HUMAN FIXATION AND VOLUNTARY PURSUIT: THE INTERACTION BETWEEN CENTRAL AND PERIPHERAL MOTION STIMULI

MENSELIJKE FIXATIE EN OOGVOLGBEWEGINGEN: DE INTERAKTIE TUSSEN CENTRALE EN PERIFERE BEWEGINGSSTIMULI

PROEFSCHRIFT

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PROMOTOR : PROF. DR. H. COLLEWIJN

aan Hermine,
aan Bastiaan en Ewoud

VOORWOORD

Velen hebben een bijdrage geleverd bij de totstandkoming van dit proefschrift. Hiervan wil ik er enkele in het bijzonder noemen:

Prof. dr. H. Collewijn als promotor, begeleider, kollega, lid van de promotiekommissie en als aandrager van vele, originele ideeen.

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Tenslotte alle proefpersonen die hun tijd en inzet ter beschikking stelden en zonder wie dit onderzoek nooit plaats had kunnen vinden.

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CHAPTER 1

INTRODUCTION

Vision is, for a human being, one of the most important senses. The basic function of vision, which is relevant for all species which have a form of vision, is spatial orientation. This function is important for postural control in tasks such as standing upright, walking around, guiding a hand to touch an object, etc. The important beneficial effect of vision above other senses is that it allows the subject to acquire information about objects not located in the close vicinity of the subject. A second function of vision, which is only found in the higher primates and which requires a high visual acuity, is the intake of symbolic information in tasks such as reading or looking at a photograph. Vision allows a human brain to collect, select and process an enormous amount of information in a relatively short period of time.

Notwithstanding the fact that we can observe almost one half of the visual world without moving our head or eyes (Fig. 1.1) only the fovea,

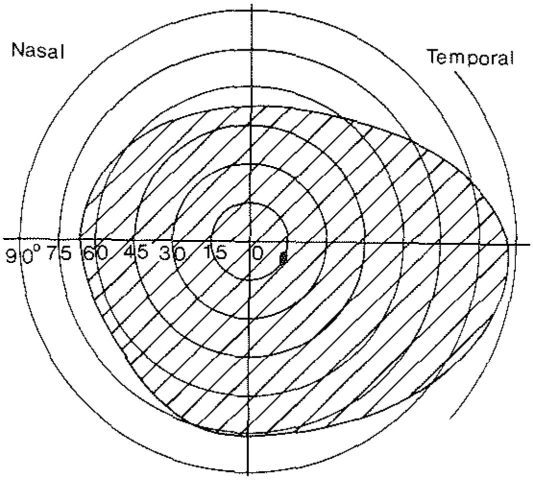


Fig. 1.1. Visual field of the right eye. The blind spot is located in the temporal half of the visual field (drawn black), from Voorhoeve, 1978.

a small part of the central retina (Fig. 1.2), is capable of resolving objects in great detail.

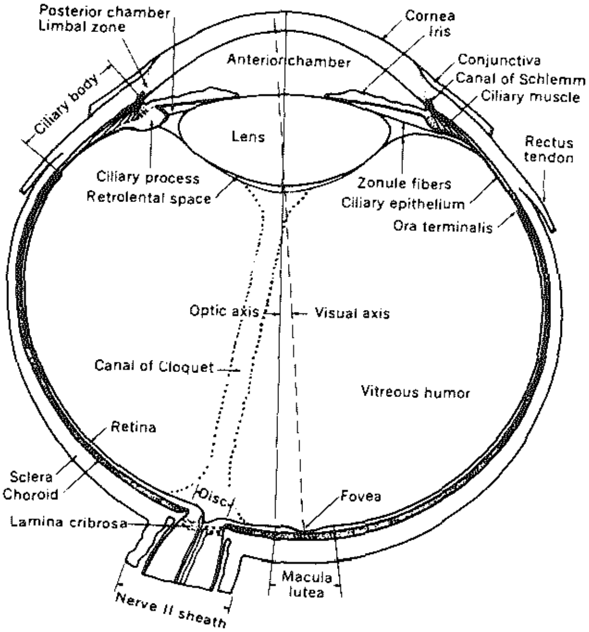


Fig. 1.2.
Horizontal section of right human eye (From Walls, 1942)

Fig. 1.3 shows the acuity as a function of the eccentricity; visual acuity is maximal in the fovea, but drops readily below 30% of the foveal level at an eccentricity of only 5°. The fovea occupies only 0.01% of the surface of the retina and thus covers only a very small part of the visual field. To enable a good observation of this visual world, the fovea must be directed at the objects of interest by means of a combination of body-, head- and eye movements. The mechanism which controls the eye position must be very precise. Accidental head and eye movements must be compensated by opposite eye movements to prevent chaotic movements of the image on the retina, but at the same time complete stabilization of the eye is not allowed because of fading of the visual image due to adaptation processes in the receptors of the visual system.

To fulfill the variety of functions of the visual system, the eye is driven by an oculomotor system which executes, in general, two different types of eye movements: (1) steplike discrete eye movements, called saccades, which rotate the eye very fast (within 10 to 100 ms) from one position to the other and (2) smooth continuous eye movements which are used to compensate for smooth head and body rotations (via the vestibular-ocular reflex in combination with the optokinetic reflex) and to pursue slowly, continuously moving objects. Fig. 1.4 shows an example of the two types of eye movement.

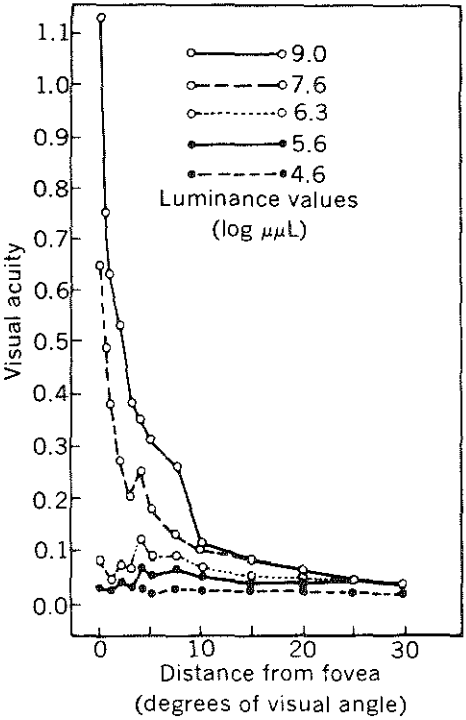


Fig. 1.3. Visual acuity as a function of distance from the fovea at five different luminance levels. Visual acuity is tested with Landolt C rings and expressed in arbitrary units on a relative scale. Measurements were made along the horizontal meridian of the retina on the temporal side (from Mandelbaum & Sloan, 1947).

Fig. 1.4. Example of a combination of the two types of eye movement: saccades (small steps) and smooth pursuit (in between saccades), from Fender & Nye, 1961.

If we want to inspect a moving object in detail, we make voluntary pursuit eye movements to keep the image of the object as close as possible to the centre of the fovea. 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 voluntary pursuit is a combination of smooth pursuit and saccades and that smooth pursuit gain (ratio of smooth pursuit velocity and target velocity or the ratio of the amplitudes of these signals) is as a rule smaller than unity (Puckett & Steinman, 1969; Murphy, Kowler & Steinman, 1975; Murphy, 1978). The contribution of smooth pursuit and saccades to the total displacement of the eye (composite eye movement) depends on various stimulus parameters such as predictability, velocity, frequency, etc. For constant velocity target movements smooth pursuit gain is near 1.0 for trained subjects and low target velocities (below 5^o/s). For higher velocity target movements, however, smooth pursuit is supplemented by saccades to maintain foveation of the moving target as pointed out recently by Mackeben, Haegerstrom-Portnoy & Brown (1980), but also visible in early recordings (e.g. Fender & Nye, 1961).

A precise study of the contribution of smooth and saccadic components requires sufficiently reliable recording and separation techniques, because eye movements are normally a combination of the two components; smooth pursuit is normally interspersed with saccades of various sizes and velocities. 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, Vossius & Young, 1962; Dallos & Jones, 1963; Michael & Jones, 1966; St-Cyr & Fender, 1969a, b; Stark, 1971; Young, 1971). In several of these studies predictability has been identified as an important stimulus parameter influencing pursuit performance. Stark, Vossius & Young (1962) and Dallos & Jones (1963) showed a clear difference between voluntary pursuit of single sinusoids and sinusoids which were a component of a pseudo-random motion. The predictability of the stimulus apparently permits both the pursuit and the saccadic component to reduce the phase lag which is inherent to their reaction time. It was later shown by Michael & Jones (1966) that predictability is not an all or nothing phenomenon but that there is a continuum of degrees of predictability of signals. The gain and phase of eye movements depend upon the degree of predictability or the narrowness of the bandwidth of the input spectrum, with wide-band random noise and single sinusoids representing the two extremes. There is no superposition of the responses to the different input signals. This clearly shows that a single linear model of the pursuit system is inadequate. Furthermore, a systematic distinction between smooth and saccadic pursuit has usually not been made in descriptive models of the pursuit system.

Other investigators (e.g. Puckett & Steinman, 1969; Murphy, Kowler & Steinman, 1975; Murphy, 1978; Lisberger, Evinger, Johanson & Fuchs, 1981) showed that pursuit performance is not determined by frequency bandwidth and predictability of the stimulus alone, but that also velocity and acceleration of the target had their influence: the gain of the smooth component decreased when either the velocity or the acceleration of the target motion was increased.

All these stimulus parameters, however, can be quantified and manipulated by the investigator. Factors such as general attention, spatial selective visual attention as well as the perception of movement, even in the absence of a really moving target, also influence pursuit performance but these factors are, in contrast to the physical parameters of the visual stimulus, difficult, if not impossible, to measure. An example of a combination of these psychophysical parameters are the experiments done by Collewijn, Curio & Grüsser (1982), who showed that subjects were able to pursue a movement illusion (Sigma-movement) in the periphery of the visual field and even switch their attention to other parts of the visual field.

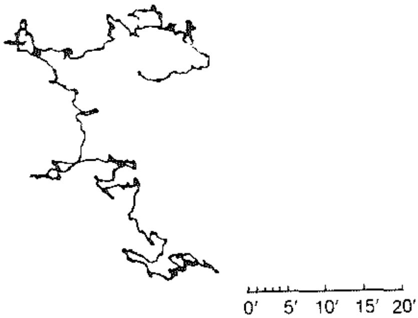


Fig. 1.5. One of the first examples of two-dimensional recording of horizontal and vertical eye movements during fixation of a small spot for a duration of 30 s (from Yarbus, 1967).

At the lower end of target velocities we find the velocity zero: a stationary target. "Pursuit" of this target motion results in a special type of eye movement: fixational eye movements. If a subject is asked to maintain foveation on a stationary target, he rotates his eyes in such a way to let the image of the target fall on the fovea, which is followed by a consistent, but idiosyncratic pattern of slow and fast miniature eye movements which keep the eye in the vicinity of the target (Fig. 1.5). This pattern has traditionally been considered to be "involuntary", "reflexive" or "spontaneous". It was shown (Fiorentini & Ercoles, 1966; Steinman, Cunitz, Timberlake & Herman, 1967; Steinman, Haddad, Skavenski & Wyman, 1973; Steinman, 1974; Steinman, Cushman & Martins 1982) that subjects were able to suppress, on instruction, the generation of miniature saccades (microsaccades) and maintain their line of sight with smooth eye movements only (Steinman, Cunitz, Timberlake & Herman, 1967, called this "slow control"). The microsaccades are not necessary to prevent a visual image from fading; the slow eye movements in combination with a high frequency tremor of the eye are sufficient to keep the image visible. Steinman, Haddad, Skavenski & Wyman (1973) suggested that one of the reasons why the saccades made during maintained fixation were described as spontaneous or involuntary was that subjects are ordinarily not aware of making them. This reason, however, is, according to Steinman, Haddad, Skavenski & Wyman (1973), not very convincing, because awareness is normally not associated with the individual acts in an overlearned motor pattern. For example, subjects are not aware of the large saccades they continuously make during reading. However, if they are asked to pay attention to their eye movements, they readily become aware that their eyes are jumping around. Once aware of each individual saccade, the overlearned pattern no longer runs itself off in exactly the same way. Similar findings can be reported for other trained motor tasks such as sports or playing musical instruments. Attention is a keyword here for the detection of an event.

One of the simplifications in most laboratory studies of pursuit and fixation is the absence of a structured background. In daily life, moving targets are normally seen against a stationary background (e.g. when one pursues a car riding in a street with buildings standing aside). Also fixation of objects is mostly done in the presence of a stationary background and sometimes even in the presence of a moving background (e.g. fixating an object in a railway station while a train leaves or enters the station behind the object). In this respect, a combination of simultaneous target and background movement is not artificial either. Fixation of an object in the presence of a stationary background might conceivably enhance the quality of fixation, if the peripheral retina were able, by using the information of the stationary background, to assist the fovea in maintaining the line of sight. On the other hand, the structures within the background might invite the visuo-motor system to scan the region around the central target and thus affect the quality of fixation in a negative way.

Pursuit of a moving object in the presence of a stationary background or fixation in the presence of a moving background will induce a concomitant (opposite) motion on the peripheral retina. The effect of this conflicting stimulus on the overall performance has been little investigated. It is theoretically possible that this conflicting stimulus by the surround is completely suppressed by a highly selective attention mechanism. Kowler, Murphy & Steinman (1978) found a non-significant interaction of a homogeneous light background with pursuit of a slowly moving target (velocity less than $6^{0}/s$). This finding does not argue for a significant interaction between target and background. On the other hand, a stationary background might inhibit smooth pursuit and a moving background might drag the eye along during fixation. Murphy, Kowler & Steinman (1975) found a modest increase in drift in the direction of the movement of a background grating (constant velocity) during fixation of a stationary target. There even might be a facilitatory effect of a background. 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 these 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. The findings of the different investigators contradict each other. This might be a result of the type of background employed in the different studies: small or large, structured or non-structured, specific structure of the background, or a result of the type of motion of the target or the background (constant velocity or sinusoidal movement).

Here I report a systematic study of

- voluntary pursuit of a foveal target
  Subjects had to pursue a single target of 7 min arc diameter as accurately as possible.

- fixation of a central target
  Subjects had to fixate a stationary target to investigate "pursuit" at a target velocity zero.

- voluntary pursuit of an eccentric target
  To test if the fovea is essential in the generation of smooth pursuit

eye movements, subjects pursued a perifoveal target. The dominance of the fovea was investigated by eccentric pursuit upon a stationary background. The instruction was to pursue the perifoveal target while the fovea was stimultated by the stationary background.

Oculomotor performance, distinguished in smooth and saccadic components, is evaluated in the

- frequency domain
  This analysis incorporated the calculation of gain and phase of the composite and the cumulative smooth eye movements with respect to the stimulus motion.

- time domain
  The retinal position error was calculated as a function of time, the quality of the eye movements is expressed in the standard deviation (S.D.) of retinal position error.

Eye movements were investigated as a function of the following stimulus variables:

- background
  To investigate the interaction between central and peripheral retina in the generation of eye movements, the targets (central or peripheral) were pursued or fixated upon three types of background: (1) dark background to present a condition without interaction; (2) diffuse background to investigate the influence of illumination of the background as such and (3) a structured background to present a motion stimulus on the peripheral retina during fixation or pursuit of a central target or to present a motion stimulus on the fovea during eccentric pursuit. I used different structured backgrounds to investigate the influence of the specific structure of the background.

- background movement
  To test if, during fixation or pursuit, eye movements are induced by a motion stimulus on the peripheral retina, not only a stationary background was applied but also a moving background.

- predictability and spectral composition of the stimulus motion
  Predictability of the stimulus motion is known to have an important

influence in the generation of smooth eye movements (see introduction above). Therefore, different motion stimuli were used: predictable (single sine wave and triangular wave stimuli) as well as non-predictable stimuli (pseudo-random motions formed by the sum of two to four sine waves of non-harmonic frequencies and different amplitudes).

- shape
  Velocity and acceleration of the stimulus motion affect the performance of the pursuit eye movements. I used (predictable) stimuli with a constant velocity (triangle wave stimuli) and stimuli which incorporate a continuous acceleration component (sine wave stimuli).

- direction and dimensionality
  The difference and independence of the horizontal and vertical pursuit eye movements are investigated by presenting the moving target in horizontal or vertical direction only or in both dimensions simultaneously. For the two-dimensional presentation, two different amplitudes are used: one in which the vectorial velocities and one in which the velocities per component (horizontal and vertical) of the one- and two-dimensional stimulus were identical.

- amplitude
  The amplitude of the stimulus influences both velocity and acceleration of the target motion and thus affects the performance of the eye movements. Therefore, subjects had to pursue a pseudo-random target motion three times, each with a different maximum amplitude in horizontal and vertical direction.

- reproducibility
  Are eye movements which are a response to a visual stimulus, stereotyped within one subject or possibly between different subjects? To get an answer to this question, some subjects pursued the same stimulus motion more than once. Only a few pilot experiments will be reported here.

- open- or closed-loop
  Normal pursuit or fixation is a closed-loop function: the visuo-motor system receives information about the effect of the eye movements by the visual feedback. One way to study the oculomotor characteristics

is to use an open-loop condition, in which eye movements made by the subject do not influence the position of the target on the retina. This open-loop condition can be created by adding the eye position to the target position. In this study, I report pursuit and fixation experiments which incorporate a visual open-loop condition.

This study was done to investigate the fundamental aspects of eye movements. On the other hand it supplied data of eye movements of normal, healthy subjects which were used as control figures in investigations of eye movements of patients. However, only the fundamental aspects will be reported here.

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

CHAPTER 2

METHODS

2.1 Subjects

Eleven different subjects, ranging in age from 21 to 47 years, were used. Some subjects were experienced in oculomotor experiments; others were not. For the results presented in the next chapters, only the data of five subjects will be described in detail (the other 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.

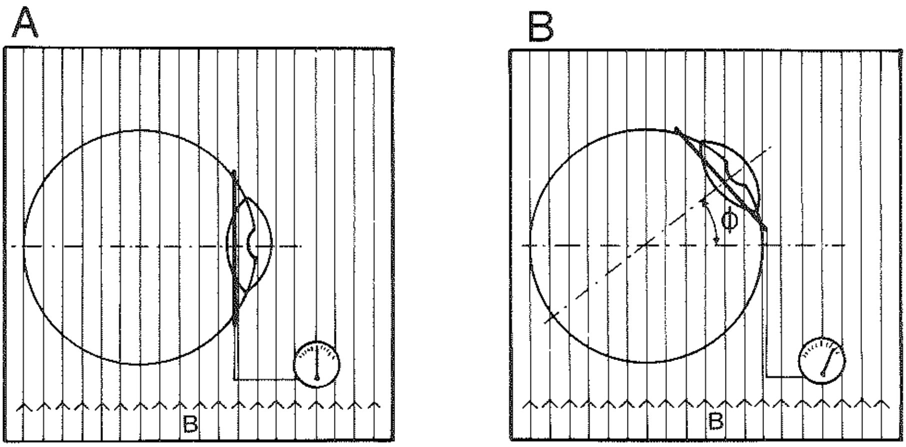


Fig. 2.1. The principle of measuring the horizontal eye position (view from above).
A:eye looking straight ahead, no potential induced in the coil because the coil is parallel to the a.c. magnetic field B.
B:eye rotated to the left. A potential is induced in the coil because a number of magnetic field lines intersects with the area of the coil. The induced potential is a measure of the rotation of the eye.

2.2 Recording technique

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). This technique enables a very precise recording of the horizontal and vertical eye position with a resolution up to 1 min arc. The basic principle of this technique is the induction of an a.c. potential in an ocular coil. Fig. 2.1 shows a schematic diagram. A coil of ten windings of copperwire of 0.05 mm diameter was embedded in a flexible silicone ring which fitted on the limbic area, concentric with the cornea. The coil was placed within a horizontal a.c. magnetic field of 10 kHz using a Helmholtz configuration. The voltage e_i induced in the coil was:

$$e_i = N\ A\ \sin\phi\ B\ \sin\omega t \qquad (1)$$

N = number of windings of the coil
A = area of the coil
ϕ = rotation of the coil
B = strength of the magnetic field
ω = radian frequency of the magnetic field

By using a phase-lock amplifier (Princeton Applied Research lock-in amplifier model 128A and 129A) a d.c. potential e_d was produced, which was proportional to $\sin\phi$. Because rotations of the eye with the induction coil were limited to 20^o, $\sin\phi$ was used as an approximation of the rotation of the eye ϕ, which resulted in a non-linearity of less than 2%. A second, vertical magnetic field, in spatial and phase quadrature with the first one, was used to measure the vertical eye movements simultaneously. The dynamic range of the recording system was better than 100 Hz and noise level less than 3 min arc.

Before the insertion of the scleral induction coil, the surface of the eye was anaesthetized with two drops of Novesine 0.4%. The ring was wetted with Ringer's solution, put on the limbus with the leads of copper wire at the side of the inner cantus and pressed firmly upon the eye. In this way, fluid between eye and ring was evacuated and the elasticity of the ring caused an underpressure which kept the ring firmly in place once it was released. Once placed, the ring could be worn during 30 to 45 min without serious discomfort. The motion of the right eye was recorded; the left eye was covered. Head movements were minimized by head and chin supports. The experimental room was almost completely dark during measurements which employed a dark background and dimly lit for measurements with a diffuse or a structured background.

2.3 Visual stimuli

The target (diameter 7 min arc) was formed by the spot of a He-Ne laser, backprojected 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 or 12 bits D/A converters, low pass filtered (-3 dB at 10Hz) and connected to two servo-controlled scanning mirror units with position output (General Scanning, Watertown, Massachusetts), mounted in the light pathway. A neutral density filter attenuated the luminance of the laser spot to about 200 cd/m^2. A background could be superimposed which filled the whole visible part of the screen (subtending about 90 x 90 degrees arc; limited by the field coils of the recording system). The backgrounds used were darkness (luminance < 1 cd/m^2); diffuse illumination (11 cd/m^2) or a black-and-white random dot pattern with individual elements of 15 min arc (Julesz, 1971, Fig. 2.6.2.). The luminance of the white parts was 16.8 cd/m^2, of the black parts 3.6 cd/m^2. The luminance of the diffuse background was equal to the average luminance of the random dot background. For the experiments described in paragraph 4.1.4 twelve other black and white backgrounds were used: horizontal and vertical sine wave and square wave gratings with wavelengths of 4.76 and 9.46°; two random dot patterns with individual elements of 1.05 x 1.05 and 2.1 x 2.1° and two checkerboard patterns with elements of 3.23 x 3.23 and 6.46 x 6.46°. Examples are shown in Fig. 2.2.

2.4 Experimental procedures

The data recording for each subject was divided over different sessions. Before the insertion of the induction coil, the head of the subject was positioned by means of head and chin supports with the aid of a peephole in such a way that the right eye of the subject was in the centre of the magnetic field (homogeneous part) and that the visual axis

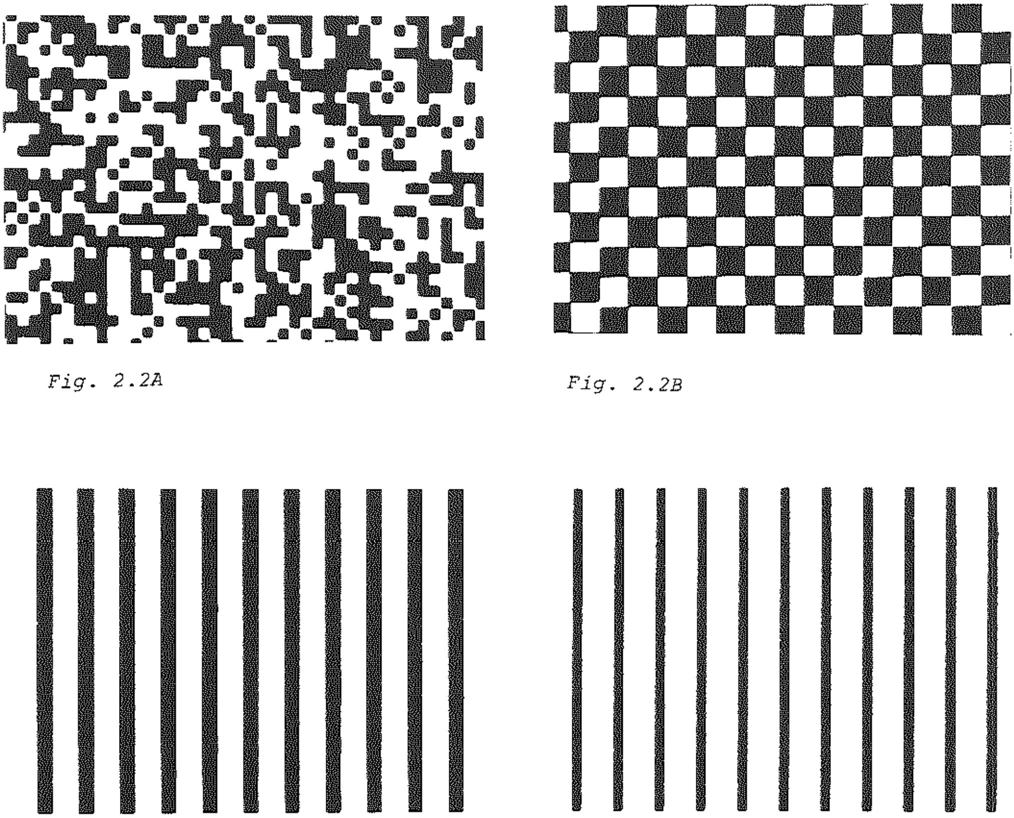


Fig. 2.2A

Fig. 2.2B

Fig. 2.2C

Fig. 2.2D

Fig. 2.2. Examples of types of background used. Random dot (2.2A), checkerboard (2.2B), square wave grating (2.2C) and sine wave grating (2.2D).

was aligned with the centre of screen. Before the data recording started, gain and offset were manually adjusted to obtain standard values for fixation of the target at a number of known positions. This procedure also corrected for any magnification or reduction factors caused by the spectacles of the subject. This manual procedure was followed by a calibration measurement in which the computer displaced the target to fixed positions in the visual field. The subject fixated these positions for about 2.5 s. These calibration measurements were used for off-line further correction of the calibration done by hand at the start of the experiment. To check for significant changes during the experiment, calibration was repeated at the end of the session.
Between the two calibration measurements, about 30 to 40 measurements were done, each lasting 32.77 s (4096 points sampled at a rate of 125/s). The target and/or background were displaced using stimuli calculated and stored before the experiment. Data recording was started a few seconds after the start of the stimulus movement. The order of the measurements was altered between subjects to balance for effects of practice.

A session was limited to about 30 minutes of recording. After the last calibration measurement, the induction coil was taken out of the eye using a pair of tweezers to lift the edge of the coil. To summarize the experiments which were done, the computer printed a data report.

2.5 Data analysis

The horizontal and vertical component of eye and target position and if necessary the horizontal background position were digitized on line (resolution 0.02° or better) at a rate of 125 samples/s and stored on disk. All data analysis was done off-line. The first stage was the adjustment of the eye position signals on the basis of 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 by 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 $0.2 - 0.3^{\circ}$ for offset. Adjustment differences between the calibration at the beginning and the end of the session did not exceed 2 - 3% for gain and $0.3 - 0.4^{\circ}$ for offset. The experiment was repeated if larger differences occured.

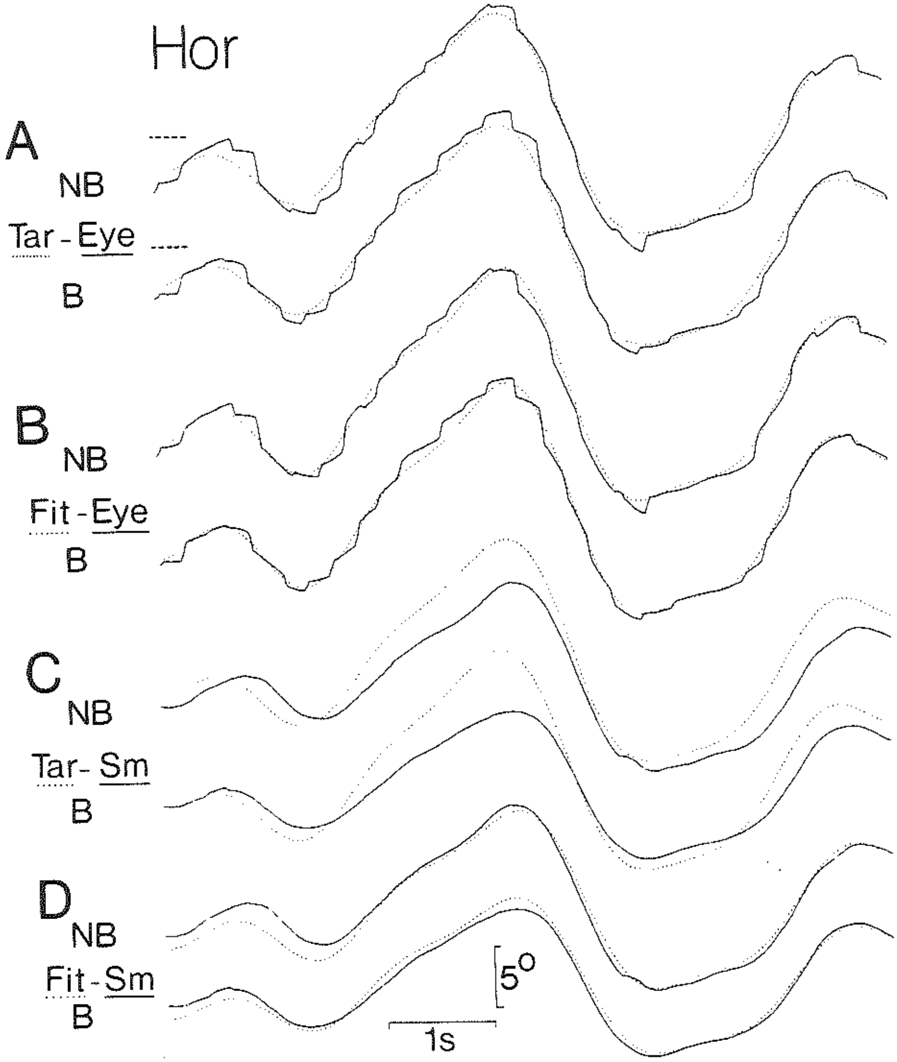


Fig. 2.3A. Combinations of horizontal target and composite eye movement (A), fitted and real eye movement (B), target and cumulative smooth eye movement (C), and fitted and real smooth eye movement (D) for pursuit upon a dark (NB) and a structured background (B). Fitted signals were calculated via a forward and inverse Fourier transformation, see text.

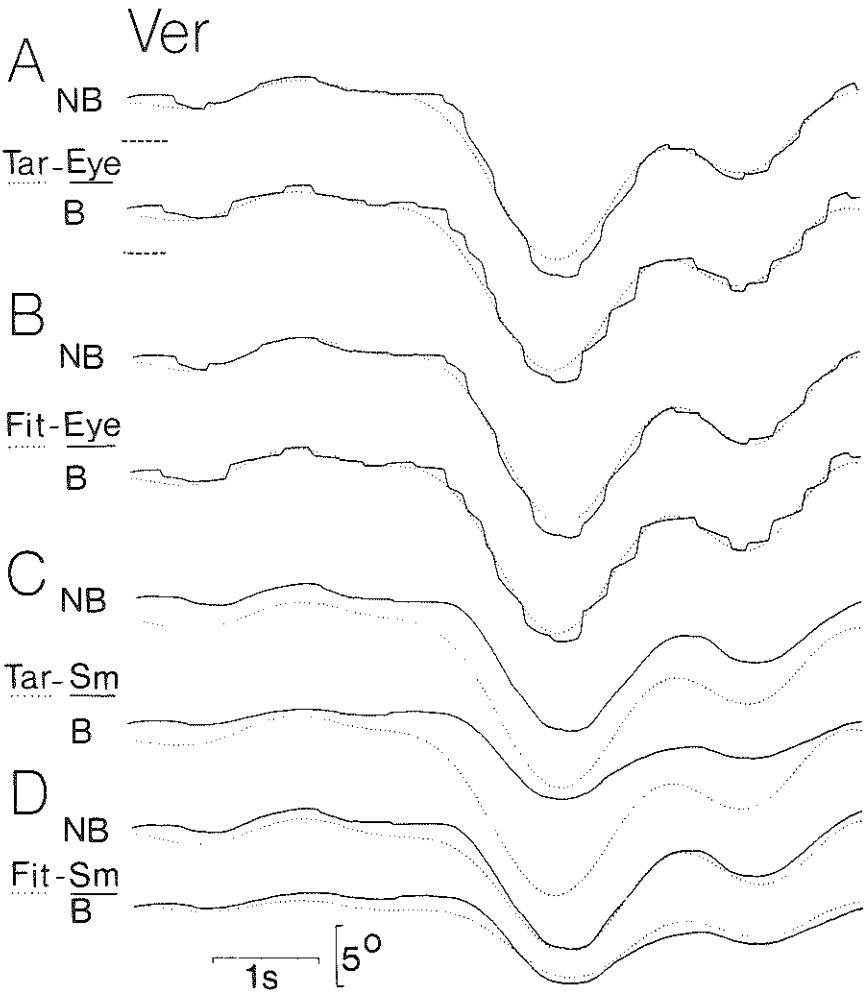


Fig. 2.3B. As Fig. 2.3A for vertical target and eye movements.

To analyze the smooth pursuit component of the eye movement, software (described in 2.6) was developed to detect the saccades in the eye position signal and to separate the eye movement into a smooth and a saccadic component. The missing parts in both components (the saccades in the smooth component and the smooth eye movement in the saccadic 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 the trend was removed by means of a least squares method. For sinewave stimuli, the eye and target position signals were Fourier transformed with a Fast Fourier Transform (FFT) routine. Gain (ratio of peak to peak amplitude 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 square fitting of sinewave stimuli. Fig. 2.3A and 2.3B show examples of this process for the horizontal and vertical component of the composite as well as the cumulative smooth eye movement. 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. For pursuit of pseudo-random stimuli more than 98% of the energy of the composite eye movement and more than 75% of the energy of the cumulative smooth eye movement was contained within the four remaining frequencies. For single sinewave stimuli, these figures were 99% and 90% respectively for the single frequency component used. Therefore, the cumulative smooth eye position produced by the computer provides 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 (Fig. 2.4); 12.5% at the beginning and at the end of the slope in horizontal or vertical direction were excluded from the analysis.

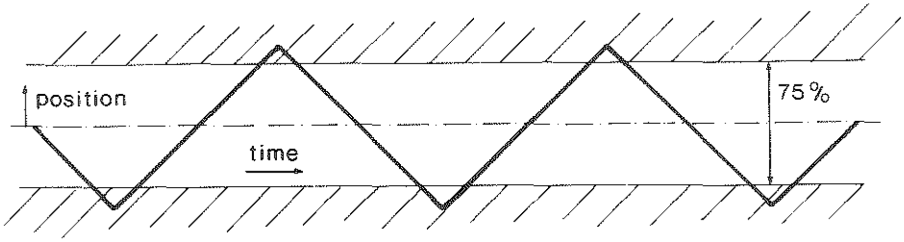


Fig. 2.4. The central 75% of the horizontal or vertical slopes of the triangular wave stimuli were used to calculate the gain of the composite and smooth eye movement. For the calculation of retinal error, 100% of the recording was used.

For these stimuli, separate gains were calculated for the pursuit of left- and rightward and up- and downward directed target movements. The retinal position error was calculated by subtraction of the eye position from the target position. Paired t-tests were used to test for differences between different stimulus conditions; p values shown are for two-tailed testing.

2.6 Separation of smooth and saccadic eye movements

To analyze the function and performance of the smooth and saccadic eye movements, software was developed to separate the composite eye movement into a cumulative smooth and saccadic component. Separation of the two components of pursuit eye movements was based upon the detection of saccades within the eye movement. Saccades are steplike, discrete eye movements with high peak velocities and accelerations, in contrast to smooth pursuit which is limited in velocity and acceleration.

Detection of saccades was basically a three stage problem:

1. All parts of the eye position which were candidates for being a saccade were flagged on the basis of a velocity and acceleration

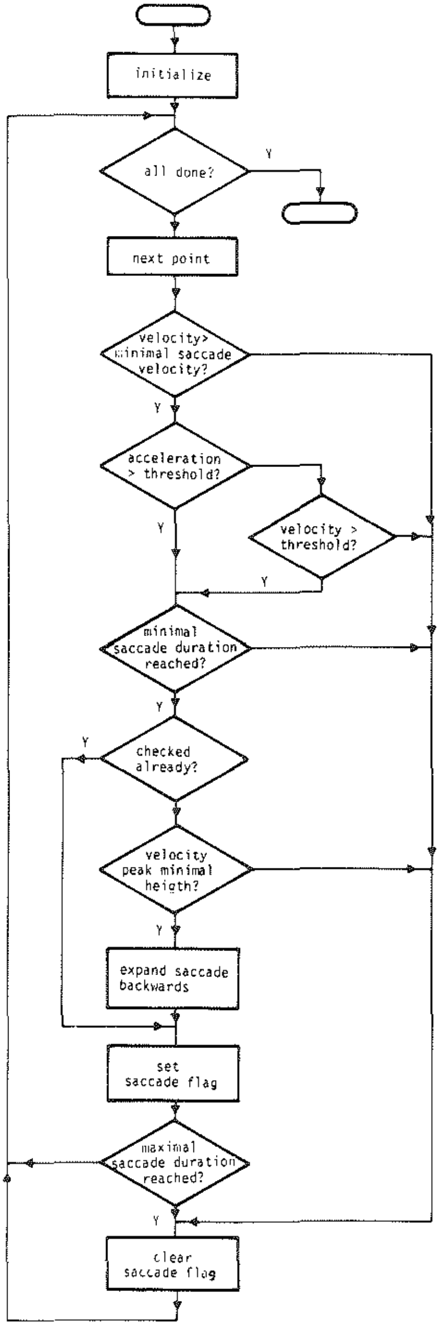


Fig. 2.5. Flowchart of the algorithm to detect saccades in the eye position signal.

threshold (fast preselection).

2. Each part selected in 1. was checked for minimal duration. Noise in the eye position signal could result in high velocities and accelerations of short duration. The use of a minimal saccadic duration test eliminated detection of noise as saccades.
3. If the first two conditions were met, the velocity profile of the eye movement was analyzed for the presence of a peak of minimal height and maximal duration. The use of a maximal duration test on detected saccades prevented the program from treating parts of high velocity smooth pursuit as saccades.

Fig. 2.5 is a flow chart of the basic algorithm.

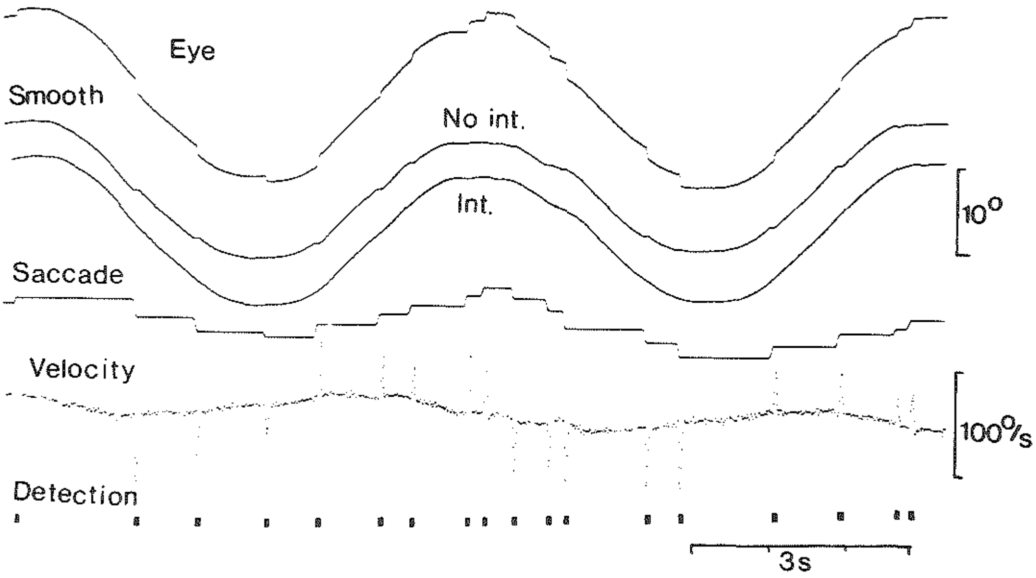


Fig. 2.6. An example of separation of composite eye movement in response to a sinusoidal target movement of 0.28 Hz into a cumulative smooth (with and without interpolation) and saccadic component based upon the eye velocity and acceleration. The saccade detection signal was stored for further analysis.

A number of detection parameters (e.g. thresholds and duration limits) could be adjusted to obtain a reliable detection of saccades. Saccadic characteristics could vary due to different stimulus conditions. For example, a low target velocity resulted in pursuit which contained a few saccades of short duration and low peak velocities. Fast target motions on the other hand, led to a more frequent use of saccades to pursue the target and those saccades were larger and reached higher peak velocities. The determination of an appropriate set of parameters was a trial and error process. Once a satisfactory set was found, it was used for all comparable experiments. In practice, a velocity range of the target from $5^{\circ}/s$ to $30^{\circ}/s$ together with a maximum amplitude of $7-10^{\circ}$ and a sample frequency of 125 Hz resulted in the same set of parameters for detection of saccades (velocity threshold $10^{\circ}/s$, acceleration threshold $400^{\circ}/s^{2}$, minimal saccade duration 15 ms, maximal duration 75 ms). Saccades as small as 0.2° could be reliably detected.

The smooth and saccadic eye movements were separated using the saccade detection signal (Fig. 2.6). The consecutive segments of smooth pursuit and saccades were connected by zero-velocity elements to obtain the cumulative smooth and saccadic eye movement. Optionially, the consecutive elements of smooth pursuit could be connected by linear interpolation of the smooth eye velocity to obtain a gradually changing smooth pursuit velocity. The saccade detection signal was saved to calculate the gain of the smooth component during pursuit of triangular wave stimuli and to analyze the correctivity of saccades.

CHAPTER 3

PURSUIT UPON A DARK BACKGROUND

3.1 Gain and phase

3.1.1 Single sine waves

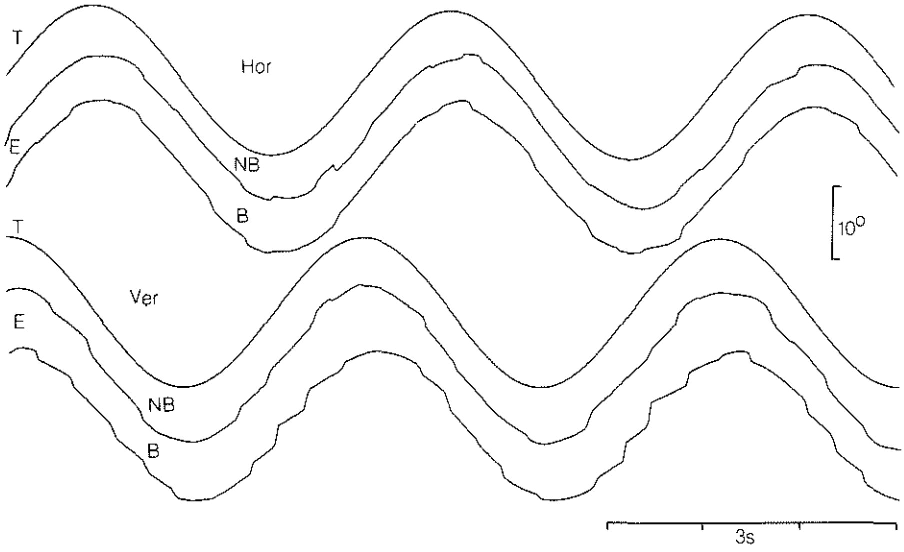


Fig. 3.1. Recordings of the horizontal and vertical component of a sinusoidal target movement (T) and pursuit eye movements (E) without (NB) and with (B) a stationary background.

Fig. 3.1 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 (NB). The horizontal and vertical component of the target movement were single sine waves of the same frequency (0.28 Hz) and amplitude (10^0), shifted 90° in phase. Most of the pursuit was achieved by smooth eye movements; the saccadic component was small.

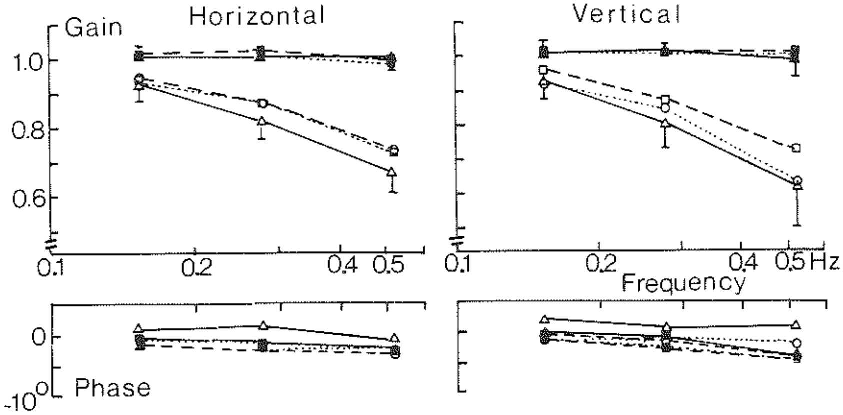


Fig. 3.2. Gain and phase of the composite (filled symbols) and cumulative smooth eye movement (open symbols) in response to one-dimensional single sine wave stimuli (amplitude 10°, solid lines), or two-dimensional stimuli with an amplitude of 7.07° (dashed lines) or 10° (dotted lines). Means ± S.D. for 5 subjects. The S.D. is indicated by a vertical line for one condition only. The S.D. of the other conditions were comparable.

Fig. 3.2 shows mean gain and phase as a function of frequency for 5 subjects for one-dimensional target motion (amplitude 10°) and two-dimensional target motion with an amplitude of 7.07° or 10°. 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 ± 0.02 (S.D.; n = 30 = 5 subjects x 3 situations x 2 dimensions). Gain decreased only to 0.99 ± 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. For the composite eye movement, there was no significant difference between the gain and phase of the horizontal and vertical component.

The pursuit eye movements were not 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 ± 0.04 (S.D.) and of the vertical component 0.93 ± 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 in 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.).

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 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 of the smooth pursuit component was not systematically different from the phase of the composite eye movement. Smooth pursuit gain of the horizontal component was significantly higher than the vertical component, mean difference 0.03 ± 0.06 (S.D.; $p < 0.05$).

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.

3.1.2 Pseudo-random motion

Fig. 2.3A and 2.3B show a recording of pursuit of a two-dimensionally moving pseudo-random stimulus (frequency range 0.15 - 0.70 Hz). Compared to the single sine wave stimulus (Fig. 3.1) more saccades were used to pursue the target.

Fig. 3.3A and B show Bode plots of the mean results for the same 5 subjects illustrated before for the two pseudo-random stimuli (with different bandwidth, see Table 3.1 for the precise composition of these stimuli) 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.

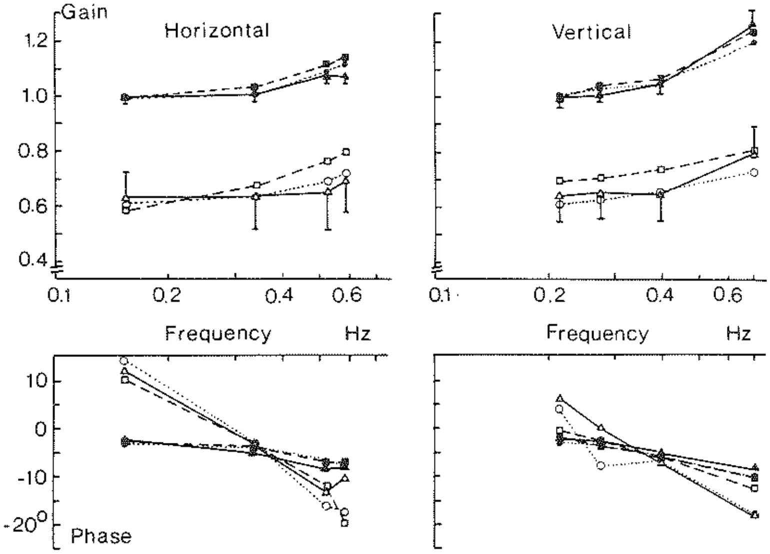


Fig. 3.3A

Fig. 3.3B

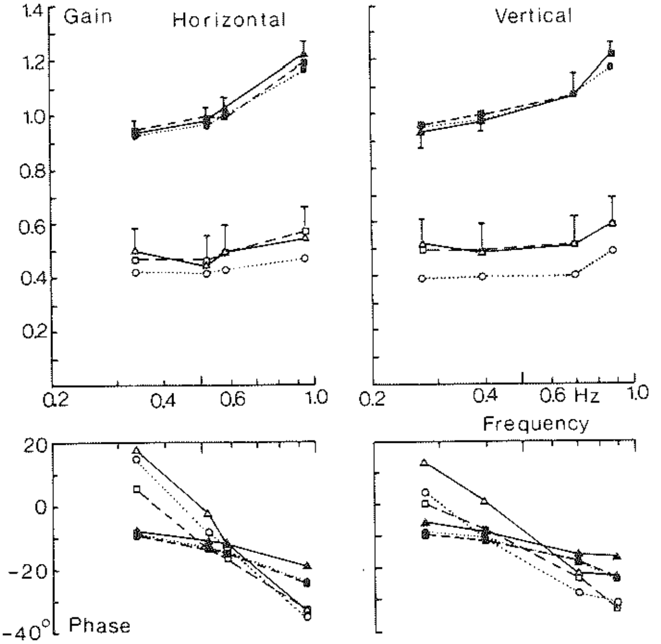


Fig.3.3. Gain and phase of the composite (filled symbols) and cumulative smooth eye movement (open symbols) in response to a pseudo-random target motion in one dimension with an amplitude of 10° (solid lines), in two dimensions with an amplitude of 7.07° (dashed lines) or 10° (dotted lines). Fig. 3.3A and 3.3B show results for pseudo-random target motions with different frequency ranges. Means ± S.D. for 5 subjects.

Table 3.1. Spectral composition of two pseudo-random stimuli with a maximum amplitude of 10° in horizontal and vertical direction. The amplitude of the components is inversely proportional to frequency.

	SUM 1			SUM 2		
	Frequency (Hz)	Amplitude (deg)	Phase (deg)	Frequency (Hz)	Amplitude (deg)	Phase (deg)
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

The gain of the composite eye movement increased from a value of about unity for the lowest frequency component in the pseudo-random stimuli to a value above 1.1 for the highest frequency component. For example, for the pseudo-random motion with the lowest frequency range the gain of the composite eye movement was 1.0 at 0.15 Hz for the horizontal component and 1.0 at 0.21 Hz for the vertical component (both the lowest frequency component in this stimulus). These gains increased to about 1.12 at 0.58 Hz for the horizontal component and to about 1.24 at 0.70 Hz for the vertical component of the composite eye movement. 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 gain of the smooth component during pursuit of pseudo-random stimuli was lower than that for single sine wave stimuli of comparable frequencies; during pursuit of pseudo-random stimuli the relative contribution of the saccadic component increased compared to pursuit of a single sinusoidal trajectory. The results for horizontal and vertical eye movements for these two pseudo-random stimuli are not completely comparable because different frequencies had to be used to form the sum for the horizontal and vertical component of the target movement (Uncorrelated horizontal and vertical target movements were required).

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. For the stimulus with the frequency range of 0.15 - 0.70 Hz (Fig. 3.3A), the gain of the smooth component during the one-dimensional pursuit task (maximum target amplitude 10°) was comparable to the gain of the smooth component during pursuit of two-dimensional target motions with a maximum amplitude of 10°. For the stimulus with the higher frequency range, however, (Fig. 3.3B) the gain of the smooth component during pursuit of a one-dimensionally moving target was comparable to the gain of the smooth component during pursuit of two-dimensional target motions with a maximum amplitude of 7.07°.

The phase lag of the composite eye movement during pursuit of pseudo-random stimuli was larger than during pursuit of single sinewave stimuli and in contrast to single sinewave 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 of the same frequency in common, the stimulus with the highest frequency range resulted in larger phase lags of the composite eye movement over the whole frequency range.

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 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 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 in 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 systematical differences between the one-dimensional and two-dimensional pursuit tasks.

To measure the influence of the amplitude of the target movement on pursuit performance, experiments were done in which the subject had to track the same pseudo-random target motion for different maximum target amplitudes, viz. 2, 5 and 10°. Horizontal and vertical target motions were again formed by the sum of four non-harmonic sinewaves of different amplitudes and were mutually uncorrelated (see Table 3.2).

Table 3.2. Spectral composition of the pseudo-random stimuli used for experiments with different target amplitudes and for a match between horizontal and vertical component. This specification if for a maximum amplitude of the target motion of 10°, the specification for a maximum amplitude of 2 and 5° can be obtained by dividing the amplitudes of the components by 5 or 2 respectively.

SUM 3			SUM 4		
Frequency (Hz)	Amplitude (deg)	Phase (deg)	Frequency (Hz)	Amplitude (deg)	Phase (deg)
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

In order to compare the horizontal and vertical eye movements, the same pseudo-random stimulus had to be followed in a situation in which the composition of the horizontal and vertical component of the target movement had been interchanged.

Fig. 3.4 summarizes the results for the two combinations used. Although during the experiments the horizontal component of Fig. 3.4A was combined with the vertical component of Fig. 3.4B (and in an other experiment the vertical component of Fig. 3.4A with the horizontal component of Fig. 3.4B), the results for identical composition of horizontal and vertical component have been grouped in the same figures for convenience of comparison.

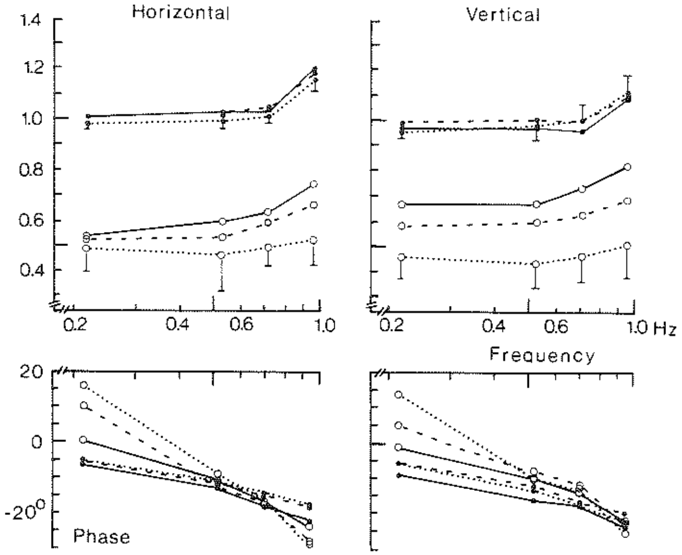


Fig. 3.4A

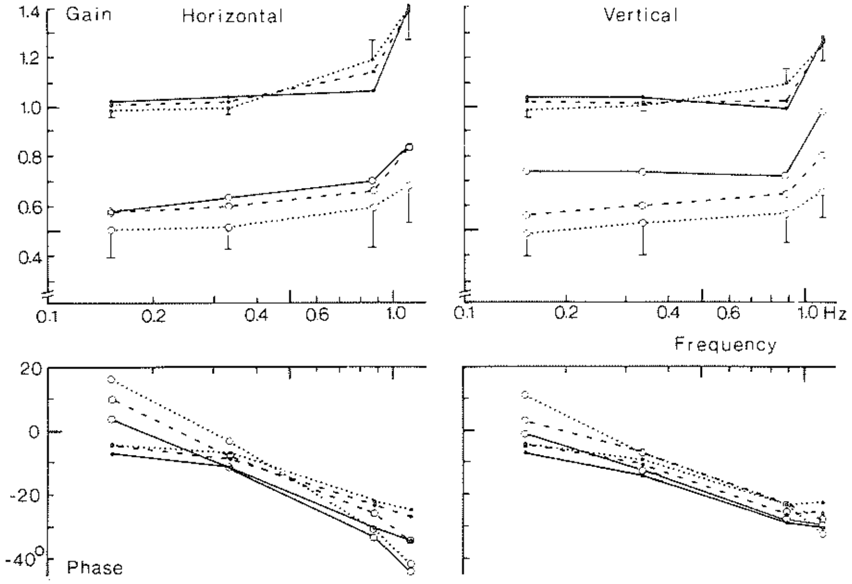


Fig. 3.4B

Fig. 3.4. Mean ± S.D. gain and phase for 5 subjects of the composite (filled symbols) and cumulative smooth eye movement (open symbols) in response to a pseudo-random target motion in two dimensions with an amplitude of 2° (solid lines), 5° (dashed lines) or 10° (dotted lines). Fig. 3.4A and 3.4B show results for pseudo-random target motions with different frequency ranges. The horizontal component of Fig. 3.4A was in the experiment combined with the vertical component of Fig. 3.4B and the vertical component of Fig. 3.4A with the horizontal component of Fig. 3.4B.

The gain of the composite eye movement was not significantly influenced by the stimulus amplitude. Although the 10° stimulus contained velocities which were five times higher than the 2° stimulus, the eye pursued both stimuli with a comparable gain. This result applies to both the horizontal and vertical component of the eye movement. The gain of the horizontal component of the composite eye movement was higher than that of the vertical component (mean difference 0.06 ± 0.11 S.D., $p < 0.001$).

However, the phase lag of the composite eye movement did increase with increasing frequency (as shown earlier) and was, in general, larger for a smaller stimulus amplitude. For example, the phase lag of the horizontal component was 6.3° at 0.15 Hz and increased to 21.8° at 1.13 Hz for a maximum amplitude of 2°, while for a maximum target amplitude of 10° these data were 5.0 and 17.5° respectively.

The gain of the smooth component was lower than that of the composite eye movement and in contrast to the composite eye movement, was affected by the amplitude of the stimulus. A larger stimulus amplitude resulted in a lower smooth pursuit gain. The difference was significant over the whole frequency range and for both the horizontal and vertical component, although the effect of amplitude was larger for the vertical component. The mean decrease in the gain of the smooth eye movement for the horizontal component was 0.04 ± 0.06 (S.D.) when the maximum stimulus amplitude was increased from 2 to 5° and 0.09 ± 0.06 (S.D.) when the amplitude increased further from 5 to 10°. The vertical component of the smooth eye movement was more sensitive to an increase in the stimulus amplitude. The decreases amounted 0.12 ± 0.08 (S.D.) for an amplitude increase from 2 to 5° and 0.12 ± 0.08 (S.D.) for an increase from 5 to 10° for this component. All differences were highly significant ($p < 0.001$).

The phase of the smooth eye movement showed in general, for a larger stimulus amplitude, a larger phase lead for the lowest frequency component and a smaller phase lag for the highest frequency component of the pseudo-random stimulus. For example, the phase of the smooth horizontal component (as shown in Fig. 3.4A) was 16.0° (phase lead) at 0.21 Hz which decreased to -28.7° (phase lag) at 0.95 Hz and an amplitude of 10°. For a stimulus amplitude of 2° these data were 0.7 and -23.5° respectively. Only the decrease in phase between a stimulus amplitude of 2 and 5° was significant: 3.6 ± 5.4°, $p < 0.001$ (mean and S.D. of the horizontal and vertical component over the whole frequency range).

3.1.3 Triangular waves

In contrast to sine wave stimuli, triangular wave stimuli have a measure the pursuit performance with constant stimulus velocity triangular wave stimuli of the same frequencies (0.15, 0.28 and 0.52 Hz) and amplitudes (7.07 and 10°) as the single sine wave stimuli and in addition triangular waves of 0.06, 0.09 and 0.12 Hz of the same amplitudes were used. This resulted in target velocities in the range from 1.7 to 20.8°/s. The corners of the triangular wave stimuli were excluded from the calculation of gain of the composite and cumulative smooth eye movements. Fig. 3.5 shows a recording of pursuit of a rhomboid stimulus trajectory.

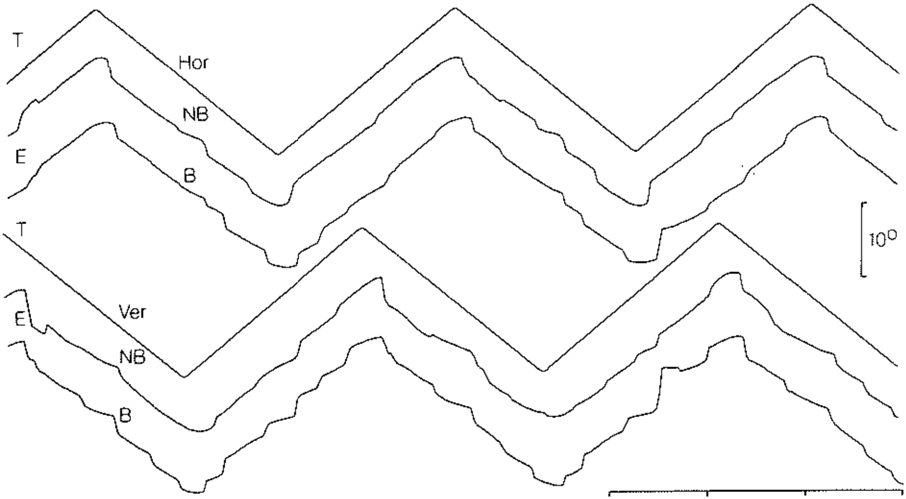


Fig. 3.5. Recordings of the horizontal and vertical component of a triangular target motion (T) of 0.28 Hz and pursuit eye movements (E) upon a dark (NB) or a structured (B) background.

Fig. 3.6A

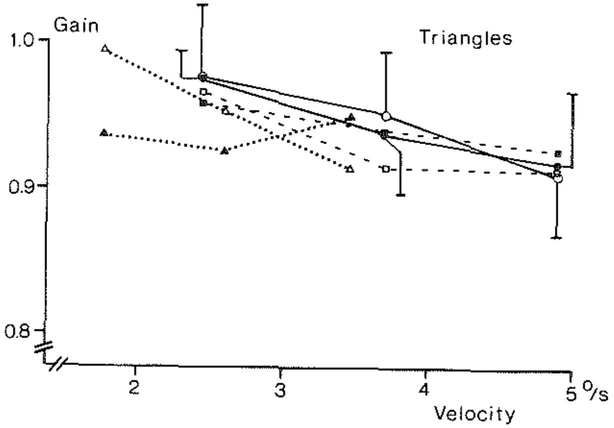


Fig. 3.6B

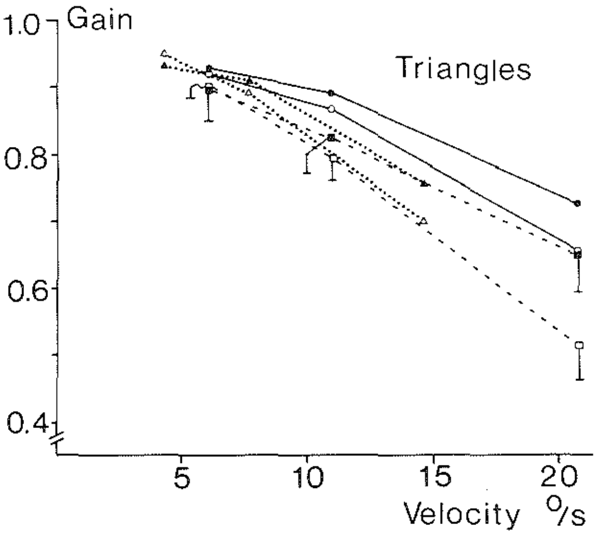


Fig. 3.6. Gain of the horizontal (filled symbols) and vertical (open symbols) smooth eye movement in response to triangular wave stimuli moving in one dimension with an amplitude of 10° (solid lines), or in two dimensions simultaneously with an amplitude of 7.07° (dotted lines) or 10° (dashed lines). Fig. 3.6A is for low and Fig. 3.6B for high target velocities. Means ± S.D. for 5 subjects.

The horizontal and vertical components of the target movement were triangular waves of the same frequency (0.28 Hz) and amplitude (10^{o}), shifted 90^{o} in phase.

The gain of the composite eye movement was unity for all frequencies, directions of target movement and stimulus situations. Although more saccades were used to pursue a triangular wave stimulus of $20.8^{o}/s$ than of $1.7^{o}/s$, the amplitude of the composite eye movement remained equal to the target amplitude and the gain was independent from velocity. Fig. 3.6 summarizes the gains of the smooth component of the eye movement, averaged over 5 subjects, during pursuit of one-dimensionally moving (amplitude 10^{o}, 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^{o} each) for low target velocities (Fig. 3.6A) and for high velocities (Fig. 3.6B). There was a progressive shift from smooth towards saccadic pursuit when the velocity of the stimulus increased from $1.7^{o}/s$ to $20.8^{o}/s$. The gain of the smooth pursuit component decreased from 0.96 at $1.7^{o}/s$ to 0.58 at $20.8^{o}/s$ (means of 5 subjects and of the horizontal and vertical component). The standard deviations of the gain of the smooth component were relatively small for the triangular wave of $1.7^{o}/s$, but increased when the velocity increased to $20.8^{o}/s$. This relative increase was due to the differences between subjects. Some subjects were able to pursue the triangular wave of $20.8^{o}/s$ relatively smoothly, which resulted in a high gain of the smooth component, while other subjects pursued this triangular wave almost completely with saccades, while the smooth component had a low gain. The gain of the vertical smooth component was lower than of the horizontal smooth component (mean difference 0.04 ± 0.07 S.D.; $p < 0.02$). There was no significant difference in gain of the smooth component between right- and leftward and between up- and downward target movements. The gain of the smooth component appeared to be largely determined by the velocity of the stimulus. As can be seen in Fig. 3.6B, a decrease in horizontal and vertical smooth pursuit gain occurred when the horizontal and vertical target motions were combined. It should be emphasized that these gains were calculated as the ratio horizontal eye movements / 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.

A remarkable error of direction occured when the frequency (and thus the velocity) of the rhomboid target motion was increased (see Fig. 3.7).

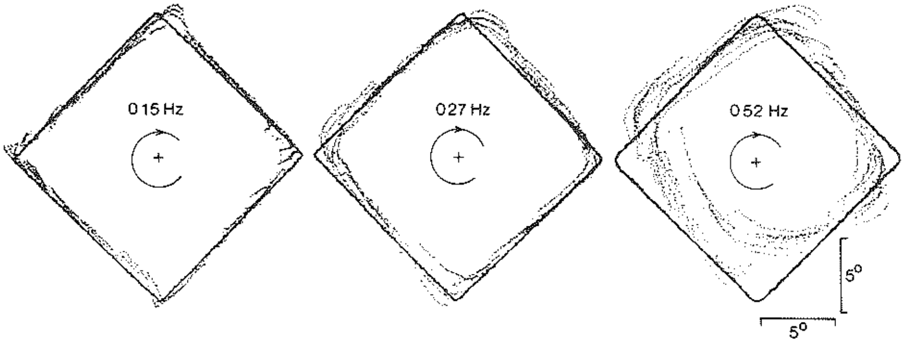


Fig. 3.7. Rotation of the eye movement trajectory with respect to the rhomboid traget trajectory when the frequency of the target increased from 0.15 Hz to 0.52 Hz. A period of 16.39 s of the target and eye movement recording are shown.

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 corner 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 was done not exactly in the direction of the target movement, but in a somewhat tilted direction. The rhomboid trajectory of the eye movements was rotated in the direction of the target motion. Is seems as though the subjects anticipated the changes of direction of the target.

3.2 Retinal position error during pursuit

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. I assumed a normal distribution and characterized this by a mean value and a standard deviation (S.D.).

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 (NB) and a stationary random dot background (B) are shown in Fig. 3.8.

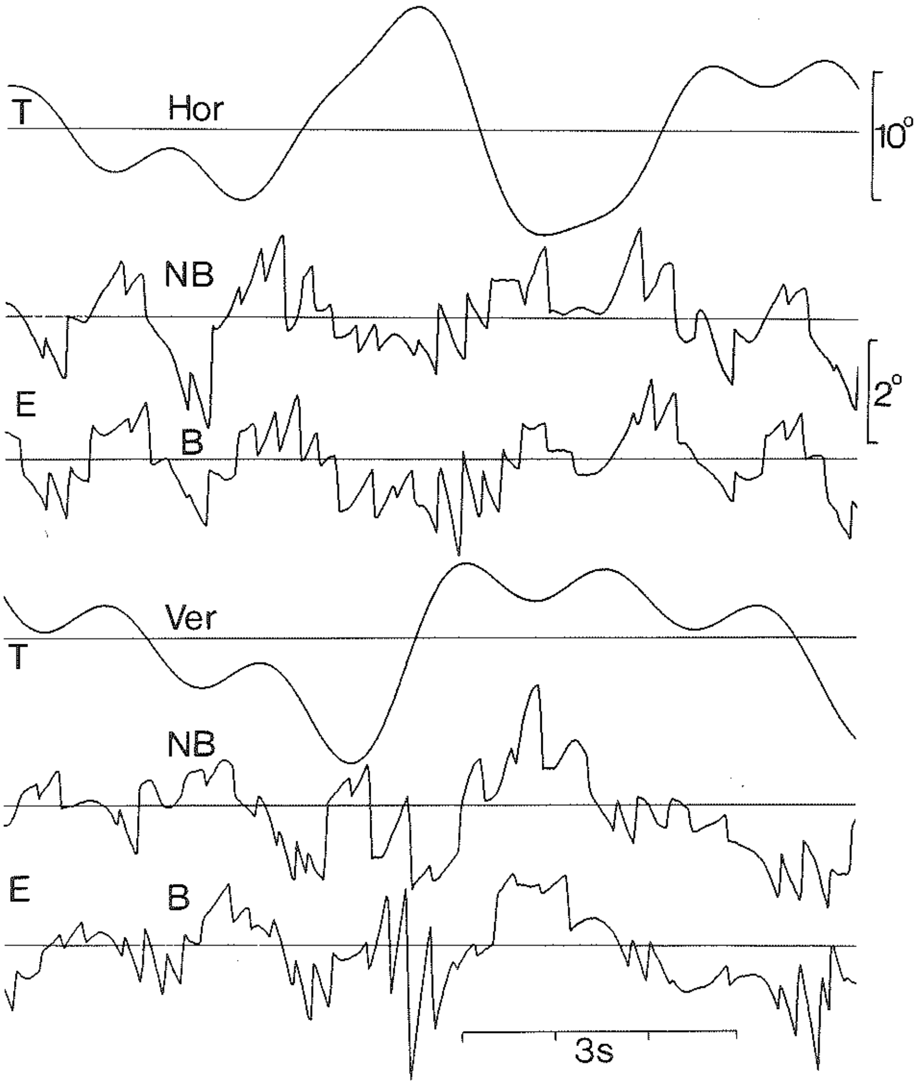


Fig. 3.8. Recordings of the horizontal and vertical retinal position error (E) during pursuit of a pseudo-random target motion (T) upon a dark (NB) or a structured (B) background. Notice the different calibrations for target and error.

The effects of a background on pursuit will be discussed in detail in chapter 4. An example of the two-dimensional distribution of the retinal position of the target during pursuit of one cycle of a circular movement is shown in Fig. 3.9.

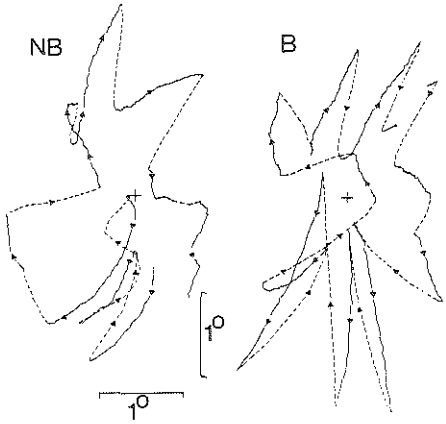


Fig. 3.9. Recordings of the combined horizontal and vertical retinal position error during pursuit of one period of a circular target motion of 0.28 Hz and an amplitude of 10° upon a dark (NB) or a structured (B) background. The occurrence of a saccade is indicated by an interrupted line and the arrows indicate the direction of the retinal position error.

Examples of the distribution of horizontal and vertical retinal position error are shown in Fig. 3.10. 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. 3.8). 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. 3.10). Therefore, for practical purposes, the distributions were considered to be unimodal and mean and standard deviation of retinal position error were chosen to characterize its distribution. Means and standard deviations were calculated for all stimulus conditions described sofar. 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.

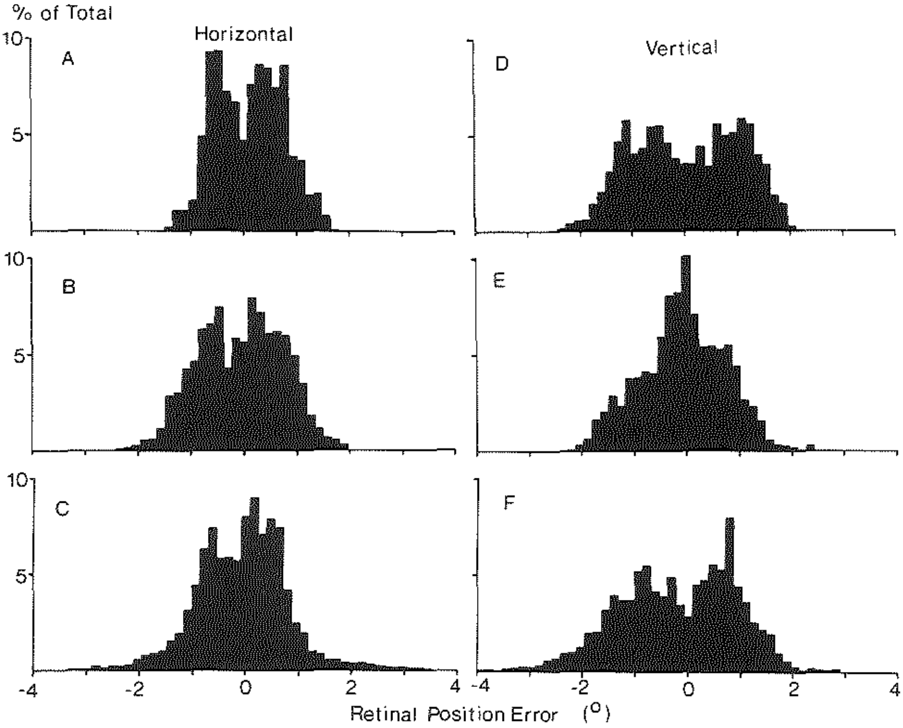


Fig. 3.10. Distributions of retinal position error in horizontal (A, B, C) and vertical (D, E, F) direction for a two-dimensionally moving sinusoidal stimulus of 0.28 Hz (A, D), a pseudo-random stimulus with a frequency range of 0.15 - 0.70 Hz (B, E) and a triangular wave stimulus of 0.28 Hz (C, F).

3.2.1 Single sine wave stimuli

For single sinewave stimuli, the S.D. of retinal position error increased with frequency (Fig. 3.11).

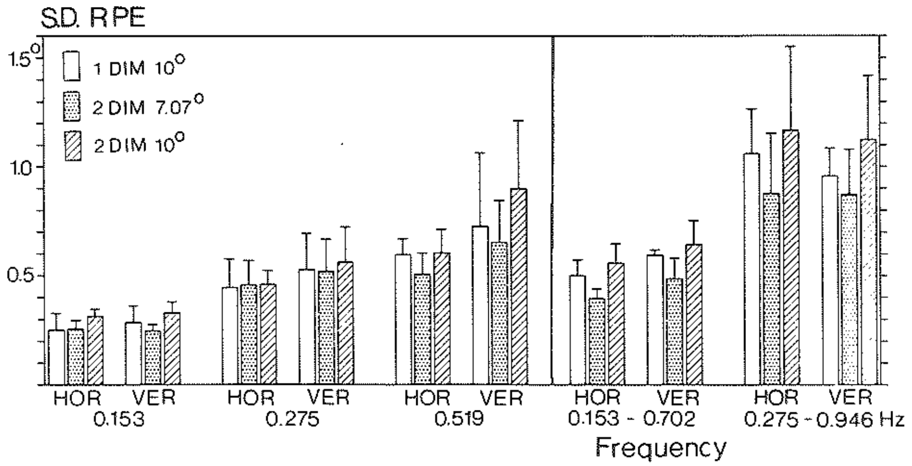


Fig. 3.11. Standard deviations (mean values for 5 subjects, S.D. of this mean is indicated by vertical lines) of retinal position error during pursuit of single sine wave or pseudo random stimuli in one dimension with an amplitude of 10° (open bars) and two dimensions with an amplitude of 7.07° (dotted bars) or 10° (hatched bars).

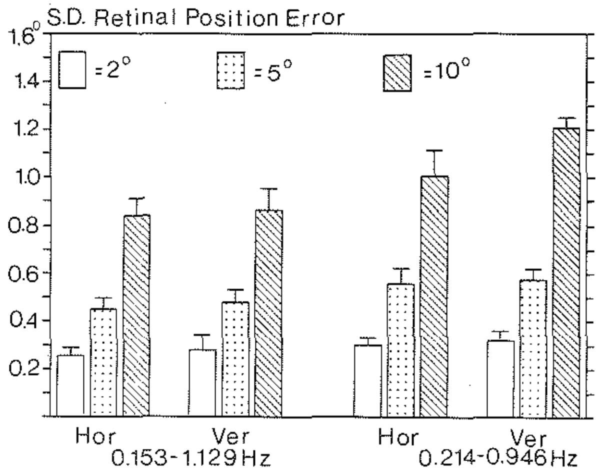
Within each frequency, two-dimensional target movements with an amplitude of 7.07° resulted in the lowest S.D. for each frequency. For one- and two-dimensional pursuit at an amplitude of 10° the error was larger. However, only the difference with the two-dimensional stimulus with an amplitude of 10° was significant (mean difference 0.09 ± 0.12 S.D.; $p < 0.001$). The S.D. of the vertical retinal position error was significantly higher than the S.D. of the horizontal error (mean difference 0.10 ± 0.16 S.D.; $p < 0.01$).

3.2.2 Pseudo-random stimuli

For the two pseudo-random stimuli as specified in Table 3.1, the movement with the higher frequency range resulted in a significantly larger S.D. of retinal position error than the stimulus with the lower frequency range (Fig. 3.11). Similarly as for the single sine wave stimuli, the S.D. 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).

To measure the influence of the amplitude of the target movement one pseudo-random stimulus (see Table 3.2) was shown at three different maximum amplitudes: 2, 5 and 10°. To compare the horizontal and vertical retinal position error, the same stimulus had also to be pursued in a situation in which the composition of the horizontal and vertical component of the target motion had been interchanged. The results of these balanced tests have been regrouped in Fig. 3.12.

Fig. 3.12. Standard deviations (mean values for 5 subjects, S.D. for this mean is indicated by vertical lines) of the horizontal and vertical 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).



In general, a larger stimulus amplitude (and thus a higher target velocity) resulted in a larger S.D. of retinal position error (Fig. 3.12). For example, for the stimulus with the frequency range of 0.15-1.13 Hz a stimulus amplitude of 2° resulted in a mean S.D. of retinal position error of 0.27 ± 0.05° (S.D.), an amplitude of 5° in 0.46 ± 0.05° (S.D.) and 10° in 0.85 ± 0.08° (S.D.). The vertical component of the retinal position error was only slightly, but significantly higher than the horizontal component (mean difference 0.05 ± 0.1° S.D., $p < 0.02$).

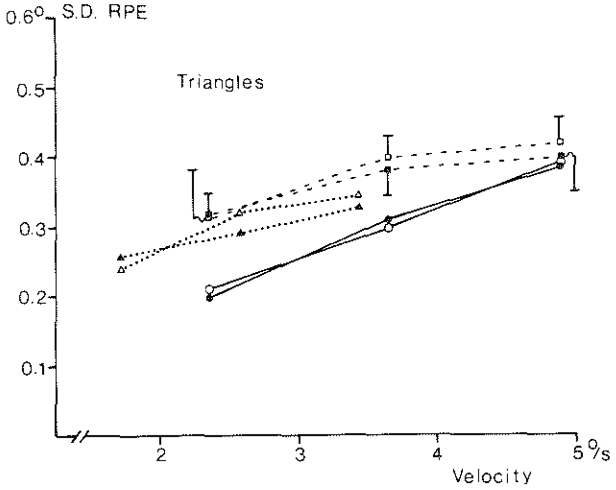


Fig. 3.13A

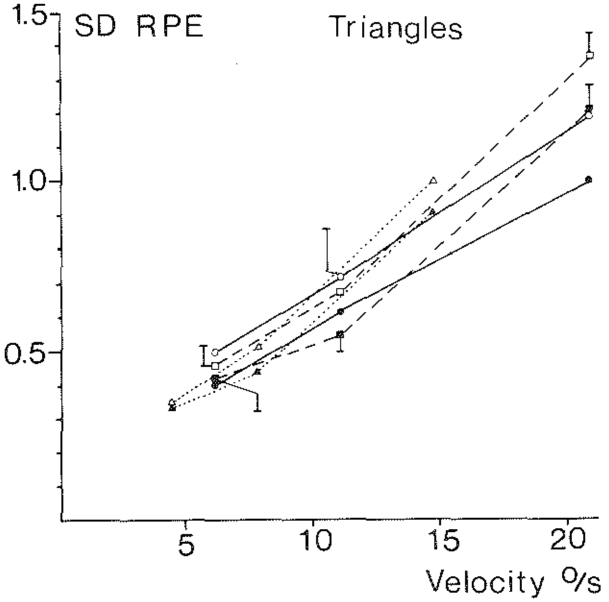


Fig. 3.13B

Fig. 3.13. Standard deviations of horizontal (filled symbols) and vertical (open symbols) retinal position error (RPE) during pursuit of triangular wave stimuli moving in one dimension only with an amplitude of 10° (solid lines) or in two dimensions simultaneously with an amplitude of 7.07° (dotted lines) or 10° (dashed lines). Fig. 3.13A is for low and Fig. 3.13B for high target velocities. Means ± S.D. for 5 subjects.

3.2.3 Triangular wave stimuli

For triangular target movements, the S.D. of retinal position error increased with velocity (Fig. 3.13A for the lower and Fig. 3.13B for the higher target velocities). Similarly as for the single sine wave stimuli, the S.D. of retinal position error of the horizontal component was lower than that of the vertical component (mean difference 0.06 ± 0.13 S.D.; $p < 0.001$).

3.2.4 Similarity of retinal position error

To investigate the reproducibility of the eye movement patterns in time (and thus of retinal position error) for the same stimulus condition in different trials, three subjects had to pursue the same pseudo-random target motion three times. Two of these three measurements were done in the same session (separated about 20 minutes in time); the third measurement was done in another session with the same subject. Fig. 3.14 shows the recording of retinal position error over these three trials for two different subjects.

The following remarks may be made:

1. There is a large similarity of retinal position error within one subject over different trials under the same stimulus conditions. One subject (EP) showed this similarity to a larger extent than the other subject (HC).
2. There was no systematic difference between the trials done within one session and the trial done in the other session with the same subject.
3. The pattern of the retinal position error and thus the corresponding pursuit eye movements was idiosyncratic. Subject HC used fewer saccades to correct his eye position, his eye movement was more smooth than that of subject EP.
4. Although the strategies of these two subjects in pursuing the target differed (smooth vs. saccadic), the S.D. of retinal position error as a function of time and thus the quality of pursuit was not significantly different (mean S.D. of retinal position error of subject HC $1.17 \pm 0.4^{\circ}$ S.D. between measurements; of subject EP $0.96 \pm 0.04^{\circ}$ S.D.).

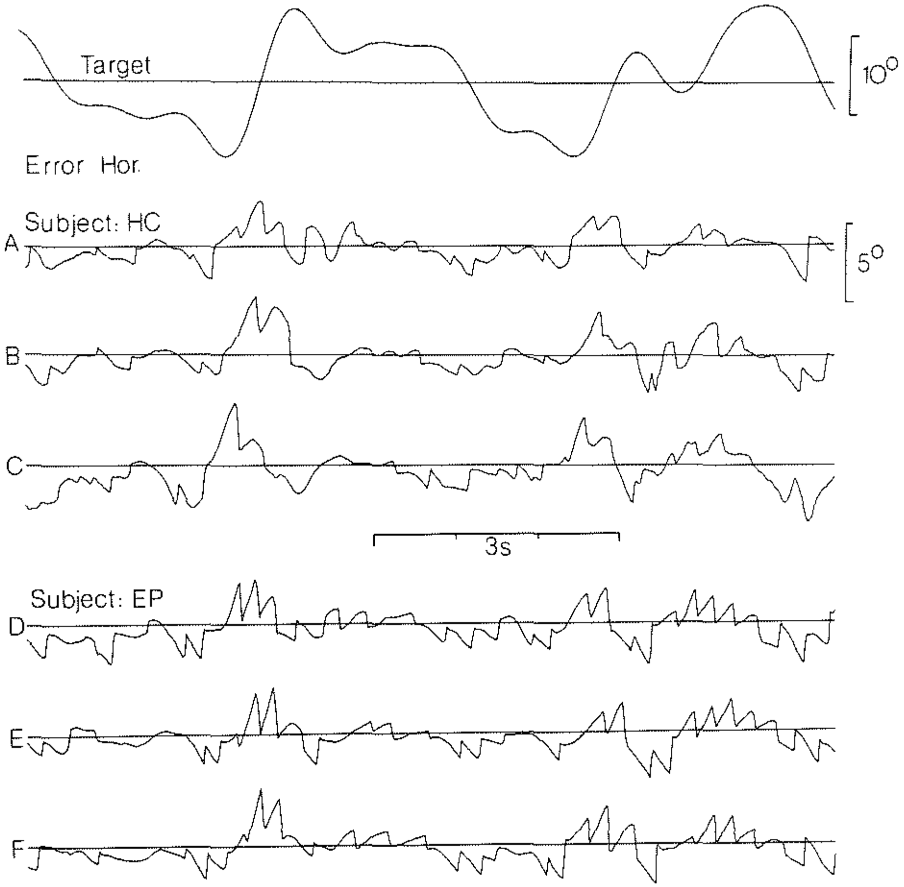


Fig. 3.14. Recordings of horizontal target movement and retinal position error of two subjects for three different trials under the same stimulus condition (pursuit of a pseudo-random target motion with a maximum amplitude of 10° upon a dark background). Recording B and C for subject HC (and recording E and F for subject EP) were the results of measurements done in the same session, separated about 20 minutes in time, recording A (and D for EP) was done in another session about one week earlier.

3.3 Saccades during pursuit

Recordings of the retinal position error (Figs. 3.8 and 3.9) 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 analyze the correctivity of saccades during pursuit, scatter plots were made which show the retinal position error in the horizontal and vertical direction at the beginning and at the end of saccades.

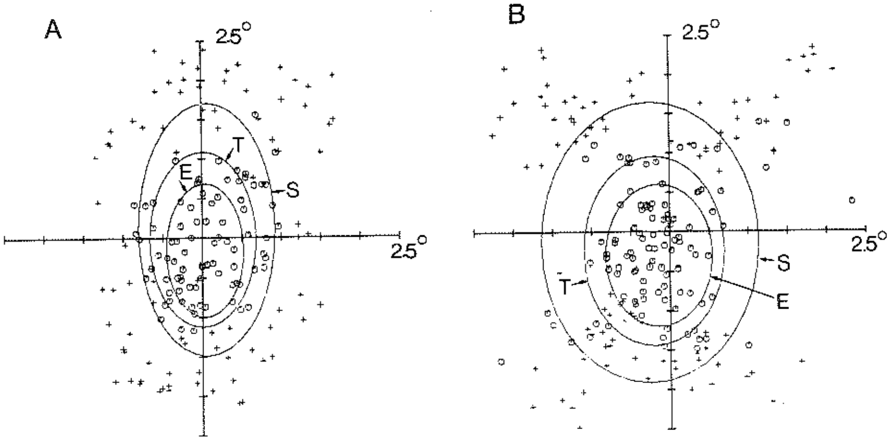


Fig. 3.15. Diagram of combined horizontal and vertical retinal position error at the start (+) and end (o) of saccades during pursuit of a circular (A) or a rhomboid (B) target motion of 0.28 Hz upon a structured background, with insertion of three ellipses which indicate the retinal position error at the beginning of saccades (S), the end of saccades (E) and during the total measurement of 32.77 s (T).

Fig. 3.15 shows two examples of such plots, one for pursuit of a circular trajectory (Fig. 3.15A, frequency 0.28 Hz, amplitude 10°) and a second for pursuit of a rhomboid trajectory of the same frequency and amplitude (Fig. 3.15B). In both situations, pursuit was done upon a structured background.

In Fig. 3.15B, (rhomboid trajectory) the starting points of saccades are mainly located at the 45 degree 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 (see chapter 4). Therefore the saccades were mostly in the direction of the target motion. The slopes of the rhomboid target trajectory made angles of 45^{o} 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^{o} 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. One 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 centres and half the length of the axes represent the means and standard deviations of the retinal position errors.

The mean error during pursuit was small compared to the S.D. 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 S.D. of retinal position error was larger in vertical direction than in horizontal direction.

Fig. 3.15 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 ellipse S and E shows that the retinal position error during pursuit was in between the errors at the start and end of saccades.

3.4 Discussion

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 0.96 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, Murphy & Steinman (1978). The latter investigators reported that subjects could only match 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 I showed 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.

The performance of the pursuit system depends on the spectral composition of the stimulus. Even if two stimuli have three components of the same frequency and differ in only one frequency, a completely different response and performance can be obtained (Figs. 3.3 and 3.11). Sinusoidal target movements are pursued with a higher smooth pursuit gain and a smaller phase lag than more complex pseudo-random signals. This was expected on the basis of the literature (Stark, Vossius & Young, 1962; Michael & Jones, 1966; Bahill, Iandolo & Troost. 1980; Lisberger, Evinger, Johanson, & Fuchs, 1981; Lisberger, Evinger, Johanson, & Fuchs, 1981).

New results are that the gain of the composite eye movement and the cumulative smooth eye movement increase with frequency during pursuit of pseudo-random stimuli, that the composite gain can rise above unity for the higher frequency components in these stimuli (Figs. 3.3 and 3.4) and that the cumulative smooth eye movements can have a phase lead with respect to the target motion for the lower frequency components.

A composite gain above unity is due to saccades which overshoot the target movement (Figs. 2.3A and B). Although the composite gain could be larger than one, smooth pursuit gain was always smaller than unity.

Lisberger, Evinger, Johanson, & Fuchs (1981) found that smooth pursuit is a function of maximum acceleration of the target. This is not corroborated by my results of pursuit of pseudo-random stimuli. I chose the amplitude of the frequency components of this type of stimuli 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 the amplitude times the square of its frequency, the components had a maximum acceleration which increased linearly with frequency. If the findings of Lisberger, Evinger, Johanson, & Fuchs (1981) would apply for my results as well, I should have found a smooth pursuit gain which decreased with increasing frequency, but I did not (Figs. 3.3 and 3.4). Lisberger, Evinger, Johanson, & Fuchs (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. I used a sum of four sine waves of different frequencies and although a maximum acceleration is defined for each of those frequencies when they would be used as single sine wave stimuli, the composite signal contains only one maximum acceleration which is present only once in the complete recording period. Comparison of the results presented here with those of Lisberger, Evinger, Johanson, & Fuchs (1981) may therefore be perilous. I confirm, however, that the gain of the smooth component does not only depend on frequency of the stimulus, but on a combination of frequency and amplitude. For a stimulus with a certain amplitude, a higher frequency (range) results in a lower gain of the smooth component (Fig. 3.2) and similarly, for a stimulus with a certain frequency (range) a larger amplitude results in a lower smooth pursuit gain (Fig. 3.4).

My results are in partial agreement with St-Cyr & Fender's (1969a) findings that composite gain increased with frequency within a narrow frequency band, but in contrast to their results I found that gain could reach values in excess of unity. One difference between the present study and that of St-Cyr & Fender is that I used a maximum stimulus amplitude of 2, 5, 7.07 or 10^o and components which had an amplitude inversely proportional to frequency. St-Cyr & Fender used a maximum amplitude of 1.5^o for the composed signal; the amplitudes of the different components as such were not specified. Given the fact that small differences in composition of the stimulus can result in a markedly different pursuit performance, one can expect discrepancies between different studies.

It remains unclear why the cumulative smooth eye movement shows a phase lead for the lower frequencies during pursuit of a pseudo-random target motion. It is not an artifact caused by the zero-velocity filling of the gaps (due to saccade removal) in the smooth eye movement, nor it is caused by the removal of the trend of the cumulative smooth eye movement. Interpolation of the consecutive segments of the smooth eye movement by a second order polynomial still resulted in a phase lead and omission of the trend correction led to erroneous results for gain and phase. A phase lead of the smooth pursuit eye movements occurred only with pseudo-random target motions. A sinusoidal target motion was followed in general with a phase lag.

For triangular wave stimuli, smooth pursuit gain was lower for a two-dimensional than for a one-dimensional target motion, This is in contrast to sinusoidal wave stimuli where a one-dimensionally moving target was pursued with a lower smooth pursuit gain than a two-dimensionally moving, circular stimulus (Fig. 3.2). There is, however, a substantial difference between single sinusoidal (one-dimensional) and circular (two-dimensional) target motions. Although the horizontal and vertical components of both types of stimuli are equal, the vectorial velocity (square root of sum of the squares of horizontal and vertical velocity) and acceleration are different. The velocity and acceleration of one-dimensional sinusoidal target movements changes continuously whereas the vectorial velocity and (centripetal) acceleration of the circular target motion are constant. On the other hand, the vectorial velocity of a rhomboid trajectory shows frequent abrupt directional changes.

I found that horizontal pursuit contained a higher proportion of smooth pursuit and was more accurate in terms of retinal position error than vertical pursuit. This could be due to a difference in training in horizontal and vertical tracking. Kowler, Murphy & Steinman (1978) described 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 every day 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 may not be fundamental.

Saccades during pursuit are 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. This saccade brings the target closer to the fovea and the remaining retinal error 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 overall retinal position error during pursuit is substantial (Figs. 3.8, 3.9 and 3.14). The same kind of imperfection of pursuit and saccadic correctivity was found by Mackeben, Haegerstrom-Portnoy & Brown (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: pursuit of a single moving 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 would require a better foveation of the moving target. Even in the present situations, however, saccades brought the target already to an area where visual acuity is relatively high. Fig. 3.15 shows that the standard deviation of the position of the line of sight on a single meridian is about 35' at the end of saccades. So, during pursuit, the precision of gaze with respect to position is sufficient to permit clear vision, particularly if modern acuity measurements are considered which show that the diameter of the isoacuity area is as large as 50' (Millodot, 1972).

It is also interesting to notice that fixation of a stationary target during active oscillation of the head (Steinman, Cushman & Martins, 1982) results in the same level of foveation as pursuit of an oscillating target while the head is stationary, provided that the frequency and amplitude of head and target are comparable. Apparently, the fixation and pursuit system yield a comparable precision of gaze, indicating that both systems may have large parts of the visuo-motor system in common.

Collewijn, Conijn, Martins, Tamminga & Van Die (1982) found that the trajectory of the retinal image of a moving target is highly stereotyped within one subject and one session and independent of the position or velocity of the eye in the head during coordinated head and eye movements. The results presented in Fig 3.14 confirm this finding for pursuit without head movements and they furthermore show that there is no systematic difference between the trials done in one session and those done in another session. The trajectory of retinal position error during pursuit of a pseudo-random stimulus is, however, idiosyncratic. Subjects have different strategies to pursue a moving target. Some subjects pursue relatively smoothly whereas others use saccades more frequently. As a consequence, the trajectory of the retinal position of the image of the moving target differs between subjects. However, the pursuit strategy did not significantly influence the S.D. of retinal position error.

The rotation of the trajectory of the pursuit eye movements with respect to the rhomboid trajectory of the target may be due to expectation of the direction 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 and 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 the increase in frequency of direction changes (and thus of the rhomboid motion) would lead to a larger rotation of the eye movement trajectory with respect to the targets trajectory. For the rhomboid target motion with a frequency of 0.52 Hz (rightmost rhomboid of Fig. 3.7) 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. 3.7).

CHAPTER 4

PURSUIT UPON A DIFFUSE OR STRUCTURED BACKGROUND

4.1 Gain and phase

One of the simplifications in most laboratory studies of pursuit is the absence of a structured background. In a normal physiological situation, moving targets are seen against a stationary background and pursuit of the target will induce a concomitant opposite motion on the peripheral retina. To measure the influence of a stationary background the single sine wave, triangular wave and two of the pseudo-random stimuli were also pursued upon a black and white random dot pattern which filled about 90 x 90° of the visual field, limited by the field coils of the recording system. The effect of illumination as such was also tested by presenting the stimuli on a diffusely illuminated background with a luminance equal to the average luminance of the random dot background.

Some examples of recordings of pursuit upon a structured background (B) were shown in previous chapters: in Fig. 3.1 (circular target motion at 0.28 Hz), Fig. 2.3A and 2.3B (pseudo-random stimulus) and Fig. 3.5 (rhomboid target trajectory, frequency 0.28 Hz). The main effect of a structured background was a slowing down of smooth pursuit and, concomitantly, the insertion of more saccades. In the next part of this section, only the results for the two-dimensional stimulus condition with a maximum amplitude of 10° will be presented in detail to illustrate and quantify 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.

4.1.1 Single sine wave

Bode plots of the mean gain and phase of the composite and the smooth eye movements for pursuit of single sine wave stimuli are shown in Fig. 4.1.

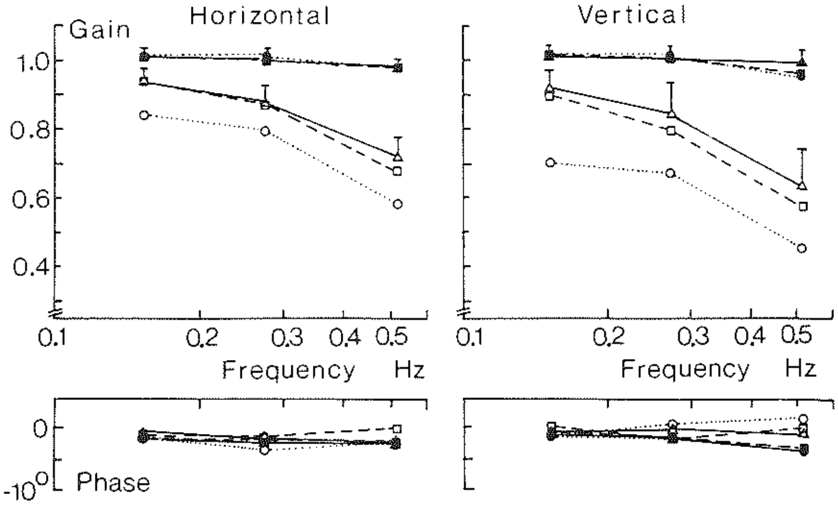


Fig. 4.1. Gain and phase of composite (filled symbols) and cumulative smooth eye movement (open symbols) during pursuit of circular stimuli with an amplitude of 10° upon a dark (solid lines), diffuse (dashed lines) or structured background (dotted lines). Means ± S.D. for 5 subjects.

The introduction of a structured or a diffuse background 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 component was unaffected by a diffuse background but lowered in the presence of a structured background. The mean decrease in gain of the smooth component for single sine wave stimuli was 0.07 ± 0.08 (S.D.; $p < 0.001$) for the horizontal component and 0.19 ± 0.13 (S.D.; $p < 0.001$) for the vertical component. Clearly, vertical smooth pursuit was more inhibited by the structured background than horizontal smooth pursuit.

The phase of neither the composite eye movement nor the smooth component was systematically changed by a diffuse or structured background.

4.1.2 Pseudo-random stimuli

A summary of the results of pursuit of two pseudo-random stimuli upon the three different backgrounds used (dark, diffuse and random dot) is shown in Fig. 4.2. The influence of a background on pursuit of pseudo-random stimuli is similar to the one on pursuit of single sine waves. The presence of a structured or a diffuse background had no systematical influence on the gain of the composite eye movement. There was no significant difference in smooth pursuit gain between pursuit upon a dark or a diffuse background, but the presence of a structured background lowered the gain of the smooth component. The mean decreases were 0.08 ± 0.09 (S.D.; $p < 0.001$) for the horizontal component and 0.19 ± 0.10 (S.D.; $p < 0.001$) for the vertical component (means and S.D. for the two pseudo-random stimuli pooled). Similarly as for the single sine wave stimuli, the random dot background inhibited the vertical component more than the horizontal component of the smooth eye movements.

The phase of neither the composite nor the smooth eye movement was systematically altered when the dark background was replaced by the diffuse or the structured background.

4.1.3 Triangular wave stimuli

A structured background had a similar effect on the pursuit of a triangular waveform. 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 (Fig. 4.3). This decrease was very small for the diffuse background: 0.03 ± 0.08 (S.D.; $p < 0.02$) for the horizontal component and 0.03 ± 0.06 (S.D.; $p < 0.01$) for the vertical component (note: only the three higher velocity triangular wave stimuli were pursued upon a diffuse background). The decrease in smooth pursuit gain was larger for the structured background: 0.09 ± 0.08 (S.D.; $p < 0.001$) for the horizontal and 0.17 ± 0.10 (S.D.; $p < 0.001$) for the vertical component. These values are comparable to those obtained with the sine wave stimuli.

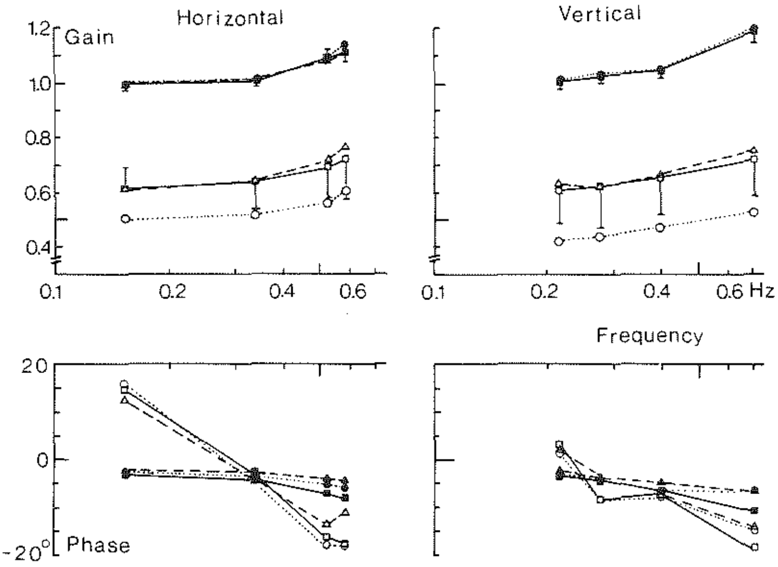


Fig. 4.2A

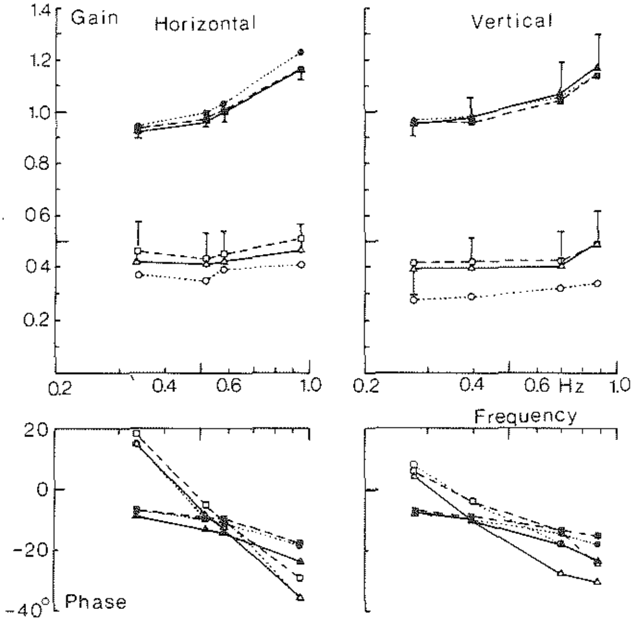


Fig. 4.2B

Fig. 4.2. Gain and phase of composite (filled symbols) and cumulative smooth eye movement (open symbols) during pursuit of two (A and B) two-dimensional pseudo-random stimuli with a maximum amplitude of 10° upon a dark (solid lines), diffuse (dashed lines) or structured background (dotted lines). Means ± S.D. for 5 subjects.

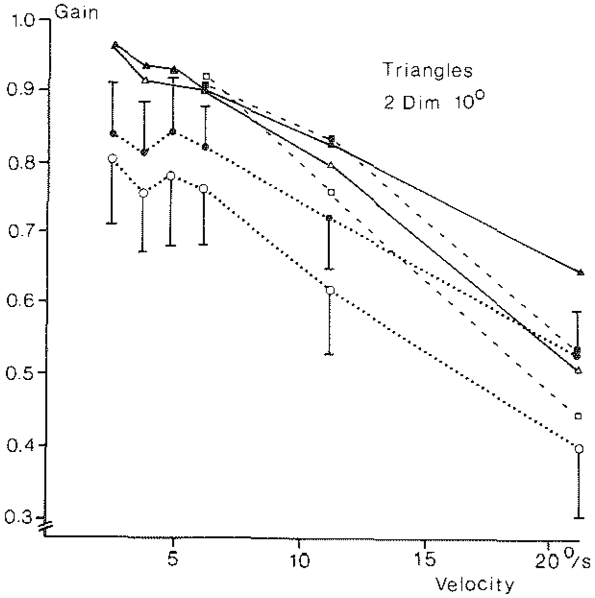


Fig. 4.3. Horizontal (filled symbols) and vertical (open symbols) smooth pursuit gain in response to two-dimensional triangular wave stimuli with an amplitude of 10° during pursuit upon a dark (solid lines), diffuse (dashed lines) or structured (dotted lines) background. Means ± S.D. for 5 subjects.

On the basis of these results I 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.

4.1.4 Different structured backgrounds

In order to test the influence of the type of structured background on the decrease in smooth pursuit gain, one pseudo-random stimulus (described in Table 3.2) had to be pursued upon twelve different structured backgrounds: sine wave and square wave gratings with two different wave lengths and edges in horizontal or vertical direction, two checkerboard patterns with different element sizes and two random dot backgrounds, also with two different element sizes (all backgrounds are specified in Chapter 2, page 13). With these backgrounds the following questions were answered:

1. Does the orientation of the contrast edges (horizontal or vertical) of the background have a differential effect on pursuit eye movements in horizontal or vertical direction?
2. Is a sharp contrast within the background more inhibitory on smooth pursuit than a soft contrast?
3. Does the wavelength or the size of the structures of the background affects its influence on pursuit?
4. Is the influence of a structured background different for pursuit of target motions with different maximum amplitudes?

Based upon the results which were obtained, the following answers can be given.

Ad. 1. The orientation of the contrast edges (tested with the horizontal and vertical sine and square wave gratings) had a different inhibitory influence on the smooth eye movements in the direction of the contrast edge and in the direction orthogonal to the edge. For the horizontal component of the smooth eye movements, a vertical edge was more inhibitive than a horizontal one. Complementary, for the vertical component a horizontal direction of the contrast edge was more inhibitive than a vertical edge. The mean difference was small (0.04 ± 0.1 S.D.), but significant ($p < 0.001$).

Fig. 4.4. Gain and phase of the composite (filled symbols) and cumulative smooth eye movement (open symbols) in response to a pseudo-random target motion in two dimensions with an amplitude of 2° (solid lines), 5° (dashed lines) or 10° (dotted lines) upon a random dot background with elements of 2.1°. Fig. 4.4A and 4.4B show the results for pseudo-random target motions with different frequency ranges. During the sessions, the horizontal component of Fig. 4.4A was combined with the vertical component of Fig. 4.4B and the vertical component of Fig. 4.4A with the horizontal component of Fig. 4.4B, in order to have uncorrelated horizontal and vertical stimulus motions. Mean ± S.D. for 5 subjects.

▶

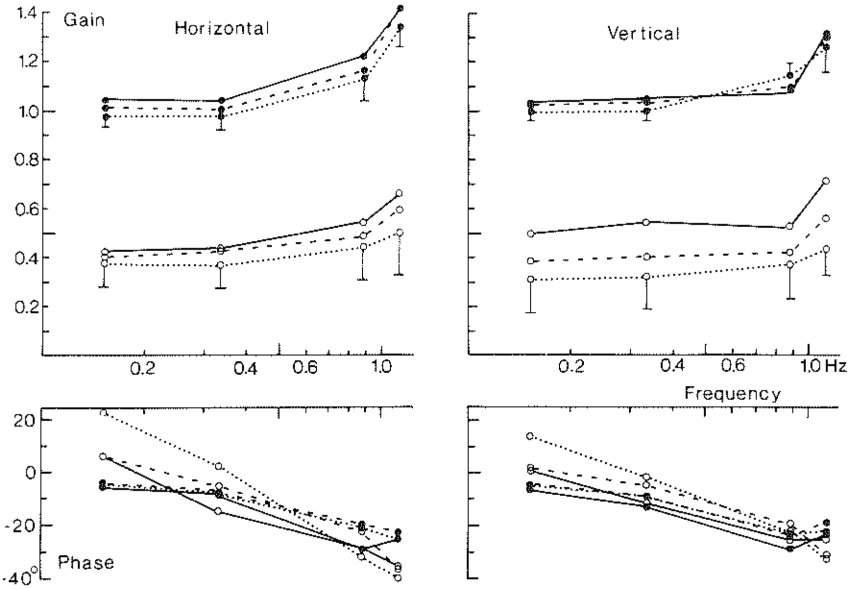


Fig. 4.4A

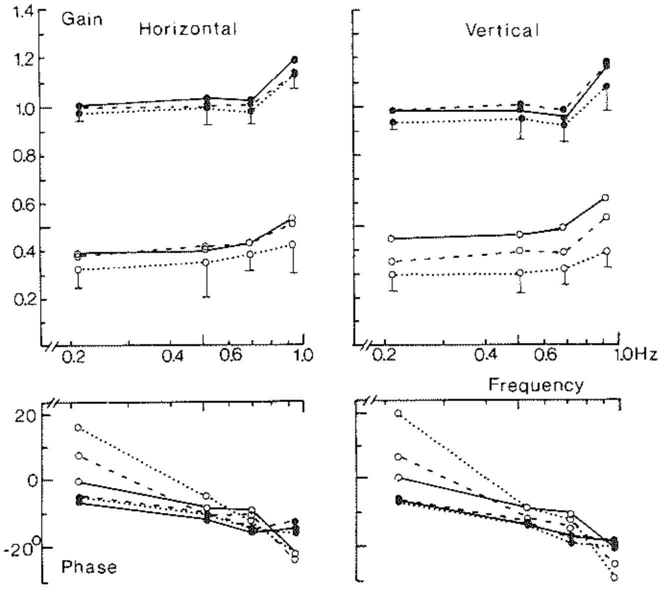


Fig. 4.4B

Ad. 2. A structured background with a soft contrast edge between the black and white parts (sine wave grating) resulted in a similar decrease in gain of the smooth component as a background with sharp edges (square wave grating).

Ad. 3. The size of the elements of the background had no influence on the decrease in smooth pursuit gain.

Ad. 4. The decrease in smooth pursuit gain due to the stationary background was larger for a smaller stimulus amplitude. Fig 4.4 shows results for pursuit upon the random dot background with an element size of 2.1°. Compared with the results for pursuit upon a dark background (Fig. 3.4) the differences in smooth pursuit gain between the different stimulus amplitudes is smaller. The mean decrease in smooth pursuit gain when the random dot background was introduced was, for a maximum stimulus amplitude of 2°: 0.20 ± 0.13 (S.D.); for an amplitude of 5°: 0.18 ± 0.1 (S.D.) and for an amplitude of 10°: 0.15 ± 0.08 (S.D.).

In summary: a structured background has an inhibitory influence on smooth pursuit, but the specific structure of the background is only of marginal importance. The decrease in gain of the smooth component is larger when the stimulus is slower (= amplitude smaller).

4.2 Retinal position error

4.2.1 Diffuse and random dot background

A typical example of retinal position error of pursuit of a pseudo-random target motion upon a random dot background was shown in Fig. 3.8 (recording marked with B). Fig. 3.9 showed an example of the two dimensional distribution of the retinal position error during pursuit of one cycle of a circular target motion upon a dark (NB) and random dot background (B). Both figures illustrate the effect of a structured background on pursuit movements: the smooth component slowed down and extra saccades were inserted to supplement the smooth component. The S.D. of the retinal position error during pursuit upon a diffuse or structured background are shown in Fig. 4.5 (single sine wave and pseudo-random stimuli) and Fig. 4.6 (rhomboid target trajectories).

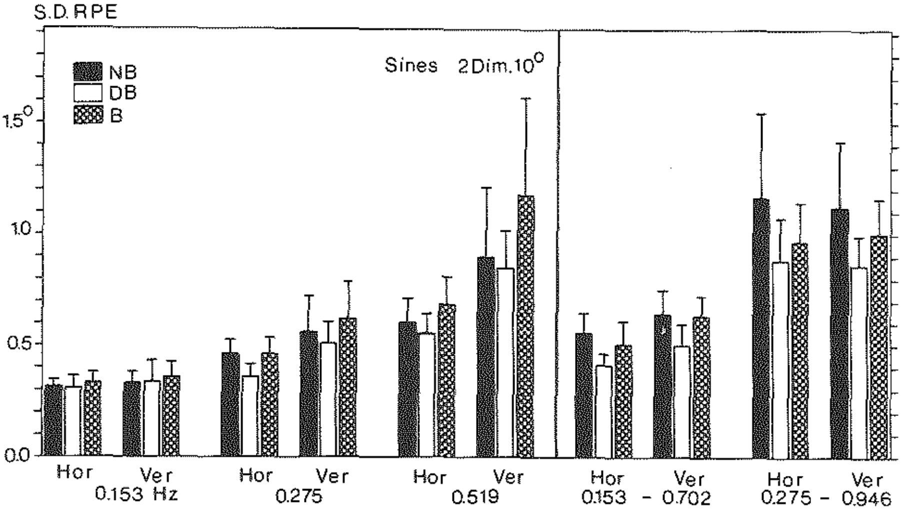


Fig. 4.5. Standard deviations (mean values for 5 subjects, S.D. of this mean indicated by vertical lines) of retinal position error during pursuit of circular or two-dimensional pseudo-random stimuli with a maximum amplitude of 10° upon a dark (black bars), diffuse (open bars) or a structured (checkerboard bars) background.

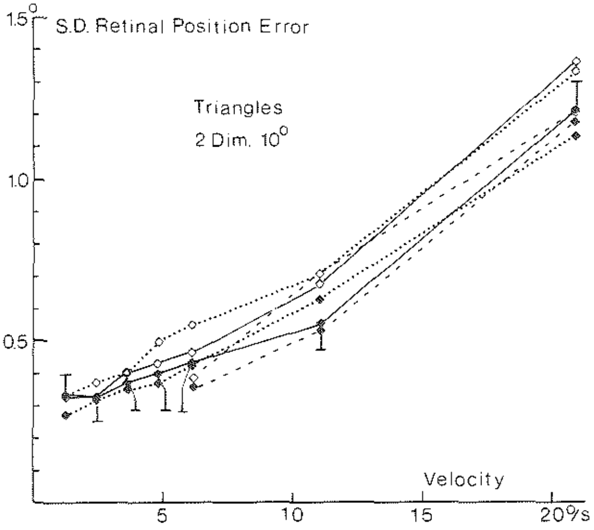


Fig. 4.6. Standard deviations of the horizontal (filled symbols) and vertical (open symbols) component of retinal position error as a function of target velocity during pursuit of rhomboidal stimuli with a maximum amplitude of 10° upon a dark (solid lines), diffuse (dashed lines) or a structured (dotted lines) background. Mean ± S.D. for 5 subjects.

For all types of stimuli used, the S.D. of retinal position error increased with increasing frequency and velocity. For single sine waves the S.D. increased from 0.28° to 0.73° when the frequency increased from 0.15 to 0.52 Hz. The S.D for triangular wave stimuli was larger: 0.30° for a stimulus velocity of 1.22°/s and 1.30° for 20.8°/s (inclusive corners). From the two pseudo-random stimuli specified in Table 3.1, the one with the higher frequency components resulted in a higher S.D of retinal error: 0.89° versus 0.51° for the pseudo-random stimulus with the lower frequency range. The S.D. of the horizontal error was smaller than the S.D 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.; $p < 0.001$). In nearly all situations, the S.D. 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. 4.5 and the dashed line in Fig. 4.6). The mean difference for single sine wave stimuli was 0.06° ± 0.22° (S.D.; $p < 0.02$) and for the two pseudo-random 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 S.D. of retinal position error showed no significant differences between pursuit upon a dark or a structured background. Although the smooth component slowed down when the structured background was introduced, the S D. of retinal position error was not significantly increased. Apparently the insertion of saccades was effective in preventing an increase in the S.D. of the retinal position error. The two pseudo-random stimuli were pursued with a slightly larger S D. of retinal position error upon a dark background than upon a structured background (mean difference 0.06 ± 0.16 S.D.; $p < 0.01$).

4.2.2 Effects of structure of backgrounds

In general, the introduction of the random dot background did not significantly influence the S.D. of retinal position error. The performance of the eye movements (measured in time) was not degraded by the shift from smooth towards saccadic pursuit. To measure if the type of structure within the background had any systematical influence on retinal position error, one pseudo-random stimulus (Table 3.2) was pursued upon twelve different structured backgrounds (see section 4.1.4) with three different stimulus amplitudes (2, 5 and 10°). All these conditions (12 x 3) were used twice with interchange of the horizontal and vertical target motion to balance for the composition of the stimulus in both orthogonal directions. Figs. 4.7 and 4.8 show the S.D. of retinal position error for the two compositions used.

The type of structured background present during pursuit (dark or any of the twelve other backgrounds) did not systematically influence the S.D. of retinal position error. Within each frame of Figs. 4.7 and 4.8, the bars are of comparable height. It was shown (section 3.2.2) that, for a dark background, a larger stimulus amplitude resulted in a larger S.D. of retinal position error. This result applies for pursuit upon a structured background as well.

Another spectral composition of the stimulus resulted in another retinal error. The S.D of retinal error during pursuit of a pseudo-random stimulus was lower for the frequency range of 0.15 - 1.13 Hz than for a pseudo-random stimulus with a frequency range of 0.21 - 0.95 Hz. The average difference for a maximum target amplitude of 10^o was 0.22 ± 0.16 (S.D, $p < 0.001$), for 5^o amplitude 0.10 ± 0.07 (S.D., $p < 0.001$) and for the 2^o amplitude 0.04 ± 0.04 (S.D., $p < 0.001$).

The vertical component of retinal position error was, in general, larger than the horizontal component. For the pseudo-random stimulus with the frequency range 0.159 - 1.13 Hz (Fig. 4.7) the mean difference between the horizontal and vertical component was 0.01 ± 0.05 (S.D., $p < 0.05$) for a 2^o stimulus amplitude, 0.05 ± 0.08 (S.D.) for a 5^o amplitude and 0.06 ± 0.15 (S.D.) for 10^o. For the other spectral composition (Fig. 4.8) these figures were 0.04 ± 0.05 (S.D.); 0.07 ± 0.11 (S.D) and 0.22 ± 0.22 (S.D.) respectively. The last five differences were highly significant ($p < 0.001$).

Thus, the retinal position error was not significantly influenced by any of the structured backgrounds. The spectral composition of the stimulus together with the maximum amplitude determined the error (in time) of the pursuit eye movements. The vertical component of the retinal error is, in similar conditions, larger than the horizontal component.

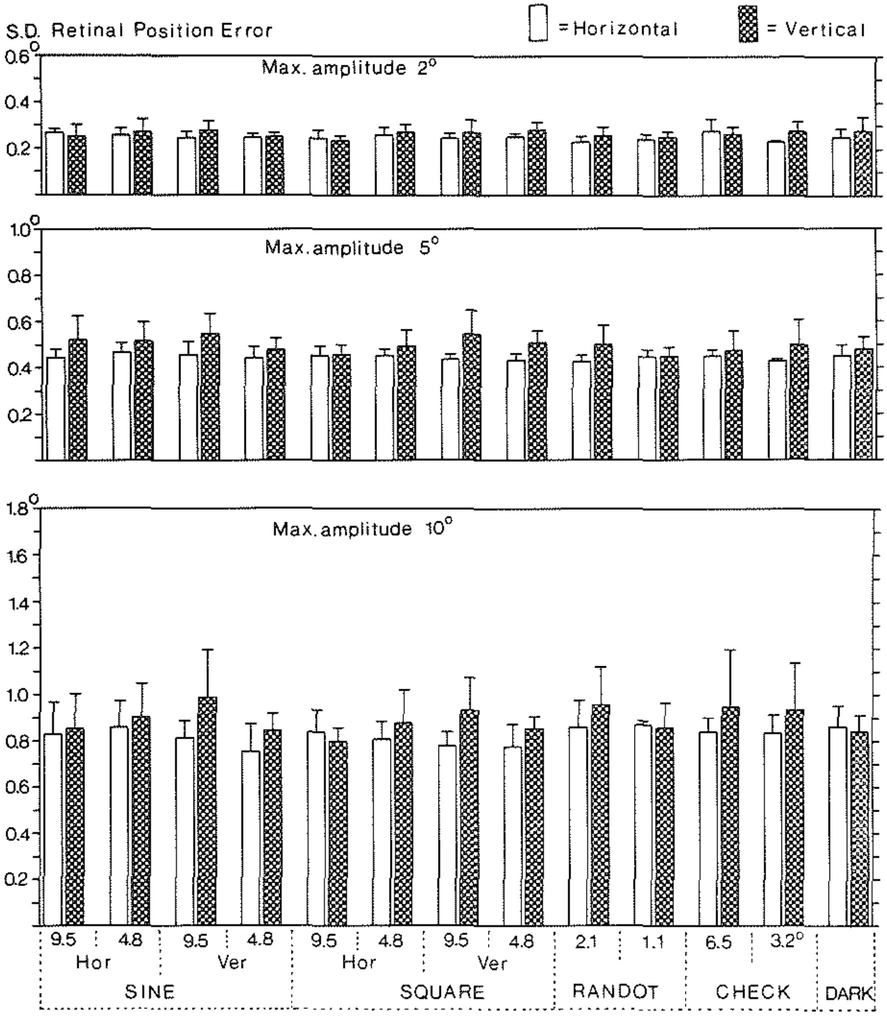


Fig. 4.7. Standard deviations (mean values for 5 subjects, S.D. of this mean indicated by vertical lines) of the horizontal (open bars) and vertical (checkerboard bars) retinal position error during pursuit of pseudo-random stimuli in two dimensions with an amplitude of 2, 5 or 10° as a function of the 13 different backgrounds used. The frequency range of the stimulus was 0.15 - 1.13 Hz.

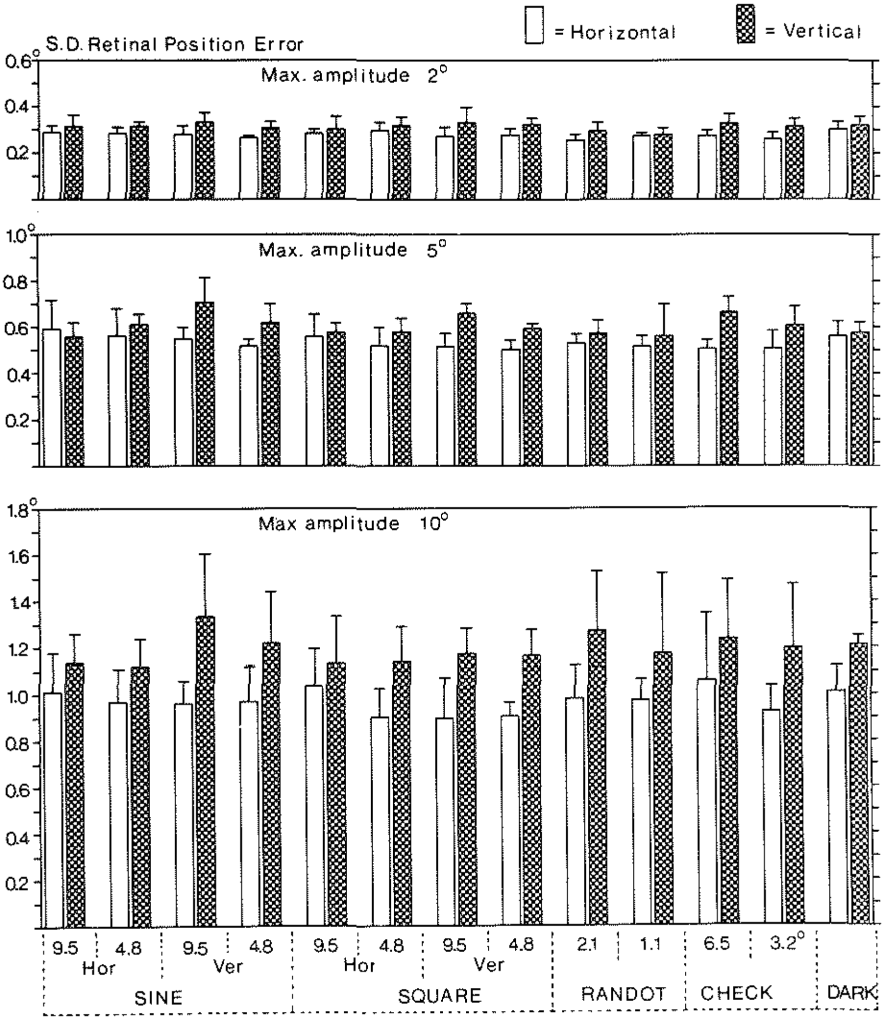


Fig. 4.8. As Fig. 4.7 for a pseudo-random target motion with a frequency range of 0.21 - 0.95 Hz.

4.3 Open-loop pursuit

One way to study oculomotor characteristics and to identify the oculomotor system directly is to use an open-loop condition. In this condition, eye movements made by the subject do not influence the position of the target on the retina. The open-loop condition was created by adding (electronically) the eye position to the target position (Fig. 4.9).

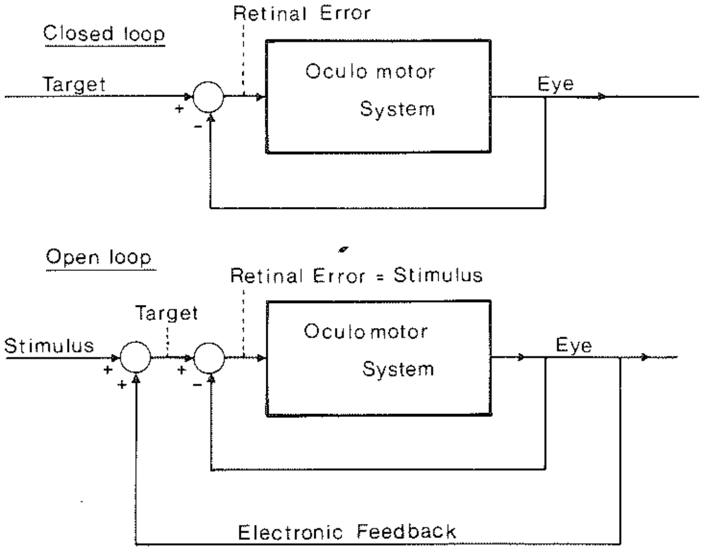


Fig. 4.9. Schematic diagram of the normal closed-loop and artificially open-loop pursuit condition. In the open-loop condition, the retinal error signal is equal to the presented stimulus motion.

Only a number of pilot experiments was done. In these experiments, some of the measurements were open-loop, others were not. Only the feedback loop for the horizontal eye movements was opened. One pseudo-random stimulus (Table 3.1; horizontal component of SUM 1) was displayed in horizontal direction with an amplitude of 0.5, 1 or 2^o for the open-loop condition (in these measurements the retinal error signal was equal to the stimulus) and with an amplitude of 1, 2 or 4^o for the closed-loop condition. Subjects were told before the experimental session that open-loop measurements would be done (all knew what an open-loop condition was) and instructed to pursue the target in a normal way. In practice, subjects immediately recognized an open-loop condition.

The results obtained with these open-loop experiments were very idiosyncratic. Fig. 4.10 shows five examples of open-loop pursuit, one for every subject serving in these experiments.

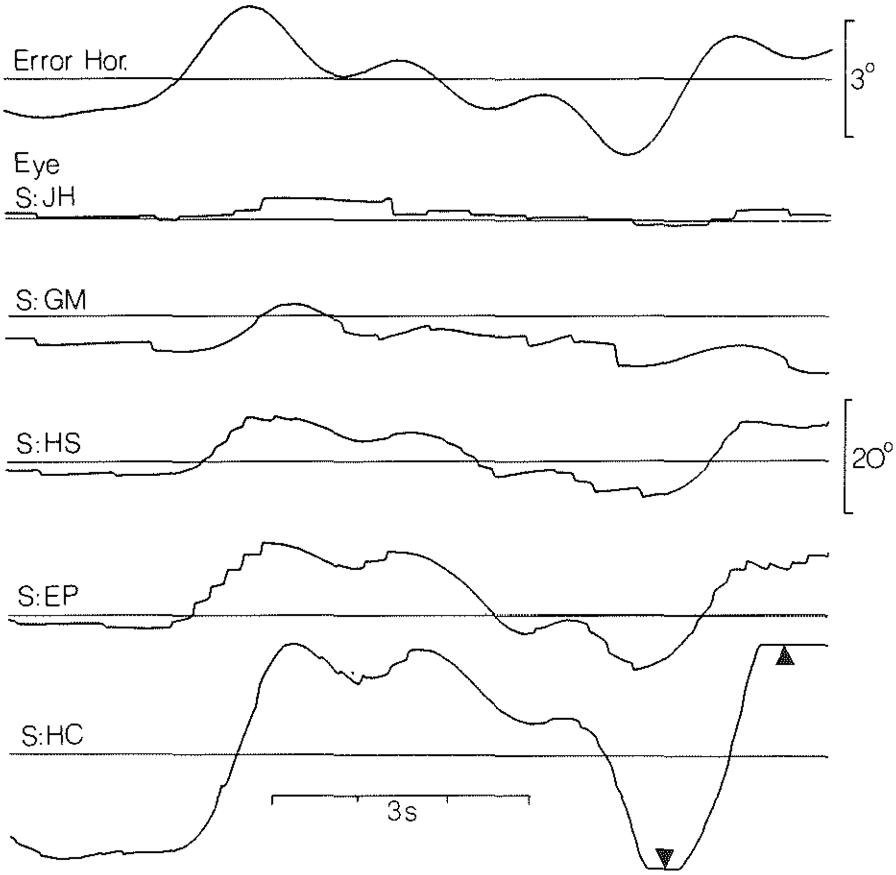


Fig. 4.10. Recordings of the horizontal eye movements of 5 subjects in response to a stimulus (= retinal error) presented in an open-loop condition. Notice the different calibrations used for error and eye motion. The arrows in the lower trace indicate that the deviation of the eye exceeded the range of the recording equipment (20°).

A completely different response can be seen for the different subjects. One subjects (HC) responded to the stimulus (= retinal error signal) with very large eye movements which exceeded the range of the apparatus. The gain of his eye movements (measured with the stimulus = retinal error signal serving as input signal) varied between approximately 5 and 20. Another subject (JH) responded only with small eye movements (gain values varied between 0.5 and 2). Subject GM on the other hand reported that she voluntary modified her eye movements (i.e. the gain of her eye movements) in order to keep the target within a limited area (about 20°) around the centre of the screen (which she managed quite well).

On the basis of these results, no further attempts were made to investigate the influence of a background on the pursuit system in an open-loop condition.

4.4 Discussion

4.4.1 Effect of background and attention

The results presented in this chapter 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 whereas the overall 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.

Smooth pursuit and saccades subserve two different functions. The effect of smooth pursuit eye movements is to reduce the slip of the image on the fovea and thereby prevent an increase in retinal position error. This stabilization is not perfect. Therefore saccades frequently interrupt the smooth eye movements to correct the eye position. Smooth pursuit movements do not minimize the unweighted retinal slip velocity; rather they minimize the sum of retinal slip velocities at different parts of the retina after weighting with different factors. These factors are partially determined by the structure of the visual system, but they can, on the other hand, be modified by the subject. The structure of the visual system, such as ganglion cell density and cortical mapping area of different parts of the retina, determines the relatively large weight of the central part of the retina as compared to the peripheral part. Van Die & Collewijn (1982) described that, in the generation of optokinetic nystagmus, the influence of the central 10° of the visual field is disproportionally large compared to the contribution of the peripheral retina (beyond 15^o eccentricity). Selective attention, on the other hand, enables the subject to modify the weighting factors to some extent (Collewijn, Curio & Grüsser, 1982).

The decrease in smooth pursuit was compensated by another part of the visuo-motor system: the saccade generation system. As a result, the gain of the composite eye movement did not decrease and the S D. of retinal position error did not increase. There is some penalty for this strategy. Firstly, the target will be less stable on the retina due to the degradation of smooth pursuit. Secondly, the time spent to make saccades to compensate for the decrease in smooth pursuit will increase the total amount of time in which threshold for vision is elevated (Zuber & Stark, 1966; Beeler, 1967; Campbell & Wurtz, 1978). One possible explanation for the strategy to replace part of the smooth component by saccades is that if, during foveal pursuit, the visual information coming from the surrounding of the moving target is completely neglected, any object of interest or danger which is in this surrounding will remain unnoticed by the subject. This is an unwanted and possibly dangerous situation. Therefore, visual information from the periphery of the retina is processed up till a certain extent, although it interferes with the primary task of the visuo-motor system: pursuing the moving target.

Kowler, Murphy & Steinman (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, Murphy & Steinman (1978) I found only a minimal effect of a diffusely illuminated background. For all types of target motion, the S.D. of retinal position error was even slightly smaller (Figs. 4.5 and 4.6) 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 I 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 small saccades more frequently to foveate the target, which resulted in a smaller S D. of retinal position error.

My results contrast with the preliminary 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, blurring of the image of the background may occur and no effect of the background may be found. 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, than the background might interact more strongly with the smooth pursuit eye movements. The results in this chapter show that the decrease in smooth pursuit gain is relatively larger for a smaller stimulus amplitude, thus when the stimulus is slower (see Fig. 4.4). 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 my results.

Hood (1975) did some preliminary experiments on pursuit of a target which moved in darkness or upon a striped background, using EOG recording. In normal subjects he found no effect. The background in his experiments, however, contained relatively little contrast (narrow white stripes at intervals of 15^o) 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 ($< 1.0^o$) 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, but much stronger than the one I 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, Gogan, 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 exerted by a background.

The decrease in smooth pursuit gain during pursuit upon a structured background as presented in this study, is somewhat smaller than the one reported earlier (Tamminga & Collewijn, 1981). This may be due to the fact that a number of subjects were used extensively in the background paradigm since the report in 1981. As a result, some of these subjects have learned to counteract the inhibitive influence of the background with as a result a smaller decrease in smooth pursuit gain. It also indicates that training can have a beneficial effect on pursuit in the presence of a background. Thus, the inhibitory effect of a stationary surround can sometimes be overcome by sufficient training and/or specific attention. It is known that training can also improve the quality of pursuit without a background (Kowler, Murphy & Steinman, 1978). Another difference is that for the experiments described in this study, I used a small target (7 min arc) of high luminance whereas the results of Tamminga & Collewijn (1981) were obtained with a fairly large (40 min arc) and transparent target, i.e. the background was not concealed by a solid target. This means that any retinal velocity detectors in the central retina were stimulated by the opposite stimuli of target and background, which could lower the velocity dependent drive for pursuit by straightforward competitive interaction.

4.4.2 Open-loop pursuit

Several investigators have done experiments on pursuit in an open-loop condition (e.g. Heywood & Churcher, 1971; Yasui & Young, 1975; Wyatt & Pola, 1979; Cushman, Tangney, Steinman & Ferguson, 1983). Their general finding was that small target motions or displacements on the retina gave rise to relatively large eye movements. This high open-loop gain is thought to be the mechanism that brings about accurate pursuit under normal closed-loop conditions encountered in the real world. However, the experiments done to investigate the influence of a stationary background upon pursuit under open-loop conditions (this study) were not successful. The results obtained showed gains of the open-loop system which were for one subject a tenfold higher than for another subject. Although the open-loop measurements were intermixed with normal closed-loop measurements, subjects recognized an open-loop condition almost immediately. Furthermore, at least one subject was able to modify her open-loop pursuit response in such a way that the target remained within a limited area around the centre of the screen. The open-loop condition must be considered as an unnatural situation for pursuit. During closed-loop conditions (normal visual feedback), eye movements are used to control the amount of retinal error: smooth eye movements minimize the retinal slip velocity and saccades interrupt the smooth eye movements to correct the eye position if the retinal position error rises above a certain unacceptably high level (see Figs. 3.8, 3.9, 3.14 and 3.15). In an open-loop condition, eye movements are unable to influence the retinal position of the image of the target; retinal slip and position error are completely determined by the stimulus motion. This artificiality of retinal error resulted in large individual differences. Such differences, however, were small during pursuit in a closed-loop condition.

Wyatt & Pola (1979) obtained, in contrast to the results presented in this chapter, consistent results in a comparable open-loop situation. They used sinusoidal stimuli of comparable amplitude (2 or 3° peak to peak) and frequency (0.3 - 1.5 Hz). There are, however, a number of differences which could account for this (apparent) consistency. Wyatt & Pola did experiments with two subjects and illustrate their findings with the results of one subject only. Furthermore, they used recording equipment with a low resolution (0.25°) and used a feedback loop to create the open-loop condition with an accuracy of 0.25 - 0.5° and limited bandwidth (75 Hz) in combination with a relatively large target (1.5° in diameter). This configuration is possibly not sufficient to provide a complete open-loop condition and to eliminate any influence of the eye movement on the retinal error. Cushman, Tangney, Steinman & Ferguson (1983) showed that even a minimal amount of retinal slip allows the subject to overcome the idiosyncratic characteristics of his smooth pursuit subsystem. Slip, even when unnatural, wiped out virtually all individual differences. Wyatt & Pola reported that the gain at a given frequency of target motion was found to shift somewhat from day to day. Their results, however, lack the specification of the S.D. of this gain.

On the basis of my results, I conclude that in an open-loop condition pursuit eye movements primarily reflect idiosyncracies of the particular subject used in the experiment. The results do not contribute to the understanding of the interaction between pursuit and a stationary background.

CHAPTER 5

INDUCED EYE MOVEMENTS DURING FIXATION OR PURSUIT

5.1 Fixation

In the previous chapter it was shown that the presence of a conflicting stimulus during pursuit -a stationary structured background- influenced the pursuit eye movements; although the overall precision of the composite eye movements, measured in time and frequency, was not degraded, the smooth eye movements slowed down and there was a shift from smooth towards saccadic pursuit. To extend the range of target velocities to the lowest velocity possible (= zero), fixation experiments were done. To investigate the influence of a stationary or structured background upon the eye movements during fixation, subjects had to fixate a stationary target during 32.77 s under various conditions: with or without a stationary diffuse or random dot background (section 5.2) or in the presence of a moving random dot background in a closed- (section 5.3) or open-loop condition (section 5.4). During the fixation experiments, the sensitivity of the recording equipment was 2.5 times higher than during the pursuit experiments. Each fixation measurement was repeated once, with a time interval of about 15 min.

5.2 Fixation with a stationary background

During fixation the eye was not completely stable. Eye movements consisted of combination of small saccades (also called microsaccades) and drift. The amount of instability of the eye varied between subjects. Fig. 5.1A shows the combined horizontal and vertical eye movements during fixation with a dark background for two subjects. The eye of subject HS was relatively unstable and moved in a small area around the central target. Subject DP, however, demonstrated an almost complete stabilization of the eye during fixation. The S D. of the retinal error was calculated as a measure of the quality of the fixation.

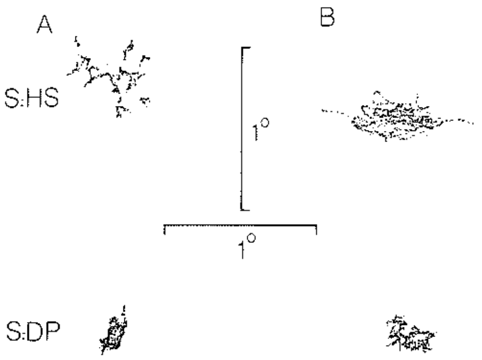


Fig. 5.1. Registration of the combined horizontal and vertical eye movements of two subjects (HS and DP) during fixation of a spot of 7' diameter upon a dark background (A) or random dot background in horizontal, sinusoidal motion (B). Duration about 8 s.

Table 5.1 presents the results for the horizontal and vertical component of the eye movement during fixation upon the three different stationary backgrounds used: dark, diffuse or structured.

There was no significant difference in the quality of fixation between the three different backgrounds. Although the structured background formed a larger stationary stimulus, the S.D. of retinal position error did not decrease by the presence of this background. The horizontal component of the S.D. of retinal position error was generally smaller than the vertical component although the difference was not significant. The S.D. of retinal position error is comparable to the values obtained if the results for tracking of a slope (Fig. 3.13A) are extrapolated to a zero target velocity: 0.10° for the horizontal and 0.12° for the vertical component.

5.3 Fixation with a moving background

The complement of pursuit with a stationary background is fixation with a moving background. During fixation of a central target, the moving background formes a large moving visual stimulus on the peripheral retina. To measure the influence of this moving stimulus upon the quality of fixation and to investigate if eye movements were induced by the background movement, subjects had to fixate the stationary target while the background moved sinusoidally with the following frequencies and amplitudes:

Table 5.1. Horizontal and vertical component of the S.D. of retinal position error (in degrees) during fixation upon different backgrounds. Results of 4 subjects and 2 trials per subject.

Subject	Dark Background	Diffuse Background	Random dot Background
Horizontal component			
EP	0.169	0.140	0.135
	0.127	0.070	0.161
GM	0.062	0.050	0.073
	0.092	0.111	0.071
HC	0.085	0.135	0.089
	0.066	0.093	0.092
HS	0.098	0.058	0.069
	0.089	0.129	0.199
Mean (S D)	0.099 (0.035)	0.098 (0.036)	0.111 (0.049)
Vertical component			
EP	0.174	0.089	0.107
	0.067	0.087	0.102
GM	0.060	0.048	0.058
	0.069	0.060	0.053
HC	0.122	0.238	0.171
	0.106	0.168	0.152
HS	0.080	0.088	0.058
	0.133	0.159	0.147
Mean (S D)	0.101 (0.040)	0.117 (0.065)	0.106 (0.047)

(a) 0.153 Hz and 4.94°; (b) 0.275 Hz and 2.68°; (c) 0.397 Hz and 1.84° and (d) 0.580 Hz and 1.26°. The amplitudes of the background motions were inversely proportional to the frequency to obtain stimuli with equal maximum velocities. To test the superposition of the effects of the single sine wave stimuli, the background was also displaced pseudo-randomly with the sum of a and c; b and d; a, b and c; b, c and d; and all four single sine waves. Due to technical limitations, the background was displaced in horizontal direction only.

5.3.1 Gain and phase

Fixation was influenced by the presence of a moving background, although the induction of motion was small and varied between subjects and between different background movements.

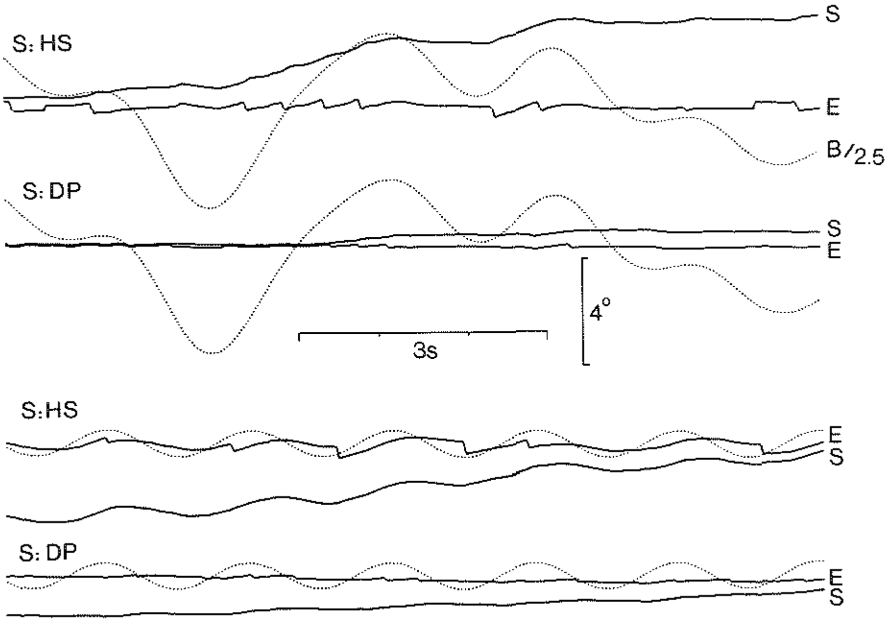


Fig. 5.2. Registration of the horizontal composite (E) and cumulative smooth (S) eye movements of two subjects (HS and DP) during fixation in the presence of pseudo-randomly or sinusoidally moving background (dotted lines). The amplitude of the background movement during the experiment was 2.5 x larger than shown here.

Fig. 5.2 shows the recordings of the background (divided by 2.5 in amplitude) and composite and smooth eye movements during fixation with a sinusoidally and pseudo-randomly moving background Subject HS showed a relatively large induction of eye movement, while the induced eye movements in subject DP were very small. Subjects reported that, although they knew that the target was stable and only the background was displaced, they perceived a motion of the target, especially during background movements with a small amplitude. In general, but by no means always, the saccades in the composite eye movement were, in contrast to saccades during pursuit, opposite to the smooth eye movements. They brought the eye back to the point of fixation if the eye had drifted away. Therefore, only the gain and phase of the cumulative smooth eye movements with respect to the background movement were analyzed. Fig. 5.3 shows mean gain and phase of the induced smooth eye movements for the different background movements.

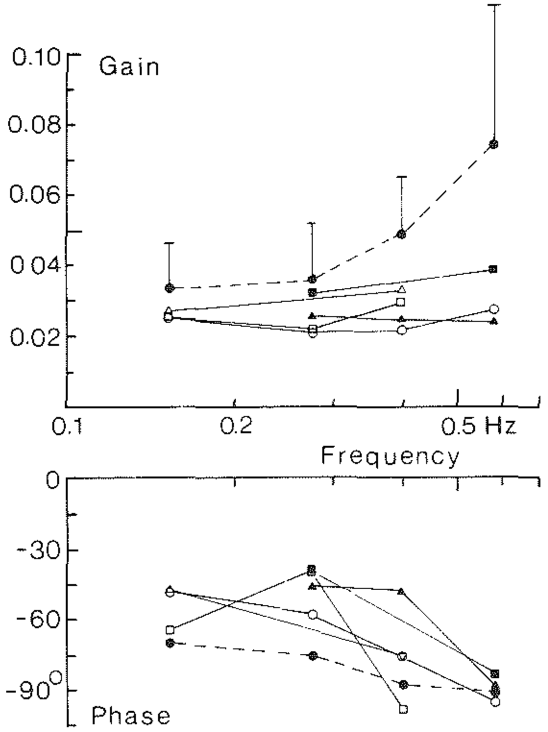


Fig. 5.3. Mean gain and phase of the cumulative horizontal smooth eye movements which were induced by a sinusoidally (dashed lines) or a pseudo-randomly (solid lines) moving random dot background of different spectral compositions. Mean ± S.D. of 4 subjects, two trials each. The background moved in horizontal direction.

For single sine wave stimuli, the gain increased with frequency. The amplitude of the induced eye movements, however, decreased with increasing frequency, because the increase in gain was less than the increase in frequency (stimulus amplitude was inversely proportional to frequency). For a background motion with an amplitude of 4.94° at 0.15 Hz, the amplitude of the cumulative smooth eye movements was 0.17° (= stimulus amplitude x gain). This amplitude decreased to 0.09° for a background movement of 1.26° at 0.58 Hz.

There was no superposition of the motion induced by the single sine waves. The induced motion was smaller for pseudo-random stimuli than for single sine wave stimuli and decreased when the number of components in the stimulus increased. The induced eye movements were not clearly in phase, nor in counter phase with the background motion. The phase of the smooth eye movements varied between -30 and -100°, and decreased with the increase in frequency.

5.3.2 Retinal error

Fig. 5.4 summarizes the S.D. of retinal position error for fixation in darkness and in the presence of a stationary or moving background.

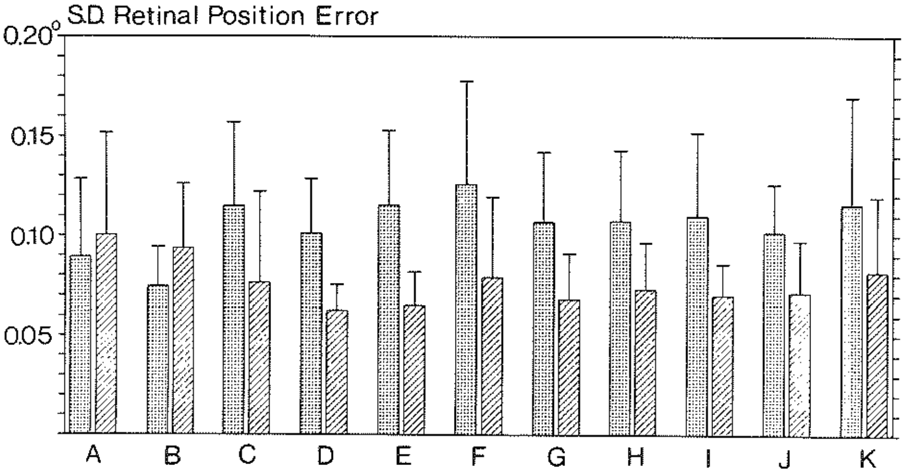


Fig. 5.4. S.D. of the horizontal (dotted bars) and vertical (hatched bars) component of retinal position error during fixation of a spot of 7' diameter upon a dark background (A); stationary random dot background (B); sinusoidally moving background of 0.15 Hz and 4.94° (C); 0.28 Hz and 2.68° (D); 0.40 Hz and 1.84° (E); 0.58 Hz and 1.26° (F); or a pseudo-randomly moving background with a spectral composition equal to the sum of C and E (G); D and F (H); C, D and E (I); D, E and F (J); and all four single sine waves (K). Mean and S.D. (indicated by a vertical line) of four subjects. Note: These fixation experiments incorporated other subjects than the ones reported in Table 5.1.

Due to the induction of motion by the background which moved in horizontal direction, the S D. of the horizontal component of retinal error increased (mean increase 0.03°). The S.D. of the vertical component, however, decreased. This decrease in vertical direction is also visible in Fig. 5.1B. The vertical eye movements decreased in amplitude when the background was moved horizontally. There was no significant difference in retinal error during fixation between the different movements of the background.

5.4 Fixation of a central target in an open-loop condition

The visual feedback during fixation enabled the visual system to correct the eye position with a saccade whenever the eye deviated from the target position. To eliminate this visual feedback, open-loop experiments were done in which the target was stabilized in horizontal direction within the foveal region. During this stabilization, subjects which showed a very stable fixation in vertical direction, reported that the target faded (which indicates a good stabilization) but that the target could be made visible by making small vertical eye movements. During these experiments, the background was displaced with a pseudo-random stimulus (sum of four sine waves; Table 3.1, horizontal component SUM 1) with three different maximum amplitudes: 0.5, 1 and 2°. Fig. 5.5 shows two examples of the resulting composite and cumulative smooth eye movements.

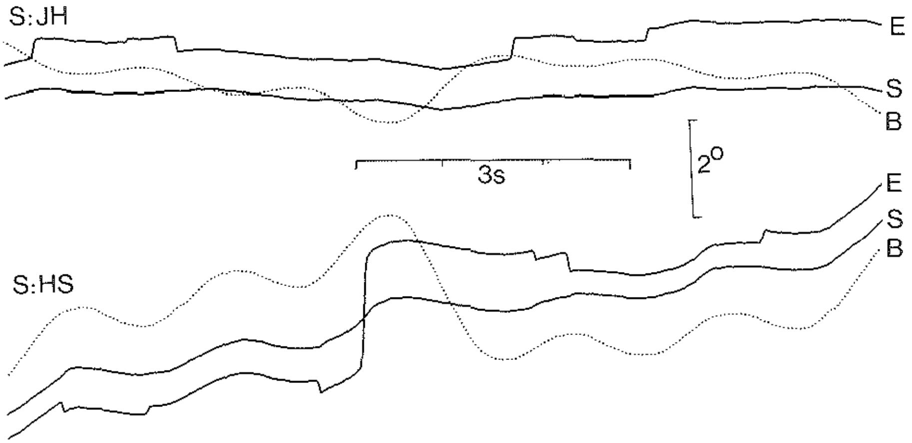


Fig. 5.5. Registration of the horizontal composite (E) and cumulative smooth (S) eye movements of two subjects (JH and HS) during fixation in open-loop condition in the presence of pseudo-randomly moving background (dotted lines).

The induced movement varied between subjects but amounted to only a fraction of the movement of the background. Fig. 5.6 summarizes mean gain and phase of the cumulative smooth eye movements for the three different amplitudes of the background motion.

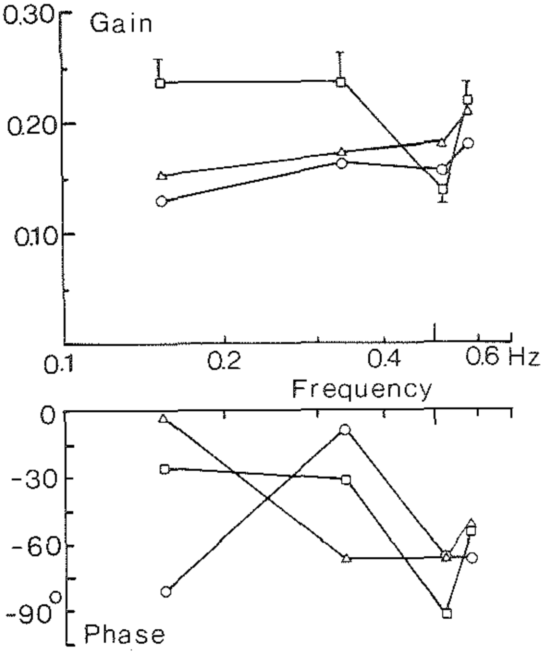


Fig. 5.6. Mean gain and phase of the horizontal component of the cumulative smooth eye movements which were induced by a pseudo-randomly moving random dot background with a maximum movement amplitude of 0.5° (squares), 1.0° (circles) or 2.0° (triangles) during fixation of a horizontally stabilized target (open-loop fixation). Mean ± S.D. of 5 subjects.

Even under open-loop conditions, the gain of the smooth component was small: less than 0.25. There was no clear relationship between the gain and the amplitude of the background motion. The background movement with the maximum amplitude of 2^{o} resulted in a lower gain than the 0.5^{o} motion, but in a higher gain of the smooth component than the 1^{o} background movement. The phase of the smooth eye movements varied between 0 and -90^{o} and showed a tendency to decrease with the increase in frequency.

Although there was a large moving visual stimulus on the perifoveal retina and no visual feedback from the central retina due to the open-loop condition, the eye movements which were induced were small and not in phase nor in counterphase with the motion of the background.

5.5 Induced motion during pursuit

To investigate the induction of motion by a moving background during pursuit, five subjects had to pursue a pseudo-random target motion (sum of four sinewaves; Table 3.1, vertical component SUM 1) in horizontal or in vertical direction while a random dot background was displaced in horizontal direction with a pseudo-random motion (sum of four sinewaves; Table 3.1, horizontal component SUM 1). Target and background motion were uncorrelated. The amplitudes of the components of target and background motion were scaled to obtain maximum amplitudes of 1, 2 or 4°. Subjects were not informed that the target and background would be displaced simultaneously; they were instructed to pursue the target attentively.

During simultaneous horizontal target and background movements, subjects perceived that the target and background were moving both in horizontal direction with uncorrelated motions. However, when the target was moved in vertical direction only and the background in horizontal direction only, subjects had the strong illusion that the target was moving both in horizontal and vertical direction. During pursuit, there was induction of eye movements by the moving background, but the induced eye movements were small. During horizontal pursuit, it was not possible to separate the induced smooth eye movements from the pursuit smooth eye movements, because the amplitude (and thus the energy) of the induced motion was overwhelmed by the pursuit motion. Therefore, Fig. 5.7 shows only mean gain and phase of the horizontal induced smooth eye movements during pursuit in vertical direction.

Not withstanding the strong illusion that during vertical pursuit the target was displaced in horizontal direction as well, the gain of the induced horizontal eye movements was small: less than 0.15 over the complete frequency range of the background motion. A smaller amplitude of the background motion tended to induce a smaller eye movement. The standard deviations of the gains were relatively large, due to large differences between the subjects. The phase lag of the smooth eye movements was larger for a smaller background amplitude and showed a tendency to increase with frequency. The phase varied between -12 and -105°.

Compared to the induced eye movements during fixation (Fig. 5.3) the induced eye movements during pursuit (Fig. 5.7) were larger. Apparently, the induction of motion is larger when the eye is moving than when the eye is stationary. The cumulative amplitude of the smooth eye movements, however, was limited in both conditions to only a fraction of the background movement. Furthermore, the smooth eye movements were neither in phase nor in counterphase with the background motion.

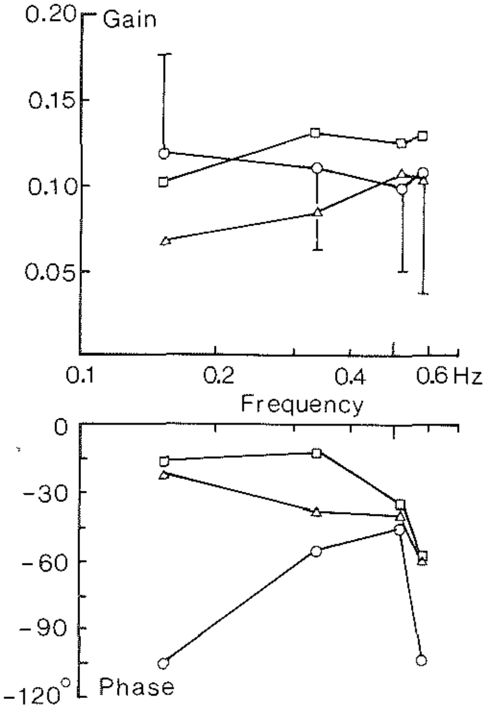


Fig. 5.7. Mean gain and phase of the horizontal component of the cumulative smooth eye movements which were induced by a random-dot background moving pseudo-randomly with a maximum amplitude of 1.0° (circles), 2.0° (triangles) or 4.0° (squares) during pursuit of an uncorrelated pseudo-random target motion with the same amplitude in vertical direction. Mean ± S.D. for 5 subjects.

5.6 Discussion

The results in this chapter show that, during fixation, the eye is never completely stable. Even if a large stationary pattern was added to support the eye to fixate the central target, eye movements remained a combination of small saccades and drift and the S D. of retinal position error was not influenced Although the illusion of target motion was strong during fixation in the presence of a moving random dot background (in closed- or in open-loop), the eye movements did not reflect this perceived target motion. Even in the absence of any visual feedback due to an open-loop condition, the induced eye movements amounted to only a fraction of the movement of the background.

The eye movements during fixation varied between subjects. Some subjects showed, even in the presence of a moving background, a very stable fixation almost without saccades and drift; other subjects moved their eye in a small region near the target or drifted strongly in the direction of the moving background. This intersubject variability was reported before by other investigators (Fiorentini & Ercoles, 1966; St-Cyr & Fender, 1969c; Steinman, Haddad, Skavenski & Wyman, 1973; Steinman, Cushman & Martins, 1982). The S.D. of retinal error as reported in this study is somewhat larger than values typically mentioned in the literature. This may be due to the fact that the recording periods used in this study were rather long and sometimes contained blinks. Furthermore, the target which was used (laser spot) was not the optimal target for eliciting a maximal stable fixation. Murphy, Haddad & Steinman (1974) showed that a small annulus was a more effective stimulus for fixation than a small spot. The aim of my study, however, was to investigate the influence of a background during pursuit or fixation with the same target and backgrounds in both situations.

During fixation, the eye movement pattern is composed of three kinds of eye movements: (micro)saccades, drift and tremor. In this study, no special arrangements were made to analyze tremor. This type of eye movement has a frequency of 20 to 100 Hz and a median amplitude of about 20" (Findlay, 1971). There are several theories about the function of the microsaccades and drift during fixation. One theory is that if the eye does not move, the visual image is stabilized on the retina and the image fades from perception after several seconds. In 1956, Cornsweet showed that neither the frequency of saccades nor the size of drift samples correlated with the fading of stabilized images. The drift in combination with the smooth eye movements provide enough motion of the eye to prevent the visual image from fading.

Fiorentini & Ercoles (1966) and Steinman, Cunitz, Timberlake & Herman (1967) showed that microsaccades can be eliminated by simple instructions and that when they are absent, precise control of the line of sight is accomplished entirely by smooth eye movements. A current theory (Steinman, Cunitz, Timberlake & Herman, 1967) of the significance of saccades during fixation, which fits to the results shown in this chapter, is that during normal visual search, the eye rests in an attended region for several seconds at the most, a sufficient time to take in all relevant visual information without any microsaccades. If, under laboratory conditions, the subject is asked to fixate a very small target for a longer period of time, the subject is never entirely sure that his line of sight is perfectly centered and therefore he uses small saccades to scan a small region around the target.

The scanning eye movements disappeared when motion was induced by a moving background (Fig. 5.1B). The induced smooth eye movements tended to move the eye away from the point of fixation. To prevent an increase in retinal error, saccades were used to bring the target back to the centre of vision (Fig. 5.2). Apparently, the task of correcting the eye position to counteract the induced eye movements forced the visuo-motor system to abolish the small scanning eye movements; the system was too much involved in correction of the eye position. There is, however, in literature some controversy concerning the significance of the various fixational eye movements; see Ditchburn (1980) and Kowler & Steinman (1980) for a recent overview. The small saccades, functional or not, are not detrimental to vision; they do not move the target away from the part of the retina where objects can be seen well.

The induction and perception of motion during fixation has been investigated earlier. Murphy, Kowler & Steinman (1975), Mack, Fendrich & Pleune (1979) and Mack, Fendrich & Wong (1982) used backgrounds which moved at constant velocity, while Yasui & Young (1975), Wyatt & Pola (1979), Pola & Wyatt (1980), Mack, Fendrich & Wong (1982) and Collewijn, Conijn, Martins, Tamminga & Van Die (1982) used a sinusoidal movement of a background or a structure surrounding the central target which was viewed in closed- or open-loop. New results in the current study are that the effects of different single sine wave stimuli did not add, that the smooth eye movements lagged the background with 90° of phase and that the induction of motion was larger during pursuit.

Murphy, Kowler & Steinman (1975), using a background formed by a square wave grating which moved in horizontal direction with a constant velocity, found that most of the eye motion was in the direction of the background movement, although the fastest mean drift velocity was less than 6% of the velocity of their most influential background motion (0.8°/s). Mack, Fendrich & Pleune (1979) also reported that the eye drifted in the direction of a frame of reference, which consisted of four points which marked the corners of a rectangle 3° high and 0.5° wide.

The results of experiments done with sinusoidal background motions contradict each other. Wyatt & Pola (1979) found that the eye movement was in phase with perceived movement of the target and in counterphase with the movement of the background, which was formed by a frame consisting of two thin strips which formed the upper and lower border of a rectangle 27° wide and 22° high. The eye viewed a central target which was stabilized on the retina (open-loop). In addition to this experiment, Wyatt & Pola (1979) found that pursuit of a sinusoidally moving target in open-loop was augmented by the movement of the frame in counterphase with the stimulus motion. Mack, Fendrich & Wong (1982), however, replicated the experiments done by Wyatt & Pola and found the opposite of what Wyatt & Pola reported: the amplitude of pursuit was substantially reduced when a counterphase frame was present. This is consistent with my finding that smooth pursuit in the presence of a stationary background is slowed down. Collewijn, Conijn, Martins, Tamminga & Van Die (1982) reported that the eye motion induced by a sinusoidally moving random dot background in closed-loop condition had a phase lag of about 90° with respect to the background motion, thus was neither in phase nor in counterphase with the background motion. The present study shows that the induced eye movements tend to lag 90° in phase with respect to the background, especially for background movements with a small amplitude (which is what Collewijn, Conijn, Martins, Tamminga & Van Die, 1982, used). Such background movements induce smooth eye movements with a relatively high gain. Collewijn, Conijn, Martins, Tamminga & Van Die (1982) found a mean gain of about 0.2, which is somewhat higher than the data presented in Fig. 5.3.

There are factors which may account for the different results of the various studies. First of all, there is the recording technique. Wyatt & Pola (1979) used an infrared reflection technique with a resolution of about 0.25°; Mack, Fendrich & Wong (1982) used a Purkinje image tracker which had a precision of about 2 min arc, whereas Collewijn, Conijn, Martins, Tamminga & Van Die (1982) and I used a scleral induction coil technique with a resolution better than 1 min arc. Especially in the open-loop condition, the use of a very precise recording technique is of crucial importance (see discussion in the previous chapter). A second factor of major importance is the idiosyncrasy of the induced eye movements in different subjects (Figs. 5.1 and 5.2). A third factor is the type of motion of the background. In the current study, a sinusoidal background movement with a small amplitude and a high frequency induced smooth eye movements with a higher gain than a stimulus with large amplitude and low frequency, although the maximum velocities of all single sine waves were equal. The use of a more complex background motion resulted in a smaller induction of movement; if the background motion contained more components, the gain of the cumulative smooth eye movements was lower. Another important factor was the nature of the background which was used in the different studies. Most investigators used a background or frame of reference which contained relatively little structural information: a couple of small points or small stripes located in the periphery. Murphy, Kowler & Steinman (1975) used a richer background (square wave grating) although it was rather small (4^o). Collewijn, Conijn, Martins, Tamminga & Van Die (1982) and I used a background which was large and contained many contrast edges: a random dot background of 90×90^o in size. The results obtained with this background are consistent: the induced eye movement lagged the background motion by 90^o.

During pursuit and probably also during fixation, smooth eye movements serve to minimize the weighted sum of central and peripheral slip velocity. Therefore, they should be maximal when this weighted sum is maximal. If the target is stable (fixation), smooth eye movements should be determined by the velocity of the background only. Therefore, induction should be larger when the background motion is faster (limited of course by the velocity at which blurring of the background occurs).

This explanation is corroborated by the results of Murphy, Kowler & Steinman (1975) and Mack, Fendrich & Pleune (1979) who found that the eye drifted in the direction of the background motion and not in a direction opposite to the background displacement. They used, however, background displacements with constant velocities. With these type of stimuli it is impossible to clarify the exact phase relation between background movement and induced eye movement. The lagging of the eye in my experiments and those of Collewijn, Conijn, Martins, Tamminga & Van Die (1982) suggests that induction needs some time to build up and that this risetime is correlated with the frequency of the background motion.

There was, during fixation, no superposition of the motion which was induced by the single sine waves (Fig. 5.3). The induction was smaller for pseudo-random stimuli and reduced further when the number of components in the pseudo-random stimulus increased. This decrease in gain may be due to the difference in the velocity distribution (Fig. 5.8). The pseudo-random stimulus contained, due to the summation of the different components, higher velocities than the single sine wave stimulus. These higher velocities probably resulted in blurring of the background motion. Murphy, Kowler & Steinman (1975) found that the induction of motion was smaller for a background moving at $8^o/s$ than for a background moving at $0.8^o/s$. Furthermore, induction probably needs some time to build up; single sine wave stimuli enable this build-up, while pseudo-random stimuli cancel the build-up because of the frequent and irregular changes of direction. On the other hand, single sine wave stimuli are known to induce a different type of response than (pseudo-) random stimuli.

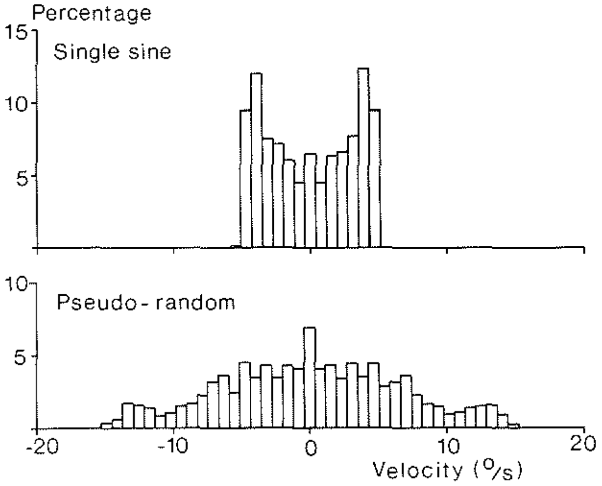


Fig. 5.8. Distribution of velocity of a single sine wave of 0.15 Hz and an amplitude of 4.94° (top) and of a pseudo-random motion (bottom) which was the sum of four non-harmonic sine waves (0.15 Hz and 4.94°; 0.28 Hz and 2.68°; 0.40 Hz and 1.84°; 0.58 Hz and 1.26°).

Pursuit experiments with single sine wave stimuli result in eye movements with a higher gain and a smaller phase lag than pseudo-random stimuli (see e.g. chapter 3 and 4 of this study). If the eye is fixating a stationary object in the presence of a sinusoidal background movement, prediction of the background movement might interfere with the fixation task and lead to a larger induction.

The eye movements which were induced by a background during fixation of a central target in open-loop condition were only a fraction of the movements of the background. This was also reported by Mack, Fendrich & Pleune (1979) and Mack, Fendrich & Wong (1982) who found that, even in an open-loop condition, the eye remained relatively stable. This finding can only be explained by the imperfection of the open-loop condition or the existence of additional feedback loops in the visuo-motor system. The recording technique and the projection apparatus of the target, however, were very precise and had a bandwidth large enough to provide an appropriate feedback of the eye position, even during saccades. Furthermore, all possible care was taken to eliminate secondary artifacts and to create a feedback loop with a gain of unity and without offset.

It is possible that, in the open loop condition, there was a remaining visual feedback from stationary objects in the surrounding of the subject, e.g. the field coils of the recording system. These objects could serve as an earth fixed frame of reference in an otherwise moving visual world. Although the coils were located in the periphery of the visual field (45^{0} out of centre) and only dimly lit by the reflection of the illumination of the background, they marked the edges of the random dot background.

Another way for the oculomotor system to get information about the position of the eye is the proprioceptive feedback loop. This loop was not nullified by the opening of the retinal feedback loop of the visual system. Proprioceptive feedback from the muscles of the eye may signal the position of the eye with respect to the head and may, in combination with the head position, give the subject information about the position of the eye in space.

Information about the position of the eye, however, may also be established if the brain monitors the outflow of the eye position command generator (outflow principle, efferent copy or corollary discharge) and the commands which go to the eye muscles. Data summarized by Skavenski & Hansen (1978) have led to the conclusion that the visuo-motor system has accurate eye position information at all times and for all types of eye movement. My results of experiments with fixation in a (visual) open-loop condition in the presence of a moving background endorse this view.

A new result of my experiments is that the induction of movement is enhanced when the eye is pursuing a target in an orthogonal direction. This may be a result of the limited processing capacity of the visuo-motor system. During fixation with a moving background, all attention can be used to counteract the movement of the background During pursuit, however, eye movements did not only serve to counteract the background motion, but were also used to pursue the pseudo-random target motion, which required attention. Therefore, less attention could be paid to the minimizing of the induced movement. As a result, induction during pursuit was larger.

CHAPTER 6

PERIPHERAL PURSUIT

6.1 Peripheral versus foveal pursuit

The experiments described in the previous chapters incorporated the fixation or pursuit of a target with the fovea, the small central part of the retina which has maximal visual acuity. The introduction of a conflicting stimulus on the peripheral retina modified the pursuit eye movements or induced eye movements during fixation but the influence was limited if maximal attention was paid to the central stimulus. To investigate if subjects were able to pursue moving targets projected on the peripheral retina, eccentric pursuit experiments were done with four subjects. These subjects had to pursue the imaginary midpoint between two green symmetrical arrows which had a vertical distance of 10° (Fig. 6.1).

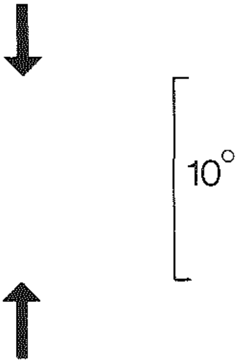


Fig. 6.1. Target for peripheral pursuit. Subjects had to fixate an imaginary point in the centre between the two (green) arrows moving together in horizontal direction. The vertical distance between the points of the two arrows was 10°.

The arrows were displaced together in horizontal direction with single sine wave stimuli of 0.15 and 0.52 Hz and an amplitude of 10°; with two pseudo-random stimuli with frequency ranges of 0.21 - 0.70 and 0.28 - 0.89 Hz and a maximum amplitude of 10° (sum of four sine waves; Table 3.1, vertical components of SUM 1 and SUM 2) or with four triangular wave stimuli with velocities of 1.2, 3.7, 6.1 and 20.8°/s. To investigate if the presence of a stationary background influenced pursuit performance, these stimuli had to be pursued upon a dark, diffuse and random dot background.

6.2 Gain and phase

Subjects were able to pursue peripheral targets. Fig. 6.2 shows recordings of pursuit of a triangular wave stimulus of 3.7°/s upon the dark and the random dot background.

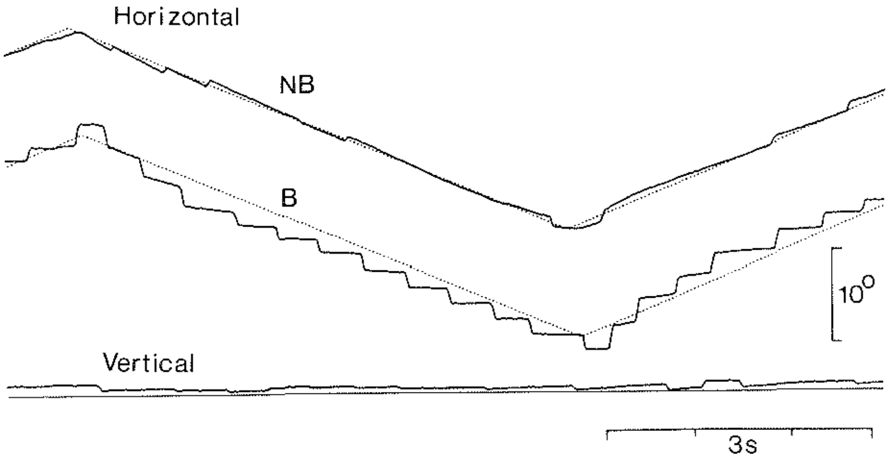
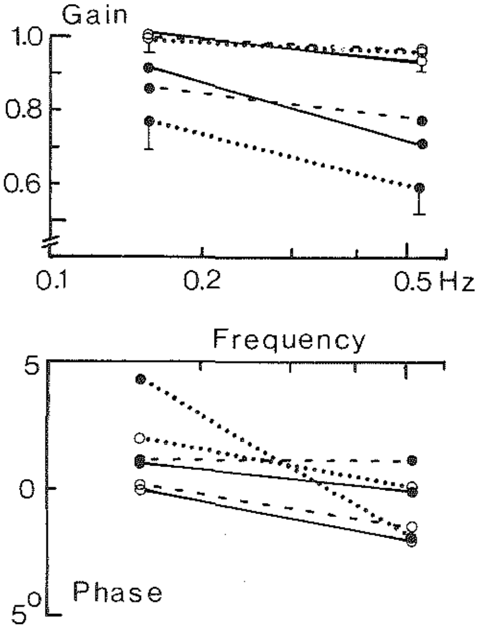


Fig. 6.2. Recordings of the eye movements (solid lines) during peripheral pursuit of the two-arrow target with a velocity of 3.7°/s (dotted line) upon a dark (NB) or structured (B) background. The lower trace shows the vertical eye position with respect to the centre of the two arrows during peripheral pursuit upon the structured background.

Even in the absence of a foveal target, pursuit upon a dark background was almost completely smooth and only a few saccades were made (back and forth) to correct the eye position. In the presence of a stationary background there was a shift from smooth towards saccadic pursuit and almost no smooth eye movements were left. This effect is illustrated in Fig. 6.2 for the stimulus type which showed this effect most dramatically, i.e. a slow target motion at constant velocity. The eye showed a tendency to anticipate the target position and saccades were used to keep the eye ahead of the imaginary target. Vertical eye position was maintained in between the peripheral targets. The eye remained, in general, within a range of 2^{o} above or below the horizontal position of the imaginary target. Normally, no significant drift in up- or downward direction was found; the measurement was repeated if a large deviation in vertical direction occurred.

Fig. 6.3 shows mean gain and phase of the composite and the smooth eye movements as a function of frequency for the two single sine wave stimuli used upon the three different backgrounds.

Fig. 6.3. Mean gain and phase of the horizontal composite (open circles) and cumulative smooth eye movements (filled circles) during peripheral pursuit of single sine wave stimuli upon a dark (solid lines), diffuse (dashed lines) or random dot background (dotted lines). Mean ± S.D. of four subjects.



For peripheral pursuit, the introduction of a diffuse or a structured background did not systematically change the gain of the composite eye movement. This gain decreased from 1.00 ± 0.02 (S.D.) at 0.15 Hz (which is comparable to foveal pursuit) to 0.96 ± 0.03 (S.D.) at 0.52 Hz (slightly less than the composite gain during foveal pursuit). The pursuit eye movements were not completely smooth. In the presence of a dark background, the gain of the smooth component was 0.92 ± 0.04 (S.D.) at 0.15 Hz which decreased to 0.72 ± 0.06 (S.D.) at 0.52 Hz, values comparable to the normal pursuit condition. The introduction of a diffuse background did not systematically affect smooth pursuit gain, but the presence of a structured background lowered the gain of the smooth component. The average decrease in smooth pursuit gain was 0.13 ± 0.12 (S.D.) which is larger than the decrease during foveal pursuit, which amounted to 0.07 ± 0.09 (S.D). The phase of the composite and the smooth eye movement was small and decreased little with the increase in frequency.

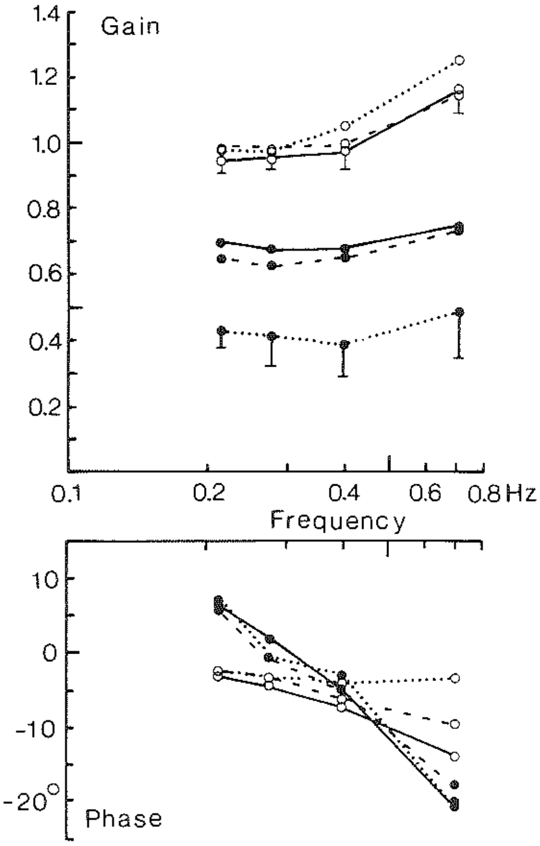


Fig. 6.4. Mean gain and phase of the horizontal composite (open circles) and cumulative smooth eye movements (filled circles) during peripheral pursuit of a pseudo-random stimulus with four components in the frequency range of 0.21 - 0.70 Hz upon a dark (solid lines), diffuse (dashed lines) or structured background (dotted lines). Mean ± S.D. of four subjects.

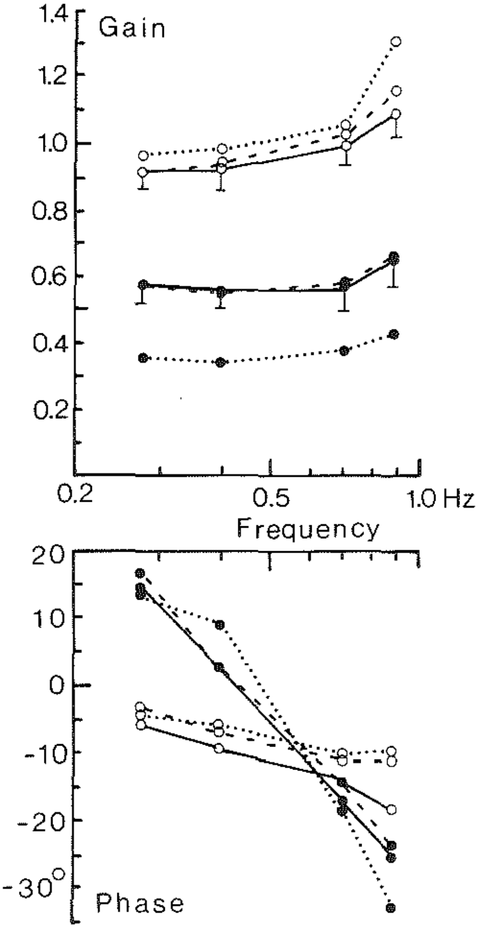


Fig. 6.5. As Fig. 6.4 for a pseudo-random stimulus with a frequency range of 0.28 - 0.89 Hz.

For pseudo-random stimuli (Figs. 6.4 and 6.5) the introduction of a structured background increased the gain of the composite eye movement. Although the increase was small (0.08 ± 0.1 S.D) it was significant ($p < 0.001$). Apparently, overshoot of the motion of the virtual target by the eye was larger in the presence of a structured background. For the contribution of the smooth eye movements, pseudo-random stimuli showed a similar trend as single sine wave stimuli: a diffuse background did not influence smooth pursuit gain, but the introduction of a structured background lowered it. The difference in smooth pursuit gain between a dark and a structured background (0.24 ± 0.1) was larger than during foveal pursuit (0.07 ± 0.09, Fig. 4.2). During peripheral pursuit, the eye movements were never completely saccadic; the mean gain of the smooth component remained larger than 0.35. The phase of neither the composite nor the smooth eye movement was systematically altered when the dark background was replaced by the diffuse or the random dot background. The phases were comparable to those obtained with foveal pursuit of a central target. Similarly as for foveal pursuit, gain and phase of the composite and the smooth eye movement depended upon the spectral composition of the stimulus motion.

The mean gain of the smooth component during peripheral pursuit of triangular wave motions is shown in Fig. 6.6

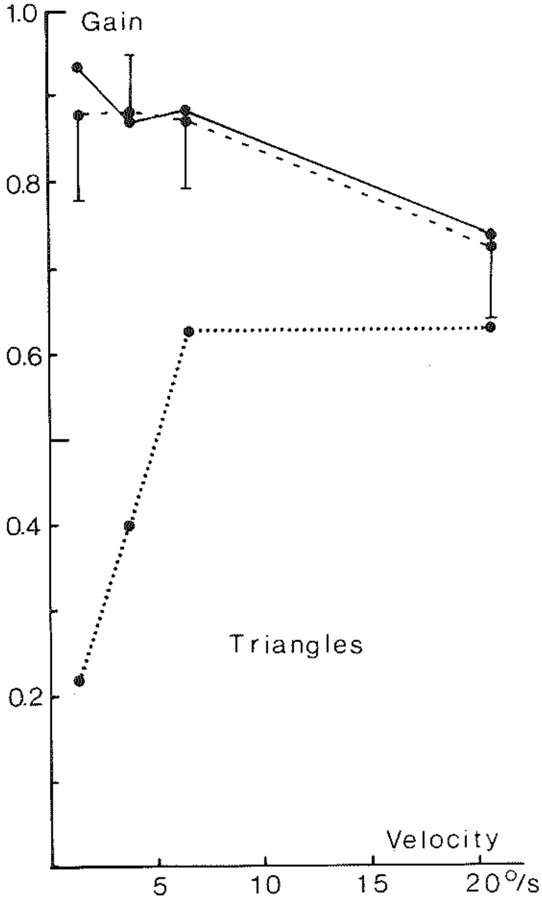


Fig. 6.6. Gain of the cumulative smooth eye movement during peripheral pursuit of triangular wave stimuli of different velocities upon a dark (solid line), diffuse (dashed line) or random dot background (dotted line). Only the central 75% of the slope of the target motion was used to calculate gain. Mean ± S.D. for 4 subjects.

For the two higher velocity triangular wave stimuli, the results obtained resembled those of the single sine wave and pseudo-random stimuli. The gain of the smooth component was not affected by the introduction of a diffuse background, but lowered when the structured background was presented. For the two lower velocity stimuli the decrease in smooth pursuit gain for pursuit upon a structured background was very large: from 0.94 ± 0.04 (S.D.) to 0.22 ± 0.16 (S.D.) for a stimulus velocity of 1.2°/s and from 0.87 ± 0.09 (S.D.) to 0.40 ± 0.18 (S.D.) for a stimulus velocity of 3.7°/s. The gain of the smooth component in these conditions was much lower than during foveal pursuit. Apparently, peripheral smooth pursuit of very slow target motions is inhibited heavily by the presence of a stationary central stimulus.

6.3 Retinal position error

Similarly as for foveal pursuit, a retinal position error could be calculated for the difference between the point of fixation and the imaginary target: the centre between the two arrows. Fig. 6.7 summarizes the results for the S.D. of retinal position error for peripheral pursuit of the motion stimuli described in the previous section upon the three different backgrounds used: dark, diffuse and structured.

In general, the S.D. of retinal position error increased with velocity for triangular wave stimuli and with frequency or frequency range for single sine wave and pseudo-random stimuli and was -in contrast to foveal pursuit- larger for a structured than for a diffuse or a dark background, although the differences were small. The S.D of retinal position error during peripheral pursuit was larger than during foveal pursuit (mean increase about 35%).

In summary: even in in the absence of a real foveal target, subjects were able to pursue an imaginary centre between two peripheral structures. The peripheral target motions were pursued with a gain of the composite eye movement comparable to the gain during foveal pursuit. In both conditions, the gain was relatively independent of the type of background used. Smooth pursuit gain during peripheral pursuit was comparable to foveal pursuit for tracking upon a dark or a diffuse background, but lower in the presence of a structured background. The difference in smooth pursuit gain between peripheral and foveal pursuit was small for higher velocity target motions, but large for slow target displacements. For these slow stimuli, peripheral pursuit in the presence of a structured background was almost completely saccadic.

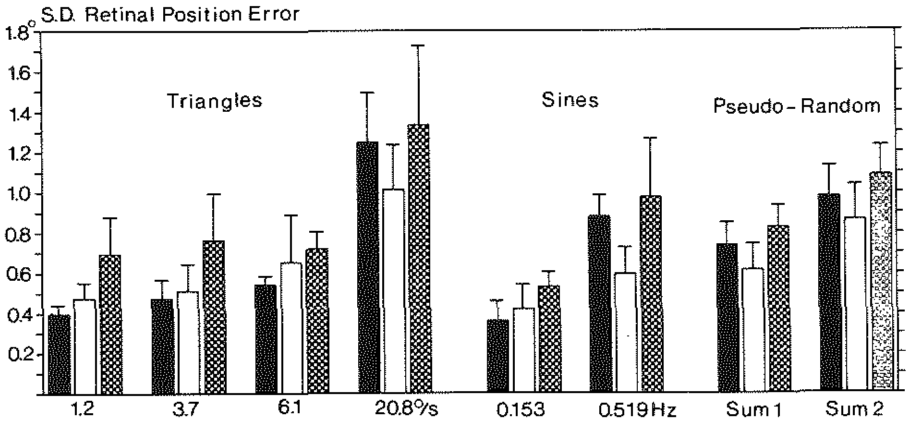


Fig. 6.7. Horizontal component of the S.D. of retinal position error between the centre of the peripheral targets and the eye position during horizontal pursuit of triangular wave, sine wave or pseudo-random peripheral motion stimuli (pseudo-random stimulus Sum 1 had a frequency range of 0.21 - 0.70 Hz, Sum 2 a range of 0.28 - 0.89 Hz, see Table 3.1, vertical component SUM 1 and SUM 2). Mean ± S.D. of four subjects.

In contrast to foveal pursuit, the S.D. of retinal position error of the imaginary target during peripheral pursuit was larger for pursuit upon a structured than upon a dark or diffuse background.

6.4 Discussion

Pursuit is not only a function of the fovea. Most system-analytical studies describe smooth pursuit as the foveal fixation of a smoothly moving target (Robinson, 1976). This description is acceptable because humans (and other foveate animals) will normally use saccades to bring the image of the target to the fovea and then start to pursue. The experiments described in this chapter show that this method of pursuit is a preference but not the result of incompetence of the peripheral retina to control pursuit behaviour.

Targets moving in the perifoveal region are capable of generating smooth pursuit eye movements. A similar result was found, although not quantified, by Steinbach (1976), and also described by Winterson & Steinman (1978) and Collewijn, Curio & Grüsser (1982). The latter investigators described that, even in the absence of real movement, perceived motion in the periphery generated by Sigma movement was an effective stimulus for generating smooth pursuit eye movements (Sigma movement is a movement illusion elicited when a stationary regular pattern is stroboscopically illuminated and the eye moves along this pattern at a specified velocity). The first two investigations used a condition where the fovea was not stimulated by any, possibly conflicting, visual stimulus.

The results in this chapter show that smooth pursuit can be elicited by moving objects in the perifoveal retina, even if the fovea is stimulated by a stationary background In the absence of foveal stimulation, the gain of the smooth eye movements of peripheral pursuit was comparable to foveal pursuit. In the presence of a stationary background, however, peripheral pursuit resulted in a lower smooth pursuit gain, although the difference in gain was limited to about 20%. Only if the object in the periphery moved very slowly (below $5^{o}/s$), smooth pursuit gain decreased dramatically (Fig. 6.6). Although peripheral pursuit was not as precise as its foveal counterpart, the mean difference in S.D. of retinal position error amounted only to about 35%.

My findings seem to contrast with the results of Van Die & Collewijn (1982), who reported that, during optokinetic nystagmus (OKN), the gain of the smooth eye movements decreased dramatically when the fovea was not stimulated by the moving stimulus (a vertical grating which extended 90^{o} to the left and right). During whole field stimulation, mean gain of 10 subjects was 0.77 for stimulus velocities of 12 and $30^{o}/s$. If the central sector of 10^{o} was occluded, leaving the whole peripheral stimulus intact, gain reduced to 0.42.

There are, however, substantial differences between the peripheral stimulus of the present study and that of Van Die & Collewijn (1982). The masking of the central 10^{o} in the experiments of Van Die & Collewijn (1982) occluded a vertical sector with a width of 10^{o} of the moving stimulus. Subjects had, in the configuration of Van Die & Collewijn (1982), no possibility to align their horizontal eye position with the peripheral stimulus, because the occlusion was locked to the eye position. In my experiments, subjects could align their horizontal eye position with the vertical midline of the two arrows which were projected 5^{o} eccentric in upper- and lower half of the visual field Van Die (pers. comm) found in supplementary experiments that occlusion of a horizontal sector of 20^{o} in height resulted in a mean OKN gain of 0.55, which is a much smaller decrease in gain than during vertical occlusion.

A second difference is that the two peripheral structures in my experiments contained clear horizontal position information; there was only one midpoint of the two arrows. The visual stimulus with the horizontal occlusion used by Van Die (pers. comm.) did not contain clear horizontal position information; the vertical bars of his visual stimulus were identical and numerous and there was no single (imaginary) target to attend to.

The results of Van Die & Collewijn (1982), however, support the view that the fovea is not essential in the generation of smooth pursuit eye movements. A further corroboration of this view is provided by the results of Steinbach (1976), who described that the occurrence of pursuit movement depended on the observer's appreciation of a moving object, rather than on the sensory information which led to the percept. Horizontal pursuit could even occur when the only physical stimulus present on the retina moved in vertical direction.

There is a biological function of this eccentric pursuit in higher primates. It permits the visuo-motor system to pursue targets moving under scotopic conditions when the fovea is not providing visual information. Furthermore, perifoveal pursuit can support foveal pursuit under photopic conditions if a large object is pursued.

A critical factor in all these experiments is the attention of the subject. During pursuit of perifoveal targets, subjects must shift their attention from the fovea to the periphery (spatially selective visual attention). Collewijn, Curio & Grüsser (1982) called this a shift of the "attention fovea". Whenever the attention fovea did not coincide with the retinal fovea, the part of the retina corresponding to the attention fovea controlled the pursuit eye movement and the speed of the Sigma-OKN slow phase. Thus the role of the fovea in the generation of smooth pursuit can be minimized (weighted with a small factor). However, movement or perception of movement on the perifovea must be large enough to overrule the motion information of the fovea. Tynan & Sekuler (1982) found that the threshold for perception of motion is higher if the moving object is more eccentric. It would be interesting to investigate if the amount of movement on the peripheral retina which is needed to outweigh the central retina is correlated with the eccentricity of the moving object.

The results described in this chapter have implications for the models which describe the smooth pursuit control system. Servo-mechanical models of the pursuit system that operate on retinal slip velocity and retinal position error alone are far too simple. General attention and spatially selective visual attention as well as the percept of movement are factors which should be taken into consideration during further development of such models, although this will be difficult. For a human being, however, the effect of the relative visuo-motor independency is beneficial: it allows us to look at and pursue objects of our choice rather than to have our eye movements controlled by the properties of the objects around us.

CHAPTER 7

CONCLUDING REMARKS

In this chapter I will summarize some of the general findings of the different experiments described in the previous chapters.

Common to all experiments was that the eye movements, voluntary or reflexive, depended heavily on the type of stimulus motion which was used. Single sine wave stimuli were pursued with a higher smooth pursuit gain and a smaller phase lag than pseudo-random stimuli. Pseudo-random stimuli with different spectral compositions resulted in a different performance in time and in frequency; the result could not be predicted from other experiments. A larger stimulus amplitude resulted, for an identical frequency composition, in a lower gain of the smooth component and in a higher S.D. of retinal position error. The induction of eye movements was larger for a single sine wave background motion than for a pseudo-random motion. This dependence on the type of stimulus shows that the visuo-motor system is non-linear. This non-linearity makes it difficult to compare results of one study or experiment with those of others. Furthermore, generalization of results is hazardous if these results are based upon one class of stimuli only (single sine wave, pseudo-random, noise, constant velocity, randomized constant velocities, etc). A further complicating factor in the generalization of the results is the idiosyncrasy of the response, which was most clearly visible in the open-loop pursuit experiments and in the fixation experiments. During open-loop pursuit, the eye movements of one subject were a tenfold larger than for another subject. Idiosyncrasy, however, is not limited to eye movements. Also other weltrained motor tasks, such as walking, eating, etc , show differences between different subjects. Idiosyncrasy is inherent to the functioning of a human being.

Another general finding was the interaction between central and peripheral retina. If a subject pursued a foveal target, information presented on the peripheral retina (background) was not completely neglected, but taken into account in the generation of smooth pursuit. This finding could be extended to a target velocity zero (fixation), where smooth eye movements were induced by motion on the peripheral retina. In all experiments (fixation, foveal or peripheral pursuit), smooth eye movements served to minimize a weighed sum of central and peripheral retinal slip velocities. The actual weights were determined both by the attention of the subject and the physiological structure of the visual system.

The influence of the background on the composite eye movements, however, was limited: saccades compensated for the deficiency of the smooth eye movements. During pursuit, saccades supplemented the smooth eye movements to pursue the target with the proper amplitude. Even if the contribution of smooth pursuit degraded due to the presence of a stationary background, saccades were able to prevent an overall decrease in precision in time and frequency. During fixation, saccades brought the fovea back to the point of fixation if the eye drifted away due to spontaneous drift or motion induced by the movement of the background. In general, saccades were corrections of the eye position (see Fig. 3.15).

The saccadic system can be found in other species (e.g. the rabbit) as well, but smooth pursuit is a highly specialized function which is only present in foveate animals. Apparently this specialization makes the smooth pursuit system more susceptible to disturbing factors such as conflicting visual stimuli. If the visuo-motor system encounters a situation where the smooth pursuit system fails to execute a specified task, it resorts to saccadic eye movements to supplement the smooth pursuit system. However, this reliance on the saccadic system is, at least partially, under voluntary control. Puckett & Steinman (1969) showed that subjects were able to adopt a highly saccadic or almost saccade-free mode of pursuit, although the last strategy led to large retinal position errors. During the experiments described in this study, no explicit instructions were given to the subject to abolish the use of saccades in pursuit or fixation. In all experiments the instruction was to pursue or fixate the target as accurately as possible. It might be that this instruction was not enough to elicit a more uniform response.

Attention is an important factor between the visual input and the resulting motor activity of the eye. A current theory about attention (see e.g. Sperling, 1983) is to describe it as the "allocation of processing resources". The amount of information supplied to the brain via the visual or other sensory systems is almost unlimited. The actual processing capacity of the brain, however, is limited and unable to process all information which is presented. Therefore, the processing capacity must be shared between the different systems. The way in which the processing resources are allocated to the multiple sources of information is called "attention". The amount of information and the way in which this information is presented to the brain is determined by the physiological structure of the receptive system. For example, the structure of the retina, ganglion cell density and cortical mapping area of the different parts of the retina determine that the amount of information from the central retina is disproportionally large compared to the amount of information of the peripheral retina. Nevertheless, subjects were able to shift their attention from the fovea to the perifoveal retina (deallocate processing resources from the central retina and allocate this capacity to the processing of information of the peripheral retina) and pursue objects moving in the perifoveal retina, although the central retina was, at the same time, stimulated by an opposite stimulus motion.

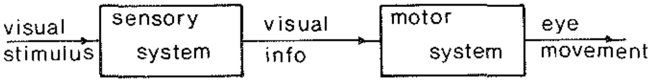


Fig. 7.1. Servo-mechanical model of the visuo-motor system.

It is clear from the experiments and results described in the previous chapters that the visuo-motor system is complex and susceptible to a variety of visual as well as non-visual stimuli. Modelling the visuo-motor system as a servo-mechanical system (Fig. 7.1) gives some insight in the working of parts of the visuo-motor system, but ignores the fact that there is a complex information processing system which receives the visual information, combines this information with information originating from other, possibly non-visual sources and finally generates commands which enter the eye motor system (Fig. 7.2) and possibly other systems as well.

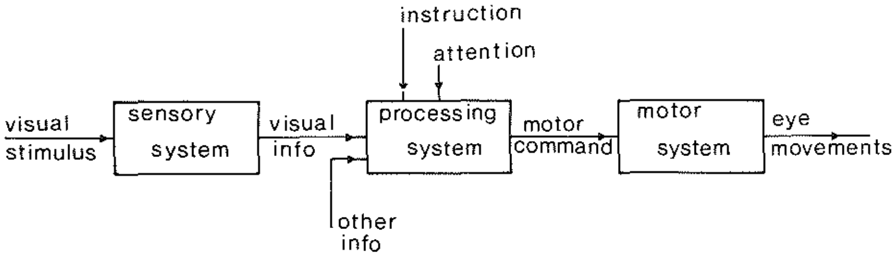


Fig. 7.2. Model of the visuo-motor system, incorporating a processing element which is influenced by non-visual sources of information.

Retinal events as such are not enough to predict and explain the eye movements which are made. Despite the fact that interpretation of the results is difficult and susceptible to misunderstanding, investigations as to how eye movements are determined by visual stimuli, instructions, attention, training and possibly many other factors should learn us something about the most complex and intriguing part of the human body: the brain.

SUMMARY

To investigate the interaction of (conflicting) moving visual stimuli presented on the central and peripheral retina upon the generation of pursuit eye movements, horizontal and vertical eye movements of 11 human subjects were recorded with a scleral induction coil technique during voluntary foveal and peripheral pursuit and during fixation Stimulus motions consisted of single sine wave, triangular wave and pseudo-random stimuli of different frequency, amplitude and dimensionality. Pursuit and fixation was done upon a dark, diffusely lighted or structured stationary or moving background. For some pursuit and fixation experiments the visual feedback loop was electronically opened.

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 or background movement and analysis of retinal position error.

I found that pursuit eye movements were never completely smooth. Smooth pursuit gain was always lower than 0.96 and saccades were used to supplement the smooth eye movements in pursuing the target with the proper amplitude. A structured background had an inhibitory influence on smooth pursuit and diminished its gain by about 10% for horizontal and 20% for vertical during foveal pursuit. The inhibition of smooth pursuit was fully compensated by the insertion of saccades, with as overall result a shift from smooth towards saccadic pursuit. The specific structure of the background was only of marginal importance. The influence of diffuse illumination of the background was minimal. Horizontal foveal pursuit contained a higher proportion of smooth components and was more accurate in terms of retinal position error than vertical foveal pursuit.

Gain and phase as well as retinal position error of pursuit eye movements were strongly affected by the spectral composition of the stimulus motion. Sinusoidal target motions were pursued with a higher smooth pursuit gain and a smaller phase lag than pseudo-random target motions. A larger amplitude of the target motion resulted in a lower gain of the smooth component and a higher S D. of retinal position error. Smooth pursuit gain decreased and retinal position error increased as a function of frequency for single sine wave stimuli and as a function of velocity for triangular wave stimuli. The cumulative smooth eye movements showed, during pursuit, a phase lead with respect

to the target movement for the lower frequency components of pseudo-random stimuli.

Open-loop pursuit led to eye movements which were very idiosyncratic. The gain of the eye movements varied between 0.5 and 20. At least one subject could control the amplitude of the composite eye movements during open-loop stimulation.

Saccades during pursuit corrected the eye position, although not perfectly. During pursuit of pseudo-random stimuli, saccades overshot the target position. This resulted in a gain of the composite eye movement above unity for the higher frequency components.

The distribution of retinal position error during pursuit was symmetrical around zero. Its standard deviation varied from 0.2^{o} to about 1.5^{o}. During fixation, the S.D. of retinal position error was not influenced by the presence of a diffuse or a structured background and was about equal for horizontal and vertical component (0.1^{o}). The S.D. of retinal position error increased in horizontal direction to about 0.13^{o} and decreased in vertical direction to about 0.07^{o} when a background was moved in horizontal direction. These differences were independent of the type of movement of the background.

The induction of motion by a moving background during fixation was small. The mean gain of the cumulative smooth eye movements was less than 0.1 and tended to lag the background by 90^{o}. The induction of movement by the motion of the background was larger for sinusoidal than for pseudo-random background motions. There was no superposition of the motion induced by the single sine waves. The induction of motion by a horizontally moving background was larger during open-loop fixation of a central target and during closed-loop pursuit of a vertical target motion than during closed-loop fixation, although the induced smooth eye movements remained only a fraction of the movement of the background (mean gain of the smooth component was less than 0.25).

Subjects were able to pursue perifoveal targets even upon a stationary background. Gain and phase of the eye movements during perifoveal pursuit were comparable to foveal pursuit upon a dark or diffuse background, but lower upon a structered background. Peripheral smooth pursuit of slow target movements (below 5^{o}/s) was, in contrast to foveal pursuit, inhibited heavily by the presence of a stationary background. The S.D. of retinal position error during peripheral pursuit was about 35% larger than during foveal pursuit.

I conclude that smooth and saccadic eye movements during pursuit and fixation subserve, in general, two different functions. Saccades correct the eye position and, if necessary, supplement for a deficiency of the smooth eye movements The smooth eye movements serve to minimize a weighted sum of slip velocities of central and peripheral retina. The weighting factors are determined both by the structure of the visual system and by spatially selective visual attention of the subject.

SAMENVATTING

Om de interaktie te bepalen tussen (konflikterende) visuele stimuli die gepresenteerd worden op het centrale en perifere gedeelte van de retina, zijn de horizontale en vertikale oogbewegingen, die gemaakt worden tijdens vrijwillig volgen en fixatie, met behulp van een sclerale induktiespoel gemeten bij 11 menselijke proefpersonen. Stimulus bewegingen bestonden uit enkelvoudige sinussen, driehoekvormige signalen en semi-willekeurige bewegingen van verschillende frekwentie, amplitude en dimensionaliteit. Het volgen of fixeren werd gedaan op een donkere, diffuus verlichte of gestruktureerde achtergrond die stilstond of werd bewogen. Voor enkele volg- en fixatie experimenten werd de visuele terugkoppeling langs elektronische weg opgeheven.

Het verwerken van de meetgegevens bestond uit het scheiden van de samengestelde oogbeweging in een kumulatieve gladde oogbeweging en een saccadische oogbeweging; berekening van de versterkingsfaktor en faseverschuiving van de samengestelde en gladde oogbeweging met betrekking tot de stimulusbeweging en het analyseren van de retinale positiefout (positieverschil tussen fovea en het beeld van het doel op de retina).

Oogvolgbewegingen waren altijd een kombinatie van gladde en saccadische oogbewegingen. De versterkingsfaktor van de kumulatieve gladde oogbeweging was altijd kleiner dan 0.96. Saccades vulden de gladde oogbeweging aan om de doelbeweging met de juiste amplitude te volgen. Een gestruktureerde achtergrond had een remmend effekt op de gladde oogbeweging: de versterkingsfaktor verminderde met ongeveer 10% voor de horizontale en 20% voor de vertikale komponent. De achteruitgang in gladde oogbeweging werd volledig gekompenseerd door saccades met als resultaat een verschuiving van glad naar saccadisch volgen. De specifieke struktuur van de achtergrond zelf was niet belangrijk en ook de verlichting van de achtergrond als zodanig had weinig invloed. Het aandeel van de gladde komponent was groter voor de horizontale dan voor de vertikale komponent van de oogvolgbeweging. Tevens was de horizontale volgbeweging nauwkeuriger met betrekking tot retinale positiefout dan de vertikale volgbeweging.

De spektrale samenstelling van de stimulus had een grote invloed op de oogvolgbeweging. Enkelvoudige sinusoidale bewegingen werden gevolgd met een grotere versterkingsfaktor en een kleinere faseachterstand dan semi-willekeurige bewegingen. Een grotere amplitude van de doelbeweging

resulteerde in een kleinere versterkingsfaktor van de gladde komponent en een grotere retinale positiefout. De versterkingsfaktor van de gladde komponent werd kleiner en de retinale positiefout werd groter als funktie van de frekwentie van de enkelvoudige sinusoidale stimuli en als funktie van snelheid voor de driehoekvormige doelbewegingen. De gladde volgbeweging had een fasevoorsprong ten opzichte van de doelbeweging voor de laagste frekwentiekomponenten van de semi-willekeurige stimuli.

Het openen van de visuele terugkoppeling tijdens het volgen leidde tot oogbewegingen die sterk afhankelijk waren van de proefpersonen. De versterkingsfaktor van de samengestelde oogbeweging varieerde tussen 0.5 en 20. Tenmiste 1 proefpersoon was in staat om de ampltiude van de oogbeweging in deze sitiatie te beïnvloeden.

Saccades korrigeerden de oogpositie tijdens het volgen, alhoewel niet perfekt. Tijdens het volgen van semi-willekeurige bewegingen vertoonden de saccades een doorschot ten opzichte van de doelbeweging en dit resulteerde in een versterkingsfaktor van de oogbeweging die groter was dan één.

De retinale positiefout was tijdens het volgen symmetrisch rond de nul verdeeld. De standaarddeviatie van de retinale positiefout (een maat voor de nauwkeurigheid van de oogbeweging) varieerde van 0.2° tot 1.5°. De standaarddeviatie werd, tijdens fixeren, niet beinvloed door de aanwezigheid van een stilstaande gestruktureerde achtergrond en was ongeveer gelijk voor de horizontale en vertikale komponent (0.1°). De standaarddeviatie vergrootte in horizontale richting tot ongeveer 0.13° en verkleinde in vertikale richting tot ongeveer 0.07°, wanneer de achtergrond in horizontale richting werd bewogen. Deze verschillen waren onafhankelijk van de soort beweging van de achtergrond

De bewegende achtergrond induceerde een kleine oogbeweging tijdens het fixeren; de kumulatieve gladde oogbeweging had een gemiddelde versterkingsfaktor die kleiner was dan 0.1 en een faseachterstand van ongeveer 90° tenopzichte van de achtergrondbeweging. Een sinusoidale achtergrond beweging resulteerde in een grotere induktie van oogbeweging dan een semi-willekeurige achtergrondbeweging. Het openen van de visuele terugkoppeling of het volgen van een vertikale doelbeweging leidde tot een grotere induktie van horizontale oogbeweging door de horizontaal bewegende achtergrond. Desondanks bleven de oogbewegingen beperkt tot een fraktie van de totale beweging van de achtergrond (de versterkingsfaktor van de gladde oogbeweging bleef kleiner dan 0.25).

Proefpersonen waren in staat om een bewegend doel te volgen dat gepresenteerd werd op het perifere gedeelte van de retina, zelfs als er foveaal een stilstaande achtergrond aanwezig was. De versterkingsfaktoren en faseverschuivingen van de oogbewegingen waren vergelijkbaar met foveaal volgen tijdens volgen op een donkere of een diffuse achtergrond, maar lager tijdens het perifeer volgen op een gestruktureerde achtergrond. In tegenstelling tot foveaal volgen was het glad volgen van langzaam bewegende perifoveale doelen (snelheid kleiner dan 5^o/s) moeilijk en was de volgbeweging bijna volledig saccadisch. De standaard deviatie van de retinale positiefout tijdens perifoveaal volgen was ongeveer 35% groter dan bij foveaal volgen.

Ik konkludeer dat gladde en saccadische oogbewegingen tijdens volgen en fixeren verschillende funkties hebben. Saccades korrigeren de oogpositie en vullen de gladde oogbeweging aan als deze tekort schiet. De gladde oogbeweging daarintegen dient om een gewogen som van retinale slipsnelheden te minimaliseren. De weegfaktoren van de slipsnelheden van centrale en perifere retina worden enerzijds bepaald door de struktuur van he visuele systeem, maar kunnen anderzijds door de proefpersoon sterk beinvloed worden door selektieve aandacht te schenken aan bepaalde gedeelten van het gezichtsveld

REFERENCES

BAHILL, A.T., IANDOLO, M.J., TROOST, B.T. (1980). Smooth pursuit eye movements in response to unpredictable target waveforms. Vision Res., 20, 923-931.

BEELER, G.W. (1967). Visual threshold changes resulting from spontaneous saccadic eye movements Vision Res., 7, 769-775.

CAMPBELL, F.W., WURTZ, H. (1978). Saccadic omission: why we do not see a grey-out during a saccadic eye movement. Vision Res., 18, 1297-1303.

COLLEWIJN, H., CONIJN, P., MARTINS, A.J., TAMMINGA, E.P., VAN DIE, G.C. (1982). Control in gaze of man: synthesis of pursuit, optokinetic and vestibulo-ocular systems. Doc. Ophthal. Proc., 34, 3-22.

COLLEWIJN, H., CURIO, G., GRÜSSER, O.J. (1982). Spatially selective visual attention and generation of eye pursuit movements. Human Neurobiol., 1, 129-139.

COLLEWIJN, H., VAN DER MARK, F., JANSEN, T.C. (1975). Precise recording of human eye movements. Vision Res., 15, 447-450.

CORNSWEET, T.N. (1956). Determination of the stimuli for involuntary drifts and saccadic eye movements. J. Opt. Soc. Am., 46, 987-993

CUSHMAN, W.B., TANGNEY, J.F., STEIMAN, R.M., FERGUSON, J.L. (1983). Characteristics of smooth eye movements under open loop conditions. Arvo 1980, Supplement to Invest. Ophtalmol. and Visual Science, 81, and to be published.

DALLOS, P.J., JONES, R.W. (1963). Learning behaviour of the eye fixation control system. IEEE Trans. Auto. Control, AC-8, 218-227.

DITCHBURN, R.W. (1980). The function of small saccades. Vision Res., 20, 271-272

FENDER, D.H., NYE, P.W. (1961). An investigation of the mechanisms of eye movement control. Kybernetik, 1, 81-88.

FINDLAY, J.M. (1971). Frequency analysis of human involuntary eye movement. Kybernetik, 8, 207-214.

FIORENTINI, A., ERCOLES, A.M. (1966). Involuntary eye movements during attempted monocular fixation. Atti Fond. Ronchi, 21, 199-217.

HEYWOOD, S., CHURCER, J. (1971). Eye movements and the after-image - I. Tracking the after-image. Vision Res. 11, 1163-1168

HOOD, J.D. (1975). Observations upon the role of the peripheral retina in the execution of eye movements. Oto Rhino Laryngol., 37, 65-73.

JULESZ, B. (1972). Foundations of Cyclopean Perception. Chicago: University of Chicago Press.

KOWLER, E., MURPHY, B.J., STEINMAN, R.M. (1978). Velocity matching during smooth pursuit of different targets on different backgrounds. Vision Res., 18, 603-605.

KOWLER, E., STEINMAN, R.M. (1979a). The effect of expectations on slow oculomotor control - I: periodic target steps. Vision Res., 19, 619-632.

KOWLER, E., STEINMAN, R.M. (1979b). The effect of expectations on slow oculomotor control - II: single target displacements. Vision Res., 19, 633-646

KOWLER, E., STEINMAN, R.M. (1980). Small saccades serve no useful purpose: reply to a letter by R.W. Ditchburn. Vision Res., 20, 273-276.

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. J. Neurophysiol., 46, 229-249

MACK, A., FENDRICH, R., PLEUNE, J. (1979). Smooth pursuit eye movements: is perceived motion necessary? Science, 203, 1361-1363.

MACK, A., FENDRICH, R., WONG, E. (1982). Is perceived motion a stimulus for smooth pursuit. Vision Res., 22, 77-88.

MACKEBEN, M., HAEGERSTROM-PORTNOY, G., BROWN, B. (1980). Correctional movements during foveal pursuit in man. Proc. OMS 80 Conf., Pasadena, California.

MICHAEL, J.A., JONES, G.M. (1966). Dependence of visual tracking capability upon stimulus predictability. Vision Res., 6, 707-716

MILLODOT, M. (1972). Variation of visual acuity in the central region of the retina. Brit. J. Physiol. Opt., 27, 24-28.

MURPHY, B.J., HADDAD, G M., STEINMAN, R.M. (1974). Simple forms and fluctuations of the line of sight. Percept. Psychophys., 16, 557-563.

MURPHY, B.J., KOWLER, E., STEINMAN, R.M. (1975). Slow oculomotor control in the presence of moving backgrounds. Vision Res., 15, 1263-1268.

MURPHY, B.J. (1978). Pattern thresholds for moving and stationary gratings during smooth eye movement. Vision Res., 18, 521-530.

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

PUCKETT, J. DE W., STEINMAN, R.M. (1969). Tracking eye movements with and without saccadic correction. Vision Res., 9, 695-703.

RASHBASS, C. (1961). The relationship between saccadic and smooth tracking eye movements. J. Physiol., 159, 326-338.

ROBINSON, D.A. (1963). A method of measuring eye movement using a scleral search coil in a magnetic field. IEEE Trans. Biomed. Electron., BME-10, 137-145.

ROBINSON, D.A. (1965). The mechanics of human smooth pursuit eye movement. J. Physiol., 180, 569-591

ROBINSON, D.A. (1976). The physiology of pursuit eye movements. In: Eye movements and psychological processes, ed. MONTY, R.A. & SENDERS, J.W., New Jersey, Lawrence Erlbaum associates, publishers.

SKAVENSKI, A.A., HANSEN, R.M. (1978). Role of eye postion information in visual perception. In: Eye movements and their higher psychological functions, ed. SENDERS, J.W., FISHER, D F. & MONTY, R.A., pp. 15-34, New Jersey, Lawrence Erlbaum associates, publishers.

SPERLING, G. (1983). A unified theory of attention and signal detection. In: Varieties of attention, ed. PARASURAMAN, R. & DAVIES, D.R., New York, NY: Academic Press, in press.

STARK, L., VOSSIUS, G., YOUNG, L.R. (1962). Predictive control of eye tracking movements. IRE Trans. on Human Factors Electron., 3, 53-57.

STARK, L. (1971). The control system for versional eye movements. In: The Control of Eye Movements, ed. BACH-Y-RITA, P. & COLLINS, C.C., pp. 363-428, New York and London: Academic press.

ST-CYR, G.J., FENDER, D.H. (1969a). Nonlinearities of the human oculomotor system: gain. Vision Res., 9, 1235-1246.

ST-CYR, G.J., FENDER, D H. (1969b). Nonlinearities of the human oculomotor system: time delays. Vision Res., 9, 1491-1503.

ST-CYR, G J., FENDER, D H. (1969c). The interplay of drifts and flicks in binocular fixation. Vision Res., 9, 245-265.

STEINBACH, M.J. (1976). Pursuing the perceptual rather than the retinal stimulus. Vision Res., 16, 1371-1376.

STEINMAN, R.M. (1974). Oculomotor effects on vision. In: Basic mechanisms of oculomotor motility and their clinical implications, ed LENNERSTRAND, G. & BACH-Y-RITA, P., pp. 385-415, Oxford, Pergamon Press.

STEINMAN, R.M., CUNITZ, R.J., TIMBERLAKE, G.T., HERMAN, M. (1967). Voluntary control of microsaccades during maintained monocular fixation. Science, 155, 1577-1579.

STEINMAN, R.M., CUSHMAN, W.B., MARTINS, A.J. (1982). The precision of gaze. Human Neurobiol. 1, 97-109.

STEINMAN, R.M., HADDAD, G.M., SKAVENSKI, A.A., WYMAN, D. (1973). Miniature eye movement. Science, 181, 810-819.

TAMMINGA, E.P., COLLEWIJN, H. (1981). The effect of a structured background on human oculomotor pursuit of visual targets. Doc. Ophthal. Proc., 30, 134-143.

TER BRAAK, J.W.G (1957). "Ambivalent" optokinetic stimulation. Fol. Psychiat. Neurol. Neurochir. Neerl., 60, 131-135.

TER BRAAK, J.W.G (1962). Optokinetic control of eye movements, in particular optokinetic nystagmus. Proc. 22th Int. Congr. Physiol. Sci. (Leiden) 1, 502-505.

TYNAN, P.D., SEKULER, R. (1982). Motion processing in peripheral vision: reaction time and perceived velocity. Vision Res., 22, 61-68.

VAN DIE, G., COLLEWIJN, H. (1982) Optokinetic nystagmus in man. Human Neurobiol., 1, 111-119.

VOORHOEVE, P.E. (1978). Leerboek der neurofysiologie. Amsterdam/Brussel: Agon Elsevier.

WESTHEIMER, G (1954). Eye movement responses to a horizontally moving visual stimulus. A.M.A. Arch. Ophthal. N.Y., 52, 932-941.

WINTERSON, B.J., STEINMAN, R.M. (1978). The effect of luminance on human smooth pursuit of perifoveal and foveal targets. Vision Res., 18, 1165-1172.

WYATT, H.J., POLA, J. (1979). The role of perceived motion in smooth pursuit eye movements. Vision Res., 19, 613-618.

YARBUS, A.L. (1967). Eye movements and vision. New York: Plenum Press.

YASUI, S., YOUNG, L.R. (1975). Perceived visual motion as effective stimulus to pursuit eye movement system. Science, 190. 906-907.

YOUNG, L.R. (1971). Pursuit eye tracking movements. In: The Control of Eye Movements, ed. BACH-Y-RITA, P. & COLLINS, C.C., pp. 429-443, New York and London: Academic press.

ZEE, D S., YEE, R.D., COGAN, D G , ROBINSON, D A., ENGEL, W.K. Oculomotor abnormalities in hereditary cerebellar ataxia. Brain, 99, 207-234.

ZEE, D.S., YAMAZAKI, A., BUTLER, P.H., GÜÇER, G (1981). Effects of ablation of flocculus and paraflocculus on eye movements in primates. J. Neurophysiol., 4, 878-899.

ZUBER, B.L., STARK, L. (1966). Saccadic suppression: elevation of visual threshold associated with saccadic eye movements. Exp. Neurol., 16, 65-79.

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