HUMAN SMOOTH PURSUIT AND OPTOKINETIC NYSTAGMUS: EFFECTS OF STIMULUS FACTORS AND INSTRUCTIONS

GLAD VOLGEN EN OPTOKINETISCHE NYSTAGMUS VAN DE MENS: EFFECTEN VAN STIMULUSFACTOREN EN INSTRUCTIES

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR
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Albert Victor van den Berg

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PROMOTIECOMMISSIE

PROMOTOR : PROF. DR. H. COLLEWIJN
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Contents

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CHAPTER I: GENERAL INTRODUCTION

Some basic notions on eye movements

Eye movements are made to improve vision. A high slip velocity of the image over the retina precludes the detection of image details. For example, the sleepers of a railway track, which are easily distinguished from one another when the train is stationary, become blurred and hard to discern when one looks down through the window of a train moving at a high speed.

Visual acuity would thus be served best by fixating the eye with respect to the environment while the animal moves about. This goal is achieved approximately by the reflexive *compensatory* eye movements which are found in all vertebrates. These eye movements consist of a typical alternation of slow rotations of the eye *opposite* to the body motion and fast (saccadic) eye movements which carry the eye in the direction of the resting position. When the body motion consists of a unidirectional rotation or translation, a typical rhythmic alternation of *slow* and *quick* phases occurs which is called *nystagmus*. During the slow phases vision is improved, because the orientation of the eye is approximately fixed with respect to the environment, while during the brief quick phases visual sensitivity is reduced (see Matin, 1974, for a review).

Several sensory modalities are involved in the generation of compensatory eye movements. Proprioceptive input from the neck provides the oculomotor system with information about the motion of the head with respect to the body. The visual system and the vestibular organs monitor the motion of the head in space; this information is used to generate compensatory eye movements with the right direction and velocity. Most research has concentrated on visually evoked nystagmus (OKN) and nystagmus generated by vestibular stimulation. The reflex systems involved are, in the same order, the optokinetic reflex (OKR) and the vestibulo-ocular reflex (VOR). In real life these systems operate nearly always together and their properties are well matched in order to achieve image stability for as wide a range of motions of the head as possible. In the laboratory, the OKR and the VOR are easily studied in isolation, by rotating a visual surround around the stationary subject, or by rotating the subject in the dark, respectively. Theoretically, eye movements can compensate perfectly for a pure rotation of the visual surroundings with respect to the eye. However, there exists good evidence that the angular velocity of the eye falls short of that of the scene by a few percent at low velocities, and by considerably more at higher velocities (Van Die and Collewijn, 1984, 1986; Howard and Ohmi, 1984). Moreover, head motion usually involves a translatory component as well, for which eye rotations can at best compensate in only part of the visual field. For example, when an animal makes a pure translation, the local angular velocity of the visual scene with respect to the eye will depend on the visual direction and the distance of the objects to the eye. Thus, the angular velocity of the eye rotation compensates the angular velocity of the scene due to body motion only for a limited number of visual directions.

In view of these limitations of oculomotor compensation for head motion it is necessary that the human visual system tolerates retinal slip to some extent to prevent degraded vision during locomotion. Indeed, Westheimer and McKee (1975) found that an imposed retinal slip velocity up to 2.5 deg/sec had little influence on visual acuity. Similarly, Murphy (1978) reported that during fixation of a stationary point target the contrast threshold of a moving pattern was not strongly elevated up to velocities of 100 min arc/sec. The function of reflexive eye movements is therefore to reduce the slip of the image to a level optimal for vision in as large a part of the visual field as possible. This does not imply that every part of the visual field is equally effective in the generation of nystagmus. For example, moving stimuli confined to the visual streak of the rabbit (a specialized region of the retina with a higher density of receptor cells) are much more powerful in evoking nystagmus than identical stimuli presented to the retinal periphery (Dubois and Collewijn, 1979a). Similarly, many studies have shown that the central part of the human retina is much more effective in generating nystagmus than the retinal periphery(Dubois and Collewijn, 1979b; Cheng and Outerbridge 1975; Van Die and Collewijn, 1982; Howard and Ohmi, 1984).

In animals with frontally placed eyes such as the cat, the monkey and man the retina becomes increasingly inhomogeneous. Vision in these animals is course in the largest part of the visual field. In addition a high grade version, which allows for the perception of fine details, is available in the small (diameter ca. 1 deg) central part of the visual field which corresponds to the fovea. In addition to the reduction of retinal slip velocity by compensatory eye movements, voluntary eye movements occur in these animals in order to direct this small region of high quality vision - irrespective of head or body motions - to those parts of the visual field which are most attended to. (Consequently, these eye movements are an overt indicator of where attention is most likely directed in space - a phenomenon used by every teacher to screen his class for absent-minded students). Similarly to reflexive eye movements, voluntary eye movements consist of saccadic motions for fast changes of the viewing direction, capturing the target on the fovea, and slow voluntary smooth pursuit eye movements which prevent the image of the target from slipping off the fovea.

The different properties of the optokinetic reflex and smooth pursuit.

From the functional point of view the OKR and smooth pursuit are easily distinguished. The OKR is concerned with the reduction of the global motion in the entire field of view, whereas smooth pursuit attemps to stabilize the image at a selected location in the visual field. Typically, small point targets have been used for stimulation of the smooth pursuit system and full-field stimuli for the OKR. These stimuli are not completely selective for stimulation of either system. For example, reflexive eye movements occur in response to moving point stimuli (Cheng and Outerbridge, 1975; Barnes and Hill, 1984; Pola and Wyatt, 1985) and of course the details of a large moving pattern are adequate targets for pursuit. The reflexive and voluntary eye movements are not activated differentially by the mere stimulus parameters, but by specific intructions to the subject. Humans can relax voluntary control, leaving their response under involuntary control (Rademaker and Ter Braak, 1948). When the subject consciously attends to the details of a moving stimulus, 'active' or 'look' nystagmus is evoked, which is believed to reflect the activity of the smooth pursuit system. On the other hand, with relaxed attention 'passive' or 'stare' nystagmus (OKN) is evoked, which has properties in common with the reflexive eye movements present in animals without a fovea. For both systems the gains (defined as the ratio of the amplitudes or velocities of the eye movement and the target motion) depend on the frequency, velocity and predictability of the motion of the visual stimulus ,albeit in quantitatively different ways. Human smooth pursuit and the OKR are also qualitatively different in a number of respects:

(1) When the lights are turned off after prolonged unidirectional stimulation of the OKR the eye velocity shows an initial fast decline followed by a slowly decaying nystagmus (optokinetic after nystagmus, OKAN) which may reverse its direction after some time (Brandt, 1974; Cohen et al., 1981). In contrast, pursuit of a sawtooth movement for several minutes results in weak pursuit after nystagmus (PAN) in only a minority of the subjects and shows no reversals (Muratore and Zee, 1979). OKAN reflects the activity of a velocity storage mechanism which is involved in the generation of eye movements. The smooth pursuit system has apparently no access to the velocity-storage mechanism. Velocity-storage probably enables the OKR to operate in a higher velocity range, because labyrinthine defects have been reported to reduce the responses to high stimulus velocities and to attenuate human OKAN (Zee et al, 1976; Zasorin et al., 1983).

(2) Pursuit of a moving target is only slightly more saccadic in the presence of a stationary background (Murphy et al, 1975;Collewijn and Tamminga, 1984) or an effect of the stationary background is completely absent (Kowler et al., 1984). In contrast, the optokinetic response to a large moving field is strongly inhibited by stationary edges perpendicular to the direction of the target motion, even if they are visible in the periphery of the visual field only (Schor and Narayan, 1981; Howard and Ohmi, 1984).

(3) Both systems appear to use some kind of predictive mechanism to overcome the phase lag due to the oculomotor delay, but for the OKR the operation of this mechanism seems to be limited to simple periodical pattern motions like single sine waves (Yasui and Young, 1984) whereas the smooth pursuit of complex waveforms also shows predictive properties (Yasui and Young, 1984; Collewijn and Tamminga, 1984).

(4) Directional asymmetries of monocularly evoked OKN have been reported occasionally for horizontal (Van Die and Collewijn, 1982; Thompson and Saunders, 1984) and vertical (Takahashi et al., 1978) pattern motion although other reports suggested that the human OKN is essentially directionally symmetrical (Schor and Narayan, 1981). Especially for vertical pattern motion the reported directional asymmetries have been conflicting. On the other hand there is general agreement that normal smooth pursuit of small targets is directionally symmetrical, horizontally as well as vertically (Collewijn and Tamminga, 1984; Ranalli and Sharpe, 1987).

Remarkably, a direct comparison of the image stability achieved by the OKR and human smooth pursuit has been undertaken only incidentally. At first sight it might seem appropriate to compare the gain-velocity characteristics of the smooth component of pursuit (Collewijn and Tamminga, 1984; Buizza and Schmid, 1986) to those reported for the smooth component of the OKR (Schor and Narayan, 1981; Van Die and Collewijn, 1982), but in such a comparison effects of stimulus extent, of the instruction to the subject and of the constraints imposed on the frequency of the nystagmus by the fixed trajectory of a small target in opposition to the freedom in this respect offered by the large optokinetic stimulus would be confounded. Honrubia (1968) compared the nystagmus evoked by a large pattern rotating around subjects who were instructed to <u>stare</u> to the pattern, to the nystagmus when subjects attempted to <u>look</u> at the details of the striped pattern. The mean eye velocity during the slow phases of the 'stare' nystagmus was lower than during 'look' nystagmus. However, these EOG measurements were not sufficiently accurate to detect small saccades in the direction of the pattern motion during the slow phases. Hence, the higher mean eye velocity during the 'look' nystagmus might simply have resulted from a larger number of saccades in the direction of the pattern motion.

The specific objectives of the present investigations

Two questions were central during the first part of the presently reported investigations: (1) are directional asymmetries a true property of the normal human OKR, but not of human smooth pursuit? (2) is there a difference in the amount of image stability achieved by the smooth components of the eye movement during smooth pursuit and during OKN?

To answer these questions, 'stare' and 'look' nystagmus were investigated on the presence of directional asymmetries of the gain-velocity characteristic of the smooth component (chapters II and III). In addition, for 'stare' nystagmus the effects on the gain-velocity characteristic of binocular and monocular viewing with either eye were determined and the gains of the right and the left eye were compared to investigate whether the eyes move perfectly yoked during optokinetic nystagmus (chapter II). To relate pursuit of small targets to the pursuit of details of a large pattern (look nystagmus), the effects of the target extent and the constraints imposed by the fixed trajectory of a small target on the smooth pursuit gain were determined (chapter III).

In the second part of this thesis the smooth pursuit system was further studied. When a small target is pursued on a large stationary background or fixated on a moving background, the attempt to keep the target on the fovea results in concomitant opposite motion in large parts of the visual field. Theoretically, the retinal slip of the background would provide a powerful input to the OKR. Nevertheless, smooth pursuit of a small target on stationary backgrounds and fixation on moving backgounds are little affected by the retinal motion of the backgound. Smooth pursuit possibly achieves this independence of the background motion by preferential weighting of the retinal motion of the target and suppression of the optokinetic response to the background. When the target is artificially stabilized on the fovea, the retinal target motion is zero, irrespective of the motion of the eye. Under this condition the eye movements induced by the background should reflect the weight attributed to the backgound motion, or, formulated differently, the eye movements would reflect the activity of the incompletely suppressed OKR (Wyatt and Pola, 1984). Experiments along these lines were done by several groups but the results have been conflicting. My interest in these experiments was raised because the apparently conflicting results seemed to point into the direction of opposite drives of pursuit by the retinal periphery and the central retina *evoked by the intent to fixate or pursue a small target*. Such opposite drives would largely cancel the effect of en bloc motion over the retina and would thus offer an interesting hypothesis to account for the very moderate effects of backgrounds on pursuit. Moreover, such a mechanism would correlate well with the surprising result, reported in chapter III, that the pursuit of a *particular* detail of a large pattern results in slower eye movements than when *any detail* of the pattern is valid as a target. Thus, it seemed worth while to investigate the effects of masking of the central or the peripheral part of the background on the movement induced by the background motion during fixation of a foveally stabilized point target on a large moving background. These experiments (reported in chapter IV) gave inconsistent and idiosyncratic results, which raised the question whether foveal stabilization was a useful technique to study the interactions between target and background, because a consistent relationship to normal pursuit eye movements was absent. This led to an investigation of voluntary influences on smooth eye movements made with foveally stabilized targets (chapter V), which resulted in a proposal how the foveal stabilization technique may be used to obtain results relevant to normal pursuit. Finally, in chapter VI the predictive properties of smooth pursuit were investigated, using, amongst other stimuli, targets which were stabilized temporarily on the fovea, to probe the state of the predictive mechanism at different moments during pursuit of predictable and unpredictable target movement.

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CHAPTER II: DIRECTIONAL ASYMMETRIES OF HUMAN OPTOKINETIC NYSTAGMUS

INTRODUCTION

Rotation of the visual surroundings around a subject evokes slow eye movements in the direction of the pattern motion, interrupted by oppositely directed saccades. This combination is commonly called optokinetic nystagmus (OKN). OKN constitutes the visual component of the visuo-vestibular reflex eye movements, which serve the purpose of stabilizing the retinal image of the surroundings as a whole during rotation of the head. For mammals with lateral eyes the horizontal OKN in one direction is practically completely controlled by the contralateral eye. In the rabbit (Collewijn, 1969) and the rat (Hess et al., 1985) the gain of OKN elicited with monocular viewing is approximately equal to the gain of binocularly evoked OKN when the pattern rotates from the temporal to the nasal part of the monocular visual field. The response to monocularly viewed pattern rotation in the temporal direction is much smaller. Animals with frontally placed eyes show, in parallel to the development of the fovea and the visual cortex, a more symmetrical monocular response of the optokinetic reflex (cat: Hoffmann, 1982; Cynader and Harris, 1980). Recent neurophysiological evidence indicates that the different degree of horizontal directional preponderance of monocularly elicited OKN is related to the different organization of the inputs to the nucleus of the optic tract (NOT), which is involved in the generation of slow eye movements towards the ipsilateral side. The symmetrical monocular OKN in monkeys may result from the dominance of the connections descending from the visual cortex to the NOT, which convey binocular information (Hoffmann and Distler, 1986). In contrast, the NOT in the rabbit receives its input predominantly directly from the contralateral eye (Collewijn, 1975). In line with this evolutionary trend, monocularly elicited horizontal OKN of normal humans has been generally reported to be symmetrical or to show a marginal preference for temporal to nasal pattern movement (Van Die and Collewijn 1982).

Vertical binocular OKN is asymmetrical in many species and usually shows the largest response to upward pattern movement (chicken: Wallman and Velez 1985, cat: King and Leigh, 1982; Collins et al, 1970, monkey: Matsuo and Cohen, 1984; Takahashi and Igarashi, 1977) although in some instances a preference for downward pattern movement has been reported (rabbit:Erickson and Barmack, 1980, monkey: Kömpf et al, 1979). For humans the results are less clear. A number of studies indicates the occurrence of idiosyncratic differences in the directional asymmetry without a significant group effect on the OKN of the direction of the vertical pattern movement (Collins et al, 1970; Schor and Narayan, 1981; Baloh et al. 1983). Takahashi et al. (1978), however, reported the occurrence of significantly faster slow phases of the OKN for upward pattern movement for pattern velocities exceeding 70 deg/sec. All of these studies except one (Schor and Narayan, 1981) used the EOG technique. This technique has been criticized as unsuitable for recording vertical eye movement because the EOG signal is contaminated with a component due to the vertical movement of the eye lid over the globe (Barry and Melvill-Jones, 1965; Schlag et al. 1983; Collewijn et al. 1985).

In view of the scarcity of reliable data on human vertical OKN it seemed important to reinvestigate the occurrence of vertical directional asymmetries with a precise recording technique in human OKN. Horizontal OKN was recorded in the same subjects to compare the stabilizing qualities of the OKN in the vertical and horizontal directions. In addition, we investigated the effects of binocular and monocular viewing conditions on the OKN gain. As the effects might be different for the viewing and the non-viewing eye, we recorded from both eyes simultaneously.

We found no evidence for an overall asymmetry for rightward or leftward motion. When the pattern moved upward, gain was larger than for downward motion. The decrease of the gain of vertical OKN for increasing pattern velocity was steeper than for the horizontal OKN. The eyes moved nearly perfectly yoked for vertical pattern movement irrespective of the viewing conditions. For horizontal motion gain was largest for the eye which moved in the nasal direction.

METHODS

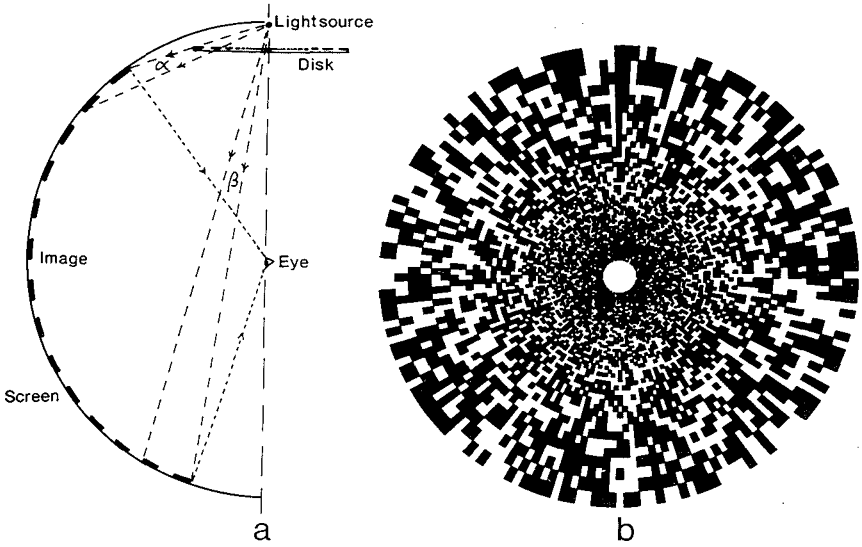
Eye movements were recorded with an electro-magnetic technique as described in Van Die and Collewijn (1982). Briefly, the phase of the voltage induced in a search coil by a rotating magnetic field is measured. When the field rotates in the horizontal plane, the phase is a linear function of the horizontal eye position. Similarly, vertical eye position may be measured when the field rotates in the sagittal plane. Horizontal and vertical OKN was recorded in separate sessions, with different sets of field coils active. The noise level was less than 4 minarc and the bandwidth was dc to 80 Hz (-3 dB).

The subject was seated in front of a hemispherical projection screen (radius: 80 cm) mounted within the coil system. A point source, mounted above the subject at the circumference of the hemisphere, projected an image onto the screen of a random dot pattern on a disk, which was positioned horizontally below the point source (Fig 2.1). The size of the pixels forming the pattern on the disk showed a radial gradient in order to compensate for the projection on a spherical surface. Consequently, the subject viewed a uniform random dot pattern with square elements of 2 x 2 deg extending throughout the visual field. When the disk was rotated about the vertical axis through the centre of the hemisphere and the lamp, the pattern was seen to rotate horizontally.

The projection system could also be placed in a lateral position with the axis of rotation in a transverse orientation. Rotation about this axis caused the pattern to move vertically. Tests were regularly done to ensure that the pattern velocity was within 2% of the nominal values.

The subjects viewed the pattern under three conditions: right eye

Fig. 2.1. (a) A vertical cross-section of the stimulus generating equipment. Indicated are the lamp at the circumference of the screen, the subject's eye at the center of the hemispherical screen and the horizontal disk carrying the random dot pattern, which is shown in (b). The disk is concentric with and rotates about the vertical axis through the lamp and the centre of the hemisphere. On top the vertical extent (120 deg) of the projection is limited by the radius of the disk (26.5 cm) and below it is limited by the radius of the blank area around the center of the pattern (1.9 cm). (b) The distorted random dot pattern used to project a random dot pattern with 2x2 deg square pixels on the hemispherical projection screen by an approximate point source positioned 7 cm above the center of the pattern. The distortion of the projection on the hemispherical screen was compensated for by the radial size-gradient of the pixels in the negative.



viewing (left eye covered), left eye viewing (right eye covered) and both eyes viewing. The head was stabilized with a bite bar which was adjusted to position in the centre of the sphere either viewing eye (for monocular conditions) or the bridge of the nose (for binocular viewing conditions). OKN was recorded for 4 directions of pattern movement (right,left,up and down) each at 4 velocities (9,23,36,57 deg/sec). Each session started with a calibration procedure as described in chapter III. The 24 different stimulus conditions (2 directions x 3 viewing conditions x 4 velocities) were presented in random order. Measurements were started at variable times (usually less than 30 sec) after stimulus-onset, when the subject indicated that he was ready. Each measurement lasted 8 sec.

Complete data on horizontal and vertical nystagmus were recorded in 7 subjects. An incomplete data set was obtained from two more subjects;

these were not included in the analysis but were consistent with the presented results. None of the subjects had visual defects other than refractive anomalies (four myopes and one hypermetrope). None of the subjects wore corrective spectacles during the experiments in order not to compromise the extent of the visual field. No effects related to uncorrected visual acuity were found. Subjects were instructed to look at an imaginary fixation point straight ahead in the same depth plane as the pattern and not to pay attention to the pattern motion. In preliminary experiments we established that under this instruction the average gain of the horizontal nystagmus did not differ significantly from the nystagmus observed with the usual 'stare' instruction, but showed a smaller amount of variability.

Horizontal or vertical eye movement was recorded from both eyes simultaneously. Signals were low pass filtered (-12 dB/octave and 62.5 Hz cut-off frequency) and sampled at 125 Hz. Eye velocity was computed by a program which removed the saccades from the record on the basis of velocity criteria (a detailed description may be found in chapter III), differentiated the cumulative smooth eye position and averaged the resulting smooth eye velocities over the entire recording period. OKN gain was computed as the ratio between the averaged smooth eye velocity and the velocity of the pattern motion.

RESULTS

The mean gain of OKN in the four principal directions is shown in Figs 2.2 through 2.4 for binocular viewing and monocular viewing with the right and the left eye, respectively. Mean OKN gain was always less than 0.85 and decreased when the velocity of the pattern movement increased. For instance, the mean gain of the horizontal OKN (pooled over both directions) decreased from 0.79 at 9 deg/sec to 0.54 at 57 deg/sec. The decrease was steeper for vertical pattern motion. For upward motion mean gain decreased from 0.80 at 9 deg/sec to 0.49 at 57 deg/sec; for downward motion the mean gain decreased from 0.68 at 9 deg/sec to 0.35 at 57 deg/sec.

Differences in gain between the right and the left eye

To our surprise, the gain of the horizontal OKN was not identical for the two eyes. The gain of the eye moving towards the nose was higher than the gain of the eye moving in the nasal-to-temporal direction. This was true irrespective of the viewing conditions. For instance, when the pattern moved towards the right at 23 deg/sec, the gain of the right eye was lower than the gain of the left eye. The difference in gain of the right and the left eye (g_r-g_l averaged across all subjects) amounted to -0.025, -0.086 and -0.063 for monocular viewing with the right eye,

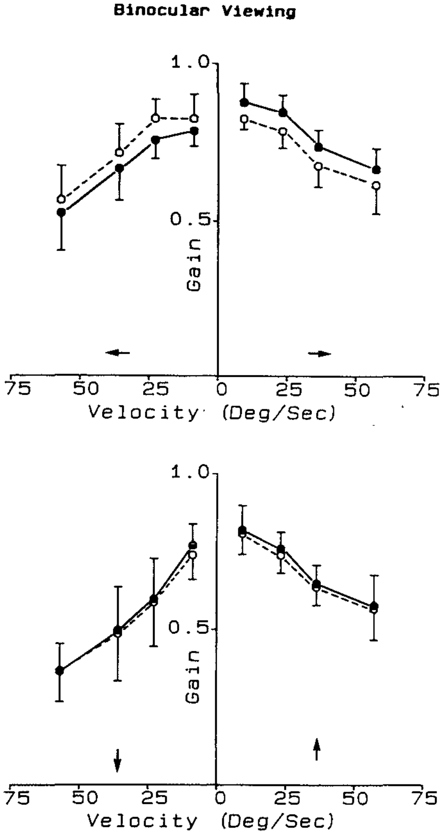


Fig. 2.2. OKN gain as a function of the stimulus velocity and the direction of motion when both eyes were viewing. Mean values of 7 subjects; bars indicate 1 SD. Horizontal OKN gain is shown in the upper panel. Vertical OKN gain is shown in the lower panel. The arrows in each panel indicate the direction of the target motion. Broken lines and open symbols indicate the gain of the right eye. Continuous lines and filled symbols indicate the gain of the left eye.

monocular viewing with the left eye and binocular viewing repectively. When the pattern moved at the same speed to the left, the right eye moved faster than the left eye and the differences in gain were (in the same order of the viewing conditions) 0.064, 0.041 and 0.059. This pattern of disjunctive eye movements occurred in all subjects but one (HC), who showed a more variable response. On the other hand the grand mean of the difference in gain between the right and the left eye (pooled over subjects,viewing conditions, velocities and horizontal directions of motion) was nearly zero (-0.001 ± 0.077; p>0.2). Thus, there was no overall difference in gain between the eyes.

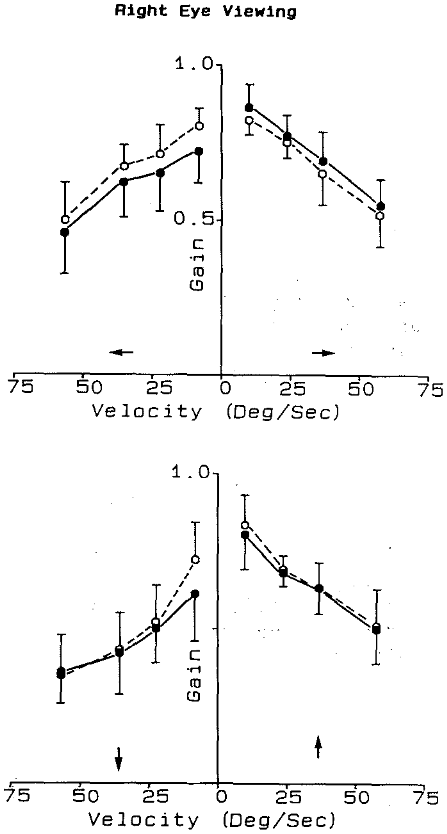


Fig. 2.3. OKN gain as a function of the stimulus velocity and the direction of motion when the right eye was viewing. Labels and other conventions as in Fig. 2.2.

For vertical pattern motion the gain of the left eye was marginally higher than the gain of the right eye (difference: -0.0077 ± 0.035). Although this difference was significantly different from zero ($p<0.01$) it was similar in size to potential errors of calibration (less than 1% or 0.1 deg) of the eye movement recordings. Therefore the difference may not be real.

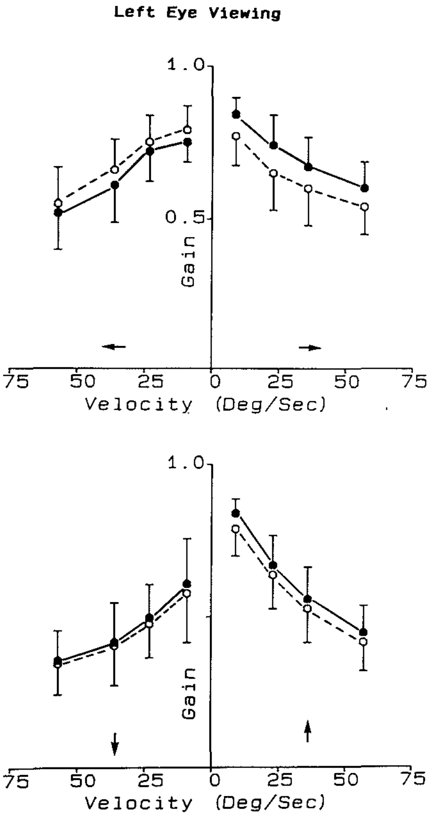


Fig. 2.4. OKN gain as a function of the stimulus velocity and the direction of motion when the left eye was viewing. Labels and other conventions as in Fig. 2.2.

OKN asymmetries with respect to the direction of motion

Gain was substantially higher for upward than for downward pattern motion. The grand mean of the gain difference (averaged over viewing conditions, subjects, recorded eyes and velocity) was 0.150 ± 0.149 ($p<0.001$). This asymmetry was clearly present in six subjects. A seventh subject (HS) showed a variable difference in gain between upward and downward pattern motion without a clear preference. For the 6 subjects with a clear preference the gain for upward pattern motion exceeded the gain of downward OKN by more than 0.05 in 80% of the measurements.

Idiosyncratic preferences for one direction of horizontal motion occurred, but a clear group effect was absent. In three subjects the rightward OKN gain of either eye generally exceeded the OKN gain for leftward pattern motion, for otherwise identical stimulus conditions. In the other subjects, however, a gain difference was absent, or the preferred directions were oppositely directed for each eye. The grand mean of the OKN gain for rightward motion of the pattern was 0.037 ± 0.104 ($p<0.001$) larger than for leftward pattern motion. As the pattern velocity was reliably known to within 2% of the intended value only, this gain difference may have been caused by a systematically larger pattern velocity to the right and we feel that this difference does not provide convincing evidence for a horizontal OKN asymmetry.

Temporo-nasal asymmetries

In order to determine the occurrence of temporal-to-nasal asymmetries we computed for each subject the difference between the gain of monocular OKN elicited by nasalward and temporalward stimulus motion. For monocular viewing of the right eye, the gain for rightward motion was subtracted from the gain for leftward motion; when the left eye was viewing the subtraction was reversed. For each subject these differences in gain were pooled over viewing conditions, recorded eyes and velocities. A positive grand mean gain would indicate a preference for temporal-to-nasal stimulus motion. The gain differences as defined ranged from 0.005 ± 0.124 to -0.083 ± 0.15 among our subjects. The mean differed significantly from zero only in one subject (CE: -0.083 ± 0.15; $p < 0.05$), but the preference was in the nasal-to-temporal direction. Hence, none of our subjects showed a true preference for temporal-to-nasal pattern motion.

There was, however, an effect of the viewing eye on the magnitude of the gain difference between the right and the left eye (Table 2.1). As described before, on average the left eye moved faster than the right eye during slow phases to the right (the difference in gain, pooled over subjects and velocities, was negative). For leftward motion the right eye moved faster than the left eye (difference in gain positive). As shown in Table 2.1, the magnitude of the difference in gain was largest when the right eye saw leftward motion and when the left eye saw rightward motion. Hence, the mean difference in gain between the right and the left eye was largest when the subject viewed monocularly a pattern motion towards the nose. This suggests that the inherent preference of each eye to move towards the nose may be slightly enhanced by the viewing of nasalward motion and diminished by viewing of temporalward motion. This effect was not consistently present for all subjects and all stimulus conditions.

	Direction of Pattern Motion	
	Right	Left
Right Eye Viewing	-0.030 ± 0.041	0.064 ± 0.076
Left Eye Viewing	-0.071 ± 0.051	0.040 ± 0.068

Table 2.1. The difference in gain between the right eye and the left eye pooled over velocities and subjects for different viewing conditions and directions of horizontal motion.

Binocular and monocular viewing

The gain of binocularly elicited OKN was on average higher than of monocularly elicited OKN gain of either eye, although this effect was not consistently present for all stimulus conditions in each subject. The grand mean difference in gain (averaged over subjects, recorded eyes, directions and velocities) between binocular viewing and monocular viewing with the right and the left eye were 0.055 ± 0.067 ($p<0.001$) and 0.073 ± 0.079 ($p<0.001$), respectively.

Statistical analysis

These trends were confirmed with a number of four way analyses of variance (subject x viewing eye x direction x velocity). Separate ANOVA's were performed for horizontal and vertical pattern motion with either the gain of the right eye (g_r), the gain of the left eye (g_l) or the difference in gain of the right and the left eye (g_{r-l}) as the dependent variable. Only main effects and two way interactions were considered. In all tests of g_r and g_l there was -as expected- a significant effect of velocity which will not be discussed further.

In a first ANOVA only the monocular data for horizontal pattern motion were selected. There were significant differences between the subjects in the effects of direction and velocity on the OKN gain. This follows from the occurrence of significant interactions between subject and direction and subject and velocity for all dependent variables ($p<0.001$ in all cases) In addition, a significant interaction was found between direction and the viewing eye on g_r ($F(1,63)=11$; $p<0.005$) and g_l ($F(1,63)=6.2$; $p<0.05$). This temporal-to-nasal asymmetry may be attributed largely to the contribution of one subject (CE) as mentioned above. There were significant main effects of horizontal direction on g_l ($F(1,63)=91$; $p<0.001$) but not on g_r ($F(1,63)=3.7$; $p>0.05$). This may also be observed from Figs 2.2-2.4. The mean OKN gain showed no clear directional asymmetry for the right eye, but for the left eye the mean rightward OKN gain was clearly larger than the mean leftward OKN gain. In the right eye, the preference of either eye for moving towards the nose has apparently compensated the apparent directional 'preference' of the horizontal OKN for rightward motion. On the other hand, the tendency of the left eye to move faster towards the nose has enhanced the OKN 'preference' for rightward motion. The effects of the horizontal direction ($F(1,63)=21$; $p<0.001$) of the pattern motion and of the monocularly viewing eye ($F(1,63)=21$; $p<0.001$) on g_{r-l} were also significant.

In a second set of 4 way analyses of variance (subject x viewing condition x direction x velocity) the monocular data of each eye were pooled and compared to the binocular data. For horizontal as well as vertical motion, the OKN gain of either eye increased significantly when binocular viewing was compared to monocular viewing, but there was no effect on the difference in gain between the eyes. In agreement with the above, a significant effect of the viewing condition (monocular or binocular) occurred for horizontal pattern motion on g_r ($F(1,119)=48$; $p<0.001$) and g_l ($F(1,119)=67$; $p<0.001$) but not on g_{r-l} ($F(1,119)=3.2$; $p>0.05$). Similarly, for vertical pattern motion significant effects were found of the viewing condition (monocular or binocular) on g_r ($F(1,119)=49$; $p<0.001$) and g_l ($F(1,119)=68$; $p<0.001$) but not on g_{r-l} ($F(1,119)=1.8$; $p>0.1$).

Finally, for vertical pattern motion there was a significant interaction effect of subject and direction on g_r ($F(6,119)=38$; $p<0.001$), g_l ($F(6,119)=48$; $p<0.001$) and on g_{r-l} ($F(6,119)=4.3$; $p<0.001$) and there were significant effects of the direction on g_r ($F(1,119)=301$; $p<0.001$) and g_l ($F(1,119)=376$; $p<0.001$) but not on g_{r-l} ($F(1,119)=1.8$; $p>0.1$). Thus, for either eye the OKN gain for upward pattern motion is sigificantly larger than for downward motion but the effect depends on the subject tested.

DISCUSSION

The finding that the eye moving smoothly towards the nose moved faster than the eye moving in te nasal-to-temporal direction was unexpected and has, to our knowledge, not been reported before. We carefully checked our data on potential artefacts. Because the stimulus was not seen at optical infinity we looked into the possibility that the unequal movement of the eyes might have resulted from differences in the pattern velocities seen by each eye. When the eye is positioned off the axis of rotation, the local velocity of the pattern seen by the eye depends on the visual direction. For instance, when the (vertical) axis of rotation intersects the bridge of the nose (as was the case in the present experiments for binocular viewing) the velocity seen by the right eye is higher in the right hemifield, and lower in the left hemifield, compared to the angular velocity of the pattern. Similarly, the left eye will observe a higher pattern velocity in the left hemifield. As the eyes generally deviate in the direction of the fast phases during OKN, faster motion will be seen by the left eye for rightward pattern movement, and by the right eye for leftward pattern motion. This differential stimulation of the eyes might then result in a faster movement of the eye with the slow phases towards the nose. Although this effect may have contributed to the occurrence of the gain-difference between the eyes, we may conclude that the phenomenon as such reveals a property of the OKN, for the following reasons. Firstly, when one eye was patched and the viewing eye was positioned on the axis of rotation, the angular velocity seen by the eye was independent of the visual direction. Nevertheless, the gain was higher in the eye which moved towards the nose. Secondly, for an interocular distance of 7 cm, a radius of the projection screen of 80 cm and a deviation of 15 deg into the direction of the fast phases, the difference in stimulus velocity observed by each eye would be only 2% of the pattern velocity. The difference in gain was larger and amounted to 0.048 ± 0.060 and -0.055 ± 0.036 (pooled over subjects and viewing conditions) for pattern motion towards the left and right, respectively. Consequently, we believe that the finding that the gain of the eye which moves towards the nose is higher than that of the eye moving temporally, reflects a physiological phenomenon.

It must be stressed that the faster motion of the eye which moves medially does not necessarily result in a preference of each eye for moving towards the nose, because in addition to this preference other asymmetries may occur, such as a rightward or leftward preference. For instance, in three subjects there was a preference for rightward pattern motion, which resulted in a nearly symmetrical OKN gain for the right eye and a strong temporo-nasal asymmetry for the left eye. However, when such a right-left asymmetry is absent, the reported gain difference between the eyes is equivalent to a preference of each eye for moving towards the nose. Consequently, when recording the movement of the monocularly viewing eye only, temporo-nasal OKN asymmetries related, to the viewing eye are confounded with temporo-nasal asymmetries, related to the recorded eye, when a preference for one direction of pattern motion is absent. This was e.g. the case in the study by Van Die and Collewijn (1982), who reported for monocular OKN a small, but significant preference for nasalward pattern motion, in the absence of a left-right asymmetry. We found no evidence in any of our subjects for a clear preference for nasalward pattern motion of the monocular horizontal OKN for either monocularly viewing eye, when the gains of the right and the left eye were averaged. This result is in line with the results of earlier studies (Schor and Narayan, 1981; Westall and Schor, 1985). However, the difference in gain between the eyes increased when the motion of the monocular stimulus was in the nasal direction, which suggests that human OKN may show a marginal sensory preference for temporal-to-nasal motion. This possible sensory preference for nasalward stimulus motion is much weaker and less consistently present than the motor preference for temporal-to-nasal motion of the eye. Thus, we conclude that the small but statistically significant temporal-to-nasal asymmetry reported by Collewijn and van Die (1982) most likely reflects the preference of each eye to move towards the nose rather than a preference of the monocular OKN for pattern movement towards the nose.

As the described motor preference of the smooth component of OKN results in a convergent eye movement irrespective of the direction of stimulus motion, prolonged optokinetic stimulation would lead to considerable convergence of the eyes, unless the convergence would be cancelled during the quick phases. We never observed a clear increase in the convergence during our relatively brief (8 sec) recording periods. The low sample frequency (125 Hz) did not permit an accurate analysis of possible differences between the saccades of the right and the left eye. Interestingly, Erkelens et al. (in prep.) recently found that the saccades of a temporally moving eye showed a larger amplitude and peak-velocity than the nasally directed saccades of the other eye, when subjects saccaded between targets positioned on an iso-vergence contour.

We could not confirm another asymmetry reported by Van Die and Collewijn (1982), viz. a larger gain of monocularly elicited horizontal OKN for the right than for the left eye. The grand mean of the gain difference, for a sample of 10 subjects, was found by these authors to be as large as 0.05 ± 0.11. We found no significant gain difference between the eyes for horizontal pattern motion. Since Van Die and Collewijn recorded monocular OKN of the viewing eye only, whereas we also recorded the movement of the patched eye and in addition measured binocular OKN, the different outcomes might mean that the gain difference between the viewing eyes was compensated by an equal but opposite difference in gain between the patched eyes in our sample. To test this possibility we computed the mean gain difference of the left and the right eye for monocular viewing, taking into account only the gains of the viewing eye. Also for this subset of our data the mean difference of the gain (pooled over all subjects, horizontal directions and velocities: -0.003 ± 0.080) was not significant ($p>0.3$). Unfortunately, we have no explanation for the different outcome with respect to Van Die and Collewijn's results.

In Fig 2.5 the gain-velocity characteristics for horizontal full-field pattern motion, derived in two other studies, are compared to our present findings. We consider these studies the most appropriate ones for a comparison, because a precise recording technique was used and

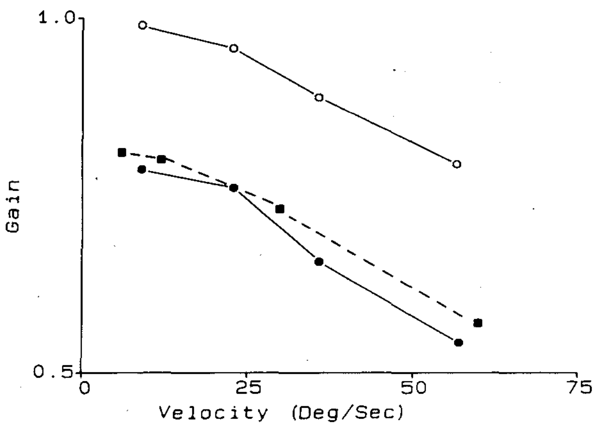


Fig. 2.5. Horizontal OKN gain as a function of the stimulus velocity. Our data are compared to data from the literature which are most comparable with respect to the methods employed. Continuous line, dots: our present data. Broken line, squares: Van Die and Collewijn (1982). Continuous line, open circles: results from chapter III (Van den Berg and Collewijn, 1986).

the gain of the smooth component of the eye movement, averaged over a fixed period of time, was computed. Our data, pooled over the direction of pattern motion, viewing conditions, recorded eyes and subjects are very similar to those obtained by Van Die and Collewijn (1982). The latter authors instructed their subjects to pay full attention to the pattern, without deliberately attempting to pursue a stripe, while we instructed our subjects to fixate an imaginary fixation point at the same distance as the pattern. Apparently, such variations in the instruction have a very limited effect on the gain of the OKN. On the other hand, when subjects (five of who participated also in the present study) were instructed to pursue a stripe of their choice, much higher gains at all velocities were found (see chapter III). The downward slope of the gain as a function of pattern velocity was remarkably similar in all three studies. This suggests that active pursuit of pattern elements and 'stare' nystagmus share a single non-linearity, causing the fall-off of the gain for larger stimulus velocities. The effect of the instruction to pursue a pattern element may simply be described as an overall increase of the gain. Similarly, Pola and Wyatt (1985) reported that the attempt to foveally fixate a stabilized oscillating point target increased the gain of the eye movements over the whole frequency range tested, compared to 'passively' watching of the same stimulus.

The gain for upward nystagmus was comparable to the horizontal OKN gain but downward nystagmus showed a clearly lower gain. Takahashi et al. (1978), using the EOG technique, found a similar preference of the human OKN for upward pattern motion if the velocity exceeded 70 deg/sec. In contrast to our findings, no vertical directional asymmetry was found for lower velocities. Takahashi et al. instructed their subjects to pursue the striped pattern as rapidly as possible. Thus their instruction -in contrast to ours- evoked smooth pursuit of the pattern. It is well known that human smooth pursuit is directionally symmetrical, horizontally as well as vertically (Collewijn and Tamminga, 1984; Ranalli and Sharpe, 1987). Possibly, directionally symmetrical smooth pursuit dominated the response at the lower velocities and precluded the detection by Takahashi et al. (1978) of the vertical asymmetry of the OKN.

As stated in the introduction, a similar preference for upward pattern motion has been reported for the OKN of several other species. Takahashi and Igarashi (1977) e.g. reported that the OKN gain of the monkey was close to unity for either vertical direction up to 40 deg/sec, but that for higher velocities the decline of the gain was much steeper for downward pattern motion. Matsuo and Cohen (1984) provided evidence that the reduced gain of downward nystagmus of the monkey could be attributed to a reduced velocity storage for downward motion. Unlike the monkey, humans do not show a slow build-up of the velocity of the slow phases, and horizontal optokinetic after nystagmus (OKAN) is irregular and sometimes absent in subjects with normal OKN (Baloh et al. 1983). This suggests that velocity storage is relatively unimportant in the generation of horizontal OKN. Human OKAN elicited by vertical pattern motion has been rarely measured. In the only study known to us, human OKAN seemed to occur more frequently after prolonged stimulation with upward pattern motion than after stimulation with with downward pattern motion (Baloh et al, 1983) but a clear asymmetry of vertical OKN was absent. Thus, the preference of the human OKN for upward pattern motion reported here may be attributable to a reduced operation of the velocity storage mechanism for downward motion but more data are clearly necessary to firmly support this possibility.

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CHAPTER III: HUMAN SMOOTH PURSUIT: EFFECTS OF STIMULUS EXTENT AND OF SPATIAL AND TEMPORAL CONSTRAINTS OF THE PURSUIT TRAJECTORY

INTRODUCTION

Constant velocity visual stimuli have been used extensively to investigate reflexive and voluntary eye movements. Typically, small targets moving along a sawtooth or triangular trajectory have been used to investigate voluntary pursuit while large structured patterns have been used to evoke optokinetic nystagmus (OKN). Traditionally, a distinction has been made between reflexive 'stare' OKN and 'look' OKN (Ter Braak, 1936). The latter is probably similar to voluntary pursuit. In recent years, precise recording techniques such as the scleral search coil method and computerized segregation of eye movements in their smooth and saccadic components have facilitated the analysis of smooth tracking of visual stimuli. Using such methods, Collewijn and Tamminga (1984) and Van Die and Collewijn (1982) described smooth pursuit of a point target and the smooth component of 'stare' OKN evoked by a full-field striped pattern, respectively. In both studies, the gain of the smooth component decreased markedly when the target velocity increased. The fall-off was steeper for the pursuit of the point target but it is not clear whether the difference should be attributed to the difference in stimulus extent, the different instructions or both. It is known, on the other hand, that the OKN decreases for smaller stimuli (Cheng and Outerbridge, 1975; Dubois and Collewijn, 1979; Van Die and Collewijn, 1982). Therefore, as a step towards a clearer demarcation of reflexive and voluntary smooth pursuit it would seem to be of interest to compare the voluntary smooth pursuit of a small target with the pursuit of a detail of a traditional OKN stimulus, i.e. a large textured pattern.

There are a number of reasons why a textured pattern might elicit better pursuit than a single point target. A large target stimulates more velocity detectors simultaneously which may lead to a stronger sensory stimulus by spatial integration (cf. Koenderink et al. 1978) or to a better estimate of the slip velocity by averaging. Also, a full-field pattern stimulates peripheral velocity detectors that may operate in a different velocity range than the central detectors. Third, during parts of its trajectory a small target will stimulate the retina outside the foveal region with a diameter of about 1 deg, especially when the target velocity is high. Studies which have dealt with extra-foveal pursuit (Barnes and Hill, 1984; Behrens and Grusser, 1979; Collewijn et al. 1982; Collewijn and Tamminga, 1986; Winterson and Steinman, 1978) indicate that foveal pursuit is superior to extra- foveal pursuit, although Collewijn and Tamminga (1986) reported that there was no difference for targets in the near periphery if the background was featureless. On the other hand, the many contours of a striped pattern may be expected to provide a foveal stimulus during a larger part of the pursuit movement than the point target.

In this study we compared the smooth pursuit of a spot (diameter: 10 min arc) with that of a nearly full-field stripe pattern, for a number of velocities. This comparison is complicated by the fact that a small target restricts the pursuit eye movements to its fixed trajectory whereas the pursuit of a stripe in the pattern allows the subject to pursue in a preferred eye position range (henceforth: the pursuit range) because the subject has the freedom to saccade to another target any time. Moreover, in the large pattern the subject may shift his attention gradually from one target to another while this is clearly impossible during the pursuit of a small target. Hence the effect of extent of the target could be confounded with the effect of a preferred pursuit range or different pursuit strategies. To resolve this ambiguity we investigated the effect of releasing the subject from possible restrictions caused by the fixed trajectory of the small target. This was achieved by resetting the spot to the fovea whenever the subject made a saccade in a direction opposite to the target movement.

Conceivably, different pursuit strategies might be used when the subject was either free to track a stripe of his choice or when he was instructed to track the spot superimposed on the pattern and moving at the same velocity. Therefore we investigated both conditions. Pursuit in the latter condition compared to pursuit of the spot on a dark background should reveal the effect of target extent. Pursuit of a stripe compared to pursuit of the spot superimposed on the pattern should reveal the effect of different pursuit strategies. The latter could result in different pursuit ranges or different nystagmic movements. Therefore in addition to the gain, (the ratio of smooth eye velocity and target velocity) the pursuit range and the structure of the nystagmic eye movements were analyzed to characterize pursuit.

Finally, we looked for the occurrence of directional asymmetries of the smooth pursuit system. It is well known that directional preferences occur in the OKN of afoveate species (Ter Braak 1936; Hess et al., 1985; Tauber and Atkin, 1968). Recently, a small but statistically significant preference of human monocular 'stare' OKN for temporal to nasal movement has been described by Van Die and Collewijn (1982). It would seem of interest whether directional preferences occur during voluntary pursuit of image details of a full-field stimulus, which is an effective stimulus for 'stare' OKN.

In the following it will be shown that pursuit of a small target improved when the subject was free to choose the pursuit range. When a large pattern moved in conjunction with the spot smooth pursuit improved further. The smooth pursuit improved once more when the subject could freely track any detail of the pattern.

METHODS

Recording and stimulus generation

Horizontal gaze was measured by phase detection of the voltage induced in a scleral coil by a magnetic field rotating in the horizontal plane (for details see Collewijn, 1977; Van Die and Collewijn, 1982). We used a range of 40 deg to each side of the straight ahead position out of the 360 deg linear recording range available. The noise level was less than 4 min arc and the bandwidth was DC to 80 Hz (-3 dB). The eye position signal was differentiated (Grass Polygraph Differentiator 7P20C) to obtain the eye velocity.

The subject was seated in the centre of a hemicylindrical screen (radius: 80 cm). The head was stabilized by means of a chin support which was adjusted to position the viewing eye, which also wore the scleral coil, in the central axis of the screen. The other eye was patched.

Above the subject a cylindrical grating was positioned concentric with the screen. A lamp with a vertical tungsten filament in the central axis of the cylinder projected an image of the grating on the screen. The pattern of the black and white stripes (each with a width of 2.5 degrees) covered an area of 180 degrees horizontally and 105 degrees vertically. The pattern could be rotated horizontally at different velocities in both directions. Details can be found in van Die and Collewijn (1982).

To create a point target, a He-Ne laser beam was reflected onto the screen by a servo-controlled mirror (General Scanning G300PD) mounted near one edge of the screen and on its circumference. This arrangement allowed a horizontal deflection of the spot over a linear range of at least 45 degrees to each side. The position of the spot was controlled by the output of an electronic integrator. Feeding this integrator with a DC voltage resulted in a constant velocity displacement of the spot. In the 'free range' condition logic circuitry was used to reset the integrator whenever the eye velocity in the direction opposite to the movement of the spot exceeded a criterion value. Following a reset the initial value of the integrator was made equal to the output of the eye position monitor. Hence, if the gains of the amplifiers were properly calibrated the spot position equalled the eye position after a reset. The target was thus foveally stabilized during return saccades but moved at a constant velocity otherwise. In this way, the spot moved through a range which was determined by the subject. In addition, we used for comparison a 'fixed range' condition, which consisted of a traditional sawtooth trajectory with fixed starting point (the straight ahead position) and end point (27 or 40 deg to the right).

Tests were regularly done to ensure that the stabilization of the spot was precise to at least 10 min arc and pattern velocity to within 2% of the intended values. The relative velocity between the spot and the pattern was always below 1% of the intended velocity of either target.

The position output of the eye movement monitor and the scanner control unit were low pass filtered (cut off: 67.5 Hz) to prevent aliasing, digitized (sample rate: 125 Hz) and stored on computer disk memory for later analysis. Details of the data acquisition can be found in Collewijn and Tamminga (1984).

Procedures and subjects.

In preliminary observations it became clear that differences of the pursuit gain for the different targets appeared especially at high target velocities. Hence pursuit gain was investigated at 6 velocities covering a decade: 9,18,23 ,36,57 and 90 deg/sec. To determine whether pursuit asymmetries occurred, targets were moved in both directions and monocular pursuit with either eye was tested in two sessions lasting about 45 min each. The target consisted of either the spot on a dark background, the pattern or the combination of spot and pattern. In each session the 36 different stimuli (6 velocities, 3 patterns, 2 directions) were presented in a pseudo-random order. Sessions typically started and ended with a calibration measurement, during which the subject was asked to fixate the laser spot which was displaced 10 degrees to either side of the straight ahead position to confirm correct calibration. Between two successive measurements a 15-60 sec period was scheduled to select the next stimulus conditions on a switch board and to permit the subject to recuperate from motion after effects, if any. Each measurement took 16 seconds.

Five subjects were tested. All had some practice with the stabilized return technique from preliminary experiments. None had visual defects other than refractive anomalies. One subject possessed 20/20 Snellen acuity; the four remaining subjects were myopic(-3D to -7D). One of the myopes wore his contact lenses during the experiment. The remaining three myopes were not allowed to wear their glasses as the frame of the spectacles would limit the visual field. It was felt that in the present investigation, in which much effort was made to allow the subjects to pursue the target in a preferred pursuit range, the extent of the horizontal visual field could not be compromised. On the other hand the mild blur affected the visibility neither of the stripes nor of the laser spot. Actually it was found that the subject with the highest degree of myopia had the best overall performance, which suggests that blur caused only little - if any - deterioration of pursuit. Subjects were instructed to pursue the spot exclusively whenever it was visible and to track a single stripe otherwise.

Data analysis

As a first step in the off-line data analysis the calibration of the eye position signal was checked by means of the calibration measurements. A detailed description of this procedure can be found in Collewijn and Tamminga (1984). Typical values of the eye position offset were below 0.5 deg. The sensitivity of the eye position monitor as computed from the calibration records usually differed by less than 2% from the intended value of 250 mV per degree. The eye position record was differentiated with a 6 point central difference algorithm and inverted if necessary to obtain positive eye velocity during the slow pursuit phase. Return saccades could then be detected by a negative velocity criterion (-20 to -30 deg/sec) while saccades in the direction of stimulus movement were characterized by the lower of the two following criterions:

(1) A forward saccade exceeds the (unsigned) stimulus velocity by at least 10 deg/sec;

(2) A forward saccade exceeds the mean smooth eye velocity by at least 125%.

These simple criteria sufficed to reliably detect saccades in the nystagmic pattern of eye movements elicited by the unidirectionally moving stimuli.

Prior to the computation of the mean and standard deviation of the smooth eye velocity of the entire 16 sec record, segments of 50 msec prior to saccade onset and of 150 msec following saccade onset were removed from the record. Smooth pursuit gain was computed as the ratio of the mean smooth eye velocity and the stimulus velocity.
As a further characteristic of the pursuit movement, histograms of the frequency of occurrence of a given gaze position during a measurement were computed.
To characterize the structure of the nystagmic pursuit movements histograms of three more parameters were computed for each measurement:

(1) The time interval between two successive return saccades.

(2) The amplitude of the slow phase between two successive return saccades.

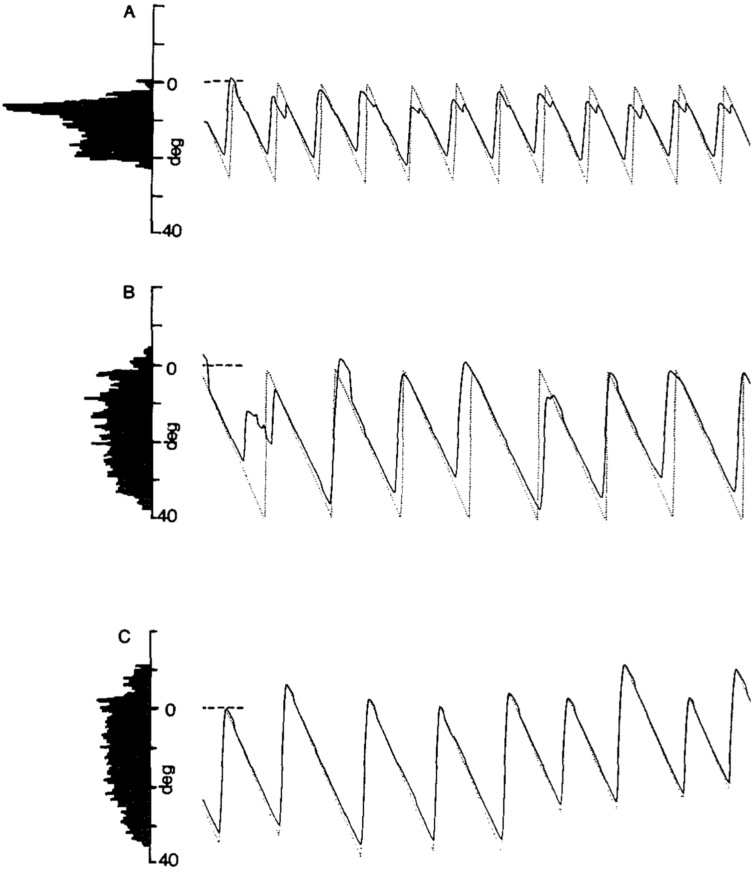
(3) The eye position at the beginning of a slow phase.

Note that the amplitude of the slow phase thus computed is determined by smooth as well as saccadic components. The histograms were digitally filtered to reduce noise with the following smoothing function:

$$Y(n) = 0.25*X(n-1) + 0.5*X(n) + 0.25*X(n+1)$$

The filtered n-th bin (Y(n)) is obtained from the weighted sum of the unfiltered n-th bin (X(n)) and its neighbouring bars X(n-1) and X(n+1). The smoothed histograms are estimates of the probability density functions of the duration, the amplitude and the starting eye position of the slow phase.

Fig. 3.1. Gaze during pursuit of the spot moving with a velocity of 23 deg/sec to the right. The spot moved in a fixed range with an amplitude of 27 deg (a) or 40 deg (b), or the spot moved in a free range (c). The dotted line indicates the spot position, the continuous line indicates gaze. The broken horizontal line marks the straight ahead position. Corresponding histograms of gaze during pursuit are plotted along the ordinate.



RESULTS

Effect of the free range technique on pursuit

Fig 3.1 shows typical recordings of the pursuit eye movements elicited by the spot moving along a sawtooth trajectory. The matching eye position histograms are plotted along the ordinate of each record.

In the fixed range condition, the eye movement showed the usual nystagmic wave form with return saccades followed by a relatively slow smooth pursuit and one or several catch up saccades that corrected the retinal error. Although the fixed sawtooth trajectory of the target was regular and would seem to be highly predictable, the return saccade seldom brought the eye on target. The return saccade often preceded the reset of the spot position by 100 msec or more (see Fig 3.1a,b) and often fell short of the return position of the target by several degrees. Especially in the low-amplitude fixed range condition the subsequent pursuit of the at that moment eccentric target tended to be slower and often a second saccade corrected the retinal error. Part of this slow onset of pursuit was removed from the computation of the smooth eye velocity by saccade elimination.

In the free range condition, time differences between the return movement of the spot and that of the eye were absent since the return movement of the spot was coupled to the return saccade (see Fig 3.1c). In this condition, slow phases with a large amplitude were often preceded by a return saccade which crossed the center position. In general, pursuit eye movements did not carry the eye beyond 40 degrees eccentricity. The amplitude of the pursuit movement was only occasionally larger than 40 degrees. In general the stabilization of the spot during the return saccade made the pursuit movements more regular. Note that, although the subject was free to determine the eye position range, the gaze position histograms during the 'free range' pursuit and the 40 deg 'fixed range' pursuit were nearly identical.

Fig 3.2 shows smooth pursuit gain averaged over the 5 subjects as a function of the target velocity. Gain was highest in the free range condition over the whole velocity range investigated. Gain was 6 to 10 % higher than in the fixed range, 40 deg amplitude condition.

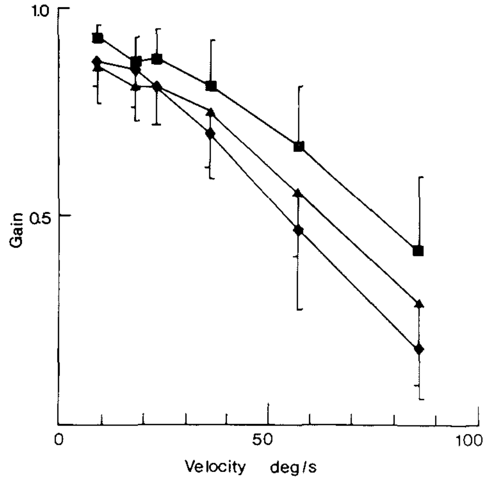


Fig. 3.2. Smooth pursuit gain (mean and 1 SD of 5 subjects) during the pursuit of the spot to the right. The spot moved in a free range (squares) or followed a fixed sawtooth trajectory with an amplitude of 27 deg (diamonds, SD marked by rightward bars) or 40 deg (triangles, SD marked by leftward bars).

The difference between the free range and fixed range smooth pursuit gain was even higher when the amplitude of the fixed range sawtooth was reduced to 27 degrees. The gain reduction may in part be attributed to the slow onset of pursuit after a return saccade in the fixed range condition. In all conditions, when the target velocity increased, pursuit became more saccadic and the smooth pursuit gain decreased. Although stabilization of the spot during return saccades clearly improved smooth pursuit, a substantial part of pursuit was still saccadic. At 90 deg/sec the gain of the smooth component had dropped to 0.45 indicating a mean slip velocity of nearly 50 deg/sec. During individual beats, however, the smooth eye velocity could occasionally reach values of 70 deg/sec and more.

Apparently, releasing the eye from the temporal or spatial confinements imposed by the fixed range target movement improved the performance of the smooth pursuit system. In the remaining part of the paper the free range technique was used whenever the the point target was pursued.

Pursuit asymmetries

We systematically varied the type of target, the target velocity, direction of motion and the viewing eye and determined the smooth pursuit gain. Neither viewing eye nor direction of target motion evoked a consistent difference in gain at all target velocities in any of our subjects. The same applied to possible temporo-nasal asymmetries. To investigate whether our subjects as a group showed any asymmetries we used Student's t-test. Pursuit to the right seemed to be slightly better than pursuit to the left (difference in gain(m): 0.023 ± 0.101; $p<0.01$). This difference, although statistically significant, could be caused by a systematic difference in the stimulus velocity between rightward and leftward moving targets. The target velocity was reliably known within 2% of the intended value. Our data therefore do not provide evidence for a preference of smooth pursuit to the right. The gain of temporal-to-nasal pursuit did not differ significantly from the gain of naso-temporal pursuit ($m=0.0079 \pm 0.103$;$p>0.2$). Also, when naso-temporal asymmetries in the eye movements were considered for the targets separately, no significant differences were found (spot: $m=0.012 \pm 0.131$; $p>0.4$, pattern: $m=0.006 \pm 0.09$; $p>0.4$, spot+pattern: $m=0.0059 \pm 0.083$;$p>0.4$). Finally, no significant difference was found between the two eyes (difference in gain: $m=-0.01 \pm 0.0899$; $p>0.05$).

The structure of the nystagmic movement was analyzed by calculating the distribution of several parameters from the pooled data of the 5 subjects. No differences that were correlated with the direction of the target movement or the viewing eye were found in the distributions of the beat interval or the slow phase amplitude. The histograms of the gaze position at the start of a slow phase were displaced with respect to the midposition in a direction opposite to the movement of the stimulus (Fig 3.3). Thus the slow phases tended to start in the headcentric half field which the target was leaving. The shift was about equal for both directions of the stimulus movement and there was no directional asymmetry in the beat pattern. Velocity did not affect these histograms systematically but, when the pattern was pursued, the slow phases tended to start at more eccentric eye positions than when the spot was pursued.

Fig. 3.3. Histograms of the gaze position at the beginning of the slow phase at two target velocities (23 deg/sec and 57 deg/sec). Data are pooled over subjects and viewing eyes. Each plot contains two histograms; the upper for target movement to the right (R) the lower for target movement to the left (L). The direction of the target movement is indicated by a white arrow in each histogram. A white vertical line marks the straight ahead position in each histogram. The upper two panels show the gaze distributions when the spot was tracked in the free range condition on a featureless background. The lower two panels show the gaze distributions when a stripe in the pattern was pursued.

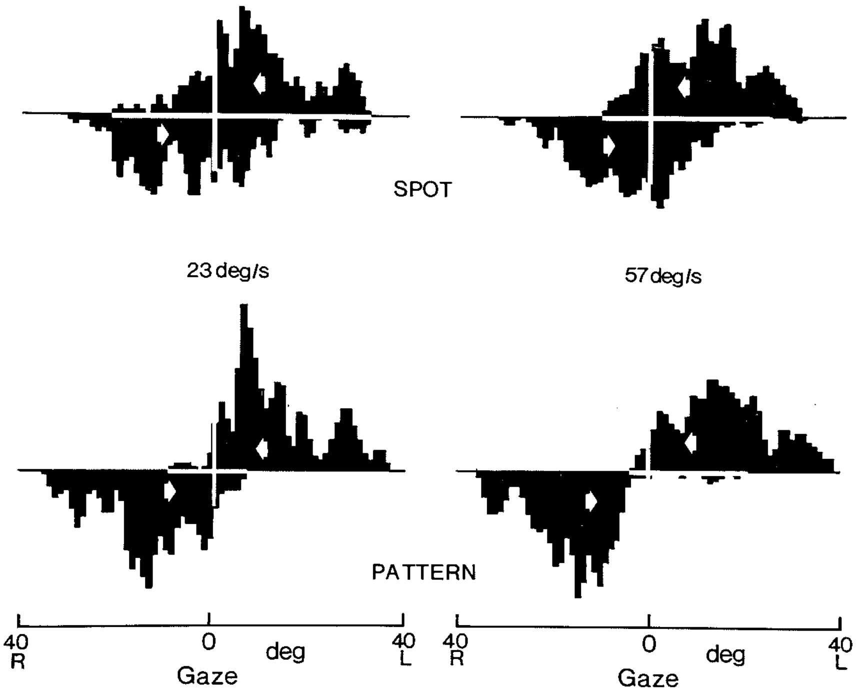
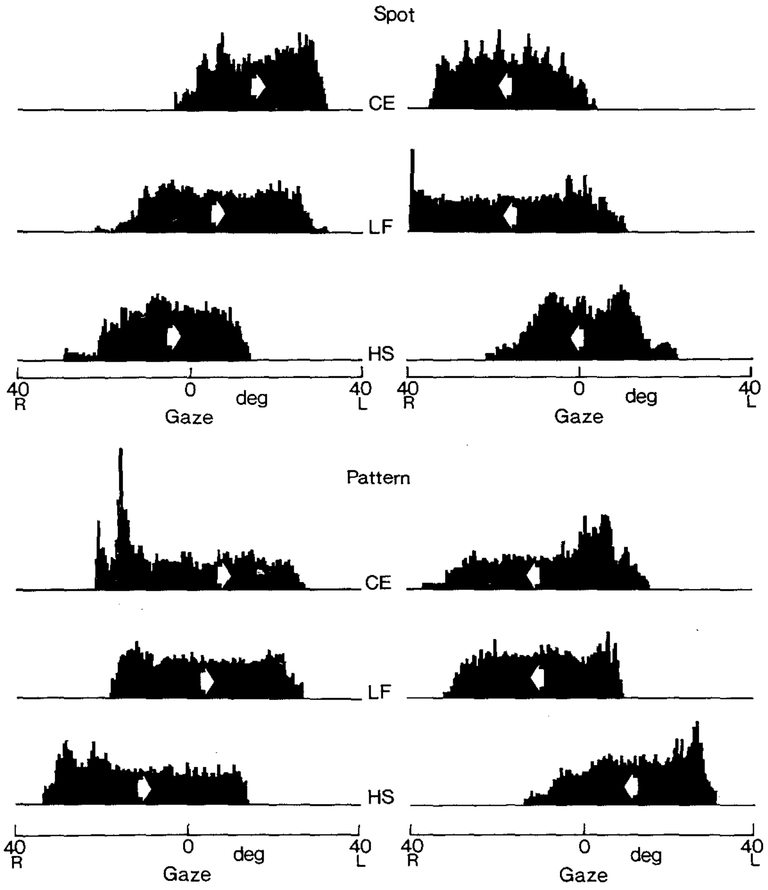


Fig. 3.4. Distributions of gaze position during pursuit of the spot in the free range condition (upper 6 histograms) or the stripe pattern (lower 6 histograms) of 3 subjects (CE, LF, HS). The white arrow indicates the direction of the target movement. Target velocity is 23 deg/sec.



It can not be concluded, though, that the target was generally pursued up to the midposition. All gaze position histograms were flat and the 30 to 60 deg wide distributions included gaze positions on both sides of the midposition. The gaze position histograms of the subjects largely overlapped, although for some subjects the mean gaze position could be shifted into the direction of the stimulus movement (subjects CE and LF, Fig 3.4) and for others in the opposite direction (subject HS, Fig 3.4).

Mean gaze position was never shifted from the straight ahead position by more than 20 deg. Neither target velocity nor target type had a consistent effect on the mean gaze position. Some subjects tended to shift the mean gaze position in the direction of the stimulus movement at higher velocities for pursuit of the spot but not for pursuit of the pattern. Other subjects tended to shift mean gaze in the direction opposite to the movement of the spot for higher target velocities or a clear tendency was absent.

The effect of the target extent on pursuit

In view of the absence of asymmetries in the gain, the beat interval or the slow phase amplitude histograms the data were pooled over both eyes and both directions. Mean and SD of the gain are depicted as a function of stimulus velocity in Fig 3.5. Gain was always lower than unity and decreased progressively with increasing stimulus velocity.

At all velocities the mean pursuit gain of the spot increased when the striped background moving at the same velocity was also visible. The effect was consistently present at all stimulus velocities and for all subjects. Table 3.1 presents the individual gain pooled over viewing eye and the direction of target motion at two target velocities. The difference in mean gain was largest at the highest target velocities: 0.25 at 57 deg/sec and even 0.34 at 90 deg/sec. The perception of the spot correlated well with the effect of the striped background on the gain.

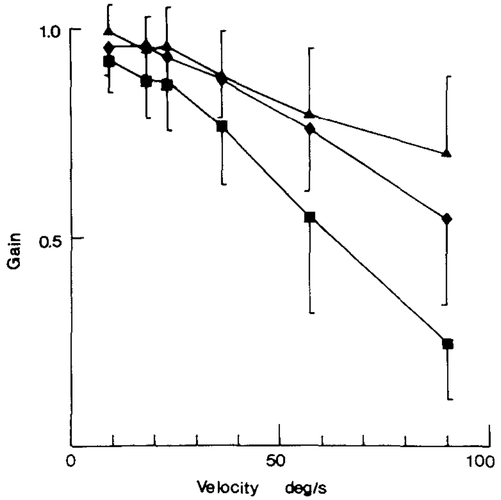


Fig. 3.5. Smooth pursuit gain as a function of the target velocity during pursuit of a 10 min arc spot alone (squares), the stripe pattern alone (triangles) or the spot in combination with the stripe pattern (diamonds). Mean and 1 SD of 5 subjects.

At the two highest velocities pursuit of the spot alone was very difficult for most subjects and this target was seen only intermittently as a spot; otherwise it was seen as a red blurred line. The spot was seen much better at these velocities if the stripe pattern moved in conjunction with the spot.

Remarkably, the pattern alone was pursued even better than the spot superimposed on the pattern. The effect was consistently present for all subjects at the highest three target velocities but not at the other target velocities (Table 3.1). When all the data were pooled a small but significant difference in pursuit gain was found between the pattern and the spot superimposed on the pattern. ($m=0.0481 \pm 0.0919$; $p<0.001$). This result was surprising since the spot moved at the same velocity as the stripe pattern and merely added a small detail to the otherwise unaltered pattern. We wondered whether this difference could be due to an adverse effect of the free range technique. Perhaps the gain was reduced because a stationary spot was seen on the fovea during the return saccades. To test this possibility, we investigated whether the gain would improve when the laserspot was made invisible during the return saccade. The laserbeam could be interrupted during a saccade by a fast

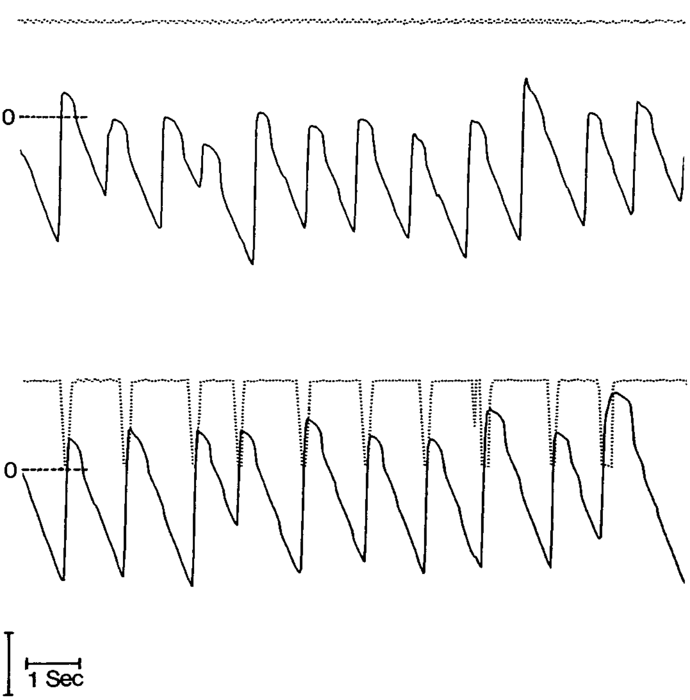


Fig. 3.6. Smooth pursuit of the spot moving at 23 deg/sec to the right in the free range condition. The laser beam was interrupted during a return saccade (lower panel) or the spot was continuously visible (upper panel). The dotted line indicates the output of the light detector; during an interrupt the output of the detector is low (0 Volt).

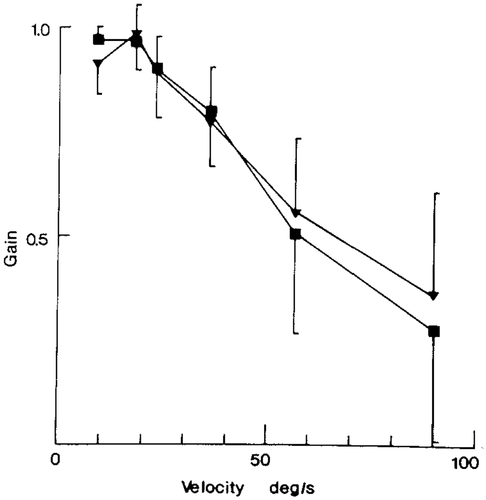


Fig. 3.7. Smooth pursuit gain during tracking of the spot in the free range condition to the right. During the return saccade the spot was masked (squares) or visible (triangles). Mean and 1 SD of 5 subjects.

Table 3.1. Individual data of the smooth pursuit gain during pursuit of the spot (s), the spot superimposed on the pattern (sp) and the pattern (p) at two target velocities (18 deg/sec, 57 deg/sec). Mean and one s.d. of the gain pooled over direction of stimulus movement and viewing eye are presented.

	18 DEG/SEC			57 DEG/SEC		
SUBJECT	S	P	SP	S	P	SP
AB	0.91 ±0.02	0.97 ±0.07	0.98 ±0.04	0.31 ±0.21	0.81 ±0.09	0.67 ±0.13
CE	0.78 ±0.04	0.90 ±0.08	0.93 ±0.04	0.32 ±0.18	0.62 ±0.08	0.57 ±0.11
HC	0.93 ±0.03	0.99 ±0.02	0.95 ±0.03	0.62 ±0.09	0.89 ±0.03	0.75 ±0.05
HS	0.97 ±0.02	0.98 ±0.04	0.99 ±0.01	0.73 ±0.07	0.90 ±0.03	0.89 ±0.02
LF	0.91 ±0.07	0.99 ±0.05	0.96 ±0.06	0.73 ±0.11	0.92 ±0.04	0.87 ±0.03

electro-magnetic shutter. The shutter was driven by the same logic circuitry that was used to stabilize the spot. A semi-transparent mirror behind the shutter deflected part of the laser beam onto a light detector which signalled the interruption of the laserbeam.

Fig 3.6 shows two registrations of the eye movements with the laser beam either interrupted or continuously visible. The upper trace shows the output of the light detector. Pursuit did not improve when the laser beam was interrupted during the stabilization. Fig 3.7 plots the mean and SD of smooth pursuit gain with or without target interruption as a function of the velocity of the spot which moved to the right. The gain did not change significantly by interruption of the laserbeam ($m=-0.009 \pm 0.078$; $p>0.2$).

The beat interval and slow phase amplitude histograms are shown in Figs 3.8 and 3.9 for the three targets at three velocities. Each plot contains two histograms that refer to the same stimulus conditions except the target type.

Fig. 3.8. Histograms of the interval between two successive return saccades at three target velocities (23,57,90 deg/sec). Data were pooled over subjects, directions of the target movement, and viewing eyes. Histograms are plotted in pairs to show the effect of the target on the structure of the nystagmic movements. Left side: interval histograms during pursuit of the spot on a dark background (upper) or in combination with the moving stripe pattern (lower). Right side: interval histograms during pursuit of the spot in combination with the pattern (upper) compared to the pursuit of the pattern alone (lower). The scale of the ordinate is identical for all panels.

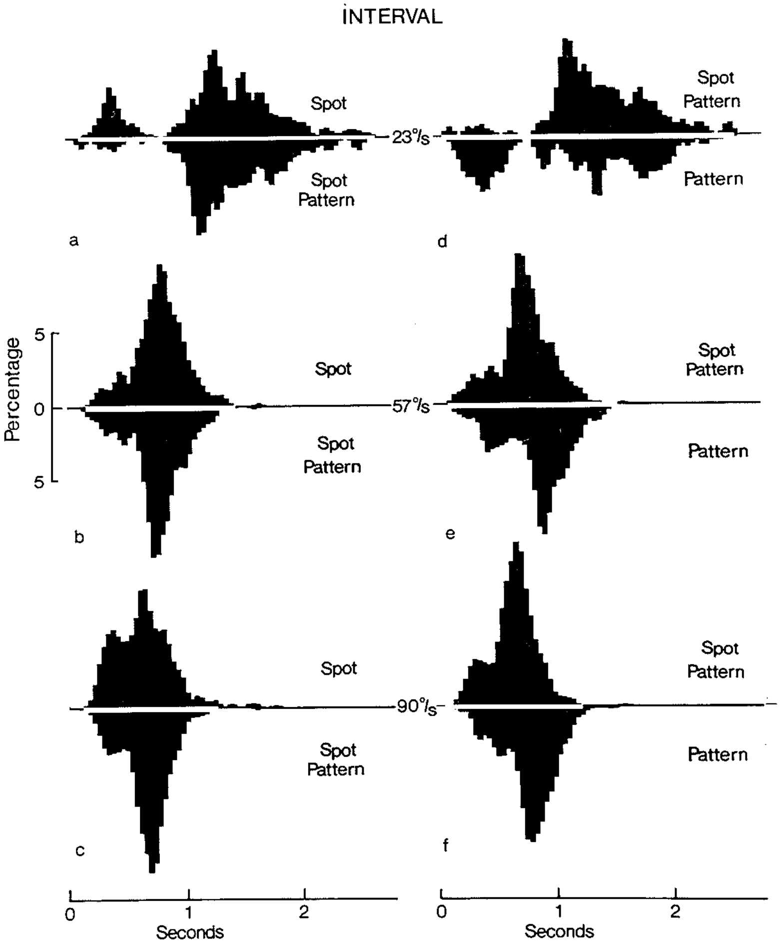
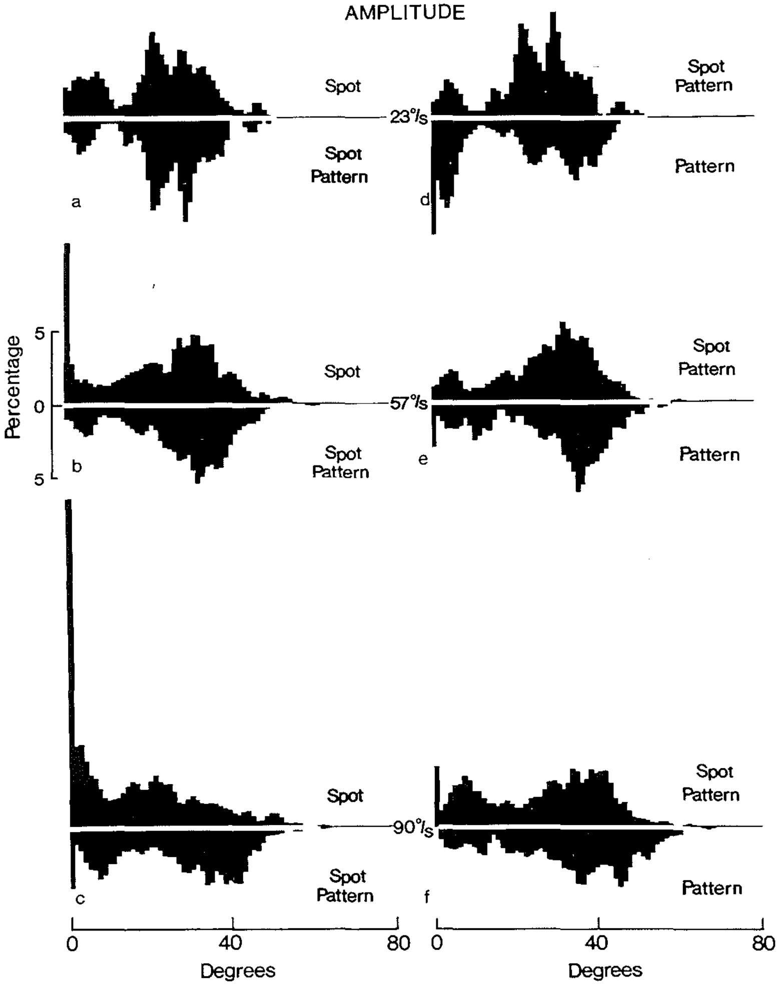


Fig. 3.9. Histograms of the amplitude of the slow phase of pursuit at stimulus velocities of 23 deg/sec, 57 deg/sec or 90 deg/sec. Data were pooled and plotted as described in the legend of Fig. 3.8.



In the first set of plots the histograms of the beat pattern are compared for the spot and the spot on the pattern (Fig 3.8 a-c and Fig 3.9 a-c). In the second set of plots the distributions are compared when the subjects tracked the spot on the pattern or a stripe (Fig 3.8 d-f and Fig 3.9 d-f).

The interval distributions were multimodal. There was a frequent occurrence of beats that lasted about 400 msec. At 23 deg/sec this peak in the histogram was separated from the peaks that relate to intervals of longer duration but it merged with the rest of the histogram at higher velocities. When the velocity increased, the intervals became shorter and their duration was less dispersed. At 23 deg/sec the most frequent beats lasted 1.2-1.4 seconds; the duration declined to about 0.6-0.8 seconds at 90 deg/sec. The peaks of the interval histograms tended to sharpen at the higher stimulus velocities. In part this reflected the higher degree of certainty which could be obtained if more data were available. Because eye position records of fixed length were obtained less intervals were available for analysis at lower target velocities. For another part the distributions became narrower because the upper limit of the duration of a beat decreased. The majority of the beats were of an amplitude between 20 and 40 degrees. The amplitude never exceeded 70 degrees. The histograms hardly changed by the addition of the moving pattern when the spot was pursued (see Fig 3.8 a-c and Fig 3.9 a-c). Neither the width nor the position of the individual peaks changed consistently. However, the pursuit of a stripe rather than the spot on the pattern resulted in some consistent differences (Fig 3.8 d-f and Fig 3.9 d-f). This did not apply to the the 400 msec peak in the interval distributions which was virtually always present. At 23 deg/sec the most frequent beats lasted 1.2 sec when the spot on the pattern was pursued. During pursuit of a stripe the most frequent beats lasted 1.4 sec. Similarly,when a stripe was tracked at 57 or 90 deg/sec, the duration of the most frequent beats was longer by about 0.2 sec than when the spot superimposed on the pattern was tracked. Also, the slow phases tended to be somewhat larger in amplitude when a stripe rather than the spot formed the detail of the pattern which was pursued. In the latter condition the peaks in the amplitude histograms were shifted to about 3 deg lower values.

Apparently, the spot was pursued with a similar beat pattern whether a striped pattern moved in conjunction or not. The gain of the smooth component, however, increased at all target velocities by the addition of the moving pattern. When an arbitrary stripe was tracked, rather than the spot superimposed on the pattern, the beats lasted longer and tended to be larger and a significant increase of the smooth pursuit gain occurred.

DISCUSSION

Effect of the free range condition on the pursuit of a small target

Pursuit of a single point target moving in a fixed sawtooth trajectory imposes a fixed spatial range as well as a fixed temporal rhythm upon the subject. The free range condition relaxed both of these restrictions. Although our data do not allow us to determine the relative importance of these two factors definitely, they suggest that the freedom to program saccades at any time was more important than the freedom to program them between any eye positions desired. In the first place, when the range of the spot trajectory was determined by the subject, the return saccades of most subjects carried the eye only a few degrees across the midposition. The spot was subsequently tracked towards 20 to 40 degrees eccentricity. Thus, during free range pursuit, the eye tracked the spot in the same part of the head centric field as when the spot followed the (fixed range) 40 degrees amplitude sawtooth trajectory. Yet, the mean pursuit gain was improved by 0.06 to 0.12 in the free range condition. Secondly, if the smooth pursuit gain would be affected by e.g. elastic forces opposing the pursuit movement of the eye towards more eccentric positions it would be expected that pursuit would improve if the amplitude of the (fixed range) sawtooth was decreased. We found quite the opposite trend. Reduction of the amplitude of the sawtooth from 40 to 27 degrees lowered the smooth pursuit gain by another 0.05 to 0.10. Probably, the use of the free range technique improved smooth pursuit primarily because it allowed the subject to program return saccades any time rather than in a rhythm imposed by the spot.

Collewijn and Tamminga (1984) investigated smooth pursuit of a spot using triangular wave stimuli with an amplitude of 10 degrees. Target velocity ranged from 1.7 deg/sec to 20.8 deg/sec. The smooth component of pursuit was isolated and mean speed of the eye movement during 32 sec of pursuit was computed, with exclusion from the analysis of the periods of reversal of the target movement. Smooth pursuit gain was found to decrease from 0.92 at 6.6 deg/sec to 0.73 at 20.8 deg/sec (their Fig 7b). This decline of the gain is larger than in any of the conditions we investigated (see Fig 3.2). However, this result fits well in the trend, observed in our data, that at smaller amplitudes of the target movement a faster decline of the gain occurs with increasing target velocity.

At the highest target velocities (57 or 90 deg/sec), the slip velocity of the spot was often tens of deg/sec during the slow phase. The mean eye velocity pooled over our 5 subjects was at most 36 deg/sec. The performance of individuals, however, as determined by the highest mean eye velocity during a measurement, ranged from 26 deg/sec for our worst pursuing subject up to 51 deg/sec for our best subject. All subjects showed considerable variation in the eye velocity during a measurement. Maximum eye velocity could exceed 70 deg/sec during a single slow phase. Recently, Meyer et al. (1985) reported maximum smooth eye velocities of ca. 100 deg/sec. The target started at an eccentric position of 45 degrees and moved over 90 degrees with a velocity unknown to the subject. The start of the movement was indicated by a buzzer but the interval between trials was randomized. Although our subjects were free to use an 80 degree range for pursuit, symmetrical with respect to the center position, most of their beats were smaller than 40 degrees and their pursuit range was never larger than 70 degrees. Collewijn et al.(1985) found maximum smooth pursuit velocities far in excess of 100 deg/sec when the subject pursued a target. These high velocities critically depended on the prior knowledge of the subject concerning the shape of the trajectory and the start of the target movement. When the target was moved by the subject, smooth eye velocities up to 200 deg/sec occurred. On the other hand, when the target was moved by the experimenter, smooth eye velocity was no larger than about 75 deg/sec. Apparently, the performance of the smooth pursuit system may be even better than we found when it operates in a 'single shot' mode using the full power of predictive tracking or the full range over which the eye is able to move to pursue a small target.

Directional asymmetries

There was no preference regarding the direction (rightward vs. leftward) of the target movement. This confirms data of Collewijn and Tamminga (1984) who found no right-left asymmetries when a spot, moving along a triangular trajectory, was pursued. The present investigation extends this observation to the full-field target. Also, in the retinal reference frame (nasalward vs. temporalward target movement) directional preferences were not found, either for the different targets considered separately, or for all the data pooled. This result is in contrast to the finding of Van Die and Collewijn (1982),who -with the same equipment- found a small preference for temporal to nasal movement. However, their subjects were instructed to watch the stripe pattern without following a particular detail. Thus, the instruction was aimed at eliciting the 'stare' type of optokinetic nystagmus. It is well known that directional preferences are enhanced if foveal function is lowered. This has been described e.g. in patients with achromatopsia (Baloh et al., 1980) and amblyopes (Schor and Levi, 1980). Our finding that directional preferences are absent when the subject actively pursues the target probably reflects the other end of this trend. The stronger cortical guidance of the eye movements during pursuit increases the invariance of the smooth eye movements with respect to the direction of the stimulus movement.

The effect of the extent of the stimulus on pursuit

We found that compared to the smooth pursuit of a small spot on a dark background, a striped pattern moving at the same velocity as the spot improved smooth pursuit at all velocities. However, the nystagmic pattern was not altered with respect to the interval distribution. The amplitude histograms of the slow phase differed only at the highest target velocity where the pursuit of the spot on a dark background was disrupted during large parts of the records. Apparently, the stochastic structure of the nystagmic pattern was identical whether the spot was pursued on a dark surface or on a stripe pattern moving at the same velocity as the spot.

Assuming that 'stare' OKN contributes to the pursuit response, it could be suggested that the smooth pursuit gain of the spot superimposed on the full field pattern is larger than the gain of pursuit of the spot alone because a large stimulus is more effective in generating 'stare' OKN (cf. Van Die and Collewijn, 1982 ; Dubois and Collewijn, 1979). We believe this is unlikely. It is well known that whenever there is relative movement between a target which is attended to and a background, the influence of the background on the eye movement is small or absent. This applies to moving targets and stationary backgrounds as well as the reverse conditions of movement of the background and the target (Collewijn and Tamminga, 1984; Murpy et al., 1975; Kowler et al., 1984). Even when a fixation target is stabilized on the fovea the eye movement induced by a moving background is small (Collewijn and Tamminga, 1986; Wyatt and Pola 1984) and usually amounts to a small fraction of the 'stare' OKN evoked by the same background when no target is visible (Wyatt and Pola, 1984). Apparently, OKN is suppressed during pursuit or fixation of a target. Also, retinal slip or position error of the target does not seem essential for the suppression (Wyatt and Pola, 1984) and the mere intention to attend to the target whenever it is visible may have caused the suppression. It is not clear to what extent the absence of relative motion between the target and the background in our experiments has influenced the suppression of OKN, but we believe that our instruction to exclusively attend to the spot whenever it was visible has evoked a similar suppression of OKN. We feel that this view is supported by the fact that intersaccadic intervals of ca. 400 msec duration - a typical duration of the intervals between fast phases of 'stare' OKN (Cheng and Outerbridge, 1974) - did not occur more frequently when the spot moved in conjunction with the striped pattern than when the spot moved on the dark background. Such a result is not suggestive of a larger contribution of the OKN during the pursuit of a spot when a stripe pattern moves in conjunction.

Our results are in agreement with the data of Collewijn and Tamminga (1984) in the sense that a background influences smooth pursuit. A full-field background moving in conjunction with the spot improved the smooth pursuit. Despite the instruction to attend to the spot exclusively, some velocity information of the background seemed to exert control over the smooth pursuit system. This suggests that optimal target selection may require a minimum size of the target. Our 10 min arc spot - like the target used by Collewijn and Tamminga (1984) - would seem to be below this limit. As a consequence the background inhibited or improved the smooth pursuit depending on the relative velocity between target and background. There may be several reasons why the movement of a small spot may not be entirely seperated from the background movement to drive the pursuit system. The 10 min arc spot may have been smaller than the size of the receptive fields of velocity detectors. Nakayama (1985) suggested in central vision an elongated receptive field for motion detectors with a major axis of about 15 min arc perpendicular to the direction of highest sensitivity for motion. Hence, such velocity detectors would integrate motion over a larger area than the size of the spot and background motion would in part determine the output of the detector. Furthermore, the retinal slip of the target implies that the spot may stimulate several velocity detectors successively during pursuit. A perfect selection of the target velocity information might require 'switching circuitry' with temporal properties the visual system may not be able to meet. Finally, a small spot possibly does not allow the subject to exclusively attend to the target because the advantage of a better pursuit is traded off against the disadvantage of a reduced capability to make visual judgements of the background (cf. Murphy 1978).

We found that smooth pursuit improved significantly when an arbitrary feature of the striped pattern in stead of the spot, superimposed on the pattern, was pursued. This result was surprising, because the spot merely added a small detail to the otherwise unaltered pattern. Hence, the target extent could not account for the difference. Also, the difference was not caused by a detrimental effect of the image stabilization during the return saccade when the spot was pursued. In view of the physical equivalence of the stimuli, an explanation in terms of a difference in mental set or a different pursuit strategy seems more appropriate. Perhaps, during pursuit of a stripe the selection mechanism is relaxed because of the repetative nature of the pattern, causing a larger drive to the pursuit system by attention to a larger part of the stimulus than when the spot is pursued. Moreover, assuming that redirection of the attention to another detail in the stripe pattern is determined by the retinal eccentricity of the current target, a shift of the attention to another stripe may be necessary less frequently than the resetting of the spot on the fovea by a return saccade, because a stripe is pursued with a higher gain. This would result in a tendency of the slow phases to be of longer duration and larger amplitude for the pursuit of a stripe than for the pursuit of the spot on the pattern, as we indeed observed. An alternative explanation could be that during pursuit of a grating attention may shift gradually from one stripe to the next. This would allow the subject to pay attention to that part of the pattern that happens to stimulate the fovea or the near periphery whereas during the pursuit of the spot on the pattern, attention had to be directed to an extra foveal location, because the eye movement was always slower than the target movement. Hence, in this explanation the dissociation of the 'attentional fovea' (Collewijn et al., 1982) and the anatomical fovea would have caused the decrease of smooth pursuit of the stripe pattern when the spot was pursued exclusively. In conclusion, we believe that smooth pursuit of a stripe pattern is improved in comparison to to the pursuit of a spot for three reasons: the larger extent of the stimulus which provides more moving contours to drive the pursuit system, the relaxed temporal restrictions with respect to the pursuit movement and the use of a pursuit strategy in which the target is chosen more globally.

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CHAPTER IV: PURSUIT OR FIXATION OF A TARGET ON BACKGROUNDS WITH CENTRAL OR PERIPHERAL OCCLUSIONS

INTRODUCTION

A large stationary structured background has been shown to inhibit the horizontal smooth pursuit of a small target by about 10% (Collewijn and Tamminga 1984). Similarly, retinal stability of the target image is decreased only slightly by the movement of either small (Murphy et al., 1975; Mack et al., 1979) or large (Collewijn and Tamminga, 1986; Kowler et al., 1984) structured backgrounds. On the other hand, the motion of a large stimulus with respect to the observer induces optokinetic nystagmus (OKN) when a subject stares at the display, and no stationary fixation target is available. The small influence of the relative motion between the target and the background on pursuit or fixation of a target suggests that OKN has been suppressed to a large extent by an as yet ill-understood mechanism.

It has been proposed that the influence of a background is reduced by the preferential weighting of contributions by the target to the integrated retinal position or velocity error. Collewijn and Tamminga (1986) found that, when a subject fixated a spot which was stabilized on the fovea, the eye movements induced by a large random dot background were not larger than 25% of the background movement and lagged the background motion by no more than 90 degrees in phase. Pola and Wyatt (1980) using a similar paradigm, reported the induction of slow eye movements lagging the sinusoidally moving background by about 180 degrees. Hence, despite the absence of contributions by the target to the retinal error or slip velocity (because the target was stabilized), the eye movements induced by the background were small. This may not be a surprising outcome in the study of Pola and Wyatt, who used a background consisting of two thin horizontal bars, 10 deg above and below the target. Such a pattern is hardly an effective stimulus for evoking OKN. This argument does not apply to the study of Collewijn and Tamminga (1986) and an explanation of the small size of the induced eye movements is lacking. The results of Pola and Wyatt suggested to us the possibility that central and peripheral parts of the background may influence the fixation of a stabilized spot differently. We wondered whether background motion in the central part of the retina might cause the eye to move nearly in phase with the background whereas background motion in the more distant periphery would induce eye movements opposite to the background movement, i.e. with about 180 deg phase lag for oscillating backgrounds, as found by Pola and Wyatt (1980). Spatial integration of such antagonistic inputs might largely cancel the influence of retinal slip caused by a large background on the eye movement.

For this hypothetical antagonistic action to occur, fixation or pursuit of a visible target would be crucial. The facilitatory effect on pursuit of a background, moving at the same speed and in the same direction as a point target, is reduced when the subject attends to the point target solely instead of to the entire moving background (chapter III). This observation correlates well with a hypothesis as outlined above. Without the attempted fixation of such a target, 'stare' OKN will dominate the response to the moving background. The roles of the central and peripheral retina in the generation of 'stare' OKN have been described before (Cheng and Outerbridge, 1975; Dubois and Collewijn, 1979; Van Die and Collewijn, 1982; Howard and Ohmi 1984). These studies agree in their conclusions that, while the dominant contribution comes from the central retina, central and peripheral parts of the retina are synergistic in inducing reflexive following movements.

To test the hypothetical antagonistic effect of central and peripheral motion stimuli under conditions of selective fixation or pursuit, we investigated the eye movements induced by a moving background during fixation of a small stabilized target and during pursuit of the same point-target on a stationary background. Central or peripheral parts of the background were masked.

GENERAL METHODS

The phase of the voltage induced in a scleral coil by a rotating, horizontal magnetic field was measured as described by Collewijn (1977). This phase is linearly related to the horizontal angle of rotation over a range of 360 deg. For the present purpose, we used a 40 deg range. Noise level was below 4 min arc and the dynamic range was 80 Hz.

The subject was seated in front of a hemispherical projection screen as decribed in chapter II. The head was stabilized by a bite bar adjusted to position the right eye at the center of the hemisphere. The left eye was patched. Stimuli consisted of a point-target and a random-dot pattern with square elements of a uniform size (2 x 2 deg). The target was a small (diameter: 7 minarc) laser spot, reflected onto the screen in front of the observer by a servo-controlled mirror (General Scanning; bandwidth better than 200 Hz). The spot could be displaced over at least 50 deg to either side with respect to the midposition. The random dot pattern was projected onto the screen with the technique described in chapter II. On top of the pattern-disk a second disk could be mounted and rotated independently. This transparant disk carried black masks, which occluded central or peripheral parts of the pattern.

Data acquisition was under control of a PDP 11/10 mini computer. Signals representing target position, background position and gaze were filtered, to prevent aliasing (cut off frequency: 67.5 Hz), digitized (sample rate: 125 Hz) and stored on disk-memory for off-line analysis. Each measurement lasted 16 sec.

To confirm the accuracy of the gain and offset settings of the eye movement monitor, 2-4 calibration measurements were done during each recording session. In these trials the subject fixated the (non-stabilized) target, positioned straight ahead or 10 deg to either side of the midposition. The sensitivity differed by no more than 2% from the intended value of 500 mV/deg and offset was below 0.3 deg. A computer program was used to remove saccades from the eye position recordings and to synthesize a cumulative smooth eye position signal.

The gain of the eye movements was computed as the ratio between the cumulative smooth eye velocity (mean of the entire 16 sec recording period) and the background velocity or the target velocity. Details concerning the data acquisition and data analysis can be found in Collewijn and Tamminga (1984).

EXPERIMENT 1:
Fixation of a stabilized target on a unidirectionally moving background

Methods

The mirror position was controlled by the horizontal eye position signal to achieve target stabilization. Before each session the stabilization was carefully adjusted. The subject was instructed to fixate calibration marks straight ahead and 10 deg to either side of the midposition successively; the stabilized target was also visible. Offset and gain of the stabilization circuitry were adjusted until the subject reported that the target and the fixation marks coincided at all calibration positions. In some long sessions (lasting about 45 min) the adjustment procedure was repeated about halfway the session. The setting of the gain was never altered but occasionally the offset had to be adjusted by about 0.1 deg to compensate for a tendency of the subject to drift in one direction.

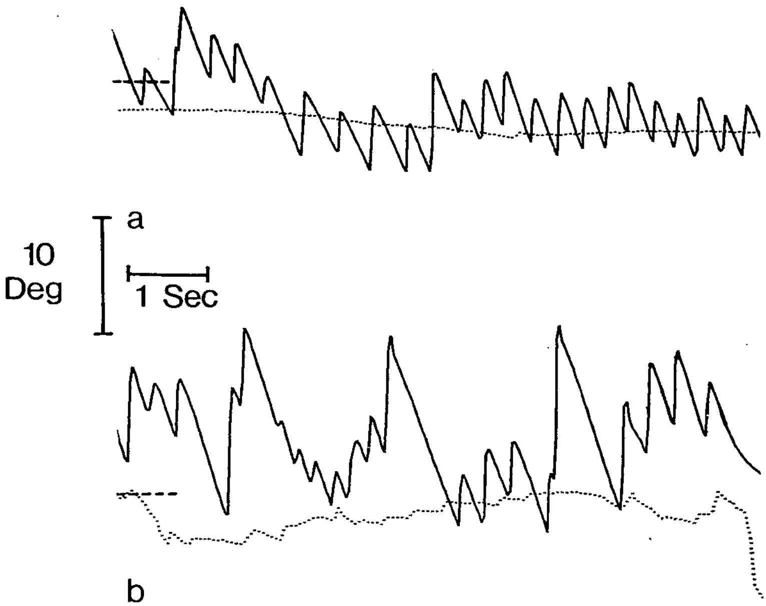
The eye position signal was also used to control the mask position, in order to stabilize the image of the mask on the retina. The masks used in this experiment were a 15 deg diameter circle occluding the central part of the pattern, concentric with the fixation target, or the complement of this mask. Hence, either a circular area of the pattern around the fovea was masked (central mask) or the pattern was occluded completely, except for this same central circular area (peripheral mask).

The pattern moved at 9, 23 or 57 deg/sec in either horizontal direction. The whole pattern was visible, or one of the masks occluded it partially. The fixation spot was either visible or absent (the laser beam could be interrupted by a shutter). The 12 stimulus conditions (3 velocities, 2 directions, 2 fixation conditions) were presented in a pseudo-random order. For practical reasons, the masks were changed in a fixed order: no mask, central mask and peripheral mask successively. Each session consisted of 4 calibration measurements and 36 different fixation trials.

Twelve subjects without visual defects other than refractive anomalies participated (1 hypermetrope, 6 myopes, 5 emmetropes with 20/20 Snellen acuity). None wore their corrective spectacles because we did not want to compromise the extent of the visual field. All subjects could easily distinguish the laser spot from the pattern elements. We found no differences between subjects correlating with their refractive anomaly.

The instruction to the subjects varied with the visual stimulus. When the laser spot was not visible, the subject was instructed to fixate an imagined stationary point, located straight ahead at the same distance as the pattern. When a mask was used the subject was told to imagine the fixation point at the center of the mask. Using these instructions reflexive eye movements were induced by the moving background. These data provided a 'baseline' from which the effect of a visible target on OKN could be estimated, when different parts of this background were masked. When the stabilized spot was visible, subjects should fixate the target exclusively and not attend to the background. Whenever the target was seen to move, it should be tracked. No explicit information was given about the target motion to be expected.

Fig. 4.1. Monocular OKN of the right eye evoked by the whole background. The subject attended to an imagined stationary target (continuous line) or fixated a real, retinally stabilized target (dotted line). The horizontal broken line marks the straight ahead gaze position. During fixation of the stationary target, OKN of subject HN (upper graph) was virtually completely absent whereas for subject JA (lower graph) OKN was suppressed by ca 90%. Background movement was to the right (23 deg/sec).



When the moving background was shown only in a circular area around the fovea and subjects fixated an imagined target, OKN with a lower gain than during full-field stimulation was evoked. The mean gain of the smooth component decreased from 0.30 at 9 deg/sec to 0.04 at 57 deg/sec (Fig 4.3). When the stabilized laser spot was fixated, in combination with this central stimulus, the induced eye movements decreased further and mean gain was below 0.05 at all velocities.

When the central part of the background was masked, induced eye movements were variable, with fixation of either the imagined target or the laser spot. In about 90% of the measurements slow, smooth eye movements with a gain below 0.15 were induced when the target was imagined. The majority of these eye movements was in the direction of the background movement. However, all subjects occasionally made eye movements opposite to the background movement.

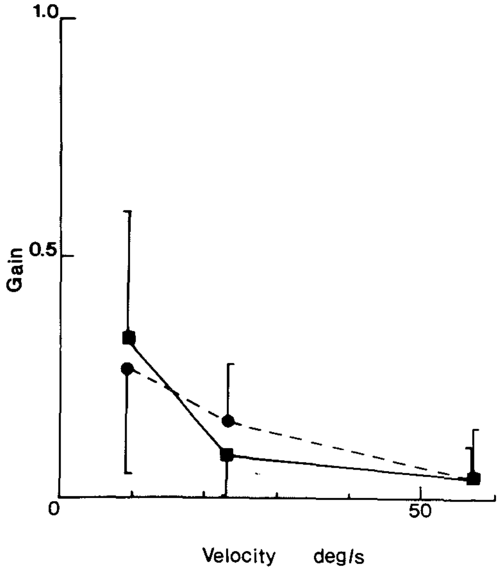


Fig. 4.3. Mean and 1 SD of the velocity gain of monocular OKN of the right eye evoked by the central part of the background. The fixation target was imagined. Background movement to the left is marked by the continuous line and leftward bars. Background movement to the right is indicated by the broken line and rightward SD bars.

Results

In all subjects, OKN was evoked by the whole background viewed in the absence a fixation target (Fig 4.1). Mean and SD of the gain of the smooth component of the OKN are plotted in Fig 4.2. There was a large variation of the smooth eye velocity among our subjects, as reflected in the large standard deviations of the mean gain. Gain decreased when target velocity increased. With a real, stabilized target, the optokinetic response to whole field stimulation was reduced to only 10-20% of the smooth eye velocity in the absence of the target. The majority of the subjects showed slow drifts in the direction of the background movement (Fig 4.1). In about 10% of the measurements, however, mean eye velocity during a measurement was in a direction opposite to that of the background. None of the subjects showed such opposite drift for both directions of the background movement. On the other hand, whenever subjects perceived the target as moving, this induced motion was opposite to the background movement.

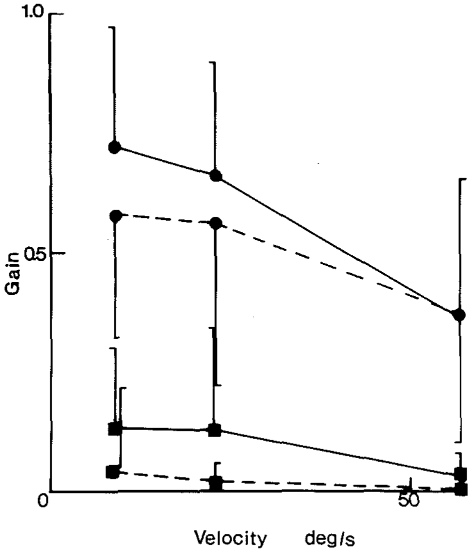


Fig. 4.2. Mean velocity gain of monocular OKN of the right eye evoked by the whole background. Subjects attended to an imagined, head-stationary fixation target (dots) or a real, stabilized fixation target was fixated (squares). Background movement was to the left (continuous lines) or to the right (broken lines). Bars indicate 1 SD.

When the stabilized laser spot, centred on the central mask, was fixated such opposite eye movements were induced more often. Six of the twelve subjects made opposite eye movements for both directions of the peripheral background movement, although not consistently at all velocities. These opposite eye movements were slow with gain below 0.10 (Fig 4.4; subjects AB, AR, CE, HC, HS, JA). The other subjects made either no eye movements at all (MR, JH, LF), showed slow pendular movements (HN) or drifted slowly in the direction of the background movement (HR, JT). Thus, when the spot was fixated and the central part of the background masked, the eye movements were dominated by idiosyncrasies. On the other hand, all subjects experienced illusory target motion opposite to the background movement.

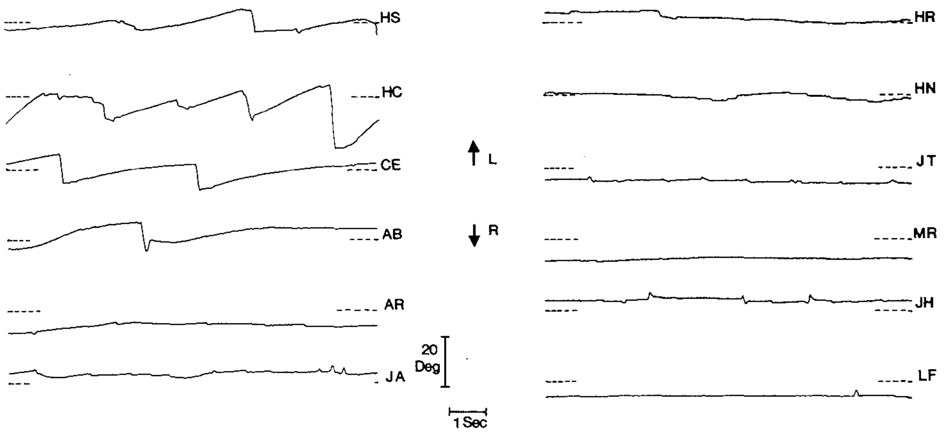


Fig. 4.4. Eye movements evoked by the background are shown for 12 subjects fixating a stabilized laser spot. The central part of the background was occluded by a stabilized, circular mask concentric with the fixation target. The background moved at 23 deg/sec to the right (=downward deflections in the graph). The broken line in each graph shows the straight ahead position.

Discussion

Masking of parts of the background lowered the gain of the induced eye movements when an imagined target at the center of the mask was fixated. Van Die and Collewijn (1982) found an OKN gain of 0.65 when a vertical stabilized occlusion masked the periphery of a stripe pattern. In contrast, we found under similar conditions a mean gain not exceeding 0.3. We attribute this difference to the different instructions employed. Our instruction directed the attention of the subject to the center of the mask. It has been reported before that attention directed to a stabilized mask rather than to the moving pattern reduces the gain of the eye movements (Dubois and Collewijn, 1979). Probably, our subjects used the borders of the mask as an eccentric fixation target. When the mask covered the central part of the background, gain was usually at its minimum. Since the borders of the complementary masks were at the same retinal location, the masks offered a similar stimulus for eccentric fixation. Hence, the slower eye movements induced when the mask covered the central part of the pattern once more confirm previous demonstrations that the central retina is dominant in the generation of reflexive eye movements (Cheng and Outerbridge, 1975; Dubois and Collewijn, 1979; Van Die and Collewijn, 1982; Howard and Ohmi, 1984).

The fixation of the foveally stabilized laser spot instead of the imagined target reduced the eye movements evoked by the whole-field background by 80 to 90%. This result is in agreement with the data of Wyatt and Pola (1984) indicating that OKN evoked by a sinusoidally moving background in most subjects is reduced in gain and increased in phase lag by a stabilized fixation target. The present data extend this observation to a full-field background moving at constant velocity. This suggests that visibility of the target is both necessary and sufficient to largely suppress OKN. Our data, however, do not provide evidence for a suppression mechanism relying on antagonistic contributions by the retinal periphery and the center to the induction of eye movements. Eye movements opposite to the background were occasionally induced with either the periphery or the center of the background occluded, albeit more often in the latter case.

These opposite movements were idiosyncratic to an extent that would not be expected from involuntary mechanisms operating at a low integrational level. Possibly, eye movements with a foveally stabilized target are prone to willful manipulation by the subject. If this would be true, it would render the foveal stabilization technique unsuitable for the investigation of the interaction between target and background motion, because effects of motion induced by the background would be confounded with smooth eye movements generated by the volition of the subject. This problem will be explored further in chapter V.

EXPERIMENT 2:

Pursuit of a point-target on a stationary background

Methods

In the second experiment we avoided stabilization of the target but instead attempted to obtain indirect evidence for antagonistic contributions by the central and the peripheral parts of the retina to the generation of pursuit of a small target. Six subjects, five of whom had participated in the first experiment, were investigated.

Subjects pursued the point target which moved to the right at velocities ranging from 9 to 90 deg/sec (9,23,36,57,90 deg/sec). The point target was stabilized foveally during saccades which returned the eye to the straight ahead position. This technique (described in chapter II) enabled the subject to determine the frequency and the amplitude of his nystagmic beats. The target was pursued on a dark field, on the full-field stationary random dot pattern or on the random dot pattern with the central part masked by a stationary horizontal black band 180 deg wide and 13 deg high. The target moved in the center of the band. The different stimulus conditions were presented in a pseudo-random order. Subjects were instructed to attend exclusively to the point target.

If the background-contours in the neighbourhood of the pursued target would inhibit pursuit whereas background features in the periphery would facilitate pursuit, the gain would be expected to be improved by the masking of the central part of the background in comparison to the gain of pursuit on the full-field stationary pattern as well as with respect to the gain of pursuit on a dark field.

Results and Discussion

Mean gain of the 6 subjects as a function of target velocity and the type of background is shown in Fig 4.5. In all subjects gain was largest when the target was pursued on the dark field irrespective of the target velocity. Gain decreased when a background was seen in the periphery, and decreased even further when the stationary background extended through the entire visual field.

This result argues against a facilitatory influence of the background motion in the periphery. Miles et al. (1986) recently reported for the monkey that the optimal stimulus for pursuit of ramp motion was not an en-bloc motion of a large pattern. The eye velocity (measured ca 120 msec after the onset of the ramp motion) was larger (by about 70%) when the motions presented in the 40 deg diameter central zone and the peripheral part of the pattern were directed oppositely. When motion was shown only in the periphery, the eye moved in the direction of the pattern motion. Miles et al. concluded that there is a dual contribution to pursuit of the motion in the periphery. Firstly, it contributes, with a small weight, to the generation of pursuit eye movements in the same direction as the pattern motion. Secondly, the motion in the periphery would enhance the gain of pursuit of a target moving in the central part of the visual field, when the motion in the peripheral retina is directed oppositely to the motion in the center ('anti-phase enhancement'). Our results do not support the hypothesis that a similar mechanism operates in humans during on-going pursuit. However, our mask covered a horizontal band of 13 deg height of the background. Thus, background details were visible at eccentricities beyond 6.5 deg. Miles et al. reported that results were variable, when a circular mask of only 10 deg diameter was used the; a clear effect on the eye velocity pointing to anti-phase enhancement was absent. Another point is, that the properties of the initial response of pursuit with respect to target background interactions may be quite different from those of on-going pursuit. For example, Keller and Kahn (1986) showed that in the monkey a stationary background reduces the initial eye acceleration of smooth pursuit of ramp motion of a point target by 40% compared to pursuit on a dark field. In contrast, the reduction of steady state velocity gain by the stationary background was only 7%, in good agreement with the slight effect of stationary backgrounds on the human smooth pursuit gain as reported by Collewijn and Tamminga (1984).

In conclusion, we found no evidence that the small effect of a stationary background on the gain during on-going pursuit of a point target may be attributed to antagonistic influences of central and peripheral retinal zones to the generation of pursuit. A stationary background reduces the smooth pursuit gain even when the background is limited to retinal locations of 6.5 deg eccentricity or more.

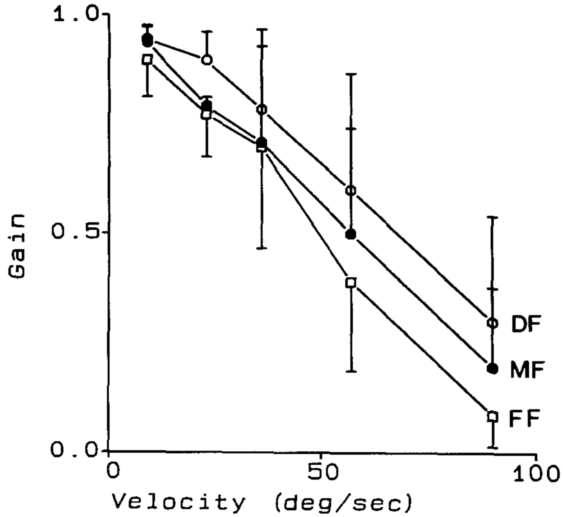


Fig. 4.5. Mean and 1 SD of the velocity gain of monocular smooth pursuit of the point target, on the dark field (DF), stationary full-field random dot background (FF) and the random dot background with the central part masked (MF).

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CHAPTER V: VOLUNTARY SMOOTH EYE MOVEMENTS WITH FOVEALLY STABILIZED TARGETS.

INTRODUCTION

Several investigators have used retinally stabilized stimuli to investigate the properties of the oculomotor system. Imposed retinal target movement with the oculomotor feedback loop opened has been used to investigate the dynamics of the oculomotor controller (Wyatt and Pola, 1983; Collewijn and Tamminga, 1986) or the effect of perceived motion on pursuit (Pola and Wyatt, 1980; Mack et al., 1982) whereas foveally stabilized, non-moving targets have been used to investigate the interaction between target and background during pursuit (Pola and Wyatt, 1985; Collewijn and Tamminga, 1986) or the role of perceived motion during fixation (Yasui and Young, 1975; Wyatt and Pola, 1979). Unfortunately, the results have often been conflicting. Wyatt and Pola (1979) e.g. have reported that open-loop pursuit of a small target was improved by a peripheral frame that moved in counterphase. They argued that illusory target motion evoked by the counterphase movement of the frame had increased perceived target motion resulting in larger pursuit movements. However, Mack et al. (1982) repeated the experiment and reported that counterphase motion of the frame inhibited open-loop smooth pursuit.

In these studies the subjects were usually not explicitly informed about the stabilized condition. In one study in which the target moved with respect to the retina it was reported that such an attempt to keep the subjects unaware about the stabilization was futile since the subjects immediately noticed that their pursuit eye movements did not reduce the retinal error or slip velocity (Collewijn and Tamminga, 1986). When subjects become aware that the target is elusive they may alter their pursuit effort and such a voluntary influence may have been responsible for the conflicting results mentioned if the subjects possess voluntary control over their eye movements with stabilized targets.

Cushman et al. (1984) investigated the ability of two subjects to imitate with a foveally stabilized target their previous tracking eye movements of triangular stimulus motion. A foveally stabilized target provides neither retinal position nor velocity error, which have been presumed to be the main visual inputs to the smooth pursuit system. Although the subjects pursued the triangular stimulus equally well and hardly differed in their estimates of the velocity of the triangular stimulus, one of the subjects could not control the frequency of his eye movements with the foveally stabilized target and the other subject imitated pursuit with a frequency which was systematically too high. These results seem to suggest that the ability of subjects to influence their open-loop pursuit eye movements may be very limited. Cushman et al. (1984) used a target which was foveally stabilized in both the horizontal and the vertical direction while the formerly mentioned studies used only horizontal stabilization. In line with these previous investigations we investigated the ability to imitate pursuit eye movements with a target stabilized in the horizontal direction only. We found that all our subjects possessed crude control over the frequency and the amplitude of their eye movements during imitation of pursuit.

In a second experiment we concentrated on the evidence obtained with stabilized targets concerning the effects of a moving background on fixation stability. The feedback loop is opened in such experiments with the anticipation that if the background motion exerts some control over the oculomotor system during fixation of the target, its effects will become more clearly manifest in the absence of visual feedback about the target position. Using such a stimulus arrangement both counterphase eye movements (Pola and Wyatt, 1980; Wyatt and Pola, 1984) as well as eye movements lagging the background by less than 90 deg have been observed (Collewijn and Tamminga, 1986; Wyatt and Pola, 1984) which have been interpreted as pursuit of apparent motion induced by the background movement and an optokinetic influence of the background, respectively. In contrast, Mack et al. (1982) found in a similar experiment that no eye movements related to the movement of the background or apparent motion of the target occurred. In all these experiments the target was stabilized horizontally only. It has been suggested that the different responses may have resulted from differences in the number of contours, the location and the size of the background (Wyatt and Pola, 1984) or the waveform of the background motion (Collewijn and Tamminga, 1986). Such explanations cannot account for the large idiosyncratic differences in the response in a single experiment as reported by Wyatt and Pola (1984). The results of our first experiment suggested that the influence of volition might partly explain the prior inconsistent results. This prompted the second experiment in which the voluntary control of subjects over the phase of their eye movements with a stabilized target on a moving background was investigated. We found that subjects fixating a foveally stabilized point target on a large sinusoidally moving background were able to make either no eye movements, eye movements nearly in phase with or eye movements nearly in counterphase with the background movement, depending on the instruction to imagine the target as head-stationary, moving in phase, or moving in counterphase with the background. Subjects were generally able to shift within a few cycles the imagined target motion from stationary to moving and made a shift in the eye movements accordingly. This suggests that with predictable background movement the volition of the subject rather than the movement of the background determines the eye movements when the subject fixates the foveally stabilized target.

METHODS

General

We used the scleral search coil technique to measure horizontal and vertical eye position in a range of 25 deg to either side of the straight ahead position. Our configuration was similar to the one described by Robinson (1963). Noise level was below 3 minarc and bandwidth d.c. to 100 Hz. Details may be found in Collewijn and Tamminga (1984).

The visual stimuli were backprojected on a tangent screen 147 cm in front of the subject by two servo controlled mirrors (General Scanning G300PD). We used a point target (diameter: 24 min arc) for pursuit and a background consisting of a 70 x 70 deg Julesz random dot pattern (pixel size: 42 x 42 min arc) with a central horizontal band (5 x 70 deg) occluded by a mask. Thus, if the target and the background were shown, the target was seen in the middle of the dark band. This band was used to dissociate the target from the background and to help the subject to not pursue the perifoveal details of the background but to exclusively attend to the target. The point target could be stabilized horizontally by driving the mirror controlling horizontal target position with the horizontal eye position signal. The background was never stabilized.

The experiments were performed in one or two sessions that lasted 20-40 min. Each session started with a calibration of the eye position monitor. Three calibration marks positioned in the straight ahead direction and 10 deg to the right and to the left of the central target were projected on the screen and the subject was instructed to fixate them in turn. If necessary, the gain of the eye position monitor was adjusted to obtain the same sensitivity as that of the mirror servo-control unit. The point target was then shown in the open-loop condition and the offset of the eye position monitor was adjusted until the subject reported that the point target could be fixated in the straight ahead direction without a tendency to drift in either horizontal direction. The subject then looked ca. 15 deg to the right and to the left and if a tendency to drift was reported the calibration procedure was repeated. Occasionally the offset of the eye position monitor was adjusted during an experiment by ca. 0.1 deg to compensate for a tendency of the subject to drift in one direction.

Procedures and Subjects

In the first experiment we investigated to what extent our subjects possessed voluntary control over the frequency of their eye movements when fixating a foveally stabilized target. Subjects pursued the moving point target (amplitude: 3.5 deg; frequency: 0.21, 0.4 and 0.7 Hz) with normal visual feedback on a dark field during 16 sec. Subsequently a switch under control of the computer used for data-acquisition shut off the sine wave and instead connected the mirror drive to the eye position signal. During the next 16 sec period, in which the point target was foveally stabilized, the subject was instructed to reproduce the previous pursuit movement. The target was stabilized in the horizontal direction only. Eye position and target position were recorded during the last 24 sec of each measurement. Thus, pursuit under conditions of normal visual feedback was recorded for 8 sec followed by the recording of the eye movement in the subsequent 16 sec period in which the point target was foveally stabilized. At all frequencies two measurements were done to obtain enough cycles for the analysis of frequency control with a stabilized target (see below). Since possible differences between the smooth eye movements during pursuit and imitation of pursuit might result from inaccurately remembered target motion we determined in 5 subjects (out of the six that had partaken in the experiment) the accuracy with which target frequency and amplitude was remembered. Subjects pursued computer driven target movement for about 30 sec. Immediately afterwards subjects adjusted the frequency and the amplitude of a function generator set at a random frequency until the subject saw the target moving similarly as when the target was driven by the computer.

In the second experiment we investigated to what extent subjects could control the frequency and the phase of their eye movements when fixating a foveally stabilized target on the moving background. During the entire 16 sec recording period the point target was foveally stabilized in the horizontal direction only. We did not attempt to stabilize the target in the vertical direction as well since a small drift in the vertical direction would carry the line of sight outside the dark band into the moving background. We used the same frequencies and amplitude for the background movement as used in the first experiment for the movement of the point target. In a further experiment the background was moved with a pseudo-random stimulus (see Table 5.1 for the spectral composition) to investigate the effect of the predictability of the background motion on the control of the subject over his eye movements with the stabilized target.

Frequency (Hz)	Amplitude (Deg)	Phase (Deg)
0.214	5.0	0
0.396	2.5	45
0.702	1.0	90

Table 5.1. Spectral composition of the pseudo-random stimulus.

To investigate phase-control, subjects were instructed to imagine the target as being dragged by the background or as moving in a direction opposite to the background movement. Of course, these instructions did not direct the attention to the target exclusively as some attention had to be directed to the background also. In half of the measurements subjects were instructed to 'hold' the target at first i.e. to imagine the target as head-stationary; after 3 sec of recording the subjects received the instruction to imagine the target as moving (either in phase with or in counterphase to the background motion). Thus, in these measurements the change of the eye movement due to the change of the instruction was recorded. In the other measurements the target was imagined as moving from the start of the background movement, and recording was started when the subject felt he had attained a steady response. Thus the subjects fixated the target on the moving background under 4 different instructions: drag, hold-drag, opposite and hold-opposite.

In both experiments the different stimuli were offered in a pseudo-random order but the different instructions in the second experiment were given in a fixed order (opposite, hold-opposite, drag, hold-drag).

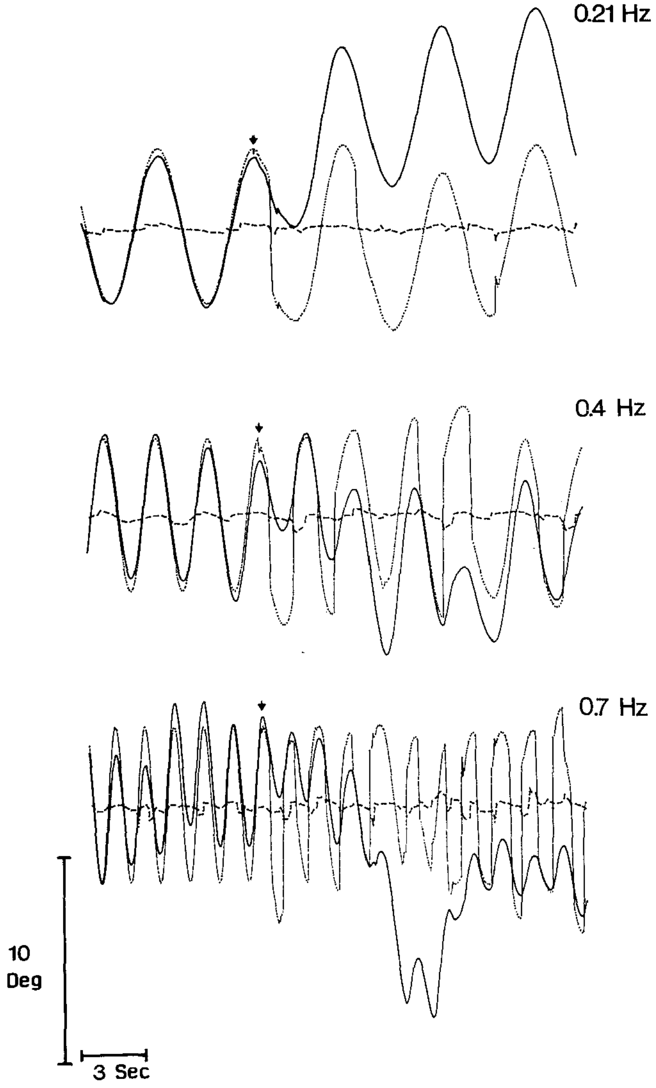
Six subjects were tested. All possessed 20/20 Snellen acuity or their refractive errors were corrected to this value by spectacles or contact lenses. Four subjects were highly experienced in oculomotor tasks; the other two had only occasionally served as a subject in oculomotor experiments. The head was stabilized by means of chin and forehead supports. We recorded the movement of the right eye. The left eye was patched.

Data analysis

Data acquisition was under control of a PDP 11/73 mini computer. Horizontal and vertical eye position, target and background position were digitized (sample frequency:125 Hz) and stored on tape for off-line analysis. Sampling causes an artefact known as aliasing which may be understood as 'backfolding' of the frequency components exceeding half the sample frequency on the low-frequency part of the spectrum of the signal. To suppress aliasing we low-pass filtered (corner frequency:62.5 Hz; roll-off: 12 dB/oct) the signals prior to sampling. As a first step in the off-line analysis, saccades were removed from the record by an algorithm that detected saccades as small as 0.5 deg based on velocity and acceleration criteria. The resulting cumulative smooth eye movement signals were used for further analysis. For the analysis of the frequency control by the subjects the smooth horizontal eye position signal was differentiated with a 5 point central difference algorithm and intervals between successive zero crossings of the eye velocity were obtained under manual control from a plot of the eye velocity signal on the screen of the terminal. Six to twenty half-cycles were averaged to obtain mean and SD of the frequency of eye oscillation during either the pursuit phase or the imitation of pursuit. The amplitude of the same half-cycles was used to estimate mean and SD of the amplitude of the smooth eye movements during pursuit and imitation.

To analyse phase control in the second experiment, a fast Fourier transform was applied to the horizontal smooth eye position signal and the background position signal after removal of bias and -if necessary- a linear trend. The spectrum of the gaze signal was smoothed by a Tukey window (Priestley, 1982). From the complex ratio of the smoothed component and the corresponding component of the background movement gain and phase were computed.

Fig. 5.1. Eye movements of subject AR during normal pursuit of the sinusoidal target movement and during the consecutive imitation of pursuit with the foveally stabilized target at 0.21 Hz (top graphs), 0.4 Hz (middle graphs) and at 0.7 Hz (lower graphs). Each panel shows graphs of cumulative smooth horizontal eye movement (continuous line), vertical eye movement (dashed line) and target movement (dotted line). At the time indicated by the arrow the target was stabilized on the fovea. Thus the target movement equals the composite (smooth + saccadic) horizontal eye movement during the period of stabilization.



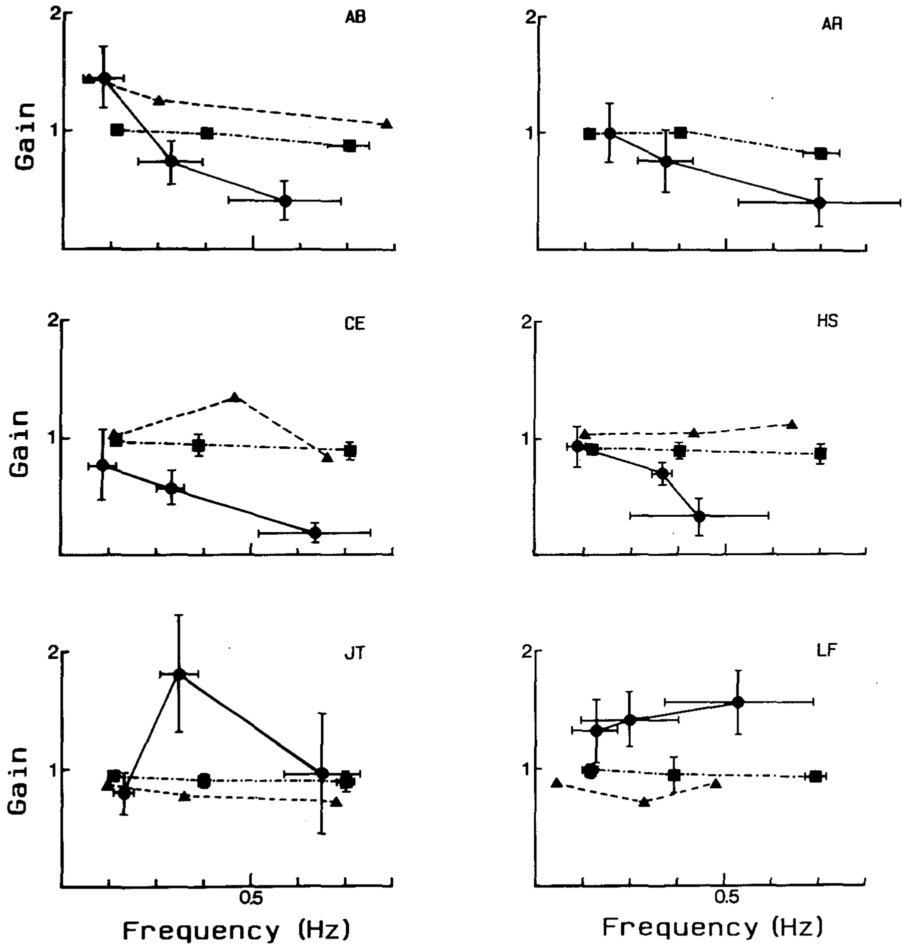
RESULTS

Imitation of pursuit with a foveally stabilized target

A qualitative impression of the smooth eye movements made by our subjects when they imitated with a foveally stabilized target their preceding pursuit eye movements may be gained from Fig 5.1. All subjects were able to make smooth oscillatory eye movements with the foveally stabilized target although the number of saccades generally increased compared to the preceding period of smooth pursuit. As described previously by Cushman et al. (1984) the smooth eye movements during the imitation differed from the pursuit eye movements. The frequency and the amplitude of the eye oscillation during imitation always differed from those during pursuit. At the lowest frequency the amplitude during imitation was often larger than the amplitude of the preceding smooth pursuit eye movements but at 0.7 Hz the amplitude during imitation was clearly reduced with respect to the amplitude during pursuit in 4 out of 6 subjects. In some subjects the imitation of the horizontal pursuit eye movements was accompanied by increased vertical eye movements although the target was not stabilized in the vertical direction. These vertical eye movements were always smaller than 10% of the horizontal eye movements.

Quantitative results concerning frequency control during imitation are offered in Fig 5.2. Mean and SD of the frequency and the amplitude (normalized with respect to the amplitude of the preceding target movement) of the eye movement during imitation and during pursuit are given for 6 subjects. Clearly, all our subjects possessed some amount of frequency control as is evident from the increase in the frequency of the eye oscillations during imitation when the preceding pursuit movement was of a higher frequency. However, this control was rather crude for most of our subjects. At 0.7 Hz the mean frequency of the imitating eye movements was consistently lower (range: 2%-35%) than during pursuit. Also, the regularity of the frequency of the eye oscillation decreased during the imitation of pursuit: the SD of the frequency (as computed

Fig. 5.2. Individual gain and frequency of the smooth eye movements during pursuit of sinusoidal target movement and imitation of pursuit with the target stabilized on the fovea. Each point indicates mean gain and mean frequency of the smooth eye movement during pursuit (squares; dot/stripe line) and imitation (circles; continuous line). Mean frequency during pursuit equals target frequency. Vertical bars indicate 1 SD of the gain and horizontal bars indicate 1 SD of the frequency of the smooth eye movement when these exceed the size of the symbols. Triangles mark the frequency and the amplitude (as a ratio of the target movement during pursuit) of the sine wave remembered by the subject in the psychophysical experiment.



from the SD of the duration of a half-cycle of the eye oscillation) was consistently higher than during pursuit.

All our subjects also possessed to some extent control over the amplitude of their eye movements during imitation. In 4 subjects the mean amplitude of the smooth component decreased when the frequency increased. The loss in amplitude of the smooth component was compensated by an increase in the number of large saccades. Thus the amplitude of the composite (smooth + saccadic) eye movement was similar to or even larger than the amplitude of the previous pursuit eye movement. In the other two subjects a clear fall-off of the smooth component was not present. Across subjects and frequencies the ratio of the mean amplitude of smooth eye movement during imitation and pursuit ranged from 0.4 to 2.0. The reduced precision of the smooth eye movement during imitation was also reflected in the larger SD of the amplitude during imitation. The SD during imitation was 0.4-1.9 deg whereas it was only 0.06-0.6 deg during pursuit.

In the psychophysical task the subjects in general reset amplitude and frequency of the function generator driving the target to values very similar to those of the corresponding parameters of the target movement during pursuit. Only for one subject (LF) the frequency (but not the amplitude) of the remembered target movement was more similar to the frequency of the imitating eye movement, which was clearly lower than the pursuit eye movements of this subject at 0.4 and 0.7 Hz.

We conclude that all our subjects possessed voluntary control over frequency and amplitude of their smooth eye movements during imitation of pursuit with a foveal horizontally stabilized target although this control was not very accurate. The differences in frequency and amplitude between the imitating and the pursuit eye movement did not correlate with the inaccuracies in the subject's estimates of frequency and amplitude of the target movement.

Table 5.2. Frequency, gain and phase of the individual eye movements with a foveally stabilized target on a sinusoidally moving background. Motion of the target was imagined by the subject and was in counterphase to the background movement (opposite) or in phase with the background movement (drag). One SD of the frequency of the eye movement was determined from the duration of 10-20 half-cycles.

Target Freq.		Instruction											
		Drag						Opposite					
		Subjects						Subjects					
		AB	AR	CE	HS	JT	LF	AB	AR	CE	HS	JT	LF
	Gain	1.10	0.83	0.53	0.58	1.20	1.08	0.39	0.62	0.42	0.57	1.23	0.58
0.21	Phase	-16	-19	-50	-5	27	-7	-174	-176	-167	-188	-116	-180
	Freq.	0.21	0.22	0.20	0.22	0.21	0.21	0.21	0.22	0.23	0.21	0.22	0.22
	± 1 SD	0.02	0.02	0.05	0.02	0.02	0.02	0.04	0.05	0.03	0.02	0.08	0.02
	Gain	0.77	0.90	0.16	1.05	1.37	0.88	0.31	0.45	0.20	0.06	1.16	0.57
0.40	Phase	-55	-80	-134	-37	-7	-28	-153	-181	-160	-133	-142	-188
	Freq.	0.39	0.39	0.40	0.40	0.40	0.40	0.39	0.37	0.40	0.46	0.40	0.40
	± 1 SD	0.05	0.06	0.06	0.04	0.08	0.03	0.06	0.17	0.05	0.21	0.08	0.06
	Gain	0.29	0.74	0.09	0.60	1.07	0.65	0.21	0.27	0.10	0.12	0.86	0.29
0.70	Phase	-60	-29	-83	-14	-9	-97	-170	-176	-190	-124	-172	-194
	Freq.	0.70	0.71	0.70	0.72	0.70	0.65	0.70	0.69	0.70	0.71	0.68	0.70
	± 1 SD	0.10	0.10	0.13	0.07	0.15	0.12	0.11	0.08	0.11	0.15	0.14	0.08

Eye movements with a foveally stabilized target on a moving background: Sinusoidal background movement.

It was essential for a proper interpretation of the results of the second experiment that the subject kept his line of sight on the target vertically. Mean vertical eye position never varied by more than twice the diameter of the target from the vertical target position. Occasionally one subject (JT) made saccades that displaced the line of sight vertically by 1-2 deg. However, the vertical misalignment of the gaze lasted less than 1 sec. Hence, this subject -like the other subjects- kept the line of sight on the target during most of the time during the measurements.

The mean frequency of the horizontal eye movements with the foveally stabilized target on the moving background was identical to the frequency of the background movement (Table 5.2). The SD of the frequency however was larger than during pursuit of the target in the first experiment (Fig 5.2). Hence, when the movement which had to be imitated with the stabilized target was visible in the retinal periphery (as in the second experiment) the accuracy of the frequency of the smooth eye movement during imitation was larger than when this movement was only shown in advance (as in the first experiment). However, the SD of the frequency of the smooth eye movements with the stabilized target was always larger than for normal pursuit of the target. As shown in table 5.2 the phase of the eye movements parallelled the phase of the target movement as imagined by the subject. Grand mean phase lag was 42 ± 37 deg when the target was imagined as dragged by the background and 166 ± 23 deg when the target was imagined as moving in counterphase with the background. In parallel with the results of Experiment 1 the gain of the smooth eye movement decreased when the background moved at a higher frequency.

Fig 5.3 gives an example of the smooth eye movements made when a subject altered his 'mental set' concerning the target movement from head-stationary to moving in phase with the background (Fig 5.3a) or moving in counterphase with the background movement (Fig 5.3b).

The response of this subject was exceptional in the sense that vertical saccades of ca. 1-2 deg occurred when he increased the amplitude of his eye movements. In other subjects only horizontal saccades occurred when they imagined target movement. Clearly, when the subject considered the target as head-stationary little or no eye movements occurred (the amplitude was typically about 0.5 deg) but after the instruction to

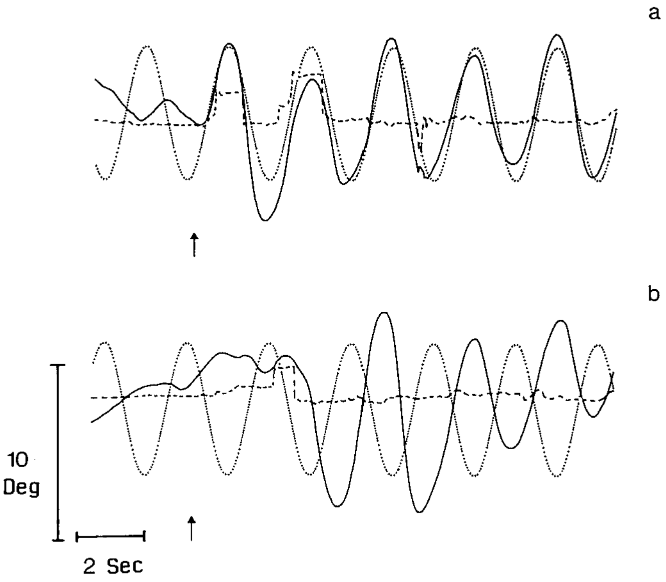


Fig. 5.3. Horizontal cumulative smooth eye movements (continuous line) of subject JT with the foveally stabilized target on the moving background (dotted line). The target was imagined to be head-stationary at the start of the recording and at the time marked by the arrow the target was imagined to move opposite to the background (lower panel) or the target was imagined to be dragged by the background (upper panel). This subject least controlled his vertical eye movements (dashed line) which displaced the line of sight occasionally by 1-2 deg although the subject was explicitly instructed to keep the line of sight on the target vertically. The drift prior to the time indicated by the arrow in (b) is an artefact arising from the removal of a linear trend from the entire eye position record although the trend started only after the instruction to imagine the target as moving.

imagine the target as moving the eye movement rose in amplitude and the phase approached the imagined phase of the target movement in a few cycles. Only at 0.7 Hz many subjects reported difficulty in willfully attaining a stable 'mental set' concerning the target movement, although the phase lag of their steady state eye movements (instructions: opposite and drag) kept showing differences depending on the instruction concerning the imagined target movement (Table 5.2). When the eye movements of the subjects lost the required phase relationship with respect to the background they succeeded to restore the original phase relationship only after a transient reduction of the amplitude of their smooth eye movements (Fig 5.4).

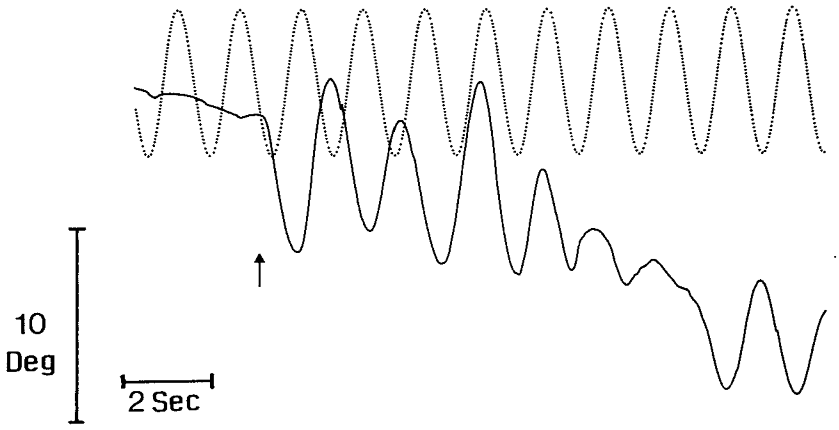


Fig. 5.4. Horizontal cumulative smooth eye movements of subject LF (continuous line). The background oscillated at 0.7 Hz (dotted line). When LF attempted to imagine opposite target movement at the time marked by the arrow he made opposite eye movements for about two cycles of the background movement. Subsequently, his eye movements became approximately in phase with the background movement. Opposite eye movements recurred after about 4 cycles in which the amplitude of the smooth eye movement was gradually reduced and then restored.

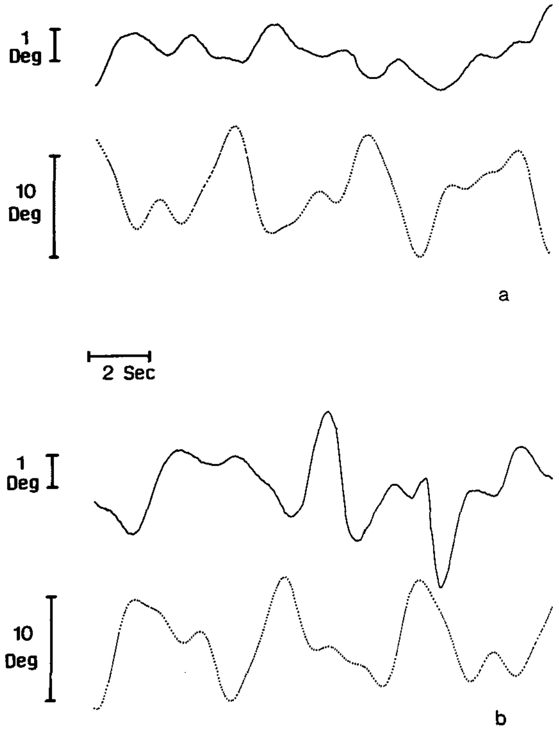


Fig. 5.5. Cumulative smooth eye movements (continuous line) of subjects CE (a) and AB (b) when they imagined opposite target movement with the foveally stabilized target. The background moved pseudo-randomly (dotted line; spectral composition of Table 5.1). For clarity, background movement is plotted on a three times smaller scale.

Eye movements with a foveally stabilized target on a moving background: Pseudo-random background movement.

When the background movement was unpredictable the control over the phase of the eye movement with the stabilized target was considerably less. Subjects had in general not much difficulty in attaining the head-fixed representation and the accompanying virtual absence of eye movements but when they were instructed to imagine the target as moving the subjects were successfull in making appreciable eye movements at the end of the 16 sec recording period only when they imagined target drag. Even when the subjects were given ample time (as with the instruction 'opposite') to

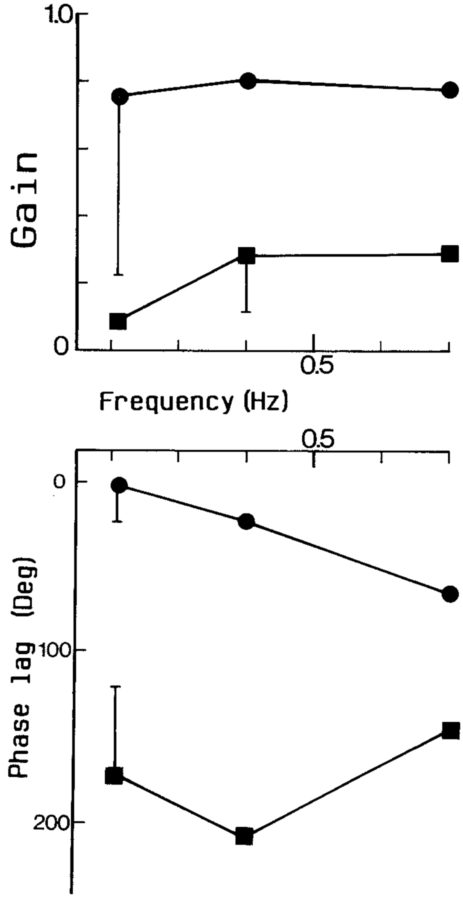


Fig. 5.6. Gain and phase of the cumulative smooth eye movement with the foveally stabilized target with pseudo-random background movement. The subject attempted to imagine the target as dragged by the background (dots) or opposite target movement was imagined (squares). Mean gain, phase and error bars representing 1 SD are given for 6 subjects when the target was imagined as being dragged by the background. Mean and SD are based on the data of two subjects (CE and AB) for the condition in which subjects imagined the target as moving opposite to the background.

obtain a steady representation of opposite target movement only two subjects were marginally able to make opposite eye movements of small amplitude (Fig 5.5). Mean gain and phase of these two subjects during imagined opposite eye movement are plotted with representative standard deviations (bars) in Fig 5.6. The other subjects made no eye movements at all or slightly lagged the background when they tried to imagine the target as moving opposite to the background movement.

On the other hand, all subjects were able to shift their mental set to seeing the target as dragged along with the pseudo-random background motion and made considerable eye movements approximately in phase with the background movement. Gain for each subject varied little with frequency and mean gain (of all six subjects) ranged from 0.76 to 0.81 for the three frequencies. Intersubject variability, however, was quite large as is reflected in the large SD of the mean gain. Apparently, when the background movement was predictable and frequency was low, subjects were able to make smooth eye movements with the same frequency as the background motion with a foveally stabilized target or to inhibit such eye movements at will. Moreover the subjects could voluntary control the direction of the eye movement with respect to the background motion. With unpredictable background movement on the other hand, most subjects could not control their pursuit eye movements to such an extent that the smooth movements were reversed in direction with respect to the background motion although they could still inhibit their smooth eye movements.

DISCUSSION

Several groups have used open-loop techniques to tackle a variety of questions concerning the operation of the human smooth pursuit system. The popularity of image stabilization techniques is not surprising since a great prize may be gained by opening the feedback loop. In normal (closed loop) conditions the properties of the oculomotor controller (which drives the eye using retinal input and additional non-visual inputs) are reflected rather indirectly in the relationship between the eye movement and the target movement whereas in the open-loop condition the relationship between the retinal motion and the the eye movement is studied directly. The basic assumption of studies employing stabilized targets is that the dynamics and the structure of the oculomotor controller are not changed by the opening of the unity-gain feedback loop. Providing this is true, simple relationships hold between the open-loop and the closed-loop response when the system is linear (Wyatt and Pola, 1983) or, in an approach not assuming linearity, the non-linear differential equation governing closed-loop pursuit may be formulated from the limit cycles observed during open-loop fixation (Scotto and Oliva, 1984). The precondition is then that during open-loop experiments the non-visual inputs -e.g. cognitive inputs like attention and expectations concerning the target movement (c.f. Kowler and Steinman 1981)- must not alter the state of the pursuit system. This precondition is not necessarily met since it is well known that humans can to some extent influence the performance of the pursuit system according to instructions. Subjects can voluntarily suppress saccades (DeWeese-Puckett and Steinman, 1969) and can smoothly pursue at a fraction of target velocity (Steinman et al., 1969). Also in the open-loop condition it has been noted that subjects can voluntarily influence the gain of their open-loop pursuit eye movements (Collewijn and Tamminga, 1986) and the number of saccades (Kommerell and Täumer, 1972), possibly by modulation of the amount of attention directed to the target (Kommerell and Täumer, 1972; Pola and Wyatt, 1985).

The ability to voluntarily influence smooth pursuit eye movements is not limited to stimulus conditions in which stabilized targets are displaced with respect to the fovea as is the case in open-loop pursuit experiments. Even when the target was foveally stabilized, all our subjects were able to imitate sinusoidal smooth pursuit eye movements with a foveally stabilized target, although the amplitude often differed from that during smooth pursuit and the frequency was generally lower. This result is in two respects contrary to the findings of Cushman et al., 1984). Firstly, their subjects showed large unexplained idiosyncratic differences in the capacity to make voluntary eye movements with a foveally stabilized target. Secondly, one out of the 4 subjects screened by Cushman et al. possessed control over the frequency of his eye movements but during imitation the frequency of his eye movements was systematically higher than during pursuit. Cushman et al. used image stabilization in two dimensions while we used a target which was foveally stabilized in the horizontal direction only. Possibly the smooth pursuit system behaves differently for a target stabilized in two dimensions. Unfortunately, with our present equipment we could not satisfactorily stabilize the point target in the horizontal and the vertical direction simultaneously due to slight asymmetries in the vertical stabilization circuitry. Hence, we could not test this possibility directly.

Self generated smooth eye movement with targets stationary on the retina have been reported before. Grüsser (1986) described smooth horizontal oscillating eye movements with a pair of horizontal point targets, stabilized at symmetrical positions with respect to the fovea, when the subjects attended to each point target in turn in response to a periodical auditory signal. Similarly, Kommerell and Täumer (1972) showed that a subject made a smooth eye movement with a foveally stabilized target in the direction in which he attempted to look when he attended to a blank zone close to the foveal target. The direction of the smooth eye movement reversed when the subject directed his attention to the other side of the foveal target. The latter authors concluded that attention directed to an eccentric visual direction can be as valid as a visible target to elicit a smooth eye movement. Our results are not incompatible with this notion since we did not explicitly instruct our subjects to direct their focus of attention to the center of the point target. However, if our subjects made smooth oscillating eye movements by periodically shifting their focus of attention with respect to the stabilized target, the dynamics of this strategy seems to be relatively slow since the imitation of pursuit eye movements with a frequency of 0.7 Hz was of clearly lower frequency in all subjects but one.

In the presence of a sinusoidally moving background subjects possessed control over the direction of the eye movement with respect to the background. For pseudo-random background motion most subjects lost such control over their eye movement and the eye lagged the background motion by less than 90 deg. It might be suggested that these latter eye movements are the result of peripheral pursuit of background details. Collewijn and Tamminga (1986) investigated pursuit of an extra-foveal target which consisted of two arrows 10 deg apart vertically. Subjects pursued the arrows -keeping the line of sight between the two arrows vertically- which followed a horizontal pseudo-random movement of a similar spectral composition as our stimulus. The gain of the cumulative smooth eye movements was similar to our findings but a clear phase lead of about 10 deg occurred at 0.21 Hz changing to a phase lag of about 20 deg at 0.70 Hz. Such a phase lead has been reported for foveal pursuit of pseudo random target motion as well (Collewijn and Tamminga, 1984; Yasui and Young, 1984) but is absent in the slow phase of optokinetic nystagmus (Yasui and Young, 1984). Thus the phase lag of smooth pursuit of the imagined movement of a foveally stabilized target on the moving background is not suggestive of peripheral pursuit of background details.

If subjects have extensive voluntary control over their smooth eye movements with a foveally stabilized target on a moving background it is essential that the instruction directs the volition of the subjects unequivocally. In the studies in which such a stimulus arrangement was used (Pola and Wyatt, 1980; Wyatt and Pola, 1984; Mack et al., 1982; Collewijn and Tamminga, 1984) the subject was usually instructed to look at the target or to fixate the target when it was stationary and to track it when the target moved. Hence, the subject was uncertain about the occurrence of target motion. When in such experiments the subject recognizes that the target is foveally stabilized the logic of the instruction is corrupted because the subject then knows that the target moves with the eye. Consequently, the subject may be tempted to formulate another goal than the ordinary one (i.e. to keep the target on the fovea) for pursuit. For instance, one subject in Collewijn and Tamminga's study reported that during open-loop pursuit of pseudo-random target motion she voluntarily reduced her eye movements to keep the target within a limited area around the centre of the screen. When a subject changes the goal of his pursuit effort the resulting open-loop eye movements loose their relevance for the study of normal closed-loop pursuit. Hence it seems essential that the subjects do not detect the occurrence of the target stabilization at all or only after the stabilization has been terminated because only then we may expect unequivocal responses in an open-loop experiment using instructions which suggest that the subject is confronted with a normal pursuit task. In our experience it is nearly impossible to keep the subjects naive with respect to the stabilized condition during the 16 sec recording intervals employed. This does not rule out the possibility that subjects may be unable to detect brief intervals of stabilization during normal pursuit which might be a useful paradigm to study open-loop pursuit.

We conclude that for predictable background movement voluntary influences on eye movements with a foveally stabilized target may be large. In earlier studies using this stimulus arrangement the effect of such voluntary influences was not investigated nor controlled for. Hence the conclusions of these older studies that the background movement evokes eye movement through illusory perceived motion or through the optokinetic system during fixation of a foveally stabilized target are premature.

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CHAPTER VI: HUMAN SMOOTH PURSUIT DURING TRANSIENT PERTURBATIONS OF PREDICTABLE AND UNPREDICTABLE TARGET MOVEMENT

INTRODUCTION

Humans pursue a moving object of interest with a combination of saccadic and smooth eye movements. This composite pursuit movement shows practically no phase lag or even a phase lead for a periodic, predictable target motion. In contrast, the onset of the eye movement in response to an unexpected target movement occurs with a delay of about 100-130 msec (Robinson, 1965; Carl and Gellman 1986) and composite pursuit of unpredictable target movement shows considerable phase lags (Stark et al., 1962; Dallos and Jones, 1963; Michael and Melvill Jones, 1966; St Cyr and Fender, 1969; Yasui and Young, 1984; Collewijn and Tamminga, 1984). The smooth component of pursuit reveals a similarly small phase lag for predictable target movement, but for pseudo-random target movement a conspicuous phase lead at the lowest frequencies of the stimulus, changing into a phase lag at the higher frequencies, has been reported (Collewijn and Tamminga, 1984; Yasui and Young 1984).

Dallos and Jones (1963) introduced the concept of a "predictor", which formally expressed the effect on the gain and phase lag of the ability of the human brain to detect periodicities, or to recognize known waveforms and to employ this knowledge to improve pursuit of predictable target movement. Thus, a distinction was made between pursuit eye movements driven by retinal information alone (as for unpredictable target motion), and eye movements driven by a combination of retinal information and a predictive mechanism (as for predictable target motion). However, the assumption that prediction could be neglected for unpredictable target motion was rejected by Kowler and Steinman (1982), on the basis of evidence that humans make smooth eye movements in the guessed direction of target movement prior to the unpredictable onset of target steps or ramps. Thus, for a better understanding of smooth pursuit it is of interest to determine the contribution of prediction during pursuit of periodic as well as pseudo-random motion.

Whittaker and Eaholtz (1982) attempted to isolate the predictive component of pursuit of sine waves by blanking the target for brief periods, thus removing the retinal drive to the smooth pursuit system during the blank. The eye continued to oscillate for at least a second at aproximately the same phase and frequency (0.8 or 1 Hz) as prior to the target blanking. The authors suggested that in order to achieve a reduced phase-lag for pursuit, the predictive mechanism does not rely on the addition of a compensatory signal to the delayed retinal slip signal because such a signal should lead the target movement, in contrast to their finding. This conclusion rests on the assumption that prior to the target blank the retinal input to the pursuit system is not outweighed by the extra-retinal predictive input because this would imply that a large phase lead of the predictive mechanism would be unnecessary to compensate the delay of the weak retinal drive. This assumption was not investigated further. The crude analysis by Whittaker and Eaholtz precluded the detection of small differences in phase between pursuit prior to and during the blank which might be compatible with an additive predictive process. Moreover, Whittaker and Eaholtz did not isolate the smooth component of pursuit; therefore their data are difficult to interpret with respect to prediction by the smooth pursuit system. Another point of concern is the target blanking. Subjects immediately notice a target's disappearance. It is not known whether the removal from sight of the target influences the output of the predictive mechanism. Becker and Fuchs(1985) used a similar paradigm to investigate prediction during ramp tracking. Although they encouraged their subjects to make predictive eye movements by the instruction to continue the ramp tracking during the dark period, so as to be on target when it reappeared, they found a fast decline of the eye velocity, starting within 200 msec after the shut-off of the target whereupon eye velocity settled at ca. 40% - 60% of the target velocity.

I was not convinced that extra instructions would guarantee the continued operation of the predictive mechanism as during normal pursuit of a continuously visible target. I sought a method for isolating the predictive component of smooth pursuit under conditions which resembled normal pursuit as closely as possible. As pointed out by Becker and Fuchs(1985), the smooth pursuit system may also be deprived of retinal motion input by foveally stabilizing the target. Such a stimulus provides neither retinal error nor retinal slip velocity, which have been presumed to be the main visual inputs to the smooth pursuit system. Since the target is continuously visible, no extra instructions to the subject are necessary, provided that the subject does not notice the onset of the stabilization. To this end special precautions were taken to mask the onset of the stabilization.

After foveal stabilization, the eye continued to oscillate at the frequency of the preceding target movement (with a small phase lead) when the onset of the stabilization was masked. The mean eye acceleration up to the first velocity peak after the stabilization was ca. 70 % of the unidirectional target acceleration prior to the stabilization. When the onset was not masked the eye velocity dropped to zero within ca 300 msec. The eye oscillated at the highest frequency present in the stimulus after a sudden stabilization on the fovea during pursuit of a pseudo-random stimulus. The oscillation was usually damped within one cycle. These results suggest that pursuit of oscillatory target motion is largely under control of the predictive component, but that the predictive component needs continuous updating by the actual target motion.

METHODS

Recording conditions

The subject was seated in a dark room in front of a tangential screen at a distance of 147 cm. A He-Ne laser beam was backprojected onto the screen via two General Scanning servo-controlled mirror galvanometers creating a 10 minarc diameter point target. The luminance of the laser spot was reduced by a neutral density filter to a level well above foveal detection threshold. The target moved horizontally only.

The head was supported by a chin rest and a forehead abutment. Horizontal and vertical movement of the right eye was recorded with the scleral induction coil method (Robinson 1963). The left eye was patched.

Horizontal and vertical eye movement, horizontal target movement and a logic signal indicating the occurrence of stabilization were fed through anti-aliasing filters (corner frequency: 62.5 Hz; roll-off: -12 dB/oct) and sampled at 125 Hz with a 12 bit ADC. Each measurement lasted 16.38 sec.

Prior to each experimental session the eye position monitor was calibrated and sensitivity was adjusted to 400 mV/deg while the subject in turn fixated three calibration marks, positioned at 10 deg horizontal intervals with the central mark in the straight-ahead direction. This sensitivity permitted a 50 deg horizontal recording range. Maximum deviations from linearity occurred at the extreme right and left positions within this range and were limited to 3.2%. This large range was chosen because a priori it was not known through what range the eye would move when it pursued the temporarily foveally stabilized target. Subsequently, the stabilization circuitry was calibrated. The laser spot was stabilized horizontally by feeding the eye position signal to the horizontal mirror drive. The subject was asked to look straight ahead without paying attention to the spot. Then the subject was asked to fixate the spot and if the spot was seen to move, the offset of the eye position monitor was adjusted until the subject reported that the target was seen as stationary. This procedure was repeated for two visual directions ca. 15 deg to either (horizontal) side of the straight-ahead position. If additional adjustment of the offset of the eye position monitor was necessary to obtain the percept of a stationary target in one of these eccentric visual directions, the calibration procedure was repeated from the beginning. This happened in only two out of a total of fifteen sessions.

Stimuli and procedures

Horizontal target movement was under control of the computer. Our aim in the first experiment was to describe how smooth eye movements continue when during smooth pursuit of predictable target motion the pursuit system is suddenly deprived of retinal image motion. It is known that subjects can alter the properties of their smooth pursuit under specific instructions (De Weese-Puckett and Steinman, 1969; chapter V). Therefore, I wanted to refrain from special pursuit instructions to direct the subject's effort when the retinal motion of the target was nullified, since the effect of the extra instructions would be confounded with the effect of the foveal stabilization. My aim to use normal pursuit instructions required that subjects did not notice the occurrence of the altered conditions of pursuit at all, or only after the termination of the test period. Therefore, I stabilized the target only briefly (1.5 sec) at unpredictable times during the tracking and took special measures to mask the transitions from normal pursuit conditions to open-loop conditions and vice versa.

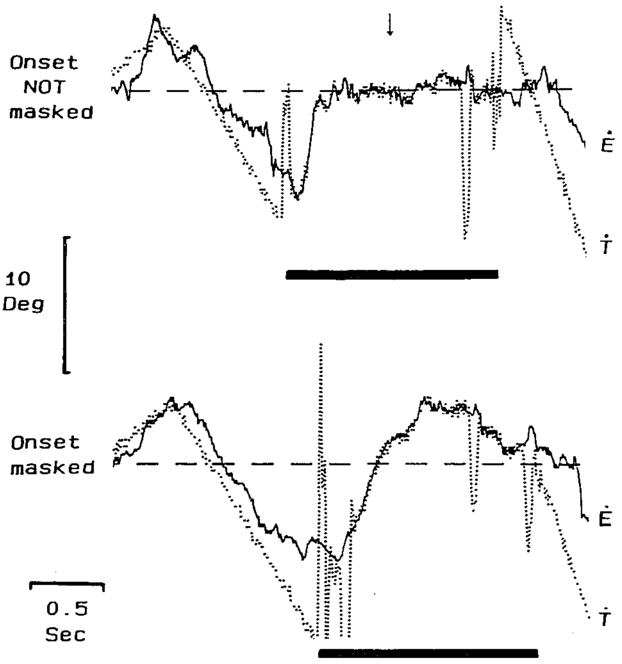
The computer made a logic signal true at a specified phase of the sinusoidal target movement. The duration of this time-window for the onset of stabilization was chosen at 10% of the cycle duration. During this time-window stabilization started only when one of the following conditions was satisfied:

(1) the subject made a saccade which was detected by a velocity criterion (1.5 times the peak velocity of the target)

(2) the retinal error position was less than 0.25 deg.

Thus, foveal stabilization started during a saccade or when the target image was nearly at the fovea. Analog circuitry was used to detect these conditions and to disconnect the mirror drive from the computer. Instead the mirror was then driven by the output of the eye position monitor. When the stabilization was terminated the mirror was again driven by the computer but an additional offset was given, to compensate for the difference between the output of the eye position monitor and the target signal generated by the computer at the end of the stabilization. As a result, target position was a continuous function of time, despite the stabilization switch-off.

Fig. 6.1. Cumulative smooth eye velocity (continuous line) and target velocity (dotted line) during transient foveal stabilization of the target. The bar in the lower half of each panel indicates the occurrence of target stabilization; the arrow indicates the detection of the stabilization by the subject. When the stabilization started during a saccade (lower panel) the subject did not detect the stabilization and the eye continued to oscillate although the target was stationary on the fovea. When the target stabilization started indiscriminately at the onset of the stabilization window (upper panel) the oscillation was abolished within 300 msec and the subject indicated the detection of the stabilization ca 700 msec after its onset. The occurrence of saccades during the foveal stabilization period may be observed as 'spikes' in the target velocity record for which no saccade removal was performed.



The importance of the masking of the stabilization onset may be appreciated from Fig 6.1. Both panels show target velocity and cumulative smooth eye velocity. When the velocity criterion for saccade detection was set at zero (upper panel) the target jumped to the fovea at the start of the stabilization window. The eye started to decelerate within 150 msec and came to rest within 300 msec. On the other hand, when the onset of the stabilization was locked to the occurrence of a saccade, then -for the same stimulus conditions- the eye continued to oscillate with a slowly decreasing amplitude (lower panel). In the first experiment the target moved sinusoidally at 0.488, 0.671 or 0.854 Hz. Peak velocity was constant at 18 deg/dec. The stabilization window started briefly before the zero-crossing of the target velocity (position phase: 72 or 252 deg) or its peak (position phase: 162 or 342 deg). The stabilization window never occurred in the first cycle. The 12 different stimulus conditions were offered in a pseudo-random order. In some measurements stabilization did not occur because the subject's response did not satisfy either of the criteria for stabilization during the stabilization window. Half of the measurements was repeated for each subject to obtain at least one response for stabilization starting at the velocity zero-crossing or at the velocity peak for each frequency.

To investigate the contribution of retinal slip to the pursuit of predictable target movement, the smooth eye movement during transient foveal stabilization was compared to the pursuit of an unexpected modification of the sinusoidal target trajectory. The modification consisted of an interruption, lasting one half-cycle, in which the target continued to move at a constant velocity equal to the velocity directly preceding the onset of the disturbance. At the end of the test period, the sinusoidal target movement was reinstated with the same phase as at the start of the disturbance and in addition an offset was given equal to the target diplacement during the test period. Thus the modification of the sine wave consisted of a ramp displacement, smoothly inserted into the sinusoidal trajectory. The frequencies and the phase at which the ramp started were chosen as in the foveal stabilization experiment. Peak velocity was constant across frequencies at 18 deg/sec.

Duration (sec)	Sequence							
0.512	+80	-60	+40	-80	* +120	-140	* +160	-120
0.512	-80	+60	-40	+80	* -120	+140	* -160	+120
1.024	+20	-15	+10	-20	* +40	-35	* +40	-30
1.024	-20	+15	-10	+20	* -40	+35	* -40	+30

Table 6.1. The sequences of acceleration levels used for the pseudo-random target movement. The duration of each epoch of constant acceleration was 0.512 or 1.024 sec. The acceleration level during successive epochs is indicated by the sequence in units of (1.024) deg/sec^2. In trials with stabilization, one stabilization window occcurred during the first presentation of the acceleration sequence at either one of the acceleration steps indicated by the asterisks.

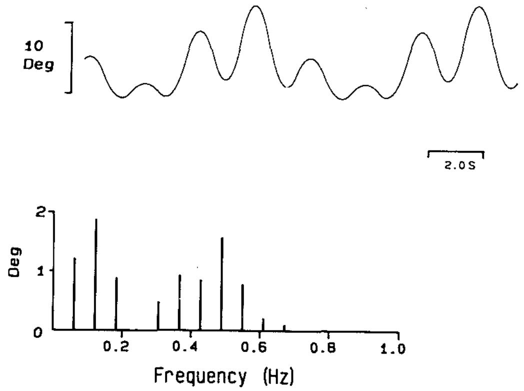


Fig. 6.2. The top panel shows the waveform (position as a function of time) of the pseudorandom sequence of target acceleration steps for the long step interval (1.024 sec). The spectral content of this stimulus is shown in the lower panel. The waveform of the sequence with the short step interval is identical, when the time axis is compressed by a factor 2.

In a second series of experiments the target movement was pseudo-random, and at various times the target could be stabilized. During a session, measurements with stabilization were randomly alternated with trials in which no stabilization occurred. The subjects had to indicate with a push-button the detection of target stabilization. The push-button controlled a logic signal which was recorded in addition to the signals mentioned above. The target motion consisted of a sequence of acceleration steps. The interval between two successive steps was constant (0.512 or 1.024 sec) but the amplitude was randomized. Successive steps were of opposite polarity. Thus, the stimulus was predictable in the sense that rightward and leftward accelerations alternated with regular intervals, but unpredictable with respect to the size of the acceleration. Table 6.1 describes the sequence of acceleration steps. Fig 6.2 shows the target position waveform for the stimulus with the long step interval and its spectral content. The sequences of Table 6.1 were presented twice during a measurement for the long interval between the steps, and four times per measurement for the short interval. In trials with stabilization (40% of all measurements) one stabilization window (duration: 400 msec) occurred during the first presentation of the acceleration sequence at either one of the acceleration steps indicated by the asterisk in Table 6.1. To minimize learning of the target trajectory by our subjects, a different acceleration sequence with approximately the same spectral content was offered in half of the measurements without stabilization.

Subjects and Instructions

A complete set of data was obtained for 5 subjects without visual defects except refractive errors. Subjects wore their corrective spectacles during the experiments. Subjects were instructed to pursue the point target.

In the first experiment three subjects (including the author) knew that the target would be stabilized briefly during the experiment because they had partaken in pilot experiments. Two other subjects (MR and HR) who were familiar with the stabilization technique from previous experiments were not informed about the transient target stabilization but were instead told that the sinusoidal target movement would be replaced transiently by other waveforms. The latter subjects did not detect that the disturbance was caused by their own eye movements deviating from the sinusoidal trajectory after the stabilization on the fovea.

In the second experiment all subjects knew that the target would be stabilized on the fovea. They were instructed to pursue the target and to indicate the onset of the target stabilization by pressing a push-button (see before). I did not attempt to use this procedure for sinusoidal target movement since, in view of the subject's familiarity with such a waveform, any deviation from the sinusoidal trajectory would provide a cue for the onset of stabilization.

Data Analysis

Off-line data analysis started with the removal of the saccades from the records. Saccades were detected by a computer algorithm based on acceleration and velocity criteria and replaced by ramps with a velocity which was the mean of the pre- and post-saccadic smooth eye velocity. The post-saccadic part of the eye position record was given an offset equal to the difference between the amplitude of the saccade and the displacement by the ramp which replaced the saccade to create the cumulative smooth eye position record (CSEP). Eye velocity was obtained by digital differentiation of the CSEP with a sliding window algorithm computing mean eye velocity in overlapping intervals of 40 msec duration, the onsets of which were one sample interval apart (8 msec). Parameters -to be discussed below- to characterize the response during the foveal stabilization were obtained from the smooth eye velocity records interactively. A computer program created a plot of the smooth eye velocity on the terminal screen and eye velocity, acceleration and their time of occurrence, or their means over an interval, specified with hairlines, could be computed.

For the measurements without stabilization, Fourier analysis was performed on the target position signal and the CSEP signal to obtain gain-phase characteristics of smooth pursuit. If necessary, a linear trend and an offset were removed from the CSEP prior to the Fourier analysis.

All data in the figures represent across-subject means after averaging repeated measurements within the subjects unless stated otherwise.

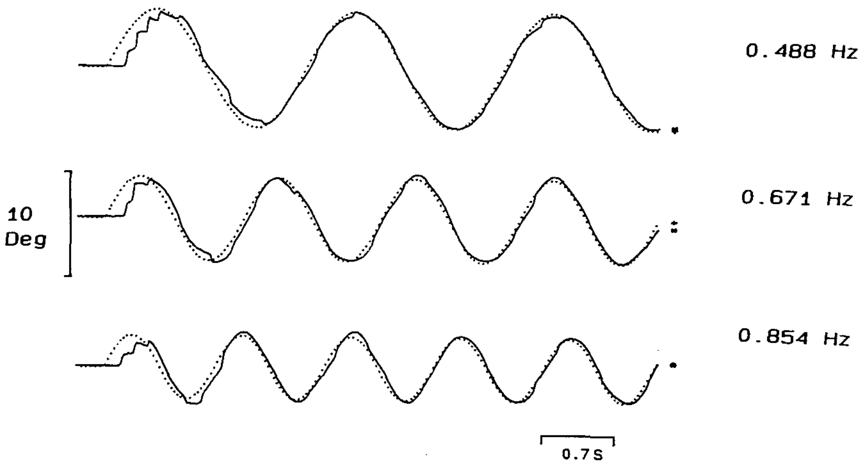


Fig. 6.3. Target position (dotted line) and eye position (continuous line) during smooth pursuit of sine waves at three different frequencies. The amplitude of the sine was inversely proportional to the frequency. One cycle after the onset of the stimulus motion (left side of the traces) pursuit is largely smooth and few saccades occur.

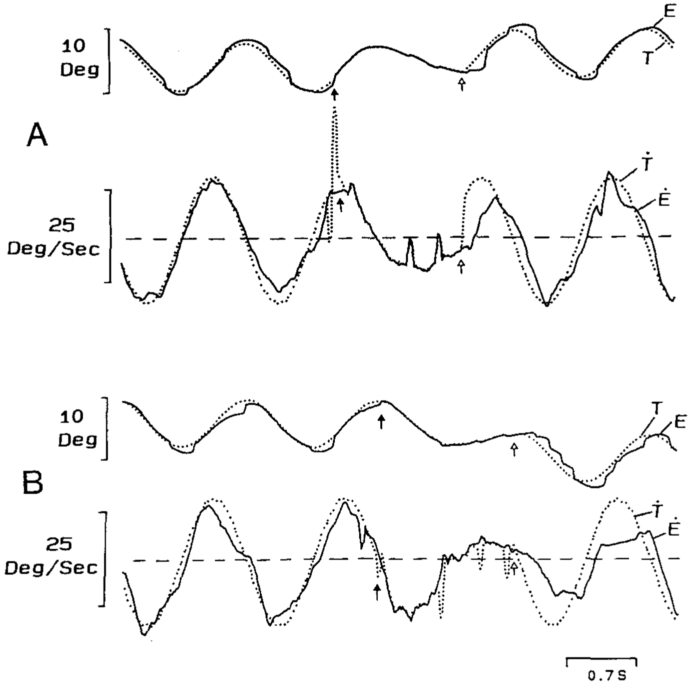
RESULTS

Transient foveal stabilization during pursuit of single sine waves

Qualitative observations

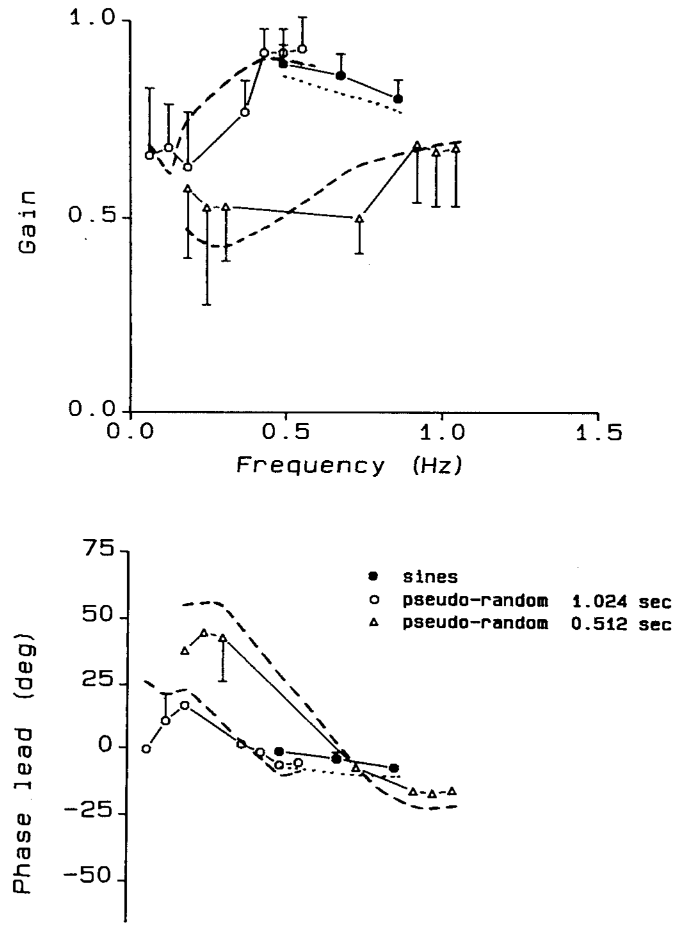
Subjects usually tracked the sinusoidal target movement with nearly zero phase-lag within one half-cycle after the onset of the target motion. Pursuit after the first cycle was largely smooth, as shown in Fig 6.3, and contained few saccades. Typically, the peak velocity of the smooth eye movement was 80-90% of the peak target velocity and the lag was close to zero, or CSEP even led the target by a small amount in some subjects, indicating that prediction had compensated the 100-130 msec delay. When the target was stabilized briefly before the target reached its peak velocity, the eye acceleration reversed its direction after a brief delay. On the other hand when stabilization occurred briefly before the target velocity zero-crossing, the eye continued to accelerate in the same direction. Thus the stabilization of the target on the fovea was not followed by a reversal of the eye acceleration after a constant delay. This argues against an interpretation that the reversal of the eye acceleration was caused by the sudden reduction of the retinal slip associated with the onset of the stabilization. The reversed eye acceleration after stabilization at the peak target velocity and the continued acceleration after stabilization at the target velocity zero-crossing were labeled the "initial eye acceleration". At the end of the initial eye acceleration the eye moved in the direction opposite to that directly preceding the target stabilization. The peak velocity reached at the end of the initial eye acceleration was usually lower than the peak velocity prior to the stabilization. Typical eye velocity profiles after stabilization are shown in Fig 6.4. The direction of the initial acceleration was not related in a consistent way to the retinal slip directly preceding the stabilization on the fovea. For example, in Fig 6.4a the positive retinal slip prior to the foveal stabilization is followed by a negative initial acceleration while in Fig 6.4b a similarly negative initial acceleration is preceded by a negative slip velocity.

Fig. 6.4. Foveal stabilization during smooth pursuit of a sine wave. Stabilization started near the velocity peak (a) or near the velocity zero-crossing (b) of the target. In each panel position (target: dotted line; eye: continuous line) and velocity are plotted in the upper and the lower traces respectively. The onset and the shut-off of the stabilization are indicated by the filled and the open arrow heads respectively. Saccades were removed from the eye velocity record. The occurrence of saccades during the foveal stabilization period may be observed as 'spikes' in the target velocity record for which no saccade removal was was performed. (Two small saccades which were not detected by our saccade elimination routine occur in the eye velocity trace also in a).



In the great majority of the cases (86%) the initial eye acceleration was followed by a reduced eye acceleration in the opposite direction. Thus the amplitude of the oscillation rapidly declined after the onset of the foveal stabilization. The change of the initial eye acceleration into the secondary eye acceleration could be very abrupt, resembling an eye acceleration step (48% of the cases). About equally often the eye acceleration declined gradually before the reversal (38% of the cases).

Fig. 6.5. Frequency characteristics of smooth pursuit of single sine waves (filled symbols) and pseudo-random target movement (open symbols) consisting of a sequence of acceleration steps with intervals of 1.024 sec duration (circles) or 0.512 sec duration (triangles). The frequency characteristics of the model's response to the same target motion signals are indicated by the broken lines (pseudo-random signals) or the dotted line (sines).



In 11% of the measurements the secondary acceleration was absent, and instead the eye continued to move at a constant velocity after the initial acceleration. The latter response type tended to occur more frequently at 0.488 and 0.671 Hz. In the remaining 3% of the cases the eye decelerated to a standstill along a (single) exponential course. These measurements were excluded from the analysis.

There was neither a difference in the types of responses nor in the relative frequencies of occurrence of the different response types between the experienced and the naive subjects. This indicates that -given the unpredictability and the masking of the stabilization onset and the brief duration of the stabilization- the knowledge that the target would become stabilized during a measurement did not affect the response.

Quantitative observations

Fig 6.5 shows gain and phase of the smooth component of pursuit as a function of frequency for measurements without stabilization. Gain was consistently less than unity and decreased with the increase in frequency from 0.89 at 0.488 Hz to 0.81 at 0.854 Hz. The mean phase lag was small and increased with frequency from 1.7 deg at 0.488 Hz to 7.7 deg at 0.854 Hz. The SD reflects the inter subject differences. Typically, one SD of the gain was about 0.05 and one SD of the phase was 2.5 deg. The initial acceleration seemed the most appropriate part of the response to analyze quantitatively. Firstly, it occurred consistently for all subjects and stimulus conditions, whereas the secondary eye acceleration was more variable. Secondly, it was probably influenced least by possible changes of the tracking strategy. The magnitude of the initial acceleration (a_I) was computed as the mean unidirectional eye acceleration starting 100 msec after the onset of the stabilization until the first successive peak of the eye velocity. In addition the time interval (T_{pd}) between the peak velocity of the eye at the end of the initial acceleration and the peak target velocity of the same sign in the cycle preceding the stabilization was computed. If the output of the predictive mechanism shows a phase lead (ϕ; degrees) with respect to the target movement then

T_{pd} is reduced with respect to the cycle duration by

$$\frac{\phi}{360} * 100\%$$

The initial eye acceleration increased for larger target frequencies, irrespective of the phase of the onset of target stabilization. Since the peak target velocity was equal across frequencies, the initial eye acceleration was not a function of the peak target velocity but of the peak target acceleration which increased for increasing frequency. Fig 6.6 shows the initial eye acceleration (a_I) versus the peak target acceleration during the half-cycle prior to the onset of the stabilization (a_T) for one subject. A linear relationship between a_I and a_T was consistently present for all subjects and phases of stabilization. Table 6.2 shows the linear regression coefficients for all subjects. The ratio of a_I and a_T did not vary much across the subjects and phase of stabilization. For stabilization at the peak

<u>Stabilization at the velocity peak</u>

Subject	α	β	r^2	g_P
AB	-0.515	2.9	0.98	0.809
MP	-0.495	-2.1	0.98	0.775
HS	-0.447	0.1	0.96	0.702
HR	-0.487	4.4	0.98	0.765
MR	-0.488	-0.3	0.98	0.767

<u>Stabilization at the velocity zero-crossing</u>

Subject	α	β	r^2	g_P
AB	-0.518	3.0	0.94	0.814
MP	-0.512	-8.2	0.94	0.804
HS	-0.455	5.3	0.90	0.715
HR	-0.476	6.8	0.99	0.748
MR	-0.478	2.7	0.99	0.751

Table 6.2. Regression coefficients and coefficient of determination (r^2) of a_I versus a_T for sinusoidal target movement. $a_I = \alpha\ a_T + \beta$. g_P equals $|2/\pi\ \alpha|$ and indicates the ratio between a_I and the <u>mean</u> unidirectional target acceleration.

target velocity this ratio ranged between -0.447 and -0.515, and for stabilization at the target velocity zero-crossing the ratio ranged between -0.455 and -0.518. There was no consistent difference between the ratios in relation to the phase of the target stabilization. In some subjects the ratio was larger for stabilization starting at the peak target velocity; for other subjects the ratio was larger when the stabilization started at the zero crossing. The initial acceleration was larger than ca 45% of the peak target acceleration. For a sine wave the ratio between the mean acceleration in one direction and the peak acceleration equals $2/\pi$. Thus the mean initial eye acceleration exceeded 70% of the mean target acceleration in one direction prior to the stabilization. Fig 6.7 shows T_{pd} as a function of the cycle duration. Each point represents the average of 3-6 measurements in which only the phase of the onset of the target stabilization varied. T_{pd} was not consistently related to the phase in which the stabilization started. For 0.488 Hz and 0.854 Hz T_{pd} averaged across subjects was larger by 20 and 5 msec respectively when the stabilization started at a velocity zero-crossing but for 0.671 Hz T_{pd} was longer by 25 msec when the stabilization started at the peak velocity. One SD for each point was ca 5% of the mean value. The mean of T_{pd} was equal to or lower than the cycle duration in all subjects for all frequencies. This may be interpreted as a phase lead of the predictive component if it is assumed that the predictive process is precisely tuned to the target frequency. We computed a phase lead angle ϕ_p of the predictive eye acceleration from T_{pd} and the cycle duration T.

$$\phi_p = (T - T_{pd})/T*360 \ \mathrm{deg}$$

For 0.488 Hz ϕ_p ranged between -1.6 deg and 16.3 deg for different subjects while for 0.671 Hz and 0.854 Hz ϕ_p ranged between 0 and 20.1 and between 0 and 13.8 deg respectively. Thus a tendency of the predictive eye acceleration occurred a small phase lead with respect to the target movement.

If we consider ϕ_p and g_p (see Table 6.2) as estimates of phase lead

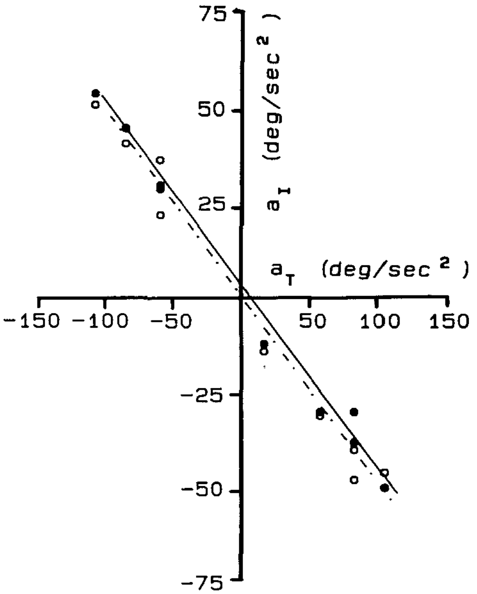


Fig. 6.6. Initial eye acceleration (a_I) as a function of the peak target acceleration in the half-cycle directly preceding the stabilization on the fovea (a_T) for subject MR. Stabilization started at the peak target velocity (open symbols) or at the velocity zero-crossing (filled symbols). With the exception of a small difference in the constant the linear regression coefficients were equal.

and gain of the predictive component we may, under the assumption that normal pursuit consists of the sum of a retinal and a predictive, extra-retinal component of the same frequency, compute the gain (g_r) of the retinal contribution to pursuit of sine waves from the gain (g) and phase lead (ϕ) of normal pursuit (see Fig 6.5).

$$g_r^2 = g_p^2 + g^2 - 2g{*}g_p{*}\cos(-\phi + \phi_p)$$

Since gain and phase of normal pursuit and of the predictive component of pursuit differed only slightly for different subjects we computed g_r for each frequency from the gains and phases averaged across subjects. The gain of the retinal contribution did not depend on frequency and equalled 0.196 ± 0.006 averaged across frequencies. Thus, g_r is about 3.5 times lower than g_p indicating that for pursuit of sine waves more than 75% of the response must be attributed to the predictive component of pursuit.

Unexpected perturbations of the sinusoidal target trajectory

How fast is the output of the predictive process modified when the target movement deviates from the predicted trajectory? This was investigated in the experiment in which the target continued to move for one half period at a constant velocity, equal to the target velocity directly preceding the moment the perturbation started. The constant velocity epoch started at the peak target velocity (position phase: 342 or 162 deg) or at the target velocity zero-crossing (position phase: 72

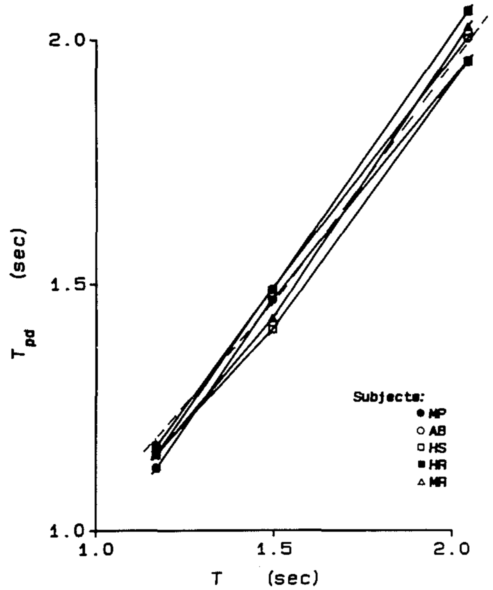


Fig. 6.7. The time interval between the first peak velocity of the eye after foveal stabilization and the peak target velocity of the same sign which occurred prior to the stabilization period (T_{pd}) as a function of the cycle duration (T) for each subject. For most subjects T_{pd} was slightly shorter than T indicating that the eye movement during the foveal stabilization period showed a small phase lead with respect to the target movement. The broken line indicates T_{pd} of the model in response to the same stimuli.

or 252 deg). A typical response is shown in Fig 6.8. Irrespective of the phase at which the constant velocity epoch started, the eye initially accelerated as if the sinusoidal target movement had continued. This eye acceleration thus carried the eye away from the target and created retinal error and retinal slip velocity. At a variable time after the onset of the perturbation the eye acceleration reversed its direction. This corrective acceleration reduced the retinal slip. When the ramp started at the peak target velocity the corrective acceleration was preceded by an eye velocity plateau in 56% of the cases. The occurrence of the velocity plateau did not systematically depend on the frequency nor did it occur in each subject. The time after the onset of the perturbation at which the smooth eye acceleration became zero was considered the reaction time (T_c) of the smooth pursuit system to the perturbation. This reaction time depended both upon the phase in which the perturbation started and upon the frequency. Fig 6.9 (left panel) shows T_c as a function of frequency and phase of the start of the constant velocity epoch. When the target remained stationary following the target velocity zero-crossing, T_c was independent of frequency and equalled about 0.18 sec. On the other hand, when the target moved at the maximum velocity of the sine for half a period following the velocity peak, T_c decreased with frequency (F) and approximately satisfied the following relationship:

$$T_c = 1/(4*F) + 0.08 \text{ sec.}$$

Thus, more than a quarter of a period elapsed before the eye acceleration became zero. The peak slip velocity ($\dot{\epsilon}_c$) -which occurred at T_c- varied considerably among the subjects but the peak slip velocity was consistently larger when the constant velocity epoch started at the peak velocity of the target. Fig 6.9 (right panel) shows the magnitude ϵ_c as a function of frequency and the phase of the target movement in which the constant velocity epoch starts. $\dot{\epsilon}_c$ increased as a function of the frequency and was about twice as large for ramps starting at the velocity peak (phase: 342 or 162 deg) as for ramps starting at the velocity zero-crossing (phase: 72 or 252 deg). Thus, the predicted target velocity seems to be modified very fast when the target remains stationary at the peak target position, but when the target continues

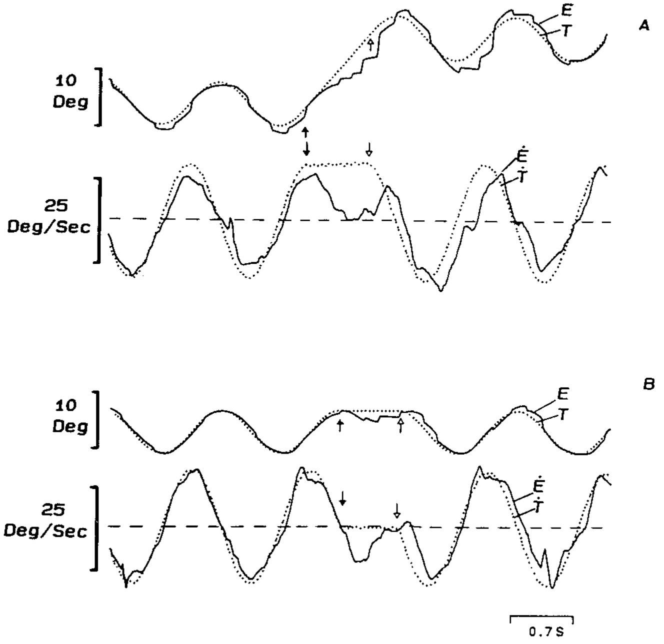


Fig. 6.8. Pursuit of constant velocity epochs smoothly inserted into the sinusoidal target movement. The perturbation of the sinusoidal trajectory started near the velocity peak (a) or near the velocity zero-crossing (b) of the target. In each panel position (target: dotted line; eye: continuous line) as well as velocity are plotted in the upper and the lower half respectively. The eye continues to accelerate as if the sinusoidal target movement continues for more than a quarter cycle (a) or eye acceleration is reduced to zero within 200 msec (b) after the start of the constant velocity segment. The onset and the termination of the disturbance are indicated by the filled and the open arrow heads respectively.

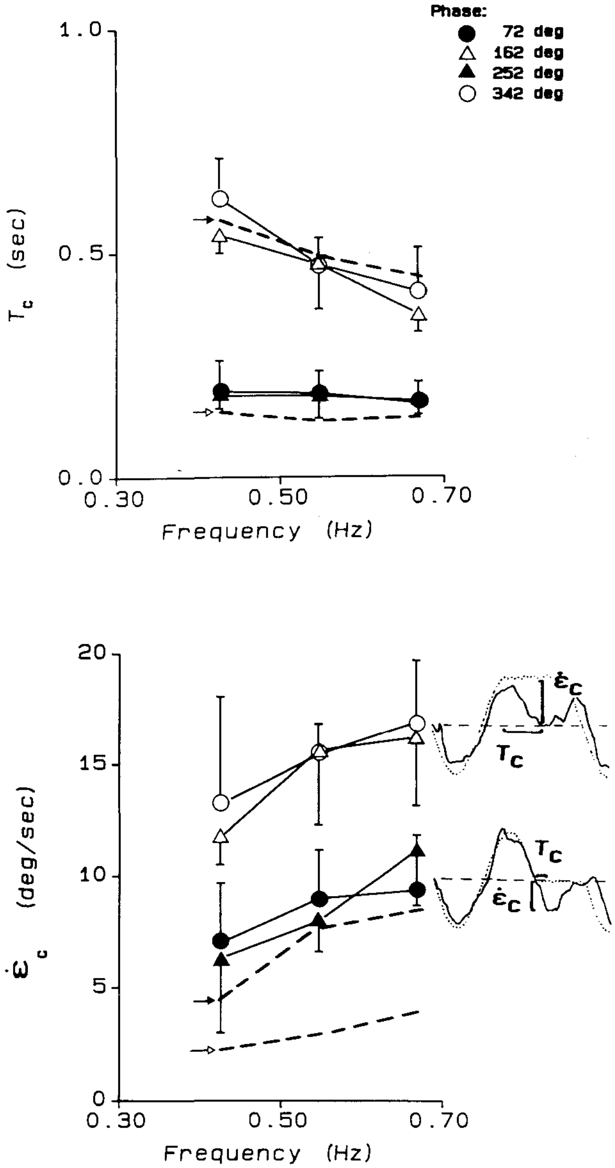


Fig. 6.9. Left panel: T_C as a function of frequency and the phase at which the constant velocity segment started. Right panel: peak retinal slip velocity ($\dot{\epsilon}_C$) after the start of the constant velocity segment as a function of frequency and the phase at which the perturbation started. T_C and $\dot{\epsilon}_C$ of the model are indicated by the broken lines. Open arrows indicate the model's response when the disturbance started at the velocity zero-crossing (72 deg or 252 deg). Filled arrows indicate the model's response when the interruption started at the peak target velocity (162 deg or 342 deg). The inset shows two examples of T_C and $\dot{\epsilon}_C$ when the disturbance started at the peak velocity (upper part) or at the velocity zero-crossing (lower part; dotted lines: target velocity, continuous lines: eye velocity).

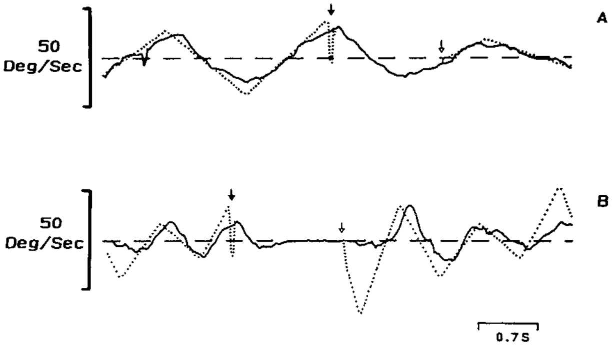
to move at the peak target velocity the eye accelerates for more than a quarter of a period, as if the sinusoidal target movement had continued.

Foveal stabilization during pursuit of pseudo-random target motion

Fig 6.5 shows the frequency characteristics of the smooth component of pursuit of the pseudo-random sequence of acceleration steps with an interval of 0.512 or 1.024 sec. The frequency characteristic depended on the frequency content of the stimulus. For the stimulus with the long step interval and hence the lower frequency content the gain was larger and the phase differed less from zero for the entire frequency band.

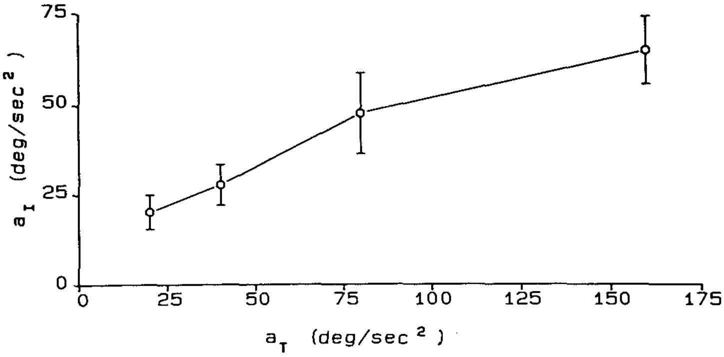
Gain reached its highest values for the highest frequency within the band. For the long step interval (1.024 sec) mean gain rose from 0.66 ± 0.16 at 0.061 Hz to 0.93 ± 0.08 at 0.549 Hz, and the phase showed a maximum lead of 16 deg at 0.183 Hz which decreased to a phase-lag of 6 deg at 0.549 Hz. Similarly, gain increased from 0.53 ± 0.15 at 0.244 Hz to 0.68 ± 0.15 at 1.04 Hz, and the phase lead of 44 deg at 0.244 Hz turned into a phase lag of 16 deg at 1.04 Hz for the stimulus with the short intervals between the acceleration steps. Thus, pursuit of the sequence of acceleration steps showed a frequency characteristic which was typical for pursuit of pseudo-random wave forms (Collewijn and Tamminga, 1984; Yasui and Young, 1984). Stabilization occurred in 37% of the measurements. When the target was stabilized on the fovea briefly before an acceleration step, the eye continued to accelerate in the same direction for ca. 100 msec. Subsequently, the direction of the eye acceleration reversed, which was considered the onset of the predictive eye acceleration (the initial eye acceleration). In more than 50% of the measurements the stabilization on the fovea was not detected by the subject. The subjects pressed the push button in 24% of the measurements. However, in 20% of these cases stabilization had not taken place or the stabilization had terminated more than 5 sec before the response. In the other cases the subjects pressed the button nearly always after the the stabilization had terminated and subjects told that they had inferred the occurrence of the target stabilization from the unexpectedly slow target movement when the eye stopped at the end of the stabilization period.

Fig. 6.10. Foveal stabilization during pursuit of pseudo-random target movement. Interval duration was 0.512 sec (b) or 1.024 sec (a). The initial acceleration after the stabilization onset is larger in b although the peak of the eye velocity (continuous line) and the peak target velocity (dotted line) prior to the stabilization are smaller than for the long acceleration step duration. Consequently, it is not the peak velocity of either the target or the eye which determines the magnitude of the initial acceleration but the target acceleration prior to the stabilization onset.



At the end of the initial eye acceleration, the eye velocity was reversed in direction but its speed was much lower than the peak eye velocity at the start of the initial acceleration (Fig 6.10). Thus, the eye oscillation rapidly declined after the start of the foveal stabilization, and usually the eye stopped to move before the end of the 1.5 sec stabilization interval. The duration of the initial acceleration depended on the duration of interval between the acceleration steps. All subjects showed the same response pattern. For the 1.024 sec step interval the grand mean duration of the initial eye acceleration was 0.85 ± 0.12 sec, while for the 0.512 sec interval between the acceleration steps the initial eye acceleration lasted an average 0.48 ± 0.11 sec. The initial acceleration averaged over subjects and direction of the preceding target acceleration step was plotted as a function of the target acceleration plateau during the interval directly preceding the stabilization interval (a_T) in Fig 6.11. Results for the two different pseudo-random signals are combined in this figure. The mean initial acceleration (aI) was about equal to a_T for the ± 20 deg/sec^2 step.

Fig. 6.11. The initial eye acceleration (a_I) during the stabilization when pseudo-random target movement was pursued as a function of the target acceleration (a_T) during the step prior to the stabilization averaged across subjects and the direction of a_T.



a_I increased less than proportionally to a_T for larger target acceleration steps which may be interpreted as a saturation effect. The averaged mean initial acceleration was about 75%, 64% and 40% of the preceding target acceleration plateau for 40, 80 and 160 deg/sec^2 respectively. Thus when the magnitude of a_T doubled, then the initial eye acceleration, expressed as a fraction of a_T, decreased by 25% for the 20-40 and the 80-160 deg/sec^2 pairs but only by 10% when these ratio's are compared for 40 and 80 deg/sec^2 acceleration plateau levels. Thus when these ratio's are compared in pairs drawn from one stimulus signal (20 and 40 deg/sec^2 levels were offered in the stimulus with 1.024 sec interval durations; 80 and 160 deg/sec^2 levels were offered in the stimulus with 0.512 sec interval durations) the decrease was larger. The peak acceleration of the stimulus (which occurred only once in each presentation of the sequence) equalled 40 and 160 deg/sec^2 for the sequence with the long and the short step intervals respectively. Hence, the ratio between the predictive eye acceleration and the preceding target acceleration step appears to decrease for an increasing probability that the next acceleration level will be smaller.

DISCUSSION

The present report describes human smooth eye oscillations while the target is briefly stabilized on the fovea during pursuit of sinusoidal target movement. Our findings are consistent with previous observations (Whittaker and Eaholtz 1982; Von Noorden and Mackensen, 1962) that eye oscillations continue in dark intervals during pursuit of sine waves. In these earlier reports it was suggested that the oscillation continues undisturbed when the interruption lasts less than a second (Von Noorden and Mackensen, 1962) or that the oscillation continues undisturbed for more than a cycle (Whittaker and Eaholtz, 1982). In contrast, I find that after the foveal stabilization the smooth eye acceleration is always reduced with respect to the eye acceleration during normal pursuit. The mean eye acceleration after the onset of the stabilization till the next peak velocity of the eye was about 70% of the mean unidirectional target acceleration prior to the stabilization. The end of the initial acceleration ocurred in general slightly before the moment at which the target velocity would have peaked if no stabilization had taken place. The magnitude and the small phase lead of the initial acceleration suggest that ongoing pursuit of sine waves is dominated by the predictive component, and that eye acceleration generated directly by retinal slip (cf. Lisberger et al., 1981) is relatively unimportant. Does this imply that pursuit of a predictable target motion is under the control of a pattern generator, as soon as the waveform is identified, as was hypothesized among others by Bahill and McDonald (1983)? I feel this is not the case because the secondary acceleration, which was directed in the opposite direction as the initial eye acceleration, was always of a considerably reduced size. This suggests that the predictive eye acceleration is dependent on continuous updating by a retinal motion signal, even for a regular stimulus like a sine wave.

Both subjects in Whittaker and Eaholtz's study expected to make sinusoidal eye movements during the dark period. Thus it is difficult to establish the relevance of these measurements to normal pursuit, as it is unknown to what extent the response during the dark period was affected by the special expectations of these subjects. The expectation of the subject as to what he is supposed to do or to imagine concerning the target movement during the target disappearance may be crucial for the type of response. Becker and Fuchs (1985) reported the occurrence of a residual eye velocity lasting up to 4 seconds when the target was blanked during pursuit of ramp target motion. The residual eye velocity was about 40 to 60% of the normal pursuit eye velocity of the target ramp. The subjects had been instructed to track the invisible target movement in order to 'catch' the target when it reappeared. On the other hand Mitrani and Dimitrov (1978) found that eye velocity dropped to zero within 0.6 sec after target disappearance which indicated the end of the target movement. None of our subjects received special instructions on what to do or what to imagine concerning the target movement during the period of stabilization. Instead we assumed that the eye movements during the stabilization provide the best possible description of the normal state of the predictive component of the smooth pursuit system, when a subject does not detect the special pursuit condition. Indeed, when the onset of the stabilization was not masked, the eye rapidly decelerated to a standstill and the stabilization was detected within 500 msec after its onset. In the same subject the eye continued to oscillate for more than a second when the target stabilization was not detected, because its onset was locked to the occurrence of a saccade. In addition, we found no systematic differences in the response of experienced subjects and naive subjects, provided that the onset of the stabilization was masked. Thus, our study shows that in the absence of a retinal drive, continued eye oscillations - although rapidly damped - are a phenomenon of normal smooth pursuit of periodic motion, and are not the result of special instructions to the subject.

We found that the eye also continued to oscillate for less than a cycle when the target was stabilized on the fovea at an unpredictable instant during pursuit of the sequence of acceleration steps of random amplitude. This stimulus was periodic in the sense that the duration of the acceleration steps was constant. However, the shape of the frequency characteristic of smooth pursuit of this stimulus strongly suggests that the target motion was 'unpredictable'. The frequency characteristic showed a phase-lead and gain reduction at the lower frequencies, which has also been reported for pursuit of a pseudo-random signal consisting of a sum of 4 harmonically unrelated sine waves (Collewijn and Tamminga, 1984). This result is consistent with the view that the predictive mechanism of smooth pursuit continues to operate, even when the target movement is pseudo-random or 'unpredictable'. The duration of the initial eye acceleration depended on the duration of the acceleration steps and lasted 0.48 sec for acceleration steps of 0.512 sec duration but 0.85 sec for steps of 1.024 sec duration. Moreover, the magnitude of the initial eye acceleration increased for larger values of the preceding acceleration step. The increase was less than proportional in contrast to the results for sine waves.

Thus, two features of the predictive mechanism emerged consistently for pseudo-random as well sinusoidal target movement:
(1) The duration and the magnitude of the initial acceleration increase when the duration and the magnitude of the unidirectional target acceleration in the cycle prior to the stabilization increased;
(2) The eye movement after the foveal stabilization is rapidly damped (usually within one cycle) indicating that the predictive mechanism is dependent on continuous updating by retinal motion signals.
There is a class of pursuit models in which an efference copy of the eye velocity command signal is added to the retinal slip signal to create an internal copy of target velocity with respect to the head (Young 1977; Yasui and Young, 1975; Robinson, 1982). The positive feedback acts like a velocity integrator, which results in a sustained or exponentially decaying eye velocity when the retinal slip is zero. This is clearly in contrast to the oscillatory behaviour of the eye after the onset of the foveal target stabilization. A more elaborate version of such a model contains a predictive element which adds a signal representing predicted target acceleration to the internal copy of the target velocity (Robinson, 1982). The structure of this predictive element is as yet not clear. It has been hypothesized that the smooth pursuit system achieves zero latency pursuit of predictable target movement by a lead-element

Fig. 6.12. The model structure. The model is a modification of Robinson's (1982) pursuit model. Retinal delay ($\tau 1$: 40 msec), central delay ($\tau 2$: 40 msec) and motor delay ($\tau 3$: 20 msec) were chosen to create a total delay of 100 msec. The delay of the efference copy ($\tau 4$: 60 msec) matches the delay's external to the positive feedback loop to maintain stability (Robinson et al., 1986). The plant model was derived from Robinson et al.(1986) and is represented by a single lag with a time constant of 0.015 sec. The slipvelocity ($\dot{\epsilon}$) and an efference copy of the desired eye velocity ($\dot{E}_d$) are combined to create an internal copy of the target velocity($\dot{T}'$). $\dot{T}'$ passed through an adaptive lead element and the central delay results in $\dot{E}_d$. The adaptive lead element is represented by a direct path carrying reconstructed target velocity ($\dot{T}'$) from which $\dot{T}'$ passed through an adaptive lag and a variable gain is subtracted. The transfer function of the lead element is given by

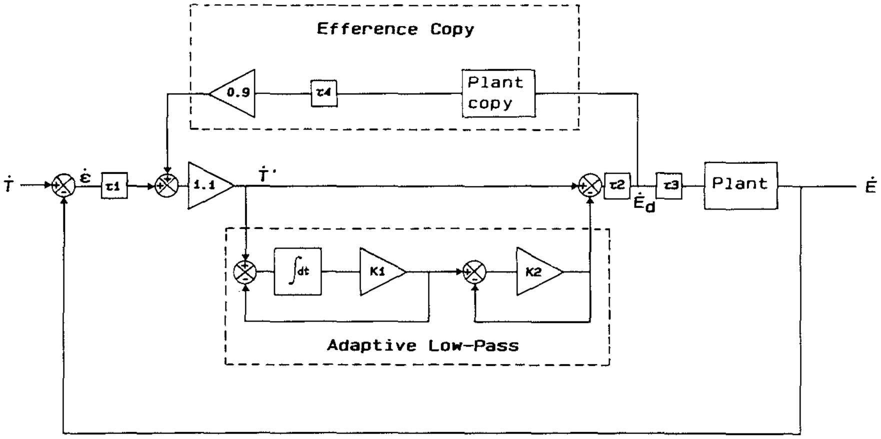
$$H(s) = 1 - K2/((K2+1) * (K1*s + 1)) = ((K2+1)*K1*s + 1)/(K1*s + 1)$$

The two parameters of the adaptive lag element (K1,K2) are modified during pursuit depending on frequency of the stimulus (f). K1 and K2 depended on f in such a way that the phase lag of the oculomotor delay was fully compensated at a slightly lower frequency ($f_c = f * 0.87$).

$$K1 = f_c$$

$$K2 = \tan\left(\pi/8 + (\tau 1+\tau 2+\tau 3)*f_c\right) - 1$$

During the simulation of foveal stabilization the retinal slip ($\dot{\epsilon}$) was set to zero.



(Vossius, 1961 as cited in Becker and Fuchs, 1985). The frequency characteristic of the smooth component of pursuit of pseudo-random target movement is indeed reminiscent of that of a lead-element, tuned to achieve zero phase lag at an intermediate frequency of the spectrum of the target motion leading to low frequency phase lead (Yasui and Young, 1984; Collewijn and Tamminga, 1984) and low frequency gain reduction (Collewijn and Tamminga, 1984; this chapter). The parameters of the lead-element would depend on the input waveform. Another piece of evidence which points into the direction of a lead-element, enclosed within the positive feedback loop, is our finding that when the target remains stationary for half a cycle after the target velocity zero-crossing, a corrective eye acceleration starts much earlier than when the target continues to move at the peak velocity after the sinusoidal target motion reached its peak velocity. In the former case the onset of the constant velocity epoch is coincident with a target acceleration step, because the target acceleration is maximum at the extreme positions of the sine wave but zero when the target remains stationary, while in the latter case target acceleration is zero at the onset of the ramp motion. Hence, if the eye velocity is in part determined by the target acceleration (which is the case when a lead element is present between retinal input and the motor output), then the early start of the corrective eye acceleration when the target remains stationary in an extreme position may be interpreted as the response to the target acceleration step.

Fig 6.12 shows the model structure which incorporated the above notions. The model was implemented as a FORTRAN program on our PDP 11/73 mini computer. The parameters of the lead element depended on frequency of the stimulus. The frequency was estimated in the model from the time interval (T_z) between two successive velocity zero crossings of the target.

$$f = 1/(2*T_z)$$

Thus the parameters of the lead element were constant for at least one half-cycle of the stimulus. The relationships between the parameters and the frequency (f) were chosen suitably to compensate the phase lag due to the oculomotor delay (100 msec: Carl and Gellman, 1986) at a frequency slightly below the current estimate of the oscillation frequency.

As shown, the frequency characterists of smooth pursuit of the pseudo-random as well as the sinusoidal target movement were simulated with reasonable accuracy (Fig 6.5). The main deviations are the overestimated low frequency gain reduction for the pseudo-random stimulus with a high frequency content and the ca 10 deg larger phase lead of the model at the low frequencies of the pseudo-random stimulus. Qualitatively, the model simulated the response to foveal stabilization and constant velocity epochs quite well. The model generated after foveal stabilization a damped sinusoidal eye movement with an appropriate duration of the initial eye acceleration (Fig 6.7), but the magnitude of the initial eye acceleration generated by the model was too small. The slope factor of a_I as a function of a_T of the model was -0.27 whereas the same slope factor for our subjects ranged from -0.447 to -0.518. When the target remained stationary for half a period after the target velocity zero-crossing the model generated a corrective eye acceleration after 140 msec (observed T_c values were on the average 180 msec) but when the target continued to move at the peak velocity for half a period the model responded with eye velocity decaying to a plateau level which was reached after more than a quarter of a period (Fig 6.9). A decay of the eye velocity to a plateau level was observed only in 56% of the measurements in which the target continued to move at the peak velocity, while in the other cases the subjects made a corrective eye acceleration after slightly more than a quarter period of decreasing eye velocity in reponse to the ramp motion of the target. Like the observed responses, the peak slip velocity of the model in response to the ramp motion of the target increased for increasing target frequency, and was about twice as large for ramp target motion starting at the peak velocity as for the target remaining stationary at the peak target position. However, the magnitude of the peak slip velocity of the model was for every condition less than the observed values (Fig 6.9). Both the initial acceleration and ϵ_c simulated by the model were too small. Increasing the gain in the forward path from 1.1 to 1.4 decreased the discrepancy between the subject's responses and the model response to stabilization, but the low frequency gain reduction and phase lead of the model for tracking of the pseudo-random stimulus became larger.

Thus, although the model simulates the frequency characteristics of smooth pursuit of sine waves and pseudo-random target motion quite satisfactorily it clearly fails to reproduce (with the same parameters) the responses of the smooth pursuit system to foveal stabilization or to a disturbance of the sine with a ramp motion of the target. However, in view of the qualitative correspondence between the model and the observed responses I interpret the discrepancies not as decisive evidence against a role of adaptive lead compensation for smooth pursuit but rather feel that the model is incomplete. Perhaps, prediction in human smooth pursuit results from contributions of a hierarchy of control systems, depending to an increasingly larger extent on cognitive processes to predict the future course of the target, of which the control system here presented may constitute the lowest level. The present model cannot reproduce predictive eye movements like the smooth drift of the eye before expected target steps or the expected onset of a ramp (Kowler and Steinman, 1981; Becker and Fuchs, 1985) since prediction of the model depends on the slip velocity and the recent history of the periodicity of the target motion. Different expectations about the duration of the disturbance of the sine may be responsible for the occurrence of a corrective eye acceleration in some measurements but not in other ones when the sinusoidal target movement was replaced by a ramp motion at the peak velocity of the sine. Also, the occasionally observed abrupt reversals of the eye acceleration during foveal stabilization are hard to simulate with sums of exponential functions, but may be compatible with abrupt reversals in the expectation of the subject concerning the direction of the target motion. However, it seems premature to incorporate into the model an effect of target movement expected by the subject since there is a lack of data concerning the way expected target movement depends on prior target movement for continuous target motion.

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CHAPTER VII: CONCLUDING REMARKS

The purpose of OKN and smooth pursuit eye movements is to achieve a high degree of image stability for the entire visual field or at selected locations on the retina, respectively. The quality of the image stability attained depends on several factors. Properties of the stimulus (motion parameters, structure and extent of the target), the retinal location stimulated (central or peripheral), central processes (attention, expectations concerning the target motion, use of non-visual sensory information concerning the target motion) and motor factors influence the properties of the smooth eye movements. A number of these factors was investigated and the main findings will be summarized and discussed.

Stimulus factors

The gain of the smooth component of following eye movements depended on the velocity and the extent of the target. The gain decreased as a function of increasing velocity, commonly resulting in slip velocities in excess of 20 deg/sec at the highest stimulus velocity (90 deg/sec). These high slip velocities adversely affected visual acuity. Most subjects perceived a point target as smeared into a line. Gain increased markedly when the extent of the target increased from a point target to a nearly full-field stimulus. However, details of a moving pattern were not only better pursued because of the larger extent of the stimulus, but also because the point target constrained the trajectory for pursuit to its own sawtooth trajectory whereas the full-field pattern allowed the subject to pursue with a nystagmus of his own preferred rhythm and amplitude. The planning of the saccades, in the fixed rhythm imposed by the trajectory of the point target, somehow appeared to affect the smooth component of pursuit adversely.

Another stimulus factor screened in the present investigations was the direction of stimulus motion. Horizontal direction of stimulus motion affected tracking idiosyncratically. I could not find evidence for a temoporo-nasal asymmetry of the OKN or smooth pursuit either. This contrasts with the clear preference for temoporal-to-nasal stimulus motion of the OKN, as described for animals with the eyes placed laterally. In humans, the OKN is largely under cortical control, using binocular information, resulting in an absence of horizontal directional preponderance of the OKN. For vertical OKN, however, a clear preference for upward pattern motion occurred, which conforms to the vertical directional asymmetries observed in other animals. This may reflect a lower performance of the velocity-storage mechanism for downward stimulus motion but this hypothesis must be tested in additional experiments involving human optokinetic after-nystagmus.

Prediction in human smooth pursuit

The non-linearity of the smooth pursuit system is of a larger complexity than a velocity saturation. This is evident from the dependency of the frequency characteristic of smooth pursuit on the waveform of the target motion. Such a non-linearity pervades the entire operating range of the smooth pursuit system. This non-linearity has been interpreted as evidence for the input-adaptive character of the smooth pursuit system (Yasui and Young, 1984). My attempt to describe these so called predictive properties of smooth pursuit quantitatively were only partly successful. A model in which the rhythm of the target oscillations was used to tune the smooth pursuit system to the higher frequency components in the stimulus was reasonably accurate in its description of the frequency characteristics of normal pursuit. However, results were inaccurate for pursuit of unexpected 'disturbances' of a predictable target motion.

The prediction of 'events' like the onset of target motion (resulting in anticipatory eye movements; Kowler and Steinman, 1979ab, 1981) may involve predictive processes of a different kind than the prediction of on-going target motion. The magnitude and direction of anticipatory eye movements is clearly not (as in the above model) related to the immediate history of target motion, which is zero. Rather, the change in the direction and magnitude of the anticipatory eye movements appears to be determined in a probabilistic way by the correspondence between the anticipated and the actual target motion in the previous trials (Kowler et al., 1984a).

An even higher level of prediction may be conceived of, which involves associative relations between different items in the visual field. For example, when during pursuit of a running rabbit I recognize a dark blob in my visual field as the rabbit's burrow, I most likely use this information to direct the eye, as the knowledge that the rabbit is likely to head for its burrow constrains the future trajectory of the target considerably.

Clearly, the latter two examples involve the use of extra-visual information to generate anticipatory eye movements. Hence, (non-linear) servo-models by itself provide only a limited tool to understand the predictive properties of pursuit.

Attentional factors

Attention constitutes the interface between sensory information and motor activity. It is under voluntary control and may be directed by instructions. Attention is selective in the sense that higher order processing (which is assumed to be limited in capacity; cf. Koch and Ullman, 1986) is allocated to a limited number of (sensory) inputs or motor activities at a time. It is well known that the general level of attention affects the probability and speed of identification of targets in psychophysical experiments. Similarly, the performance on oculomotor tasks is affected by the level of attention; the gain of the vestibulo-ocular reflex decreases when the subject is distracted by performing mental arithmetic and the following eye movements decrease in speed when the subject's attention to the moving stimulus is lowered by the instruction to attend to an imaginary stationary target. This does not imply that the OKN elicited by the stimulus under the latter instruction may be equated to smooth pursuit with a lower gain. OKN has properties of its own (as vertical directional asymmetries and those summarized in the introduction) which make it likely that OKN and smooth pursuit involve different neural circuitry to a large extent.

In psychophysical tasks, spatial cues are an especially important guide to direct attention. The speed of detection of a target is enhanced by advance cueing of the location of the target (see Johnston and Dark, 1986, for a review) and detection of the target is inhibited when an invalid cue is given. The focus of attention can thus be directed to retinal locations other than the fovea to enhance performance in that region. A related phenomenon is the ability of humans to pursue extra-foveal targets (Winterson and Steinman, 1978; Barnes and Hill, 1984; Collewijn and Tamminga, 1984) which involves the reduction of retinal slip at a selected region in the peripheral retina. Selective attention to the target may even be counter-productive for pursuit in special stimulus conditions. When subjects attended to a *particular* detail of a rotating multi-contoured pattern, pursuit eye velocity was lower than when *any* detail was valid as a target. The mechanism by which selective attention reduced the facilitatory effect of the background, moving in conjunction with the point target, is not understood. It is clear, though, that the proposed mechanism (chapter IV) of antagonistic weighting of the slip velocity in the central and the peripheral part of the retina must be rejected.

A single mechanism of selective attention may be common to smooth pursuit eye movements and perception (Khurana and Kowler, 1986). In a concurrent pursuit/psychophysical task, subjects searched in an array of 4 moving strings of 4 characters for the occurrence of 2 numerals. One numeral appeared in a pair of 'target' strings the other numeral in a pair of 'background' strings. Target and background moved at different velocities. Search performance was 2 to 3 times better for a pursued target than for the background. As attention was directed to both moving pairs of strings, pursuit eye velocity was influenced by the motion of the target and the background. The gain for pursuit of the target increased or decreased when the background moved faster or slower than the target, respectively. On the other hand, smooth pursuit eye velocity may practically equal the velocity of the target stimulus when the target and the background are superimposed and consist of similarly structured patterns of equal luminance, provided the subject attends exclusively to the target (Kowler et al, 1984b). These latter authors suggested that for instances in which stationary backgrounds inhibited smooth pursuit, the inhibitory effect was mainly caused by insufficient effort of the subject to attend to the target. My data do not support this notion; a stationary background reduced the smooth pursuit of a point target by 10 to 75% depending on the target velocity although subjects were instructed to attend exclusively to the target. Even when the target and the background were shown in different retinal locations, the stationary background exerted an inhibitory effect on pursuit of the point target. Apparently, the degree of dissociation of target and background motion for pursuit depends on the configuration of the target and the background, and their relative velocity. Thus, attentional mechanisms may be only partly successful in transmitting exclusively the velocity information of the target to the motor system. This does not necessarily point to limitations of the mechanism of selective attention. It may also result from target-background interactions at the level of the velocity detectors; i.e. the attentional mechanism may correctly identify the retinal channels which carry information about the target but the information conveyed by these channels may not be necessarily determined exclusively by the motion of the target.

Stabilization of the image

It is a common technique in the study of servo-control systems to artificially open the feedback loop in order to determine the properties of the controller directly. A recent trend in the literature is to consider the open-loop technique unsuitable for the study of the smooth pursuit system because the results would be dominated by idiosyncrasies and not reveal the properties of normal smooth pursuit (Steinman, 1986; Cushman et al., 1984). In my view this rejection of the open-loop technique needs to be qualified. By stabilizing the image on the retina the subject gains control over the target motion when he has voluntary control over his smooth eye movements. My results indicate that voluntary control over the smooth eye movements is large whith a horizontally foveally stabilized target, even if non-stabilized motion is presented in the retinal periphery. The significant idiosyncrasies, reported in the literature, of smooth eye movements with horizontally stabilized targets, may result from voluntary influences of the subject which are not adequately constrained by instructions to pursue normally. Such instructions become paradoxical when a subject notices that the target is stabilized, as the subject then knows that part of the motion is self-generated. Thus the open-loop technique allows a direct investigation of the relationship between retinal motion and pursuit eye movements, but its value is limited because the properties of the system may change by voluntary influences on the part of the subject. The way out of this dilemma is to prevent the subject from noticing the occurrence of the stabilization. My results indicate that this is possible for brief periods of stabilization on the fovea, provided that the onset of the stabilization is masked. Indeed, for such a stimulus the degree of variation in the response to stabilization across subjects is comparable to the degree of idiosyncracy in normal pursuit experiments. In conclusion, I consider the open-loop technique not entirely unsuitable for the study of the smooth pursuit system. However, adequate precautions must be taken to minimize the likelihood of the subject changing his tracking strategy in response to the stabilization.

Motor effects

It was a surprising result that the eyes did not move perfectly yoked during horizontal OKN. The velocity of the temporally moving eye was lower than that of the nasally moving eye. This occurred for monocular viewing with either eye and for binocular viewing, which suggests not a visual but a motor origin of the asymmetry. Progressive convergence of the eyes, as may be expected to occur for unidirectional stimulus motion in the presence of such an asymmetry, was not observed in our recordings; possibly a similar but oppositely directed asymmetry of the quick-phases had compensated the unequal displacements of the eyes during the slow-phases. It seems prudent to postpone speculations concerning the function - if any - of this asymmetry until its motor nature and its quantitative relationship to the (as yet hypothetical) asymmetry of the quick-phases is better understood.

Despite a wealth of descriptive physiological observations on the properties of human OKN and smooth pursuit we have only a limited insight in the basic processes determining the observed relationships between the eye movements and the stimulus motion. Especially for smooth pursuit, it has become clear that apart from visual information, non-visual sources of information (sensory and memory-related) are used suitably to acquire the goal of maintaining the target on the fovea. For a full understanding of the anticipatory and attention-related properties of smooth pursuit, incorporation of models of cognitive processing into the existing servo-control models seems necessary. This, in turn, may require a much more detailed modelling of the visual process than the usual reference to the visual system in terms of retinal slip velocity and retinal position error in servo-control models.

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SUMMARY

The properties of human optokinetic nystagmus and smooth pursuit were investigated by means of a scleral coil induction method. Horizontal and/or vertical eye movements were routinely decomposed in their smooth and saccadic parts; only the smooth component was analyzed. Stimuli consisted of point targets or full-field patterns moving sinusoidally, pseudo-randomly or with a constant velocity. Different instructions, aimed at eliciting reflexive or voluntary eye movements, were given to the subjects.

Neither OKN nor smooth pursuit showed asymmetries related to the horizontal direction of the stimulus motion. In contrast, the OKN showed a clear preference for upward pattern motion. The mean gain was ca. 0.15 larger for upward than for downward motion of the pattern. Vertical pursuit was not investigated in the present studies but, according to the literature, vertical pursuit of small targets is symmetrical. A statistically significant increase in the gain of the OKN occurred when the pattern motion was viewed binocularly instead of monocularly with either eye, but the effect was not consistently present. Remarkably, the eye movement during horizontal OKN was not perfectly conjugate. The motion of the eye moving in the nasalward direction was faster (difference in gain: ca. 4%) than the motion of the other eye, irrespective of the viewing conditions. This suggests that the asymmetry is located in the efferent path of the OKR.

The mean gain of the OKN elicited by unidirectional rotation of a full-field pattern, was always less than 0.85 and decreased as a function of increasing stimulus velocity. The decline of the OKN gain was steeper for vertical than for horizontal motion. Increased attention of the subject to the stimulus resulted in an increase of the gain; when the subject tracked arbitrary details of a horizontally moving pattern, the gain of the smooth component of the following eye movement was ca. 0.15 larger than for OKN. However, the decline of the gain as a function of increasing stimulus velocity was similar for OKN and smooth pursuit.

The gain of smooth pursuit depended on the extent of the stimulus. For identical stimulus velocities, pursuit of a point target on a dark field was always slower than when a striped pattern moved in conjunction with the same point target. This held true even when special measures were taken to remove the temporal and spatial constraints, imposed on pursuit by the fixed trajectory of a point target, which are absent for pursuit of details of a rotating full-field pattern. By the addition of the moving pattern to the point target the gain increased by ca. 0.05-0.20, depending on the stimulus velocity.

Surprisingly, pursuit of arbitrary details of a rotating pattern was even better than pursuit of the point target on the pattern. The instruction to direct the attention to a particular detail of the moving pattern apparently influenced pursuit adversely.

Based on results from open-loop fixation experiments in the literature, the hypothesis was raised that the attempt to foveate a particular detail might invoke an antagonistic weighting of the slip velocity in the central and the peripheral part of the retina. Spatial integration of these antagonistic inputs would reduce the facilitatory effect on the gain of the background moving in conjunction with the point target. This hypothesis was not confirmed by the experiments. Open-loop experiments aimed at a direct test of this hypothesis gave idiosyncratic results. Unidirectional horizontal background motion in the retinal periphery induced either opposite or following eye movements or a mixture of both, in different subjects.

Similarly, I could not find evidence for a facilitatory effect of slip velocity, opposite to the motion of a pursued point target, in the retinal periphery. The gain for pursuit of a point target on a stationary background, confined to the retinal periphery, was reduced compared to pursuit of a point target on a dark field.

The idiosyncratic differences in the eye movements induced by a moving background during fixation of a foveally stabilized target appeared to reflect idiosyncratic differences in the subject's preference to make either opposite or following eye movements. Subjects possessed considerable voluntary control over their smooth eye movements with a foveally stabilized target. When the target was viewed on a dark field, all subjects were able to make smooth oscillatory eye movements when they attempted to imitate their own normal pursuit of a sinusoidal target movement (0.2 - 0.7 Hz), directly preceding the (horizontal) stabilization on the fovea. The frequency of the imitating eye movement was in general lower than the frequency of normal pursuit by 2 - 35%. While fixating a foveally stabilized point target superimposed on a large, sinusoidally moving non-stabilized background, all subjects were able to make either no eye movements, eye movements nearly in phase with or eye movements nearly in counterphase with the background movement, depending on the instruction to imagine the target as head-stationary, moving in phase, or moving in counterphase with the background. In most subjects the ability to make eye movements opposite to the background motion was limited to predictable, periodic motion. Thus, the results of open-loop experiments are prone to willful manipulation by the subject which makes such experiments difficult to interpret with respect to normal pursuit. On the other hand, when the stabilization is brief and its onset carefully masked, idiosyncrasies in the response are moderate and results relevant to the normal operation of the smooth pursuit system may be obtained.

The frequency characteristics of human smooth pursuit depended on the frequency content of the stimulus. The gain of the smooth component was close to unity and the phase lag nearly zero for sinusoidal target movement. For pseudo-random stimuli, the gain of the lower frequency components was reduced and a phase lead occurred with respect to the target motion. This non-linear behaviour of the smooth pursuit system is generally attributed to the activity of an intelligent brain, attempting to predict the future course of the target. The state of the predictive process was probed by temporarily stabilizing the target on the fovea at unexpected instants. After stabilization during pursuit of sine waves, the eye continued to oscillate at approximately the same frequency as prior to the stabilization, but usually for less than one period. The unidirectional eye acceleration was ca. 70% of the unidirectional target acceleration prior to the stabilization. After foveal stabilization during pseudo-random target motion, the eye continued to oscillate at approximately the highest frequency of the target motion. Thus, the smooth pursuit system adapted to the waveform of the input signal and was tuned to the highest frequency component in the stimulus. When sinusoidal target motion was briefly replaced by a ramp motion with a smooth transition in the target acceleration, the eye continued first to oscillate for more than a quarter of a period despite the retinal slip velocity and the position error created by this eye movement; only after this delay a corrective eye acceleration started. In contrast, when a step in the target acceleration was coincident with the onset of the ramp motion, a corrective eye acceleration occurred ca. 180 msec after the transition. This suggests that target acceleration is monitored by the smooth pursuit system and possibly used by the predictive process.

SAMENVATTING

Een belangrijke functie van de beweeglijkheid van onze ogen is het voorkomen van bewegingsonscherpte. Deze treedt op wanneer het beeld van de omgeving snel over het netvlies slipt. Retinale slip wordt gereduceerd door een oogbeweging te maken in de richting waarin het beeld zich verplaatst. De aanleiding tot het ontstaan van retinale slip kan gelegen zijn in een beweging van het lichaam of het hoofd, waarvan het effect dan gecompenseerd moet worden door een oogbeweging. Het is duidelijk dat dergelijke bewegingen altijd een verschuiving van het hele beeld over het netvlies veroorzaken. Anderzijds kan de retinale slip haar oorsprong vinden in de beweging van een voorwerp in de buitenwereld. De slip is dan niet even groot in alle blikrichtingen en wordt dan gereduceerd in slechts een deel van het blikveld door een volgbeweging.

Compensatoire oogbewegingen verlopen automatisch en komen voor bij zulke uiteenlopende diergroepen als kreeftachtigen, vissen, reptielen en zoogdieren. Zij worden in het algemeen opgewekt door een combinatie van visuele prikkels en prikkeling van zintuigen die de beweging van het hoofd in de ruimte en t.o.v. de nek detecteren. Visuele prikkeling alleen is echter voldoende om compensatoire oogbewegingen op te wekken -de z.g. optokinetische nystagmus (OKN). OKN treedt op in alledaagse situaties als wanneer we uit het raam van een trein staren, die met constante snelheid rijdt.

Gladde volgbewegingen zijn kenmerkend voor dieren met een goed ontwikkelde fovea. De fovea vormt het centrale deel van het netvlies, waar de gezichtsscherpte het grootst is. Zij bestrijkt slechts 0.01% van het retinale oppervlak. Om een (bewegend) voorwerp scherp te zien moet het op de fovea afgebeeld blijven. Dit is een tweede functie van de oogbewegingen. Volgbewegingen treden niet reflexmatig op maar vereisen de intentie van de waarnemer.

OKN en vrijwillige volgbewegingen worden gezien als het product van twee verschillende neurale systemen, die de oogbeweging sturen. In dit proefschrift wordt de vraag behandeld in hoeverre deze twee systemen verschillen met betrekking tot hun vermogen het beeld te stabiliseren. Daartoe werd de gladde component van de oogbeweging gemeten m.b.v. een op het oog geplaatste siliconen ring, die een aantal windingen koperdraad bevatte. In een homogeen magneetveld leiden oogbewegingen tot inductiespanningen in de met het oog meedraaiende spoel, die een maat vormen voor de verdraaiing van het oog.

De belangrijkste gegevens, die dit onderzoek heeft opgeleverd zijn de volgende,

- OKN noch glad volgen leidt tot een volledige compensatie van de slip van het beeld. OKN reduceert de slipsnelheid minder dan het gladde volgsysteem ongeacht de snelheid van de patroon beweging. Voor horizontale patroon beweging is de compensatie even goed in beide richtingen voor beide systemen, maar de OKN vertoont een uitgesproken betere stabilisatie van het beeld voor opwaartse patroonbeweging dan voor neerwaartse patroon beweging.

- In tegenstelling tot dieren met lateraal geplaatste ogen en zonder fovea (b.v. ratten en konijnen) is er bij de mens geen asymmetrie aantoonbaar in de stabiliserende eigenschappen van de monoculaire OKN met betrekking tot temporo-nasale stimulus beweging. Echter, de ogen bewegen tijdens horizontale OKN niet zuiver conjugaat. Het oog dat naar de neus draait beweegt significant sneller tijdens de langzame fasen dan het andere oog, dat tegelijkertijd naar de slaap draait. Het gegeven, dat dit verschil niet afhankelijk is van de wijze van waarnemen (monoculair of binoculair) suggereert, dat deze asymmetrie van motorische oorsprong is.

- Het gladde volgen van puntdoelen (een vogel tegen een onbewolkte hemel) resulteert in een grotere retinale slip dan het volgen van details van een en-bloc bewegend patroon (b.v. de gezichten van passagiers in een trein, die het station binnen rijdt). Dit verschil wordt niet alleen veroorzaakt doordat het grotere patroon een grotere informatie stroom omtrent de beweging verschaft dan het puntdoel, maar ook doordat het puntdoel het traject dat het oog moet volgen volledig vastlegt, waar het grote patroon op willekeurige momenten de fixatie van een ander detail toelaat, waardoor de waarnemer gedeeltelijk zeggenschap heeft over het door het oog te volgen traject.

- Een veelgebruikte techniek om de dynamische eigenschappen van het gladde volgsysteem en OKN te onderzoeken is retinale stabilisatie van de visuele prikkel. Langs electronische weg wordt de stimulus met het oog meebewogen, zodat de volgbeweging geen effect heeft op de positie van het beeld op de retina. Dit type experimenten heeft meermaals tot tegenstrijdige resultaten geleid. Onderzoek beschreven in hoofdstuk V heeft aangetoond, dat mensen op commando verschillende soorten gladde oogbewegingen kunnen maken met een foveaal gestabiliseerd doel, dat gezien werd tegen een bewegende achtergrond. Wilsinvloeden van de proefpersoon kunnen de resultaten van open-loop experimenten dus in hoge mate beinvloeden en bemoeilijken de interpretatie ervan met betrekking tot het normale (d.w.z. zonder compensatie van de visuele terugkoppeling) gladde volgen. Pogingen om de proefpersoon onwetend te houden van de stabilisatie van het doelwit falen voor langdurige stabilisatie (16 sec) maar dit blijkt wel mogelijk wanneer de stabilisatie kort (1.5 sec) duurt en haar aanvang en beeindiging gemaskeerd worden.

CURRICULUM VITAE

De auteur werd geboren te Amstelveen in 1957. Na in Rotterdam het Marnix Gymnasium te hebben doorlopen studeerde hij van 1975 tot 1982 Biologie aan de Rijks Universiteit te Utrecht. Van 1982 tot 1984 vervulde hij de vervangende dienstplicht aan het Laboratorium voor Vergelijkende Fysiologie te Utrecht. Het betrof een onderzoek naar akoestische orientatie vermogens van vissen onder leiding van Dr. Ir. A. Schuijf. In 1984 trad hij in dienst van ZWO (Medigon) om als medewerker van Prof. H. Collewijn het onderhavige onderzoek uit te voeren.

De auteur is getrouwd, heeft een zoon en werkt momenteel in dienst van ZWO (Psychon) aan een onderzoek naar bewegings perceptie door de mens op zijn voormalige Utrechtse werkplek.