INFLUENCE OF EYE MOVEMENTS ON VISUAL PERCEPTION

De invloed van oogbewegingen op de visuele waarneming

(Met een samenvatting in het Nederlands)

Proefschrift ter verkrijging van de graad van doctor

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Stellingen

Een ieder die beter weet zal het beamen: dom en eigenwijs gaan altijd samen.

De veelheid aan diagnostische apparatuur vertroebelt de analytische blik van de medicus. De mogelijkheid om e.e.a. 'voor de zekerheid even te laten nakijken' ondermijnt zijn expertise, en is daarom bedreigend voor zowel de geneesheer als voor zijn cliënt.

Van onoverkomelijk belang bij het schrijven van een proefschrift is de handleiding van de tekstverwerker.

Kants argumentatie over het negatieve karakter van de menselijke kennis kan juist aan de hand van, en dus dankzij, het door hem gehanteerde kausaliteitsbegrip weerlegd worden. (Immanuel Kant, Kritik der reinen Vernunft)

Gezien het feit dat de monopoliepositie van de engelstalige wetenschapper voortvloeit uit het gebruik van het engels als wetenschappelijke voertaal, verdient het een sterke aanbeveling voortaan een 'dode taal', bij voorkeur Latijn, als middel voor kennisoverdracht te gebruiken. Iedere wetenschapper, onafhankelijk van zijn landsaard, kampt dan met eenzelfde handicap.

Een evenwichtig mens is iemand die de juiste balans vindt tussen waarnemen en zich blind houden.

De maatschappij is democratischer geworden: in alle geledingen kan men mensen waarnemen die de kleren van de keizer dragen.

Een gelukkig man is hij, die een vrouw heeft, een dochtertje en een zoontje, een leuke nieuwe baan, een nieuw oud huis, en een proefschrift!

Voorwoord

Op het Instituut voor Zintuigfysiologie is het goed toeven voor een NWO'er. De (hier zo gekoesterde) meerwaarde die een samenwerkingsverband kan bieden, kwam mijn werk zeer ten goede. Niet alleen de bereidheid tot (samen)werken, maar vooral ook de lol erin, maakt dat menig medewerker mij in de afgelopen drie jaar wist te inspireren. Ook de hier niet met name genoemde collega's ben ik hiervoor erkentelijk. Sommigen ben ik echter meer erkentelijk dan anderen: Leo Spiekman, Johan Alferdinck, Aart Everts, Jan Varkevisser, Koos Wolff, Walter van Dijk, Arno Krul en Leny van de Boon voor de voortreffelijke ondersteuning. Hans Vos en Dick van Norren voor hun liefdevolle maar genadeloze kritiek. Lex Wertheim, mijn supervisor, voor vele, vele uren van woeste maar ook verfijnende discussie, en Wim Bles voor een wijds en boeiend toekomstperspectief. Tenslotte, mijn opleider Wim van de Grind, die bereid was als promotor te fungeren wanneer mijn werk van wetenschappelijk gehalte zou blijken te zijn. Ik heb hem daar niet meer over gehoord, het zal wel in orde zijn.

Dit werk is opgedragen aan de puber die ondanks actieve tegenstand van enige walgende middelbareschooldocenten zijn eigen weg ging, en aan zijn ouders die hem hierbij steunden.

Ik ben een god in 't diepst van mijn gedachten,

maar in de bibliotheek een volontair.

(Annie M.G. Schmidt)

CONTENTS

General introduction

Why not start with an analogy: when your hand moves across this booklet, the hand is perceived as moving and the booklet as a stationary object. But when the booklet is moved across the skin of your stationary hand, it is definitively the booklet which is perceived as moving. Finally, when you move your hand (or your hand is moved) with the booklet lying on it, both hand and object are perceived as moving in space. This is, of course, surprising. You are fortunate in having a very sophisticated multidimensional perceptual system which is capable to orient itself by means of proprioceptive, egocentric and exocentric information. How does it work? Before I get too enthusiastic about this topic and inevitably tedious: this introduction concerns a dissertation about the influence of eye movements on perception, not about hands. In principle, however, the perceptual problems to be solved by the haptic and visual systems are quite similar. The shift in topic will, therefore, neither change the question nor my enthusiasm.

When we move around, the reflected light from objects in our environment shifts continuously across the retinae. Notwithstanding these shifts, caused by eye, head and body movements, we perceive our world as stable. Shifts caused by actual moving objects are identified and properly interpreted, too. Also when a moving object is carefully pursued by the eyes, thus maintaining a stabilized 'retinal image' of the object (no shift at all), the object is (nevertheless) correctly perceived as moving. How does the visual system identify these shifts? How does it distinguish between shifts caused, for instance, by eye movements and those due to object motion?

It is rather difficult to investigate this sophisticated perceptual mechanism because it functions so well under normal conditions. We therefore have to study it in isolated parts and in extraordinary situations, open to artifacts which might threaten our generalisations. But enough knowledge is gathered so far to divide at least the investigators in two main groups, both with a respectable number of arguments. A rough classification can be made between researchers who understand perception as a 'direct' process versus those who expect perception to be an 'indirect' process. The point of view of the direct perceptionists is that the shifts in the light flux on the retina contain necessary *and* sufficient information for the (visual) perceptual system to operate on. Perception is seen as the direct process of tuning to and picking up this available information. The standpoint of the members of the other group is that besides retinal afferent stimulation also signals about the (eye, head and body) movements of the observer her/himself have to be taken into account by the perceptual mechanism. Perception is seen by them as an indirect process of comparing and calculating sensations from such different sources. Relevant information has to be made, not simply picked up. I will not go into more details on this controversy here. Both viewpoints are thoroughly discussed in the literature (Gibson, 1966; Lombardo, 1987; Van de Grind, 1984; Ullman, 1980; Mack, 1986; Grüsser, 1986; Wertheim, 1990). When necessary, arguments from both groups will be discussed in the following chapters. However, I was taught to put most weight on the phenomena themselves and investigate them in a original and proper way, and not get too much into scholasticism. This guiding principle will be followed. Many of the visual phenomena described in this dissertation were discovered long ago and have been thoroughly disputed. Despite this I had the pretension to study them myself. The combined articles of this dissertation reflect this research. In order to obtain psychophysical information about the functioning of the visual perceptual system two main questions were posed: Do eye movements affect the perception of the world, and if so, in what way? And secondly, what is the relevant information for the perceptual (sub)mechanism involved? Three types of eye movements, one voluntary and two reflexive, and their influence on perception were subjected to investigation. Firstly, smooth pursuit eye movements and perception of object motion (part I). Secondly, optokinetic nystagmus and perception of self motion (part II). Finally, ocular counterrotation and orientation towards the horizontal (part III).

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Part I: Smooth pursuit eye movements and perception of object motion

I.1. THE PERCEPTION OF OBJECT MOTION DURING SMOOTH PURSUIT EYE MOVEMENTS: Adjacency is not a factor contributing to the Filehne illusion

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Abstract:

During smooth pursuit eye movement performance an illusionary motion of background objects is often perceived. This so called Filehne illusion has been quantified and explored by Mack and Herman (1973, 1978). According to them two independent factors contribute to the Filehne illusion: 1) a subject relative factor, viz. the underregistration of pursuit eye movements by the perceptual system, and 2) an object relative factor, viz. adjacency of the pursued fixation point and the background stimulus. The evidence of the present experiment supports the former but rejects the latter as a contributing factor. Instead of the concept of adjacency, an alternative theoretical extension of the subject relative factor is offered.

Introduction

Visual perception of object movement can be understood as the outcome of a comparison between two signals, a retinal signal, encoding retinal image movement, and a reference signal, encoding the movements of the retinae in space. Only when the magnitudes of the two signals differ significantly (at least one JND: Wertheim, 1981), object motion is perceived; otherwise retinal image motion is interpreted as due to eye movements and the object is perceived as stationary. However, since Filehne (1922) it is known that during smooth pursuit eye movements (made to a moving fixation point), stationary objects, whose images consequently move across the retinae, often appear to move in the direction opposite to the eye.

This phenomenon, known as the Filehne illusion, has been nicely quantified by Mack and Herman (1973). They measured the compensatory velocity that a large background stimulus had to be given to restore its subjective stationarity. This compensatory motion indeed always turned out to be in the direction of the eye movement. At the point of subjective stationarity (PSS), the magnitudes of retinal and reference signals are equal by definition. Thus, since subjective stationarity is reached by decreasing retinal image velocity of the background stimulus, actual eye velocity must have been underrated in the reference signal. Therefore Mack and Herman concluded that the Filehne illusion is a consequence of this underregistration of pursuit ocular velocity in the reference signal.

In a later paper Mack and Herman (1978) mentioned an additional factor that contributes to the Filehne illusion; a factor which is unrelated to the comparison mechanism mentioned above. They claimed that close adjacency of a small background stimulus dot and a moving fixation point will cause a substantial increase of the Filehne illusion. This claim was based on their observation that the Filehne illusion is less pronounced when the background stimulus dot was visible for 1.2 s than when it was visible for only 0.2 s. Their argument was that with very brief exposure of the background stimulus, the images of the untracked background stimulus dot and the tracked fixation point are close together and herefore subject to the biasing effect of object-relative motion cues.

When the background stimulus dot is seen for a longer period of time, the two images become separated and consequently the salience of object relative displacement cues decreases. The perceived motion of the background stimulus will then be determined mainly by subject-relative information, i.e. by the outcome of the comparison of retinal and reference signals. This results in a much smaller Filehne illusion because it is now caused by only one factor; the underregistration of ocular velocity.

Mack and Herman tested their adjacency hypothesis with an additional experiment in which the moving fixation point disappeared while the background stimulus dot was briefly exposed, thus eliminating object-

relative displacements cues. This indeed resulted in a small Filehne illusion, similar to that in their original long background stimulus exposure condition. This suggested that background stimulus exposure time per se does not affect the Filehne illusion. However, their data are somewhat difficult to interpret, because the eye velocity of their (highly trained) subjects shows a sudden drop after disappearance of the fixation point, i.e. during the background stimulus exposure.
Since the reference signal may have been affected by this change in eye velocity, the reduced Filehne illusion could also have been caused by this factor.
To test the adjacency hypothesis of Mack and Herman more thoroughly we performed an experiment in which background stimulus exposure time was varied while adjacency remained constant, but with continuous visibility of the moving fixation point. For this purpose we needed a background stimulus pattern which was always projected onto the same part of the retinae during the pursuit eye movement. Therefore we used a window through which only part of a large background stimulus pattern was visible and had this window move with the same velocity as the fixation point.
In one condition the window (through which the background stimulus pattern was visible) was centered around the fixation point, so both the background stimulus and the fixation point were presented foveally. Therefore adjacency was high and constant, irrespective of the duration of the background stimulus. In another condition the window again moved with the same velocity as the fixation point, but now it was presented in the retinal periphery. The background stimulus pattern was thus always projected onto the same peripheral area of the retinae whilst the pursued moving fixation point was always presented foveally. So here adjacency was low but still constant, irrespective of the duration of the background stimulus exposure.
Within both these 'high' and 'low' adjacency conditions we then varied the period during which the stimulus pattern was visible. Suppose differences in adjacency were indeed the underlying reason for the difference in the strength of the Filehne illusion between the short and long stimulus duration conditions in the Mack and Herman study. Then the duration of the background stimulus exposure should have no effect within the present conditions where adjacency is kept constant. There should, however, be a significant difference in the strength of the Filehne illusion between the 'high' and 'low' adjacency conditions. According to Mack and Herman, the condition with low adjacency should cause a small Filehne illusion and the condition with high adjacency should cause a substantial one.
Two control conditions were included. In one of them the window remained stationary in the visual field rather than on the retina. Thus adjacency then varied between the short and long background stimulus exposure in the same way as in the Mack and Herman study. In the second control condition

the full background stimulus pattern was visible. Here, during the performance of a pursuit eye movement, adjacency remained high and constant in the foveal areas but varied in the peripheral areas of the retinae between short and long background stimulus exposure.

Methods

Apparatus

A moving fixation point (a small plus sign), the pursuit stimulus, was swept with a constant velocity of 12 deg/s across a CRT screen (a Hewlett-Packard high-speed graphics display model 1321A with a rapidly decaying phosphor [P4]). Then, temporally located in the middle of this sweep a background stimulus pattern was made visible for a fixed exposure time of either 0.3 or 1.5 s. This background stimulus pattern was a 30 x 30 deg array of randomly positioned white dots (dot diameter 10.8 min of arc, interdot distance at least 1,2 deg) that could be moved en masse in either horizontal direction.

In three conditions only part of the background stimulus pattern was visible throug a 6 x 6 deg window. This window was created by localised Z-modulation, and possessed fuzzy borders to prevent sudden (dis)appearance of the dots at its edges. In two of the three conditions the window moved with the same velocity and in the same direction as the fixation point. In the first, the foveal window condition (FovW), the window was placed symmetrically around the fixation point, which ensured foveal perception of the stimulus pattern during the pursuit eye movement. In the second, the peripheral window condition (PerW), the midpoint of the window was positioned 20 deg vertically above the fixation point. Thus the stimulus pattern always projected onto the same area of the peripheral retinae during smooth pursuit. In the third condition, the stationary window condition (StatW), the window did not move but remained stationary in the middle of the screen.

In a last condition, the large pattern condition (NoW), no window was used and the complete 30 x 30 deg background stimulus pattern was visible on the screen.

Eye movements were measured with an IR reflection device mounted on a frame of spectacles (Haines model 52). Eye movements were monitored on line with a BBC computer, which also controlled the stimuli on the CRT screen. In parallel, the eye movements were digitized (sample rate 100 Hz), stored and analysed with an IBM AT computer. The experimental environment was completely dark. Average luminance of the dot pattern on the screen was 2 x 10^{-4} cd/m^2.

Subjects were seated in a dentist chair, the head completely fixed in a rigid (vacuum) cushion which was attached to the headrest of the chair.
The viewing distance was 52 cm.

Procedure

After calibration of the IR eye movement recording system, subjects were instructed to track the moving fixation point with their eyes. Then, near the middle of the fixation point sweep, the background stimulus pattern was made visible, in such way that exposure time was symmetrical around the exact midpoint of the sweep. To determine the point of subjective stationarity (PSS) of the background stimulus two thresholds were measured. One was the threshold for perceiving background stimulus motion in the direction opposite to the eyes, i.e. opposite to the direction in which the fixation point moved (against-threshold). The other was the threshold for the perception of background stimulus movement in the same direction as the eyes (with-threshold). The PSS was defined as the midpoint between these two thresholds.
Thresholds were measured using the single staircase method. At the end of each sweep of the fixation point the subject reported verbally whether the background stimulus had been perceived as stationary or as moving in the same or opposite direction to that of the fixation point. Then the experimenter increased or reduced the background stimulus velocity by 0.35 deg/s, depending on the subjects response. (Actually initial steps of 2.6 and 1.3 deg/s were used to converge quickly onto the threshold area). Mean background stimulus velocity across the first six consecutive turning points of a staircase served as the threshold stimulus velocity. For each sweep on which a turning point had occurred, the eye movement trace was stored and the eye velocity was computed exclusively during the background stimulus exposure period. The mean of these six eye velocity values served as the ocular velocity score associated with that particular threshold. Trials with bad tracking on which saccades occurred during the stimulus presentation were discarded.
The determination of a PSS took about 10 to 15 minutes, after which rest was allowed in normal light conditions. Then the IR eye movement recording system was calibrated again. In each of the four conditions (FovW, PerW, StatW and NoW) two background stimulus exposure durations were used, lasting either 0.3 s or 1.5 s. Thus eight PSS measurements were obtained for each subject, presented in random order. The order of the 'with-threshold' and the 'against- threshold' in a PSS measurement was balanced between conditions. All 10 (male and female) subjects were paid, and naive with respect to the hypothesis. They were between 20 and 33 years old.

Results

The results of two subjects were excluded from analysis because they could not perform proper smooth eye movements in the experimental situation. The remaining eight subjects had no such problems. The sudden appearance of the background stimulus did not disrupt the smooth eye movement nor did it change ocular velocity (see Fig. 1). Mean ocular velocity was 11.44 deg/s across all conditions. An ANOVA performed on the ocular velocity scores revealed no significant differences in eye movement velocity between short (0.3 s) and long (1.5 s) background stimulus exposure situations nor between any of the eight PSS measurement groups.

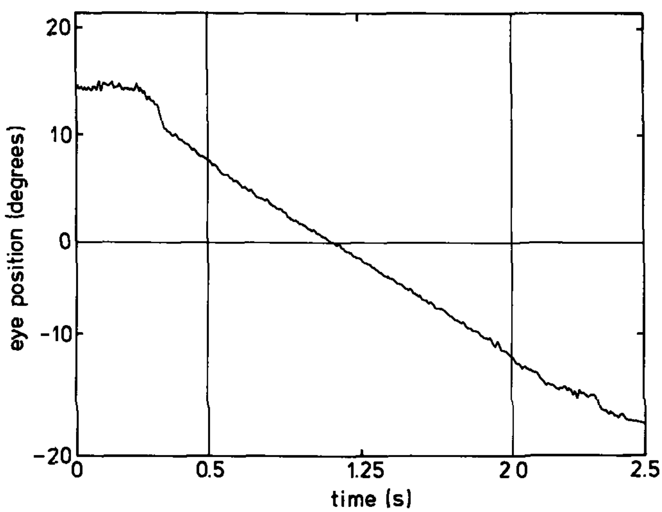

Fig. 1 Example of smooth pursuit eye movement performance during the long stimulus exposure situation (1.5 s between vertical bars).

However, an ANOVA performed on the PSS background stimulus velocity scores revealed a significant difference ($F = 3.14$; d.f. $= 21,21$; $p < 0.01$, 12% variance explained) in the strength of the Filehne illusion between short and long background stimulus exposure durations. The illusion was always stronger in the brief background stimulus presentation situation (see Fig. 2).

The strength of the Filehne illusion was also significantly different between the four background stimulus conditions ($F = 12.7$; d.f. 3,21; $p < .001$, 28% variance explained). Post hoc Newman-Keuls analysis revealed that the illusion was significantly stronger in the PerW condition than in all other conditions ($p < .01$), which did not differ significantly from each other (see Fig. 2).

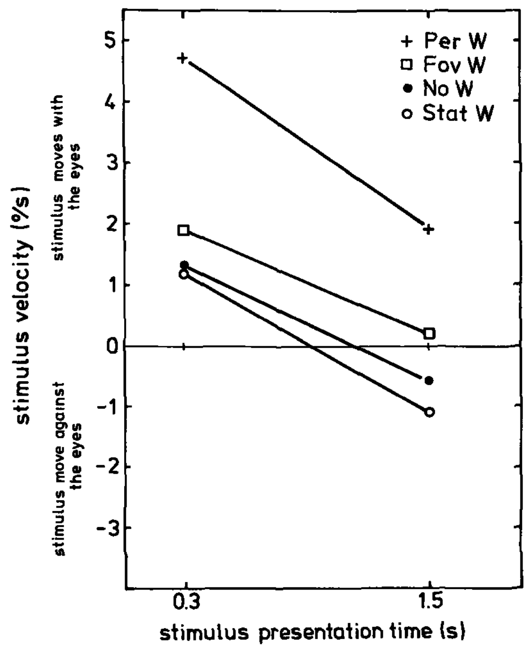

Fig. 2 Compensatory stimulus velocity at the point of subjective stationarity (group means of eight subjects). The extent of stimulus velocity - with the eyes - quantifies the strength of the Filehne illusion. Note the difference in strength of the Filehne illusion within all conditions between short and long stimulus exposure durations. In addition, the Filehne illusion is stronger in the peripheral window (PerW) than in all other conditions.

Discussion

The results confirm Mack and Herman's finding that background stimulus exposure time is critical for the strength of the Filehne illusion. However, adjacency between background stimulus and fixation point seems not to be the underlying cause. There was a significant difference in strength of the Filehne illusion within conditions where background stimulus exposure time was varied even though adjacency was kept constant (FovW, PerW).

In addition, according to the Mack and Herman hypothesis, there should be differences in strength of the Filehne illusion between conditions with different levels of adjacency. In fact there was a difference. The condition responsible, the peripheral window condition which had the lowest adjacency, produced the largest Filehne illusion. This seems to imply an effect of adjacency opposite to what was predicted. But actually adjacency is not a determinant at all, because all other conditions, despite their different levels of adjacency, did not differ significantly from each other.

Consequently, adjacency must be rejected as a contributing factor for the Filehne illusion. How then should one explain the importance of background stimulus exposure time for the strength of the illusion? Let us briefly explore a possible answer. We endorse the view (Mack and Herman; 1973) that underregistration of ocular velocity in the reference signal causes the Filehne illusion, but claim that the reference signal does not merely refer to eye velocity alone but is a signal whose purpose is to register the velocity of the retinal surface in space. The reference signal is therefore proposed to be the result of a parallel processing of (1) efferent ocular (eyes in their orbits) and (2) afferent vestibular (head movement) velocity information and (3) additional afferent retinal optokinetic information. The latter kind of information is available in the smearing of images of background objects across the retina, and is known to have the potential to generate a perception of self motion (Helmholtz, 1962; Dichgans and Brandt, 1978; Berthoz and Droulez, 1982; Schmidt, Buizza and Zambarbieri, 1985). Self motion implies movement of the retina in space. So optokinetic stimulation implies information about movement of the retinae in space.

Physiological evidence for such an integration of information from at least these 3 sources stems from electro-physiological measurements of mossy fibers in the cerebellar flocculus (of monkeys). These fibers receive converging inputs from structures related to visual, oculomotor and vestibular functions (Noda, 1985; Ito, 1982; Miles and Lisberger, 1981; Lisberger, Morris and Tychsen, 1987; Buttner and Waespe, 1984). Examples of mossy fiber visuomotor unit responses to combination of retinal smear information, eye velocity information and head velocity information (Noda, 1985) give a strong indication that the reference signal originates in the flocculus. With psychophysical methods Wertheim (1987) demonstrated that retinal afferent stimuli with optokinetic potential (i.e. rather large stimuli with low spatial frequency which move across the retinae for at least one second) do indeed affect, namely increase the magnitude of, the reference signal[1].

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[1] The hypothesis that optokinetic stimulation affects the magnitude of the reference signal does not necessarily imply that this happens only when self motion is consciously experienced. There may be a perceptual threshold. In other words, the reference signal might already be affected before sensations of self motion reach consciousness [see Dichgans and Brandt (1978) for a similar suggestion that optokinetic stimulation may affect object motion perception before it affects ego motion perception].

On basis of these arguments we think it is reasonable to assume that integration of ocular velocity information, head velocity information and optokinetic information can normally optimize the gain of the reference signal so that the Filehne illusion will not occur. But when the head of a subject is fixed and the background stimulus presented has no optokinetic power (e.g. it is small and/or very briefly presented), then the gain of the reference signal is less than one, due to (underregistered) ocular velocity information only, and this causes the Filehne illusion.

In their (1978) experiments Mack and Herman used a single small background-stimulus dot, which was presented for a very short (0.2 s) or a little, but crucially, longer (1.2 s) time. In the brief exposure situation visual (i.e. optokinetic) modulation of the reference signal could not play a role. But, according to our explanation, a small visual component in the reference signal may have been induced in the long background stimulus situation, slightly increasing the reference signal size. This explains why Mack and Herman found a somewhat smaller Filehne illusion in the latter condition.
In the present experiment we used more or less the same background stimulus exposure durations as Mack and Herman did, but a much larger background stimulus pattern. In our long exposure situation this must have induced a larger visual component in the reference signal. The Filehne illusion did indeed disappear in three conditions and became much smaller in the fourth, peripheral, condition.

The question remains why the overall strength of the Filehne illusion was significantly larger in the peripheral window condition than in all other conditions (Fig. 2). We think that besides time there is another factor determining the strength of the illusion, namely position on the retina. It seems reasonable to assume that retinal eccentricity affects the build-up of visual modulation of the reference signal. Possibly the peripheral retinae require a larger area of stimulation or a longer background stimulus exposure. Future research will deal with this matter.

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I.2. THE PERCEPTION OF OBJECT MOTION DURING SMOOTH PURSUIT EYE MOVEMENTS: the Filehne illusion reconsidered

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Abstract

During smooth pursuit eye movement performance an illusory motion of background objects is often perceived. According to the quantitative analysis by Mack and Herman (1973) this so called Filehne illusion is caused by a permanent underregistration of pursuit eye movements by the perceptual system. This explanation is at variance, however, with the fact that the Filehne illusion sometimes does not appear. The experiments presented in this paper suggest that this will happen in conditions where object-background relative information is available, a finding which is also at variance with predictions from a model proposed by ourselves (Wertheim, 1987; De Graaf and Wertheim, 1988).

Introduction

Since Filehne (1922) it is known that during smooth pursuit eye movements (made to a moving fixation point), stationary objects, whose images consequently move across the retinae, often appear to move in the direction opposite to the eye movement. This phenomenon, known as the Filehne illusion, has been quantified by Mack and Herman (1973). They measured the compensatory velocity that a stimulus pattern had to be given to restore its subjective stationarity. This compensatory motion always turned out to be in the direction of the eye movement. Therefore Mack and Herman, who advocate a model in which object motion perception is understood as the outcome of a comparison between a **retinal** signal (encoding retinal image movement) and an **extraretinal** signal (which encodes the movement of the eyes in their orbits), concluded that the Filehne illusion is a consequence of a permanent underregistration of pursuit ocular velocity in the extraretinal signal[2]. In a later paper Mack and Herman (1978) observed that the Filehne illusion was less pronounced when the stimulus was visible for 1.2 sec than when it was visible for only 0.2 sec. Their explanation for this in terms of an object relative factor, viz. adjacency of the pursued fixation point and the stimulus, was falsified by us, although their data were replicated (De Graaf and Wertheim, 1988). In addition, we found that there was no Filehne illusion at all with a 1.5 sec stimulus exposure duration. This was in line with an extended concept of the extraretinal signal as proposed by Wertheim (1987), who suggested an additional component in the extraretinal signal which could compensate for the permanent underregistration of pursuit eye movements. This model will be dealt with later in the text.

However, we have now noticed another, very influential and dominant effect on the Filehne illusion. Subjects who were adapted to the normal light conditions in our laboratory showed, after light offset, the frequently measured Filehne illusion. This illusion did not appear, though, when we remeasured 15 minutes later in the dark. In other words, subjects optimally adapted to the dark did not "misjudge" stimulus velocity anymore while performing pursuit eye movements. To investigate this issue we began by postulating that the transitional state of dark adaptation might somehow have been responsible for the appearance of the Filehne illusion. The first experiment was set up to test this hypothesis. We created three conditions. In one the measurements took place in the dark while the subjects were dark

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[2] At the *point of subjective stationarity (PSS)*, the *magnitudes of* retinal and extraretinal signals are equal by definition. Thus, since subjective stationarity is reached by decreasing the retinal image velocity of the stimulus, actual eye velocity must have been underrated in the extraretinal signal.

adapted for 15 min. In the other two conditions the subjects were normal (day)light adapted, but in the first the measurements took place within an illuminated environment and in the second in total darkness. The idea was that the Filehne illusion would only appear in the condition where the subjects were in a (strong) transitional state of dark adaptation. In the two other conditions no Filehne illusion was expected.

We also varied stimulus exposure time, which had already been found to sort effect on the appearance of the Filehne illusion, reasoning that there might be an interaction between stimulus exposure time and level of dark adaptation.

Two 'follow up' experiments will also be presented in this paper.

EXPERIMENT 1

Methods

Apparatus

A moving fixation point (a dot of 0.6 x 0.6 deg), the pursuit stimulus, was swept with a constant velocity of 12 deg/sec along a horizontal trajectory of 40 degrees across a large projection screen of 68 x 21 degrees. In the middle of the sweep a large stimulus pattern was made visible for a fixed exposure time of either 0.3 or 1.5 sec. This pattern was a sinusoidally modulated grating of 32 x 21 degrees, with a contrast $[(L_1 - L_2)/(L_1 + L_2)]$ of 25%. Both fixation point and stimulus pattern were projected on the screen from slides and could be moved independently in either horizontal direction with the help of mirrors mounted on computer controlled galvanometers. Viewing distance was 6.05 m. There were three experimental main conditions : LIGHT, DARKNOT and DARKAD. In the LIGHT condition we illuminated the environment (a black painted room without windows) as highly as permitted without seriously veiling the slide projection. Consequently, the environment was dimly illuminated (5 lux at the screen), but clearly visible, resulting in an average screen luminance of 10^{-1} cd/m^2 when nothing else was projected on it. The luminance of the fixation point was 10 cd/m^2, the mean luminance of the stimulus pattern on the screen 4×10^{-1} cd/m^2. In the DARKNOT and DARKAD conditions the room lights were off. In the DARKNOT condition, where the subjects were not dark adapted, the luminance of the screen was 5×10^{-4} cd/m^2 when there was nothing else projected on it. The luminance of the fixation point was 9.6 cd/m^2. To make the stimulus pattern subjectively equal to that in the LIGHT condition, we needed a mean luminance of 2.2×10^{-2} cd/m^2. In the DARKAD condition, where the subjects were adapted to the dark, luminance of the screen was again 5×10^{-4} cd/m^2. The luminance of the fixation point was 9.6 cd/m^2. To keep the stimulus pattern

subjectively equal to that in the other two conditions we needed an average stimulus luminance of 2.9×10^{-3} cd/m^2.
Eye movements were measured with an IR reflection device mounted on a frame of spectacles (Haines model 52). Eye movements were monitored on line, digitized (sample rate 200 Hz), stored and analyzed with an IBM AT computer, which simultaneously controlled the stimuli on the screen.

Procedure
Luminance and adaptation conditions are summarized in Table 1. In the LIGHT and DARKNOT conditions prior to measurements the subject adapted for 15 minutes to normal day light (mean luminance of the surroundings >1500 cd/m^2), somewhere in our Institute. Then calibration of the IR eye movement recording system took place in the experimental room with the normal lights on (about 400 lux, resulting in 100 cd/m^2 luminance of the screen). In the LIGHT conditions measurements took place 30 sec after the normal room lights were switched off. In the DARKNOT conditions the measurements also started 30 sec after light offset.

Table 1 Experimental design. The course of the mean luminance of the surroundings in the three experimental situations.

experimental situation	circ. before measurement	calibration procedure	threshold measurement
LIGHT	15 min light ($\geq$1500 cd/m^2)	3 min light (100 cd/m^2)	5 min low light (1×10^{-1} cd/m^2)
DARKNOT	15 min light ($\geq$1500 cd/m^2)	3 min light (100 cd/m^2)	5 min dark (5×10^{-4} cd/m^2)
DARKAD	15 min dark (5×10^{-4} cd/m^2)	3 min dark (5×10^{-4} cd/m^2)	5 min dark (5×10^{-4} cd/m^2)

In the DARKAD conditions the subject first sat 15 minutes in the dark whereafter calibration and measurements took place in the dark. In each of the three experimental conditions two stimulus exposure durations were used, lasting either 0.3 or 1.5 sec.

For the measurements subjects were instructed to track the moving fixation point with their eyes. Then the stimulus pattern was projected, with the exposure time symmetrical around the exact midpoint of the sweep. To determine the point of subjective stationarity (PSS) of the stimulus two thresholds were measured. One was the threshold for perceiving stimulus motion in the direction opposite to the eyes, i.e. opposite to the direction in which the fixation point moved ('against threshold'). The other was the threshold for perceiving stimulus motion in the same direction as the eyes ('with-threshold'). The PSS was defined as the midpoint between these two thresholds.

Thresholds were measured using a staircase method. At the end of each sweep of the fixation point the subject reported verbally whether the stimulus had been perceived as stationary or as moving in the same or opposite direction to that of the fixation point. Then the experimenter increased or reduced the stimulus velocity by 0.50 deg/sec, depending on the subject's response. (The starting point of the staircase procedure was determined randomly and could vary between 0 and 20 deg/sec with or against the eye movement, <u>in</u>dependent of which threshold condition was measured. Initial steps of 4, 2 and 1 deg/s were used to converge quickly onto the threshold area). Mean stimulus velocity across the first six consecutive turning points of a staircase served as the threshold stimulus velocity. For each sweep on which a turning point had occurred, eye velocity was computed over the stimulus exposure period. The mean of these six eye velocity values served as the ocular velocity score associated with that particular threshold. Trials with bad tracking on which saccades occurred during the stimulus presentation were discarded (see De Graaf and Wertheim, 1988 Fig.1, for details).

Determination of a threshold took about 5 minutes, after which the normal lights were switched on. Then subjects were adapted again for 15 minutes (to the day light or to the dark, depending on the next condition). Twelve threshold measurements (six PSS measurements) were obtained from each subject, presented in random order. All 10 paid subjects, five male and five female, were naive with respect to the apparatus and the hypothesis. They were between 21 and 29 years old. Subjects were seated on a comfortable seat with a (fixating) headrest.

Results

None of the subjects had difficulties in performing proper smooth eye movements in the experimental situation. The sudden appearance of the stimulus did not disrupt the smooth eye movement nor did it change ocular velocity. Mean ocular velocity was 10.8 deg/sec across all conditions and did not differ between conditions.

The results of the experiment are shown in Fig. 3.

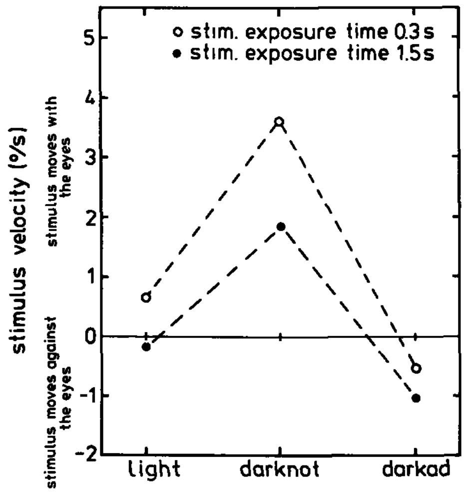

Fig. 3 Compensatory stimulus velocity at the Point of Subjective Stationarity (group means of ten subjects). The extent of stimulus velocity - with the eyes - quantifies the strength of the Filehne illusion. There appears to be a strong Filehne illusion in the DARKNOT (not adapted to the dark) conditions. In addition, note the difference in strength of the Filehne illusion within all conditions between brief and long stimulus exposure durations.

ANOVA performed on the stimulus velocity scores at PSS, revealed a significant difference in strength of the Filehne illusion ($F = 59.2$; d.f.= 2,18; $P < 0.001$, 56% variance explained) between the LIGHT, DARKNOT and DARKAD conditions. Post hoc Newman-Keuls analysis revealed that the LIGHT, DARKNOT and DARKAD conditions all differed significantly ($P < 0.01$) from each other.

ANOVA also revealed a significant difference ($F = 7.63$; d.f.=1,9; $P < 0.05$, 6% variance explained) between brief and long stimulus exposure durations. The Filehne illusion was always stronger in the brief stimulus exposure situation. There was no interaction between stimulus exposure time and level of dark adaptation.

Discussion

The data are in line with the hypothesis that the transitional state of dark adaptation is a powerful determinant of the appearance of the Filehne illusion. But is there a direct causal relationship? Is the process of dark adaptation itself responsible for this bias in object motion perception, or is it an intermediate for another process. In the ecological perception theory of Gibson (1966, 1968) motion perception is seen as an active, direct process of picking up the dynamic relation between stimulus (object) and environment (background). Perhaps this object-background relative information could not manifest itself during the transitional state of dark adaptation. In the light as well as when adapted to the dark, subjects presumably would not have problems to obtain object-background relative information and consequently perceive object motion directly and therefore correctly[3]. But in the dark, while not properly adapted the environmental background information is subthreshold. According to Mack (1978) then a subject-relative process of comparison between retinal and extraretinal signal will take place (with the permanent bias due to underregistration of eye velocity in the extraretinal signal). Therefore, the difference found between our DARKAD and DARKNOT conditions could be due to a different mode of perception, object-background relative ('direct' in Gibsonian context) versus object-subject relative ('indirect'). A second experiment was performed to test this hypothesis. It was a replication of the first experiment, but with an additional background projected on the screen. This stable background was dim, but well perceivable in all experimental conditions. Thus object-background relative perception was made explicitly possible, also in conditions where subjects were not properly dark adapted. Consequently, perception should remain veridical (no Filehne illusion) in all three situations. However, if indeed the transitional state of dark adaptation (and not the availability of object-background relative motion) would be the cause, then the results from experiment 1 should be replicated.

To test these hypotheses it was not necessary to vary the stimulus exposure time. We chose the 0.3 s stimulus exposure duration because in this condition the largest Filehne illusion had been observed (see Fig. 3).

EXPERIMENT 2

Methods

Apart from fixation point and stimulus pattern, a continuously visible stationary background pattern (44.8 deg of visual angle) was projected onto

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[3] According to the Gibsonian standpoint active perception, based on object-background relative information, is always veridical if there is sufficient information available and if this information can be picked up. This is essentially different from the 'object relative' mode of perception, postulated by Mack (1978, 1986). According to Mack, the latter could be responsible for considerable illusions (see however De Graaf and Wertheim, 1988).

the screen. It consisted of randomly positioned dark, cloud like blobs (0.3 x 0.3 up to 6.5 x 4 deg of visual angle) in a white setting. The total amount of dark and white areas was equal. In the LIGHT situation the mean luminance of the fixation point, the stimulus and the background pattern was 9.5, 3.8 x 10^{-1} and 2.2 x 10^{-1} cd/m^2 respectively. Because of the continuous presence of the dim background pattern, mean luminance of fixation point, stimulus and background pattern in the DARKNOT and DARKAD conditions was set at 8.9, 2.2 x 10^{-1} and 7.4 x 10^{-2} cd/m2, respectively.
In terms of light, the presence of the background pattern lessened the difference in circumstances during the threshold-measurements between LIGHT and DARKNOT conditions. Therefore, to maintain a relevant difference between these two conditions, we introduced a large difference in level of light adaptation. As previously, in the DARKNOT condition the subjects were adapted for 15 min to the daylight (>1500 cd/m^2) before the calibration and measurement procedure started (as in experiment 1), but in the LIGHT condition the subjects were adapted for 15 min to the normal lights in the room (100 cd/m^2, as during the calibration procedure). If the transitional state of dark adaptation is the main determinant, then the results should reflect this difference.
For the rest the procedure was the same as in the first experiment. Eight new subjects were involved, 7 male and 1 female. They were naive with respect to the apparatus and the purpose of the experiment.

<u>Results experiment 2</u>
None of the subjects had difficulties in performing proper smooth eye movements in the experimental situation. Mean ocular velocity was 10.5 across all conditions, similar to that in experiment 1.
Fig. 4 presents the data of the second experiment.

Despite the differences in level of adaptation in the LIGHT, DARKNOT and DARKAD conditions, the mean PSS' did not differ between conditions nor from 0. As compared to the data of experiment 1, a post hoc Newman-Keuls analysis revealed that the difference between the experiments (with or without background pattern) only had a significant effect in the DARKNOT situation. This is evident in Fig. 4.

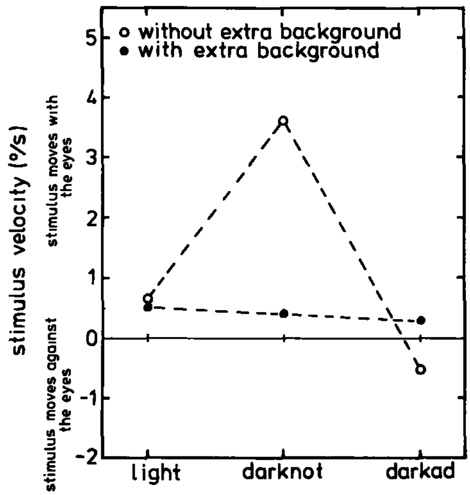

Fig. 4 Mean stimulus velocity at PSS. • = data obtained in experiment 2. When a background pattern was added no differences between LIGHT, DARKNOT and DARKAD were found. As compared to the data of experiment 1 (o), the difference between the experiments (with or without background pattern) was in evidence only in the DARKNOT situation.

<u>Discussion</u>

The evidence from both experiments suggests a 'two modes of motion perception' theory. Direct perception when object-background relative information is available, and object-subject relative perception when there is no background information. The former is a consequence of mere afferent information, the latter mode is based on a comparison of afferent (retinal smear) and efferent ocular information and contains a 'built in' permanent biased output due to underregistration of ocular velocity.

As mentioned already in the introduction, Wertheim (1987) and De Graaf and Wertheim (1988) suggested an alternative model by means of an extended version of one mode, namely the object-subject relative. It was assumed that motion perception was the outcome of a comparison between afferent 'retinal image' velocity information and a complex of efferent ocular and afferent head velocity information and afferent optokinetic information, named the **reference signal**. In this view the optokinetic information about the motion of the retinae in space could optimize the gain of the reference signal, and compensate for the underregistration of ocular velocity. This model had the same prediction about the PSS in the DARKNOT situation of experiment 2 as had the direct, object-background relative, approach.

Because of the permanent presence of the large background pattern a visual modulation of the reference signal could appear, with an unbiased PSS as consequence. With a final experiment we wanted to investigate a situation where this extended object-subject relative model and the direct (object-background relative) perception theory make different predictions.
To this purpose we measured the PSS of subjects in a transient state of dark adaptation (the DARKNOT condition) while the background pattern was made visible only during the 0.3 sec stimulus presentation. According to the direct theory this brief background pattern exposure duration should make no difference with the data obtained in experiment 2: 0.3 sec is long enough to perceive stimulus motion against its background, and therefore no Filehne illusion should appear. According to our extended object-subject relative model however, a 0.3 sec exposure duration would be too brief to generate an optokinetic contribution to the reference signal (Wertheim, 1987). Therefore no compensation will occur for the underregistration of ocular velocity, and consequently the Filehne illusion should appear.
This time we only measured in the DARKNOT situation. In addition to the condition mentioned above, two control conditions were included. In one the background pattern was continuously visible, like in experiment 2. In the other no background pattern was visible during the sweep, as in the (traditional) Filehne condition of experiment 1.

EXPERIMENT 3

Methods

The same background pattern as in experiment 2 was used. Its luminance, however, was somewhat lower, 2 x 10^{-2} cd/m^2, because of the transmission characteristics of a silent polaroid shutter which was placed in its projection path. Therefore, a neutral density filter (0.2 log unit) was placed in the lightpath of the stimulus pattern, reducing mean stimulus luminance to 1.6 x 10^{-1} cd/m^2. The stimulus pattern was also made somewhat smaller in horizontal direction which made it easier to distinguish from the background pattern. Its size was 18.8 x 21 deg of visual angle in all conditions. The measurements were taken under the same circumstances as in the DARKNOT conditions of the former two experiments. Six threshold measurements (three PSS measurements) were obtained from each subject, presented in random order. Seven new naive subjects were involved, six male and one female.

Results experiment 3

Again no subject had difficulties in performing proper smooth eye movements. Mean ocular velocity was 10.7 across conditions, similar to the ocular velocities in experiment 1 and 2. The results are shown in Fig. 5.

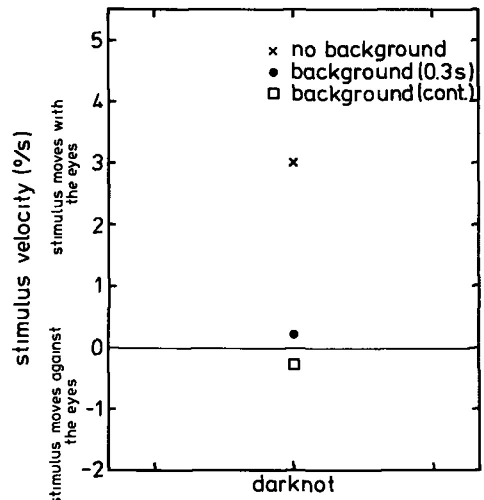

Fig. 5 Compensatory stimulus velocity at PSS. The data obtained with subjects in a transient state of dark adaptation (DARKNOT situation) show a difference in the PSS between the condition without background pattern (×) and the conditions were the background was permanently visible (□) or visible for 0.3 s (•). The latter two conditions did not differ from each other or from 0.

A difference was found between conditions (ANOVA: F= 37.9; d.f.= 2,12; P < 0.001, 68% variance explained). A post hoc Newman-Keuls analysis performed on these data revealed that the PSS in the condition without background pattern differed from the PSS in the conditions were the background was permanently visible or visible for 0.3 sec. The latter two conditions did not differ from each other or from 0.

Discussion

The data obtained in the control conditions replicated the findings in the DARKNOT conditions of experiment 1 and 2. A Filehne illusion appeared when subjects were in a transient state of dark adaptation and had no background information available (experiment 1). But whenever a background pattern was added, no illusory stimulus motion was perceived. This was also true when the background pattern was only visible for 0.3 sec together with the stimulus pattern. This is in accordance with the prediction made by the direct, object-background relative model, and is at variance with the prediction from the alternative model suggested by Wertheim (1987)[4] and De Graaf and Wertheim (1988). Consequently a two modes of motion perception theory still seems the most plausible. Direct (mere afferent) perception occurs when object-background relative information is available, which concerns most of our everyday experience. But, when no such information is available the perceptive system switches to the object-subject relative mode. This mode is biased and therefore responsible for illusions like the Filehne illusion. The idea that ocular velocity during pursuit is permanently underregistrated is perhaps intuitively not satisfactory, but at the moment the only one with explanatory power as to the perceptual effects which occur when no object-background relative information is available.

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[4] But note that in that paper it was shown that the Filehne illusion can be inverted, which in turn seems to be at variance with a direct perception model.

Part II: Optokinetic nystagmus and perception of self motion

II.1 ANGULAR VELOCITY, NOT TEMPORAL FREQUENCY DETERMINES CIRCULAR VECTION

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Abstract

This paper shows that the experienced speed of circular vection depends on stimulus speed, not on stimulus temporal frequency. But why would anyone think the contrary? The point is that many modelers in the field of motion perception believe that perceived speed is determined by temporal frequency. Moreover, the optokinetic behaviour of the fly is said to be dependent on the temporal frequency, not the speed, of the stimulus pattern (Reichardt, 1987). It was the aim of the present experiment to test the notion that the experienced speed of circular vection is proportional to stimulus velocity information, which is carried by the temporal and the spatial characteristics of light.

Introduction

It has been known for a long time that exposure solely to visual stimuli can generate a sensation of selfmotion (among others: Mach, 1875; Helmholz, 1896; Fischer and Kornmüller, 1930). In the laboratory this sensation of selfmotion can be induced for instance by a large moving scene which rotates around a stationary subject. The subject then experiences an apparent selfrotation (called circular vection), opposite in direction to that of the visual stimulus and phenomenally indistinguishable from actual selfrotation. Circular vection has been thoroughly studied and measured quantitatively by Dichgans and Brandt (1973, 1978). In 1973 Brandt et al. reported that the speed of circular vection varies as a function of stimulus speed. Later Wong and Frost (1978) confirmed these findings. In both experiments the researchers used an optokinetic drum, the inside wall of which was lined with alternating vertical black and white stripes. During the experiments only the angular velocity of the drum was manipulated. Because information for the visual system is carried by the spatiotemporal modulation of light, the only motion information available to the observer inside of the optokinetic drum consists of the changes in light flux caused by the moving stimulus pattern. This constitutes the <u>input</u> to the (self) motion detection mechanism. The detection of motion, its direction and velocity are supposed to be the <u>output</u> of this mechanism (Reichhardt, 1987 ; Van Santen and Sperling, 1985 ; Nakayama, 1985 ; Van de Grind et al, 1986). A manipulation of optokinetic drum speed therefore, keeping the spatial period of the pattern constant, yields a change of temporal frequency (the adequate stimulus). So, unless we do believe that motion per se is an input for the visual apparatus (but how then is it picked up?), the experiment of Brandt et al showed that (at least) the temporal frequency of a moving stimulus pattern has an influence on circular vection.

The angular velocity (V) of a stimulus can be simply described in the frequency domain as the temporal frequency (TF) divided by the spatial frequency (SF)

$$V = TF/SF \tag{1}$$

According to Brandt et al (1973) there exists a linear relationship between angular stimulus velocity and estimated speed of circular vection (CV), and therefore

$$CV = k \cdot TF/SF \tag{2}$$

Consequently, we may hypothesize that the spatial frequency characteristics of the stimulus should also have an effect on circular vection. In their prominent review article, however, Dichgans and Brandt (1978, page 769) stated that the speed of CV does not exhibit a strong dependency upon the spatial frequency of the optokinetic stimulus. They did not offer data or explanations, but at face value this statement implies that temporal frequency controls circular vection

$$CV = k \cdot TF^1/SF^0 \tag{3}$$

This is in harmony with models from the (analogous) field of object motion perception. It has been extensively argued that motion sensitive elements of the visual system (of flies, humans) respond to temporal (contrast) frequency, and not to velocity (Pantle, 1974; Sekuler et al, 1976; Diener, Wist, Dichgans and Brandt, 1976; Reichardt, 1987[5]. But there is counter evidence. Perceived shifts in apparent velocity depend on the velocity of the adapting stimulus, not its temporal frequency (Thompson, 1981). Also, McKee et al (1986) convincingly showed that human observers respond to the velocity of sinusoidal gratings, not to temporal frequency only. We, on basis of the rationale given by formula 1 and 2, join this latter group. Therefore, if (some) moving stimuli have the ability to generate circular vection, we expect not only that their temporal, but also their spatial characteristics will have an effect on visual self motion perception.

It was the aim of the present experiment to test this hypothesis. For this purpose we had to overcome two practical difficulties. First, we had to generate stimuli with a single pure spatial frequency. Therefore the inner wall of the optokinetic drum had to be covered (successively) with singular sinusoidally modulated vertical gratings of different spatial frequency. Second, to obtain <u>direct</u> evidence for the influence of spatial frequency characteristics of visual stimuli on the speed of circular vection we had to isolate them from temporal frequency characteristics. The latter normally co-varies when we manipulate the former: doubling the spatial frequency of a (moving) black and white grating also doubles the temporal frequency. However, with an optokinetic drum it is possible to dissociate the two. The experimenter can manipulate the angular velocity of the drum in such a way that the temporal frequency remains constant in two subsequent situations with patterns of different spatial frequency. If, for example, the spatial frequency of a given stimulus pattern is four times

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[5] During a visit at our institute in 1989 Prof. Reichardt was rather explicit about this viewpoint. A reviewer of the present paper, however, mentioned a very interesting (earlier) publication of Egelhaaf and Reichardt (1987) which is more in line with our present arguments.

lower than that of an other pattern, the angular velocity of the drum has to be increased by a factor of four to keep the temporal frequency the same for both situations[6]. If the observers do not experience a difference in speed of circular vection, then we must concede that temporal frequency controls vection. But if they do experience a significant difference in speed of selfmotion, then we can conclude that the speed of circular vection is directly related to stimulus velocity information, which is carried by the temporal <u>and</u> the spatial characteristics of light.

The same argument will serve for another response of the human organism to a big moving scene, namely optokinetic eye movements. We therefore, besides the estimated speed of circular vection, also measured the speed of the optokinetic nystagmus.

<u>Methods</u>

Apparatus

For this experiment we used a rotary chair and drum system (Tonnies, Freiburg), which permits independent or coupled chair/drum rotations around the vertical axis. In our experiment only the drum, 1.5 m in diameter, moved. Its inner wall was covered with a band (4.72 m length by .5 m high) of photographic stimulus material. We used three bands, each of a single sinusoidally modulated spatial frequency, which could easily be attached to or detached from the inner drum wall by the use of Velcro ribbons. Their spatial frequencies were respectively 0.023, 0.094 and 0.378 cycles per degree. Mean luminance [(L1+L2)/2] was 1.8 cd/m^2 and the contrast [(L1-L2)/(L1+L2)] was 70-90%. See Fig. 6a for a verification of the quality of the three stimulus bands.

To prevent information from sources other than the stimulus material the subject wore an adjusted (motorcyclists) pair of glasses, which restricted the visual field to 35 deg vertically and 200 deg horizontally, and a headset intercom with ear muffs, to overcome acoustic information about drum movement and about position with regard to the outside world during conversation with the experimenter. Fig. 6b illustrates the experimental situation.

[6] Such a manipulation of the velocity of the drum is allowed because, as mentioned earlier, velocity per se is not an input to the (self) motion detection mechanism. Our sinusoidal stimuli contain no other possible cues for motion perception (like sharp contrasts and reference points), so the only motion information available for the observer inside the drum is the spatial and temporal modulation of light, which effects we will investigate here.

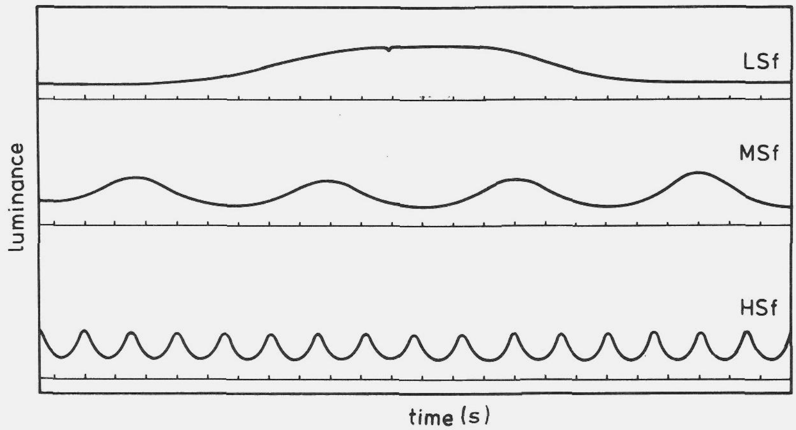


Fig. 6a Registration of the three stimulus bands (rotating with 1 deg per s) by a luminance meter, which was placed in the inside of the drum about 2 cm from the wall. The little notch on top of the curvature of (only) the registration of LSf was due to adhesive tape and unfortunately unavoidable, but invisible to an observer who was seated at 75 cm distance from the pattern and was wearing motorcyclists glasses (see Fig. 6b). The values of the spatial frequencies are respectively 0.023 (LSf), 0.094 (MSf) and 0.378 (HSf) cycles per degree.

Fig. 6b An illustrative example of the experimental situation. The stimulus band shown is MSF.

We had two dependent variables; (1) experienced speed of circular vection and (2) the speed of the slow phase of optokinetic nystagmus. The first was measured by means of a small handle which could be rotated through 360 deg with one or two fingers of the right hand. Subjects were instructed to point the handle to an imagined (fixed) point outside the drum (like a compass needle). In this way subjective position was continuously indicated, which offers a registration of experienced self motion speed as a function of time. Second, we registered horizontal (OKN) eye movements by means of EOG skin electrodes placed at the outer canthi of the eyes. The actual drum velocity, eye movements, the speed of circular vection as indicated by the handle, and information about the lights inside the drum (on/off) were registered on paper with a multi channel recorder. The 10 subjects, 4 male and 6 female, were between 21 and 29 years old. They were paid and totally naive with respect to the apparatus, the experimental paradigm and the purpose of the experiment.

Procedure

We simultaneously received three subjects per day, showed them the optokinetic drum and the possibility to rotate chair and drum independently. Then the subjects were taken to a waiting-room and invited one by one to come to the experimental room again. EOG-electrodes were placed and the subject was invited to enter the drum. Then instructions followed about the use of the handle if (and only when) selfmotion is experienced. A pilot test trial was performed, with the standard striped inner drum wall as stimulus. Every subject experienced saturated circular vection, i.e. had a strong sensation of selfrotation while perceiving the drum as stationary, and no one found it difficult to indicate this by rotating the handle.

Next, we attached one of the three stimulus patterns to the wall of the drum and exposed the subject to it in a random order of temporal frequency. Figure 7 shows the various temporal frequencies used for each of the three spatial frequency patterns and the associated drum angular velocities.

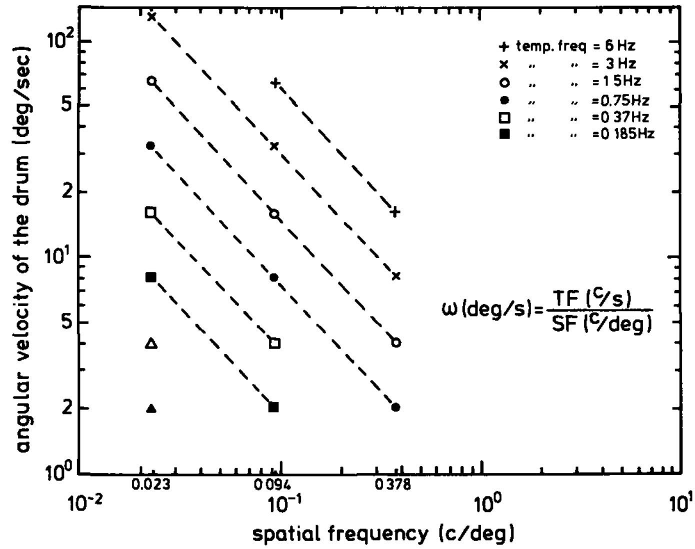


Fig. 7 Stimulus conditions and their mutual relations. The points on the vertical columns represents measurements with one stimulus pattern. The pattern with the lowest spatial frequency (LSF) was presented at 7, MSF at 6 and HSF at 4 different temporal frequencies. The oblique (dotted) lines connect points with a corresponding temporal frequency.

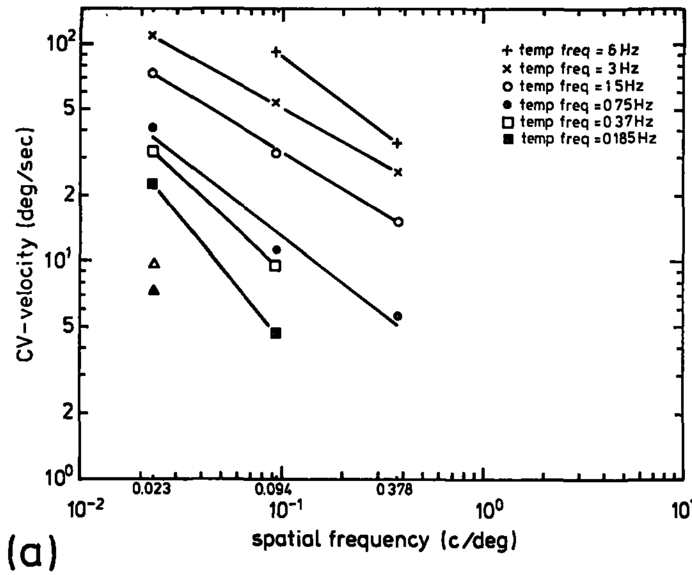
The exact measurement procedure went as follows. After EOG apparatus calibration the subject sat in complete darkness, while the experimenter adjusted the desired velocity of the drum. Then the environmental light in the drum (20 lux at the wall) *and* a fixation light, a little v-sign (0.4 deg by 1.5 deg of visual angle, luminance 20 cd/m^2) which was always projected to the same position in front of the subject, were switched on simultaneously. A few seconds thereafter the subject generally indicated selfmotion by rotating the handle (for one minute). Then the subject sat in the dark again. After one minute the light went on and the subject was exposed to the stimulus pattern moving with the same velocity as before but now in the opposite direction, and without the fixation light. This was done to register the speed of optokinetic nystagmus. Therefore the subject was asked 'to relax, to leave the handle for what it is and just to look at the stimulus pattern'. After 45 seconds the light went off and the subject sat again in the dark for one minute while the experimenter selected a new drum velocity. In the first -CV register- situation (with the handle and with fixation point) the drum always moved to the right and in the following -OKN register- situation (without the handle and without fixation point) the drum always moved to the left. In this way all required drum velocities with one stimulus band were executed. In addition the subject was asked once, at one particular (randomly chosen) temporal frequency, to register the speed of circular vection in the situation without a fixation point, i.e. during the performance of optokinetic nystagmus. This was done to investigate the possible influence of oculomotor activity on experienced speed of circular vection. Therefore, the subject was asked to continue with indicating speed of circular vection whenever the fixation point appeared or not. After an initial minute of CV speed registration during fixation, the fixation point was switched off for one minute (causing OKN) and then switched on again for another minute.

Then the subject rested, while we made measurements with the two others with the same stimulus band. This whole procedure was then repeated with each of the remaining spatial frequency stimulus bands. Thus we had three trials with each subject. The longest trial (LSF) took about 50 minutes, the next trial (MSF) about 40 minutes and the shortest (HSF) no longer than 15 minutes. At the end of the day we asked the subjects to report about their experiences and then told them that they actually had not moved during the experiment. This always caused great astonishment and disbelief.

Results

Data of two subjects could not be included because they did not meet the requirement of experiencing a constant saturated circular vection during the experimental session. One of these subjects repeatedly dropped out of vection and became worried about his perception. The other one had such a strong sensation of selfrotation that she, in her words, '..should, normally speaking, already have fallen out of the chair' and therefore concluded that it must have been the wall of the drum which was actually rotating. The other eight subjects had no such problems. They always felt themselves rotate, meanwhile perceiving the drum as stationary.

Fig. 8 reproduces the mean data from these eight subjects plotted as a function of spatial frequency (Fig. 8a) and of temporal frequency (Fig. 8b). The data show a strong increase in the speed of circular vection when spatial frequency is reduced (ANOVA: $F = 18.2$; d.f. = 2,14; $P < 0.01$, 25% variance explained). This effect of spatial frequency on circular vection is the inverse of the effect of temporal frequency (ANOVA: $F = 11.2$; d.f. = 2,14; $P < 0.01$, 15% variance explained). Both effects appear to be equally strong and independent. We therefore found no differences in estimated speed of circular vection under conditions where both the spatial and temporal frequency of the visual stimulus had been changed, but the ratio between the two was kept invariant (i.e under conditions with equal drum velocity). This is evident in Fig. 8c. Hence the speed of circular vection is clearly proportional to drum angular velocity and not to temporal frequency only.



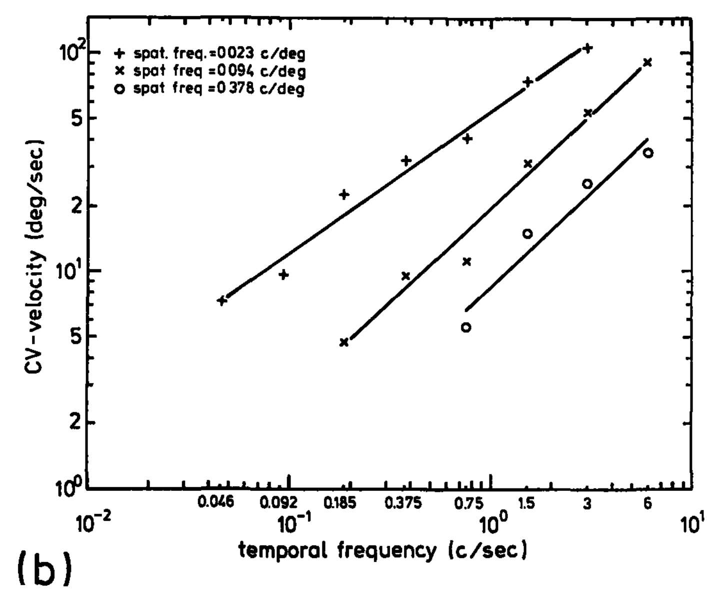
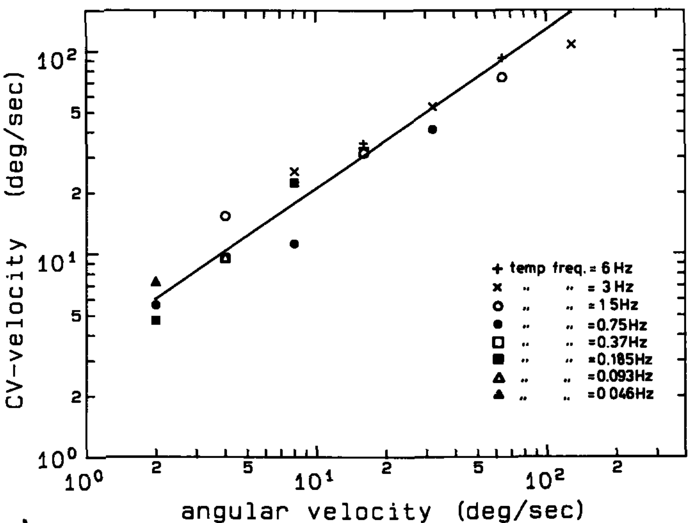


Fig. 8 (a) Group mean CV velocity (from eight subjects) plotted as a function of spatial frequency and (b) of temporal frequency. Weighted means of the slopes (-0.72 and 0.77 respectively) are not statisticly different, hence data can be replotted as a function of angular velocity of the drum (c). Best fitting straight line has a slope of 0.78. Nota Bene, the points in this figure with an identical symbol share the same temporal frequency.



(c)

The same is true for the speed of optokinetic nystagmus (see Fig. 9). We scored the eye velocity with a standard procedure, described in De Jong, Bles and Bovenlander (1981). An ANOVA performed on these data revealed a significant increase in nystagmic slow phase velocity with lower spatial frequency (F = 386; d.f. = 2,14; P < .001; 79% variance explained. See Fig. 9a). The effect of temporal frequency is as strong as that of spatial frequency, but of an inverse nature. OKN-slow phase velocity increased with higher temporal frequencies (F = 182; d.f. = 2,14; P < 0.001; 15% variance explained. See Fig. 9b). There is a slight interaction (1% variance explained) between both effects. This is probably due to the incapacity of the optokinetic nystagmus to keep up with the highest velocities. There were no differences in nystagmic slow phase velocity under conditions where both the spatial and temporal frequency were changed, but the ratio between the two was kept invariant (i.e. under conditions with equal drum velocity; cf Fig. 9c). Hence, OKN-slow phase velocity too is related to drum angular velocity and not to temporal frequency only.

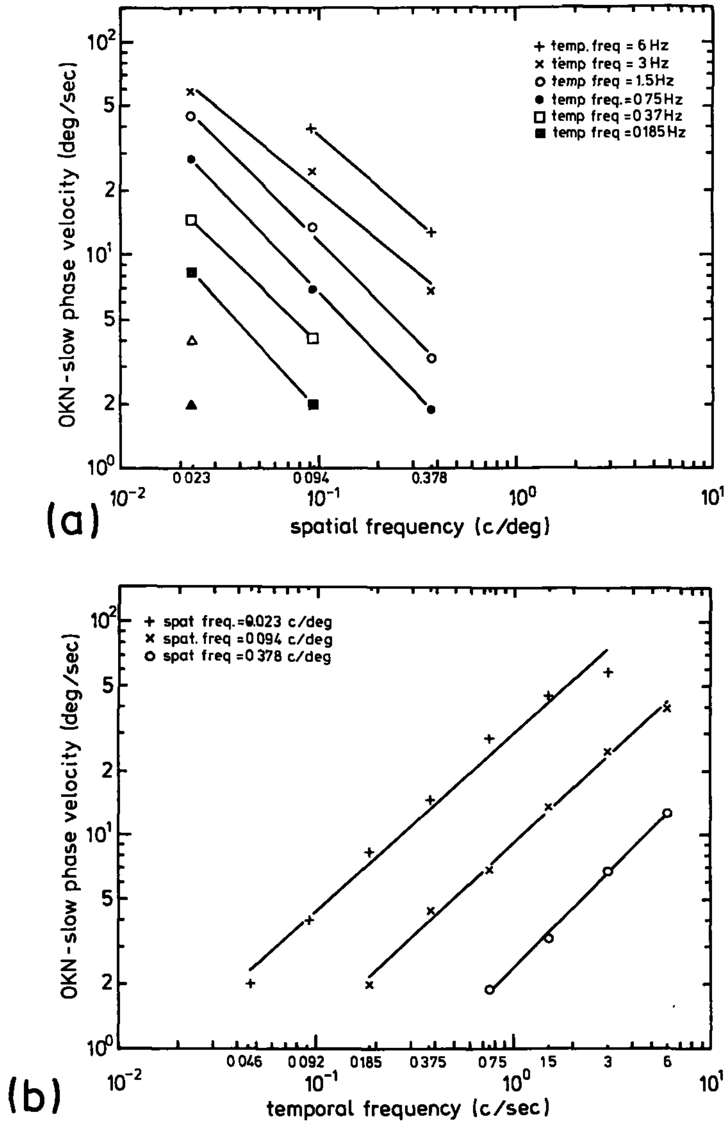
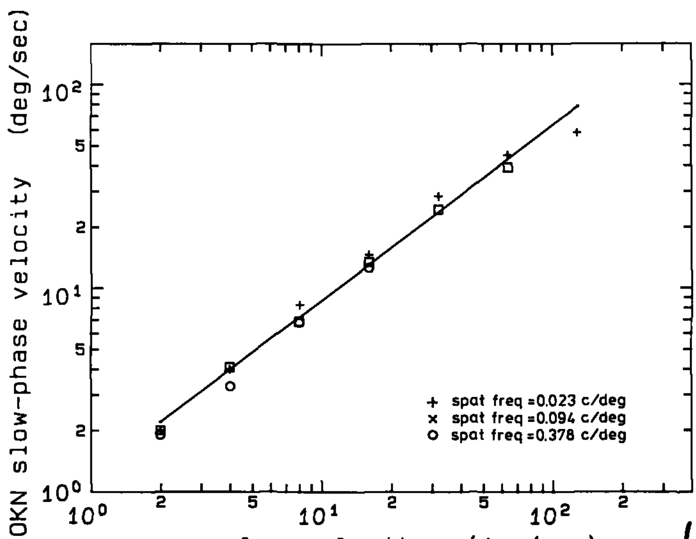


Fig. 9 (a) Group mean eye movement (OKN-slow phase velocity) data plotted as a function of spatial frequency and of (b) temporal frequency Weighted mean of the slopes is -0.90 and 0.86 respectively. Both effects are equally strong, but opposite in direction. Therefore the points associated with one and the same drum velocity, but with different spatial <u>*and*</u> *temporal frequencies, are indistinguishable (c). Fig 9c shows these mean OKN-slow phase velocity data replotted as a function of angular drum velocity. Best fitting straight line has a slope of 0.86. The points in this figure with an identical symbol share the same spatial frequency.*



(c)

In addition, the subjects experienced a difference in speed of circular vection when the eyes were kept stationary as compared to when optokinetic nystagmus occurred. In 20 out of 24 samples, taken within a range of drum velocities between 4 and 128 degrees per second, the subjects indicated a decline in selfrotation speed when the fixation light was absent, <u>and</u> an increase when they could fixate their eyes again (Fig. 10).

Subject no.

	1	2	3	4	5	6	9	10
LSf	1.61	1.08	1.30	1.08	1.73	1.28	1.12	5.38
MSf	1.06	1.17	1.17	1.16	1.76	1.11	1.28	1.13
HSf	1.50	4.54	0.95	2.47	0.80	1.80	0.91	0.60

Mean = 1.58

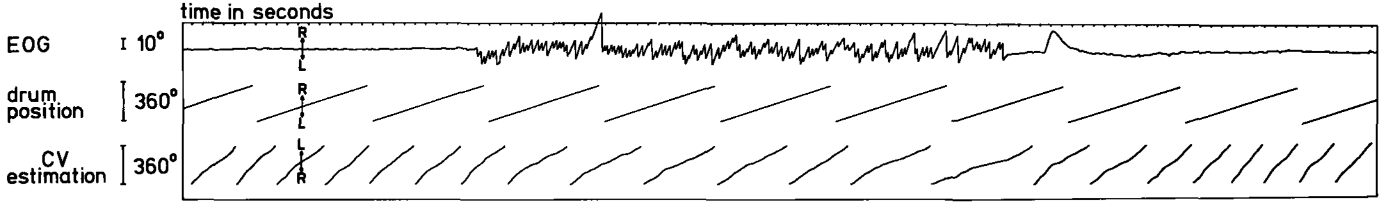


Fig. 10 Experienced differences in speed of circular vection when eyes are kept stationary as compared to when optokinetic nystagmus occurs. An example of a registration. First during ocular fixation, then without an fixation point (causing optokinetic nystagmus) and finally again with stationary eyes. From top to bottom: Time in seconds; registration of (absence or presence of) eye movements; actual speed of the optokinetic drum (one turn is 360 deg); experienced speed of CV as indicated by a subject (one full turn of the handle is one subjective selfrotation, 360 deg). Notice the lowering in "handle speed" when the fixation light is absent, and the experienced increase of selfrotation when the fixation light reappears.
The numbers in the table represent registered speed of CV with eyes fixated divided by registered speed of CV with optokinetic nystagmus.

Discussion

Both, the spatial and the temporal characteristics of a moving pattern are relevant parameters for a visually active self motion mechanism. Their influence is equally strong, although opposite in direction. Therefore the ratio between the spatial and the temporal frequency of the stimulus, the drums angular velocity (DV), determines the experienced speed of circular vection (CV). Within the stimulus range used in the present experiment we found the following relation:

$$CV = 3.5 \times (DV)^{.78}$$

The effects of spatial and temporal frequency on the functional mechanism which is responsible for the speed of optokinetic nystagmus (OKN) are rather similar. The slow phase velocity of optokinetic nystagmus is determined by drum angular velocity:

$$OKN = 1.2 \times (DV)^{.86}$$

Ecologically speaking, these results are not very surprising. In normal daily life, perceived speed of selfmotion is invariant for changes of feature scale in the visual scene, fronto-parallel as well in depth. Or, to use an analogy from the strongly related area of object motion perception, we don't expect humans to perceive the stripes of the tiger running faster than the animal. Moving objects are perceived as a whole, and this is also true for the visual scene which we perceive when we move along. Parts of the scene might have different spatial and temporal properties, which are picked up by differently tuned motion detectors, but the ratio of the properties remains invariant between parts; so all (activated) detectors will have the same velocity as output.

In addition, with respect to eye movements Dichgans and Brandt (1978, page 769), and more recently Straube and Brandt (1987), state that (with stimulus velocities up to 90 deg/s) there are no differences in perceived speed of circular vection when the eyes are kept stationary as compared to when optokinetic nystagmus occurs. We cannot endorse this. Our data show (see Fig. 10) that the experienced speed of circular vection is a factor 1.6 higher when the eyes fixate a static fixation light, a phenomenon analogous to the Aubert-Fleisschl paradox in the realm of object motion perception. We do not understand this discrepancy between the findings of Dichgans and Brandt and our results. A difference in CV-register method might be responsible [Dichgans and Brandt usually use a verbal magnitude estimation procedure according to Stevens (1957)]. However, our subjects often verbally mentioned their feelings of acceleration when the fixation point reappeared. The difference in stimulus material (sinusoidal versus rectangular) was certainly not responsible for this discrepancy; we experienced the same differences in CV velocity when we used the standard lined inner drum wall as a stimulus. The influence of oculomotor activity on experienced speed of circular vection will be subject of additional investigations.

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II.2. <u>THE AUBERT-FLEISCHL PARADOX DOES APPEAR IN VISUALLY INDUCED SELF MOTION</u>

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<u>Abstract</u>

An experiment was set up to investigate the possible influence of oculomotor activity on experienced speed of circular vection. With the standard lined inner wall of an optokinetic drum as stimulus, we found that subjects, sequentially exposed to periods with or without fixation point, experienced an increment in speed of circular vection when the eyes were kept stationary as compared to when optokinetic nystagmus occurred. No such difference, however, was found in a control condition where the influence of optokinetic nystagmus versus fixed gaze on the speed of circular vection was measured separately. These findings explain a discrepancy found in the literature.

Introduction

It has been known for a long time that exposure to moving visual stimuli can generate a sensation of selfmotion. In the laboratory this sensation of selfmotion can be induced for instance by a large scene which rotates around a stationary subject. The subject then experiences an apparent selfrotation (called circular vection), opposite in direction to that of the visual stimulus and phenomenally indistinguishable from actual selfrotation. Circular vection (CV) has been quantified by Brandt, Dichgans and Koenig (1973) and Dichgans and Brandt (1978). They used an optokinetic drum, the inside wall of which, lined with vertical black and white stripes, served as the stimulus pattern. In 1973 Brandt et al. found that the speed of CV varies as a function of stimulus speed. This finding was replicated by De Graaf et al. (1990) with a drum wall covered with a sinusoidally modulated vertical grating. Another finding was, however, not replicated. Dichgans and Brandt (1978), and recently Straube and Brandt (1987), reported that for angular velocities below 90 deg/s, perceived velocity of CV is independent of whether the subject fixates on a stationary target or reflexively tracks the moving pattern by optokinetic nystagmus (OKN). We could not confirm this finding, though. Our data showed that the experienced speed of CV was a factor of 1.6 higher when the eyes fixated a static fixation light as compared to when OKN occurred. This is a phenomenon analogous to the Aubert-Fleischl paradox in the realm of object motion perception: a stimulus is estimated as faster (by a factor of about 1.5) when the stimulus is perceived with fixed gaze as compared to when followed by the eyes (Fleischl, 1882; Aubert, 1886; Gibson et al., 1957 ; Dichgans et al., 1975).

At first glance no obvious determinant is at hand which could be responsible for this discrepancy in findings. But a comparison is hard to make because Dichgans and Brandt offered data nor references. The difference in stimulus material (sinusoidal versus rectangular) is certainly not responsible for this discrepancy; in a pilot experiment where we used the standard (rectangularly) lined inner drum wall as stimulus, we experienced the same Aubert-Fleischl like difference in perceived CV velocity as before between conditions with and without eye movements. Maybe a difference in CV-register method might have been responsible. Dichgans and Brandt generally use a verbal magnitude estimation procedure according to Stevens (1957). We measured by means of a small handle which could be rotated by hand through 360 deg[7], and thus indicates experienced change in position as a function of time. But why should two workable methods of registration, which correlated well before, suddenly deviate so radically? A more plaus-

[7] See Methods section.

ible determinant could have been a difference in experimental procedure. In our procedure the subjects were sequentially exposed to periods with and without fixation point, and were asked to continuously indicate the speed of CV. The subjects, therefore, were able to make instant comparisons. In view of the procedures commonly used by Brandt and Dichgans it is likely that they had a discontinuous procedure in which subjects had no such possibility for immediate comparison. The present experiment was set up to test this latter explanation for the discrepancy in findings. With the standard lined inner wall of the drum as an optokinetic stimulus, we created two conditions. In one, trials with and without optokinetic nystagmus alternated continuously. In the second condition, trials with and without OKN were separately presented.

Methods

Apparatus

For this experiment we used a rotary chair and drum system (Tonnies, Freiburg), which permits independent or coupled chair/drum rotations around the vertical axis. In this experiment only the drum, 1.5 m in diameter, moved. Its inner wall was lined with black and white vertical stripes (52 times 6.9 deg of visual angle per stripe).

To prevent information from sources other than the intended stimulus the subject wore a headset intercom with ear muffs, to overcome acoustic information about drum movement and about position with regard to the outside world during conversation with the experimenter.

The dependent variable was experienced speed of circular vection, measured by means of a small handle fixed on the armrest of the chair, which could be rotated through 360 deg with one or two fingers of the right hand. Subjects were instructed to point the handle to an imagined (fixed) point outside the drum (like a compass needle). In this way subjective position was continuously indicated, which offers a registration of experienced self motion speed as a function of time. Eye movements were registered by means of EOG skin electrodes placed at the outer canthi of the eyes. The actual drum velocity, eye movements and the speed of circular vection as indicated by the handle were registered on a strip chart recorder. The fixation point was a little v-sign (0.4 deg by 1.5 deg of visual angle, luminance 100 cd/m^2) projected on the wall, straight in front of the subject. Table 2 shows the experimental design.

Table 2 Experimental design. Two stimulus conditions (C and D), each with five drum velocities. In C periods with or without fixation point continuously succeeded each other. In D periods with or without fixation points were separately presented. CV-speed registrations in C and D were balanced. The order of stimuli presented (2 x 5 = 10 in each condition) was randomized.

C		D	
drum to the left		drum to the right	
deg/s		deg/s	
30	FIX-OKN-FIX	30	FIX
30	OKN-FIX-OKN	30	OKN
60	FIX-OKN-FIX	60	FIX
60	OKN-FIX-OKN	60	OKN
90	FIX-OKN-FIX	90	FIX
90	OKN-FIX-OKN	90	OKN
120	FIX-OKN-FIX	120	FIX
120	OKN-FIX-OKN	120	OKN
150	FIX-OKN-FIX	150	FIX
150	OKN-FIX-OKN	150	OKN

There were two main conditions, each carried out with five drum velocities (30, 60, 90, 120, 150 deg/s). In the Continuous (C) condition the drum always moved to the left, and trials with fixation point (FIX) and without fixation point (OKN) alternated continuously. For each drum velocity two sequences of trials were given: FIX-OKN-FIX and OKN-FIX-OKN. In the Discontinuous (D) condition the drum moved always to the right and only the FIX trial <u>or</u> the OKN trial was presented.
The 10 paid subjects, 7 male and 3 female, were between 19 and 32 years old. They were naive with respect to the apparatus, the experimental paradigm and the purpose of the experiment.

Procedure
Prior to the experiment the subject was shown the optokinetic drum and the possibility to rotate chair and drum independently. EOG-electrodes were placed and the subject was seated on the chair. Then instructions followed about the use of the handle if (and only when) selfmotion is experienced. A pilot test trial was performed in which every subject experienced saturated

circular vection (i.e. reported a sensation of selfrotation while perceiving the drum as stationary). None of them found it difficult to indicate this by rotating the handle. The subjects were also instructed to fixate the fixation light when present and otherwise to follow ('all') the stripes on the wall.
The exact measurement procedure went as follows. After EOG calibration the subject sat in complete darkness, while the experimenter adjusted the desired velocity of the drum. The order of C and D was balanced, therefore the drum moved by turn to the left (C) or to the right (D). Then the light in the drum was switched on (20 lux at the wall, resulting in a average luminance of 39 cd/m^2 of the white stripes and 3 cd/m^2 of the black stripes). A few seconds thereafter the subject generally indicated selfmotion by rotating the handle. In C conditions the subject was asked to continue with indicating speed of circular vection irrespective of whether the fixation point appeared or not. For example, after an initial one minute FIX-trial of CV speed registration, the fixation point was suddenly switched off starting a one minute OKN-trial, and then switched on again for another one minute FIX-trial. Then the subject sat in the dark again, while the experimenter adjusted a new velocity. After two minutes the light went on and the subject was exposed to the stimulus pattern but now moving to the right (D), only for a FIX-trial (<u>or</u> a OKN trial). After one minute of CV speed registration the light went off and the subject sat again in the dark for two minutes while the experimenter selected a new drum velocity. In this way all required drum velocities were executed in random order, 10 times (2 x 5 drum velocities) to the right and 10 times to the left. At the end of the experiment we asked subjects to report about their experiences and then told them that they actually had not moved during the experiment. This always caused great astonishment and disbelief.

The scoring of the CV-speed data went as follows. In the D conditions, exactly 15 s after the subject indicated selfmotion by rotating the handle, the amount of change in subjective position was scored over a fixed period of 30 s. This was the same for the first trial of the sequence in the C conditions. In the two following trials of the sequence also a period of 30 s was scored, but now 10 s after appearance (or disappearance) of the fixation point.

Results

Data of two subjects could not be included because they got sick and wanted to stop the experiment. Perhaps they made head movements despite the implicit instructions not to do so and the use of a headrest. The other eight subjects had no such problems. The results of the experiment are shown in Fig. 11.

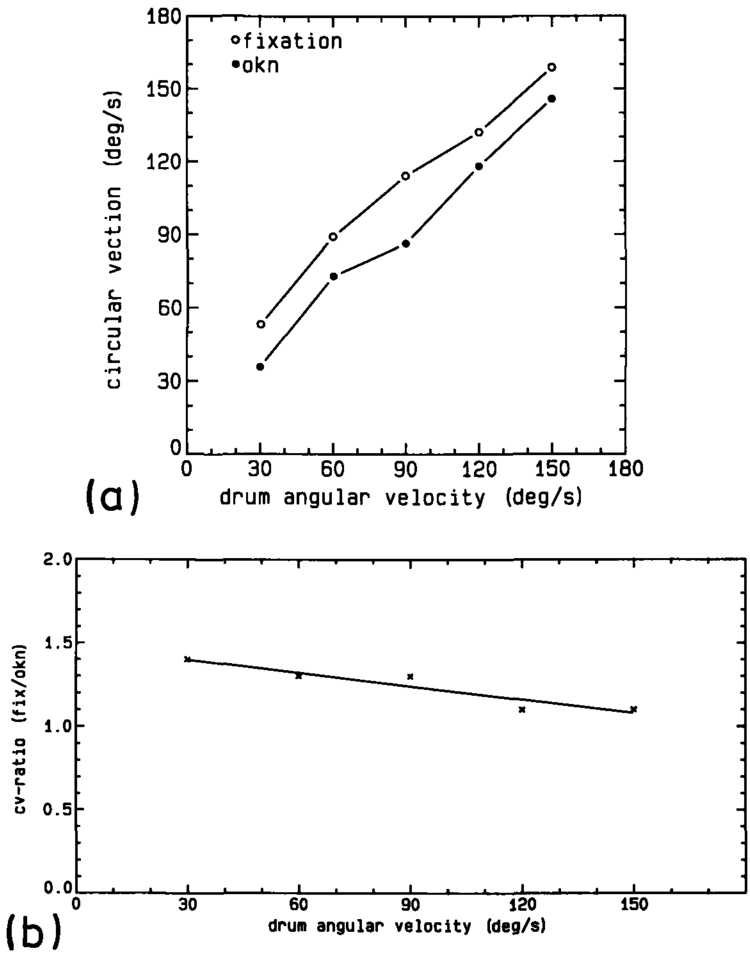

Fig. 11 (a) Group mean CV-speed (from eight subjects) plotted as a function of drum angular velocity. A significant difference in experienced CV-speed during OKN (•) and fixation (○) was only found for the C condition. The data obtained from the D condition are rather similar, but not presented here, because no significant difference was found there between OKN and fixation. (b) The course of overestimation of CV-speed during fixation (with respect to OKN) as a function of drum angular velocity.

Subjects could very well discriminate between the different stimulus velocities. ANOVA revealed that about 50% of the variance was explained by differences in experienced CV-speed as caused by differences in drum speed.

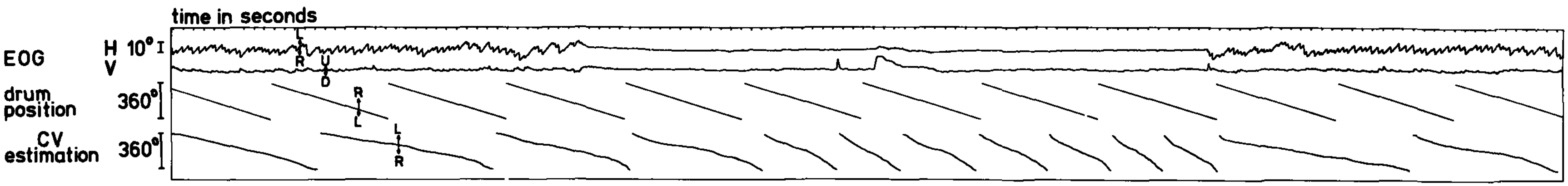

Fig. 12 Experienced differences in speed of circular vection when eyes are kept stationary as compared to when optokinetic nystagmus occurs. An example of a registration in the C conditions. First without an fixation point (causing optokinetic nystagmus), then during ocular fixation and finally again without fixation point. From top to bottom: Time in seconds; registration of (absence or presence of) the horizontal component of eye movements; registration of the vertical component of eye movements; actual speed of the optokinetic drum (one turn is 360 deg); experienced speed of CV as indicated by a subject (one full turn of the handle is one subjective selfrotation, 360 deg). Notice the experienced increase of selfrotation when the fixation light appears, and the lowering in "handle speed" when the fixation light is absent.

In the C conditions a difference in experienced CV-speed was found between ocular fixation and OKN. Subjects always indicated a higher CV-speed when the fixation point was present (ANOVA $F = 7$; d.f. $= 1,7$; $P < 0.05$, 2.9% variance explained). As is shown in Fig. 12, subjects indicated a decline in selfrotation speed when the fixation light was absent, and an increase when they could fixate their eyes again. No trial sequence effect was found, e.g. the differences in estimated CV-speed between FIX and OKN trials where independent of wether OKN came before FIX or vice versa. In the D conditions, however, no significant differences in experienced CV-speed was found between FIX and OKN trials.

A separate analysis of only the first trial (in the sequences) of the C conditions, which is in fact a replication of the D conditions (but then for drum motion to the left, see Table 2), revealed also no significant difference between FIX and OKN trials. This was, however, not the case with the two following trials in the sequences (of the C conditions). Separately analyzed, in the second trial as well as in the third trial a significant difference was found between FIX and OKN (ANOVA: respectively $F = 7.6$; d.f. $= 1,7$; $P < 0.05$, 1.8% variance explained, and $F = 7$; d.f. $= 1,7$; $P < 0.05$, 3.6% variance explained). Therefore, the difference in data obtained between the C conditions (as a whole) and the D conditions is not due to the amount of (re)measurements in C conditions.
When we compared two data sets, the D conditions and the first trial in the sequences of the C conditions, obtained from a corresponding situation, but with the drum moving in a different direction, no differences in CV-speed were found. In other words, it was not relevant whether the drum moved to the right or to the left.

<u>Discussion</u>
When sequentially exposed to periods with or without fixation point, subjects experienced an increment in speed of circular vection when the eyes were kept stationary as compared to when optokinetic nystagmus occurred. In other words, the Aubert-Fleischl paradox does also hold for visually induced self motion. The effect is small but significant (CV-ratio = FIX/OKN = 1.1-1.4), and greatest for drum velocities up to 90 deg/s (see Fig. 11b). With higher stimulus velocities the OKN has difficulties to keep up with the stimulus pattern and consequently some retinal image motion will appear (like with fixation), which will cause a small increment in CV-speed. This will reduce the Aubert-Fleischl paradox, more and more with increasing stimulus velocities.
The fact that we could not find differences in CV-speed between OKN and FIX trials when they were measured separately, probably explains the discrepancy between our former findings and those of Dichgans and Brandt as due to

a procedural difference (discontinuous versus continuous). Subjects need an instant comparison between OKN and FIX conditions to let the difference in indicated CV-speed become evident.

Finally, a contribution to an old controversy can be made. In the literature about the Aubert-Fleischl paradox conflicting opinions exist about which mode, OKN/pursuit versus straight ahead fixation, is more accurate, i.e. closest to the physical reality. While Mack (1986) speaks about an 'underestimation' of velocity during pursuit (which implies that according to her opinion estimation on basis of retinal image motion is more accurate), Dichgans et al. (1975) mention the 'overestimation' of pattern speed with fixation. Gibson (1957) found that both ways of observing, although different with respect to the impression of speed, are equally correct with respect to the relevant behaviour (a discrimination task). The latter could be true, but on basis of our data (Fig. 11a) we adhere to the opinion of Dichgans et al. The CV-speed estimations, basically a response to stimulus pattern velocity, show that subjects match almost perfectly the actual drum velocity during OKN and (thus) overestimate it during fixation.

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Part III: Ocular counterrotation and orientation to the horizontal

III.1 INFLUENCE OF VISUAL, VESTIBULAR AND CERVICAL TILT INFORMATION ON OCULAR ROTATION AND PERCEPTION OF THE HORIZONTAL

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Abstract

By combining a tilting chair and a tilting room we investigated the subjective horizontal (SH) and ocular counterrotation (OCR) as a function of body tilt, trunk tilt and tilt of a visual frame. Significant influences of (isolated or combined) vestibular and visual information were found, but no influence of neck proprioception. On basis of a comparison of OCR and SH data obtained in the dark in identical conditions, a hypothesis is generated about a relation between OCR and the Müller (E) phenomenon.

Introduction

A lot of research demonstrates the strength of a stable visual frame on the appearance of the subjective vertical (SV) or subjective horizontal (SH). Subjects, even when exposed to a severe body tilt, are able to set a line horizontal when adequate visual information is available. In the absence of such a frame however, like in the dark, considerable illusions occur. Early researchers like Aubert (1861) and Müller (1916) noticed effects of head tilt on the subjective vertical, nowadays called the A (Aubert) and E (Müller) phenomena. The A phenomenon is described (Howard, 1982) as the apparent tilt of a truly vertical line in the direction opposite to the head (c.q. body) tilt, so that the subjective vertical is tilted in the same direction as the head tilt. The E phenomenon is described as the apparent tilt of a true vertical in the same direction as the head tilt, and therefore the subjective vertical is tilted in the opposite direction of the head, c.q. body tilt. The A phenomenon is what one would expect if a subject underestimated the extent of the head tilt, and the E phenomenon is what one would expect from an overestimation of the head tilt. Müller found that most people experience the E phenomenon with small angles of head tilt and the A phenomenon with larger angles. Some people experience only the A phenomenon, however. Witkin and Asch (1948) observed that of their subjects 77% produced an E phenomenon and 23% an A phenomenon while exposed to a 28 deg body tilt, and with a body tilt of 90 deg almost all (94%) of the subjects experienced the A phenomenon.

When the head (or body) is tilted to one side, the eyes rotate in their orbits about the visual axis in the opposite direction. This response is known as ocular counterrotation (OCR). The static (residual) OCR of healthy persons is about 10% of body tilt, with a maximum of 6 deg at 60-75 deg body tilt (Schöne 1962; Miller et al. 1968). If our perceptual system failed to take this counterrotation into account, the resulting error would be in the same direction as the E phenomenon. It is therefore seductive to take the OCR responsible for the appearance of the E phenomenon, but there is evidence that it is not that simple. Fischer (1930) measured OCR and the apparent tilt of a vertical line as a function of body tilt, but found no direct or even proportional relationship. Miller et al. (1968) replicated these findings with normal subjects, and they also found E phenomena in people which showed no OCR because of vestibular malfunction.

The physiological processes responsible for the OCR and the setting of the SV or SH in darkness are not quite clear. Miller et al. (1965) showed that the function relating the magnitude of the E and A phenomena to the degree of body tilt resembles a sine function. This made Schöne (1968) to suggest that the illusions are related to the shearing force acting on the utricular surface of the vestibulum, because this is also a sine function of body tilt. Inconsistency with this utricular force theory comes from experiments with people with loss of vestibular functions. As stated before, they also show E and A phenomena. But, it may be that substitution of other sensory information to compensate for the loss of vestibular function, like neck proprioception and somaesthetic cues, is responsible for these observations (Bles et al, 1983).

Collewijn et al. (1985) used their nice scleral coil technique to measure OCR during the dynamic phase of head roll. They found an OCR from 40% to more than 70% of head motion. This high amount of compensation was probably due to activation of the semicircular canals. In situations of continuous rotation at constant velocity (and therefore without canal stimulation), Diamond and Markham (1981, 1983) showed a constant OCR of about 10% of head rotation. With static tilt of the head lasting several hours, Miller and Graybiel (1974) found that OCR is not reduced, which provides evidence that static OCR is driven by non-adapting utricular receptors.
Other factors contributing to OCR like visual information and neck proprioception are controversial. Goodenough et al. (1979) found torsional movements of the eyes of about 1 deg when subjects inspected a tilted visual framework. Collewijn et al. (1985) also reported a small but significant influence of visual cues on (dynamic and static) OCR. Howard and Templeton (1964), however, found no evidence of eye torsion when subjects look at a tilted line which subtend 10 deg at the eye. About the neck, Krejcová (1971) found that the amplitude of OCR produced by a tilt of the head alone is the same as that from the whole body, suggesting that there is not a significant contribution of the neck proprioception to the OCR. But others (Fischer, 1927; Wade, 1968; Biemond and De Jong, 1969; Schöne and Udo de Haes, 1968) suggested that an additional input from neck proprioception is likely.

In the present experiment on body tilt we investigated the isolated or combined influence of a) information from a visual frame, b) vestibular information, and c) information from neck proprioceptors, on eye rotation and subjective horizontal. A tilting chair, which made independent adjustments of head and body tilt possible, enabled us to investigate not only the vestibular but also the possible cervical influence on OCR and SH in the dark. In the light, with this chair placed in a tilting room we could investigate a possible, merely visually induced, eye rotation as well. We could also measure the possible contribution of the visual frame beyond the vestibular component both on OCR and SH, by exposing the subject to <u>one</u> particular body tilt (with respect to gravity) but with different combinations of frame (room) tilt. Finally, by comparing the data of OCR and SH obtained in the dark in identical conditions, a possible relation between OCR and the E- and A phenomena might become apparent. The range of tilts was up to 25 deg, to the left or right. It was examined with small steps of 5 deg, to provide insight into the course of the variables.

Methods

Apparatus

For this experiment we used a motor driven tilting room (Tönnies, Freiburg), which could be tilted laterally from the base. The device (2.5m x 2.5m x 2m) was completely closed, except for a door in the front side. The walls, painted in flamingo red, were fitted in a black frame. The room tilt, which was obtained by changing voltage via a potentiometer, was read by digital voltmeter (10 deg to the left up to 10 deg to the right, accuracy $\pm$ 0.1 deg). Two ceiling-lights illuminated the room dimly (35-65 lux at the back wall). We installed a tilt chair in the room, in which a subject could be tilted about the x-axis through the neck, 15 deg to the left up to 15 deg to the right. This could be done in the following ways: a) with the whole body tilted (head and trunk in line) or b) with only the trunk tilted (head upright). Soft foamrubber cushions were placed between the subject and the chair to diminish somaesthetic inputs. Fig. 13 illustrates the experimental apparatus.

The subject could indicate the subjective horizontal by means of a LED illuminated, potentiometer driven, rotatable test-bar (length 50 cm) at 125 cm distance at the back wall of the room (22,6 deg of visual angle; axis of rotation at eye level). A removable fluorescent lamp (length 50 cm) could be placed 10 cm above this test-bar in order to create an afterimage.

We had two dependent variables; (1) the deviation of the subjective horizontal (SH) with respect to the objective horizontal and (2) the amount of eye rotation in the orbit.

With regard to variable 1, subjects were instructed to put the test-bar in agreement with what they thought was horizontal. We measured the deviation (in deg) of this adjustment from the objective horizontal. With regard to variable 2, subjects were told to put the test-bar parallel to their afterimage (which was created before, with the subject in normal upright position). The difference between the actual amount of head (or body) tilt and the deviation of the test-bar (from the objective horizontal) quantified the eye rotation. The 12 paid observers, 7 male and 5 female, were between 19 and 32 years old. They were naive with respect to the apparatus, the experimental paradigm and the purpose of the experiment.

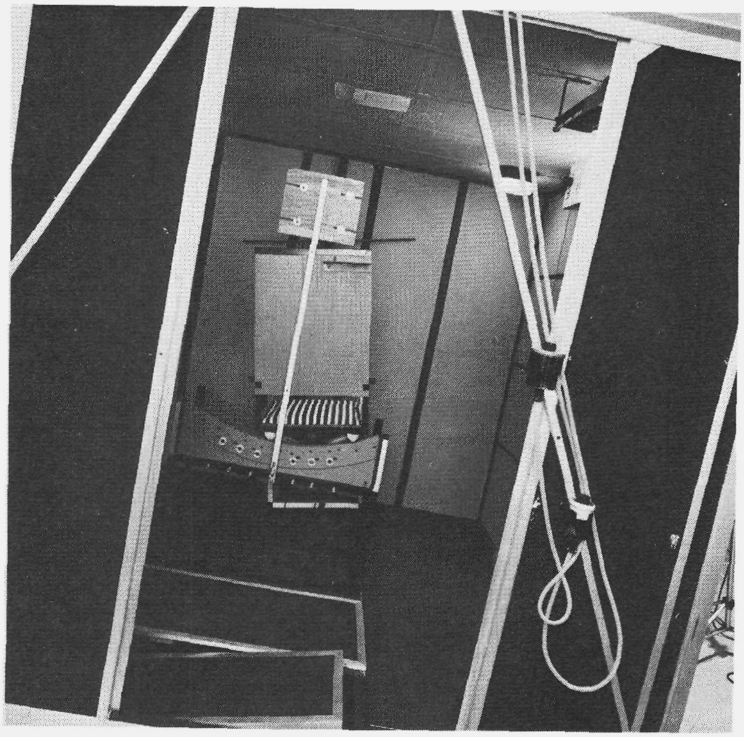


Fig. 13 A photo of the experimental apparatus. The room and the chair could both be tilted laterally. The chair could be tilted independently, but a tilt of the room also causes a tilt of the chair (it is however possible to compensate this by adjusting the chair). With the help of a lever on the chair, it is also possible to tilt the trunk of a subject independent of the head or vice versa.

Procedure

We showed the subject the tilting room and the possibility to tilt the chair and room independently. Then the subject was seated, facing the back wall of the room, and received the instructions. In the SH measurement conditions we asked the subject to level the bar with respect to the true horizontal, independent of the tilts of the room and chair, so "that a little ball placed on the test-bar will not fall off". In the OCR measurement conditions we asked the subject to adjust the bar parallel to the afterimage. The circumstances were identical for the SH and OCR conditions, except that we created an afterimage in the OCR conditions just before we installed the desired angles of tilt of chair and room.

tilt of chair (deg) \ tilt of room (deg)	-10	-5	0 on	0 off	5	10	lights
-15	a -25	a -20	c -15	a -15	a -10	a -5	off
-10	-20	-15	c -10		-5	b 0	on
-5	-15	-10	c -5		b 0	5	on
0	d -10	d -5	bcd 0	a 0	d 5	d 10	on
5	-5	b 0	c 5		10	15	on
10	b 0	5	c 10		15	20	on
15	a 5	a 10	c 15	a 15	a 20	a 25	off

tilt of trunk (deg)							lights
-15	-10	-5	0	5	10	15	off

Fig. 14 Experimental Design. The combination of tilting chair and tilting room enabled us to investigate the isolated or combined influence of visual information, vestibular information and proprioception from the neck, on ocular rotation and subjective horizontal. The design offers the ***input*** *variables:*

<u>Upper inset of the figure</u>. Each value inside the matrix represents the vestibular input, being the sum of the tilt of the chair and the tilt of the room (+ = clockwise tilt, - = counter clockwise tilt). With the lights on, the room could act as a visual frame of reference.

a. Vestibular information only.

b. Invariant vestibular, but different visual information.

c. Invariant visual frame information, with respect to the gravitational vertical. Vestibular information variates.

d. Vestibular information variates, but the visual angle between the subject and the room is always 0 deg.

N.B. Three conditions were measured both with lights on and off, to obtain additional information.

<u>Lower inset of the figure</u>. To investigate a possible cervical influence on OCR and SH, we tilted the trunk of the subjects, by tilting the chair, while the head remained upright. These measurements were performed in the dark.

The design was ran twice, once for SH and once for OCR measurements, but in different (randomized) order.

This afterimage was created by having the subject (subject and room upright) fixate the fluorescent lamp for 40 s. Then, for both the SH and OCR conditions, the subject was asked to close the eyes. The experimenter then first adjusted very slowly the desired (randomized) angle of the chair. Thereupon the room was tilted (0 deg, 5 or 10 deg to the left or right, in randomized order). After each of the tilts of the room we switched the test-bar by turns about 20 deg to the left or to the right, and then asked the subject to open the eyes and adjust the test-bar. After such a sequence of room tilts (with one particular chair tilt), which lasted about 5 minutes, the subject got a few minutes rest. Then the chair was adjusted to a new position and the room tilt sequence was repeated. The order of SH and OCR sequences of room tilt (with one particular chair tilt) was balanced. A nested variable was the light situation in the room, because some measurements were taken in the dark. Fig. 14 shows the experimental design. This design was ran twice, once for SH measurements and once for OCR measurements.

In addition, we measured the influence of cervical stimulation on the SH and OCR in darkness by tilting the trunk of the subject while leaving the head upright. For that purpose the chair was tilted in random order up to maximally 15 deg to the left or right and the room remained in horizontal position (see also Fig. 14).

Results

None of the subjects had difficulties with the adjustments of the test bar in OCR and SH conditions. Therefore the following analyses could be performed on the data gathered from 12 subjects.

OCR

The data obtained in the dark (see Fig. 15) show a strong vestibular influence on OCR (ANOVA: $F = 64.5$; d.f. $= 10,110$; $P < 0.001$, 81% variance explained). There existed a progress in strength of OCR with larger body tilts, with a mean maximum of 6 deg with tilts of 25 deg to the right or to the left. Post hoc Newman-Keuls analysis revealed significant differences ($P < 0.01$) in OCR between 0 deg tilt of the body and 5, 10 and 15 deg to the right or to the left respectively. The latter tilts on their turn caused smaller OCR's than body tilts of 20 and 25 deg.

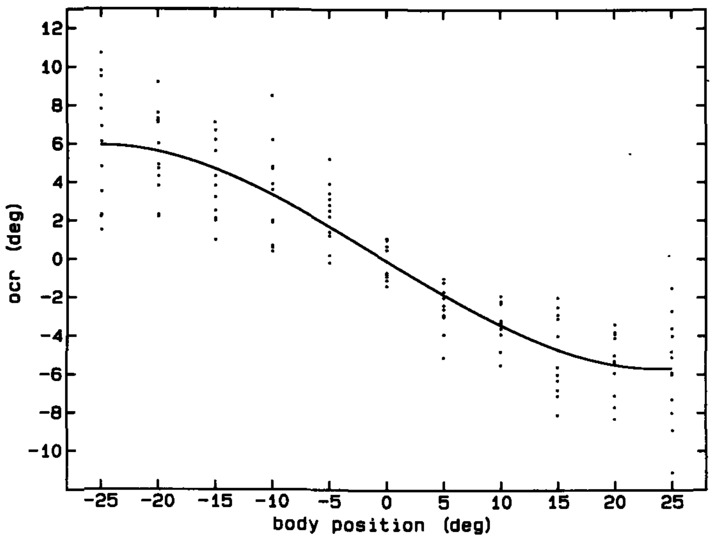


Fig. 15 Ocular counterrotation (OCR) as a function of body position in the dark (situation a, Fig. 14). A positive value stands for a tilt (x-axis) respectively rotation (y-axis) clockwise, a negative value represent a tilt (x-axis) respectively rotation (y-axis) counter clockwise. The data show a strong vestibular influence on OCR. The line drawn is a best fit 3rd deg polynome which levels at ± 6 deg.

There also exists a small but significant visual influence on OCR (Fig. 16a). In the light different tilts of the room, while the body is not tilted, revealed a difference in ocular rotation in the same direction as the room tilt (ANOVA: $F = 7.9$; d.f. $= 4,44$; $P < 0.001$, 26% variance explained)[8]. The mean maximum ocular rotation was about 1 deg with a room tilt of 10 deg to the left or to the right. We could also examine the influence of visual information on ocular rotation on other occasions. For example, in the sequence of tilts where the subject was visually locked with the tilting room (situation d, see experimental design, Fig. 14) we found a significantly smaller OCR than with the same amounts of body tilt in the dark (situation a, see also Fig. 14) (ANOVA: $F = 11.5$; d.f. $= 1,11$; $P < 0.01$, 10% variance explained, see Fig. 16b).

[8] It is therefore not always correct to maintain the term OCR (ocular counterrotation). In cases where this could lead to a misunderstanding we will use the term ocular rotation.

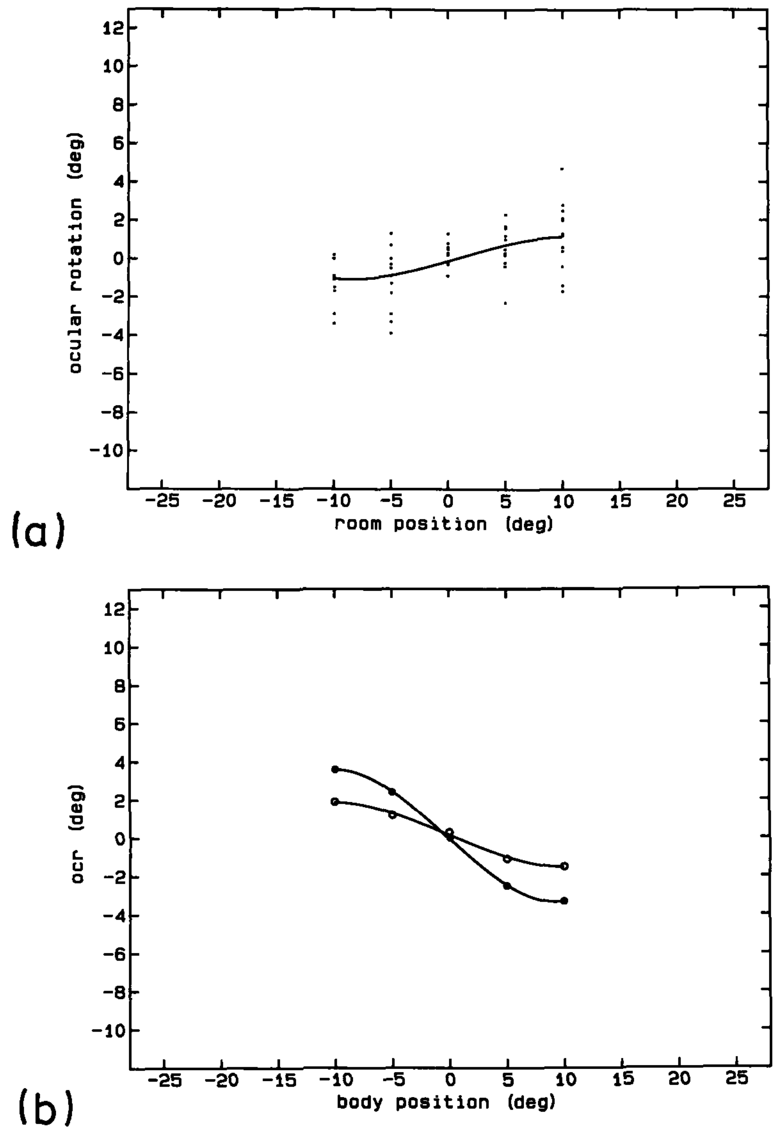


Fig. 16 (a) Ocular rotation as a function of room position in the light (situation b, Fig. 14). The data show a small but significant visually induced ocular rotation, in the same direction as the room tilt. (b) OCR as a function of body position, as measured in the light (open circles; situation d, see Fig. 14) and in the dark (filled circles; situation a, see Fig. 14). In the situation that subject and room are visually locked, i.e. tilted to the same amount, the visual frame had a restraining influence on OCR.

Obviously, a (tilted) visual frame could have a restraining influence on the OCR of a tilted subject. Also, in another situation where measured the same condition twice (in the light and in the dark), we found when the body was tilted for 15 deg to the left, but with an upright (0 deg tilted) room, in the light a significant larger OCR than in the dark (T-test; $t = 1.82$, $d.f. = 22$, $P < 0.05$). This was, however, not the case in a comparable situation where the body was tilted 15 deg to the right. On basis of these results we conclude that there exists a small visual influence on ocular rotation which could add to or subtract from a much larger vestibular component.

We found no significant influence of neck proprioception on OCR (Fig. 17). Different angles of body tilt, but with the head upright with respect to gravity, did not produce differences in the OCR of subjects. The values of the OCR unsystematicly balanced around 0, with larger standard deviations at the extremes of tilt.

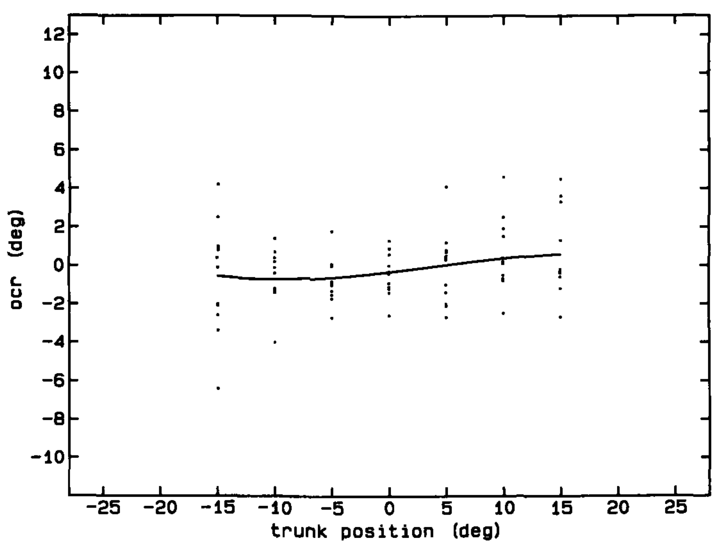


Fig. 17 OCR as a function of trunk position. No significant influence of neck proprioception on OCR was found. The values of OCR balanced around 0, with larger standard deviations at the extremes of tilt of the trunk with respect to the head.

SH

Fig. 18 reproduces the mean adjustments of the subjective horizontal. A comparison with the input variables given in Fig. 14 shows that, in the light, the room acts as a frame of reference and dominates the adjustment of the horizontal. The response was always determined by the room, despite differences in vestibular information (ANOVA: $F = 48$; d.f. $= 4,44$; $P < 0.001$, 69% variance explained. See Figs. 14 and 18, any column). Also, in situations with invariant vestibular input (like in situation b, see Fig. 14) responses were significantly different.

tilt of chair (deg) \ tilt of room (deg)	-10	-5	0 on	0 off	5	10	lights
-15	31	1.4	-0.6	1.7	0.0	1.4	off
-10	-7.8	-3.1	0.7		4.4	8.2	on
-5	-7.4	-31	0.6		4.3	7.8	on
0	-7.3	-3.7	0.3	-0.1	3.9	8.3	on
5	-6.6	-3.0	-1.1		2.0	7.1	on
10	-7.7	-4.6	-1.0		2.9	6.3	on
15	-1.0	-0.6	-0.6	-1.1	-0.5	-1.5	off

Fig. 18 Mean SH output data presented like the design of Fig. 14. The measurements taken with the lights on clearly show the dominance of a visual frame of reference on the adjustments of the subjective horizontal.

The mean SH adjustments in the dark, merely determined by vestibular information (situation a in Fig. 14), did not significantly differ from each other and from 0. See Fig. 19.

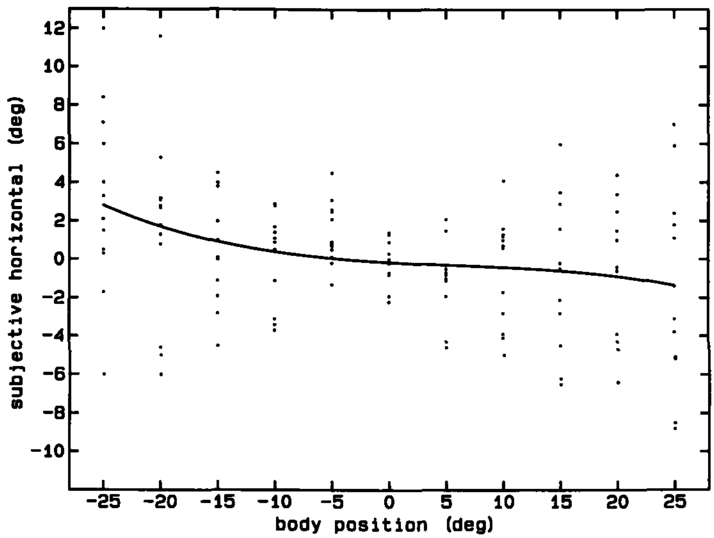


Fig. 19 Adjustments of SH as a function of body position. A positive value stands for a tilt (x-axis) respectively test bar adjustment (y-axis) clockwise, a negative value represent a tilt (x-axis) respectively adjustment (y-axis) counter clockwise. The mean data obtained in the dark, and therefore merely determined by vestibular information (situation a, see Fig. 14), did not significantly differ from each other and from 0. The line drawn is a best fit 3^{rd} deg polynome.

We found no influence of neck proprioception on the adjustment of SH (Fig. 20). Different angles of trunk tilt, but with the head upright with respect to gravity, did not produce differences in the SH of subjects. The values of the SH unsystematically balanced around 0.

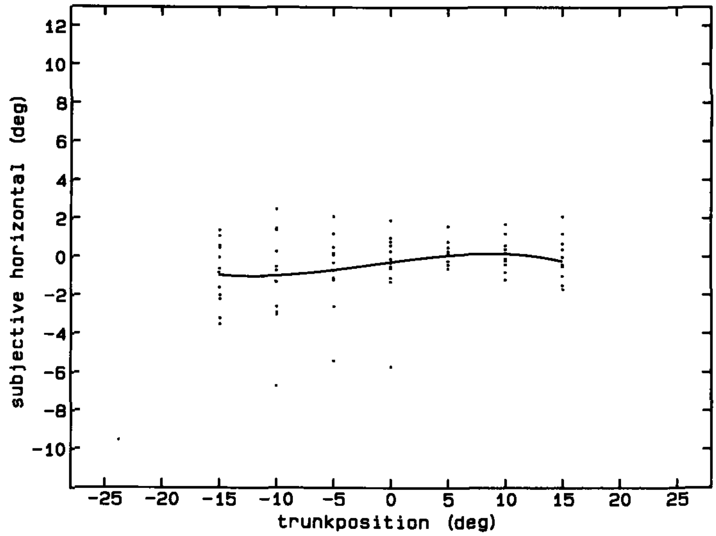


Fig. 20 SH as a function of trunk position. No significant influence of neck proprioception on SH was found. The values of SH did not significantly differ from each other and from 0.

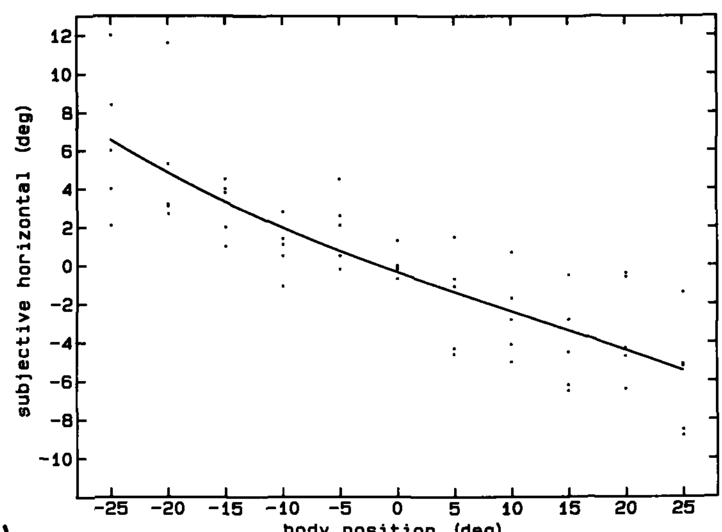
Discussion

We found that ocular counterrotation is mainly determined by vestibular information. With angles of tilt up to 25 deg we found a (static) OCR with a progressive course which will presumably saturate by 20-25 deg of body tilt, at a maximum of 6 deg. The range of the gain was 0.23-0.48, which is in correspondence with OCR data taken from the literature by Vogel et al. (1986) and conform their logarithmic description of the relation between OCR and tilt.

We found a small but significant visual influence on OCR, which could add to or subtract from the vestibular component depending on the position of the subject according to the visual frame. These results are in quantitative agreement with the results of Goodenough (1979) and Collewijn et al. (1985). Our data did not support the suggestion that there is a cervically induced contribution to OCR[9].

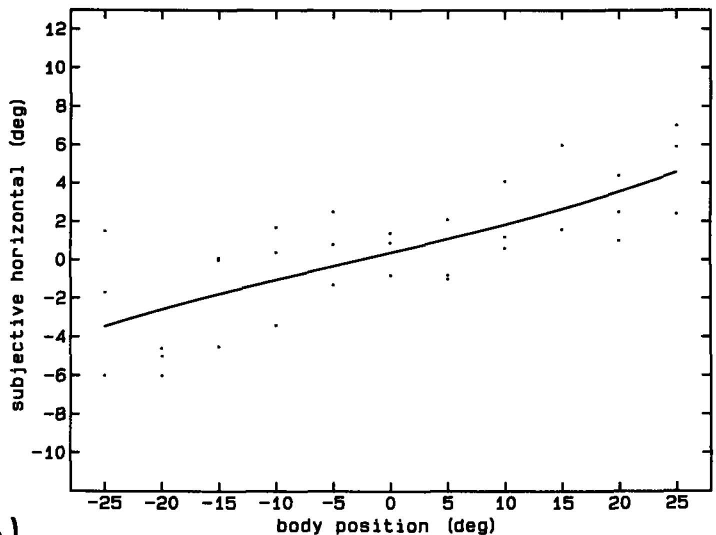
Although the subjects were instructed that the room could and would be tilted, they still adjusted their subjective horizontal according to the room. The fact that people, for example, tilted 10 deg to the right adjusted their SH according to a room which is even 5 deg more tilted to the right (15 deg to the right) says a lot about the dominance of the room acting as visual frame of reference. After our measurements the subjects explained that they were sometimes aware of a discrepancy between visual and vestibular information, but nevertheless experienced the visual information to be more valid.

In the dark, however, the mean of our data as shown in Fig. 19 appears to suggest that people are quite capable to adjust the SH according to the true horizontal. A further analysis shows that this is certainly not true. Out of the group of 12 subjects we found 5 subjects who always exhibited an E phenomenon (overestimated their body tilt, see Fig. 21a) and 3 subjects who always exhibited a specific A phenomenon (underestimated the tilt, see Fig. 21b). (The 4 subjects left were not so clearly specific, 3 of them tended to an E phenomenon and 1 tended more to an A phenomenon.) Now it is clear that the SH of the individuals deviates considerably with larger tilts, but in a very specific way. These findings replicate the observations of, for example, Witkin and Asch (1948).



(a)

Fig. 21 Reinterpretation of the data presented in Fig. 19. (a) SH data obtained from the subgroup of subjects (5) who always showed an E phenomenon, and (b) SH data obtained from the subgroup of subjects (3) who explicitly showed an A phenomenon. It is clear that the SH of individuals belonging to those subgroups deviates considerably with larger body tilts, but in a very specific way. The lines drawn are the best fit 3rd deg polynome.



(b)

We found no signs of a systematic influence of activation of the neck on the adjustment of SH. Subjects who had their trunk tilted sidewards, but with their head upright with respect to gravity, did not experience a SH different than normal, with both head and trunk upright[9].

Our final question was about a possible relationship between OCR and SH. As stated before, if our perceptual system fails to take the ocular counterrotation into account, the resulting error (in the dark!) would be in the same direction as the E phenomenon. This overcompensation should then match the OCR exactly. When the subjects are taken together, a comparison of identical OCR and SH conditions in the dark (Figs. 15 and 19) does not show such a relationship as stated before by Miller et al. (1968). However, when we compare the SH and OCR data of the subgroup who always exhibit an E phenomenon, the strength of the illusion appears to fit nicely with the strength of OCR (see Fig. 22).

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[9] However, present research on patients with vestibular deficiencies does suggest a contribution of the neck on OCR as well as on SH (in prep).

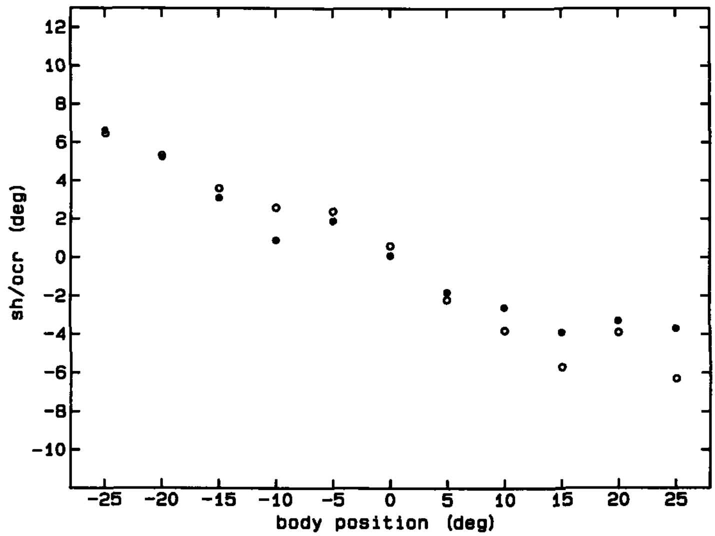

Fig. 22 Mean OCR data (filled circles) and mean SH data (open circles) from 5 subjects who always exhibited an E phenomenon, presented as a function of body position in the dark. The correlation between OCR and SH is for each of the individuals 80% or higher, and the mean OCR and SH data do not statistically deviate from each other.

We therefore suggest that with tilts up to 30 deg the OCR could be responsible for the appearance of the E phenomenon. With larger tilts the otoliths become less effective (will underestimate the tilt; Schöne and Udo de Haes, 1971), which firstly will be masked coincidentally by OCR, and with still larger tilts (and a saturized OCR) will cause the A phenomenon in all subjects (see Fig. 23). A consequence of this suggestion is that subjects who show the A phenomenon already with small tilts, are considered to have a less accurate utricular functioning (a lower gain). There is no need for them to have sleepless nights about that, because our suggestion is only valid for static tilt situations in the dark. Anyway, latent A and E phenomena are simply overruled by a visual frame of reference.

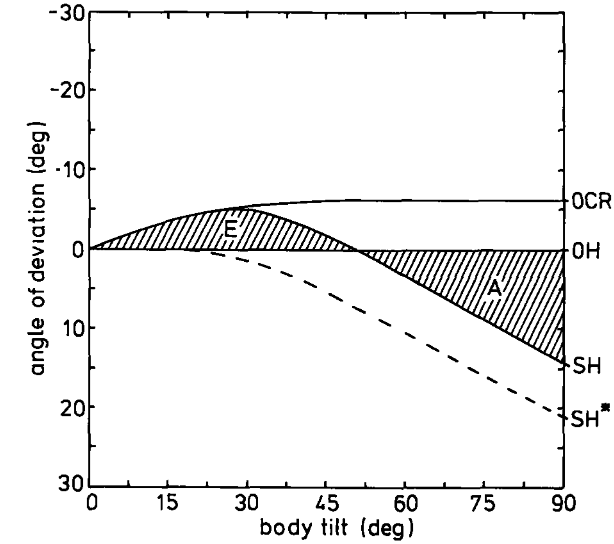

Fig. 23 A model for the course of the subjective horizontal (SH) as a function of lateral body tilt in the dark. For illustrative reasons the course of OCR is plotted as well. OH = objective horizontal; OCR = OCR as a function of body tilt; SH = hypothetical SH, based on mere vestibular information (with a gain less than 1 with larger tilts) and without appearance of OCR. SH = subjective horizontal as found in the literature (and our data). A perceptive system which bases SH on mere vestibular information without feedback about OCR could be responsible for the Müller (E) phenomenon (an overestimation of body tilt caused by addition of OCR and SH*). With larger tilts, and a corresponding larger utricular inaccuracy, the addition of SH* and OCR could not (over)-compensate for this inaccuracy. As a consequence an Aubert (A) phenomenon will appear.*

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III.2. OCULAR ROTATION AND PERCEPTION OF THE HORIZONTAL UNDER STATIC TILT CONDITIONS IN PATIENTS WITHOUT LABYRINTHINE FUNCTION

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Abstract

In a previous study (de Graaf et al., 1990) it was found that in healthy subjects Ocular (Counter) Rotation is mainly due to otolith stimulation and only to a minor extent induced by slanted visual structures. Stimulation of the neck by tilting the trunk laterally upwards did not result in a systematic rotation of the eyes.

In the present study it was found that subjects with a bilateral loss of vestibular function showed a higher visually induced ocular rotation. Tilting the head (cervical stimulation) or the whole body (somatosensory stimulation) also led to a considerable OCR, demonstrating substitution of other sensory modalities for the loss of vestibular function.

Estimates of the subjective horizontal were noisy, demonstrating the lack of an adequate gravitational reference signal.

Introduction

Patients devoid of vestibular function experience problems in balance and gait, despite the fact that the central nervous system may learn to compensate for the loss of vestibular function by substitution of relevant proprioceptive and visual information. It is especially in the dark and during quick movements that this substitution is insufficient to restore the equilibrium function completely. Because of this vulnerability patients who lost their vestibular function rather suddenly, should be examined regularly to establish the state of the compensation since a multiple deficit may inhibit the compensation process (Bles and de Jong, 1986).
Several tests have been used to quantify this compensation process. It is obvious that visual information which contains horizontally and vertically structured information is very useful to these patients for maintaining upright posture. This has been shown for instance in the tilting room: They always perceive this room as vertical even when it is laterally tilted over 10 degrees, resulting in serious postural imbalance (Bles et al., 1983a).
As for preserving gaze control, in the horizontal plane the lack of the vestibulo-ocular-reflex is at least partly compensated for by cervically and somatosensory induced eye movements: An increase in the gain has been observed in these patients in comparison to healthy controls (Bles et al., 1984 a, b).

In a recent study in healthy subjects on the orientation with respect to the gravitational vertical the influence of otoliths, vision and the neck on ocular counterrotation (OCR) and the subjective horizontal (SH) was investigated (de Graaf et al., 1990). Since the OCR was mainly determined by the otolith system, only to a lesser extent by vision, and not by the neck, we were interested in the behaviour of patients with a bilateral loss of vestibular function under these circumstances.
Therefore four subjects with a bilateral loss of vestibular function were examined on the occurrence of OCR and the perception of verticality with the same experimental setup as used for the healthy subjects. This should provide us with insight in how these subjects use the still available sensory information on verticality to compensate for the absent vestibular otolith information.

Methods

Apparatus and data analysis

For this experiment we used a motor driven tilting room (Tönnies), which could be tilted laterally from the base (10 deg to the left up to 10 deg to the right, accuracy ± 0.1 deg). The device (2.5 m x 2.5 m x 2 m) was completely closed, except for a door in the front side, and illuminated by two ceiling-lights. A tilting chair was placed on the floor of the room, in which a subject could be tilted about the x-axis through the neck, 15 deg to the left up to 15 deg to the right. This could be done as follows: a) with the whole body tilted (head and trunk in line), b) with only the head tilted (trunk upright) or c) with only the trunk tilted (head upright). By combining, *in darkness*, the different chair operation modes with the proper room tilt in condition a) a body tilt from 25 deg to the left (CCW) up to 25 deg to the right (CW) could be achieved, in conditions b) and c) head or trunk tilt from 15 deg CCW up to 15 deg CW. An additional condition, with the room illuminated, was included in which tilt of the surround relative to the upright sitting subject was possible from 10 deg CCW up to 10 deg CW (condition d). (See De Graaf et al., 1990 for more details).

In subjects without labyrinthine function this means stimulation of the somatosensory system in condition a), of the neck in condition b), of the neck minus the somatosensory system in condition c), and of the eyes in condition d).

Foamrubber cushions were used to fixate the trunk to the chair. The subject could indicate his subjective horizontal by means of a LED illuminated, potentiometer driven, rotatable test-bar (length 50 cm) at 125 cm distance at the back wall of the room (22,6 deg of visual angle; axis of rotation at eye level). A removable fluorescent lamp (length 50 cm) could be placed 10 cm above this test-bar in order to create an afterimage.

We had two dependent variables; (1) the deviation of the subjective horizontal (SH) with respect to the objective horizontal and (2) the amount of eye rotation in the orbit.

With regard to variable 1, subjects were instructed to put the test-bar in agreement with what they thought was horizontal. We measured the deviation (in deg) of this adjustment from the objective horizontal. With regard to variable 2, subjects were told to put the test-bar parallel to their afterimage (which was created when the subject was in normal upright position and requested to look into the lamp for 40 s). The difference between the actual amount of head (or body) tilt and the deviation of the test-bar (from the objective horizontal) quantified the eye rotation.

Procedure

We showed the subject the tilting room and the possibility to tilt the chair and the room independently. Then the subject was seated, facing the back wall of the room, and received the instructions. In the SH measurement conditions we asked the subject to level the bar with respect to the true horizontal, independent of the tilts of the room and chair, so "that a little ball placed on the test-bar will not fall off". In the OCR measurement conditions we asked the subject to adjust the bar parallel to or on top of the afterimage. The circumstances were identical for the SH and OCR conditions, except that we started the OCR conditions by creating an afterimage when the subject was still sitting upright. Subsequently, for both the SH and OCR conditions, the subject was asked to close the eyes. The experimenter then adjusted very slowly the desired (randomized) head and trunk tilt by a combination of the angle of the chair, head holder and/or room. Afterwards he switched the test-bar by turns about 20 deg to the left or to the right, before asking the subject to open the eyes and to adjust the test-bar. Then the chair and/or room were adjusted to a new position, etc. All conditions were ran twice, once for SH measurements and once for OCR measurements. In turn, seven randomized SH or OCR measurements were presented.

Subjects

Four subjects (age 56 to 62) with an established loss of vestibular function for at least one year participated. According to these subjects no major changes in their equilibrium function had happened during the last year which made us assume that the compensation was completed. The absence of vestibular functions was established by noting the absence of sensation and nystagmus following caloric irrigation, rotating chair examination and the absence of Coriolis effects at chair rotations of 160 deg/s. Increased postural instability in the tilting room was established in these patients too, as well as an increased gain of the cervical and somatosensory nystagmus.

<u>Results</u>

OCR. All four subjects showed in condition a) an OCR during whole body tilt (head and trunk in line). The mean OCR at 25 deg tilt was up to about 4 deg (see Fig. 24). This OCR (gain 0.24) is not different from the OCR found in the healthy controls in the same condition (gain 0.27, De Graaf et al., 1990). In the patients, however, this OCR could only be invoked by somatosensory stimulation.

Tilt of the head alone (condition b) also induced a consistent OCR (gain 0.33) (Fig. 24) which, in these patients, should be due to stimulation of the neck. Only in subject D this OCR is smaller than the somatosensory induced OCR in condition a)(see Fig. 24). The mean amplitude of OCR is not significantly different in condition a) and b).

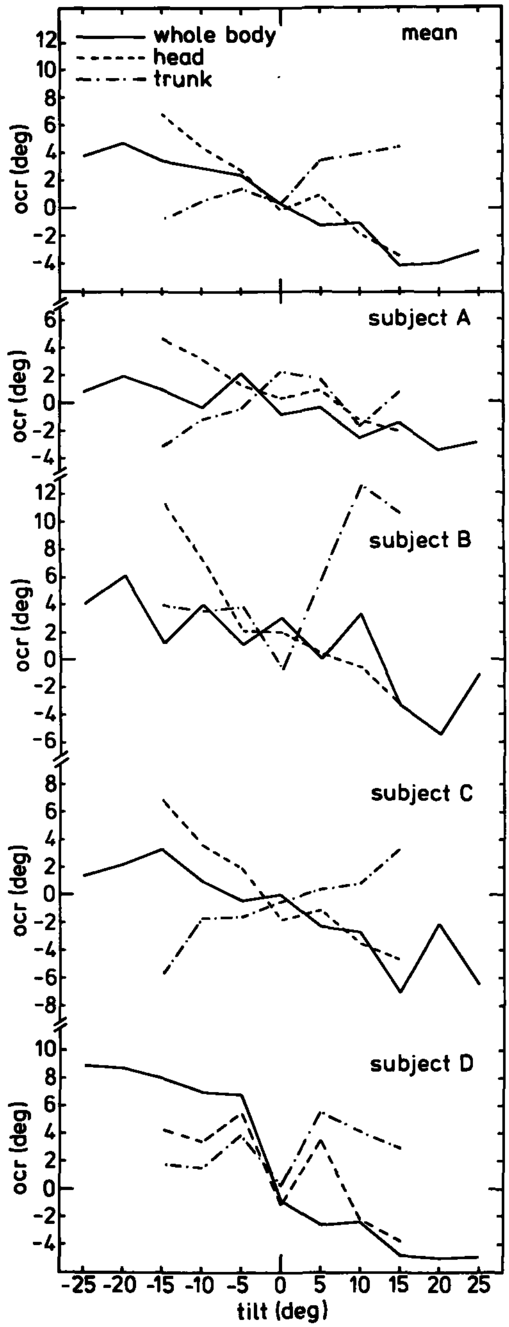

Fig. 24 Mean OCR and individual OCR data of four subjects devoid of labyrinthine function. Shown are the OCR found due to whole body tilt (—— line, condition a), to head tilt (--- line, condition b) and to trunk tilt (-•-•- line, condition c). Clockwise rotation is shown as positive values, counter clockwise as negative.

Tilt of the trunk only induced an OCR with a, small but significant, gain of 0.17 (Fig. 24). This in contrast to what was observed in healthy controls, where no OCR was found at all. It is assumed that this OCR reflects the net effect of the somatosensory and counteracting cervical OCR[10]: The OCR found in condition c) should equal the OCR found in condition b) minus the OCR found in condition a). This view is supported by the results of patients A, B and C.
The visually induced ocular rotation (condition d), Fig. 25 shows a gain of 0.30, which is significantly larger (ANOVA: $F = 5.4$; d.f. $= 1{,}14$; $P < .05$) than in normal subjects (gain 0.11, according to De Graaf et al., 1990).

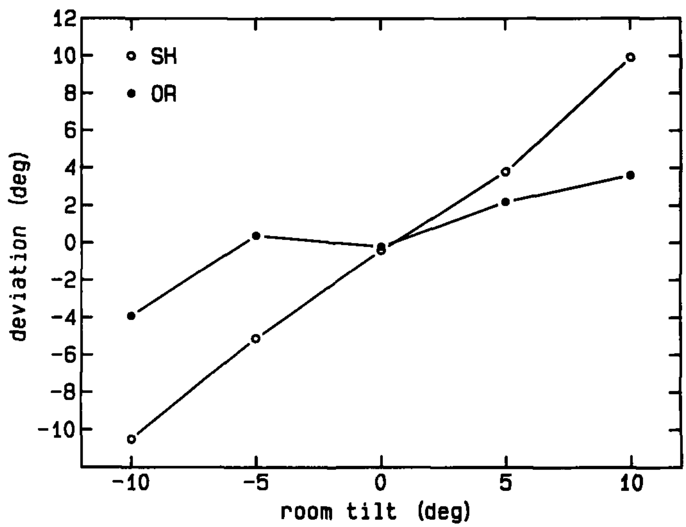

Fig. 25 Ocular rotation (•) and subjective horizontal (○) as a function of room tilt in the light (condition d). A clockwise deviation of the SH from the true horizontal (respectively clockwise ocular rotation in the orbits) is shown as positive, a counter clockwise deviation (respectively counter clockwise ocular rotation) as negative.

SH. In contrast to what was observed in the healthy controls, the data of the subjects without vestibular function are very noisy (except perhaps for subject A). This is reflected in the poor reproducibility of data at 0 deg tilt angle, where the three conditions a), b) and c) do not differ (see Fig. 26).

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[10] A clockwise tilt of the trunk causes a counter clockwise stimulation of the neck, with as result a clockwise OCR. But a clockwise tilt of the trunk also causes clockwise somatosensory stimulation, resulting in a counter clockwise OCR.

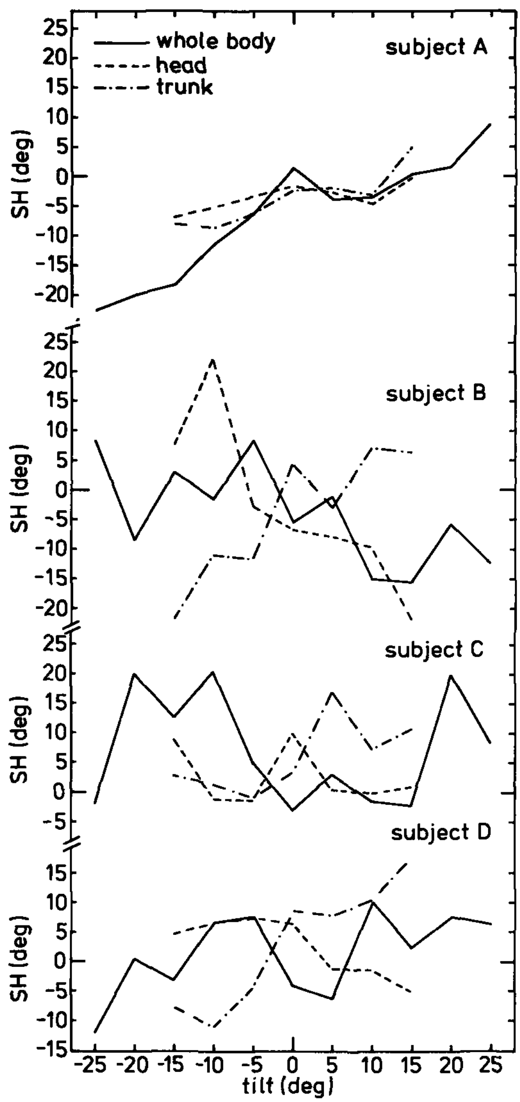

Fig. 26 Individual SH settings of the four labyrinthine defective subjects obtained during body tilt (—— line, condition a), during head tilt (--- line, condition b) and during trunk tilt (-•-•- line, condition c). A clockwise deviation of the SH from the true horizon is shown as positive, a counter clockwise deviation as negative.

The SH estimates during complete body tilt are different for each subject (Fig. 26). Subject A sets the bar almost completely perpendicular to his body, so apparently almost no tilt is perceived: He underestimates the tilt (Aubert phenomenon; Aubert, 1861). Similar behaviour is seen in subject D, be it to a lesser extent. However, subject B overestimates the amount of tilt (Müller phenomenon; Müller, 1916): she mentioned during the experiment that with the larger tilt angles to the right she was afraid to fall down. Subject C is highly variable in her estimates: e.g. at 20 deg tilt to the right the trunk serves as reference frame (SH perpendicular to the trunk) but at 20 deg to the left the amount of tilt is 100% overestimated.
Tilt of the head is estimated rather well by subjects A, C and D, but is overestimated by subject B.
A strong effect was found during trunk tilt: Apparently the subjects take in condition b) and c) their trunk as reference and perceive their head as tilted. This results in a deviation of the SH in the same direction as the trunk tilt in condition c).
As for the SH in the (illuminated) tilted room: Subjects experienced the tilted room always as vertical, and adjusted their horizontal according to this frame of reference (Fig. 25).

Discussion

OCR. The data indicate that in patients devoid of vestibular function still an OCR may be observed during body tilt (condition a), which is not significantly smaller than in healthy subjects (de Graaf et al., 1990). The amount of OCR found in our four subjects is larger than the OCR in the labyrinthine-defective subjects reported by Graybiel (1974). This may be due to the intersubject variability (note for instance the large OCR in subject D). Since this OCR cannot be of vestibular origin it must be due to somatosensory cues from the contact between body and chair.
Head tilt (condition b) induces a strong OCR as well, which should be of cervical origin in these patients. This confirms an earlier observation of Vogel et al. (1986) who found in a labyrinthine-defective subject an OCR of 5 deg during head tilt. Individual differences are present, but on the average the cervically and the somatosensory induced OCR are equally strong. In principle, this should have been reflected in the data of the situation where only the trunk was tilted (condition c): The two counteracting forces should have cancelled each other there. This was, however, not the case. A slight but significant OCR was found in that condition. We think that this remaining OCR was due to a skewed distribution in our small group of subjects: Three of the four patients had a significant larger OCR caused by somatosensory than caused by cervical stimulation (Fig. 24).

Apparently, for static tilt up to 15 deg the ocular counterrotation in subjects without labyrinthine function is of the same order of magnitude as in healthy controls. The visually induced ocular rotation is even better than in the controls, which, all together, helps to stabilize the image on the retina.

In view of the present data a reinterpretation of our data for healthy subjects (De Graaf et al., 1990) is possible: we then assumed that the contribution of the somatosensory system was negligible (cf. Graybiel, 1974) and, since in condition c) no OCR was observed, concluded that there was no cervical contribution to the OCR in healthy subjects. This was also reported by Krejcová (1971) who reached the same conclusion since there was no difference between the OCR obtained by tilting the whole body or only the head. However, our present data indicate that there is a clear somatosensory contribution to the OCR in patients and it may be incorrect to assume that this contribution is negligible when the otolithic system is working properly. In fact, the data obtained from normals and labyrinthine defective subjects do not allow us to differentiate between the assumption 1) that somatosensory and cervical information only contribute to OCR in patients and not in normals, and the assumption 2) that the otholits do not contribute to the OCR in patients as well as in normals. In view of the fact that for horizontal eye movements it was found that normals do show somatosensory and cervical nystagmus but with about half the gain of the labyrinthine defective patients (Bles et al., 1983b), a similar difference in gain may be conceivable for OCR as well. This means that in normals during body tilt, at least for the investigated range, the OCR is for 50% due to somatosensory stimulation and for 50% to the otoliths[11]. Since the cervically induced OCR roughly matches the counteracting somatosensory induced OCR, it is understandable that no OCR was found in condition c) in normals and (only a small one) in our patients.
In addition, it is understandable that no difference is observed (Krejcová, 1971) when the whole body or only the head is tilted: The contribution to the OCR by the *somatosensory system* in the *former* case, is replaced by the contribution of the neck in the latter case.

It is an inevitable conclusion that in clinical practice OCR examination is almost impossible without contaminating proprioceptive stimulation. In order to sort out the real contribution of each of the systems in normals

[11] If normals have about half of the gain (50%) of the labyrinthine defective patients with somatosensory stimulation, then only the remaining 50% could be due to the otoliths because no difference in OCR amplitude was found in condition a) between normals and patients.

and patients, it is desirable to isolate the OCR provoking systems even more, e.g. by measuring OCR during body tilt under water. This is, however, a rather cumbersome experiment. Perhaps it is more useful and of practical importance to look at the dynamic properties of the OCR (cf. Collewijn et al., 1985). It is most likely that the lack of the otolith function becomes especially then visible: After all, these patients do complain about problems mainly during and after fast head movements.

S.H. The gravitational reference frame proved to be less well determined by these patients. Most of all they rely on the visual information even when slanted over 10 deg (condition d), and despite the fact that the body is in the upright position under these circumstances. Apparently this visual dependency is very useful to them. These data confirm earlier observations on these patients in the tilting room (Bles et al., 1983a).
In the dark the subjects behave quite differently: Orientation relative to the trunk is seen to occur frequently. Body tilt leads to Aubert and Müller phenomena, but when only the trunk is tilted, the trunk is perceived as vertical and the head as tilted.
The scatter in the SH data is rather large, even in the upright position. This has been found before (Graybiel, 1974) and is in line with our clinical observations indicating that in healthy subjects the reproducibility of the SH settings is within 1 deg, whereas these labyrinthine defective subjects often show a range of up to 8 degrees. This illustrates once more the inaccuracy of the system in the absence of a properly functioning otolith system and makes the reliance on the visual information understandable.

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Concluding remarks

Concluding remarks

The first and overall conclusion is that our visual perceptual system functions optimally when a visual frame of reference is present. During voluntary or reflexive eye movements and even when subjected to conflicting information from other senses, in the presence of an adequate frame of reference the visual system offers a stable percept of the world. The motion of objects in the surroundings (see part I), the (apparent) motion of the self (see part II) and the orientation towards the horizontal (see part III), all are judged with respect to the visual frame of reference. Even when the visual information picked up is maliciously manipulated by the experimenter and consequently the percept, normally speaking, "wrong", it still dominates (for example: apparent self motion in the optokinetic drum; frame oriented subjective horizontal in a *tilted* room).
This conclusion is far from new, many researchers had similar findings and the relevance of a visual frame was already stressed by the ecological theory of Gibson (1966, 1979). But what happens if no such visual frame of reference is available to the perceiver? Then the perceptual system is deprived of important information and consequently perceptual illusions might occur. Illusions like those attributed to Filehne (see chapter I), and Aubert and Müller (see chapter III.1). Although these are rarely encountered in normal daily life, it is worthwhile to analyse the strategies used by the perceptual system under such circumstances. Mack (1973) presented a model in which the Filehne illusion and the Aubert-Fleischl paradox are attributed to underregistration of eye movements by the perceptual system. This reasoning has explicative power with regard to the Filehne illusion (see chapters I.1 and I.2), but not with regard to the Aubert-Fleischl paradox (see chapter II.2). In chapter III of this dissertation it is proposed that ocular counterrotation (OCR) influences perception of the horizontal (SH) in the dark . A model is presented (see chapter III.1) in which it is assumed that the perceptive system bases SH on mere vestibular information, without any consideration of the concurrent OCR. For subjects with an accurate utricular function the appearance of OCR is therefore responsible for the Müller (E) phenomenon with small lateral body tilts. 'Evidence' for this reasoning is yielded by the close correspondence between the amplitudes of OCR and the Müller phenomenon (in subjects who do experience the Müller phenomenon). The model has the advantage that it attributes the Aubert and Müller phenomena to one underlying cause, namely the (in)accuracy of the utriculi in combination with the appearance of residual OCR, but it has to be subjected to further examination to prove its validity.

That visual information becomes even more important for people devoid of vestibular function may seem self-evident. During tilt in the light, visual, cervical and somatosensory information interact in order to maintain a stable orientation (visual frame of reference for orientation to the horizontal; OCR provoking visual, cervical and somatosensory information to stabilize the retinal image with respect to this visual frame of reference). In the dark, however, the gravitational reference frame is poorly determined by these patients, notwithstanding the compensation by cervical and somatosensory information for the lack of otolith function.
With respect to the OCR this compensation was optimal. Both, information of cervical and of somatosensory origin could provoke an OCR with an amplitude equal to that measured in normals. This finding possibly contradicts the assumption that contribution of the somatosensory system to SH and OCR is negligible in *normals*, and the coherent negative conclusion about influence of cervical origin (see chapter III.1). In order to sort out the real contribution of each of the systems, in patients as well as in normals, it is necessary to isolate the individual systems even better.

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SAMENVATTING

Samenvatting

Het in dit proefschrift besproken onderzoek handelt over een aantal aspecten van informatieverwerking door het menselijke visuele systeem. Centraal staat de vraag hoe het maken van oogbewegingen de visuele waarneming kan beïnvloeden. Een aantal specifieke oogbewegingen zijn hiervoor onderzocht, één vrijwillige en twee reflexieve. Het eerste deel van het proefschrift behandelt de invloed van zgn. gladde oogvolgbewegingen op objectbewegingswaarneming, het tweede deel betreft optokinetische nystagmus en de consequentie daarvan op zelfbewegingswaarneming, en het derde deel, tenslotte, betreft het effect van oogtorsiebewegingen op de oriëntatie t.o.v de horizon. Een voortdurend achterliggende vraag is wat de relevante informatie is voor de betrokken zintuiglijke (sub)systemen.

Wanneer een bewegend object wordt gevolgd met de ogen dan lijken feitelijk stilstaande objecten op de achtergrond vaak óók te bewegen, en wel in tegenovergestelde richting. In het eerste deel van deze dissertatie worden de randvoorwaarden voor het optreden van deze zgn. Filehne illusie (vernoemd naar een onderzoeker uit het begin van deze eeuw, toen er nog illusies te benoemen waren) nader onderzocht. Het blijkt dat het optreden van de illusoir beweging onafhankelijk is van de relatie tussen het te volgen object en de achtergrond, maar wel afhangt van het maken van de oogbeweging zelf én van de mate van informatieve samenhang tussen de objecten op de achtergrond. Wanneer de objecten op de achtergrond zó weinig verband hebben dat zij niet als adequaat visueel referentiekader fungeren voor ons waarnemingssysteem dan zullen zij lijken te bewegen als gevolg van de beweging van de ogen. Dit soort situaties kunnen zich bijvoorbeeld in het verkeer voordoen tijdens mist, schemering of bij het binnengaan of verlaten van een donkere tunnel. Als er echter wel voldoende samenhang bestaat, zodat een percept van een stabiele achtergrond ontstaat, dan zullen feitelijk stilstaande of bewegende objecten ook dienovereenkomstig waargenomen worden, onafhankelijk van het wel of niet maken van gladde oogvolgbewegingen.

In het tweede deel van het proefschrift wordt betoogd dat de visueel geïnduceerde illusie van zelfrotatie (circular vection) afhankelijk is van de snelheid van het inducerende stimulus materiaal (in dit geval een draaiende zgn. optokinetische trommel behangen met fotomateriaal van sinusvormig gemoduleerde verticale zwart/witte balken). "Dat haalt je de koekoek", zult U brommen," Hoe harder zo'n trommel draait, hoe harder je natuurlijk denkt zelf te draaien". Het is echter een in de wetenschap nog onklare zaak hoe de snelheid van een object (of, als je zelf beweegt, de snelheid van de gehele omgeving) door ons visuele systeem wordt gedetecteerd. Wij denken te hebben bewezen dat de subjectief ervaren draaisnelheid

én ook de snelheid van de reflexief opgewekte nystagmoïde oogbewegingen proportioneel zijn aan de stimulus snelheidsinformatie, welke wordt gedragen door de temporele én de spatiële eigenschappen van het door het strepenpatroon gereflecteerde licht.
Eveneens blijkt dat er een belangrijk verschil in draaisensatie optreedt wanneer het stimuluspatroon wel of niet met de ogen wordt gevolgd. In het laatste geval wordt een beduidend snellere zelfrotatie ervaren, analoog aan de Aubert-Fleischl paradox (ook al weer bekend uit de vorige eeuw) voor objectbeweging: wanneer je het puntje van de wijzer van een metronoom volgt met de ogen lijkt hij langzamer te bewegen dan wanneer je recht vooruit fixeert (en dus geen oogbewegingen maakt).

Het laatste deel van het proefschrift betreft onderzoek naar de invloed van visuele, vestibulaire en cervicale (nekspier) informatie op oogrotatie en oriëntatie t.o.v. de horizontaal. Wanneer we ons hoofd in het donker scheef houden, zien we een horizontale lichtstreep een beetje schuin. Dit verschijnsel treedt niet op in een normaal verlichte ruimte, waar meer visuele informatie beschikbaar is. Een ander gevolg van kanteling van het hoofd is dat, door prikkeling van het evenwichtssysteem, de ogen automatisch in de tegenovergestelde richting roteren. Deze reflexmatige oogbeweging wordt ocular counterrotation (OCR) genoemd. De combinatie van een kantelstoel en een kantelkamer stelde ons in staat systematisch de invloeden van lichaams-, romp-, en kamerkantelingen te onderzoeken op zowel oogrotatie als op de waarneming van de subjectieve horizon (SH). Significante invloeden van vestibulaire en visuele informatie werden gevonden, maar geen invloed van nekpropriocepsis. Echter, toen het experiment werd herhaald met mensen zonder functionerende evenwichtsorganen, bleek een herinterpretatie noodzakelijk. Bij deze mensen bleek, naast een hogere weging van visuele informatie, de propriocepsis van de nek en ook somatosensorische informatie prominent van invloed op zowel de reflexieve oogrotatie als op de waarneming van de horizontaal. Dit demonstreert niet alleen de mogelijkheid van substitutie van andere sensorische modaliteiten voor het verlies van de vestibulaire functie, maar maakt eveneens duidelijk dat een negatieve conclusie over de invloed van de nekpropriocepsis bij normalen misschien voorbarig is. Deze laatste kan in principe wel degelijk aanwezig zijn, maar niet meetbaar omdat zij gecompenseerd wordt door tegenovergesteldgerichte somatosensorische informatie over lichaamskanteling. Ons aanvankelijke standpunt dat somatosensorische informatie bij normalen tijdens kantelingen verwaarloosbaar is, hetgeen mede gebaseerd was op de literatuur (Graybiel, 1974), dient mogelijk ook te worden herzien. Misschien dat eenzelfde experiment, maar dan uitgevoerd in het water, zodat er geen of nauwelijks somatosensorische informatie aanwezig is, uitkomst brengt over cervicale invloed op OCR en SH.

Tenslotte kan op basis van de verkregen data een verband gelegd worden tussen het vóórkomen van het door Müller (1916) gevonden E fenomeen (het verschijnsel dat bij kleine lichaamskantelingen een horizontale lijn in dezelfde richting als de lichaamskanteling wordt gezien) en de OCR. Een model hiervoor wordt gepresenteerd. Daarin wordt aangenomen dat het perceptieve systeem de SH in het donker baseert op louter vestibulaire informatie en zonder terugkoppeling van de gelijktijdig optredende oogrotatie. Als bewijs dient het gegeven dat de amplitude van de oogrotatie en de mate van deviatie van de subjectieve horizontaal t.o.v. de ware horizontaal even groot zijn. Met andere woorden: doordat deze reflexieve oogbeweging niet wordt ingecalculeerd door het waarnemingssysteem, bepaalt zij de mate waarin mensen hun kanteling overschatten.

Zo ik al talenten had
zijn deze aan de wetenschap geofferd
Het is volbracht
de geest is leeg, het blad is vol
wat ben ik toch een reuze bofferd!

Curriculum Vitae

De auteur werd geboren in 1957 te Plymouth, Engeland. Na het VWO eindexamen aan het College 'Hageveld' te Heemstede en het voldoen aan zijn militaire dienstplicht, studeerde hij tot 1986 psychologie ('cum laude') en filosofie aan de Universiteit van Amsterdam. In augustus 1986 trad hij in dienst van NWO om als medewerker van Dr. A.H. Wertheim het onderhavige onderzoek uit te voeren.
De auteur is getrouwd, heeft een dochter en een zoon en werkt momenteel als evenwichtsdeskundige in ontwikkeling (e.i.o.) op het Instituut voor Zintuigfysiologie TNO te Soesterberg.