Mark & Jansen (1975). The dynamic range of the recording system was better than 100 Hz, noise level less than 3 minutes of arc and non-linearity less than 0·5 %. The motion of the right eye was recorded; the left eye was covered. Head movements were minimized by chin and head supports. The experimental room was dark.

*Visual stimuli*

The target (diameter 7 minutes of arc) was formed by the spot of a He–Ne laser, back-projected on a translucent screen at a distance of 1·50 m in front of the subject. A minicomputer (DEC PDP 11/10), used for stimulus generation, data collection and data analysis, controlled the horizontal and vertical movements of the target independently. Pre-calculated digital target movements were converted to analog voltages via two 10-bit digital-to-analog converters, low-pass filtered ($-3$ dB at 10 Hz) and connected to two servo-controlled mirror-scanning units with position output (General Scanning, Watertown MA) which were mounted in the light pathway. A neutral density filter attenuated the luminance of the laser spot to about 200 cd/m². A background could be superimposed which filled the whole visible part of the screen (subtending about $90 \times 90°$ arc, limited by the field coils of the recording system). The backgrounds used were darkness (luminance $<1$ cd/m²), diffuse illumination (11 cd/m²) or a structured pattern. In most cases this was a black-and-white random dot pattern with individual elements of 15 minutes arc (Julesz, 1971, fig. 2.6.2.). The luminance of the white parts was 16·8 cd/m², of the black parts 3·6 cd/m². To investigate the influence of the specific structure of the background, other configurations were used in a number of experiments: horizontal and vertical sine-wave and square-wave gratings with periods of 4·76 and 9·46°; random dot patterns with individual elements of 1·05 and 2·1° and two regular checkerboard patterns with elements of 3·23 and 6·46°. The average luminance of the structured backgrounds was equal to that of the diffuse background.

*Procedures*

The data recording for each subject was divided over two or three sessions. Each session was limited to 30 min of recording in which about forty measurements were done. Each measurement lasted 32·77 s (4096 data points of each relevant signal, each sampled at a rate of 125 Hz). The stimulus was displayed for several seconds before the data recording started.

Calibration experiments were done at the beginning and at the end of each session. The subject was instructed to fixate the target which was displaced by the computer in fixed steps. The sensitivity was adjusted by hand before the start of the measurements and corrected additionally off line by the computer on the basis of the recorded response to the calibration steps. The order of the measurements was altered between subjects to balance for any effects of practice. The subjects, who were allowed to wear corrective spectacles, had to follow a set of different target wave forms under various conditions. The target wave forms used were single sine waves (0·15–0·52 Hz,

amplitude 7 or 10°); triangular wave forms (0·06–0·52 Hz, amplitude 7 or 10°) and pseudo-random stimuli in which the horizontal and vertical components consisted of the sum of four non-harmonic sine waves of different amplitudes. A number of such combinations with different band widths were used (Table 1). Each recording period contained an integer number of cycles of each component of the stimulus. To maintain a roughly similar maximal target velocity throughout the spectrum, the amplitudes of the several components were inversely proportional to the frequency.

TABLE 1. Spectral composition of the pseudo-random stimuli for a maximum amplitude of 10° in horizontal and vertical direction

| Sum 1 | | | Sum 2 | | |
|---|---|---|---|---|---|
| Frequency (Hz) | Amplitude (°) | Phase (°) | Frequency (Hz) | Amplitude (°) | Phase (°) |
| Horizontal | | | | | |
| 0·153 | 5·70 | 0 | 0·336 | 4·50 | 30 |
| 0·336 | 2·59 | 30 | 0·519 | 2·97 | 60 |
| 0·519 | 1·68 | 60 | 0·580 | 2·66 | 90 |
| 0·580 | 1·50 | 90 | 0·946 | 1·63 | 0 |
| Vertical | | | | | |
| 0·214 | 4·50 | −30 | 0·275 | 4·50 | −60 |
| 0·275 | 3·50 | −60 | 0·397 | 3·12 | −60 |
| 0·397 | 2·42 | −60 | 0·702 | 1·76 | −90 |
| 0·702 | 1·37 | −90 | 0·885 | 1·40 | 0 |

| Sum 3 | | | Sum 4 | | |
|---|---|---|---|---|---|
| Frequency (Hz) | Amplitude (°) | Phase (°) | Frequency (Hz) | Amplitude (°) | Phase (°) |
| 0·153 | 6·06 | 0 | 0·214 | 6·94 | −30 |
| 0·336 | 2·76 | 30 | 0·519 | 2·86 | −60 |
| 0·885 | 1·05 | 60 | 0·702 | 2·11 | −90 |
| 1·129 | 0·82 | 90 | 0·946 | 1·57 | −120 |

The target was moved either in one dimension (horizontal or vertical only; amplitude 10°) or in two dimensions simultaneously. For the single sines and triangles, the horizontal and vertical components of the two-dimensional stimulus were shifted 90° in phase, to produce circular and rhomboid target trajectories. Two different two-dimensional amplitudes were used: (1) vectorial sum of horizontal and vertical amplitude and velocity comparable to the one-dimensional case (amplitude of horizontal and vertical component $5\sqrt{2} = 7·07°$); (2) amplitude and velocity of horizontal and vertical component comparable to the one-dimensional case (amplitude 10°). The stimuli had to be pursued upon the dark background and the diffuse background as well as the random dot background. Five subjects were tested in all conditions, the other five were tested in all conditions except the two-dimensional pursuit with an amplitude of 10°.

*Data analysis*

The horizontal and vertical components of the eye position and the target position (as signalled by the position output of the scanner) were each digitized on line at a frequency of 125 Hz (resolution 0·02°, 8 ms) and stored on disk. All data analysis was done off line. The first stage was the recalibration of the eye position signal using the calibration measurements at the beginning and end of each experiment. The eye and target position were displayed on a graphics terminal. Parts of the recordings were selected using a manually controlled cursor to point out the beginning and end of the calibration steps. The errors in gain and offset between target and eye were then calculated and the complete experiment was corrected using the calculated values. Typically, adjustments did not exceed 1–2 % for gain and 0·2–0·3° for offset. Adjustment differences between the calibration at the beginning and the end of the session did not exceed 2–3 % for gain and 0·3–0·4° for offset. The experiment was repeated if larger differences occurred.

To analyse the smooth pursuit component of the eye movement, software (not described in detail here) was developed to detect the saccades in the eye position signal and to separate the eye movement into a smooth and a saccadic component. Fig. 1 shows a representative example of this process. The detection of the start of saccades in the eye position signal ($E$) was based upon velocity and acceleration thresholds. Velocity profile and saccade duration limits were then used to detect the end of the saccade and to check whether the detected event was a true saccade or not. Saccades as small as 0·2° could be reliably detected. With the saccade detection signal it was possible to
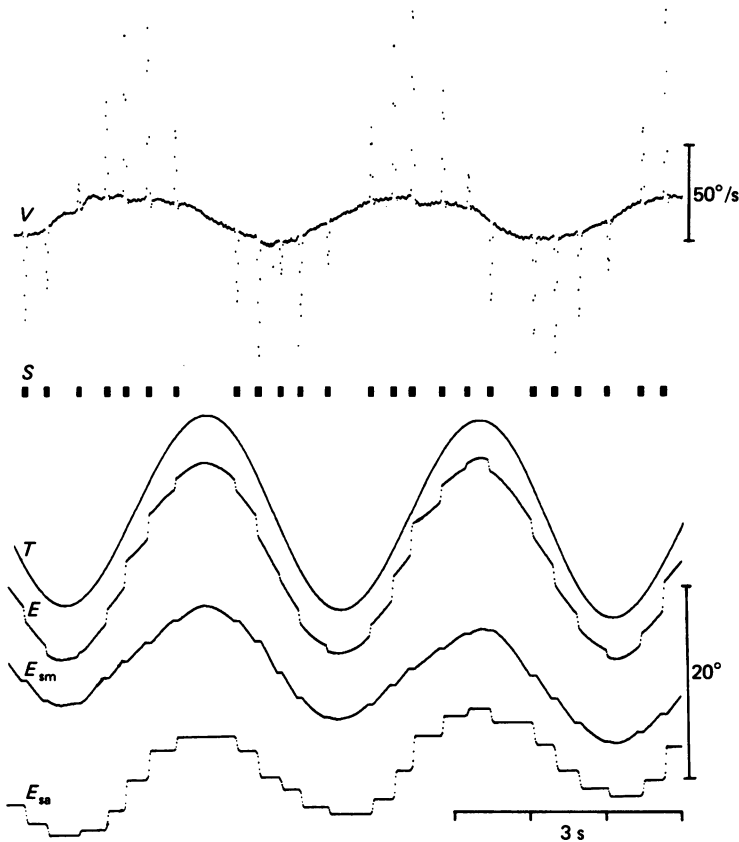


Fig 1. An example of separation of composite eye movements ($E$) in response to a sinusoidal target movement ($T$) of 0·28 Hz into a cumulative smooth ($E_{sm}$) and saccadic ($E_{sa}$) component based upon the eye velocity ($V$) and acceleration. The saccade detection signal ($S$) is stored for further analysis.

separate the eye movement into a cumulative smooth component and a cumulative saccadic component. The missing parts in both components (the saccades in the smooth component and the smooth eye movement in the sacadic component) were filled with zero-velocity elements. The cumulative smooth and saccadic signal and the saccade detection signal were saved for further analysis.

Most subjects showed a preference to make saccades in a certain direction; accordingly the cumulative smooth and saccadic eye movement showed trends in opposite directions. This trend would cause a distortion of the power spectrum and lead to errors in the computation of smooth pursuit gain and phase relationships. Therefore, for all subjects any trend was removed by means of a least-squares method, for all sine-wave and pseudo-random stimuli. For these same stimuli, eye and target position signals were Fourier transformed with a fast Fourier transform routine. Gain (ratio of peak-to-peak amplitudes of the fundamental component of eye and target position)

and phase (difference in degrees between the fundamental components of eye and target position) relationships for horizontal and vertical components were calculated by means of auto- and cross-power spectral densities.

Analysis of the fundamental components in the eye and target movement by Fourier transformation is a form of least-squares fitting of sine-wave stimuli. The fitted curves were calculated by (1) a forward Fourier transform, (2) removal of all frequencies in the signal except the four frequencies used in the stimulus and (3) an inverse Fourier transform of the stripped spectrum.
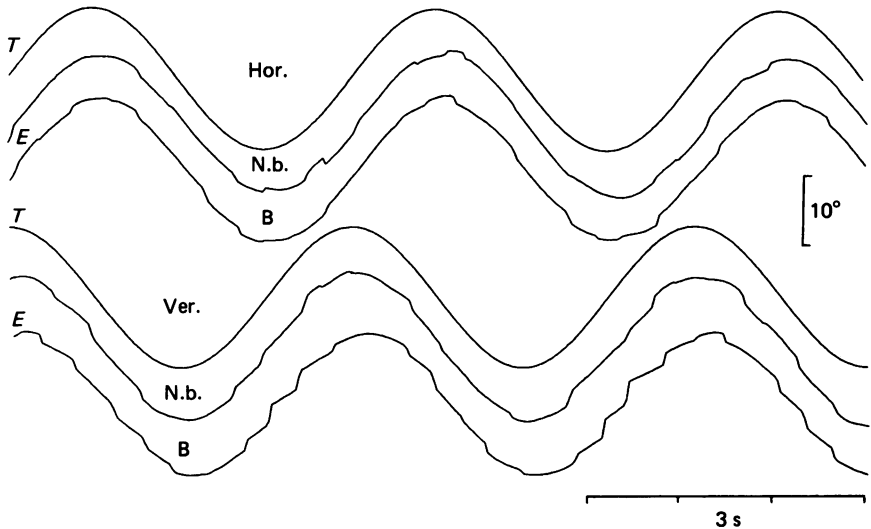


Fig. 2. Recordings of the horizontal (hor.) and vertical (ver.) component of a sinusoidal target movement (*T*) and pursuit eye movement (*E*) without (n.b.) and with (B) a stationary background.

For pseudo-random stimuli more than 98 % of the energy of the composite eye movement and more than 80 % of the energy of the cumulative smooth eye movement was contained within the four remaining frequencies. For single sine-wave stimuli, these figures were 99 and 90 % respectively for the single frequency component used. Therefore, the cumulative smooth eye position produced by the computer should provide a reliable estimate of smooth pursuit gain.

For triangular-wave stimuli the trend in the cumulative smooth eye movement was not removed. The slopes of the triangles were used to calculate the amplitude ratio (gain) of eye and target position and of cumulative smooth eye and target position. The central 75 % of the horizontal or vertical slopes of the triangles were used to calculate gain; 12·5 % at the beginning and at the end of the slopes in the horizontal or vertical directions were excluded from the analysis. For these stimuli, separate gains were calculated for the pursuit of left- and right-ward and up- and downward-directed target movements.

The retinal position error was calculated by subtraction of the eye position from the target position.

<div align="center">

RESULTS

Performance in the frequency domain

*Pursuit upon a dark background*

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*Sinusoidal motion (single sine waves)*

Fig. 2 shows an example of the horizontal and vertical component of target and eye movement during pursuit of a circular target motion upon a dark background

(n.b.). The horizontal and vertical components of the target movement were single sine waves of the same frequency (0·28 Hz) and amplitude (10°), shifted 90° in phase. Most of the pursuit was achieved by smooth eye movements; the saccadic component was small.

We shall use Bode plots to summarize the gain and phase of responses to single and composite sinusoidal target motions. This presentation does not imply that the
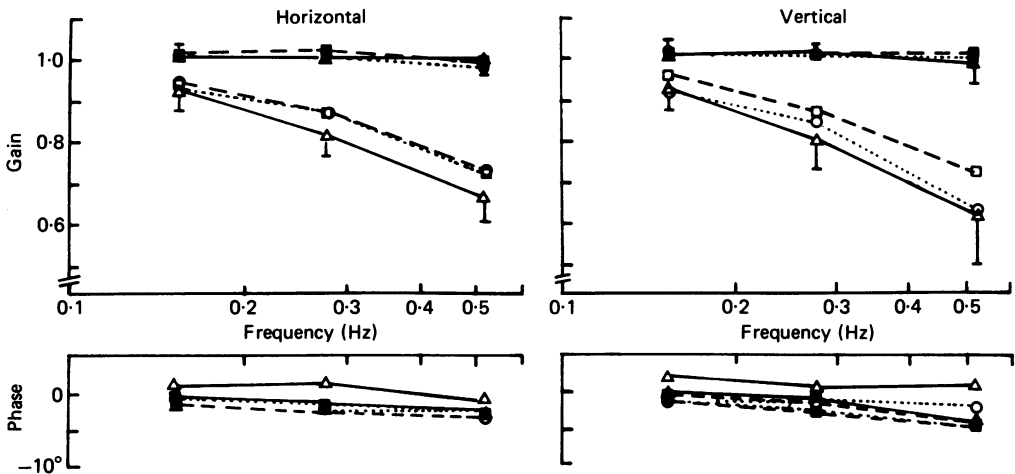


Fig. 3. Gain and phase of the composite (filled symbols) and cumulative smooth eye movement (open symbols) in response to one-dimensional single sine-wave stimuli (amplitude 10°, continuous lines), or a two-dimensional stimulus with an amplitude of 7·07° (dashed lines) or 10° (dotted lines). Means ±S.D. for five subjects.

pursuit system can be adequately described by a single frequency–response relation; on the contrary it will be shown that the system shows many non-linear properties. Therefore, the relations shown in the several diagrams describe only the response to the particular stimulus for which it was derived.

Fig. 3 shows mean gain and phase as a function of frequency for five subjects for one-dimensional target motion (amplitude 10°) and two-dimensional target motion with an amplitude of 7·07 or 10°. For the composite eye movement, there was no significant difference between the gain and phase of the horizontal and vertical components. The gain of the composite eye movement in response to single sine-wave stimuli was close to unity. For 0·15 Hz the mean gain was $1·01 \pm 0·02$ (s.D.; $n = 30 = 5$ subjects × 3 situations × 2 dimensions). Gain decreased only to $0·99 \pm 0·03$ (s.D.; $n = 30$) when the stimulus frequency increased to 0·52 Hz. The standard deviations of the gain of the composite eye movement were small, which means that the differences between subjects were small. The phase lag of the composite eye movement was less than 5° for all stimulus frequencies used, but showed a tendency to increase with frequency.

The pursuit eye movements were never completely smooth. For the one-dimensional sine-wave stimulus of 0·15 Hz, gain of the cumulative smooth component of the horizontal eye movement was $0·94 \pm 0·04$ (s.D.) and of the vertical component $0·93 \pm 0·05$ (s.D.), which means that (since the gain of the horizontal and vertical

component of the composite eye movement was about unity) 94 and 93 % respectively of the pursuit movement was accomplished by the smooth component. The remaining 6 and 7 % were achieved by saccadic eye movements.

The gain of smooth eye movement decreased with the increase of frequency. For a one-dimensional stimulus of 0·52 Hz, the gain of the cumulative smooth component of the horizontal eye movement was only 0·66 ± 0·06 (S.D.) and of the vertical eye movement 0·61 ± 0·12 (S.D.). However, on the whole this type of stimulus revealed only a slight advantage of horizontal over vertical pursuit.
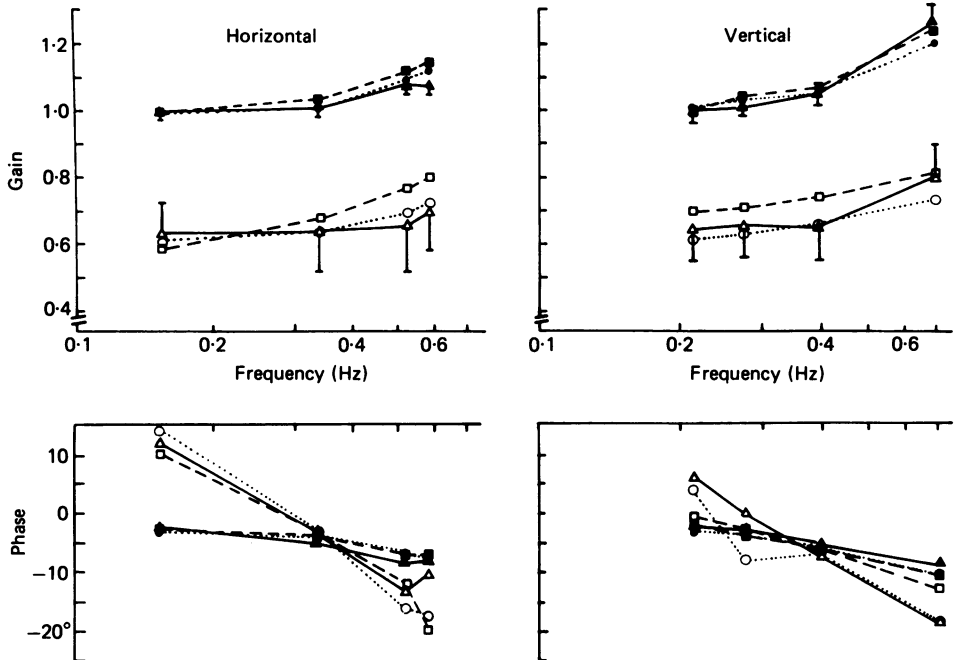


Fig. 4. Gain and phase of the composite (filled symbols) and cumulative smooth eye movement (open symbols) in response to the pseudo-random target motion with the lower band width (Table 1, sum 1) in one dimension with an amplitude of 10° (continuous lines), in two dimensions with an amplitude of 7·07° (dashed lines) or 10° (dotted lines). Means ± S.D. for five subjects.

Surprisingly, during pursuit of a circular motion the average gain of the smooth components (both horizontal and vertical) was significantly higher than for target motion restricted to one dimension. For a circular target motion with an amplitude of 7·07° the mean increase (averaged over three frequencies) amounted to 0·06 ± 0·04 (S.D.; $P < 0.001$) and for an amplitude of 10° to 0·03 ± 0·04 (S.D.; $P < 0.001$). The phase errors of the smooth pursuit component were very small, as was found also for the composite eye movement. Remarkably, there was a tendency for phase of the smooth component to occasionally show a lead (Fig. 3).

The standard deviations of the gains of the smooth pursuit eye movement were larger than those of the composite eye movement, because some subjects were able

to pursue slowly moving targets almost without saccades, while other subjects used saccades more frequently. The ability to pursue without saccades was not strongly correlated with the experience of the subject. Some experienced subjects pursued a slowly moving target with frequent saccades, while some inexperienced subjects tracked the same target motion almost without saccades. The individual difference in frequency of saccades during pursuit was persistent throughout the frequency range and over sessions.
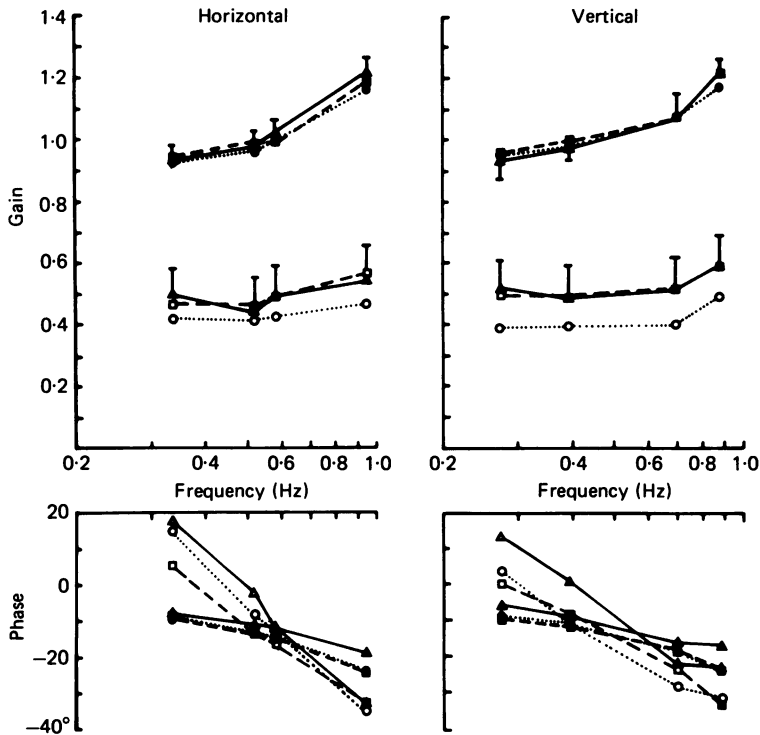


Fig. 5. Results for same subjects as in Fig. 4 for pursuit of the pseudo-random target motion with the higher band width (Table 1, sum 2).

## Pseudo-random motion

Figs. 4 and 5 show Bode plots of the mean results for the same five subjects illustrated before for two pseudo-random stimuli (with different band widths; Table 1, sums 1 and 2) used under four different experimental conditions: horizontal or vertical target movements only and combined horizontal and vertical target movements with a maximum amplitude of 7·07° or 10° in horizontal and vertical direction.

*Composite eye movements.* The gain of the composite eye movement induced by the pseudo-random stimuli showed a remarkable trend. It increased from a value of about unity for the lowest frequency component in the stimulus to a value above 1·1 for the highest frequency component. The spectral composition of the stimulus influenced the gain of the composite eye movement. Although the two pseudo-random stimuli contained three components of the same frequency, the stimulus with the higher

frequency range resulted in lower gains of the composite eye movement for identical frequency components.

The phase lag of the composite eye movement during pursuit of pseudo-random stimuli was larger than during pursuit of single sine-wave stimuli and in contrast to single sine-wave stimuli it increased with frequency. The spectral composition of the pseudo-random stimuli influenced the phase of the composite eye movement. Although both pseudo-random stimuli had three components in common, the stimulus with the highest frequency range produced larger phase lags of the composite eye movement over the whole frequency range.

*Smooth eye movements.* The gain of the smooth eye movements also showed a tendency to increase with the frequency (Figs. 4 and 5). Concomitantly with the larger contribution by saccadic pursuit, smooth pursuit gain was relatively low. In all cases it was considerably lower than for single sine waves of comparable frequencies. Furthermore, smooth pursuit gain was lowered by an increase in band width (cf. Figs. 4 and 5), even for identical frequency components occurring in both spectra. The gain of the smooth component showed no systematic difference between pursuit of one-dimensional and two-dimensional target motions for the two pseudo-random stimuli.

The phase of the smooth pursuit component showed a lead for the lowest frequency component of both pseudo-random stimuli. For the stimulus with the lower frequency range (Fig. 4) this phase lead was 12° at 0·15 Hz for the horizontal component and 3° at 0·21 Hz for the vertical component. For the pseudo-random stimulus with the higher frequency range (Fig. 5) a similar phase lead for the horizontal smooth component was found at a higher frequency (12° at 0·34 Hz) while the phase lead for the vertical smooth component was 6° at 0·28 Hz. Only the smooth pursuit component showed a phase lead at these frequencies; the composite eye movement always showed a phase lag. The phase lead of the smooth pursuit component changed into a lag with the increase of frequency. This change was larger than for the phase of the composite eye movement. The phase lag of the smooth component at the highest frequency component in both pseudo-random stimuli was larger than the phase lag of the composite eye movement at these frequencies. The phase of the composite and of the smooth eye movement showed no systematic differences between the one-dimensional and two-dimensional pursuit tasks.

The results for horizontal and vertical eye movements in these measurements are not completely comparable because different frequencies had to be used to form the sum for the horizontal and vertical components of the target movement (uncorrelated horizontal and vertical target movements were used; see Table 1, sums 1 and 2). In any case no clear differences were found. Furthermore, a smaller maximum amplitude of the target (7·07° *vs.* 10°) resulted in significantly higher gain of the smooth component (mean difference 0·085 ± 0·067 s.d.; $P < 0.001$).

*The effect of amplitude.* To measure the effects of amplitude and direction (horizontal or vertical) more reliably, a separate series of measurements was made in which the five subjects had to pursue similar pseudo-random target motions with maximum amplitudes set at 2, 5 and 10°. Horizontal and vertical motions consisted of uncorrelated sums of sine waves (Table 1, sums 3 and 4). A series of measurements in which sum 3 was the horizontal and sum 4 the vertical stimulus was complemented

by a series in which sum 3 was the vertical and sum 4 the horizontal stimulus. In this way, by suitable recombination of the responses, amplitudes as well as directions could be compared. Fig. 6 shows the horizontal and vertical responses to the pseudo-random stimulus with the band width 0·21–0·95 Hz (sum 4), obtained during two-dimensional tracking.
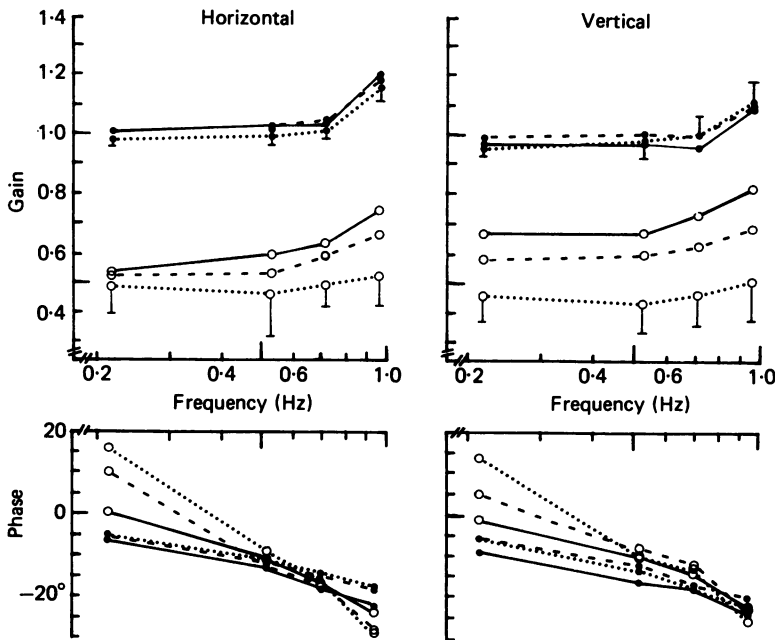


Fig. 6. Gain and phase of the composite (filled symbols) and cumulative smooth eye movements (open symbols) in response to a two-dimensional pseudo-random target motion shown at different amplitudes: 2° (continuous lines), 5° (dashed lines) and 10° (dotted lines). Composition of target motion: Table 1, sum 4. Means ± s.D. for five subjects.

The general trends of gain and phase were similar to those described above (Figs. 4 and 5). The gain of the composite eye movement was not significantly influenced by the stimulus amplitude, although the stimulus velocities varied by a factor of 5. This was true for both the horizontal and vertical component of the eye movement. However, the gain of the horizontal component was systematically higher than that of the vertical component (mean difference $0·06 \pm 0·11$ s.D.; $P < 0·001$). The phase lag of the composite eye movement increased with frequency, as described before, and in addition it tended to be somewhat larger for a smaller stimulus amplitude. However, the differences were very small.

The gain of the smooth component was markedly affected by the amplitude of the stimulus. A larger stimulus amplitude resulted in a lower gain. The difference was significant over the whole frequency range for the horizontal as well as the vertical component of pursuit, although vertical pursuit was most affected by amplitude. The mean decrease of smooth pursuit gain in the horizontal direction was $0·04 \pm 0·06$ (s.D.) when the maximal stimulus amplitude increased from 2 to 5° and $0·09 \pm 0·06$ (s.D.)

when amplitude increased further from 5 to 10°. All these differences were highly significant ($P < 0.001$).

On the other hand, these measurements do not show a consistent difference in performance between horizontal and vertical pursuit. For the 10° stimulus vertical pursuit was slightly inferior to horizontal pursuit but for the 2 and 5° stimulus amplitudes the opposite was the case.

An increase in stimulus amplitude also had a marked effect on the phase of smooth pursuit. At low frequencies a larger amplitude caused a relative advance of phase, whereas at higher frequencies the phase lag was augmented. Thus, the characteristic phase lead around 0·2 Hz seen for a stimulus amplitude of 10° (Figs. 4, 5 and 6) decreased to almost zero when the stimulus amplitude was reduced to 2°, resulting in a much flatter course of phase as a function of frequency.

### Triangular waves

In contrast to sine-wave stimuli, triangular-wave stimuli have a constant velocity which only reverses direction twice in each period. To measure the pursuit performance with constant stimulus velocity we used triangular-wave stimuli with the same frequencies (0·15, 0·28 and 0·52 Hz) as the single sine-wave stimuli and in addition frequencies of 0·06, 0·09 and 0·12 Hz, all at amplitudes of 7·07 and 10°. This resulted in target velocities ranging from 1·7 to 20·8°/s. We excluded the corners of the triangular-wave stimuli from the calculation of gain of the composite and cumulative smooth eye movements.

The gain of the composite eye movement was unity for all frequencies, directions of target movement and stimulus situations. Although there was a progressive shift from smooth towards saccadic pursuit when the stimulus velocity increased from 1·7 to 20·8°/s, the amplitude of the composite eye movement remained equal to the target amplitude and the gain was independent of velocity.

The gain of the smooth components was first calculated separately for the different directions. There was no significant difference in the gain of the smooth component between right-ward and left-ward or between upward and downward pursuit. However, the gain of the vertical smooth component was systematically lower than the gain of the horizontal smooth component (mean difference $0.036 \pm 0.076$ s.d.; $P < 0.02$).

Fig. 7 $A$ and $B$ summarizes the smooth pursuit gain for triangular target motion in the vertical direction (up and down pooled) and in the horizontal direction (right- and left-ward pooled). Average values are shown for five subjects, during pursuit of one-dimensionally moving (amplitude 10°, horizontal or vertical target movements only) and two-dimensionally moving triangular-wave stimuli (combined horizontal and vertical target movements with an amplitude 7·07 or 10° each). The gain of the smooth pursuit component decreased from 0·96 at 1·7°/s to 0·58 at 20·8°/s (means of five subjects and of the horizontal and vertical components). The standard deviations of the gain of the smooth component were relatively small for the triangular wave of 1·7°/s, but increased when the velocity increased to 20·8°/s. This relative increase was due to the differences between subjects.

As can be seen in Fig. 7, smooth pursuit gain was especially reduced by an increase in target velocity. However, an additional decrease in horizontal and vertical smooth
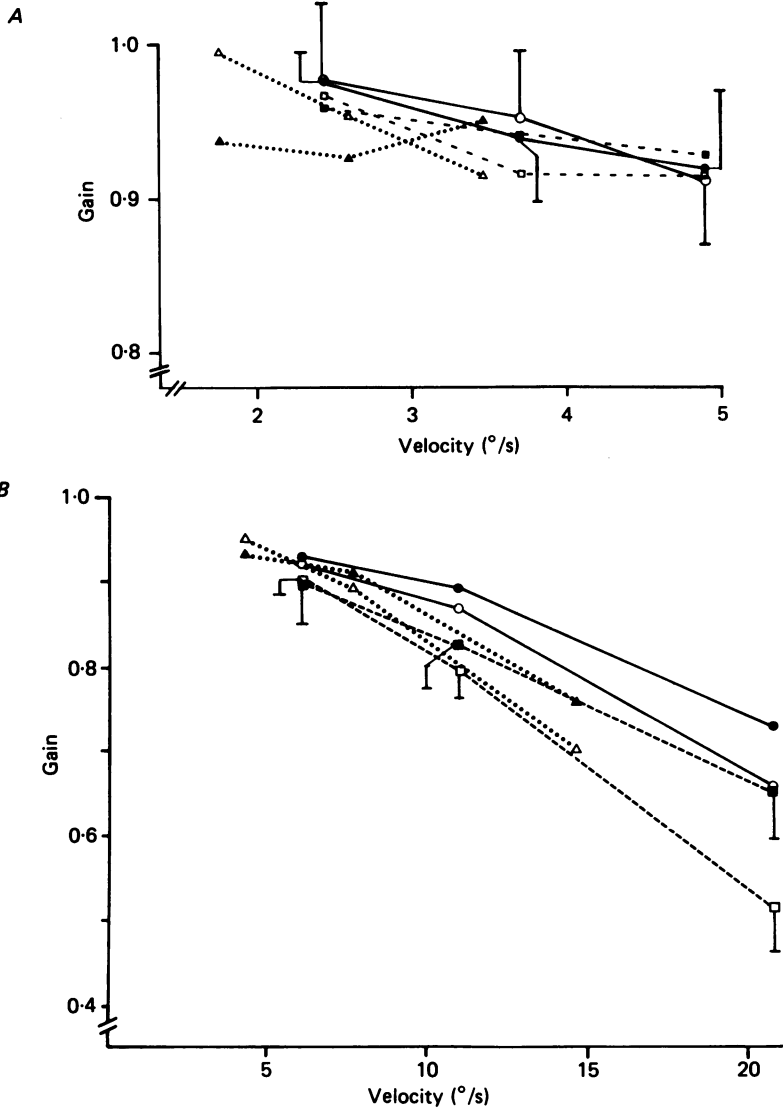
Fig. 7. Gain of the horizontal (filled symbols) and vertical (open symbols) smooth eye movement in response to triangular-wave stimuli moving in one dimension with an amplitude of 10° (continuous lines), or in two dimensions simultaneously with an amplitude of 7·07° (dotted lines) or 10° (dashed lines). Means ± s.D. for five subjects for low (*A*) and high (*B*) target velocities.

pursuit gain occurred when the horizontal and vertical target motions were combined into a two-dimensional rhomboid trajectory. It should be emphasized that gain was calculated as the ratio horizontal eye movement/horizontal target movement (and similarly for the vertical component). Therefore, the inputs to the horizontal and vertical systems remained unchanged by the two-dimensional presentation, although the total (vectorial) target velocity was increased.

*Pursuit upon a diffuse or structured background*

The main effect of a structured background was a slowing down of smooth pursuit and, concomitantly, the insertion of more saccades.

*Sinusoidal (circular) motion*

An example of the effect of a structured background upon pursuit of a circular target trajectory is shown in Fig. 2. Bode plots of the mean gain and phase of the composite and the smooth eye movements during pursuit of circular target motion are shown in Fig. 8. Only the results for the two-dimensional stimulus condition with
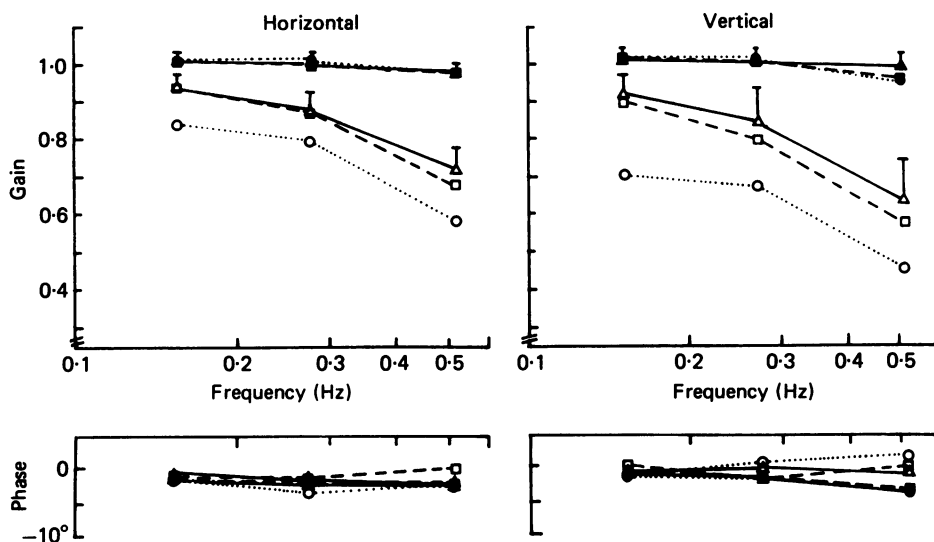


Fig. 8. Gain and phase of composite (filled symbols) and cumulative smooth eye movement (open symbols) during pursuit of circular stimuli with an amplitude of 10° upon a dark (continuous lines), diffuse (dashed lines) or structured background (dotted lines). Means ± s.D. for five subjects.

a maximum amplitude of 10° will be presented in detail to illustrate the effect of the background. The other stimulus conditions (horizontal or vertical target movements only with an amplitude of 10° and two-dimensional target movements with a maximum amplitude of 7·07°) showed the influence of a background on pursuit eye movements to a similar extent. The introduction of a diffuse or structured background (random dot pattern, elements 15 minutes of arc) did not systematically change the gain of the composite eye movement. The amplitude of the sum of the smooth and saccadic eye movements during pursuit upon a diffuse or a structured background remained comparable to the amplitude of the eye movements during pursuit without a visible background. The gain of the smooth eye movements was also unaffected by a diffuse background, but lowered by a structured background. The average decrease in gain of the smooth component for single sine-wave stimuli was $0·07 \pm 0·08$ (s.D.; $P < 0·001$) for the horizontal component and $0·19 \pm 0·13$ (s.D.; $P < 0·001$) for the vertical component. Clearly, vertical smooth pursuit was more inhibited by a back-

ground than horizontal pursuit. The phase of neither the composite nor the smooth eye movement was systematically changed by a background.

*Pseudo-random motion*

The influence of a background on pursuit of pseudo-random motion was generally similar to that on pursuit of single sine waves. The gain and phase of composite eye movements remained unaffected. The gain of the smooth component did not change with a diffuse background, but was lowered by a structured background. When this consisted of the random dot pattern with elements of 15 minutes of arc, the mean decrease was $0.08 \pm 0.09$ (s.d.; $P < 0.001$) for the horizontal and $0.19 \pm 0.10$ (s.d.; $P < 0.001$) for the vertical component (results for two pseudo-random stimuli, Table 1, sums 1 and 2, pooled). Just as we found for the circular trajectory, vertical smooth pursuit was more severely inhibited than horizontal pursuit. Also in agreement were the results for phase: this was not systematically changed by a background.

*Effects of structure of background.* To investigate which properties of the background were important, a pseudo-random motion was pursued on twelve different backgrounds (specified in Methods) which differed in orientation (horizontal or vertical bars), sharpness of contrast (square-wave or sinusoidal grating), size of the elements and regularity (random dot or checkerboard).

Orientation was a significant factor. Horizontal smooth pursuit was more inhibited by vertical than by horizontal edges, and vice versa. Thus, pursuit was more decreased when the eye moved across edges than when it moved parallel to edges. The mean difference in gain was small ($0.04 \pm 0.1$ s.d.) but significant ($P < 0.001$).

Sinusoidal and square-wave gratings caused a similar decrease in smooth pursuit gain. Also the size of the elements (in the range tested) and the regularity of the pattern proved to be immaterial for the magnitude of the effect. In summary, the specific structure of the background was only of marginal importance.

*Effect of amplitude of target motion.* Using the same pseudo-random target motions (Table 1, sums 3 and 4) as in the investigation of the amplitude effect without background, the effect of the amplitude of the target motion was measured with a random dot background containing elements of $2.1°$. The results are shown in Fig. 9. Compared with the results without background (Fig. 6), all smooth pursuit gains were lower. The mean decrease was $0.20 \pm 0.13$ (s.d.) for a stimulus amplitude of $2°$, $0.18 \pm 0.1$ (s.d.) for an amplitude of $5°$ and $0.15 \pm 0.08$ (s.d.) for an amplitude of $10°$. Thus, smooth pursuit of a target moving at a smaller amplitude (with lower velocity) had a relatively higher gain without background but was on the other hand also more inhibited by a background than pursuit of a larger target motion.

*Triangular waves*

A structured background had a similar effect on the pursuit of a triangular wave form. Also in this case, the gain of the composite eye movement was not systematically affected by a diffuse or structured background. However, the contribution of the smooth component to the total eye displacement decreased when a background was present. This decrease was very small for the diffuse background: $0.03 \pm 0.08$ (s.d.; $P < 0.02$) for the horizontal component and $0.03 \pm 0.06$ (s.d.; $P < 0.01$) for the vertical component (mean values for the triangular wave forms with frequencies of
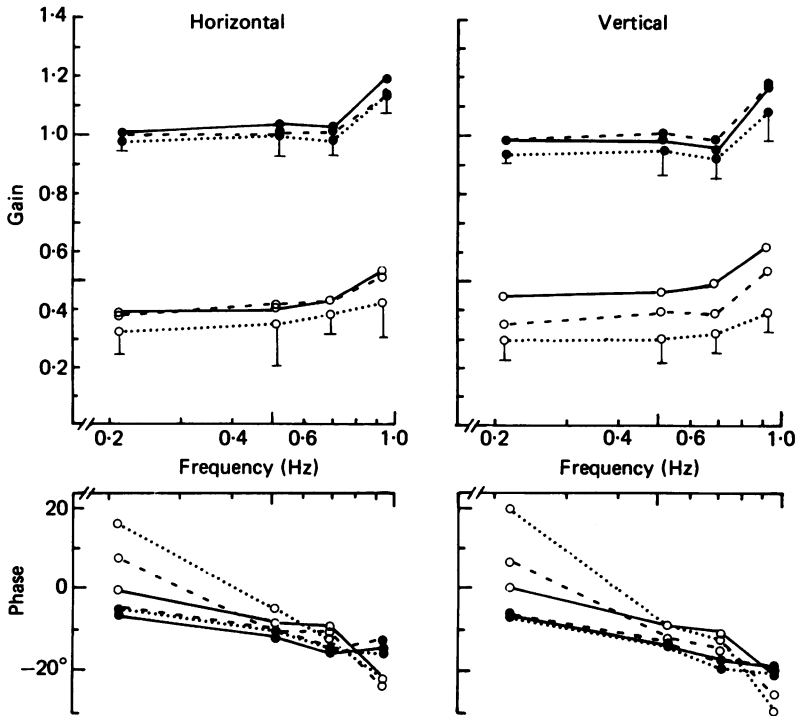
Fig. 9. Gain and phase of the composite (filled symbols) and cumulative smooth eye movement (open symbols) in response to a two-dimensional pseudo-random target motion (Table 1, sum 4) with different amplitudes: 2° (continuous lines), 5° (dashed lines) or 10° (dotted lines) upon a random dot background with elements of 2·1°.

0·15–0·52 Hz). The decrease was larger for the structured background: $0·09 \pm 0·08$ (s.d.; $P < 0·001$) for the horizontal and $0·17 \pm 0·10$ (s.d.; $P < 0·001$) for the vertical component. These values are comparable to those obtained with the sine-wave stimuli.

On the basis of these results we conclude that the presence of a large stationary structured background has an inhibitory influence on smooth pursuit eye movements; vertical smooth pursuit is more inhibited than horizontal smooth pursuit. The inhibition of smooth pursuit is fully compensated by the more frequent insertion of saccades in order to pursue the target with the proper amplitude. The influence of diffuse illumination of the background on smooth pursuit is minimal.

### Performance in the time domain

#### *Retinal position error during pursuit on a dark background*

The main purpose of pursuit eye movements is to keep the image of the target within the foveal area. If the target moves away from the foveal centre, a retinal position error between the centre of the fovea and the image of the target will occur. The distribution of this error in time is a measure of the quality of pursuit. Under the assumption of a normal distribution it can be characterized by a mean value and a standard deviation.

Some typical examples of retinal position error (target position minus eye position) as a function of time during pursuit of a stimulus in two-dimensional pseudo-random motion upon a dark (n.b.) and a stationary random dot background (B.) are shown in Fig. 10, which illustrates the effect of a structured background on pursuit eye movements: the smooth component slowed down and extra saccades were inserted to supplement the smooth component.
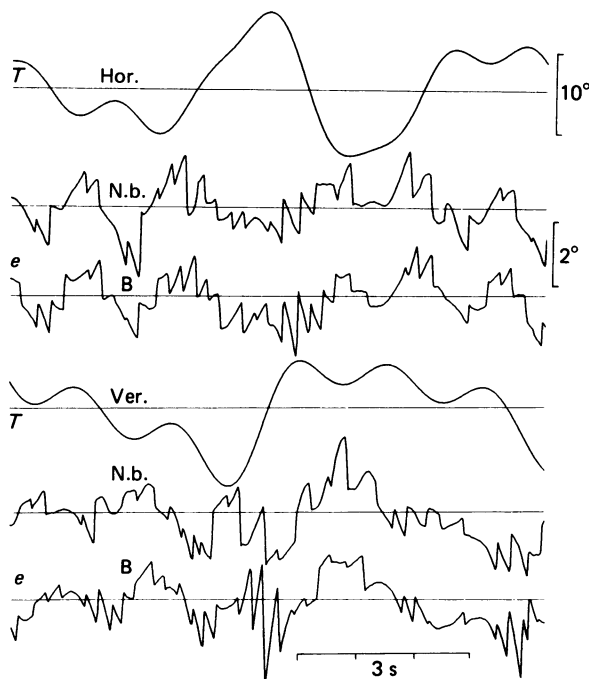


Fig. 10. Recordings of the horizontal (hor.) and vertical (ver.) retinal position error (*e*) during pursuit of a pseudo-random target motion (*T*) upon a dark (n.b.) or a structured (B) background. Notice the different calibrations for target and error.

Examples of the distribution of horizontal and vertical retinal position error are shown in Fig. 11. In principle, the distributions are bimodal, because the eye lags the target and the image of the target is in general at that side of the fovea, which is in the direction of the movement of the image (see Fig. 10). The actual distributions of retinal position error, however, show an overlap between the different parts of the distribution and the bimodality is only marginally visible (Fig. 11). Therefore, for practical purposes, we considered the distributions to be unimodal and chose the mean and standard deviation of retinal position error to characterize its distribution. Means and standard deviations were calculated for all stimulus conditions employed. The means of the retinal position error were not significantly different from zero which means that the projection of the target was distributed symmetrically around the fovea.
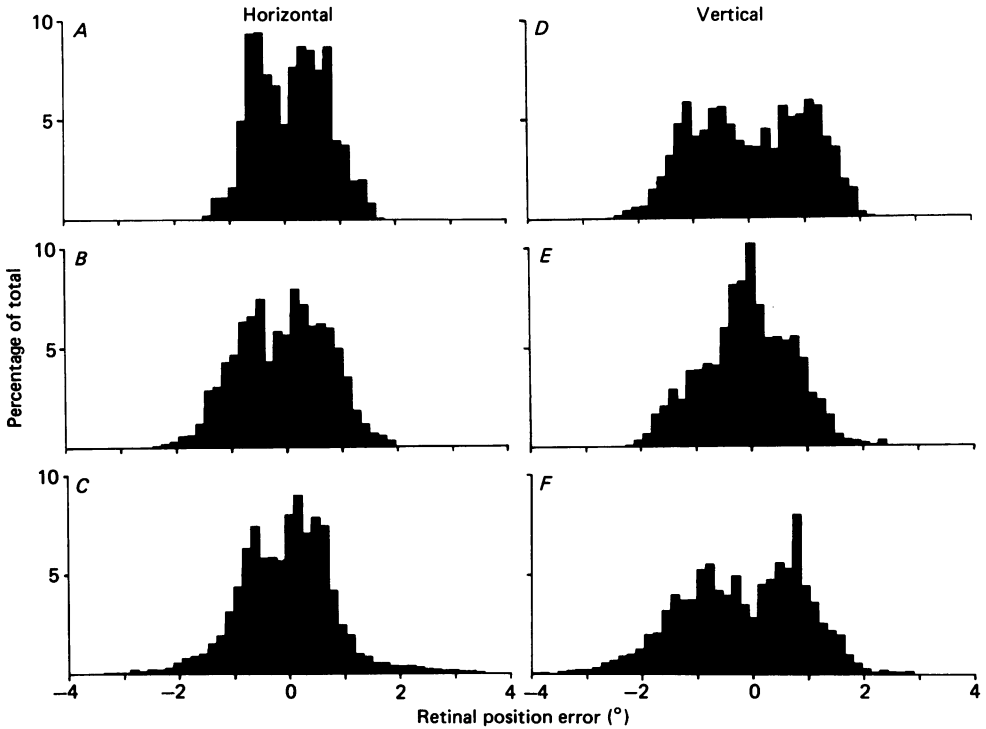
Fig. 11. Distributions of retinal position error in horizontal (*A*, *B*, *C*) and vertical (*D*, *E*, *F*) directions for a two-dimensionally moving sinusoidal stimulus with a frequency range of 0·28 Hz (*A* and *D*), a pseudo-random stimulus with a frequency range of 0·15–0·70 Hz (*B* and *E*) and a triangular-wave stimulus of 0·28 Hz (*C* and *F*).
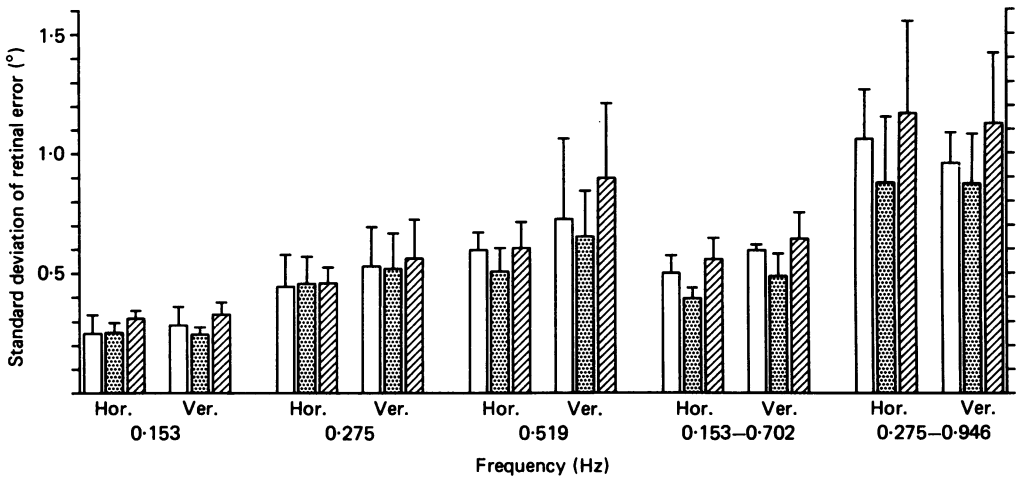


Fig. 12. Standard deviations (mean values for five subjects, s.d. of this mean is indicated by vertical lines) of horizontal (hor.) and vertical (ver.) retinal position error during pursuit of single sine-wave or pseudo-random stimuli in one dimension with an amplitude of 10° (open bars) and two dimensions with an amplitude of 7·07° (dotted bars) or 10° (hatched bars).

*Sinusoidal and pseudo-random motion*

For single sine-wave stimuli, the standard deviation of retinal position error increased with frequency (Fig. 12), from about 0·3° at 0·15 Hz to about 0·8° at 0·52 Hz. Within each frequency, two-dimensional target movements with an amplitude of 7·07° resulted in the lowest standard deviation for each frequency. For one- and two-dimensional pursuit at an amplitude of 10° the error was larger. However, these differences were small and only the difference between the responses to the two-dimensional stimuli with amplitudes of 7·07 and 10° was significant (mean difference 0·09 ± 0·12 s.d.; $P < 0.001$). The standard deviation of the vertical retinal position error was significantly higher than the standard deviation of the horizontal error (mean difference 0·10 ± 0·16 s.d.; $P < 0.01$).
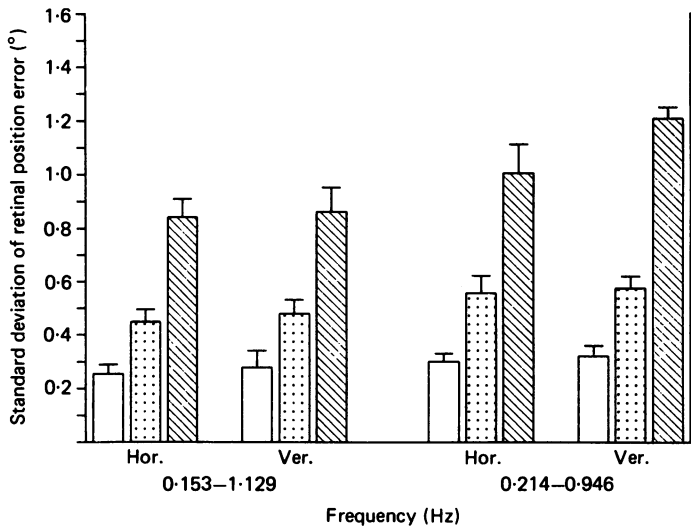


Fig. 13. Standard deviations (mean values for five subjects, s.d. for this mean is indicated by vertical lines) of the horizontal (hor.) and vertical (ver.) retinal position error during pursuit of pseudo-random stimuli in two dimensions with an amplitude of 2° (open bars), 5° (dotted bars) or 10° (hatched bars).

For the pseudo-random stimuli, the movement with the higher frequency range (Table 1, sum 2) resulted in a significantly larger standard deviation of retinal position error than the stimulus with the lower frequency range (Table 1, sum 1). Similarly, as for the single sine-wave stimuli, the standard deviation during pursuit of a two-dimensionally moving pseudo-random stimulus with an amplitude of 7·07° was lower than during pursuit of a one-dimensionally or two-dimensionally moving stimulus with an amplitude of 10° (mean difference 0·12 ± 0·11 s.d.; $P < 0.001$ and 0·22 ± 0·13 s.d.; $P < 0.001$, respectively). Due to the different spectral composition of the horizontal and vertical components it is not meaningful to compare the standard deviations of horizontal and vertical retinal position errors in Fig. 12. However, using two other pseudo-random target motions (Table 1, sums 3 and 4) in the balanced combination described before it was possible to evaluate the effects of direction as

well as amplitude on retinal position error. The regrouped results are shown in Fig. 13. In all cases, a larger stimulus amplitude resulted in a larger retinal position error. The vertical position error proved to be only marginally, although significantly, larger than the horizontal error (mean difference $0.05 \pm 0.1°$ s.d.; $P < 0.02$).

*Reproducibility of pursuit movement.* To investigate how stereotyped the pursuit movements (and thus the retinal position error) for the same target motion in
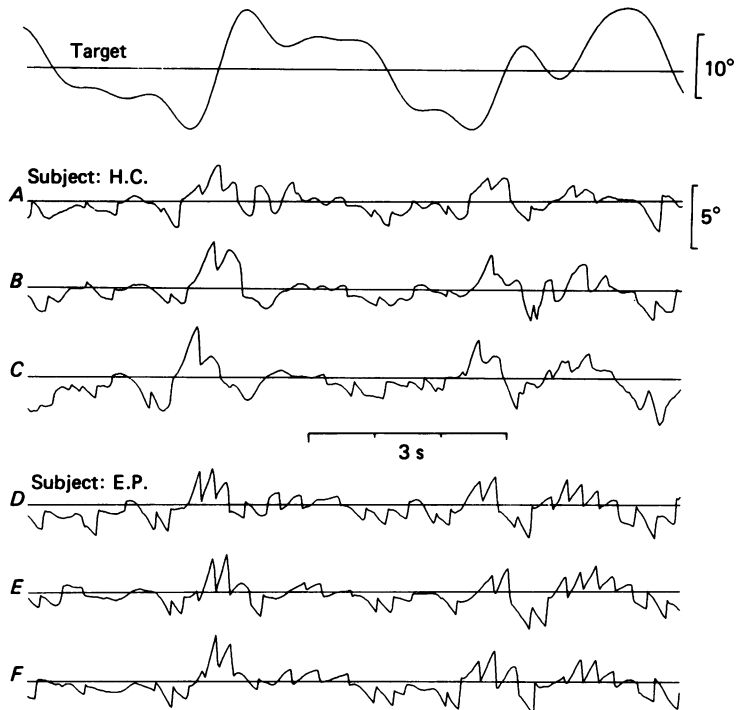


Fig. 14. Recordings of horizontal target movement and retinal position error of two subjects for three different trials under the same stimulus condition (pursuit of a pseudo-random target motion with a maximum amplitude of 10° upon a dark background). Recording $B$ and $C$ for subject H.C. and recording $E$ and $F$ for subject E.P. were obtained in the same session, separated about 20 min in time; recordings $A$ and $D$ were made in another session about one week earlier.

different trials are, some pilot experiments were done in which subjects pursued exactly the same pseudo-random target motion three times. Two of these measurements were done in the same session (with an interval of about 20 min); the third measurement was made in another session with the same subject. The recorded position errors as a function of time are shown for two subjects in Fig. 14.

Within one subject, a large similarity was found among the retinal position error traces recorded in different trials. The difference between subjects was larger than the difference between trials or sessions. Thus, the pattern of pursuit was rather constant and idiosyncratic for a particular subject. Although the strategies of the two subjects shown in Fig. 14 differed (more smooth *vs.* more saccadic), the mean standard deviation of retinal position error as a function of time and thus the quality of pursuit
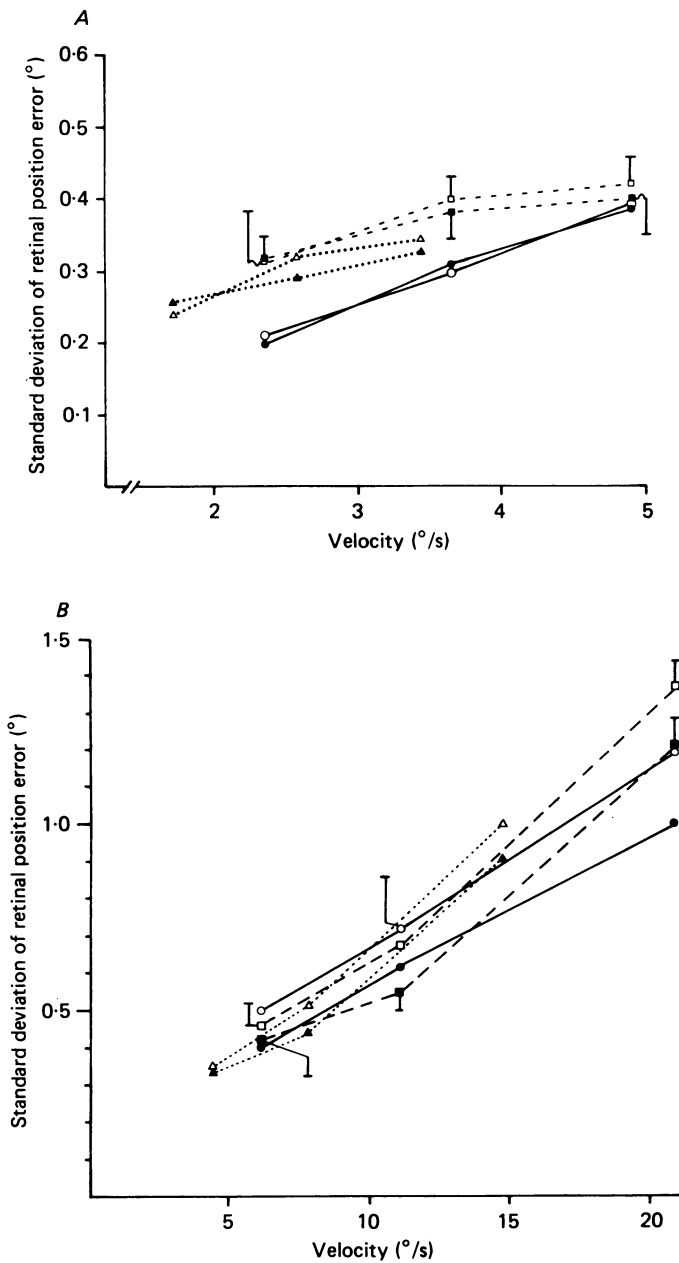
Fig. 15. Standard deviations of horizontal (filled symbols) and vertical (open symbols) retinal position error during pursuit of triangular-wave stimuli moving in one dimension only with an amplitude of 10° (continuous lines) or in two dimensions simultaneously with an amplitude of 7·07° (dotted lines) or 10° (dashed lines), for low (*A*) and high (*B*) target velocities. Means ± s.D. for five subjects.

was not significantly different between these subjects (1·17° for subject H.C.; 0·96° for subject E.P.).

*Triangular motion*

For triangular target movements, the standard deviation of retinal position error (calculated for the complete trajectory, including the corners) increased with velocity, from about 0·2° at 2°/s to about 1° at 20°/s (Fig. 15). Similarly, as for the single sine-wave stimuli, the standard deviation of retinal position error of the horizontal component was slightly lower than that of the vertical component (mean difference 0·06±0·13 s.d.; $P < 0·001$).
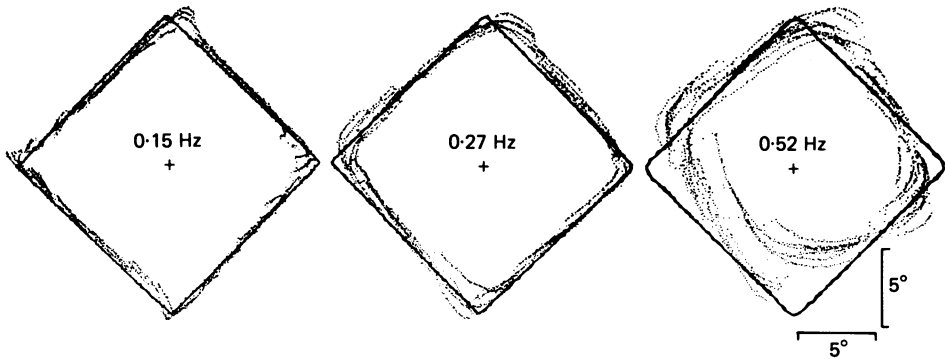


Fig. 16. Rotation of the eye movement trajectory with respect to the rhomboid target trajectory when the frequency of the target increased from 0·15 to 0·52 Hz. A period of 16·39 s of the target and eye movement recording is shown. The target moved in the clockwise direction.

*Directional errors.* A remarkable error of direction occurred in the pursuit of a rhomboid trajectory, especially when the frequency (and thus the velocity) of the target motion was increased (Fig. 16). In general, pursuit eye movements in response to a rhomboid target motion of 0·15 Hz were in the direction of the target motion. Sometimes the subject anticipated the change of direction of the target (see right corner of left rhomboid), but at other times, the eye persisted in moving into the same direction, although the target had already changed its direction (left and top corners of the left rhomboid). When the frequency of the target was increased from 0·15 to 0·52 Hz, however, eye movements were not completely aligned with the target movements: pursuit followed a somewhat tilted direction. As a result, the rhomboid trajectory of the eye movements was rotated in the direction of the target motion. It seems as though the subjects anticipated the changes of direction of the target.

*The role of saccades*

Recordings of the retinal position error (Fig. 10) indicate that saccades reduce the positional error by correcting the eye position although the remaining error is not zero. Undershoot and overshoot was associated with nearly all saccades and some saccades were not corrective at all. In order to analyse the correctivity of saccades during pursuit, scatter plots were made which show the retinal position error in the

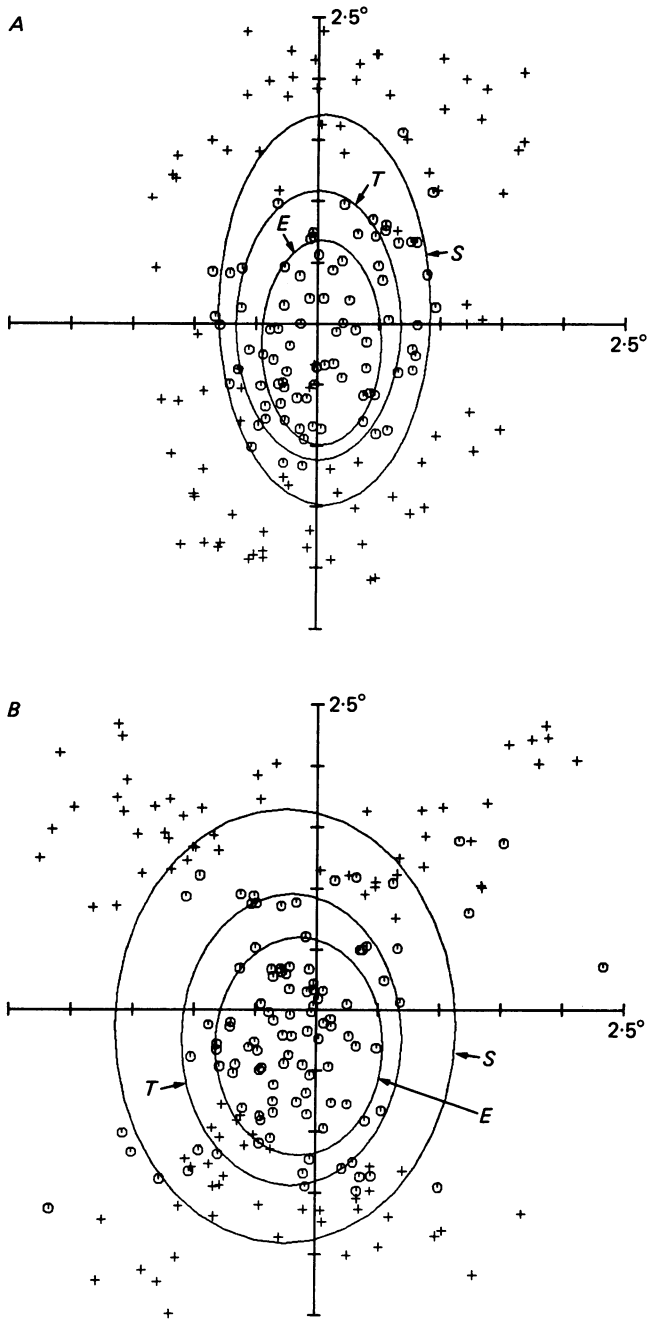Fig. 17. Diagram of combined horizontal and vertical retinal position error at the start (+) and end (○) of saccades during pursuit of a circular (*A*) or a rhomboid (*B*) target motion of 0·28 Hz upon a structured background, with insertion of three ellipses which indicate the retinal position error at the beginning of saccades (*S*), the end of saccades (*E*) and during the total measurement of 32·77 s (*T*).

horizontal and vertical direction at the beginning and at the end of saccades. Fig. 17 shows two examples of such plots for pursuit upon a structured background, one for pursuit of a circular trajectory (Fig. 17$A$, frequency 0·28 Hz, amplitude 10°) and a second for pursuit of a rhomboid trajectory of the same frequency and amplitude (Fig. 17$B$).

In Fig. 17$B$ (rhomboid trajectory) the starting points of saccades are mainly clustered around the 45° axes of the retinal position error plane. This is clearly related to the function of saccades and to the form of the trajectory of the target. Due to the presence of a structured background, smooth pursuit had a relatively low gain and saccades were mainly made to catch up with the target. Therefore the saccades were mostly in the direction of the target motion. The slopes of the rhomboid target trajectory made angles of 45° with the horizontal and vertical axes of the plane of the target movement. Accordingly, saccades in the direction of the target movement coincide with the 45° axes of the retinal position error plane. For example, a target movement from the left to the top angle of the rhomboid would result in starting points of saccades in the third (left lower) quadrant of the retinal position error plane.

Three ellipses were constructed within the retinal error plots. The centres and half the length of the axes represent the means and standard deviations of the retinal position errors. One ellipse indicates the size of the retinal position error at the start of saccades ($S$), a second the size at the end of saccades ($E$) and the third one the mean and standard deviation of retinal position error of the total measurement ($T$). The mean error during pursuit was small compared to the standard deviation of the retinal position error. Therefore, the centre of the ellipse $T$ is very close to the origin. The vertical axis of the ellipse $T$ is longer than the horizontal axis, because the standard deviation of retinal position error was larger in the vertical direction than in the horizontal direction.

Fig. 17 illustrates that saccades were not perfect corrections of the eye position as the end points of the saccades did not coincide with the origin of the retinal position error plane. Nevertheless, saccades did reduce the error as the latter was in general smaller at the end than at the start of a saccade. Accordingly, the ellipse $E$ lies completely inside the ellipse $S$. There was no sharp threshold of retinal position error at which saccades were automatically generated. The retinal position error at the start of saccades varied within and between different stimulus conditions. The starting points of saccades were not clustered in a circle or an ellipse in the retinal error plane. The location of the ellipse $T$ in between the ellipses $S$ and $E$ shows that the retinal position error during pursuit was in between the errors at the start and end of saccades.

### Effect of background on retinal position error

The effects of a diffuse or structured background upon the standard deviation of the retinal position error are shown in Fig. 18 for single sine-wave and pseudo-random stimuli. For these types of stimuli as well as for the triangular wave forms (not illustrated), the standard deviation of retinal position error increased with increasing frequency and velocity. For single sine waves the standard deviation increased from 0·28 to 0·73° when the frequency increased from 0·15 to 0·52 Hz. The standard deviations for triangular-wave stimuli were calculated for the whole trajectory,

including the corners. These values were relatively large: 0·44° for a stimulus velocity of 6·12°/s and 1·30° for 20·8°/s. The pseudo-random stimulus with the higher frequency components resulted in a higher standard deviation of retinal error than the pseudo-random stimulus with the lower frequency range: 0·89 *vs.* 0·51°. The standard deviation of the horizontal error was smaller than the standard deviation of the vertical error for single sine-wave stimuli (mean difference 0·14 ± 0·19° s.d.; $P < 0.001$) and for the triangular-wave stimuli (mean difference 0·08 ± 0·1° s.d.; $P < 0.001$).
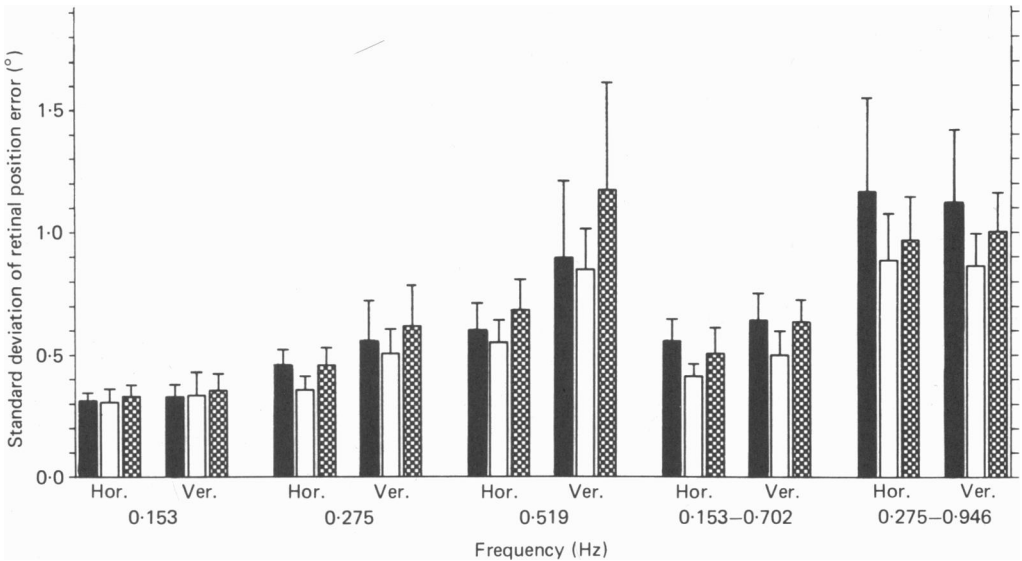


Fig. 18. Standard deviations (mean values for five subjects, s.d. of this mean is indicated by vertical lines) of retinal position error during pursuit of circular or two-dimensional pseudo-random stimuli with a maximum amplitude of 10° upon a dark (filled bars), diffuse (open bars) or a structured (checkerboard bars) background.

In nearly all situations, the standard deviation of retinal position error during pursuit upon a diffuse background was slightly lower than during pursuit upon a dark background (see open bars in Fig. 18). The mean difference for single sine-wave stimuli was 0·06 ± 0·22° (s.d.; $P < 0.02$) and for sum of sines stimuli 0·15 ± 0·18° (s.d.; $P < 0.001$). For triangular-wave stimuli the difference was not significant.

For single sine-wave and triangular-wave stimuli the standard deviation of retinal position error showed no significant differences between the pursuit upon a dark or a structured background. Although the smooth component slowed down when the structured background was introduced, the standard deviation of retinal position error was not significantly increased. Apparently the insertion of saccades was effective in preventing an increase of the standard deviation of the retinal position error. The pseudo-random stimuli were even pursued with a slightly smaller standard deviation of retinal position error upon a structured background than upon a dark background (mean difference 0·06 ± 0·16 s.d.; $P < 0.01$).

An analysis of the interaction of the type of background and the amplitude of the pseudo-random target motion showed that the retinal error was only dependent on

the amplitude of the target motion and entirely unaffected by the structure of the background.

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

### The composite nature of voluntary pursuit

Pursuit eye movements were never completely smooth. Even under conditions where background, velocity and predictability of the target movement were selected to favour smooth pursuit, it never showed a gain above 0·95 and saccades supplemented the smooth eye movements to track the target with the proper amplitude. These findings are in agreement with those of Puckett & Steinman (1969), Murphy (1978) and Kowler *et al.* (1978). The latter investigators reported that subjects could only match the velocity of slowly moving targets (2·4°/s) after considerable practice while a target moving with a higher velocity (5·4°/s) was always pursued with an appreciable retinal slip velocity. In this study we find that untrained subjects are unable to pursue targets moving at velocities between 1·7 and 20·8°/s completely smoothly and that smooth pursuit gain decreases rapidly with increasing target velocity.

Smooth pursuit and saccades subserve two different functions. The effect of smooth pursuit eye movements is to reduce the slip velocity of the image on the fovea and thereby limit the accumulation of retinal position error. This stabilization is not perfect. Therefore saccades frequently interrupt the smooth eye movements to correct the eye position. Saccades during pursuit are indeed corrective; they bring the image of the target closer to the centre of the fovea. In general, a subject makes a saccade during pursuit if the retinal error rises above a certain unacceptably high level. The saccade which is generated brings the target closer to the fovea and the remaining position error is smaller than the average retinal error during pursuit. The level of retinal position error is not constant, but varies in time and depends on stimulus conditions. The corrective saccades are not perfect and they alleviate the imprecision of pursuit only for short periods of time. The over-all retinal position error during pursuit is substantial (Fig. 10). The same kind of imperfection of pursuit and saccadic correctivity was shown by Mackeben *et al.* (1980). Apparently there is no need or it is impossible for the motor system to keep or bring the image of the target closer to the centre of the fovea. The image is kept within a region of the retina where visual acuity is high enough for the task which has to be performed: pursuing a moving single spot with a luminance well above threshold. The function of saccades is to bring the image of the target into this region whenever it slips out of it due to the insufficiency of the smooth pursuit eye movements. Therefore overshoot and undershoot is tolerated up to a certain level which can vary between subjects and depends on experimental conditions such as frequency or velocity of the target, predictability of its trajectory, etc. An interesting question is whether the saccades and the smooth pursuit eye movements would become more precise if a dynamic acuity task had to be performed, which required a better foveation of the moving target. Saccades bring the target, however, already to an area where visual acuity is relatively high. For example, Fig. 17*A* shows that during pursuit of a circular motion the standard deviation of the position of the line of sight on a single meridian was about 0·5° at the end of saccades. So, during pursuit of this trajectory, the precision of gaze with

respect to position was sufficient to permit clear vision, particularly if we consider modern acuity measurements which show that the diameter of the isoacuity area is as large as 50 minutes of arc (Millodot, 1972). It is interesting to notice that fixation of a stationary target during active oscillation of the head (Steinman, Cushman & Martins, 1982) results in a similar level of foveation to the level we found for pursuit of an oscillating target while the head was fixated, provided that the frequency and amplitude of head and target are comparable. Apparently, these two conditions result in a comparable precision of gaze, which suggests that both systems may have large parts of the visuo-motor system in common.

*The frequency response of the pursuit system*

As succinctly stated by St-Cyr & Fender (1969*a*), the behaviour of the oculomotor system is non-linear in the sense that it is not possible to predict the response to one class of target motion by linear combination of the responses to other classes of stimuli. Our results confirm this notion; frequency as such (at least in a band width up to 1 Hz) is only a weak determinant of the quality of pursuit. Gain and phase relations cannot be transferred between responses to single sinusoids and those to sums of sines, or between responses to sums of sines with a slightly different band width. Moreover, frequency responses prove to be extremely sensitive to the amplitude of the stimulus (Fig. 6). The main advantage of an analysis of the responses to single and composite sinusoidal target motion in the frequency domain is the possibility of conveniently separating the contribution of the smooth pursuit component from the composite (smooth plus saccadic) eye movement. In general, it turns out that the smooth component is the more vulnerable one, and that the relative contribution by the saccadic component increases markedly when the pursuit task is made more difficult.

For sine waves of similar amplitude, an increase of frequency is accompanied by a decrease of smooth pursuit gain (Fig. 3). However, this is more likely to be an effect of the simultaneous rise of target velocity than of frequency. A pseudo-random combination of non-harmonic sinusoids in which all components have similar maximal velocities induces a response with a relatively higher gain for the higher frequencies of the smooth as well as the composite eye movement (Figs. 4 and 5). A similar effect was found by St-Cyr & Fender (1969*a*); however, in contrast to the latter we find that the gain of composite eye movements can even exceed unity. Since the gain of the smooth component is always much lower, this overshoot must be due to saccades. It seems clear then, that in the absence of systematic velocity differences the pursuit system attempts to preferentially track the higher frequency components of a complex target motion.

Also the phase relations between eye and target motion are not an unambiguous function of frequency, but depend on the spectral composition of the stimulus. In early system-analytical investigations of pursuit (Stark *et al.* 1962; Dallos & Jones, 1963; Michael & Jones, 1966) it was noticed that phase lags of pursuit were smaller for single sinusoidal target motions than for sums of sinusoids or band-limited Gaussian noise. These differences were attributed to the degree of 'predictability' of the target motion, and Dallos & Jones (1963) modelled the transfer function of such a predictor, which was supposed to be switched on only whenever a high (cortical)

level decided that the target motion was predictable. An alternative explanation of phase lags that are smaller than expected from a linear model, avoiding the concept of prediction, was given by St-Cyr & Fender (1969a, b). They proposed that the system is not linear, and therefore phase lags do not have to follow the rules of linear systems; instead the phase lag would be mainly determined by the amount of information contained in the stimulus. A complex motion would require more central data processing and produce a larger phase lag. However, these arguments against prediction neglected the several previous reports of phase leads (Dodge et al. 1930; Westheimer, 1954; Drischel, 1958; Sunderhauf, 1960; Stark et al. 1962; Bornemann et al. 1964). Winterson & Steinman (1978) confirmed the occurrence of a phase lead of the smooth component of pursuit for frequencies below 0·5 Hz. We have found that for the composite eye movements phase is generally lagging. For single sinusoids the lag can be practically reduced to zero (Fig. 3). It is larger for pseudo-random motion, for which it increases with frequency but also with band width (Figs. 4 and 5). However, the smooth pursuit component regularly shows a phase lead. For single sine waves this lead remains very small, but for the low-frequency components of pseudo-random motion a phase lead of 10–20° was observed (Figs. 4 and 5). Phase leads as well as lags introduce a retinal error, which is partly corrected by saccades, with as a result a better behaving phase for the composite eye movement.

We interpret these phase leads as a manifestation of the anticipatory behaviour of the oculomotor system, which has been recently demonstrated for periodic as well as unpredictable target motions in elegant studies by Kowler & Steinman (1979a,b).

Also the rotation of the trajectory of the pursuit eye movements with respect to a rhomboid trajectory of the target may be due to anticipation, in this case of the directional changes of the target. Kowler & Steinman (1979a) found that subjects made anticipatory smooth eye movements during periodic steps of a small target. These smooth eye movements started about 350 ms before the displacement of the target, were independent of the frequency of the step, occurred in both horizontal and vertical meridians, were not learned and became faster as the time of the step approached. Kowler & Steinman (1979b) reported in a second paper that anticipatory smooth eye movements occurred for predictable target ramps as well. If the presence of anticipatory smooth eye movements is not only locked with a fixed interval of time to the onset of expected target displacement (such as a step or the start of a ramp), but also to the change of direction of a continuously moving target, then an increase in frequency of directional changes would lead to a larger rotation of the eye movement trajectory with respect to the target's trajectory. For the rhomboid target motion with a frequency of 0·52 Hz (right-hand rhomboid of Fig. 16) one side of the rhomboid motion had a duration of about 480 ms. If the anticipatory eye movements start 350 ms before the corner of the rhomboid, the error of direction should start after pursuit of about 1/4 of each side of the rhomboid. This is exactly what was found (Fig. 16).

Lisberger, Evinger, Johanson & Fuchs (1981) found that smooth pursuit is a function of the maximal acceleration of the target. This is not clearly supported by our results on pursuit of pseudo-random stimuli. We chose the amplitude of the frequency components of this type of stimuli to be inversely proportional to their frequency in order to obtain different components with equal maximum velocities,

independent of the frequency of the component. Since the maximum acceleration of a sine wave is proportional to its amplitude times the square of its frequency, our components had in principle a maximum acceleration which increased linearly with frequency. If the findings of Lisberger *et al.* (1981) applied for our conditions as well, we should have found a smooth pursuit gain which decreased with increasing frequency, but we did not (Figs. 4 and 5). Lisberger *et al.* (1981), however, used a completely different pseudo-random stimulus. It was essentially a single sine wave which could change its direction only when it crossed a zero-velocity point. This type of stimulus has a maximum acceleration which is determined by the frequency and amplitude of the sine wave and which is present twice in each period of the sine. We used a sum of four sine waves of different frequencies and although a maximum acceleration is defined for each of those frequencies when they are used as single sine-wave stimuli, the composite signal contains only one maximum acceleration which is present only once in the complete recording period. Therefore, a straight-forward comparison of our results with those of Lisberger *et al.* (1981) is not possible.

*Effect of target velocity*

An increase in target velocity consistently led to a decrease in gain of smooth (but not of composite) pursuit movements. This was particularly clear in the responses to triangular waves (ramps), for which smooth pursuit gain decreased monotonously throughout the target velocity range used (1·7–20·8°/s). Our findings (Fig. 7) agree well with those of Murphy (1978, his fig. 2) and once more refute the older opinion (Westheimer, 1954; Rashbass, 1961) that smooth pursuit matches target velocity up to about 30°/s with saturation effects only above this range. The same decline of gain with increase in stimulus velocity is found in optokinetic responses to large moving patterns (Van Die & Collewijn, 1982; Collewijn *et al.* 1982*a*). The results of these optokinetic experiments cannot be strictly compared to the present ones, as Van Die & Collewijn instructed their subjects to follow the pattern as a whole, not a particular detail. The decline of gain as a function of velocity appears to be steeper in the case of a single point target than for a large stripe pattern. This might be due to the size of the pattern or to the continuity of motion in one direction in case of the optokinetic stimulation, but this will have to be investigated in experiments in which both types of stimulus are directly compared.

The relation between target velocity and smooth pursuit gain is probably a major cause of the effect of frequency (below 1 Hz) on the smooth pursuit of single sine waves (Fig. 3) and the effect of amplitude on the pursuit of pseudo-random motion.

*The retinal position error*

Apart from their inability to uniformly describe pursuit behaviour, gain and phase relations are hard to interpret in terms of the precision of pursuit. In this respect the positional mismatch between the retinal projection of the target and the centre of the fovea as a function of time is easier to interpret in terms of visual function. The retinal position error reflects the precision of the pursuit movement as a whole, and is a product of smooth as well as saccadic tracking. For our stimulus conditions the standard deviation of retinal position error varied between about 0·2 and 1·3°. It increased under all conditions for which smooth pursuit decreased, even though the

gain of the composite eye movements remained at or exceeded unity. This is because saccades correct position only momentarily and imperfectly, while smooth pursuit with sufficient gain limits positional error over a longer time. The standard deviation of positional error increased monotonously with target velocity during pursuit of ramps (Fig. 15). This may again largely account for the effects of frequency for single sinusoids (Fig. 12) and amplitude for pseudo-random motion (Fig. 13).

On the basis of the findings for triangular target motion (Fig. 15) we can estimate that for velocities up to about 5°/s the standard deviation of positional error is smaller than 25 minutes of arc, which means that the target is projected for 68 % of the time within the isoacuity area according to Millodot (1972). This estimate is probably on the pessimistic side since the inversion points of the triangle were included in this calculation. For pursuit of circles with a constant velocity, a similar error of about 0·5° (s.d.) was reached at a frequency of 0·28 Hz with an amplitude of 10°, corresponding to a constant target velocity of 17·3°/s. Once more, the shape of the trajectory has a large effect on the quality of pursuit. For the pseudo-random motions velocity fluctuated continuously and could occasionally reach four times the maximal velocity of the four components by summation. In view of this random distribution of velocity, its role in determining the difference in responses to different pseudo-random motions is difficult to estimate. For similar pseudo-random motions, the error is proportional to the amplitude of the target motion (Fig. 13), which is compatible with a dependence on velocity but of course also on acceleration.

*Effects of a background*

Our results show an interaction between voluntary pursuit and the presence of a stationary structured background. Smooth pursuit is slowed down by the presence of a structured background. The resulting deficiency of pursuit is compensated by the more frequent insertion of saccades. The net result is a shift from smooth towards saccadic pursuit while the over-all accuracy of gaze is maintained, both in terms of the gain and phase relationship between eye and target movement and in terms of retinal position error. The specific structure of the background is only of marginal importance. The reduction of smooth pursuit was present with all types of stimuli and relatively larger for a slow target motion, probably because a slow relative background motion is a more effective stimulus than a faster moving one.

The inhibition of smooth pursuit by a stationary background is relatively weak. One reason may be the structure of the visual system, in which central vision is heavily favoured in terms of retinal ganglion cell density and cortical magnification factor. Also for optokinetic responses the influence of the central part of the visual field is disproportionally large compared to that of the periphery (see Van Die & Collewijn, 1982). A second important factor is probably selective attention to the target. It has been shown that the control of eye movements can be voluntarily shifted to different targets with different (extrafoveal) locations (Collewijn, Curio & Grüsser, 1982*b*).

Kowler *et al.* (1978) found no effect of a homogeneous background on smooth pursuit eye movements. Since there are no structures in this type of background, except for the edges, no retinal slip signal from this background will arise when a target is pursued and there is no conflict between central and peripheral retinal slip.

In agreement with Kowler *et al.* (1978) we found only a minimal effect of a diffusely illuminated background. For all types of target motion, the standard deviation of retinal position error was slightly smaller (Fig. 18) during pursuit upon a diffuse background than during pursuit upon a dark background. Differences in contrast could be the cause of these differences. The difference in luminance between target and background was larger for the dark background than for the diffuse background, because we used the same target luminance for all measurements, independent of the type of background. During pursuit upon a diffuse background, the target appeared to be more circumscript, due to the absence of any radiation or halo effect, which was sometimes present during pursuit upon a dark background. The smaller and better defined target probably enabled or necessitated the pursuit system to track with a smaller position error and to insert saccades more frequently to foveate the target, which resulted in a smaller standard deviation of retinal position error.

Our results contrast with the findings of Ter Braak (1957, 1962) who found a relative facilitation of pursuit in the direction opposite to the movement of the background. It remains unclear, however, whether this was a true facilitation or an effect of the relative velocity difference between target and background. If the velocity difference between target and background is large, e.g. when target and background are moving in opposite directions, the background will be less effective as a stimulus. If on the other hand there is a small velocity difference between target and background, e.g. when target and background are moving in the same direction with different velocities, then the background will interact more with the smooth pursuit eye movements. In the absence of the actual values for velocity of target and background used by Ter Braak, it is hard to compare his findings with our results.

Hood (1975) did some preliminary experiments on pursuit of a target which moved in darkness or upon a striped background. In normal subjects he found no effect. The background in his experiments, however, contained relatively little contrast (narrow white stripes at intervals of 15°) and was possibly not a very effective stimulus on the peripheral retina during foveal pursuit. The difference in recording technique could also account for the different results obtained. Most saccades during pursuit are small ( < 1·0°) and only revealed by a very precise recording technique. Hood (1975) did find an effect of the striped background on pursuit in patients with cerebellar lesions. This effect was similar to, but much stronger than the one we have recorded in normal subjects. It is well known that the cerebellum (particularly the flocculus and paraflocculus) is important for normal pursuit in primates (Zee, Yee, Cogan, Robinson & Engel, 1976; Zee, Yamazaki, Butler & Güçer, 1981). Therefore, cerebellar pathology may make the remaining smooth pursuit function more susceptible to disturbing influences such as those exerted by a background.

*Effects of direction and dimensionality*

We found that horizontal pursuit contained a higher proportion of smooth pursuit and was more accurate in terms òf retinal position error than vertical pursuit. Also, vertical pursuit was much more inhibited by a structured background than horizontal pursuit. This might be due to a difference in training in horizontal and vertical tracking. Kowler *et al.* (1978) showed that subjects were able to pursue slowly moving targets completely smoothly, i.e. without saccades, only after considerable practice.

In daily life most objects which are pursued move in a more or less horizontal plane (the predominant direction of locomotion and traffic) and subjects get an everyday training in horizontal pursuit. It would be interesting to investigate whether subjects can be trained to pursue vertically with the same gain as horizontally. If this is so, the difference between horizontal and vertical tracking is not fundamental.

Goodwin & Fender (1973) described a small interaction in the case of simultaneous horizontal and vertical pursuit. Tracking of a single sine wave in one direction slightly deteriorated when a Gaussian random motion (with limited band width) was tracked in the orthogonal direction. However, this effect was small. We also found small effects of dimensionality but these were somewhat variable and may depend on the over-all configuration of the target's trajectory. In the case of a sinusoidal motion, a one-dimensional motion was pursued with a lower smooth pursuit gain than a two-dimensional circular trajectory of the same frequency and amplitude (Fig. 3). This might be due to the extremely simple shape of a circular trajectory in which velocity and (centripetal) acceleration are constant, velocity being equal to the maximal velocity of the orthogonal components. Differences in retinal error for one and two-dimensional pursuit (amplitude 10°) were not significant. For pseudo-random target motions in both dimensions pursuit is not systematically different from that for one-dimensional motion. In this case, the two-dimensional task did not offer a simplified trajectory since horizontal and vertical motions were uncorrelated. A rhomboid motion was pursued with a lower smooth pursuit gain and a somewhat larger error (both horizontally and vertically) than the horizontal and vertical components separately. This trend was even present when the amplitude was reduced from 10 to 7·07°, to limit the total vectorial velocities to the velocity of the one-dimensional components. The difference may be again due to the over-all appearance of the trajectory, which in the two-dimensional case contains twice as many turning points with changes of direction, whereas the straight trajectories are twice as short as in the one-dimensional case.

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