THE ROLE OF COMPENSATORY EYE MOVEMENTS IN DYNAMIC VISUAL PERCEPTION

Zien onder dynamische omstandigheden: de rol van compensatoire oogbewegingen

PROEFSCHRIFT

ter verkrijging van de graad van
Doctor
aan de Erasmus Universiteit Rotterdam
op gezag van de rector magnificus
Prof.dr. C.J. Rijnvos
en volgens besluit van het College van Dekanen.
De openbare verdediging zal plaatsvinden op
woensdag 5 december 1990 om 15.45 uur

door

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Geboren te Steenbergen

universiteits Erasmus DRUKKERIJ
1990

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VOORWOORD

Dit onderzoek werd uitgevoerd binnen de vestibulaire werkkring verbonden aan de afdeling **Keel-, Neus- en Oorheelkunde** van de Faculteit der Geneeskunde en Gezondheidswetenschappen van de Erasmus Universiteit te Rotterdam.
Gezien het technische karakter van het werk bestond er een (nauw) samenwerkingsverband met de eveneens aan de Erasmus Universiteit verbonden afdelingen **Medische Technologie en Fysiologie I.**

Bij de totstandkoming van dit proefschrift zijn meerdere personen vaak op zeer uiteenlopende wijze betrokken geweest. Hun interesse en bereidwilligheid tot het geven van een kritisch oordeel, alsmede de waardevolle sociale contacten hieruit voortgekomen, verplichten tot een woord van dank aan:

De beide promotoren:
Prof.dr. C.D.A. Verwoerd en prof.dr. H. Collewijn,

De overige leden van de promotiecommissie, in het bijzonder:
Prof.dr. D. van Norren en prof.dr. G.H.M. van Lith,

De (voormalig) leden van de vestibulaire werkkring:
Mw. drs. Anne Kasteel-van Linge, dr. Marius Rodenburg, dr. Leon Boumans, en ing. Ronald Maas,

De (staf)leden van de afdeling K.N.O.-heelkunde, in het bijzonder:
Dr. G.A. van Zanten, dr. L. Ferman, dr. J. Verschuure, dr. P.P.M. Knegt en drs. R. Gerth van Wijk,

De (voormalig) leden van de afdeling Medische Technologie, in het bijzonder:
Mw. Ria van Kruining, dr. Ger Jan van der Wildt, drs. Piet Knol, ing. Cees Keemink en Cor Goedegebuur,

De beide paranimphen:
Caroline Klaver en ing. Ronald Maas,

De proefpersonen welke aan de experimenten deelnamen:
Drs. Karin van Geest, Baudowine Flipse, Caroline Klaver, Antoinette Laan, drs. Piet Knol en ir. Joan van Bruggen.

Het werk genoot de interesse van:

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is bereid geweest een tegemoedkoming in de vervaardigingskosten van dit proefschrift voor haar rekening te nemen als dank voor het feit dat wij gaarne uiting gaven aan onze goede ervaringen met het locaal anaestheticum *Novesine*®

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ABSTRACT

The smooth pursuit system is largely ineffective in reducing the amount of retinal image motion, in case the frequency of an oscillatory target movement exceeds the value of 1-2 Hz. Since it is unknown how vision itself is affected within that frequency range, the influence of pursuit eye movements on the visibility of various oscillating sine-wave gratings was investigated by simultaneous measurement of the eye rotation (infra-red reflection and scleral induction-coil method) and contrast thresholds under different viewing conditions.

It was found that the contrast sensitivity during ocular pursuit of a target superimposed on the moving grating (Expt. III) was equal to that measured during maintained fixation on a stationary target while the grating moved behind it (Expt. I, II), provided that the magnitude of retinal image motion (0-20 deg/s) was equal in both cases.

The first part of this study supported a further exploration of the visual performance under even more dynamic circumstances. Besides pursuit eye movements, head movements were introduced for the relation between visual performance and head movement is even less understood.

Since the gain of the vestibulo-ocular reflex (eye in head / head rotation) is never precisely unity, a considerable amount of retinal image motion exists during head movement. Still, the quality of vision (subjectively) remaines unaffected under these circumstances. In this context several physiologists postulated the exsistence of elaborate neural mechanisms, compensating for the surplus of retinal image motion. They based their arguments on the averaged retinal slip values, thereby discarding the effects caused by the actual sinusoidal movement of the retinal image as occurs with movement of the head.

In our view, vision might be intermittent, using exclusively the epochs of low velocity, that coincide with the reversals in head and ocular oscillation.

In order to prove our argument a number of experiments were carried out during which contrast thresholds were measured for a 6 c/deg stationary grating in the presence of sinusoidal oscillation of the head (2-6 Hz). The underlying data (Expt. IV) were analysed in two additional experiments (Expt. V, VI). The results of which showed that threshold contrast was determined by the reversal points of the ocular oscillation, where the retinal slip was *temporally* below 2 deg/s. Contrast sensitivity was highly correlated to the duration of the time intervals at which these slip values were present.

Finally, several (comparable) experiments were performed in which voluntary head movements were introduced, thereby simulating day-to-day viewing conditions (Expt. VII, VIII). The results led to the conclusion that the visibility of our environment as we experience it in the presence of natural head movement can be explained entirely from retinal phenomena.

CHAPTER 1

GENERAL INTRODUCTION

1.1 Evolution

Whether coincidental or not, the association of photoexcitable molecules with certain protein structures in the early plasma membrane, triggered the development of one of nature's most exquisite sensory systems. Although the individual photosensitive organelles merely detected changes in light intensity, they rapidly evolved into complex image decoding retinae. Subsequently, neural mechanisms, designed to screen out all but certain features of the encoded counterpart of the retinal image, led to the actual experience of vision.

The primitive eyes (like the compound eye of the insect) were firmly attached to the caput, therefore the occurence of image motion relative to the retina was omnipresent. Whereas movable eyes permitted a far more intricate and accurate scanning of the environment, the importance of retinal image motion in visual perception never became extinct. Eventually, the organisation and structure of the visual system adapated to its dynamic input in such a way that both spatial and temporal properties of the (moving) retinal image would be analysed in a comparable fashion.

To make use of the abilities of movable eyes almost equally important as the central interpretation of their neural signals was the development of a control mechanism directing them towards the object of visual interest. The necessary eye movements were generated by delicate intra-orbital muscles, innervated by various nuclei located in the pontine and mesencephalic regions of the brainstem.

Next to environmental circumstances, locomotor activity was the origin of a substantial amount of retinal image motion as well. In order to compensate for body movements, the sensory signals from the organs of equilibrium were more and more integrated in the neural networks concerned with ocular stabilization.

1.2 Retinal image motion

Ever since it became clear that human visual resolution was tuned to retinal image motion within a certain well defined velocity range (0.2-2.0 deg/s), it has been suggested that the oculomotor machinery might protect the optimal perceptual condition (Murphy, 1978; Skavenski, 1979; Duwaer, 1982). In this context, which is based on their functional support of the visual process, eye movements could be (arbitrarily) classified as either "fixational" or "compensatory". Both groups are composed of fast steplike displacements (saccades) interspaced by slow continuous movements of the eye. The small amplitude fixational eye movements provide the minimum amount of image motion required to prevent the perceptual fading of a stationary object in the environment (>0.2 deg/s; Kelly, 1979b). The larger, compensatory eye movements, to which we here confine our attention, reduce the surplus image motion (slip) to create acceptable image velocity values relative to the retina in the presence of which adequate vision of moving objects is still possible (<2.0 deg/s; Westheimer and McKee, 1975; King-Smith and Riggs, 1978; Flipse et al., 1988).

Most of our viewing stability exhibited during normal locomotor activity is brought about by the simultaneous action of two neural control mechanisms.

One mechanism, the smooth pursuit response may be regarded as a velocity servo-system with the aim of matching target velocity, largely independent of the initial position of the retinal image relative to the fovea. The other, the vestibulo-ocular reflex (VOR) is an open-loop system using information from the vestibular apparatus to generate eye movements compensatory to the angular acceleration of the head.

In a strict sense, ocular movements mediated by the neural pathways involved in the optokinetic nystagmus and the cervico-ocular reflex must be regarded as compensatory as well, however, in the presence of fixation targets their action is overruled by the former two more powerful systems (Meiry, 1971; Barnes and Forbat, 1979; Van Die, 1983).

Although the motor characteristics of the pursuit response and the vestibulo-ocular reflex have been studied extensively, their (precise) role in sustaining clear vision under dynamic day-to-day circumstances has not been fully established. In particular, serious doubts have arisen whether the relation between the magnitude of retinal image motion and the visual performance is essentially the same either with or without compensatory oculomotor activity.

1.3 Review of the literature

Miller and Ludvigh (1962) were the first to measure the perceptibility of details in moving objects, when the eyes were pursuing the test-object. Dynamic visual acuity, as they called it, remained unaltered in spite of a fivefold increase in target velocity (10-50 deg/s). Since Miller and Ludvigh (1962) did not measure the eye movements, they must have assumed that pursuit was virtually perfect within that target velocity range. Yet, further experimentation (Baloh et al., 1976 and Schalén, 1980) revealed serious imperfections in pursuit performance. With target velocities increasing from 10 to 50 deg/s a tenfold increase in averaged retinal slip (0.6-6.5 deg/s) could be measured.

Obviously, the iso-acuity values reported by Miller and Ludvigh (1962) are not easily explained by the relative motion between the optical image and the retina. Using sophisticated eye movement recording techniques, Murphy (1978) was in fact the first to describe the precise effect of pursuit eye movement on the visibility of moving objects. He simultaneously measured eye movements and the visibility of an oscillating grating (comparable to an array of small line-shaped acuity targets), while the observer smoothly pursued a target that was superimposed on the grating. The experimental results led Murphy (1978) to the conclusion that contrast sensitivity in the presence of smooth pursuit was equal to contrast sensitivity under non-pursuit conditions, provided that equal amounts of retinal image speed (unsigned velocity) were present. However, hindered by the occurence of saccades, intersperced in the smooth ocular movement, Murphy (1978) discontinued the pursuit experiment when the retinal image speed (slip) was 1.2 deg/s.

This was below the retinal speed value of 2 deg/s at which the visual performance was known to decrease (Westheimer and McKee, 1975). Therefore the question remained as to how much retinal slip, caused by inaccurate pursuit eye movement, could occur before the visual performance was affected.

The relation between averaged retinal image motion and visual performance in case head movements are allowed is even less understood.
Benson and Barnes (1978) measured the visibility of small digits during whole body oscillation. They found that a significant increase in reading errors did not occur with oscillation frequencies up to 9 Hz. Although Benson and Barnes (1978) did not measure the eye movements in the upper frequency range (5-10 Hz), estimates based on other literature reports showed that with similar head oscillations the mean retinal image speed ranged between 1.9-5.7 deg/s. In the absence of vestibulo-ocular compensation, such image speeds were at least twice the amount tolerated by the visual system (Westheimer and McKee, 1975).
Steinman and Collewijn (1980) found averaged retinal image speeds in the order of 4 deg/s during voluntary head oscillations while their subjects fixed on a distant stationary target. The head movements had, subjectively, no marked affect on detailed vision. Steinman et al. (1985), verified these impressions psychophysically and found that natural retinal image motion, which occurs during voluntary head movement, was (indeed) less harmfull to the visual performance than might be deduced from earlier more conventional experiments (Kelly, 1979a, b). Furthermore, a (hypothetical), possibly vestibular, (sub)system was postulated that might correct for the surplus of retinal image motion, thereby protecting the visual system from a decrement in performance.

1.4 Present objectives

In the absence of compensatory eye movement, retinal image speeds less than 2 deg/s have no significant effect on detailed vision (Westheimer and McKee, 1975).

Yet, it appears that the tolerated slip-level may become several times greater once the appropriate amount of oculomotor activity is introduced. Central systems, activated by either smooth pursuit or vestibular signals, might be involved in the process of visual analysis. Since our visual perception during normal locomotor activity is largely dependent on both these systems the mechanisms hypothesized above might have serious implications for visual and oculomotor physiology.
A further and more complete insight in the exact relation between retinal slip and its effect on visual perception seems crucial. Similarly, the interpretation of clinical tests for visual and vestibular control of eye movement relies first of all on a proper understanding of all mechanisms (normally) involved in dynamic vision. The objective of the present study was therefore to unravel whether the retinal phenomena, produced by relative motion between the attended object and the eye could account for the quality of vision as we experience it during normal locomotor activity.

1.5 Outline of the experiments

The first part of this study is concerned with the perceptibility of moving stimuli in the presence of pursuit eye movements. The visibility of various sine-wave gratings (0.2-12 c/deg) was investigated by the simultaneous measurement of eye movements and contrast thresholds under several different viewing conditions.
The term "grating" indicates that the visual stimulus was composed of regularly alternating (vertical) light and dark bars. The "spatial frequency" (c/deg) of which refers to the density of the bars (cycles) per unit of visual angle. "Threshold contrast" (C_{min}) or "contrast sensitivity" ($CS = 1/C_{min}$), is defined as the minimal difference in relative illumination of the bars necessary to detect the pattern rather than an uniform ulliminated field.
The first three experiments were designed to produce a - more or less - controlled amount of relative motion between the visual stimulus (grating) and the retina.

Viewing conditions were as follows:

I Both the fixation-target and the grating were stationary.
II The fixation-target was stationary, while the grating was oscillated.
III Both fixation-target and the grating were oscillated.

The results of the actual pursuit-experiment (Expt. III), were explained in terms of the former two experimental findings (Expt. I and II).
In the next two chapters both passive (2-6 Hz) and active head movements (1-4 Hz) were introduced in order to simulate more and more physiological, unrestrained, viewing conditions:

IV With passive oscillation of the head, while viewing a stationary grating.

To establish whether a major contribution to the process of vision under these circumstances (Expt. IV) could be attributed to either the averaged or the momentary velocity component of the oscillating retinal image, two additional experiments were carried out:

V With immobilized head and fixed eyes; while the grating oscillated according to a triangular-wave in order to simulate the averaged retinal velocity component measured during experiment IV.
VI with non-continuous presentation of the stationary grating in order to simulate the momentary low velocity-component of the oscillatory gaze movement (Expt. IV).

In the final experiments, the identical pattern of retinal image motion, obtained during head movement, was reimposed on to the retina, in order to exhibit the involvement of a (hypothetical) central mechanism beneficial to the process of dynamic vision:

VII With voluntary head oscillation, while viewing an earth-fixed grating.
VIII In the absence of head movement, fixating a stationary target, while the grating oscillated according to the gaze movements recorded during the previous experiment (Expt VII).

CHAPTER 2

CONTRAST SENSITIVITY FOR OSCILLATING SINE-WAVE GRATINGS DURING OCULAR FIXATION AND PURSUIT

(The essentials of this chapter have been published in Vision Research, 1988, 28, 7, 819-826)

2.1 INTRODUCTION

The influence of pursuit eye movements on the visibility of moving targets has been measured by several investigators. The first systematic approach to the problem was made by Miller and Ludvigh (1962) who studied visual acuity with Landolt C's, during unidirectional pursuit eye movement. They found that the visual acuity, - under pursuit conditions, was barely influenced by stimulus velocities between 10 and 50 deg/s. Beyond the angular velocity of 50 deg/s, a marked deterioration in visual resolution could be demonstrated. Miller and Ludvigh (1962) concluded that imperfect pursuit eye movements led to a smearing of the retinal image, reducing its contrast and therefore its visibility. Their findings were (partially) substantiated by the findings of others at that time (Blackburn, 1937; Ludvigh, 1949; Pollock, 1953; Van den Brink, 1957). However, Miller and Ludvigh (1962) did not measure eye movements.

A good estimate for the averaged amount of retinal slip was found in data available in the literature. At target velocities between 10 and 50 deg/s, Baloh et al. (1976) and Schalén (1980), measured mean gain values of ocular pursuit near 0.94 and 0.87, which corresponded to averaged retinal slip values of 0.6 and 6.5 deg/s, respectively.

Applied to the data reported by Miller and Ludvigh (1962), this might suggest that during active ocular pursuit a tenfold increase in retinal image velocity caused no significant acuity loss.

Barmack (1970) and Brown (1972) measured visual acuity as well as eye movements, but neither could predict the acuity decline from their eye movement records.

Murphy (1978) tried to prove Miller and Ludvigh's hypothesis. He simultaneously measured eye movements (scleral induction coil technique) and the contrast sensitivity for a 5.14 c/deg sine-wave grating, under several different viewing conditions.

Under the first condition adopted in his experiment the subject maintained fixation on a stationary target, while the grating moved to and fro at a constant speed across the retina. This experiment showed that retinal velocities up to 2 deg/s did not alter the contrast sensitivity, suggesting that the visual system is quite tolerant to retinal image motion. Similar findings were reported by both Westheimer and McKee (1975) and Kelly (1979a, b).

Under the second condition in Murphy's experiment, the subject smoothly pursued a target that was superimposed on the sine-wave grating and moved with it. With reference to his first experimental findings, he concluded that, contrast sensitivity during smooth pursuit was equal to contrast sensitivity during maintained fixation on a stationary target, when equal amounts of retinal image speed were present. Unfortunately Murphy (1978) discontinued his pursuit experiment when the retinal image speed was only 1.2 deg/s, corresponding to target oscillations near 1 Hz (constant target velocity of 7 deg/s). This was below the retinal speed value of 2 deg/s at which the contrast sensitivity began to decrease, according to his first experiment. Proof of Miller and Ludvigh's hypothesis required demonstration of a change in treshold contrast to be related to a corresponding change in retinal slip velocity. Although Murphy (1978) intended to do so, his (second) pursuit experiment did not reveal such a decrease in contrast sensitivity.

Liu Yumin and Baichuan (1984) measured contrast sensitivity for several sine-wave gratings (0.75-12 c/deg) under ocular pursuit conditions. Their data did not provide new information, since they were unable to record the eye movements.

Therefore the question remains how much retinal image motion, caused by inaccurate pursuit eye movement (slip), can occur before the contrast sensitivity deteriorates. This question gaines particular interest in view of the estimates based on previous reports (Miller and Ludvigh, 1962), which suggest that a substantial increase in mean retinal slip caused no significant loss of acuity.

Most studies on the relation between contrast sensitivity and eye movements have been carried out with high spatial frequency gratings or Landolt C's. Therefore a second question is whether the relation between contrast sensitivity and retinal image motion (slip) under such conditions is essentially the same for both low and high spatial frequency gratings.

In order to answer these questions we measured the contrast sensitivity for several sine-wave gratings (0.2-12 c/deg), over a wide stimulus velocity range (0-100 deg/s), while simultaneously recording the eye movements, under three different viewing conditions (Fig. 1):

I Both the fixation target and the grating were stationary.
II The fixation target was stationary, while the grating was oscillated.
III Both the fixation target and the grating were oscillated.

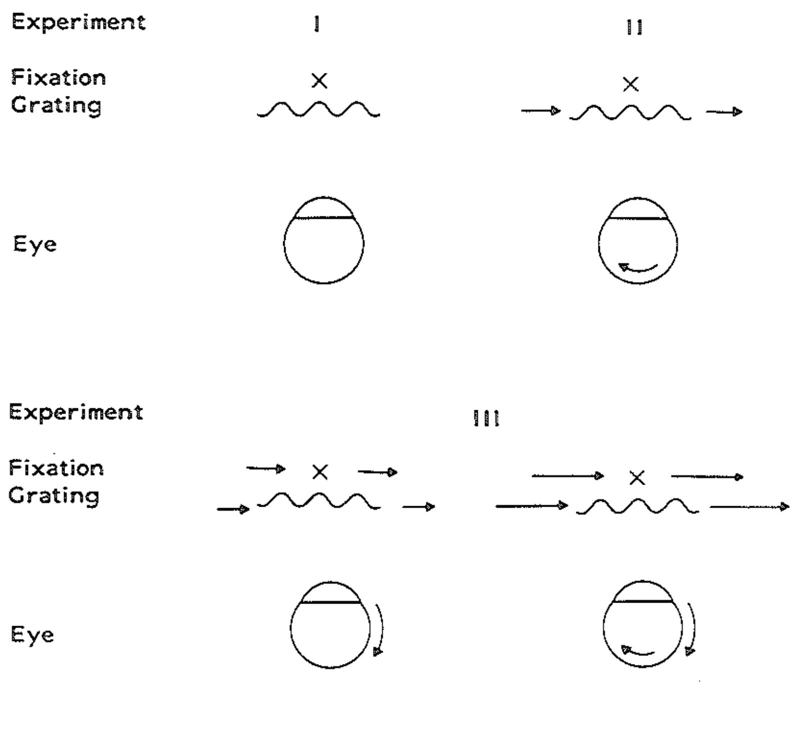


Fig. 1
The three experimental conditions. Intra-ocular arrows indicate the presence of retinal image motion. Extra-ocular arrows represent pursuit eye movements.

2.2 METHODS

The visual stimulus

The stimulus was a grating consisting of vertical bars, with the luminance sinusoidally modulated as a function of the position in the horizontal direction. The stimulus field was rectangular, with a height of 5 deg and a width of 10 deg (0.5 m in front of the viewing eye). It was viewed in a dark surround. The averaged luminance level of the stimulus was 1.6 cd/m^2 (measured with a digital photometer). A small bright fixation spot was placed in the centre of the grating. The stimulus was generated electronically and displayed on an oscilloscope screen (Tektronix 606B-monitor), at a 1000 lines/frame and a 1000 frames/s.
The grating as well as the fixation spot could be (separately) moved in a horizontal plane changing their position according to a triangular wave with a peak-to-peak amplitude of 8 deg. Although the electronic circuitry involved in stimulus motion and stimulus appearance was intemately related, both these qualities remained independent throughout all experimental conditions (stimulus velocity: 0-100 deg/s and spatial frequency 0.2-12 c/deg).
The experiments were carried out monocularly, the left eye being covered. During the experiments head movements were avoided using a chin and forehead rest, thus excluding vestibulo-ocular reflexes.
Since we used a stimulus width of 10 deg the total number of presented periods was such that the detectability of the spatial frequencies used (0.2-12 c/deg) was independent of the number of cycles displayed (Campbell and Robson, 1968; Van der Wildt et al., 1976)

Contrast sensitivity determination

Contrast (C) was defined conventionally as:

$$C = L_{max} - L_{min} / L_{max} + L_{min}$$

in which L_{max} and L_{min} represent the maximal and the minimal luminance levels present in the grating. During the actual experiments the contrast level in the grating was adjusted by electronic attenuation of the voltage on the luminance (Z-) input of the oscilloscope. Contrast values ranging from 0-90% were linearly proportional to the (Z-) input voltage. We checked this relation, measuring the luminance by means of a photodiode. The attenuator was controlled by a microprocessor, which changed the attenuation in steps of 1 dB, at a (variable) rate of 2-4 dB/s. To minimize stereotyping of the responses, slight alterations could be installed upon the contrast attenuation rate. The contrast (C) in the grating started at its maximum value ($C_{max} \approx 1$). This initial value could be decreased in case the subjects reported the occurence of afterimages during the trials.
Determination of the threshold contrast was based on a modified version of the von Békésy tracking method (Von Békésy, 1947) as described by Keemink et al. (1979). The subjects were asked to keep the continuous change in contrast on threshold detection level using a push-button which depoled the contrast attenuation. The mean value of the last 10 out of a total of 14 contrast reversals was taken as the observer's contrast threshold (C_{min}). To avoid onsett phenomena, the first 4 reversals were discarded. Contrast sensitivity (CS) was defined as the reciprocal of threshold contrast ($1/C_{min}$). At least 3 separate threshold determinations were done, of which the mean and standard deviation were calculated and plotted as such.

Recording eye movements

Eye movements were recorded with an infrared light (IR) reflection method, making use of a set of four IR-emitting diodes - two pairs on either side of the eye - and a set of four comparably situated IR photodetectors. Both sets were placed in a spectacle frame attached to the head by means of a band.
Eye rotation, within the range of this experiment (≤ 10 deg, peak-to-peak), was linearly proportional to the differential voltage between the detectors.

The deviation from linearity for horizontal eye movements over a range of 28 deg, expressed as a percentage of that range, was within 3%. The recordings permitted a precision in the eye rotation measurement of 5 minutes of arc.
Calibration of the eye movements was accomplished by voluntary saccades of 10 deg (stimulus field edges). A more detailed description of the IR reflection method is given by Reulen et al. (1988).

Analysis

Data acquisition and computation were carried out with a personal computer (Olivetti-M24) using a sample frequency of 200 Hz.
Pursuit velocity was calculated from the recorded eye rotation signal by applying a linear least-square fit to those parts that showed smooth pursuit performance. Saccades, counterphase eye movements and reversals in ocular pursuit direction were excluded and did not contribute to the calculation of the individual pursuit velocities (Fig. 2). Mean retinal speed was equal to:

$$1/N \cdot \sum_{i=1}^{N} | v_{stim} - v_{pst,i} |$$

in which v_{stim} and v_{pst} represent the stimulus and the pursuit velocity, respectively.

Subjects

The two subjects participating in these experiments had normal (corrected) eyesight and did not suffer from any neuro-ophtalmological disease. No optical aids were used during the experiments.

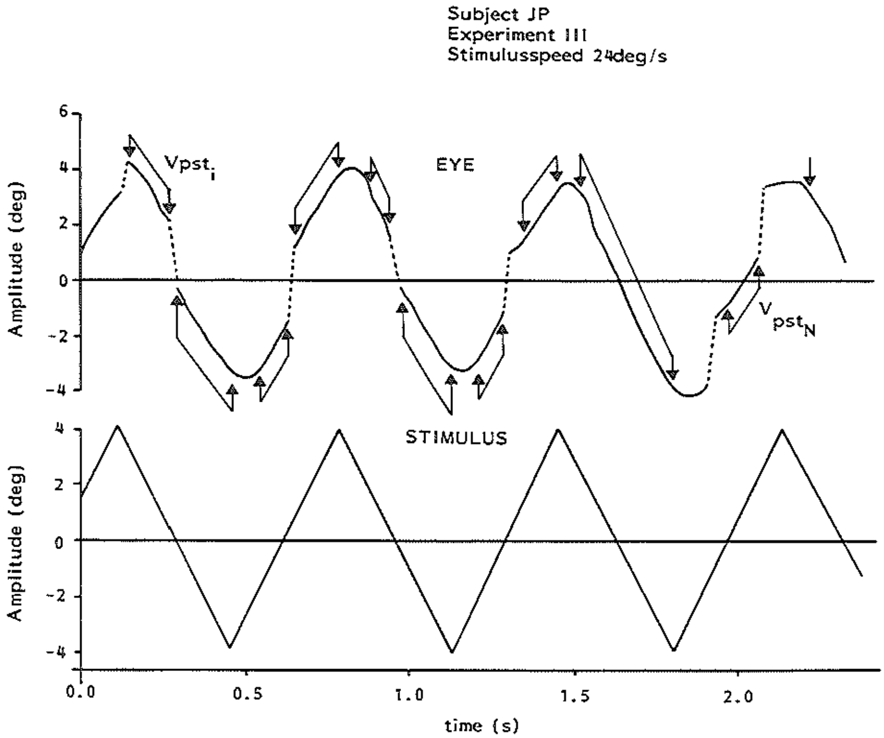


Fig. 2

Only those parts of the recorded eye movements that showed optimal pursuit performance were used to determine the (minimal) magnitude of retinal slip.

2.3 RESULTS AND DISCUSSION

Experiment I

The subject fixated a target which was superimposed on a grating. Both the fixation target and the grating were stationary. The experimental conditions are depicted in Fig.1 (Expt. I). Contrast sensitivity as a function of spatial frequency is presented in Fig. 3. The solid curves, known as contrast sensitivity functions (CSF's), were influenced by fixational eye movements.

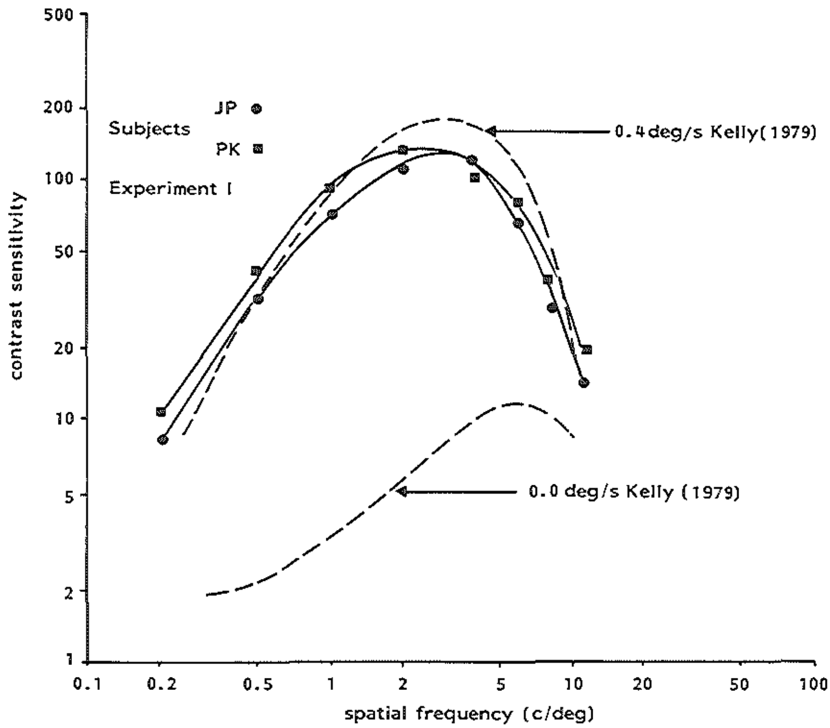


Fig. 3
The contrast sensitivity as a function of the spatial frequency of the grating. The solid curves (CSF's), show the results of experiment I. The dashed curves are taken from the stabilized contrast sensitivity results reported by Kelly (1979b).

Using more or less comparable stimulus parameters, Kelly (1979b) measured CSF's for stabilized constant velocity sinusoidal gratings, thereby excluding the effects of fixational eye movements (no major variation in contrast sensitivity was attributable to the difference in stimulus illumination between the two studies (Van Nes and Bouman, 1967)).

The CSF's obtained in experiment I were best fitted by Kelly's stabilized constant velocity results for 0.4 deg/s (Fig. 3). This might suggest that fixational eye movements of about 0.4 deg/s were present in our experimental setting.

Experiment II

In this experiment the subject fixed a stationary target, while the grating oscillated at a constant speed across the stimulus field (Fig. 1, Expt. II).

The eye movement records showed that, apart from the presence of fixational eye movements, the eyes maintained fixation on the stationary target, without being impeded by the moving grating. Others reported similar findings (Murphy et al., 1975; Murphy, 1978). So apart from fixational eye movements, retinal image speed was equal to stimulus speed under this experimental condition.

The relation between contrast sensitivity and stimulus speed (retinal image speed), for all spatial frequencies used (0.2-12 c/deg), is portrayed by the iso-contrast sensitivity contours in Fig. 4. The level of contrast sensitivity is expressed by numerical values (data points).

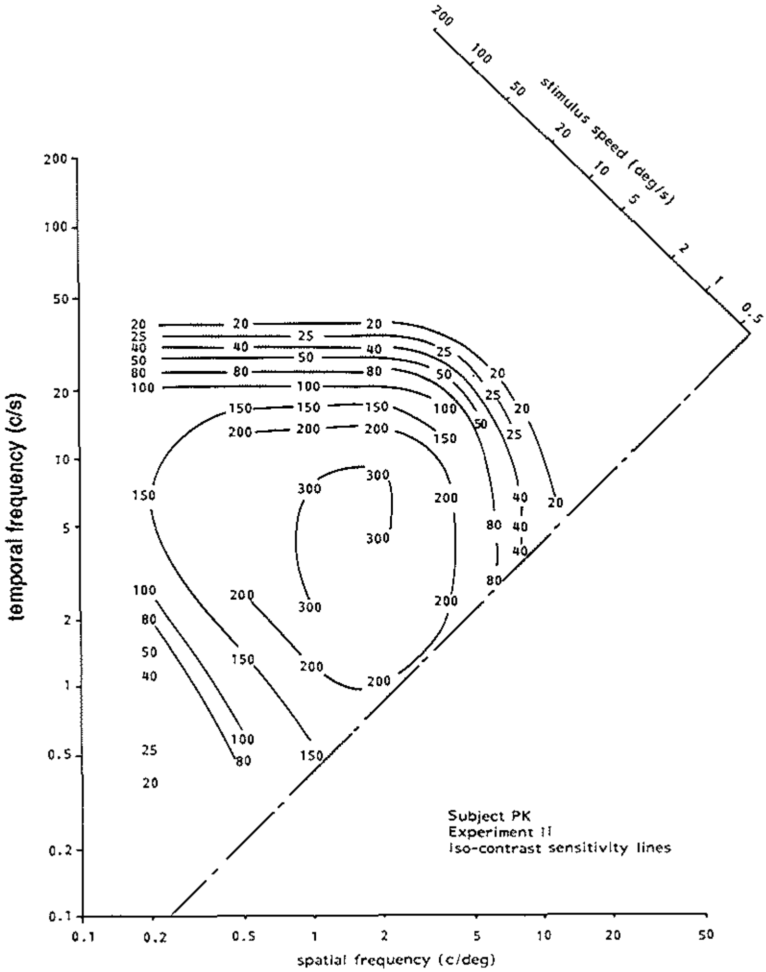


Fig. 4

Iso-contrast sensitivity contours showing contrast sensitivity versus stimulus speed (retinal speed, Expt. II). The spatial frequency of the gratings is plotted along the horizontal axis. The motion induced temporal frequency is plotted along the vertical axis. Note that optimal dynamic vision occurs with retinal image speeds near 2 deg/s (diagonal axis).

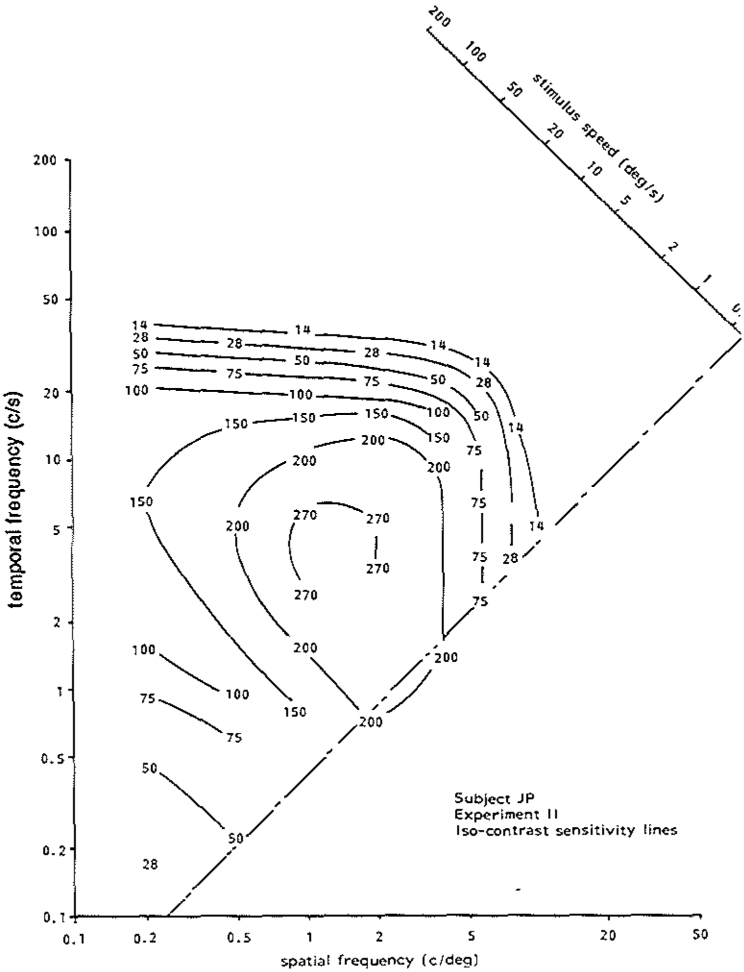

stimulus speed (deg/s)
200
100
50
20
10
5
2
1
temporal frequency (c/s)
spatial frequency (c/deg)
Subject JP
Experiment II
Iso-contrast sensitivity lines

Fig. 4
Legend (←)

Movement of a grating, relative to the retina, results in temporal illuminance changes in the stimulated area. The temporal frequency observed (f_t), is determined by two independent properties of the grating: its spatial frequency (f_s) and the amount of its displacement in time (retinal speed; μ). The relation between the spatial- and motion-induced temporal frequency is given by the following equation:

$$f_t = \mu \cdot f_s$$

Stricking parallels exist between spatial and temporal contrast perception (De Lange, 1957; Campbell and Green, 1965). Without question the symmetry of the contours reflect the age-old perceptual alliance between time and space (Van der Wildt, 1984).

The relation between contrast sensitivity and retinal image speed proved to be quite similar for the group of both low spatial frequency (<1 c/deg) and high spatial frequency gratings (>4 c/deg). Intermediate spatial frequency values (1-4 c/deg) had properties of both other groups. We therefore based our discussion on two spatial frequency values. The two selected values: 0.5 and 8 c/deg (dashed curves presented in Fig. 5) may be regarded as representatives of the low and the high spatial frequency groups, respectively. Both curves are in fact vertical cross-sections through the contourmap presented above.
The contrast sensitivity for the 0.5 c/deg-grating improved with the slightest increase in stimulus speed. Peak contrast sensitivity, at 20 deg/s (retinal speed), was followed by a rapid decline as stimulus speed further increased. These findings are in accordance with previous reports on this topic (Arend, 1976; Kelly, 1979b).

The contrast sensitivity for the 8 c/deg-grating changed only slightly as stimulus speed was increased up to 1.5 deg/s. Both Westheimer and McKee (1975) and Murphy (1978) reported similar results. Once the retinal speed of 1.5-2.0 deg/s was passed, the contrast sensitivity for the 8 c/deg-grating declined markedly.

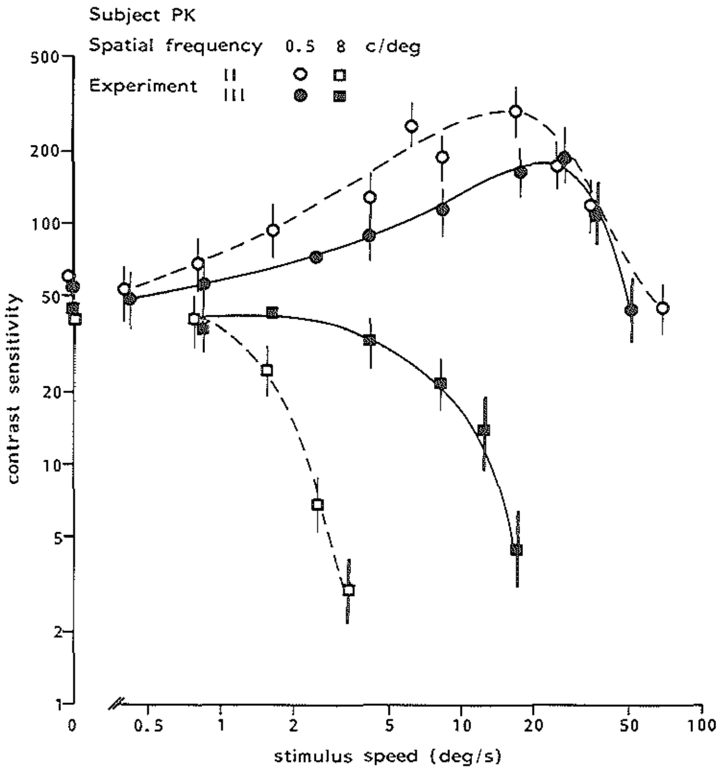
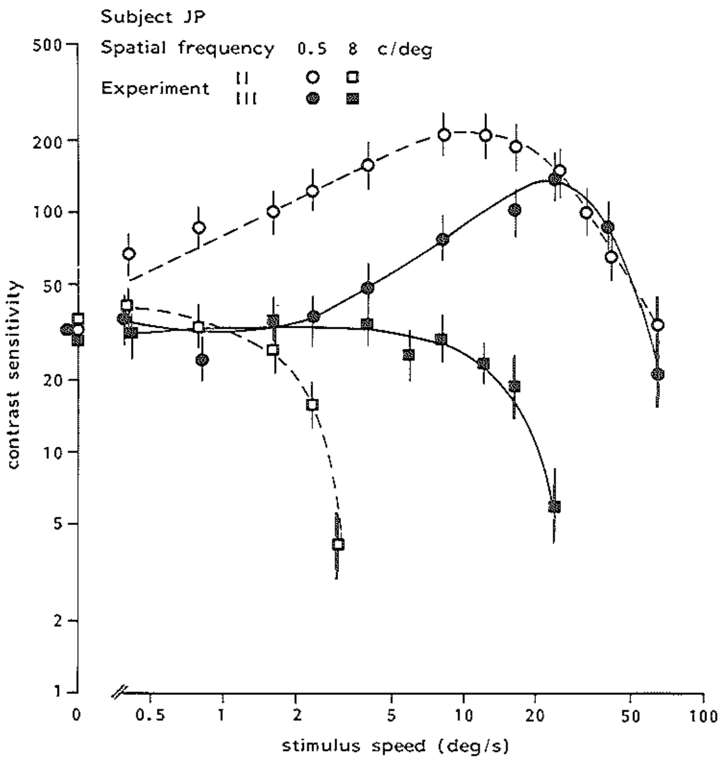


Fig. 5

Mean contrast sensitivity and standard deviation as a function of stimulus speed for two different spatial frequencies of 0.5 c/deg and 8 c/deg. The dashed curves show the results of experiment II. The solid curves show the results of experiment III.



Subject JP
Spatial frequency 0.5 8 c/deg
Experiment II
III
500
200
100
50
20
10
5
2
1
contrast sensitivity
0
0.5
1
2
5
10
20
50
100
stimulus speed (deg/s)

Fig. 5
Legend (←)

Experiment III

Both the fixation target and the grating oscillated at the same constant speed across the stimulus field. The subject was required to pursue the target as accurate as possible. As long as ocular pursuit was 'perfect', the retinal image would be stationary; hence contrast sensitivity under these circumstances was expected to be comparable with that measured in experiment I (Fig. 1, Expt. III, situation presented on the left side).

Once ocular pursuit became imperfect, additional retinal image motion would develop and therefore the contrast sensitivity would become comparable to the one measured in experiment II (Fig. 1, Expt. III, situation presented on the right side). The solid curves, presented in Fig. 5, describe the relation between contrast sensitivity and stimulus speed, as obtained during active ocular pursuit of the two gratings in question. The results for both subjects were qualitatively similar. At low stimulus speeds, contrast sensitivity values corresponded to those obtained in Expt. I (Fig. 3), indictating that there was little retinal image motion as long as pursuit performance was accurate. Once it declined, considerable retinal image motion developed and the solid curves assumed a form resembling those obtained during maintained fixation on the stationary target, as in Expt. II (Figs. 5, dashed curves). Retinal image movement proved to be favourable to the detection of spatial frequency values under 1 c/deg, therefore accurate pursuit performance led to a paradoxical suppression of the visibility of such gratings. On the other hand, adequate pursuit eye movements prevented a decline in the contrast sensitivity for spatial frequencies above 4 c/deg.

Thus, the main contribution of smooth pursuit eye movement to the process of vision is concerned with the protection of our ability to resolve spatial detail. When compared to conventional contourmaps, showing contrast sensitivity versus retinal motion (Kelly, 1979b; Fig. 4), plots picturing iso-contrast sensitivity versus target speed (Expt. III) beautifully illustrate the effect of compensatory eye movement on dynamic vision (Fig. 6).

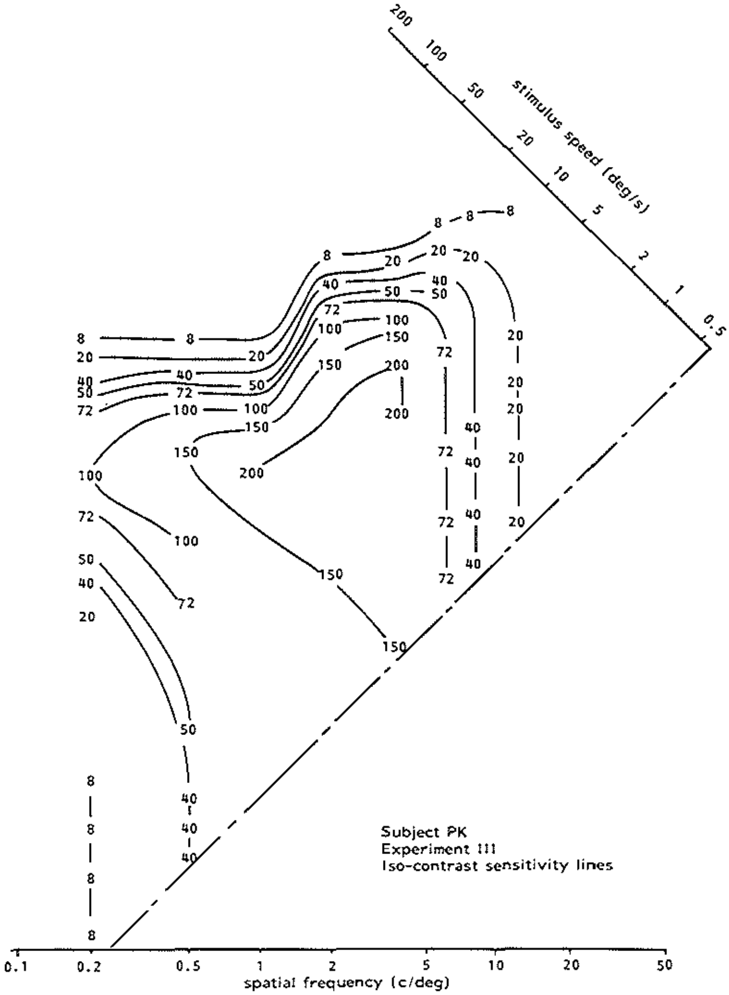


Fig. 6

Iso-contrast sensitivity contours showing contrast sensitivity versus stimulus speed (target speed, Expt. III). When compared to Fig. 4, these plots clearly illustrate the effect of accurate pursuit of various moving targets. Note the expansion of the contours in the high spatial frequency range (>4 c/deg).

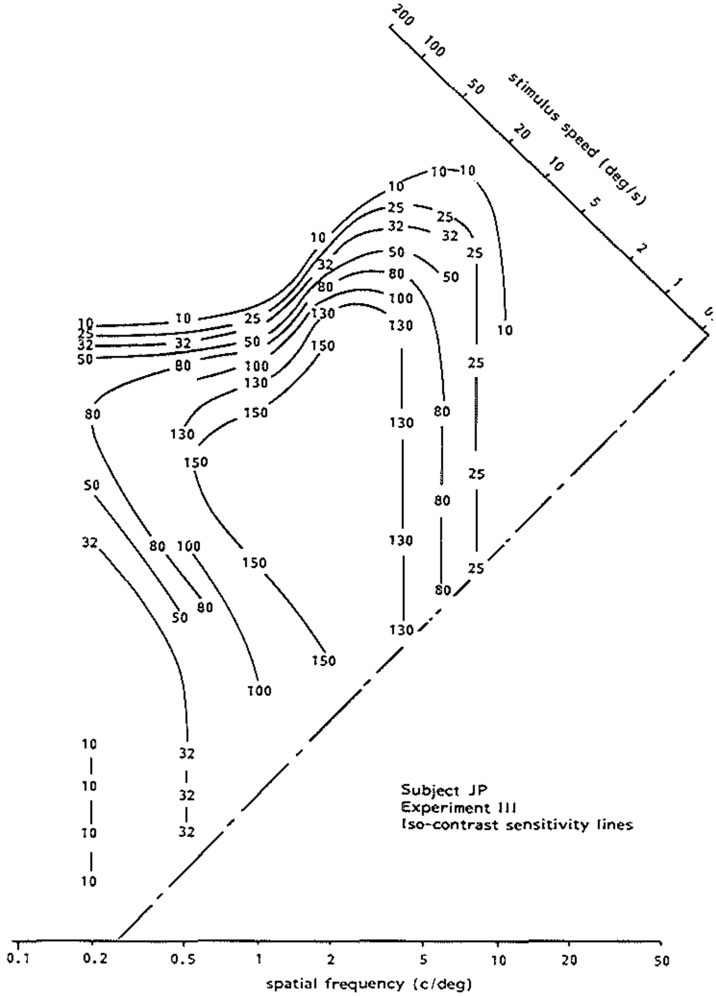

200
100
50
20
10
5
2
1
stimulus speed (deg/s)
Subject JP
Experiment III
Iso-contrast sensitivity lines
0.1
0.2
0.5
1
2
5
10
20
50
spatial frequency (c/deg)

Fig. 6
Legend (←)

Retinal image motion - especially under pursuit conditions -was expected to play a major role in causing changes in the contrast sensitivity. In order to evaluate this expectation it was necessary to establish the relation between contrast sensitivity and retinal image speed directly. Mean retinal image speed as a function of stimulus speed is presented in Fig. 7 and Table 1.

The solid curves in Fig. 8, describe the relation between contrast sensitivity and retinal image speed for both the 0.5 and the 8 c/deg grating, as obtained under pursuit conditons (Expt. III). The dashed curves presented in the same figures describe the relation between contrast sensitivity and retinal image speed as obtained during maintained fixation on a stationary target. Note that the results obtained from Expt. II (dashed curves) could be used directly without adjustment. The results showed that contrast sensitivity during pursuit is equal to contrast sensitivity during maintained fixation on a stationary target, provided that the magnitude of the retinal image motion is equal in both cases. Murphy (1978) reported the same finding. However, he discontinued his experiment at a retinal slip value of 1.2 deg/s. Since we measured retinal image speeds up to 20 deg/s, using a comparable experimental set up, our data proved the correctness of his findings far beyond a retinal image speed of 1.2 deg/s. Furthermore, the tolerated range of retinal image motion (0.2-2.0 deg/s) which inflicts no harm to the detection of acuity targets (>4 c/deg), remains unchanged under pursuit conditions. A suspected extension of this range (0.2->2.0 deg/s) was not demonstrated.

Table 1

Several parameters concerning the ocular pursuit performance. Mean and standard deviations ([ ]) are given for both subjects. Averaged smooth pursuit gain was calculated from the ratio (averaged pursuit speed / stimulus speed).

Stimulus oscillation frequency (Hz):				
00.25	00.50	00.75	01.00	01.25
Stimulus speed (deg/s):				
04.00	08.00	12.00	16.00	20.00
Subject JP:				
Pursuit speed (deg/s):				
03.74[00.13]	06.94[00.54]	10.36[01.03]	14.30[01.47]	18.26[01.54]
Smooth pursuit gain:				
00.94[00.03]	00.87[00.07]	00.86[00.08]	00.89[00.09]	00.91[00.07]
Retinal image speed (deg/s):				
00.26[00.13]	01.06[00.54]	01.64[01.03]	01.70[01.47]	01.74[01.54]
Number of tracks analysed (N):				
14.00[00.00]	20.00[00.00]	30.00[00.00]	39.00[00.00]	20.00[00.00]
Subject PK:				
Pursuit speed (deg/s):				
03.57[00.38]	07.43[00.48]	09.53[01.17]	11.56[02.36]	11.83[04.04]
Smooth pursuit gain:				
00.89[00.09]	00.93[00.06]	00.79[00.10]	00.72[00.14]	00.59[00.20]
Retinal image speed (deg/s):				
00.43[00.38]	00.57[00.48]	02.47[01.17]	04.44[02.36]	08.17[04.04]
Number of tracks analysed (N):				
12.00[00.00]	10.00[00.00]	15.00[00.00]	24.00[00.00]	21.00[00.00]

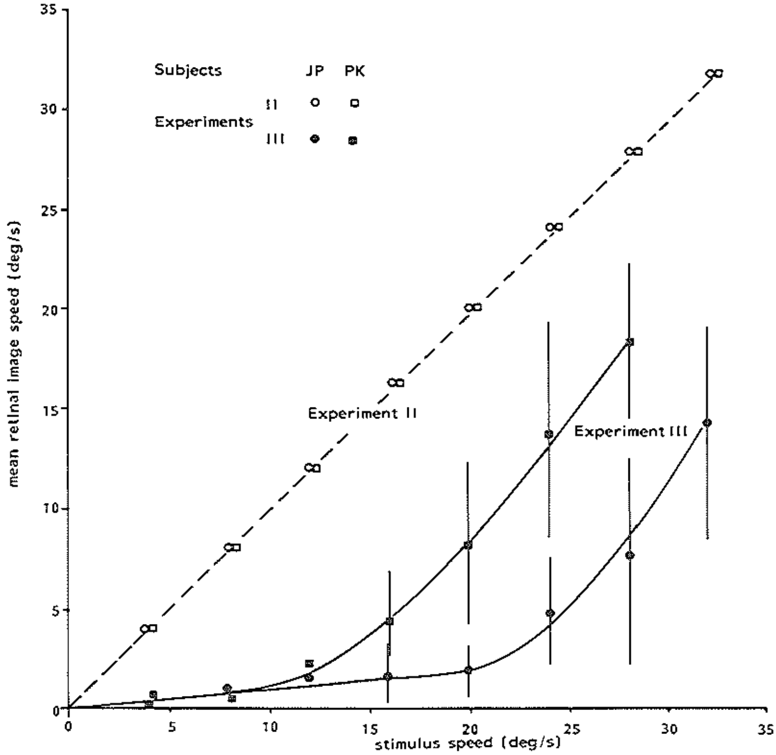


Fig. 7

Mean retinal speed and standard deviation at different stimulus speeds. The dashed line shows the results of experiment II. Note that retinal speed and stimulus speed are equal. The solid curves show the results of experiment III. Results are shown for both subjects.

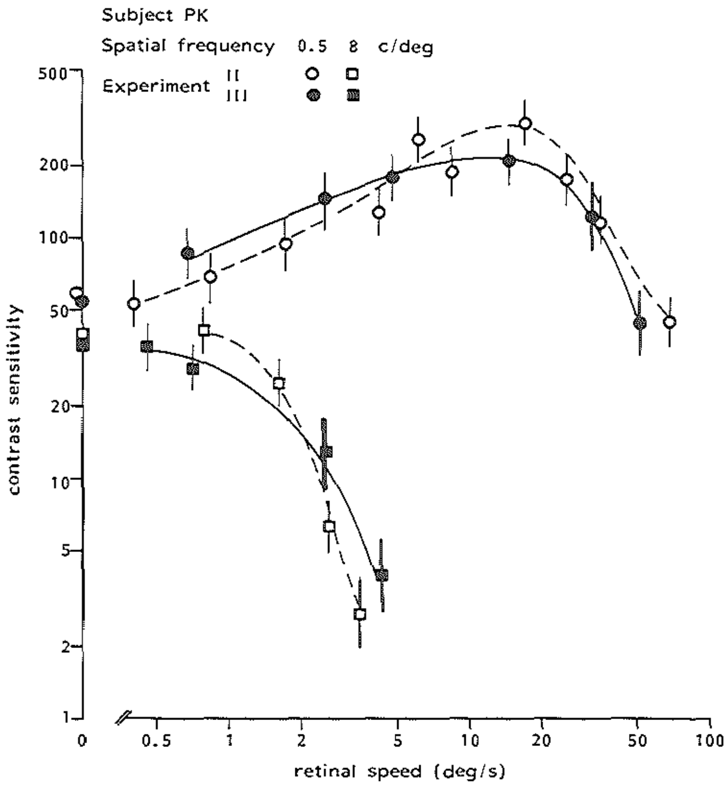


Fig. 8

Mean contrast sensitivity and standard deviation as a function of retinal speed, for two spatial frequencies of 0.5 and 8 c/deg. The dashed curves show the results of experiment II. The solid curves show the results of experiment III.

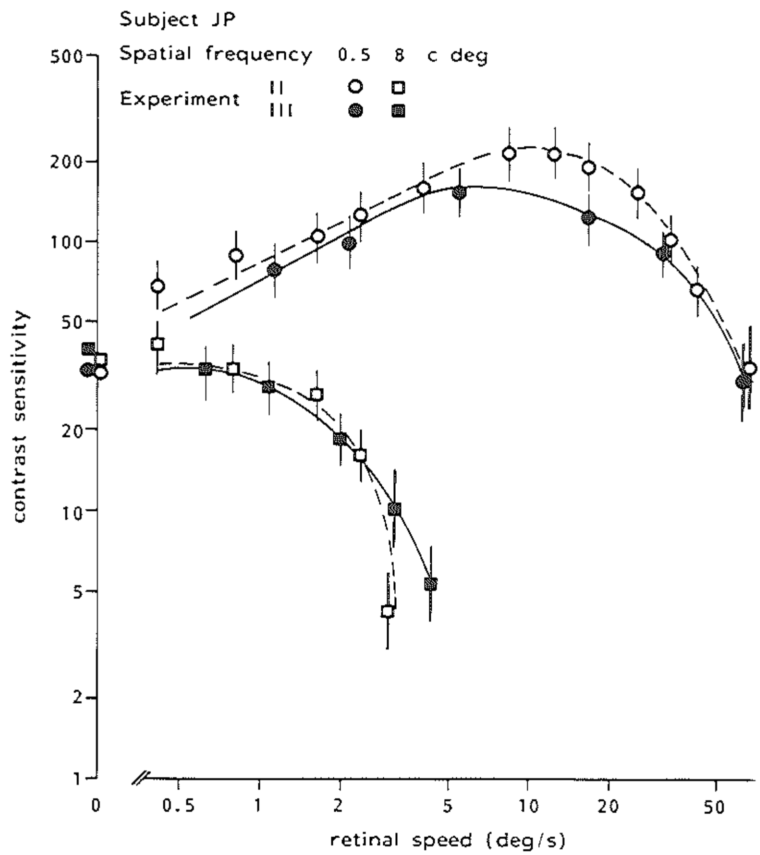

Subject JP
Spatial frequency 0.5 8 c deg
Experiment II
III
500
200
100
50
20
10
5
2
1
contrast sensitivity
0
0.5
1
2
5
10
20
50
retinal speed (deg/s)

Fig. 8

Legend (←)

Fig. 8 shows that peak contrast sensitivity values were slightly depressed during the pursuit of low spatial frequency gratings (<1 c/deg). The peak depression may be caused by the fact that we used an oscillating pattern of stimulus movement.
The visual control of eye movement is known to exhibit a severe performance decrement once the frequency of an oscillatory movement exceeds 1-2 Hz (Drischel, 1958; Fender and Nye, 1961; Stark 1971). Since we used a peak-to-peak motion amplitude of 8 deg, these oscillation frequencies corresponded to stimulus speeds ranging from 16-32 deg/s. Peak contrast sensitivity values for low spatial frequency gratings (<1 c/deg) - occuring at retinal image speeds above 20 deg/s - could not be measured in the presence of more or less accurate smooth pursuit eye movements. At target speeds beyond this critical range (16-32 deg/s), pursuit was no longer possible. Accordingly, there was no distinction between the results of experiment II and III in the high velocity range (Fig. 5 and 8, target speed >> 32 deg/s).

From the results presented in this chapter it can be concluded that, the visibility of moving objects is governed by retinal image motion (slip), irrespective whether the retinal image motion is caused by movement of the object itself or by imperfections in the oculomotor system pursuing it. A suspected enhanced acuity present during smooth pursuit oculomotor activity could not be found.

CHAPTER 3

VISUAL PROCESSING
IN THE PRESENCE OF PASSIVE HEAD OSCILLATION

(The essentials of this chapter are submitted to
Vision Research, 1990)

3.1 INTRODUCTION

At oscillatory target movements exceeding 2 Hz, the smooth pursuit system becomes totally ineffective in reducing the amount of retinal slip (Drischel, 1958; Martins et al., 1985), leading to predictable changes in the visual contrast sensitivity (Murphy, 1978; Flipse et al., 1988).
Head oscillations beyond 2 Hz however, do not alter our visual perception. This can be attributed to the actions of the vestibulo-ocular reflex (VOR) system. Its main function is to hold the image steady on the retina during head movements. An angular acceleration of the head about its vertical axis will produce a horizontal ocular movement in opposite direction and proportional in magnitude. Although the ratio of eye to head rotation, or gain of the VOR, has been studied extensively, its role in sustaining clear vision under these circumstances has been scarcely documented.

Benson and Barnes (1978) designed an experiment in which the visual perception served to quantify the VOR-gain. They measured the visibility of small digits (0.13 deg) during sinusoidal oscillation of the subject. The peak velocity of oscillation was held constant at 30 deg/s. Their results showed that a significant increase in reading errors did not occur at oscillation frequencies up to 9 Hz. They concluded that the VOR-gain must be nearly perfect up to 9 Hz.
Their experiment was founded on the assumption that adequate visibility of the digits was based solely on the stability of their retinal representation. Unfortunately, Benson and Barnes (1978) did not measure the eye movements in the upper frequency domain (5-10 Hz).

For all we know substantial retinal image oscillations might have been present, the effects of which failed to penetrate into the reading performances. So, unless the eye movements in the upper frequency domain (5-10 Hz) were measured, the validity of their argument remained subject to a considerable amount of discussion. Skavenski et al. (1979) did measure the eye movements. They found best averaged VOR-gain values of 0.75 during small artificial head rotations at 10 Hz, while the subject fixed a stationary target. With similar high frequency head oscillations, Gauthier et al. (1984) and Stott (1984) measured a mean VOR gain ranging from 0.70-0.90. The VOR-gain was never precisely unity. Deviations from unity-gain, expressed as a percentage, ranged from minus 10-30%.
Applied to the data reported by Benson and Barnes (1978) we estimated the peak gaze movement, present at head oscillations near 9 Hz, between 3 and 9 deg/s (10-30% of peak-velocity of head movement). Consequently, the averaged value of (absolute) retinal image speed, might have been 1.9-5.7 deg/s ($2/\pi$.[peak-velocity of gaze movement]). Since the quality of vestibulo-oculomotor compensation could not account for the visual performance under these particular circumstances, several other explanations had to be considered.

Vision requires a minimal amount of retinal image motion (>0.2 deg/s) to maintain visibility (King-Smith and Riggs, 1978; Kelly, 1979b). Obviously, unity-VOR-gain might impair the proper function of the visual system. In addition, the visibility of high spatial frequency targets, like the digits used in Benson and Barnes' experiment, remains unaffected by retinal speeds not exceeding 2.0 deg/s (Westheimer and McKee, 1975; Flipse et al., 1988).
Skavenski et al. (1979) suggested that the vestibular system might therefore respond to the visual needs in such a way, that the oculomotor compensation maintains the optimal range (0.2-2.0 deg/s) of retinal image motion. Notwithstanding the fact that the VOR-gain is subject to rapid adaptive changes (Gauthier and Robinson, 1975; Gonshor and Melvill Jones, 1976a; Collewijn et al., 1983), a control mechanism using information from the retina causing an immediate response from the vestibular system, is yet to be demonstrated.

Steinman and Collewijn (1980) measured binocular eye movements during voluntary horizontal head oscillation and maintained fixation on a distant target. Averaged retinal image speeds were in the order of 4 deg/s in each eye. Yet, vision remained fused, stable and clear under those circumstances. Steinman et al. (1985) examined these (subjective) impressions psychophysically by replacing the distant target for a sinusoidal grating display. They found that the adverse effects of retinal image motion on the visibility of high spatial frequency gratings (>4 c/deg) were less pronounced when compared with artificially moved stabilized gratings in the absence of head movement (Kelly, 1979b). They argued that a vestibular (sub)system might enhance acuity during head movement. In particular, one that might rearrange the neural representation of the (moving) retinal image (Julesz, 1971), using the actual cranio-oculokinetic information known to the vestibular system. This enabled the visual cortex to get a clear impression of the visual scene inspite of excessive amounts of retinal image motion (>2 deg/s).
It is unknown whether such a hypothetical mechanism would be operative only during active head movement. In this context the question as to how much retinal slip is tolerated with *passive* head movement acquires a major importance, for it might lead to clarify part of the role of the cervico-vestibular interaction.
Finally, perhaps a less spectacular explanation for the preserved visual performance during head movement might be that vision employed mostly the reversal points of ocular oscillation.
Arend (1976) described experiments in which the subject was asked to track a bright target across a stationary grating, while simultaneously adjusting its contrast. Beyond critical values of constant target speed, the patterns (>4 c/deg) were invisible across the central portion, while the striation flashed into view at each end of the sweep.
Most of the investigators cited thusfar made similar observations, which were, however, not analysed in further detail. Therefore, the visual phenomena coinciding with the reversals in the direction of the oscillatory movement of the eyes (reversal points) still remain to be established.

The main objective of the following experiments was to determine whether the visibility of a stationary grating in the presence of head movement, could be explained from the oscillatory character of the retinal image motion (gaze movement). In order to meet this request, two experimental conditions were designed in which the specific features of the (original) pattern of retinal image movement, measured with passive head movement (Expt. IV), were retested, focussing the attention on their relative effect on visual performance (Expt. V, VI). Contrast thresholds were measured under various viewing conditions:

IV **With passive oscillation of the head, while viewing a stationary earth-fixed sine-wave grating.**

With immobilized head and eyes:

V **while the grating oscillated according to a triangular-wave in order to simulate the averaged retinal velocity component;**

VI **with non-continuous presentation of the stationary grating in order to simulate the momentary retinal (low) velocity component.**

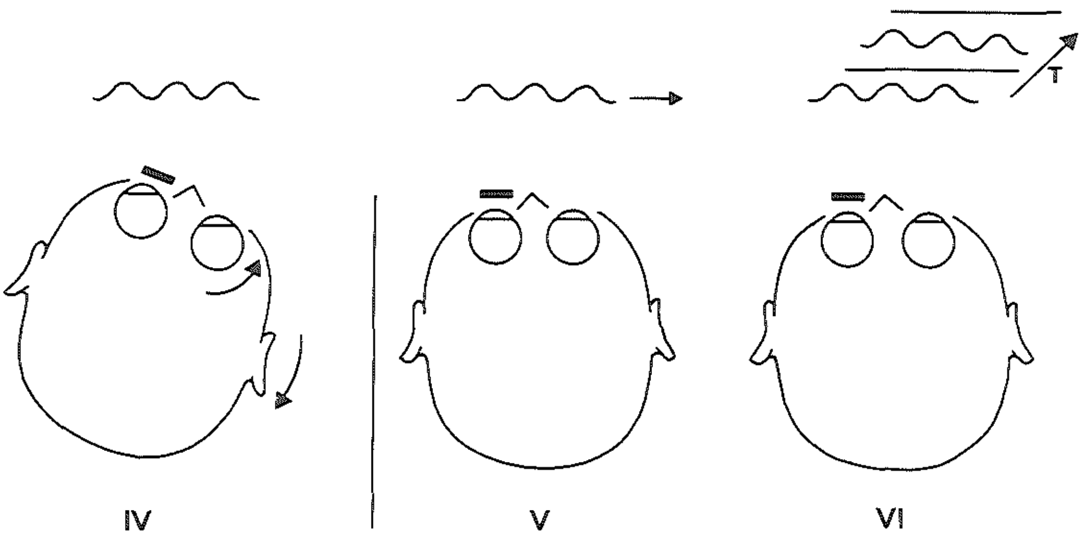


Fig. 9

Three experimental conditions.
In Expt. IV the head was moved relative to the stationary grating.
In Expt. V the grating moved relative to the fixed eye.
Finally, in Expt. VI the grating was flashed on/off.

3.2 METHODS

Experimental design

During the first experiment (Expt. IV, Fig. 9), the subjects were required to detect the striation in a stationary vertical sine-wave grating, while fixating a small target situated central to the screen. Simultaneously, head movements were induced using a biteboard of dental impression material. Under these circumstances, gaze stability was co-supported by the VOR-system. Retinal image motion (slip) was generated by the gaze movement relative to the fixed grating.
The VOR gain-error due to the non-coincidence of the rotational axes of the eye and the head was estimated to be less than 1.5% at the target distance of 4 m (Rodenburg et al., 1985). Therefore the vestibulo-ocular interaction was considered virtually similar to that measured with targets at optical infinity (Collewijn et al., 1982).
Eye and head movements were recorded with a scleral induction coil method.
The data obtained as such provided the basic information to create the conditions for a second set of experiments (Expt. V, VI) during which head movements were avoided using a fixed biteboard.

In experiment V (Fig. 9), the grating was oscillated with a constant speed across the stimulus field. Its averaged speed was equal to that calculated from the eye movement recordings from the previous experiment (Expt. IV). Stimulus speed was held constant and did not fluctuate around its averaged value. As far as the subject's capability to attend the stationary fixation target was concerned, no hinder was expected from the moving grating behind it (Murphy, Kowler and Steinman, 1975; Murphy, 1978). So apart from the fixational eye movements, stimulus speed was considered equal to its corresponding image speed relative to the retina.
Experiment VI (Fig. 9) was characterized by a non-continuous presentation of the stationary grating. The modulation was switched on/off according to a specific protocol.

The on-interval (exposure time) was calculated from the parameters of experiment IV. It equalled the time intervals during which the ocular speed was less than 2 deg/s (Westheimer and McKee, 1975; Flipse et al., 1988). In between (off-interval) the modulation dropped to 0% leaving a uniform illuminated screen. The ratio of exposure time to repetition time (duty-cycle) was inversely proportional to the frequency of the oscillatory movement.

Three successive sessions were made with each stimulus condition (Expt. IV, V and VI). There was a time delay of several days between the individual sessions. A grafical description of the mutual relation between the different experimental conditions is given by Figure 10.

Visual stimulation

The visual stimulus was a vertical 6 c/deg sine-wave grating, generated electronically and displayed on a large screen oscilloscope (Hewlett Packard 1321A/X-Y display, diagonal 56 cm). With regard to other spatial frequency values (<4 c/deg) its relation between visibility and averaged retinal image speed was in fact simple (Flipse et al., 1988), which made this particular grating an appropriate stimulus for these experiments. Low spatial frequency gratings (< 1 c/deg) were not included since pilot experiments showed that the magnitude of gaze movement, usually between 0.5-1.0 deg, was to small in comparison to the dimensions of such gratings. As expected, no improvement in their visibility could be demonstrated.
The stimulus field subtended a visual angle of 6 deg horizontally, and 4 deg vertically at 4 m. The grating was viewed in a dark surround. Due to practical limitations its averaged luminance was 0.1 Cd/m^2, which was just enough to allow photopic vision, though (Bartley, 1966).
It could be moved electronically according to a triangular wave which had a total amplitude of 1 deg. On/off flickering of the stationary grating was accomplished by a reed-switch which interrupted the modulation voltage.

Contrast (C) was defined conventionally. Its relation to the Z-input voltage proved to be linear up to 90%. Threshold contrast (C_{min}) was determined by the same method of adjustment as described in the previous chapter (Keemink et al., 1979). Each datapoint was the mean of three separate threshold determinations, during which the subjects were asked to keep the continuous change in contrast (3 dB/sec) on threshold detection level using a push-button which depoled the contrast attenuation. Contrast sensitivity (CS) was defined as the reciprocal of threshold contrast ($1/C_{min}$).

At the overall stimulus width of 6 deg, neither the number of cycles presented nor the sharp luminance discontinuities adjacent to the screen influenced the contrast sensitivity for the 6 c/deg grating (Savoy and McCann, 1975; Van der Wildt and Waarts, 1983).

After anaesthetizing the eye with 4-5 drops of Oxybuprocaine-HCl 4 mg/ml (Novesine^{R}) the annulus containing the sensor-coil was inserted using a standard application tool (Collewijn et al., 1975). The subjects adapted 5 to 10 minutes to the averaged luminance level of the visual stimulus, meanwhile several standard threshold determinations were carried out in order to monitor both the stabilization of the visual response and the process of adaptation to the inserted annulus.

The visibility of the small central opening in the fixation target provided the subjects with a critereon for normal vision. The moment it blurred they had instructions to blink several times in order to restore its visibility (if necessary, the standard threshold determinations were repeated). Although the anaesthetic had no affect on normal vision, optical blur and ocular irritation (excessive lacrimation) caused by the inserted annulus might interfere with normal contrast sensitivity (Arend and Skavenski, 1979; Marmor and Gawande, 1988). With frequent blinking no significant decrease in contrast sensitivity could be measured, when the whole experiment lasted no longer than 15-25 minutes.

Vestibular stimulation

The vestibular stimulus was generated by passive horizontal head movement using a biteboard of dental impression material. The biteboard rotated on a small vertical pin. The pin was firmly attached to a long non-metallic bar (2 m), which could be oscillated by a powerfull shaker (Derritron-Vibrator VP3/3B & TA120 amplifier: peak sine-wave force 130 N, peak acceleration 490 m/s^2). At frequencies above 2 Hz, the longitudinal oscillation of the bar resulted in angular oscillation of the head with a peak-to-peak amplitude of about 5 deg.
Due to mechanical limitations the occurrence of linear horizontal head movements proved unavoidable. On average the (estimated) fundamental translations decreased from 8 mm at 2 Hz to 4 mm at 6 Hz. The effect on linear displacement of the retinal image and its subsequent effect on contrast sensitivity was considered to be negligible.

Eye and head movement recording

A sensor-coil magnetic system was chosen to measure both head and eye rotation. The method, first introduced by Robinson (1963), is based on the voltage induced in a sensor-coil placed in an alternating magnetic field. The earth-fixed magnetic field was generated by two large square field-coils (1 m^2), placed in a cube (1 m^3) around the subject. The field frequency was 15 kHz. For small rotation angles, the amplitude of the coil-voltage (V) was linear proportional to its angle relative to the field direction (Θ). Linearity of the transduction (V/Θ) was better than 98% over a range of 20 deg (+/- 10 deg; relative to the central axis of gaze). The error due to linear displacement of the sensor-coil depended on the homogeneity of the magnetic field in its centre where the eye was positioned. The influence on the transduction (V/Θ) was measured to be less than 0.5% in a space of 8^3 cm^3 central to the cube. Based on the (relative) size of this space the effect of head translation, within the range occuring in this experiment, was negligible.
The resolution of the measuring system was better than 1 min arc (De Bie, 1986).

Calibration of eye movement was accomplished by alternated fixation of two calibration targets covering a total visual angle of 5.5 deg.
Small displacements of the annulus (<2 min arc) due to frequent blinking have been reported (De Bie, 1985). Absolute position information was not critical, though.
The rotation angle of the head was determined by a second sensor-coil which was mounted on a small plastic strip taped to the forehead. Head movements (second sensor-coil) were calibrated by means of a simple goniometer used only for this purpose.

Analysis

The signals derived from the sensor-coils were digitized at a rate of 500 samples per second. Subsequent analysis was performed by a DEC-PDP11/73 micro computer.
A correction was applied to the data in case the subject had worn spectacles during the original experiment (Expt. IV). For each Dioptre 3% of the rotation angle of the head was subtracted from the gaze signal, neutralizing the induced magnification factor (Collewijn et al., 1983).
By differentiation in the time domain, the total of 4096 stored position samples (gaze direction) were transformed to speed signals (gaze movement). Speed was defined as the absolute value of angular velocity. Saccades and blinking effects were ignored.
Vestibulo-ocular gain was calculated as follows:

$$1 - (\text{averaged gaze speed} / \text{averaged head speed}).$$

For the purpose of experiment V, the averaged ocular speed and standard deviation were calculated.

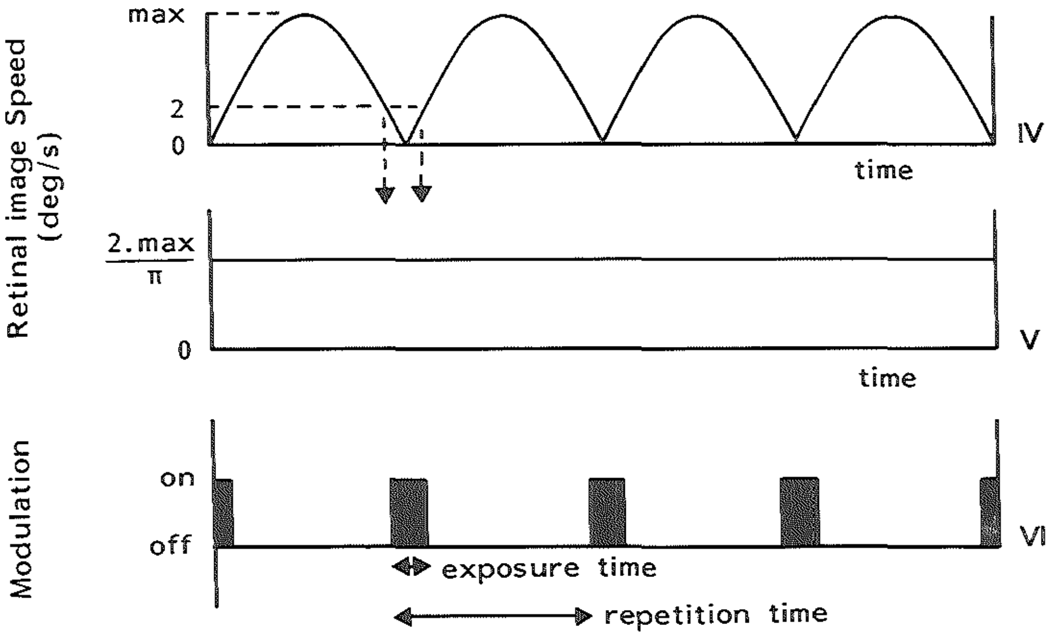


Fig. 10
Retinal speed profile in case the eye moved sinusoidally relative to the grating (Expt. IV). The effect of both the averaged and momentary (<2 deg/s) retinal velocity component on contrast perception was subsequently analysed (Expt. V and VI).

Simulation of the velocity minima, present at the reversal points of ocular oscillation (Expt. VI), involved a more complicated operation of the data. The recordings of Expt. IV showed that the eye oscillated on average sinusoidally in space.

Therefore, for each individual oscillation frequency (f), the exposure time(τ) of the grating could be calculated from the following relation:

$$| \alpha\pi f.\cos(360°.f\tau) | \leq 2.0°$$

in which α (deg) represents the peak-to-peak amplitude of gaze movement, calculated from the standard deviation (σ) of ocular gaze ($\alpha = 2\sqrt{2}.\sigma$). The precise frequency (f) with which the eye oscillated in experiment IV was determined by Fourier-analysis of the records.

Subjects

Four subjects (including one of the authors) served in the experiments. All had normal or slightly corrected eyesight (viewing eye of subject JP: -1.50 D, subject B: -1.25 D). Although some subjects wore spectacles during the experiments which introduced small perceptual changes in stimulus dimension (3%/Dioptre), no further attention was paid to these intersubject variations concerned. Non of the subjects suffered from any neuro-ophtalmological nor labyrinthal disorder that might influence the outcome of the present experiments.

3.3 RESULTS AND DISCUSSION

Experiment IV

During this experiment the subject viewed the centre of the stationary grating. Simultaneously, passive head movements were generated.

The solid symbols in Fig. 11 and Fig. 12 represent the contrast sensitivity for the 6 c/deg-grating. Plots were made as contrast sensitivity versus averaged retinal image speed (Fig. 11), and the frequency of the oscillatory head movement (Fig. 12). The level of contrast perception decreased markedly once the oscillations exceeded 3 Hz, to diminish even further at higher values, here up to 6 Hz.

It was unknown whether movement of the eye relative to the screen, producing movement of the retinal representation of its dark edges as well, might add an artefactual factor to the contrast sensitivity change. Pilot experiments, however, showed that similar contrast sensitvity values could be obtained either with the eye moving relative to the grating (Expt. IV; moving edges), or with the grating moving relative to the fixed eye (Expt. V; stationary edges), provided that comparable patterns of retinal image motion were generated. This could easily be accomplished using the (stored) signals from the scleral induction-coil (gaze movement) to move the grating relative to the screen. Consequently, the decrease in contrast sensitivity measured with movement of the head was considered essentially free from visual artefacts and solely determined by the corresponding decline in vestibulo-oculomotor compensation.

The averaged VOR-gain (Table 2) decreased from 0.91 at 2 Hz, to 0.81 at 6 Hz. The peak-to-peak amplitude of retinal image displacement (α) showed a complementary increase from 0.35 up to 0.93 deg, respectively. These findings are in agreement with those reported by Steinman and Collewijn (1980) and Collewijn et al. (1983).

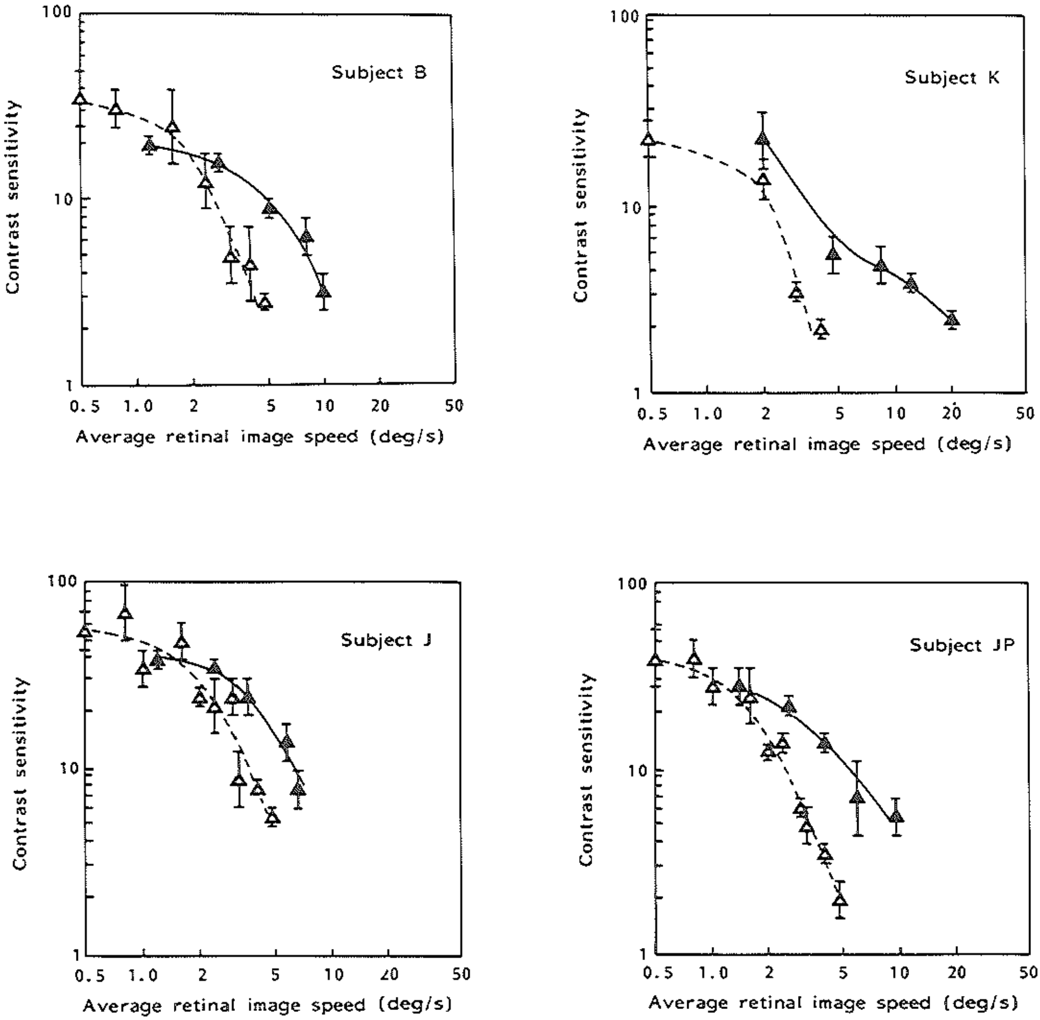


Fig. 11

Mean contrast sensitivity and standard deviation versus averaged retinal image speed. The solid symbols (Expt. IV) represent the results obtained during oscillation of the head. The open symbols (Expt V) represent the results obtained with constant motion of the stimulus relative to the fixed eye

Table 2

Several parameters concerning the passive head movement.
Mean and standard deviations ([ ]) are shown, pooled over 4 subjects.
**A correction was applied to the data in case the subjects*
wore spectacles during the experiments.

Oscillation frequency:	2 Hz	3 Hz	4 Hz	5 Hz	6 Hz
Head rotation (peak-to-peak, deg):	04.16[00.60]	04.64[00.33]	05.07[00.65]	05.03[00.78]	05.13[00.83]
Eye rotation* (peak-to-peak, deg):	00.35[00.23]	00.51[00.27]	00.45[00.10]	00.80[00.54]	00.93[00.63]
Head speed (deg/s):	16.58[02.42]	27.82[01.93]	40.55[05.26]	50.26[07.75]	61.52[10.00]
Retinal image speed (deg/s):	01.39[00.92]	03.04[01.67]	03.63[00.79]	08.80[05.39]	11.12[07.57]
VOR-gain:	00.91[00.07]	00.89[00.06]	00.91[00.03]	00.82[00.12]	00.81[00.14]

Although the size of the digits (0.13 deg) used by Benson and Barnes (1978) was quite comparable to that of each individual cycle in our grating (1 c/0.16 deg), their acuity measurements did not reveal a decline in visual performance with oscillation frequencies under near 9 Hz. This proves once more the usefullness of contrast sensitivity, in stead of simple acuity measurements, in order to quantify the visual performance.

Still, our results are not in disagreement with those reported by Benson and Barnes (1978). In case we had presented the grating with maximal contrast - as were Benson and Barnes' digits - its visibility would not have been affected by head oscillations up to 9 Hz. Note that the (extrapolated) solid curves, depicted in Fig. 12, coincide with the horizontal axis (maximal contrast) near the value of 9 Hz. Visual acuity (measured with Landolt C-rings e.g.) is strongly correlated to the contrast perception of high spatial frequency gratings (>4 c/deg; Owsley et al., 1983). So without question, Benson and Barnes (1978) would have come to quite a different conclusion regarding the VOR-gain, in case they had used much smaller digits.

Experiment V

The aim of this particular experiment was to check whether the changes in contrast sensitivity, measured with increasing head oscillation (Expt IV), might be explained by comparable changes in the averaged image speed relative to the retina. For this end the subject fixed a stationary target while the grating moved to and fro at a constant speed across the stimulus field.

The results were plotted in the same figure as were those obtained from the previous experiment (open triangles, Fig. 11). Clearly, retinal speed values exceeding 2 deg/s proved to be detrimental to the visibility of the grating. This is consistent with earlier findings (Murphy, 1978). Despite the presence of equal amounts of averaged retinal slip, measured either with (Expt. IV) or without (Expt. V) movement of the head, a major difference in the resulting contrast sensitivity persisted.

The data of experiment V (dashed curves) could however be equalled to those of experiment IV (solid curves) in case they were shifted to the right, that is towards higher values of retinal image speed. With movement of the head, the magnitude of averaged retinal slip could be seemingly 2 to 3 times larger, than without it. Eventually this led to the same visual impression of the grating.
Steinman and Collewijn (1980) and Steinman et al. (1985) made essentially similar observations with voluntary oscillations of the head. Since our data showed that "enhanced" visual performance could be measured with passive (non-voluntary) head movements as well, a major contribution to the visual process, originating in the proprioceptors of the neck muscles, seems less probable. Although this might simplify some aspects of dynamic vision, the most intriguing question, concerning the actual mechanism of contrast abstraction from the oscillating retinal image, still remains to be answered.

It has long been recognized that the organisation and structure of the visual system is directed towards a drastic reduction of information involved in the perception of a complex stimulus (Hubel and Wiesel, 1959; Campbell and Robson, 1968; Braddick et al., 1978). In order to accomplish such an input reduction, vision must be selective (Berlyne, 1970). Consequently, if one adjudges the visual system with primarily selective rather than integrative properties, the averaged retinal image speed might end up to be a poor parameter of its performance.
Therefore the idea of a central (possibly) vestibular mechanism contributing to the process of contrast detection appears to be somewhat premature.

Experiment VI

According to a large amount of experimental evidence (including the present study), retinal image speeds up to 2 deg/s proved harmless to the process of detailed vision (Westheimer and McKee, 1975; King-Smith and Riggs, 1978; Flipse et al., 1988). Sampling of these low velocity values from the profile of retinal image motion might explain the optimal level of contrast sensitivity measured with movement of the head. Since the contrast perception of high spatial frequency gratings (>4 c/deg) is unaffected by stimulus speeds between 0 and 2 deg/s, on/off flickering of the stationary grating could create visual effects similar to those present at the reversal points of the oscillatory gaze movement.
We argued that the duration of the time interval (τ), corresponding to the presence of these acceptable retinal image speeds (≤ 2 deg/s), might be the better parameter of the visual performance measured during head movement. In order to prove this argument, the exposure time of the flickered grating should correspond to the time interval at which the actual velocity of gaze movement relative to the fixed grating (Expt. IV) was less than 2 deg/s. For each oscillation frequency these (averaged) exposure durations were calculated from the eye movement records of experiment IV.

Typical recordings of the eye position signals showed that the exact direction of gaze measured at the reversal points of ocular oscillation (zero velocity) proved rather unpredictable. Consequently, the successive projections of the light and dark areas in the grating on to the retina might be mutually dislocated. Such temporal luminance gradients might seriously affect the visual contrast sensitivity.
Kulikowski and Tolhurst (1973) found that the contrast sensitivity for high spatial frequency gratings (>4 c/deg) remained unchanged whether they were on/off or counterphase flickered. Simulation of these intermittent retinal effects produced by the reversals in gaze movement using an on/off flickered 6 c/deg-grating was therefore justified.

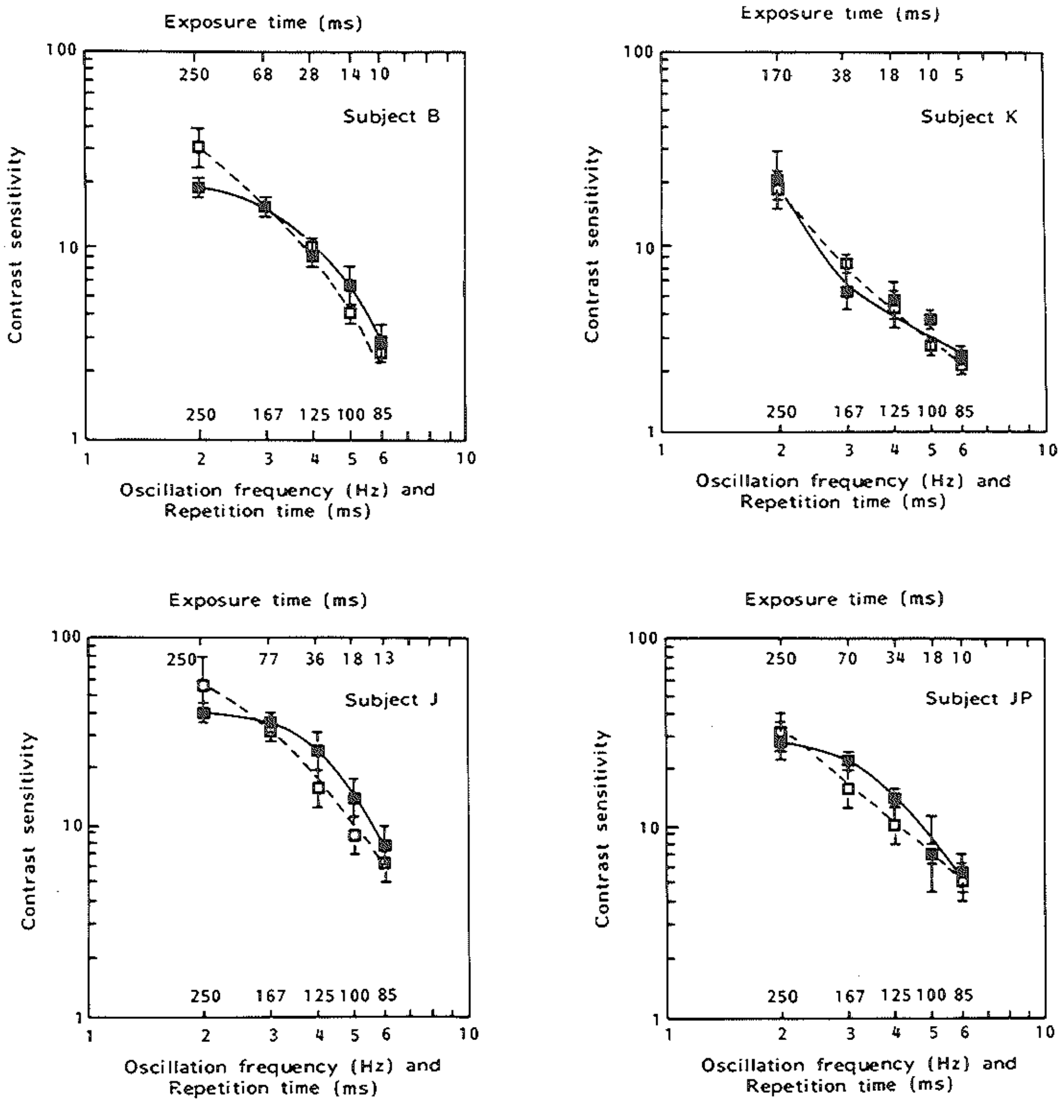


Fig. 12

Mean contrast sensitivity and standard deviation versus the oscillation frequency of the head movement is represented by the solid symbols (Expt. IV). The open symbols (Expt. VI) represent the relation between contrast sensitivity and exposure time of the on/off flickered grating (upper horizontal axis).

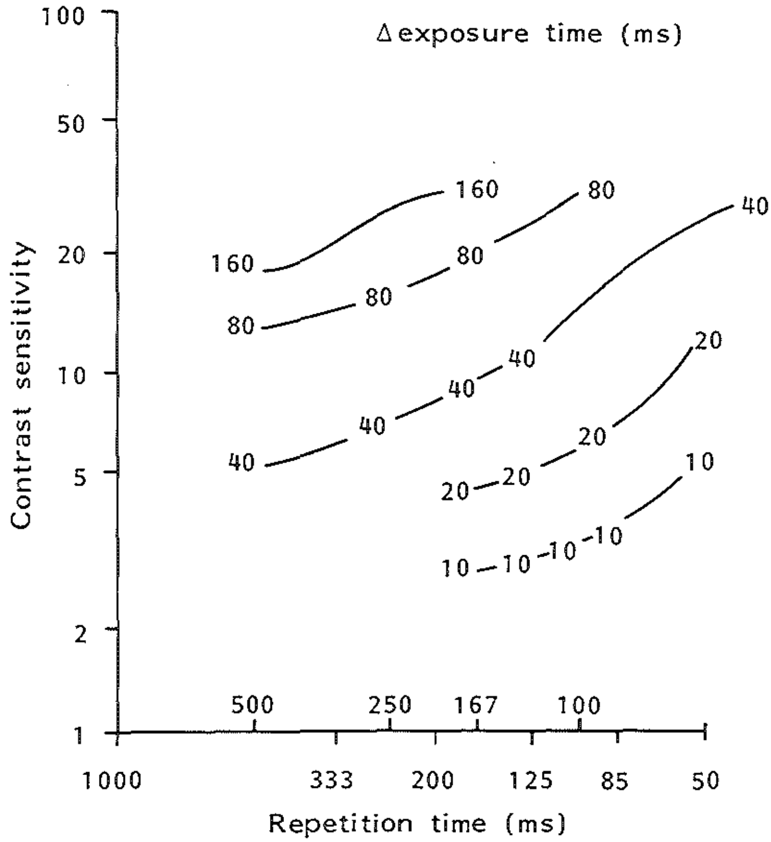


Fig. 13
Both limited exposure duration and repetition time had separate effects on contrast sensitivity. For an explanation, see text.

Contrast sensitivity versus exposure time of the 6 c/deg-grating, is plotted in Fig. 12 (Expt VI, open symbols) along with the original data measured during movement of the head (Fig. 12, solid symbols). For obvious reasons, the repetition rate (reciprocal of repetition time) was twice the oscillation frequency, for each motion cycle contained the double number of reversals.
Within the limits of experimental error, the combined data (Expt. IV and VI) were in fact equal. This provided the experimental evidence that the momentary rather than the averaged retinal image speed determined the outcome of the visual process. Optimal vision in the presence of head movement must therefore have a predominantly intermittent character. Our findings are in close agreement with the experimental results reported by Abadi and Worfolk (1989). They analysed the eye movements of patients suffering from congenital nystagmus and found a significant correlation between the visual acuity (Abadi and Sandikcioglu, 1975) and the time that the eyes were travelling at low velocities (<10 deg/s).
It appears that the vestibular support to the process of vision lies in the reduction of the magnitude of gaze movement, providing the visual system with low retinal image velocities for a sufficient amount of time during which optimal visual perception can take place. Since comparable forms of retinal stimulation led to identical contrast sensitivity levels, either with (Expt. IV) or without (Expt. VI) vestibular stimulation, our observations do not favour the existence of elaborate central mechanisms as postulated by several physiologists (Skavenski et al., 1979; Steinman and Collewijn, 1980; Steinman et al., 1985).

Close examination of the two different curves revealed a difference in trend, though (solid curves, Expt. IV; dashed curves, Expt. VI; Fig. 12). With low frequency oscillations (≤ 3 Hz) the contrast sensitivity level measured with movement of the head (Expt. IV, solid symbols) was slightly lower than that obtained during the on/off flickering experiment (Expt. VI, open symbols). Although retinal image speeds up to 2 deg/s do not harm the visual performance significantly, any increase in the amount of retinal image motion affects the contrast sensitivity in an adverse way (Expt. V, dashed curves, Fig. 11).

Presentation of the stationary grating might have led to a slightly better outcome of the contrast sensitivity. In the upper frequency range ($\geq$4 Hz) the mutual relation between the two curves seems to be reversed. We could not find a simple explanation for this phenomenon. Perhaps it originated from a (relative) lack of the minimal amount of retinal image motion. During the moments of exposure to the on/off flickering grating (Expt. VI), fixational eye movements were the only source of image motion. With very short presentation times (<20 ms), the lack of ocular movement led to a virtual stabilization of the retinal image, damaging the proper function of the visual system.
Both the exposure duration (ms) and the repetition rate (Hz) had complementary effects on the visibility of the grating (Fig. 13). Whereas exposure duration (<75 ms) was almost linearly related to the level of contrast perception (Nachmias, 1967; Kelly, 1971), increased repetition rates caused a non-linear improvement in the visibility of the grating. These effects could be attributed to the absolute amount of time the grating was in fact presented (duty-cycle).

From the insights provided by the on/off flickering experiment it was concluded that the changes in contrast sensitivity, measured during passive head oscillation, could be (in)directly related to comparable changes in vestibulo-oculomotor compensation. The process of optimal vision (threshold contrast detection) under these circumstances appeared to be sampled, and based on the (brief) moments in which the actual velocity of retinal slip was below 2 deg/s. These "observation-intervals" coincided with the reversal points in ocular oscillation.
A decrement in VOR-gain led to a complementary increase in the peak velocity of the oscillatory gaze movement (sinusoid: $\alpha\pi f$). Peak gaze velocity proved inversely proportional to the duration of the "observation-intervals", which eventually determined the level of contrast perception.
Even small changes in the VOR-gain had fairly large and predictable affects on the visual contrast sensitivity. Quantification of the VOR-gain using visual targets only, might become a usefull alternative of (clinical) tests of the labyrinthine function.

CHAPTER 4

THE INFLUENCE OF VOLUNTARY HEAD MOVEMENT ON VISUAL CONTRAST PERCEPTION

(Submitted to Vision Research, 1990)

4.1 INTRODUCTION

The introduction of new recording techniques, designed to measure the ocular rotation in the presence of unrestrained voluntary head movement, has led to a considerable interest in the quantification of human gaze stability under physiological conditions. The interest is predominantly based on the idea that some aspects of our knowledge concerning the role of the vestibulo-ocular interaction, as obtained with artificially induced head movement, may be less applicable to the natural condition then was previously assumed. In particular, many physiologists have been puzzled by the precise role of the compensatory eye movements in maintaining clear vision during natural locomotor activities.

Skavenski et al. (1979) were the first to measure the magnitude of these compensatory eye movements for natural motions of the unsupported head. When the subject was asked to sit as still as possible, ocular compensation was incomplete and resulted in substantially more retinal image motion (0.1-0.6 deg/s) than was observed when the head was supported on a biteboard (0.1-0.3 deg/s). Skavenski et al. (1979) concluded that retinal image speeds during natural bodily motion were high enough to prevent the perceptual fading of the image (>0.2 deg/s; Kelly, 1979b) and yet low enough to permit maximum acuity (<2.0 deg/s; Westheimer and McKee, 1975). According to Skavenski et al. (1979), the appropriate image motion might be regulated by a hypothetical feedback mechanism setting the actual gain of the vestibulo-ocular reflex.
In a review article, Steinman et al. (1982) described averaged retinal image speeds ranging from 1-5 deg/s, with head oscillation frequencies up to 1.33 Hz.

On average, such image speeds were twice the amount tolerated by the visual system (Westheimer and McKee, 1975). Still, vision remained clear and stable under all circumstances. Results such as these might trigger a search for central mechanisms, compensating for the adverse affects of excessive amount of retinal image motion (>2.0 deg/s) on the visual performance.

Duwaer (1982), however, doubted the validity of Steinman's experimental results, focussing much of his attention on the practical disadvantages of the scleral induction coil technique which was used to monitor the ocular rotation. Duwaer (1982), therefore, designed a suitable afterimage technique to assess the retinal image displacement while his subjects actively oscillated their heads through peak-to-peak amplitudes of 20 deg, at a frequency of 0.66 Hz. Although a drop in the precision of fixation and hence an increase in retinal image speed could indeed be demonstrated, conflicting results were obtained on the magnitude of retinal image motion.

At head oscillations near 0.66 Hz, Duwaer (1982) found averaged retinal image speeds ranging from 0.3-0.8 deg/s, which was only one third of the value reported by Steinman et al. (1.0-2.1 deg/s; 0.66 Hz). Whereas Steinman et al. (1982) concluded that oculomotor compensation for active head movement was far from perfect, Duwaer (1982) was forced to disagree on that point.

Ferman et al. (1987a), measured mean retinal image speeds between 0.6-1.3 deg/s in the presence of large amplitude voluntary head oscillation (frequency: 0.67 Hz; total amplitude 17 deg). No significant difference existed between these data and those described by both Steinman et al. (1982) and Duwaer (1982).

In spite of the fact that Duwaer (1982) reported extreme precision of gaze direction, we believe that a substantial gaze instability and concomitant retinal image motion must be regarded as a normal physiological phenomenon.

Steinman et al. (1985) were the first to quantify the visual performance during active head movement. They determined visual contrast sensitivity functions (CSF's), using a sinusoidal grating display, while their subjects actively oscillated their heads. The resulting curves (CSF's) were shifted towards lower values along the spatial frequency axis as a consequence of the retinal image motion.

The displacement however, was smaller than might be expected from the results reported by Kelly (1979b) who made measurements with artificially moved stabilized gratings. According to Steinman et al. (1985) vision was better with equal amounts of averaged *natural* retinal image motion. This finding might indeed point in the direction of a central, possibly vestibular contribution to the process of vision.
Without question their data were obtained with great care and integrity and must be regarded as free from artefacts. Still we have reason to doubt their argument, as will be discussed.

Recently, attention was drawn to the fact that the averaged retinal image speed observed in the presence of passive head oscillation (frequency: 1-6 Hz, total amplitude: 5 deg) proved to be a poor parameter of the visual contrast perception (Flipse et al., 1990). Optimal vision appeared to be intermittent and strongly related to the periods with retinal image speeds under 2 deg/s (Westheimer and McKee, 1975) which occurred around the reversal points of the oscillatory movement of the eyes. The length of the time interval at which these slip values were present determined the actual level of contrast sensitivity.
In view of these findings it is likely that Steinman et al. (1985) over-estimated the significance of these contrast thresholds obtained with voluntary head movement. However, our doubts do not discount the possibility that a vestibular subsystem indeed contributes to the process of vision. Although there are few neuro-anatomical bases to support such an idea, no experimental evidence is available on this issue. Proof of the (non)-existence of such (hypothetical) systems will be fundamental to our knowledge of the mechanisms involved in the maintainance of a proper level of visual acuity in the presence of natural, day-to-day locomotor activity.
We therefore decided to retest the most recent experiment described by Steinman et al. (1985), introducing several important methodological modifications.

The design of our experiment was such that identical patterns of retinal image motion were generated on the retina either with or without head movement.

Two different viewing conditions were applied (Fig. 14):

VII **With voluntary (high frequency 1-4 Hz) head oscillation, while viewing an earth-fixed sine-wave grating.**

VIII **In the absence of head movement, fixating a stationary target, while the grating oscillated according to the gaze movements recorded during the voluntary head movement (Expt. VII).**

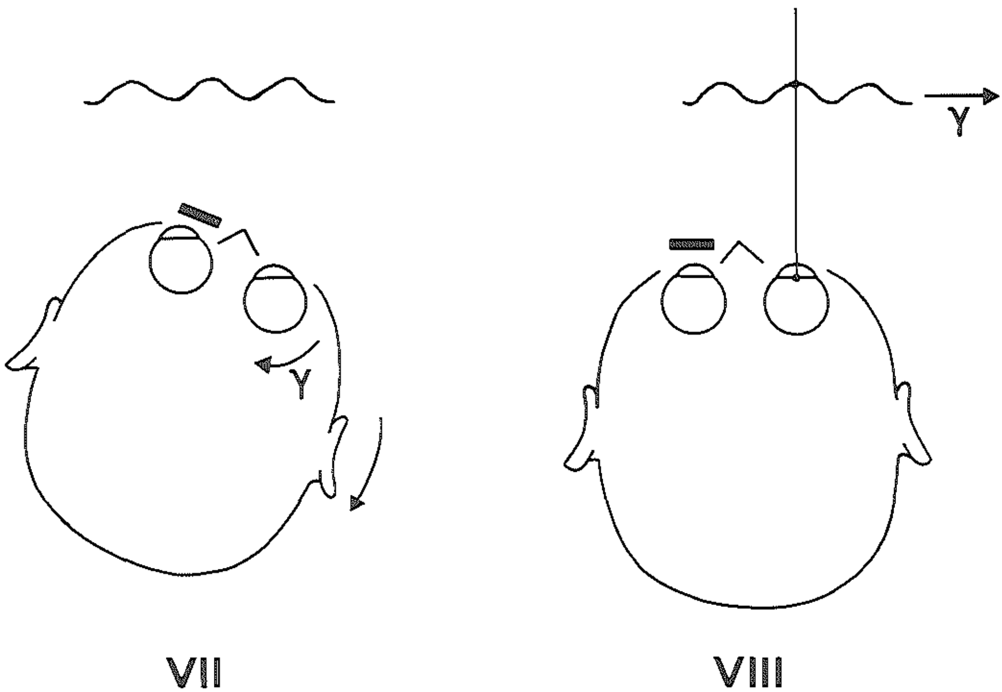


Fig. 14

The two different experimental conditions. The extra-ocular arrow in Expt. VII represents the gaze movement, which is reimposed on the retina in Expt. VIII.
The gratings are represented by sine-waves.
The vertical line in Expt. VIII symbolizes the stabilized view.

4.2 METHODS

Visual stimulation

The visual stimulus (identical to that described in the previous chapter) was a vertical 6 c/deg sine-wave grating, generated electronically and displayed on a large screen oscilloscope. The screen was positioned 4 meters in front of the subject. The stimulus field was rectangular, with a height of 4 deg and a width of 6 deg, viewed in a dark surround. Its averaged luminance was 0.1 Cd/m^2, which remained constant throughout both experimental sessions (Expt. VII, VIII). The experiments were carried out monocularly, the other eye being covered.
Contrast sensitivity was determined by a method of adjustment as described in the second chapter (Keemink et al., 1979), each datapoint was the mean of three separate settings. The subject's task was to depole the contrast attenuation using a pushbutton. As soon as the contrast was subthreshold, the button was released, which caused the contrast to increase. Repeating this procedure, the contrast of the grating varied (continuously) around the subject's detection threshold. Incidental small alterations were made to the attenuation rate (1-3 dB/s) in order to avoid stereotyping of the responses. This was not unlikely to happen, since the subjects were requested to perform several tasks simultaneously.
The fixation target, placed in the centre of the screen, was ring shaped. The visibility of its inner opening (4 min arc) provided the subject with a critereon for normal vision. This proved to be very profitable since the scleral sensor-coil, used to measure the eye movements, might irritate the eye and cause an artefactual decrease in contrast sensitivity. Once the ring blurred the subjects were asked to blink several times in order to restore its visibility. In case this proved impossible the trial was cancelled and repeated under more favourable conditions. For reasons such as these, the recording sessions were limited to approximately 20 minutes.

During the first experimental session the subjects were asked to make voluntary head oscillations while viewing the centre of a stationary sine-wave grating (Expt. VII). In the second experimental session head movements were avoided using a fixed biteboard of dental impression material (Expt. VIII). The subject now viewed a stationary fixation target, while the grating moved behind it. Stimulus movement was produced by changing its horizontal position according to the output signal of a summator which added the present- (Expt. VIII) to the previously recorded eye rotation signal (Expt. VII). Adequate attention was paid to the direction of stimulus velocity relative to the eye (+/-), so that the procedure would not be counterproductive to the objective of the second experiment. Before entering the summator both signals were submitted to a mutually independent calibration procedure:

1) Removing the modulation from the grating produced an uniform illuminated screen on which a small bright fixation spot (3 min arc) could be generated which moved according to the output signal from the scleral sensor-coil (Expt. VIII). The position of the bright spot was identical to that of the grating. Proper stabilized viewing was brought about by the alternated alignment of this moving target with one of the two fixed targets situated near the edges of the screen. After several adjustments, based on the subjects' verbal intructions, the bright spot corresponded exactly to their line of sight. During the actual experiments the bright spot was replaced by the grating.

2) In order to meet the input-requirements of the oscilloscope (Expt. VIII), the output-voltage of the computer-stored eye rotation signal obtained during the voluntary movement of the head (Expt. VII) was amplified correspondingly.

Vestibular stimulation

The vestibular stimulus was produced by high frequency voluntary head movements (1-4 Hz), paced by proper acoustic signals. Head oscillations between 1 and 4 Hz were chosen, for such values well resembled the natural frequency range of head movement.

The subjects were free to determine the amplitude of head oscillation, provided that it did not exceed a total angle of 20 deg. Since we were especially interested in high frequency motion a certain amount of vigor was recommended. Any attempt to make violent head movements was discouraged, though.

Although the fixation target was placed 4 m in front of the head, the vestibulo-ocular interaction was essentially similar to that measured with targets at optical infinity (Collewijn et al., 1982; Steinman et al., 1982; Rodenburg et al., 1985).

In addition, ocular rotation (direction of gaze) was considered equal to the retinal image displacement (Steinman et al., 1982). At all times, the basic linear displacement of the head rotation was estimated to be less than 1 cm, corresponding to a total visual angle of less than 0.13 deg. Although its maximal contribution to the retinal image displacement was in the order of 10-15%, part of it must have been removed by eye movements derived from both the pursuit and otolithic systems (Lisberger et al., 1981; Eckmiller, 1982; Gresty et al., 1987). The effect of linear translations of the head on contrast sensitivity was therefore considered to be negligible.

With regard to the orientation of the grating, no hinder was expected from (small) vertical and torsional gaze movements - which most certainly - accompanied the voluntary (horizontal) head oscillations (Ferman et al., 1987a).

Eye and head movement recording

Horizontal ocular rotation was measured with a scleral induction coil technique, first introduced by Robinson (1963). The exact technical details of the equipment have been described elsewhere (De Bie, 1986; Flipse et al., 1990a). It is however noteworthy that the instrument was insensitive to linear displacements of the sensor-coils within a cube measuring 8 cm on each side. The combined angular and linear displacement of the head, as occured during this particular experiment, was well within these dimensions. The resolution of the instrument was <2 min arc.

Calibration of the eye movement was accomplished by alterned fixation of two calibration targets situated near the edges of the screen 5.5 deg apart.

The sensor-coils were embedded in a silicon-rubber annulus which was placed on the scleral-corneal junction (Collewijn et al., 1975). To avoid any discomfort from the tight-fitting annulus a local anaesthetic was applied (Novesine^{R}).
The rotation angle of the head was determined by a second-sensor coil which was fixed to a small plastic strip taped to the forehead. Calibration of the head movement was accomplished by comparing the output signal from the sensor-coil to that of a simple goniometer.

Analysis

Data aquisition, which involved eye and head rotation (magnetic sensor-coil technique) as well as contrast sensitivity measurement, was accomplished within 10-12 seconds for it proved virtually impossible to sustain high-frequency voluntary head oscillations of a considerable magnitude (5-10 deg) for longer periods of time.
The angular position signals obtained from the sensor-coils were analysed by a DEC-PDP11/73 micro-computer (sample frequency: 500 Hz).
A correction was applied to the data of two subjects (B and JP) since they wore spectacles during the experiments. For each dioptre 3% of the rotation angle of the head was subtracted from the ocular rotation in order to neutralize the induced magnification factor (Collewijn et al., 1983).
By differentiation in the time domain velocity files were created. Speed was defined as the absolute value of angular velocity. Saccades and blinking effects were ignored. Vestibulo-ocular gain was calculated from the following relation:

1 - (averaged gaze speed / averaged head speed)

The fundamental frequency with which the head was oscillated was determined by Fourier analyses of the head movement records.

Subjects

All four subjects participating in these experiments had normal or slightly corrected eyesight (subject B: -1.25; JP: -1.50 Dioptre). Non of them suffered from any neural disorder that might influence the outcome of the present experiments. Subject A and C were naive as to the purpose of the experiment, the other two had served in comparable psychophysical experiments before.

4.3 RESULTS

During the first experiment (Expt. VII) the subjects viewed the centre of the stationary grating while actively oscillating their heads paced by proper auditory signals.

Contrast sensitivity as a function of the frequency of the oscillatory movement of the head is presented in figure 17 (solid symbols). On average the visibility of the grating decreased by a factor 3 as the frequency of the head oscillations was increased from 1-4 Hz. Although the perceptual stability of the environment was no longer guaranteed (3-4 Hz), our subjects remained under the impression that detailled vision was still possible.

Having the advantage of accurate measuring equipment, we were able to add several important parameters of voluntary head movement to these psychophysical data (Table 3.). Pooled over all four subjects, VOR-gain remained above 0.90 (1-3 Hz), which was quite a comparable - if not slightly better - result than could be obtained with passive head oscillation (Collewijn et al., 1983). As a consequence, the averaged dimension of the image excursions on the retina was less than 1 deg (peak-to-peak), which is well within the foveal area of high-acuity (Millodot, 1972).

In the next experiment (Expt. VIII) the subjects viewed the centre of the screen on which the grating was oscillated according to the gaze-records obtained in the previous experiment. The influence of fixational eye movements was ruled out by the introduction of stabilized viewing. Head movements were avoided using a biteboard. The pattern of retinal image movement was considered identical to that produced by head movement (Expt. VII).

Within the range of experimental error, the resulting contrast sensitivity values were identical as well (Fig. 15, open symbols). These data favour a purely retinal cause responsible for the outcome of the visual process.

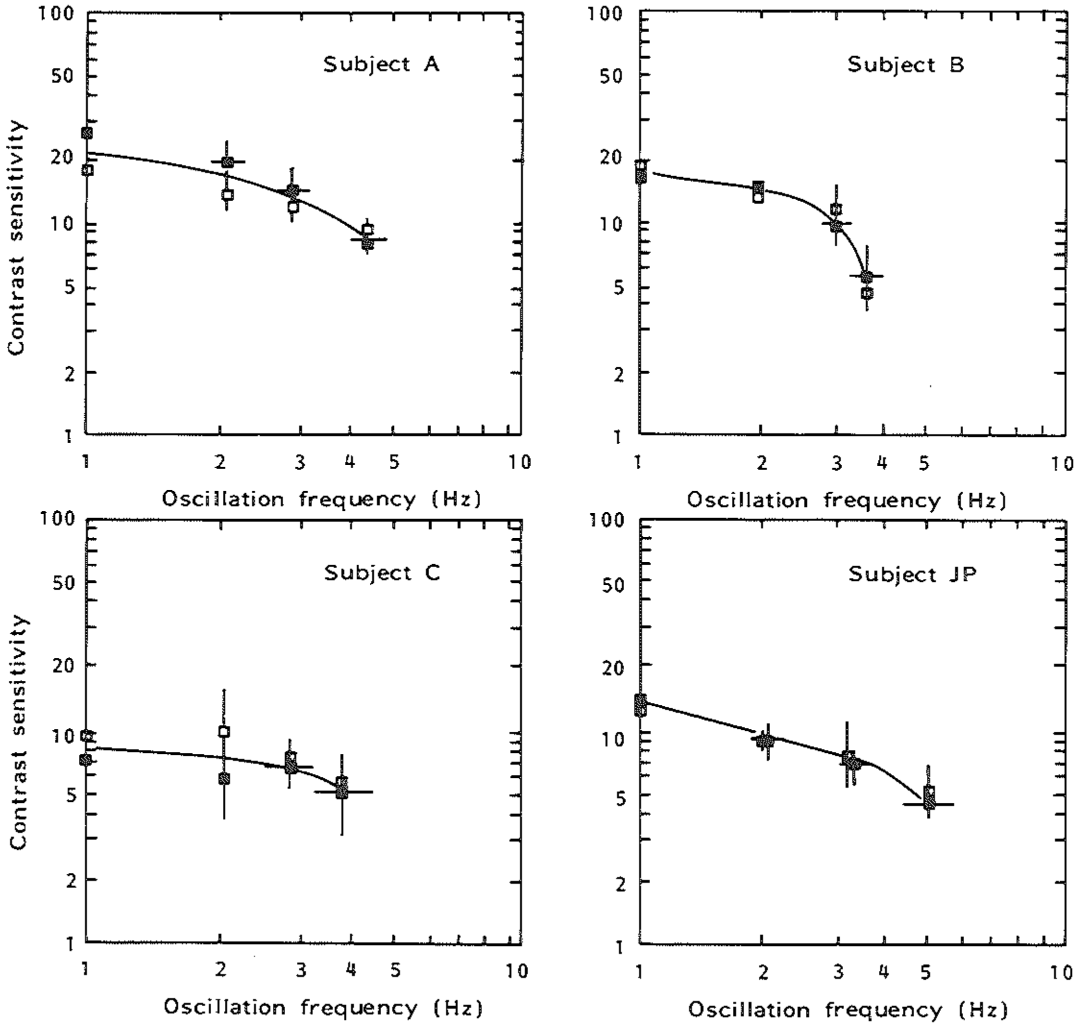


Fig. 15

Contrast sensitivity as a function of identical retinal stimulation, either with voluntary head movement (solid symbols, Expt. VII) or without it (open symbols, Expt. VIII). Mean and standard deviations are shown for both the contrast sensitivity (vertical error-bars) and frequency of voluntary head oscillation (horizontal error-bars).

Table 3

*Several parameters concerning the voluntary head movement. Mean and standard deviations ([ ]) are given, pooled over all 4 subjects. *A correction was applied in case the subjects wore spectacles during the experiments.*

Oscillation frequency:			
1 Hz	2 Hz	3 Hz	4 Hz
Head rotation (peak-to-peak, deg):			
14.89[03.32]	11.71[03.09]	09.49[02.84]	07.90[03.47]
Eye rotation* (peak-to-peak, deg):			
00.80[00.31]	00.77[00.32]	00.61[00.20]	00.78[00.26]
Head speed (deg/s):			
28.26[06.88]	47.20[12.25]	56.27[16.81]	67.12[29.55]
Retinal image speed (deg/s):			
01.68[00.71]	03.02[01.19]	03.47[01.14]	06.58[02.14]
VOR-gain:			
00.93[00.02]	00.93[00.03]	00.94[00.02]	00.89[00.03]
Fourier analysis (Hz):			
01.04[00.08]	01.99[00.08]	02.94[00.21]	04.27[00.61]

4.4 DISCUSSION

In the absence of head movement averaged retinal image speeds between 5-10 deg/s render a 6 c/deg sine-wave grating completely invisible (Flipse et al., 1988). These adverse affects on detailed vision were far less obvious in case the corresponding amount of image slip was accompanied by head movement (Fig. 15, Table 3). Steinman et al. (1985) made comparable observations and introduced the term "enhanced acuity", suggesting that vision tolerates or even benefits from a certain amount of retinal image motion, provided that it was produced by head movement.

In our view, the inconsistency between the level of slip induced loss of contrast sensitivity resulting from experiments in which head movements were either allowed (quasi sinusoidal image movement) or strictly avoided (constant image movement) could be attributed to a fundamental difference in retinal stimulation. In this context, the most important finding which emerged from the present experiments was that identical forms of complex retinal image oscillation led to similar levels of contrast sensitivity, either with (Expt. VII) or without voluntary head movement (Expt. VIII). There is no need to assume that a hypothetical, preferably vestibular (sub)system, activated by active head movement might be involved in the transformation of the moving retinal image into its central counterpart. It seems that the observed reduction in contrast sensitivity measured with increased (voluntary) head movement, merely reflects the adverse effects of a corresponding decrement in vestibulo-ocular response. (Table 3., Fig. 15).

Although the size of our grating (6x4 deg) assured a constant foveal stimulation, smaller (acuity) targets, such as Landolt C-rings, might be projected on to the periferal retina as a consequence of (large) gaze movements. The averaged amplitude of retinal image displacement, measured during this experiment, never exceeded the value of 1 deg (Table 3). Since the diameter of the foveal high-acuity area is as large as 0.85 deg (Millodot, 1972), few adverse affects are to be expected by non-foveation of small objects in the environment.

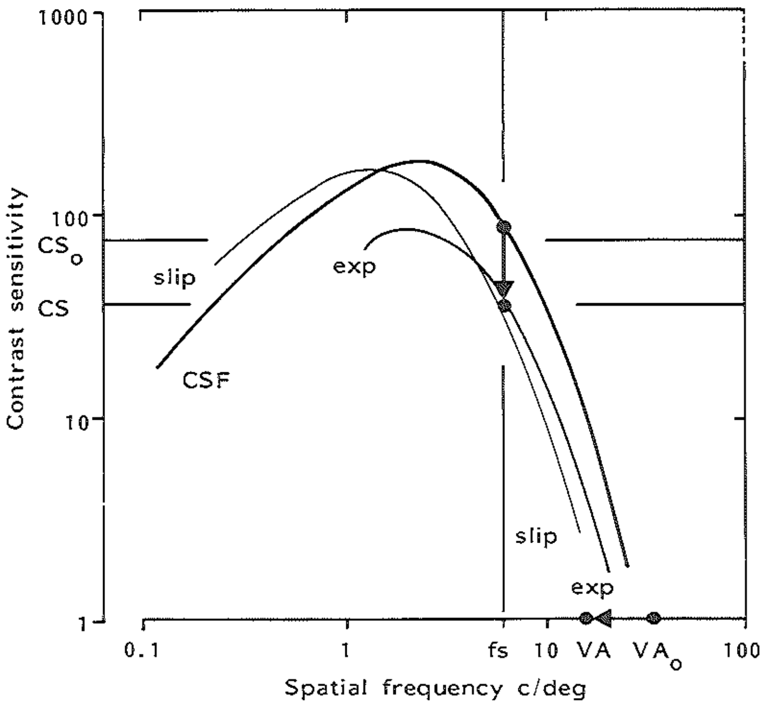


Fig. 16

Visual acuity (VA) calculated from the CSF differs whether the curves are shifted to the left as due to increasing retinal slip, or shifted downwards as occurs with limited exposure duration of the gratings.

Indeed, both common and experimental experience, suggest that accurate vision is very well maintained during locomotor activity (Steinman and Collewijn, 1980; Steinman et al., 1985). Additional proof comes from semi-quantitative data (0-5 score, 0: no hinder what so ever) on the flying performances of helicopter pilots which showed that the adverse affects on detailed vision, as produced by whole body vibration, were indeed very small (averaged score <0.69; Dupuis and Hartung, 1986). As opposed to sinusoidal head oscillations, randomized frequency spectra, as occur during natural locomotor activity, hindered the visual and flying controle performances to an even lesser extent (Lewis and Griffin, 1978; Moseley and Griffin, 1986). It can be deduced that head movement, whether it originates from artificial or natural sources, hardly affects our capacity to resolve spatial detail.

With voluntary head movement, Steinman et al. (1985) measured an averaged decrease in high spatial frequency contrast (>4 c/deg) by a factor 2. Such data are most certainly in conflict with their impression of clear vision, for a slip-induced change in high spatial frequency threshold-contrast causes a nearly identical change in visual acuity (Owsley et al., 1983). Even a central mechanism correcting the surplus of retinal image motion (Steinman et al., 1985), preventing a drastic decline in contrast sensitivity, does not explain the discrepancy between the objective measurements and the subjective impressions of unaltered accurate vision.

Obviously, a model based solely on the adverse affects of retinal slip does not account for all features of vision during oscillatory head movement.

Flipse et al. (1990a) demonstrated that contrast perception in the presence of (passive) head movement was on the moments in which the amount of retinal slip proved harmless, that is below 2 deg/s (Westheimer and McKee, 1975; Flipse et al., 1988). These observation intervals coincided with the reversals in ocular oscillation.

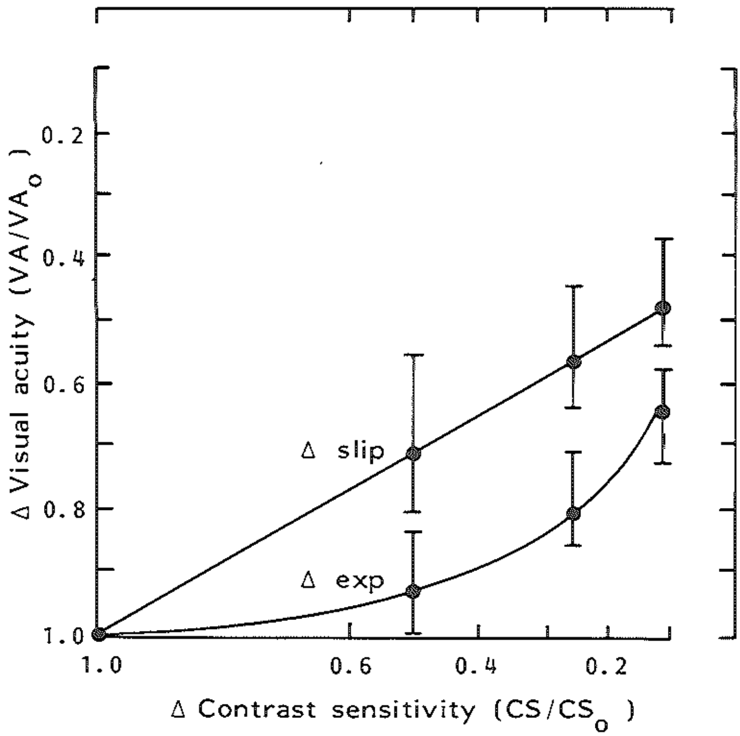


Fig. 17

The mutual relation between a change in contrast sensitivity (CS/CS_o) and visual acuity (VA/VA_o), due to either slip or limited exposure of the gratings.

The duration of these observation intervals (5-100 ms) was proportional to the level of contrast sensitivity. Baron and Westheimer (1973) described essentially similar relations between the (relative) threshold luminance level of Landolt C-rings and their exposure duration.
As will be discussed, a model relating high spatial frequency contrast sensitivity to exposure time, rather than image velocity, could account for the fact that detailed vision is not markedly affected by head movement.

Whereas retinal image motion causes the CSF (Fig. 16) to shift to the left along the horizontal axis (new situation marked "slip", Fig. 16), limited exposure duration causes a downward shift of the curve (new situation marked "exp", Fig. 16). For a given high spatial frequency value (f_s) , the relation between a decline in both contrast sensitivity ($CS_0 \rightarrow CS$) and visual acuity ($VA_0 \rightarrow VA$) as produced by movement (Kelly, 1979b; Burr and Ross, 1982), differs significantly from that produced by limited exposure (Nachmias, 1967; Kelly, 1971) of the grating.
We established these relations from a CSF based on the averaged result of 54 subjects, all having a visual acuity of ≥ 1.0 (Bulens, 1988). Visual acuity was calculated from the point of interception of the descending part of the CSF with the horizontal axis (maximal contrast, finest detail, 30 c/deg $\approx$ visual acuity 1.0). Figure 17 illustrates the relation between a change in both contrast sensitivity (CS/CS_0) and visual acuity (VA/VA_0).
Obviously, limited exposure of the gratings affects contrast sensitivity in a far more drastic manner than it does visual acuity. At oscillatory head movements near 4 Hz, we measured an averaged decrease in contrast sensitivity of almost a factor 3-4 (Fig. 15). According to the relation based on the exposure model (lower curve, Fig. 17), a decrease in contrast sensitivity to about 30% of its initial (non head movement) value, is accompanied by a corresponding decrease in visual acuity of no more than 15%. On the other hand, an identical change in contrast sensitivity based on the (averaged) amount of retinal slip (upper curve, Fig. 17), corresponds to a decrement in visual acuity of nearly 40%.

Perhaps crude subjective impressions provide an insufficient bases to distinguish between small alterations in visual acuity (<20%, model based on exposure duration), yet it seems unlikely that large(r) drops in visual acuity remain unnoticed (>50%, model based on retinal slip).

Arguments such as these, favour the concept of observation intervals during which a quasi stabilized image (<2 deg/s) is exposed to the visual system on the basis of which (intermittent) accurate vision is still possible.

CHAPTER 5
CONCLUDING REMARKS

The aim of the present study was to establish the exact effect of retinal image slip on the visibility of sine-wave gratings during eye, as well as head movement, and if possible, to provide a (simple) model that might account for certain as yet unexplained features of dynamic vision. In the course of the work increasingly physiological conditions were adopted, so that the results obtained as such would be applicable to those tasks that confront our visual and (vestibulo)-oculomotor systems most frequently in everyday life.

Murphy (1978) tried to prove that the (averaged) amount of retinal image motion (slip) was the sole determinant of contrast perception in moving objects, as postulated by Miller and Ludvigh (1962). With the eye pursuing a moving 5.14 c/deg sine-wave grating, he reported no significant decrease in contrast sensitivity with retinal slip values up to 1.2 deg/s. In spite of his efforts, this particular experimental result was insufficient to prove the correctness of Miller and Ludvigh's hypothesis, for a change in contrast sensitivity was only to be expected at higher retinal slip values (>2 deg/s; Westheimer and McKee, 1975).

The present study showed that, with moving gratings, contrast sensitivity during ocular pursuit was equal to contrast sensitivity during maintained fixation on a stationary target, provided that the magnitude of retinal image motion was equal in either case.

Since we measured slip values up to 20 deg/s, our data expanded the value of Murphy's conclusions to the full extent. Furthermore, the tolerated range of retinal image motion (0.2-2.0 deg/s) as reported by a considerable number of investigators was essentially the same under pursuit conditions.

Whereas pursuit eye movements protected the perceptibility of details in moving objects, the visibility of larger structures, such as the stationary environmental background, was impaired.

The reduced visibility measured with coarse patterns such as low spatial frequency gratings (<1 c/deg), was a consequence of the fact that accurate pursuit eye movements minimized the magnitude of retinal image motion and therefore prohibited the occurence of favourable spatio-temporal interactions on the retina. Obviously, this kind of suppression is fundamentally different from the suppression which occurs with saccadic eye movements (Matin, 1974; Riggs, 1976).
In our view, no effect on the visual performance could be traced to the activities in the oculomotor system itself.

Whereas the pursuit system becomes totally ineffective in reducing the amount of retinal slip, once the target oscillations exceed the frequency of 2 Hz, similar oscillatory movements of the head are not known to degrade our visual performance.
Benson and Barnes (1978) reported that the visual performance remained unaltered with head oscillations up to 9 Hz. Unfortunately, we could only speculate as to how much retinal slip was present during their experiment for they failed to measure the eye movements in that specific frequency range (5-10 Hz).
Steinman and Collewijn (1980) measured twice the amount of averaged retinal image motion tolerated by the visual system (4 deg/s) with voluntary head oscillations covering a frequency range of 0.25-5.0 Hz. Since vision remained stable and clear under these circumstances, they ,justly, drew attention to the implications this might have on visual and oculomotor physiology. A few years later, Steinman et al. (1985) introduced the term "enhanced" visual performance, suggesting that a (hypothetical) vestibular contribution might improve vision as we move our head. With high frequency passive (2-6 Hz) as well as active (1-4 Hz) head oscillations we measured significant reductions in contrast sensitivity for a stationary 6 c/deg sine-wave grating, which could be related to a corresponding decrease in vestibulo-oculomotor compensation.
With movement of the head, the magnitude of mean retinal image motion could (indeed) be 2 to 3 times larger than without it.

Notwithstanding the fact that our results were in agreement with those reported earlier (Steinman and Collewijn, 1980; Steinman et al., 1985), additional experimental results discouraged a further exploration of a (hypothetical) vestibular involvement in the proces of visual analysis.

Interpretation of contrast thresholds obtained with relative motion between the eye and the visual stimulus (grating) is least complicated when the speedprofile is that of a constant velocity-function. This type of retinal image motion is, however, rarely encountered under physiological conditions. The residual ocular movement (gaze movement) which occurs during movement of the head e.g., is at best described as quasi-sinusoidal. Based upon this observation, several experiments were carried out during which the emphasis was placed on elucidating the effect of momentary retinal image speed on the visibility of the gratings. From these experiments we concluded that the process of threshold contrast detection with sinusoidal movement of the head was in fact sampled and dominated by the moments during which the actual velocity of retinal slip was within the range tolerated by the visual system, that is below 2 deg/s (Westheimer and McKee, 1975). The "observation intervals" coincided with the reversal points of the oscillatory movement of the eyes. In addition, the length of the intervals (exposure time) determined the quality of visual perception, expressed in the level of contrast sensitivity.

Since the outcome of the visual process was due to retinal phenomena only, there was no need to continue the search for a hypothetical, neural mechanism, activated by (voluntary) head rotation. With reference to the concept of "observation intervals", a model based on exposure duration, rather than retinal image slip, reconciles contrast sensitivity as well as acuity measurements obtained during head movement.

Generalizing the results, it can be said that (vestibulo)-oculomotor compensation prevents a decrement in visual performance, although its action is insufficient to keep the averaged amount of retinal image motion within acceptable limits. Obviously, the visual system anticipates the imperfections in ocular guidance, directing all its attention to the (brief) moments during which acceptable image velocities do exist.

Whereas the classic view concerning the vestibulo-oculomotor compensation was based on a 'perfect' stabilization of the retinal image, thus allowing continuous clear vision in the presence of head movement, modern technology revealed a considerable image instability on the retina, forcing the visual system to make snapshot-impressions of the environmental scenery.

REFERENCES CITED

Abadi R.V. and Sandikcioglu M. (1975). Visual resolution in congenital pendular nystagmus. Am. J. Optom. physiol. Opt., 52, 573-581.

Abadi R.V. and Worfolk R. (1989). Retinal slip velocities in congenital nystagmus. Vision Res., 29 (2), 195-205.

Arend Jr. L.E. (1976). Temporal determinants of the form of the spatial contrast threshold MTF. Vision Res., 16, 1035-1042.

Arend L.E. and Skavenski A.A (1979) Free scanning of gratings produces patterned retinal exposure. Vision Res., 19, 1414-1419.

Baloh R.W., Kumley W.E., Sills A.W., Honrubia V. and Konrad H.R. (1976) Quantitative measurements of smooth pursuit eye movements. Ann. Otol. Rhinol. Lar., 85, 111-119.

Barmack N.H. (1970) Dynamic visual acuity as an index of eye movement control. Vision Res., 10, 1377-1391.

Barnes G.R. and Forbat L.N. (1979). Cervical and vestibular afferent control of oculomotor response in man. Acta. Otolaryngol., 88, 79-87.

Baron W.S. and Westheimer G. (1973) Visual acuity as a function of exposure duration. J. Opt. Soc. Am., 63, 2, 212-219.

Bartley S.H. (1966). The psychophysiology of vision. In EXPERIMENTAL PSYCHOLOGY, 24 (Edited by Stevens S.S.), Wiley & Sons, INC, New York.

Békésy von G. (1947). A new audiometer. Acta Otolaryngol. (Stockh) 34, 411-422.

Benson A.J. and Barnes G.R. (1978). Vision during angular oscillation: The dynamic interaction of visual and vestibular mechanisms. Aviat. Space Environ. Med., 49 (1), 340-345.

Berlyne D.E. (1970). Attention as a problem in behavioral theory. In ATTENTION: Contemporary theory and analysis. (Edited by Mostofsky), Appleton-Century-Crofts, New York., 25-49.

Bie de J. (1985). An afterimage vernier method for assessing the precision of eye movement monitors; results for the scleral coil technique. Vision Res., 25, 1341-1343.

Bie de J. (1986). The control properties of small eye movements. Thesis, Technical University Delft, The Netherlands.

Blackburn R.H. (1937). Perception of movement. Am. J. Optom., 14, 365.

Braddick O., Campbell F.W. and Atkinson J. (1978) Channels in vision: Basic aspects. In HANDBOOK OF SENSORY PHYSIOLOGY (Edited by Held R., Leibowitz H.W. and Teuber H.L.) Springer, New York, (8), 3-38.

Brink G. van den (1957) Retinal summation and the visibility of moving objects. Thesis, University of Utrecht, The Netherlands.

Brown B. (1972) Dynamic visual acuity, eye movements and peripheral acuity for moving targets.
Vision Res. 12 305-321.

Bulens C. (1988) Application of contrast sensitivity in clinical neurology. Thesis, Erasmus University Rotterdam, The Netherlands.

Burr D.C., Ross J. (1982) Contrast sensitivity at high velocities. Vision Res. 22, 479-484.

Campbell F.W. and Green D.G. (1965). Optical and retinal factors affecting visual resolution. J. Physiol., 181, 576-593.

Campbell F.W., Robson J.G. (1968) Application of Fourier analysis to the visibility of gratings.
J. Physiol. 197, 551-566

Collewijn H., Mark van der F. and Jansen T. C. (1975). Precise recording of human eye movements. Vision Res., 15, 447-450.

Collewijn H., Conijn P. and Tamminga E.P. (1982). Eye-head coordination in man during the pursuit of moving targets. In FUNCTIONAL BASES OF OCULAR MOTILITY DISORDERS. (Edited by Lennerstrand G., Zee D.S. and Keller E.L.), Pergamon, Oxford.

Collewijn H., Martins A.J. and Steinman R.M. (1983). Compensatory eye movements during active and passive head movements: Fast adaptation to changes in visual magnification. J. Physiol., 340, 259-286.

Die van G. (1983). Stimulus response relaties van de optokinetische nystagmus van de mens. Thesis, Erasmus University Rotterdam, The Netherlands.

Drischel H. (1958). Über den Frequenzgang der horizontalen Folgebewegungen des menschlichen Auges. Pflügers Arch. ges. Physiol., 268, 34.

Dupuis H.E. and Hartung E. (1986) Auswirkungen der Pilotenbelastung beim Fliegen mit Nachtsichtsgeraten (BiV-Bildverstarkerbrillen). Forschungsbericht aus der Wehrmedizin, FW 0038.

Duwaer A.L. (1982) Assessment of retinal image displacement during head movement using an afterimage method. Vision Res., 22, 1379-1388.

Eckmiller R. (1982) Concerning the linear acceleration input to the neural oculomotor control system in primates. In PSYSIOLOGICAL AND PATHOLOGICAL ASPECTS OF EYE MOVEMENTS. Edited by Roucoux A. and Crommelinck M.), Dr W Junk- The Hague, Boston, London, 131-137.

Fender D.H., Nye P.W. (1961) An investigtion of the mechanisms of eye movement control.
Kybernetik, 1, 81-88.

Ferman L., Collewijn H., Jansen T.C. and Berg van den A.V. (1987a) Human gaze stability in the horizontal, vertical and torsional direction during voluntary head movements, evaluated with a scleral induction coil technique. Vision Res., 27, 5, 811-828.

Flipse J.P., Wildt van der G.J., Rodenburg M., Keemink C.J. and Knol P.G.M. (1988). Contrast sensitivity for oscillating sine-wave gratings during ocular fixation and pursuit. Vision Res., 28 (7), 819-826.

Flipse J.P., Wildt van der G.J., Maas A.J.J., Keemink C.J. and Rodenburg M. (1989). Visual contrast perception during passive head oscillation. In PROCEEDINGS ECEM 5. (Edited by Schmid R. and Zambarbieri D.), University of Pavia, Pavia (Italy), 30-32.

Flipse J.P., Maas, A.J.J. and Rodenburg M. (1990) Visual processing in the presence of passive head oscillation. Vision Res. (submitted).

Flipse J.P. and Maas A.J.J. (1990). The influence of voluntary head movement on visual contrast perception. Vision. Res. (submitted).

Gauthier G.M. and Robinson D.A. (1975). Adaptation of the human vestibular-ocular reflex to magnifying lenses. Brain Res., 92, 331-335.

Gauthier G.M., Piron J.P., Roll J.P., Marchetti E. and Martin B. (1984). High-frequency vestibulo-ocular reflex activation through forced head rotation in man. Aviat. Space Environ. Med., 55 (1), 1-7.

Gonshor A. and Melvill-Jones G. (1976a). Short-term adaptive changes in the human vestibulo-ocular reflex arc. J. Physiol., 256, 361-380.

Gresty M.A., Bronstein A.M. and Barratt H. (1987) Eye movement responses to combined linear and angular head movement. Exp. Brain Res., 65, 377-384.

Hubel D.H. and Wiesel T.N. (1959). Receptive fields of single neurons in the cat's striate cortex. J. Physiol., 148, 574-591.

Julesz B. (1971). Foundations of cyclopean perception. University of Chicago Press, Chicago (U.S.A.), III.

Keemink C.J., Wildt van der G.J. and Deursen van J.B.P. (1979). Microprocessor-controlled contrast sensitivity measurements. Med. Biol. Engng. Comput., 17, 371-378.

Kelly D.H. (1971). Theory of flicker and transient responses, I. Uniform fields. J. Opt. Soc. Am., 4, 537-546.

Kelly D.H. (1979a) Motion and Vision I: Stabilized image of stationary gratings. J. Opt. Soc. Am. 69, 1266-1273.

Kelly D.H. (1979b). Motion and vision II. Stabilized spatiotemporal threshold surface. J. Opt. Soc. Am., 69, 1340-1348.

King-Smith P.E. and Riggs L.A. (1978). Visual sensitivity to controlled motion of a line or edge. Vision Res. 18, 1509-1520.

Kulikowski J.J. and Tolhurst D.J. (1973). Psychophysical evidence for sustained and transient detectors in human vision. J. Physiol., 232, 149-162.

Lange de H. (1957). Attenuation characteristics and phase shift characteristics of the human fovea-cortex systems in relation to flicker fusion phenomena. Thesis. Technical University Delft, The Netherlands.

Lewis C.H. Griffin M.J. (1978) Prediction the effect of dual frequency vertical vibration on continuous manual control performance. Ergonomics, 21, 637-650.

Lisberger S.G., Evinger C., Johanson G.W and Fuchs A.F. (1981) Relation between eye acceleration and retinal image velocity during foveal smooth pursuit in man and monkey. J. Neurophysiol., 46, 229-249.

Ludvigh E. (1949). Visual acuity while one is viewing a moving object. Arch. Ophtal., 42, 14-22.

Marmor M.F. and Gawande A. (1988). Effect of visual blur on contrast sensitivity. Ophtalmology, 95, 139-143.

Martins A.J., Kowler E. and Palmer C. (1985). Smooth pursuit of small-amplitude sinusoidal motions. J. Opt. Soc. Am., 2 (2), 234-242.

Meiry J.L. (1971). Vestibular and proprioceptive stabilization of eye movements. In THE CONTROL OF EYE MOVEMENTS. (Edited by Bach-y-Rita P., Collins C.C and Hyde J.E.), Academic Press, New York, 483-496.

Miller J.W., Ludvigh E. (1962). The effect of relative motion on visual acuity. Survey of Opthals. 7, 83-116

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

Moseley M.J. and Griffin M.J. (1986) Effects of display vibration and whole body vibration on visual performance. Ergonomics., 29, 977-983.

Murphy B.J., Kowler E. and Steinman R.M. (1975). Slow oculomotor control in the presence of moving backgrounds. Vision Res., 15, 1263-1268.

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

Nachmias J. (1967). Effect of exposure duration on visual contrast sensitivity with square-wave gratings. J. Opt. Soc. Am., 57 (3), 421-427.

Nes van F.L. and Bouman M.A. (1967). Spatial modulation transfer in the human eye. J. Opt. Soc. Am., 57, 3, 401-406.

Owsley C., Sekuler R. and Siemsen D. (1983) Contrast sensitivity throughout adulthood. Vision Res., 23, 7, 689-699.

Pollock W.T. (1953). The visibility of a target as a function of its speed and movement. J. Exp. Psychol., 45, 449-454.

Reulen J.P.H., Marcus J.T., Koops D., Vries F.R. de, Tiesinga G., Boshuizen K., Bos J.E (1988). Precise recording of the eye movement and pupilary reflects in men: The IRIS techniques. Med. Biol. Engng. Comput., 26, 20-31.

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

Rodenburg M., Kasteel-van Linge A. and Maas A.J.J. (1985). Co-ordination of head and eye position during fixation. In EYE MOVEMENTS: From Physiology to cognition. (Edited by O' Regan J.K. and Levy-Schoen A.), Elseviers Science Publishers B.V., North Holland., 211-218.

Savoy R.L. and McCann J.J. (1975). Visibility of low-spatial frequency sine-wave targets: dependence on number of cycles. J. Opt. Soc. Am., 65, 343-350.

Schalén L. (1980) A quantification of tracking eye movements on normal subjects. Acta Otolaryngol. 90, 404-413.

Skavenski A.A., Hansen R.M., Steinman R.M. and Winterson B.J. (1979). Quality of retinal image stabilization during small natural and artificial body rotations in man. Vision Res., 19, 675-683.

Stark. L. (1971) The control system for versional eye movements.
In THE CONTROL OF EYE MOVEMENTS. (Edited by Bach-y-Rita P.), Academic Press, New York.

Steinman R.M. and Collewijn H. (1980). Binocular retinal image motion during active head rotation. Vision Res., 20, 415-429.

Steinman R.M., Cushman W.B. and Martins A.J. (1982) The precision of gaze -a review. Human Neurobiol., 1, 97-109.

Steinman R.M., Levinson J.Z., Collewijn H. and Steen van der J. (1985). Vision in the presence of known natural retinal image motion. J. Opt. Soc. Am., 2, (2), 226-233.

Stott J.R.R. (1984). The vertical vestibulo-ocular reflex and ocular resonance. Vision Res., 24, (9), 949-960.

Westheimer G. and McKee S.P. (1975). Visual acuity in the presence of retinal image motion. J. Opt. Soc. Am., 65, 847-850.

Wildt van der G.J., Keemink C.J., Brink G. van den (1976) Gradient detection and contrast transfer by the human eye. Vision Res. 16, 1047-1053.

Wildt van der G.J., Waarts R.G (1983) Contrast detection and its dependence on presence of edges and lines in the stimulus field. Vision Res. 23, 821-830.

Wildt van der G.J. (1984). Interchangeability of space and time in perception. In LIMITS IN PERCEPTION. (Edited by Van Doorn et al.), VNU Science press, The Netherlands, 139-172.

Yumin L., Biachuan J. (1984) Contrast sensitivity measured during smooth pursuit movement.
Scienta Sinica (series B) XXVII, 710-721.

PUBLICATIES

(Bij dit proefschrift)

Wildt van der G.J., Flipse J.P., Rodenburg M. and Keemink C.J. (1986).
The effect of relative motion on contrast sensitivity. EYE MOVEMENTS: From Physiology to cognition. (Edited by O'Regan J.K. and Levy-Schoen A.), Elseviers Science Publishers B.V., North Holland., 156-157.

Rodenburg M., Flipse J.P. and Wildt van der G.J. (1986).
Visual contrast sensitivity for moving gratings during fixation and pursuit eye movements. 8th. Symp. Posturografy, Disorders of posture and gait, may 12-15, 2.

Rodenburg M., Flipse J.P. and Wildt van der G.J. (1987).
Visual contrast sensitivity during angular oscillation. Barany Soc. Meeting, Bologne, june 1-4, 34.

Flipse J.P., Wildt van der G.J. and Rodenburg M. (1987).
Visual performance during eye and/or head movement. Perception, 16, 2, 254.

Flipse J.P., Rodenburg M. and Wildt van der G.J. (1988).
Visual performance during passive head movement. Perception, 17, 3, 388.

Flipse J.P., Wildt van der G.J., Rodenburg M., Keemink C.J. and Knol P.G.M. (1988). Contrast sensitivity for oscillating sine-wave gratings during ocular fixation and pursuit. Vision Research, 28, 7, 819-826.

Flipse J.P., Wildt van der G.J., Maas A.J.J., Keemink C.J. and Rodenburg M. (1989). Intermittent vision during head movement. Perception, 18, 4, 496-497.

Flipse J.P., Wildt van der G.J., Maas A.J.J., Keemink C.J. and Rodenburg M. (1989). Visual contrast perception during passive head oscillation.
PROCEEDINGS E.C.E.M.5., (Edited by Schmid R. and Zambarbieri D.), University of Pavia, Pavia (Italy), 30-32.

Flipse J.P., Maas A.J.J. and Rodenburg M. (1990a). Visual processing in the presence of passive head oscillation. Vision Research, (submitted).

Flipse J.P. and Maas A.J.J. (1990b). The influence of voluntary head movement on visual contrast perception. Vision Research, (submitted).

Flipse J.P. en Maas A.J.J. (1990c). Het effect van passieve hoofdbeweging op de visuele waarneming. Nederlands Militair Geneeskundig Tijdschrift, 43, 6.

SAMENVATTING

Ofschoon de vergelijking tussen het menselijk oog en de klassieke fotocamera zich met name leent ter demonstratie van structurele overeenkomsten, laat de beeldverwerking van beide optische intrumenten een vergaande vergelijking niet toe. Zo is voor het vervaardigen van een scherpe fotografische opname een absoluut vereiste dat zowel de camera alsmede het te fotograferen object geen beweging ten opzichte van elkaar vertonen. Daarentegen is (enige) beeldbeweging op het netvlies juist een vereiste om scherp te kunnen zien. De verklaring hiervoor ligt in het feit dat het netvlies (in tegenstelling tot de fotogevoelige film in de camera) naast de ruimtelijke eigenschappen, tevens de tijdsaspecten van het door de lens gevormde (bewegende) beeld weet vast te leggen.

Afhankelijk van de gedetailleerdheid van het waar te nemen object, tolereert het visueel systeem slechts een beperkte beeldsnelheid ten opzichte van het netvlies (gemiddeld: 0,2-2,0°/s). Van nature zal het beeld nooit te langzaam bewegen daar ook tijdens fixatie van stilstaande voorwerpen, minieme - veelal onbewuste - fixatieve oogbewegingen het beeld juist voldoende bewegen over het netvlies. Naast een volledige stabilisatie is met name ook het teveel aan beeldbeweging schadelijk voor de kwaliteit van ons zien. Waar het de ongestoorde zichtbaarheid van details betreft ligt de bovengrens van beeldbewegingssnelheid ten opzichte van het netvlies reeds bij de 2°/s.
Het is dan ook niet verwonderlijk dat de mens over diverse neuronale systemen beschikt welke het dreigend teveel aan beeldbeweging op het netvlies (slip) tot aanvaardbare proporties reduceren.

Onder alledaagse omstandigheden gebruiken we met name een tweetal van deze zogenaamde beeldstabiliserende systemen. Enerzijds onderscheiden we het oogvolgsysteem, hetgeen ons in staat stelt met stilstaand hoofd bewegende objecten in de ruimte om ons heen te volgen. Anderzijds is een zeer belangrijke beeldstabiliserende taak weggelegd voor het evenwichtsorgaan, in het bijzonder de vestibulo-oculaire reflex, welke voorkómt dat bij beweging van het hoofd de ogen aan de hoofddraaiing deelnemen. Door de ogen evenveel terug te draaien ten opzichte van het hoofd blijft het mogelijk, ondanks de hoofdbeweging, de blik naar één ruimtelijk punt gericht te houden.
Hoofd en ogen kunnen niet volledig rond draaien. De bewegingsvorm is die van een "oscillatie", waarbij steeds weer de uitgangspositie wordt bereikt (vergelijkbaar met de beweging van de slinger van een klok).
Het oogvolgsysteem kan de ogen feitelijk niet sneller doen oscilleren dan met twee heen en weer gaande bewegingen per seconde (oscillatie-frekwentie: 2 Hz). Het veel krachtiger vestibulair systeem kan oogoscillaties opwekken met veel hogere frekwenties. Beide systemen werken gelijktijdig en vullen elkaar waar mogelijk aan.

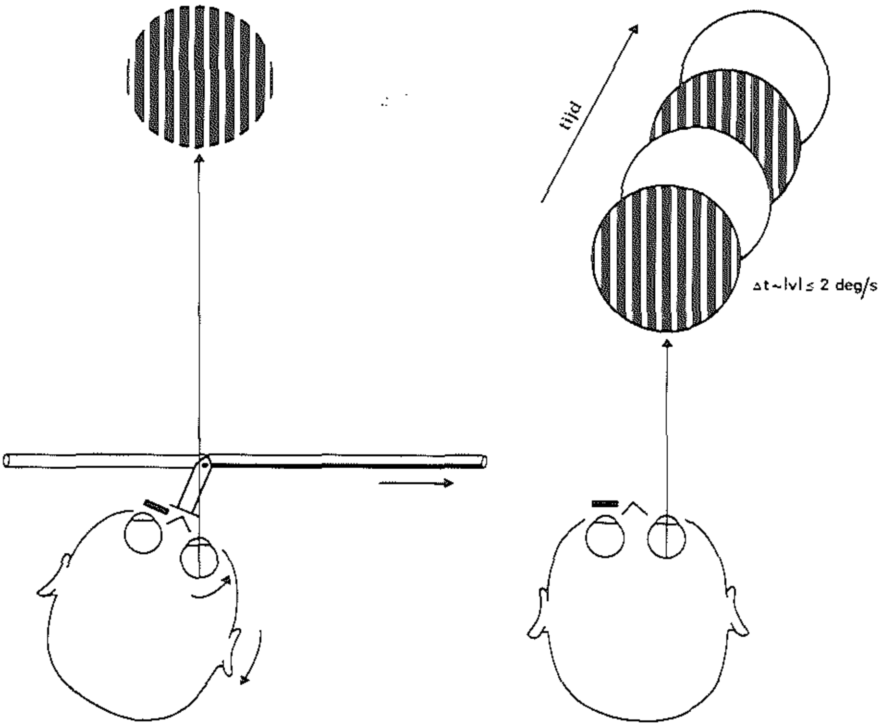
In het verleden zijn slechts enkele experimenten uitgevoerd waarbij zowel oog-en hoofdbeweging simultaan met de gezichtsscherpte werden bepaald.

In geval van het oogvolgsysteem werd reeds vroeg duidelijk dat boven een kritieke oscillatiefrekwentie (1-2 Hz) de ogen niet gefixeerd konden blijven op het object. Dientengevolge ontstond boven deze kritieke waarden een teveel aan beeldbeweging ten opzichte van het netvlies (slip), waardoor het object in kwestie niet scherp meer waargenomen kon worden. Een probleem echter werd gevormd door het feit dat de grootte van de gemiddelde beeldsnelheid niet in verhouding leek te staan tot de verminderde gezichtsscherpte. Mogelijk dat in aanwezigheid van oogvolgbewegingsactiviteit de tolerantiegrens voor beeldbeweging van het visueel systeem, doorgaans op 2°/s gesteld, enkele malen overschreden kon worden. Tijdens fixatie van een stilstaand object bij bewegend hoofd is de beeldbeweging over het netvlies een gevolg van de onvolkomenheden in het vestibulair systeem. In analogie met hetgeen bekend is over de eigenschappen van het oogvolgsysteem vermeldt de literatuur ook hier een discrepantie tussen de hoeveelheid beeldbeweging op het netvlies en de relatief goede zichtbaarheid van het object in kwestie!
De konsekwenties van deze bevindingen zijn verstrekkend. Mogelijk dat - nog onbekende - signalen afkomstig van het oogvolg- en vestibulair systeem bijdragen aan de beeldverwerking c.q. beeldbewerking welke plaatsvind in het visueel systeem. Dit zou een duidelijke waardevermindering van de huidige veelal bewegingsarm uitgevoerde (klinische) visuele tests impliceren, daar de resultaten hiermee verkregen persé geen geldigheid (meer) onder dagelijkse, dynamische, omstandigheden behoeven te hebben.
Gezien in deze contekst, en met oog voor het feit dat ons leefmilieu een toenemend dynamisch karakter krijgt waarbinnen een steeds groter beroep gedaan wordt op het visueel prestatievermogen, lijkt een studie naar de rol van deze compensatoire (slipreducerende) oogbewegingen in relatie tot de visuele beeldverwerking gerechtvaardigd.

Hiertoe werd de (visuele) contrast gevoeligheid voor al dan niet bewegende rasterpatronen bepaald onder verschillende, elkaar deels verklarende, experimentele meetcondities. Contrast gevoeligheid, als getalsmaat voor het juist waarneembaar zijn van de rasterstructuur bij een minimaal verlichtingsverschil tussen de rasterlijnen onderling, bleek een uitermate geschikte grootheid te zijn om het effect van beeldbeweging op het netvlies, en de daarmee samenhangende veranderingen in de visuele perceptie, te kwantificeren.

Door diverse, electronisch-gegenereerde, rasterpatronen een oscillatoire beweging te laten maken, waarbij de proefpersoon een meebewegend fixatiepunt volgde, werd door gelijktijdige meting van de oogrotatie (infrarood reflectie methode), het effect van de onvolkomenheden in het oogvolgbewegingssysteem verklaard (Experiment I-III). Het in de literatuur beschreven slipmodel, waarbij de (gemiddelde) snelheid van het beeld ten opzichte van het netvlies als *enige* maat voor de verandering in de visuele perceptie werd genoemd, kon middels de huidige experimenten volledig bevestigd worden. Als aanvulling hierop werd geconcludeerd dat de tolerantiegrens voor beeldbeweging van het visueel systeem, doorgaans gesteld op 2°/s, tijdens oogvolgbewegingen niet veranderd.

Het zwaartepunt van deze studie wordt echter gevormd door een serie experimenten (IV-VI) welke het effect van passieve hoofdbeweging op de visuele perceptie van in de ruimte opgestelde stilstaande rasterpatronen beschrijft. Door het hoofd door middel van een bijtstuk hoogfrekwente (2-6 Hz) oscillaties op te leggen kon voldoende beeldbeweging op het netvlies opgewekt worden om de zichtbaarheid van de rasters te doen veranderen (Fig. 18, links). Uit zeer nauwkeurige registratie van de oogbeweging (sclerale inductiespoel methode) viel af te leiden dat het beeld met een niet-constante (sinusvormige) snelheid ten opzichte van het netvlies heen en weer bewogen werd. Deze bevinding vormde de aanzet tot een differentiatie naar de invloed van enerzijds gemiddelde-, anderzijds momentane beeldsnelheid op de visuele perceptie.



Figuur 18

De drempelcontrastwaarden zoals deze gemeten werden tijdens passieve beweging van het hoofd (links), konden exact nagebootst worden door het raster in te flitsen (rechts). Hierbij was een vereiste dat de duur van de presentatie van het raster overeenkwam met de duur van de perioden dat de beeldsnelheid op het netvlies, zoals deze gemeten werd tijdens het hoofdbewegingsexperiment, niet hoger was dan 2°/s.

Volledig in overeenstemming met de literatuur konden tijdens hoofdbeweging hoge gemiddelde beeldsnelheden vastgelegd worden welke niet gepaard gingen met een corresponderende daling in contrast gevoeligheid. Alhoewel dit als mogelijk bewijs van de uitbreiding van de bewegingstolerantie van het visueel systeem onder dynamische omstandigheden beschouwd kon worden, leek een andere verklaring hiervoor meer acceptabel. Kernargument hierbij werd dan ook dat niet de gemiddelde-, maar de momentane beeldsnelheid op het netvlies de kwaliteit van de visuele waarneming bepaald.
Het mechanisme hierachter leek gebaseerd te zijn op het bestaan van zogenaamde observatie-intervallen. Deze perioden werden gekenmerkt door de aanwezigheid van lage beeldsnelheden (<2 °/s) op het netvlies, welke samenvallen met de momenten waarop de oscillatoire oogbewegingen van richting veranderen (omkeerpunten). Deze gedachte werd bevestigd door de periode waarin deze beeldsnelheden gemeten konden worden tijdens hoofdbeweging hernieuwd aan te bieden middels een inflitsexperiment, nu in afwezigheid van hoofdbeweging, waarbij de flitsduur exact overeen kwam met de (gemiddelde) duur van de lage beeldsnelheid (Fig. 18, rechts).

Tot slot werd een tweetal experimenten uitgevoerd om de invloed van actieve, vrijwillige, hoofdbeweging op de visuele perceptie vast te stellen (Expt. VII, VIII). Hieruit kwam naar voren dat uitsluitend datgene wat op het netvlies gebeurd verantwoording draagt voor een eventuele verandering in de zichtbaarheid van de omgeving.
En passant werd een verklaring gegeven voor het feit dat de gezichtsscherpte (visus), in verhouding tot de visuele contrast gevoeligheid, aanvankelijk minder geschaad wordt door beeldbeweging op het netvlies. Verschillende visuele detectie-kwaliteiten, waartoe waarschijnlijk ook kleuren-, en diepte-zien gerekend dienen te worden, lijken dus ook verschillend te lijden onder de onvolkomenheden in de beeldstabilisatie.

De tekortkomingen in het vestibulair- en - mogelijk ook - het oogvolgsysteem, inzake de reductie van het teveel aan beeldbeweging ten opzicht van het netvlies, worden in zekere zin door het visueel systeem geanticipeerd. Waar volgens de klassieke gedachte omtrent de werking van beide beeldstabiliserende systemen een continue heldere weergave van de omgeving bestaat, lijkt volgens de huidige inzichten het visueel systeem, noodgedwongen, grote discontinuiteiten in de hoeveelheid beeldbeweging op het netvlies te moeten accepteren. Hierdoor wordt de aandacht practisch geheel gericht op die momenten waarin acceptabele beeldsnelheden bestaan. Doorgaans vallen deze gunstige snelheidsmomenten samen met de omkeerpunten in de hoofd- en oogbeweging.

CURRICULUM VITAE

Geboren te Steenbergen op 30 december 1960. Later verhuisd naar Roosendaal alwaar het Norbertus College werd bezocht. Na het hoger algemeen vormend onderwijs werd het diploma Atheneum-B in 1980 behaald.
Met de studie Geneeskunde te Rotterdam werd een aanvang gemaakt in 1981. Gedurende de doctoraalfase werd als student-assistent onderzoek verricht op het gebied van de (evenwichts)fysiologie, dit in opdracht van de afdeling keel-, neus-en oorheelkunde (afdelingshoofd prof.dr. C.D.A. Verwoerd), destijds onder directe leiding van dr. M. Rodenburg en dr. G.J. van der Wildt (afdeling biomedische natuurkunde en technologie). Deze werkzaamheden, welke de basis voor dit proefschrift zouden gaan vormen, werden uiteindelijk voortgezet binnen het kader van een gastvrijheidsovereenkomst, waarbij herhaald de mogelijkheid werd geboden congressen in het buitenland te bezoeken.
Het behalen van het doctoraal examen en de bevordering tot arts vonden, respectievelijk, in 1986 en 1988 plaats.
In 1989 volgde een aanstelling als (dienstplichtig) officier-arts bij de Koninklijke Landmacht. In aansluiting daarop wordt thans de functie vervuld van arts-assistent op de afdelingen cardiologie en chirurgie van het Lievensberg ziekenhuis te Bergen op Zoom.