TORSIONAL EYE MOVEMENTS IN HUMANS

Front page: Anatomy of the human eye muscles (modified from O. Zoth (1905) Augenbewegungen und Gesichtswarnehmungen. In Nagel, W., ed: *Handbuch der Physiologie des Menschen*, vol 3, Braunsweig, 1905, Friedr Vieweg & Sohn GMBH, p. 299.). The angle of insertion of the oblique muscles and of the superior and inferior rectus muscles is not perpendicular to the equator plane. Therefore, these muscles exert part of their action in torsional direction. Of these muscles, only the superior oblique and superior rectus muscles are visible in the figure.

TORSIONAL EYE MOVEMENTS IN HUMANS

TORSIE-OOGBEWEGINGEN IN MENSEN

PROEFSCHRIFT

ter verkrijging van de graad van doctor
aan de Erasmus Universiteit Rotterdam
op gezag van de rector magnificus,
Prof. Dr P.W.C. Akkermans M.Lit.
en volgens besluit van het college van dekanen.
De openbare verdediging zal plaatsvinden
op 23 maart 1994 Om 13.45 Uur.

Door

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geboren te Leiden

universiteits
Erasmus
DRUKKERIJ

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De druk en verspreiding van dit proefschrift werd mede mogelijk gemaakt door de Stichting voor Ooglijders, de Rotterdamse Vereniging Blindenbelangen, de Prof. Dr H.J. Flieringa Stichting, de Prof. Dr Flieringa-Houët Stichting en Skalar Medical B.V.

Is this a dagger which I see before me,
The handle toward my hand? Come let me clutch thee:
I have thee not, and yet I see thee still.
Art thou not, fatal vision, sensible
To feeling as to sight? or art thou but
A dagger of the mind

(Macbeth)

CONTENTS

This thesis is based upon the following publications.

Chapter 2:

L.J. van Rijn, J. van der Steen and H. Collewijn (1994) Instability of ocular torsion during fixation: Cyclovergence is more stable than cycloversion. *Vision Research,* in press.

Chapter 3:

L.J. van Rijn, J. van der Steen and H. Collewijn (1992) Visually induced cycloversion and cyclovergence. *Vision Research, 32,* 1875-1883.

Chapter 4:

L.J. van Rijn, J. van der Steen and H. Collewijn (1994) Eye torsion elicited by oscillating gratings: role of grating orientation, cycle length and stationary contours. *Vision Research,* in press.

Chapter 5:

L.J. van Rijn and A.V van den Berg (1993) Binocular eye orientation during fixations: Listing's law extended to include eye vergence. *Vision Research, 33,* 691-708.

Chapter 6:

L.J. van Rijn and H. Collewijn (1994) Eye torsion associated with disparity-induced vertical vergence in humans. *Vision Research,* in press.

CHAPTER 1

SYNOPSIS

1.1 What are torsional eye movements?

If one has to give a description of eye movements, what first comes to mind is the possibility of the eyes to rotate in horizontal and vertical directions. It is generally less obvious that the eyes are capable of moving in a third, namely the torsional, direction. This capability is by no means hypothetical: humans, as well as other species, possess eye muscles that are pulling in torsional direction and orbital mechanics do allow for a certain amount of torsion.

Definition of torsion
Torsional eye movements can be defined in two different ways, namely as a rotation about the line of sight and as a rotation about an antero-posterior (forward-to-backward) axis that is fixed in the head.

The most 'natural' definition of a torsional eye movement is as a rotation about the line of sight. The line of sight is the imaginary line that connects the eye with the fixation target. When the eye rotates about this line, remains fixating this same target. When the eye makes any horizontal and/or vertical gaze shifts, the line of sight and, therefore, the axis of rotation for torsion, shifts as well. For example, if one looks straight ahead, eye torsion occurs about an antero-posterior (forward-to-backward) axis. If one looks *leftward*, the axis of rotation for eye torsion is also rotated *leftward*.

A major advantage of this definition of eye torsion is that torsion is directly related to the rotation of the image that we perceive of the surrounding world. This relation holds irrespective of the horizontal and vertical rotations of the eyes in the head. This may be illustrated as follows. If we look at a certain object, a projection of the object is made on the retina of the eyes. This projection is called the *retinal image*. If any torsion is made in an eye, for example in *clockwise* direction, then the retinal image of the object rotates by exactly the same amount, but in *counter-clockwise* direction.

The alternative definition of eye torsion is as a rotation about an axis that is not, as the line of sight, fixed in the eye, but that is fixed in the head. Eye torsion may be defined as a rotation about an antero-posterior axis that does not change its position when horizontal and/or vertical rotations are made. This definition of torsion has the specific advantage that calculations on combined horizontal/vertical and torsional rotations are much easier. In this definition there is, however, no direct relation between retinal image rotation and eye torsion.

Throughout this thesis, the first definition of torsion (as rotation about the line of sight) will be used, except in chapter 5, where both definitions will be used in combination.

1.2 Why investigate torsional eye movements?

Functions of eye movements in general include 1) the tracking of moving objects (*pursuit*), 2) the redirection of fixation to points of interest (*saccades*), 3) the stabilisation of the retinal images and 4) the maintenance of correspondence of the images in both eyes. Torsional eye movements are potentially important in the last two of these functions.

Stabilisation of the retinal image

In order to see the surrounding world clearly, the retinal images must be, within certain margins, stable. Stability is affected, however, by the continuous movements of the head, which may cause *motion blur*. In order to prevent motion blur, head movements are counterbalanced by compensatory eye movements. These are mediated by two reflexes, the *Vestibulo-Ocular reflex* (VOR), which senses head rotations in the equilibrium organs, and the *Opto-Kinetic Reflex* (OKR), which directly senses retinal image motion. For horizontal and vertical movements, the effects of retinal (in-) stability and the effectiveness of VOR and OKR have been very well investigated, but not for torsion.

Retinal correspondence

Since we have two eyes, the brain receives two images of the surrounding world. Yet, we perceive the world as one, because both images are combined. In order to allow combination, the images in the left and right eyes need to fall on corresponding parts of the retinas. In this situation there is said to be *correspondence* of retinal images. This causes that identical parts of the retinal images in the left and right eyes are processed by the same areas in the brain. Deviations from correspondence occur when the eyes are misaligned. Tolerances for misalignment in horizontal and vertical directions have been very well investigated. The sheer mechanical capability of the eyes of making torsional movements necessitates a regulatory system that keeps the eyes aligned in torsional direction. The properties of this system are not very well known.

Cycloversion and cyclovergence

In the description of the results of these experiments, generally, monocular eye torsion will not be considered as such, but in terms of binocular *cycloversion* and *cyclovergence*. Cycloversion is homonymous torsion. It is the component of torsion that is directed similarly in both eyes. It is calculated as the mean of the torsion of the left and right eyes:

$$\text{cycloversion} = (\text{torsion}_{\text{left eye}} + \text{torsion}_{\text{right eye}})/2$$

Cyclovergence is heteronymous torsion. This is the component of torsion that is directed oppositely in both eyes and is calculated as the difference of the torsion of the left and right eyes:

$$\text{cyclovergence} = \text{torsion}_{\text{left eye}} - \text{torsion}_{\text{right eye}}$$

Grossly, cycloversion is related to image stability; cyclovergence to image correspondence. This may be illustrated as follows. Torsional head movements will result in rotations of the retinal images that are (approximately) equally large in both eyes. Therefore, compensation of these head movement by counter-roll of the eyes also needs to be equally large in the left and right eyes. Hence this compensation requires a cycloversion movement. In contrast, cyclovergence, by definition, affects the relative orientation of both eyes. A change in relative orientation will affect correspondence of the retinal images.

1.3 Knowledge at the start of these investigations

The experiments described in this thesis are not the first that were done on eye torsion. It is by no means the objective of the author to provide a complete history of the research on eye torsion, but in the following paragraph a few investigators will be named whose research was especially important in relation to the present experiments.

The first investigator to be mentioned is Listing. This 19th century physiologist, whose work became known through the reports of Von Helmholtz (1867), predicted that torsional and horizontal/vertical eye rotations are coupled, in a way now known as *Listing's law*. By that time, objective methods of measuring eye torsion were rather inaccurate, but Listing was able to prove his law indirectly, by means of subjective techniques[1].

The next to be mentioned is Brecher, who demonstrated the existence of optically induced cycloversion, i.e. the torsional equivalent of the optokinetic reflex (Brecher, 1934).

Crone, formerly ophthalmology professor in Amsterdam, performed studies on cycloversion and cyclovergence induced by rotating optic stimuli. Using an objective method, he demonstrated the existence of optically induced cyclovergence (Crone and Everhard-Halm, 1975) and confirmed the existence of optically induced cycloversion (Crone, 1975).

Kertesz and Sullivan (1978) made a first attempt to study the dynamic behaviour of cyclovergence. They demonstrated that cyclovergence was sluggish and completed only after several seconds. They confirmed the suggestion, made by Crone, that stimulus size is important: the larger the stimulus, the larger the cyclovergence response.

A better technique for measuring eye torsion

The experimental results of these investigators demonstrated the existence of cyclovergence and cycloversion, but they did not contain a systematic evaluation of the factors that are involved in the control of torsion. Because of this incompleteness, extrapolation to the physiologic role of torsion cannot be made without difficulty. This lack of systematic analysis was due, to a large extent, to the technical difficulties involved in the accurate and reliable measurement of eye torsion. Brecher and Crone measured eye torsion by making photographs of the eyes, at certain time intervals. The temporal resolution of this technique is restricted: a study of rapid changes in eye positions cannot be performed easily. Kertesz, for his experiments, used a suction contact lens with an induction coil in a magnetic field. This technique, which will be discussed more extensively in the next paragraph, was not suited for application in a large number

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[1] One may distinguish *objective* measurement techniques, in which all observations are made by the experimentator and *subjective* techniques, which depend on the observations and subsequent reports of the investigated subject.

of subjects.

In 1963, Robinson published a technique for measuring horizontal, vertical and torsional eye movements. This technique used a suction contact lens, kept in place by means of a small tube that was connected to a vacuum pump. Embedded in this lens were a number of electrical windings (either in a coronal plane, i.e. a plane identical to that of the iris, or in a plane perpendicular to the coronal plane). If the subject, wearing this lens, was positioned in a revolving magnetic field, the induction current from the windings was proportional to the rotation angle of the lens and, thus, of the eye in the magnetic field. Advantages of this technique included a high precision, low noise and high temporal resolution. Drawbacks of this technique were that the lens had to be fitted to each subject individually and that it was rather uncomfortable to wear. In addition, lens slippage could not be avoided. These disadvantages prevented application in large numbers of subjects.

In 1975, Collewijn and co-workers (Collewijn, Van der Mark and Jansen) made a modification to this technique. Instead of a suction contact lens, they used a custom made silicon annulus that did not have to be fitted to each subject individually and, in addition, was more comfortable to wear. The original annuli could measure only horizontal and vertical rotations. Later, Collewijn, Van der Steen, Ferman and Jansen (1985) made an additional modification in order to, also, include Robinson's technique for measuring eye torsion. Since the annuli cover only the sclera of the eye and not the cornea, this technique is referred to as the *scleral coil technique.*

First extensive studies with this technique were performed by Ferman, who worked in Collewijn's lab. He investigated single-eye torsion and the relation between single-eye torsion and head movements. The results from his experiments demonstrated that spontaneous (single eye) variability in torsional direction is much larger than that in horizontal and vertical directions. In addition, torsional head movements were less effectively counterbalanced by compensatory eye movements than horizontal and vertical movements of the head (Ferman, Collewijn, Jansen and Van den Berg, 1987a). This confirms preliminary findings of Collewijn *et al.* (1985). Finally, Ferman objectively demonstrated that Listing's law is indeed largely valid (Ferman, Collewijn and Van den Berg, 1987b).

Relation to present experiments

Ferman investigated single eye torsion and the relation between single eye torsion and head movements. In contrast, the central theme in the experiments described in this thesis is the relation between the torsional movements of the left and right eye. For this purpose, cycloversion and cyclovergence eye movements were investigated under a number of experimental conditions. These conditions will be explained briefly in the next section. For measuring eye movements the accurate scleral coil recording technique of Collewijn was used. The underlying question of all experiments was how torsional movements fulfil their role in maintaining retinal stability and correspondence.

In the same period that these experiments were carried out, other investigators were also active investigating binocular torsion. In this respect, the group of Howard should be mentioned (Howard, 1991; Howard and Zacher, 1991; Cheung and Howard, 1991) and also the experiments of Mok and co-workers (Mok, Ro, Cadera, Crawford and Vilis, 1992) and Enright (1990; 1992). Except for Enright, these investigators also used the scleral coil technique for the measurement of eye positions. The results of their experiments will be discussed in the appropriate chapters of this thesis.

1.4 Description of the experiments and main results

Chapter 2 contains a description of the spontaneous variation of cycloversion and cyclovergence. Spontaneous movements in horizontal and vertical directions have been very well described, along with the consequences of these movements for visual perception (see e.g. Steinman, Cushman and Martins, 1982). For the single-eye condition it has been shown that torsion is much less stable than horizontal and vertical eye positions (Ferman *et al.*, 1987a). Chapter 2 contains a description of torsional variability in position of the two eyes simultaneously, based on measurements of cycloversion and cyclovergence, rather than single-eye torsion. The major results are that spontaneous variability of cyclovergence is much less than that of cycloversion and, in addition, that cyclovergence stability is enhanced by a visual stimulus that provides cues for torsional eye position. These findings suggest that cyclovergence, in contrast to cycloversion, is stabilized through visual feedback and that the tolerance for errors in image correspondence is less than that for image stability.

Chapter 3 deals with some dynamic aspects of cycloversion and cyclovergence. In the experiments described in this chapter, subjects were asked to look at images that oscillated about their centres; the resulting eye torsion was measured. One finding from these experiments is that cycloversion shows a rapid response to changes. It has, under our experimental conditions, no *phase lag*. In contrast, cyclovergence is more sluggish. A second finding is that the percentage of the image motion that is compensated in the motion of the eyes (*gain*) is, at the average, similar for cycloversion and cyclovergence. Finally, findings from these experiments indicate that, within subjects, cyclovergence as well as cycloversion responses are constant and reproducible, but, within subjects, the magnitude of cyclovergence is not related to that of cycloversion. These results suggest that the categorisation of torsion in cycloversion and cyclovergence is not artificial, but that these movement types really represent two different neuro-physiological subsystems, probably with different functions, as was outlined in chapter 2.

In Chapter 4, additional dynamic features are described. Here, attention is focused mainly on the role of image orientation in the induction of cyclovergence and cycloversion. In eliciting cyclovergence, it has been found that oscillating horizontal lines are much more effective than vertical lines (Crone and Everhard-Halm, 1975; Howard, 1991). The findings in this chapter confirm these results. In addition, they demonstrate that a similar phenomenon is present for cycloversion as well. These findings may point at a peculiar aspect of the role of cycloversion and cyclovergence: they may partly serve to keep the horizon aligned on the retina rather than to reduce image motion and promote correspondence only. The findings of chapter 4 confirm those of chapter 3 in that overall responses of cycloversion and cyclovergence have a similar magnitude.

Chapter 5 focuses on yet another aspect of torsion. It describes the relation between horizontal and vertical eye positions on one side and torsion on the other. When one looks around, i.e. when one makes combinations of horizontal and vertical eye movements, the torsional position of the eyes is determined by the exact horizontal and vertical positions. Until now, the nature of the relation between horizontal/vertical positions and torsion was known for the single-eye situation only and formulated in Listing's law (Von Helmholtz, 1867; Ferman *et al.*, 1987b). The model of eye positions that is presented in chapter 5 extends this description in that it gives a prediction of the torsion angles of the two eyes during fixation of targets at any distance. It turns out that the torsion that is being generated forms a compromise between optimal image correspondence and simplicity of oculo-motor control.

Chapter 6 describes the experiments that were performed in response to unanticipated results that were reported in the literature. It was found by Enright (1992) that vertical vergence, i.e. relative movement of the eyes in vertical direction, was coupled to cycloversion. Enright hypothesized that this was due to the specific action of two eye muscles, the *superior oblique muscles*. The findings presented in this chapter confirm the presence of this phenomenon, but they indicate that the cause of the association must be sought in the brain. The association may be a fortuitous result of the fact that torsional and vertical eye movements are generated by the same brain centres.

1.5 Conclusions

The experiments in chapters 2, 3, 4 and 6 are related in that they focus on torsion in absence of horizontal and vertical eye movements. In this condition there are small, spontaneous torsional eye movements: see chapter 2. Larger torsional excursions may be elicited by specific stimuli such as optic patterns that are oscillating in torsional direction (chapters 3 and 4) or by vertical disparities (chapter 6). Another specific stimulus for eye torsion is head oscillation in torsional direction (Collewijn, *et al.*, 1985). However, in the present thesis attention was focused only on torsion elicited by visual stimuli.

From the experiments in these chapters it appears that there are two different torsional regulatory systems, one for cyclovergence and one for cycloversion. Each of these systems has its own characteristics. The cycloversion system responds rapidly to changes (torsional head movements) but has a high natural noise. The cyclovergence system is more sluggish and has a low natural variability. The difference in variability and in response velocity may be related: systems that must be able to respond to rapid changes tend be more unstable than systems that may respond slowly.

These differences in dynamic characteristics suggest different roles of the cycloversion and cyclovergence subsystems: cycloversion is controlled by moment-to-moment corrections whereas errors in cyclovergence eye positions are only corrected slowly. This difference bears a close relation to the nature of the torsional errors: cycloversion must correct for head movement, which occur continuously. In contrast, cyclovergence is only affected by internal positional control errors. Once these are corrected cyclovergence does not need further changes. An interesting finding in this respect is that the gain of cyclovergence tends to decrease with increasing age (chapter 3). This fits in with the picture that once major errors are corrected, further adjustments may be small.

The suggestion, made above, that cyclovergence errors are introduced and corrected on a long time basis only implies that cyclovergence must be stable during horizontal and vertical eye movements. That this is indeed the case is one of the important results of chapter 5. It appears that torsion is coupled to horizontal and vertical eye movements in such a way that retinal correspondence is optimized, in other words, such that cyclovergence errors are minimized. This optimisation is independent of visual feedback: in the experiments in chapter 5 we used point targets that do not offer a reference for eye torsion.

At this stage, it must be emphasized that the torsional excursions of the eyes are very limited. Normal subjects only make (short term) torsional eye movements that do not exceed a few (typically 2 to 4) deg. (After training, torsion may larger: Balliet and Nakayama, 1978).

Despite these limited excursions, it is beyond doubt that knowledge about torsion may help to understand brain functioning. An important question is whether this knowledge also has any clinical relevance. Ophthalmologists frequently observe that the tolerance for torsional errors is large: lesions of the oblique eye muscles, which act especially in torsional direction, frequently remain without apparent consequences for visual perception. This tolerance seems much larger than suggested by the close regulation of, particularly, cyclovergence that we found in these experiments (chapter 2). However, it is important to notice that clear and adequate perception is a complex process that involves many factors. Torsion may be involved in aspects of visual processing that are as yet unacknowledged. The existence of such processing is made likely by the existence of torsional regulatory systems that seem designed to adequately perform functions such providing image stabilisation and image correspondence.

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CHAPTER 2

INSTABILITY OF OCULAR TORSION DURING FIXATION: CYCLOVERGENCE IS MORE STABLE THAN CYCLOVERSION

2.1 Summary

We investigated spontaneous variation of binocular torsion. Variation was expressed as SD of torsional eye positions measured over periods up to 32 s. Subjects viewed a single dot target for periods of 32 seconds. In half of the trials a large random-dot background pattern was superimposed on the dot. The movements of both eyes were measured with scleral induction coils. Spontaneous torsional movements were largely conjugate: cyclovergence was much more stable than cycloversion. This difference was not due to roll head movements. Stability of cyclovergence was improved by the background pattern. Although overall stability (SD of position) of cycloversion was unaffected by a background, the background induced or enhanced a small-amplitude torsional nystagmus in 3 out of 4 subjects. We hypothesize that the difference in stability of cycloversion vs. cyclovergence reflects the greater importance of torsional retinal correspondence, compared to absolute torsional position. In two subjects we found evidence for the existence of cyclophoria, manifested by systematic shifts in cyclovergence caused by the appearance and disappearance of the background.

2.2 Introduction

For unblurred visual perception, retinal images need to be, within certain margins, corresponding and stable on the two retinas. Correspondence prevents the perception of double images and allows full usage of stereopsis. Stability is needed because high retinal image speeds lead to motion-blur. The quality of image stability and correspondence and their effects on perception have been well evaluated for eye movements in horizontal and vertical directions (Westheimer and McKee, 1975; Skavenski, Hansen, Steinman and Winterson, 1979; Steinman and Collewijn, 1980; Steinman, Levinson, Collewijn and Van der Steen, 1985; Erkelens and Collewijn, 1985; Steinman, 1986; Ferman, Collewijn, Jansen and Van den Berg, 1987a).

The effects on perception of eye movements about the torsional axis (the line of sight, see Methods) have been less well investigated. One may expect that the effect of torsional instability is less pronounced because it induces retinal image motion predominantly in the periphery of the visual field. It has indeed been found that the stability of eye torsion is much less than of horizontal and vertical eye position. Ferman *et al.* (1987a) reported SD values of about 0.27 deg for torsion, within periods of fixation, compared to SD values of 6.7 and 8 min arc for horizontal and vertical positions. Approximately similar values were reported by Ott, Seidman and Leigh (1992).

A number of significant aspects is not covered by these previous studies of torsion stability. Firstly, they dealt with monocular torsion. Therefore, they addressed monocular torsional retinal image slip, not torsional retinal correspondence. Secondly, none of those studies contains an evaluation of the role of trial length on the variability of torsion. It has been noticed that drift, i.e., prolonged motion in one direction, is a major constituent of torsional variability (Ferman *et al.*, 1987a) Therefore, variability is likely to critically depend on the length of the sample that is considered.

A first analysis of cyclovergence variability was recently published by Enright (1990), who found that, within periods of fixation, variability of cyclovergence was much smaller than variability of monocular-torsion (SD about 4 min arc for cyclovergence and 17 min arc for monocular torsion). Between fixations, cyclovergence variability amounted to 15 min arc (SD). Due to limitations of Enright's measurement technique, temporal resolution was low.

A third issue that was not evaluated in previous papers is the role of visual feedback in ocular stabilisation. Several reports indicate that both cycloversion and cyclovergence can be elicited by adequate visual stimuli (Crone and Everhard-Halm, 1975; Kertesz, 1983; Howard and Zacher, 1991; Van Rijn, Van der Steen and Collewijn, 1992; 1994). Therefore, one would expect stability to be enhanced when such stimuli are present.

The purpose of the present study was to evaluate the stability of cyclovergence and cycloversion and to compare it to the stability of horizontal and vertical vergence and version. We recorded eye movements with scleral coils, which offer excellent temporal and spatial resolution and we were therefore able to incorporate the element of trial length into the analysis. We also studied the possible role of visual feedback, by using a single dot target with and without a large, structured background.

We found that cyclovergence was more stable than cycloversion and that cyclovergence stability was enhanced by visual feedback. An important side conclusion is that coil slippage was minimal within, but not between, trials. Some preliminary results of these experiments have been presented in abstract form (Van Rijn and Van der Steen, 1992).

2.3 Methods

Subjects

Four human subjects (3 males, 1 female, age range 26 - 57) served in this experiment, after giving informed consent. Three of them were myopic (about -2 to -3 D); one was emmetropic. All subjects had a visual acuity of at least 20/20 in each eye (measured with their own spectacle correction) and normal binocular vision. Stereoacuities were not worse than 60 sec of arc in the TNO test for stereopsis (Medical Workshop, Groningen, The Netherlands). The myopic subjects wore their spectacles during the experiment. All subjects were experienced in wearing scleral coils.

Recording of eye positions and data analysis

Eye rotations were measured with scleral induction coils of the combination type, suitable for measurements about three axes (Robinson, 1963; Ferman *et al.*, 1987a; manufactured by Skalar, Delft, The Netherlands). Angular positions of the coils were measured by a phase-lock technique (Robinson, 1963). The eye position signals were low-pass filtered at 62.5 Hz, digitized at 125 Hz and stored on disk by a minicomputer (DEC PDP 11/73) for off-line analysis.

Prior to each experiment, gains of all channels were calibrated and offsets were zeroed. During this calibration the scleral coils were mounted in a straight-ahead position on a protractor device and placed near the centre of the magnetic field, similar to the position of the eyes during the experiment. The average offset values from each first trial without background in a session were used to correct all data for coil misalignment. This correction was done using a matrix transformation described by Ferman *et al.* (1987a). (We neglected the small adduction of each visual axis (about 1.3 deg) due to the finite distance (145 cm) of the target). In this way we obtained veridical eye positions relative to an earth-fixed coordinate system that were free of cross-coupling artifacts due to coil misalignments. (Note that, as a consequence of this procedure, mean torsion was by definition zero in the first measurement without background.)

All eye rotations were expressed in Fick coordinates (see e.g. Carpenter, 1988). This implies that torsion was expressed as rotation about the line of sight. This was adequate for this experiment, because eye torsion expressed in this way is directly related to retinal image rotation. Alternatively, one may express torsion as rotation about a head-fixed antero-posterior axis (Haustein, 1989; Tweed, Cadera and Vilis, 1990).

The noise levels of the apparatus (measured as standard deviations, SD, of the signals with the coil on the stationary protractor device) were about 0.005 deg in horizontal and vertical directions and 0.01 deg in torsional direction. As the SD of torsional position with the coil mounted on the eye was in most cases at least 0.04 deg., these values were affected by apparatus noise by only about 7% (comparison of variances, see e.g. Glanz, 1987). Therefore we did not correct our data for this apparatus noise.

Protocol and visual stimuli

Subjects were seated with their eyes near the centre of the magnetic field of the eye-position measurement system. Their heads were supported by chin and forehead rests. At 145 cm distance in front of the subject a single red dot (0.24 deg of visual angle in diameter, luminance about 15 cd/m^2) was backprojected on a tangent translucent screen, in a straight-ahead position. Each experiment consisted of 20 trials. Subjects were instructed to fixate the dot continuously during each trial, lasting 32 seconds, without blinking. Successive trials were separated by a pause of approximately 15 seconds, timed by a metronome. The subject was instructed to blink several (typically about 20) times during the first 10 seconds of this pause and to abstain from blinking during the last 5 seconds. At the end of the pause, the subject started the next trial. The rationale behind this instruction was to somehow "reset" torsion and thus obtain a realistic value for inter-trial variability. As later analysis suggested that, with this procedure, inter-trial variability was largely determined by coil-slippage, values for inter-trial variability will not be reported as such. During half of the trials, a square background pattern (width x height: 55 x 52 deg of visual angle) was superimposed upon the dot. This pattern consisted of squares, measuring 0.6 deg of visual angle. The colour of each square (either black or white) was randomised (Julesz, 1965). The brightness of the background was low (about 2 cd/m^2) so as to leave the dot clearly visible. Trials with and without the background pattern were alternated ("background" and "dark"). Sessions started with the background on in subjects 1 and 2, and with the dot only in subjects 3 and 4. Throughout the experiment the room was thoroughly darkened. Therefore, in the absence of the background, there were no visual cues that could provide references for eye torsion.

Data analysis and statistical testing

Prior to analysis, all traces were inspected for the occurrence of blinks. Only 4 trials (2 in each of subjects 2 and 3) needed to be excluded on this ground from further analysis.

After correction for coil-misalignment (see above), vergence and version of all movement directions (i.e. horizontal, vertical and torsional) were calculated for each data sample.

Vergence was defined as left eye position minus right eye position (e.g. cyclovergence = left eye torsion – right eye torsion) and version was the average of the positions of the left and right eyes (hence: cycloversion = [left eye torsion + right eye torsion]/2).

Mean and SD were calculated over all version and vergence values during a 32 s trial. These SD values (SD_{32}) were taken as a measure for intra-trial variability. Data shown in Fig. 2.2 and 2.5 and Table 2.1 are averages of SD_{32} values.

Trend was calculated in each trial as the slope of the linear regression line through all data samples in that particular trial. For torsion, calculation of SD_{32} values was repeated after removal of trends (Table. 2.1).

SD_{32} values were compared in an analysis of variance (ANOVA; factors: subject and background) and in paired t-tests (cyclovergence vs. cycloversion). In order to obtain data with a (pseudo)-normal distribution, all SD values were log-transformed prior to statistical analysis. All reported P-values were calculated assuming two-sided alternative hypotheses.

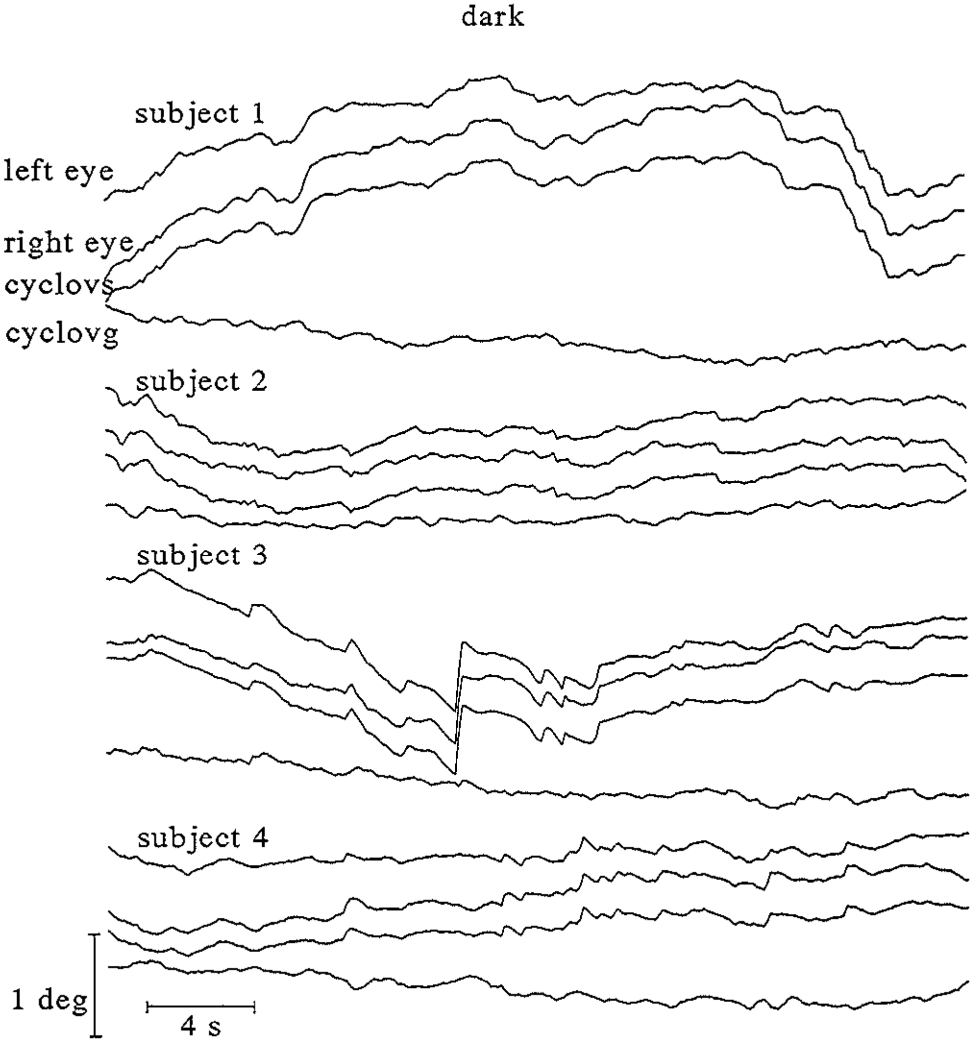
For torsion (cyclovergence and cycloversion) we also calculated the *cumulative SD* as a function of elapsed time t (SD_t) for each trial. The SD_t was calculated over all samples between time 0 and time t within a trial. The data shown in Fig. 2.3 are SD_t values, averaged across trials.

2.4 Results

Intra-trial stability

In all four subjects spontaneous, torsional movements were largely conjugate. Fig. 2.1 shows typical recordings for each subject, with and without background. The traces of torsion of the left and right eyes are largely similar. As a result, the trace of cycloversion largely corresponds to those of the separate eyes, while the trace of cyclovergence is much more stable. In agreement with this, we found that the SD_{32} values for cycloversion were much larger than those of cyclovergence (paired t-test: $P < 0.001$). This is shown in Fig. 2.2, which displays averages of SD_{32} values for each movement direction and subject.

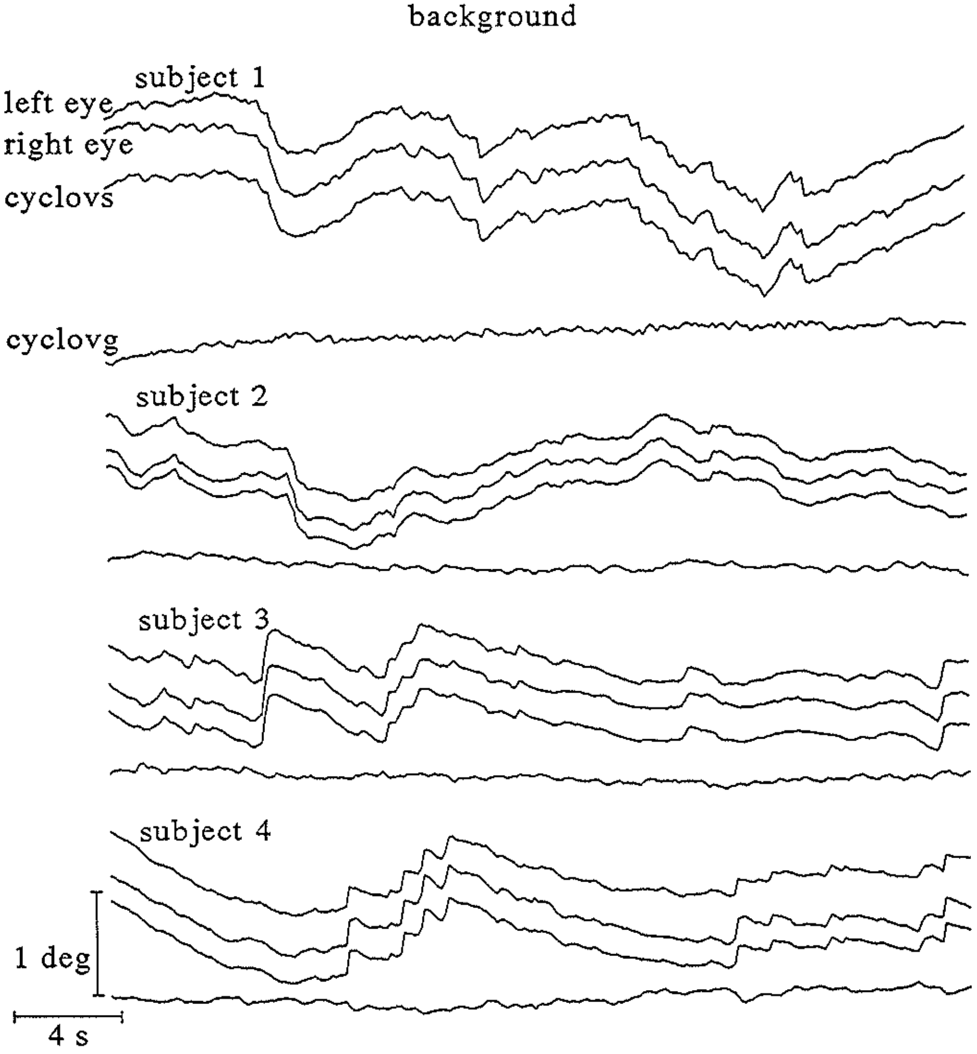
For comparison, Fig. 2.2 also shows SD_{32} values for horizontal and vertical vergence and version eye movements. These values were much lower than those for torsion but also for horizontal and vertical movements, vergence was more stable than version (both P values < 0.001).



↑ and ↗ FIGURE 2.1. Typical recordings of torsion (whole trials, lasting 32 s) of each of the 4 subjects (denoted by numbers on the left). For each subject 4 traces are shown: left eye torsion, right eye torsion, cycloversion (cyclovs) and cyclovergence (cyclovg), without (left panel) and with a Julesz background (right panel). Traces of the individual eyes correspond closely to each other and to the traces of cycloversion. As a result, the cyclovergence traces hardly show any variation.

Effect of background

In all subjects, cyclovergence stability was markedly enhanced by the background (ANOVA: $P < 0.001$). For cycloversion, such an effect was absent ($P = 0.878$).



The effect of the background on torsion stability is demonstrated in Table 2.1 (upper panel: overall variability), which shows overall variability values of cycloversion and cyclovergence, separated according to background condition. There were also effects of the background on stability about the other directions of motion (not illustrated). Horizontal vergence was more stable in the presence of the background ($P = 0.002$), but there was no effect on horizontal version ($P = 0.927$). The presence of a background did not significantly affect vertical vergence ($P = 0.136$) but vertical version was significantly *less* stable with the background ($P = 0.034$). This was due to the induction, by the background, of a small vertical nystagmus, consisting of slow and fast phases, in subjects 2 and 3. In subjects 1, 3 and 4 the background also induced a slight torsional

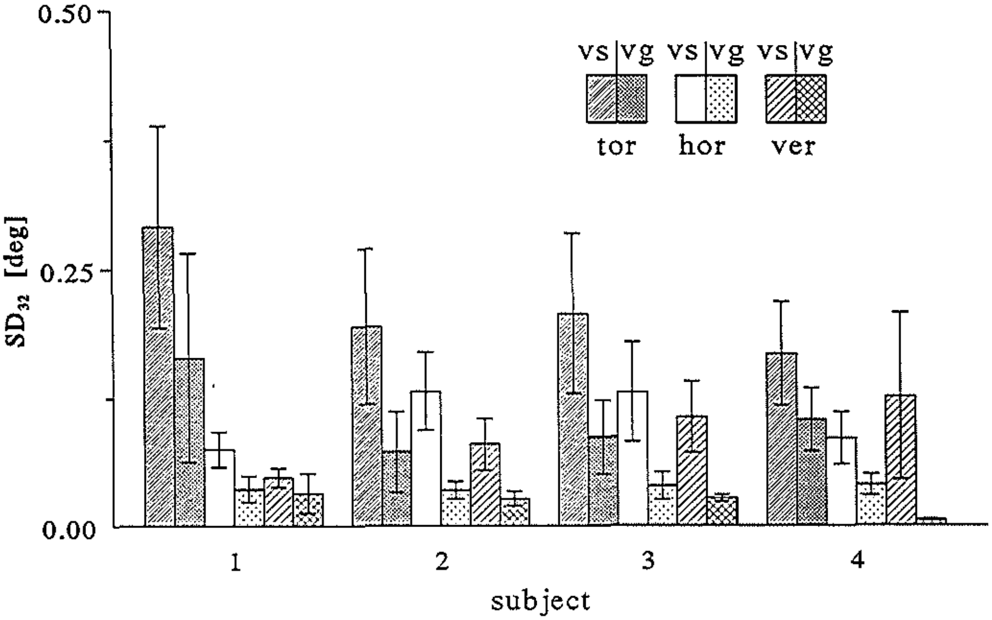


FIGURE 2.2. Variability of version (vs) and vergence (vg) in all three movement directions (horizontal, vertical and torsion), expressed as SD_{32}, i.e. as the SD of all data samples within a 32 seconds trial. Values are expressed as the mean ± SD of the SD_{32}-values of 18 trials in subjects 2 and 3 and of 20 trials in subjects 1 and 4. Stability of vergence was better than that of version in all movement directions. Horizontal and vertical version and vergence were more stable than torsional vergence and version.

(cycloversional) nystagmus (Fig. 2.1). This did not significantly affect SD_{32} values, because the amplitude of the nystagmus was small, compared to the overall variability.

Trends in cycloversion and cyclovergence

Trends in cycloversion and cyclovergence, calculated over the entire 32 s trial length were very small in subjects 2 and 3 and more substantial in subjects 1 and 4. In subject 1, trends in cyclovergence were oppositely directed in trials with background as compared to those without background (dark: 0.007 ± 0.014 deg/s; background: -0.020 ± 0.016 deg/s). These differences in trend values between subsequent trials were systematic. As will be discussed later, this kind of trend may be interpreted as the slow establishment (dark) and the slow correction (background) of a cyclophoria (the major fraction of this cyclophoria was established or corrected *between* trials; see Fig. 2.4 and below). In subject 4, trends were always in the direction of ex-cyclovergence, irrespective of background condition (-0.008 ± 0.008 deg/s and -0.008 ± 0.006 deg/s for dark and background, respectively). As will be discussed later, such a type of trend may *overall variability*

	Dark		Background	
subject	cycloversion	cyclovergence	cycloversion	cyclovergence
1	0.292 ± 0.103	0.247 ± 0.079	0.290 ± 0.097	0.081 ± 0.019
2	0.211 ± 0.090	0.098 ± 0.042	0.178 ± 0.056	0.047 ± 0.009
3	0.216 ± 0.075	0.120 ± 0.027	0.200 ± 0.083	0.061 ± 0.014
4	0.148 ± 0.039	0.115 ± 0.032	0.188 ± 0.055	0.093 ± 0.026
mean	0.217 ± 0.059	0.145 ± 0.069	0.214 ± 0.051	0.071 ± 0.020

variability after trend removal

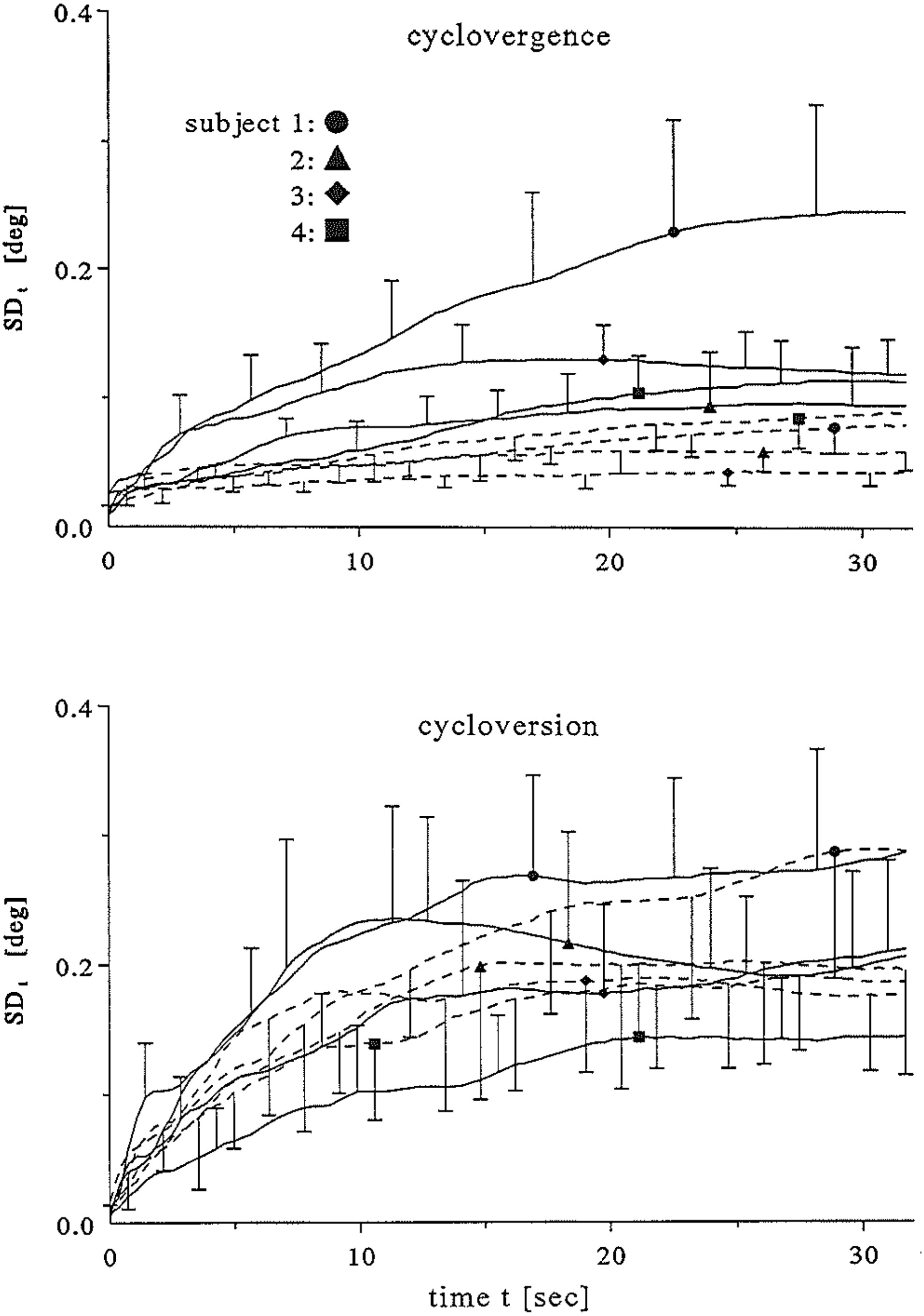
	Dark		Background	
subject	cycloversion	cyclovergence	cycloversion	cyclovergence
1	0.259 ± 0.084	0.105 ± 0.046	0.187 ± 0.051	0.042 ± 0.006
2	0.200 ± 0.089	0.081 ± 0.021	0.158 ± 0.044	0.037 ± 0.006
3	0.177 ± 0.051	0.091 ± 0.021	0.172 ± 0.080	0.053 ± 0.015
4	0.113 ± 0.038	0.060 ± 0.011	0.160 ± 0.039	0.044 ± 0.009
mean	0.187 ± 0.060	0.084 ± 0.019	0.169 ± 0.013	0.044 ± 0.007

TABLE 2.1. Variability of cycloversion and cyclovergence, expressed as SD$_{32}$, separated according to background condition. Cyclovergence was more stable with than without the background; for cycloversion there was no difference. *upper panel:* overall variability; *lower panel:* same after removal of within-trial trends. Cycloversion-cyclovergence differences and differences between background conditions were similar to those found before trend removal. All SD$_{32}$ values are expressed as mean ± SD of 9 trials in subjects 2 and 3 and of 10 trials in subjects 1 and 4.

be related to coil slippage, induced by inter-trial blinking. In subjects 2 and 3, trends were smaller (overall 0.0007 and -0.003 deg/s, respectively) and not systematic in direction or in relation to background condition. After removal of the trends, the differences between cycloversion and cyclovergence stability, as well as the effect of the background on cyclovergence stability, were still present. This is demonstrated in Table 2.1, lower panel, which shows variability values of cycloversion and cyclovergence after trend removal.

Effect of trial length

Fig. 2.3 shows the cumulative SD (SD$_t$, the SD as function of elapsed time within trials). Cyclovergence variability in subjects 2 and 3 reached a constant level after approximately 10 s. In contrast, in subjects 1 and 4, cyclovergence variability continued to rise until approximately 20 s. This continuous rise corresponds to the larger "trend" component of cyclovergence variability that was present in subjects 1 and 4 (see Table


cyclovergence
subject 1: ●
2: ▲
3: ◆
4: ■
SD$_t$ [deg]
0.4
0.2
0.0
0
10
20
30
cycloversion
SD$_t$ [deg]
0.4
0.2
0.0
0
10
20
30
time t [sec]

2.1). Cycloversion variability reached constant levels after 15 to 20 s, irrespective of subject or background condition.

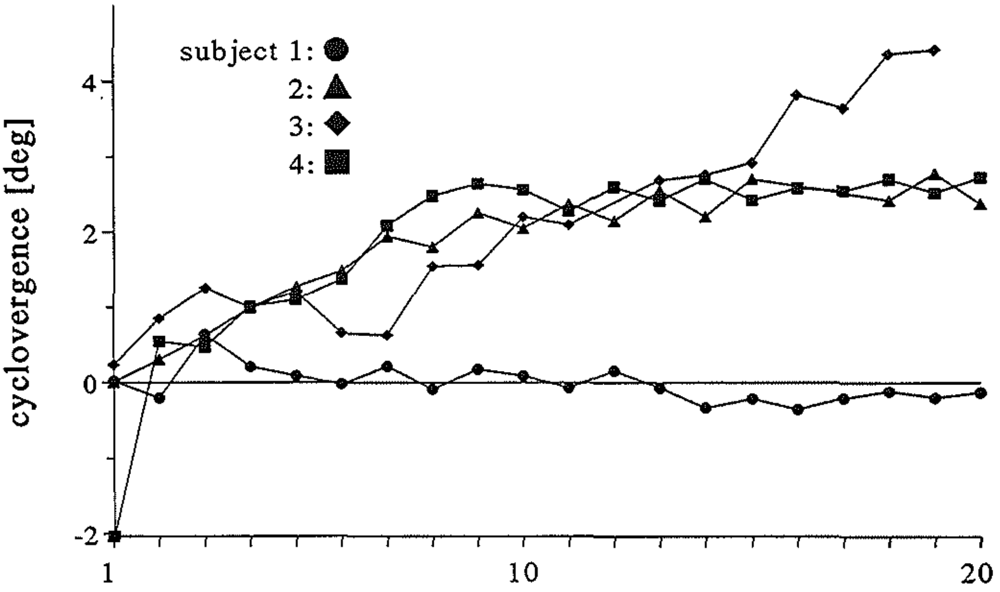
Fig. 2.3 shows once more that cyclovergence was more stable than cycloversion and that cyclovergence stability was enhanced by the background. Notice that the SD_{32} values reported in Fig. 2.2 and Table 2.1 represent the end-points of curves as shown in Fig. 2.3.

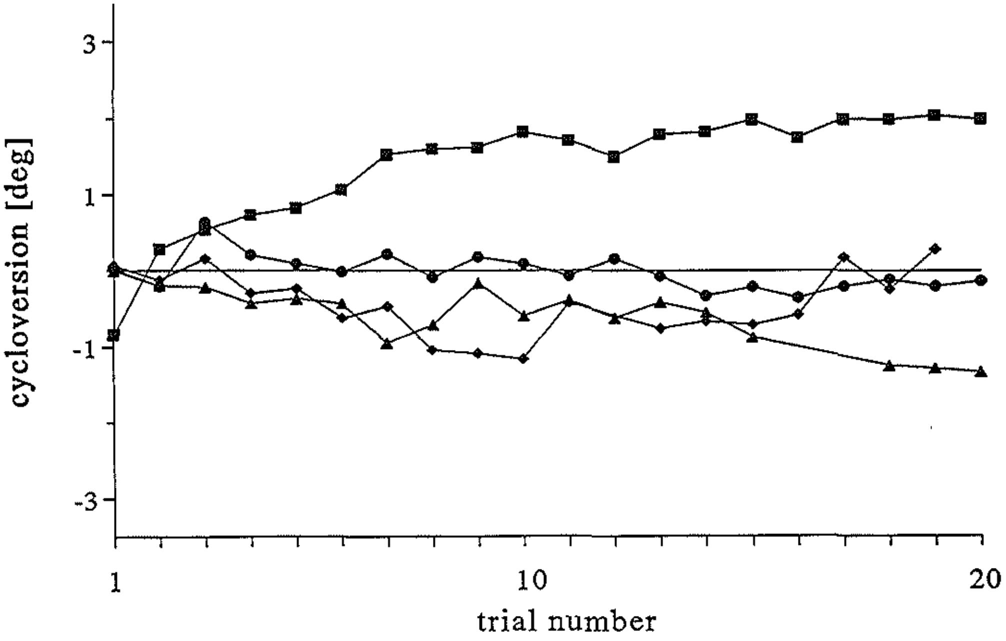
Inter-fixation stability

Fig. 2.4 displays, for each subject, the mean cyclovergence and cycloversion angles during successive trials, as function of trial number. The cyclovergence graphs for subject 1, and to a lesser extent subject 2, display a typical saw-tooth pattern in which cyclovergence alternates systematically between subsequent trials. This reflects the fact that in these two subjects cyclovergence angles with the background were systematically different from those without the background. This is a clear indication of *cyclophoria*. In subject 1, the background induced an in-cyclovergence; in subject 2 an ex-cyclovergence. In addition, in subject 1, who showed the largest cyclophoria (about 2 deg), intra-fixational trends were towards in-cyclovergence with the background and towards ex-cyclovergence without the background. Hence, the establishment and correction of cyclophoria were apparently not completed in the interval between trials. Graphs for cycloversion did not show this background dependent variation in these subjects.

Apart from these systematic changes in cyclovergence elicited by the visual background, all subjects showed, over the course of a whole session, a considerable (several degrees) shift of mean cyclovergence, always in the direction of in-cyclovergence. In our view this "long term" change reflects the effects of coil slippage (see Discussion). Inspection of the traces of separate eyes (not shown) revealed that in subject 4 the in-torsional trend occurred mainly in the left eye; in subject 2 in the right eye and in subjects 1 and 3 in both eyes. This is reflected in Fig 2.4 in long term cyclovergence changes in all subjects, whereas cycloversion only changes in subject 4 and, to a lesser extent, 2. In subjects 1, 2 and 3 there was no relation between these long term cyclovergence changes and either the direction or magnitude of intra-trial trends. In subject 4 the intra-trial cyclovergence drift was opposite to the "long-term" change (see discussion on coil slippage).

← FIGURE 2.3. Cumulative SD within trials separated according to background condition. The SD_t represents the SD, calculated over all samples between time 0 and time t. The *upper panel* shows cyclovergence variability, which was stable after about 10 seconds in subjects 2 and 3. In subjects 1 and 4 there was a continuous rise until about 20-25 seconds. Cycloversion variability, shown in the *lower panel*, reached a plateau after about 15 seconds in all subjects. Values are expressed as mean ± SD of 9 trials in subjects 2 and 3 and of 10 trials in subjects 1 and 4. In the figure, error bars are shown for every 96th data point only.


subject 1: ●
2: ▲
3: ◆
4: ■
cyclovergence [deg]
4
2
0
-2
1
10
20


cycloversion [deg]
3
1
-1
-3
1
10
20
trial number

Eye vs. head stability
Differences in stability between cycloversion and cyclovergence could, in principle, be caused by roll head movements. The torsional VOR has a low gain (on the order of 0.7 or less: Collewijn, Van der Steen, Ferman and Jansen, 1985; Seidman and Leigh, 1989). Therefore, head movements about an antero-posterior axis are compensated only partially by opposite torsional eye movements. In order to exclude roll head movements as a possible source of the cyclovergence-cycloversion stability differences, we repeated the experiment in one subject (subject 1) with one of the coils positioned on the left eye and the other coil mounted on the forehead. Except for this change in position of one coil, the protocol was identical to that of the first experiment. Results are shown in Fig. 2.5. Torsional stability values of the left eye corresponded to those found in the first experiment in this subject. As was pointed out above, this monocular torsional stability was similar to the stability of cycloversion (Fig. 2.2). Stability of the head for roll movements was far better (paired t-test: $P < 0.001$). In fact, roll head movements could account for only about 5% of left eye torsion variability (comparison of variances) and could therefore not explain the cyclovergence-cycloversion differences that we found. In contrast to torsion, for horizontal and vertical movements eye stability was significantly better than head stability (paired t-tests: $P = 0.013$ and $P < 0.001$ for horizontal and vertical movements, respectively).

2.5 Discussion

In the present experiment we investigated to which extent spontaneous torsional eye movements are conjugate, i.e. if there is a difference between cycloversion and cyclovergence (within trial) variability. Also, we looked at the effect of a structured background on this variability, as well as at the effect of trial length. Finally we considered between-trial variability, which led to some conclusions concerning the existence of cyclophoria and concerning coil-on-eye stability.

Cyclovergence vs. cycloversion variability
Previously, only monocular torsional variability has been analyzed with the scleral coil technique. Ferman *et al.* (1987a) and Ott *et al.* (1992) found that torsion was much less stable than horizontal and vertical eye position. Although Ott *et al.* measured the stability

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← FIGURE 2.4. Mean cyclovergence and cycloversion during a trial, as a function of successive trial number, indicating "long-term" changes. Trials with the background are even-numbered in subjects 1 and 2 and odd-numbered in subjects 3 and 4. The *upper panel* shows cyclovergence. In all subjects, over the total duration of the session there was a trend towards in-cyclovergence (positive cyclovergence values). In subjects 1 and 2, values in darkness were systematically different from those with the background (saw-tooth pattern), indicating cyclophoria. The *lower panel* indicates cycloversion, which is positive for clockwise rotations. Long-term trends in cycloversion were generally less than those in cyclovergence.

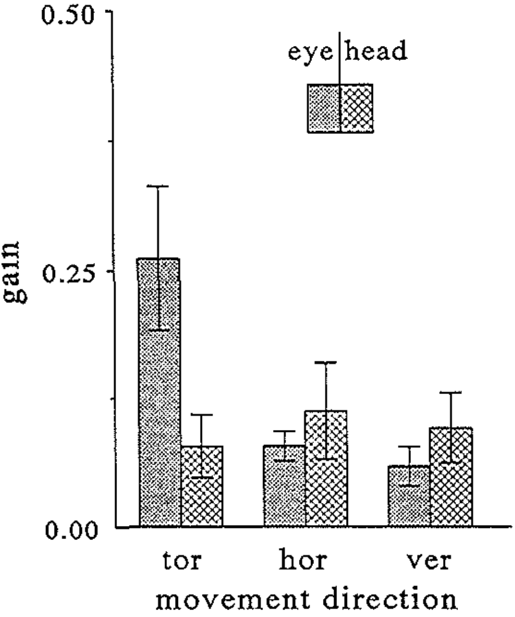

FIGURE 2.5. Variability of the left eye vs. variability of the head, in subject 1, for the three axes of motion. SD_{32} values are calculated as the SD of all samples within a 32 s trial and are expressed as mean ± SD of 20 trials. Torsional stability of the head was much better than that of the eye. However, in horizontal and vertical directions eye stability was better than head stability.

in three dimensions (i.e. including torsion) of both eyes simultaneously, they did not analyze or describe vergence-version differences. Cyclovergence stability has been previously analyzed only with photographic measurement techniques, which offer poor temporal resolution (Enright, 1990, Diamond, Markham and Money, 1990).

The results from our experiment confirm the finding of these previous investigators that torsion is less stable than horizontal and vertical eye position. In addition, we find that, at least within periods of fixation, torsion is largely conjugate. As a result, cycloversion displays much more variation than cyclovergence. This implies that these spontaneous torsional eye movements do not originate from random variation in each eye but have their source in a control mechanism that is common to both eyes. We found a similar version-vergence stability difference for horizontal and vertical positions. This may be the result of voluntary versional movements in the plane of fixation. For this reason it is less surprising than the difference for torsion since, without special training (Balliet and Nakayama, 1978) torsional movements cannot be made at will.

Effect of background

Another finding from the present experiment is that the stability of cyclovergence is much enhanced by a structured visual background. This implies that visual feedback plays an important role in maintaining cyclovergence stability. The lack of improvement by a structured background of stability of cycloversion does not imply that cycloversion is altogether unaffected by visual stimuli. In previous work (Van Rijn *et al.*, 1992; 1994) we demonstrated that gains of cycloversion movements, induced by sinusoidal oscillation about the line of sight of similar stimulus configurations as used in the present experiment, are as high as those of cyclovergence. From these observations we may conclude that dynamic cycloversion responses are superimposed on spontaneous variation. This is in agreement with the considerable drift and variable phase values that we found for dynamic cycloversion, despite good responses (Van Rijn *et al.*, 1992; 1994). Addition of spontaneous variation and dynamic responses is likely to occur in cyclovergence as well. A main difference between the two systems would then be that visual control of cyclovergence contains a marked static component, which maintains correspondence, while visual control of cycloversion is limited to a (modest) dynamic response to changes in orientation. This difference may be explained by the nature of the visual references that are available to the two systems. Cyclovergence is controlled by cyclodisparity, and optimal correspondence will be achieved by negative feedback control that minimizes any cyclodisparity by suitable cyclovergence. Thus, the set-point for cyclovergence is zero cyclodisparity, which is an unambiguous, internal reference, based on the comparison of the two retinal images. A similar set-point for the visual control of cycloversion would require both an absolute estimate of orientation of contours on the retina and knowledge about the objective orientation of the same contours in the world. Given the variety of orientations in the world and the rules of perspective and optical projection, such an estimate is unlikely to be very accurate. Curiously, our results even suggest that a large-field, structured stimulus may *destabilize* version: the background induced or enhanced the manifestation of a small, but distinct vertical nystagmus in 2 out of our 4 subjects, and a cycloversion nystagmus in 3 subjects. A similar result was reported for monocular torsion by Ferman, Collewijn and Van den Berg (1987b).

Effect of trial length

Trial length is an important factor in variability calculations. In this experiment we demonstrated that, as trial length increased, variability, expressed as SD, increased as well, up to a certain maximum. Cycloversion variability reached a plateau after about 15 to 20 seconds. Cyclovergence values were stable after 10 to 20 seconds, depending on the subject. Previous investigators used shorter intervals for measuring torsion stability. Ferman *et al.* (1987a) used 4 second periods; Enright (1990) used periods of 5 seconds, during which photographs were taken at 1 second intervals; Ott *et al.* (1992) used intervals that lasted 15 seconds. SD values based on samples of such relatively short durations should be interpreted with care.

Because SD values had reached a plateau at the end of our 32 s measurements, we feel that these end-values properly represent the total variability.

Perceptual demands

Different noise levels for cyclovergence and cycloversion could reflect different perceptual demands. The most obvious function of cyclovergence is to promote retinal correspondence. The effect of cyclovergence errors on retinal correspondence is more pronounced in the peripheral retina, but there, receptive fields are larger as well. During the viewing of three-dimensional structures, retinal correspondence can never be complete and errors are larger in the peripheral visual fields. Although full correspondence is, thus, impossible, the oculomotor system may still play a role in its optimisation. Arguments for such optimisation have been presented by Van Rijn and Van den Berg (1993).

In theory, cyclovergence errors lead to misperception of (absolute) slant angles (Ogle and Ellerbrock, 1946): a line that is slanted in the sagittal plane, viewed binocularly, gives rise to retinal images that are rotated in opposite directions in the left and right eye. Therefore, errors in cyclovergence could lead to misperception of slant. In contrast, cycloversion instability is expected to disturb the perception of tilt in the frontal plane.

Collewijn, Van der Steen and Van Rijn (1991) investigated thresholds for the perception of dynamic changes in tilt and slant of a single vertical line, oscillated at 0.25 Hz. In the absence of any frame of reference the threshold for tilt perception was about 0.6 deg and for slant perception about 2.4 deg. These values were measured as the threshold values for image cycloversion and cyclovergence, respectively, in the frontal plane, resulting from tilt and slant. They can, therefore, be directly related to ocular cycloversion and cyclovergence stability. Both threshold values are well above the instability values for cycloversion and cyclovergence that we report here and, although we found that cyclovergence is more stable than cycloversion, thresholds for slant perception were highest. This seems to indicate that there is no direct relation between torsional stability of the eyes and the thresholds of either tilt or slant perception.

More indirect effects should, however, also be considered. For example, fluctuations of cyclovergence will induce changes in the horizontal disparity of targets above or below the plane of regard. Such changes will be opposite for targets in the upper and lower visual field, and may therefore disturb the estimation of relative depth of targets that are separated by some vertical distance. This is illustrated by the results of Enright (1990), who found that (static) equidistance estimates of two visual targets that were separated vertically were less accurate than equidistance estimates of targets that were separated horizontally. He demonstrated that the difference was accounted for by cyclovergence variability. He also showed that, when alternating fixation of the targets was allowed, estimates of both horizontally and vertically separated targets was far better and he argued that, therefore, cyclovergence instability does not affect slant perception under natural conditions.

Recently, Ukwade, Bedell and White (1993) investigated patients with torsional congenital nystagmus. They found that tilt discrimination thresholds and, during foveation periods, variability values for torsion were in a similar range: tilt discrimination thresholds ranged from 0.2 to 1.4 deg and torsion variability was about 0.6 deg (SD). They found no differences between patients and controls. From their preliminary results they concluded that there is indeed a relation between tilt perception and variation of torsion.

Cyclophoria

The present experiment clearly demonstrates that in two of our subjects cyclophoria is present: in the absence of torsional visual cues, cyclovergence was systematically different from the situation in which cyclovergence could be controlled by visual feedback. Subject 1 had ex-cyclophoria, i.e. in darkness the upper poles of both eyes rotated outward, while subject 2 had in-cyclophoria. It has been argued that a distinction between cyclotropia and cyclophoria is unjustified since a cyclodeviated eye does not correct itself when the other eye is covered (Von Noorden, 1985). We think that cyclophoria should not be judged on the basis of the position of one eye only, but on the basis of the relative position of the two eyes. Of course this is only possible with techniques that allow measurement of eye positions in closed or covered eyes. This possibility is offered by the scleral coil technique. The other advantage of this technique is its sensitivity; the changes in cyclovergence amounting to about 2 deg in our subject 1 might easily remain unnoticed in clinical observation.

Does the coil slip on the eye?

Fig. 2.4 shows that, over a whole session, there was a change in mean cyclovergence amounting to between 2 and 4 degrees (depending on the subject). This "long-term" change most likely reflects coil slippage in torsional direction. It is implausible that in our subjects there was a real build-up of cyclovergence during the session, particularly since intra-trial cyclovergence was very stable. It is also unlikely that a real "long-term" change could be due to a change in the position of one eye only (as was apparently the case in subjects 2 and 4). Finally, it is not likely that the systematic sequences of corrected and uncorrected cyclophoria, which we found in two subjects, were superimposed on real long-term cyclovergence changes. All these observations point in the direction of coil slippage as the cause. There was usually no relation between these "long-term" changes and within-trial trends (except for subject 4); therefore we think that this coil-slippage occurred mainly, if not solely, during inter-trial blinking periods. Notice that we instructed our subjects to blink quite vigorously between trials. Hence, we may assume that during blinking the coil tends to intort relative to the eye. This seems plausible, because the wire-leads from the coils are positioned in the nasal angle of the eye, and therefore the downward motion of the upper eye lid will exert an inward torque on the coil. This agrees with the long-term trend in all sessions.

In subject 4, intra-fixational trends, however small, were always directed oppositely to this long-term changes. In pilot experiments with combination coils we observed that after *manual* rotation of the coil on the eye, the coil sometimes tended to drift back to its original position. This indicates that coil-slippage has several components: 1) The coil may actually rotate on the surface of the conjunctiva; 2) Rotation of the coil (e.g. by the eye lids) may cause some rotational drag of the conjunctiva on the underlying sclera, and this component may be restored by elastic forces when the external force subsides. This may be the reason of the systematic intra-trial drifts in subject 4. We emphasize that in all subjects, including subject 4, intra-trial trends were too small to account for any of the main effects (i.e. cycloversion vs. cyclovergence stability and effects of background). This is further supported by the fact that coil slippage must affect cyclovergence more than cycloversion: 1) slip is unlikely to be conjugate in any case (compare Fig 2.4a and 2.4b); 2) the major trend of the slip was towards inward rotation in both eyes (Fig. 2.4); 3) cycloversion is calculated as the average torsion, therefore coil slippage of one eye appears at only half its size in cycloversion. For these reasons, if any intra-trial slippage should have occurred, this would have decreased rather than increased the differences that we found between cyclovergence and cycloversion stability.

Photographic techniques do not have this problem of long-term slippage or drift. Enright (1990) reported inter-trial cyclovergence SD values of about 15 min arc, which was larger than the values for intra-trial stability, but far less than the values that would be expected on the basis of our 2 to 4 deg drift.

Role of head movements

Movements of the head in torsional direction are compensated only partially by torsional eye movements since the gain of torsional VOR and torsional OKN is low: the combined torsional VOR and OKN has a gain of less than 0.7 (Collewijn, *et al.*, 1985; Seidman and Leigh, 1989, see also Crawford and Vilis, 1991; Van Rijn *et al.*, 1992; 1994). Since the effect of head roll is similar on both eyes, head movements may induce "artifactual" cycloversion with respect to the earth-fixed frame of reference, the field coils. Artifactual cyclovergence cannot be induced by head movements. The results from our control experiment (see Fig. 2.5) demonstrate that the contribution of roll head movements was very minor. In fact, head movements could only account for about 5% of monocular eye torsion variability (calculated by comparing head variance to eye variance). This is far less than the differences that we found between cycloversion and cyclovergence stability. We may therefore conclude that roll head movements cannot explain this difference. Thus, cycloversion instability was much larger than torsional head instability in our measurement conditions with the head supported. In contrast we found that in horizontal and vertical directions eye stability was better than head stability. This is in agreement with higher gains for VOR and OKN in these movement directions.

Conclusions

In this study we showed that spontaneous ocular torsion is largely conjugate. This implies that cyclovergence is controlled much better than cycloversion. We also showed that visual feedback enhances the stability of cyclovergence, but does not affect cycloversion stability. This cyclovergence/cycloversion difference was not secondary to roll head movements. We hypothesized that these differences reflect demands that are placed on optimisation of torsional retinal correspondence.

2.6 References

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CHAPTER 3

VISUALLY INDUCED CYCLOVERSION AND CYCLOVERGENCE

3.1 Summary

Binocular cyclorotatory (torsional) eye movements in response to visual patterns, which oscillated sinusoidally in the frontal plane, were recorded with scleral induction coils in human subjects. Conjugate cycloversion and disjunctive cyclovergence were directly compared by in-phase and out-of-phase oscillation of the same pattern. Stimulus motion had a frequency of 0.2 Hz and amplitudes of 2-8 deg. Both response types had a similar and low gain (about 0.2 averaged over all subjects). Cycloversion showed no time lag, while cyclovergence lagged by about 600 ms. Non-fusible patterns were effective in eliciting cycloversion, but not cyclovergence. Apart from this, the nature of the pattern (random dots, rows of dots, horizontal or vertical grating, Julesz stereogram or images with a pictorial significance) had only the slightest effect on the magnitude of the responses. This finding will be discussed in relation to the role of cortical neurons sensitive to orientation in the control of torsion.

3.2 Introduction

Cyclorotatory (or torsional) eye movements can be divided into three broad categories: I. Torsion associated with horizontal and vertical (version) eye movements. Listing's law (Von Helmholtz, 1867) predicts that no torsion will occur when horizontal and/or vertical movements are made. This law has been verified by several investigators (Nakayama and Balliet, 1977; Ferman, Collewijn and Van den Berg, 1987b; Tweed, Cadera and Vilis, 1990; Tweed and Vilis, 1990). II. Torsion associated with vergence eye movements (Allen, 1954; Enright, 1980; Nakayama, 1983; Mays, Zhang, Thorstad and Gamlin, 1991). III. Torsion in response to specific stimuli for cyclorotation (visual and/or vestibular), independently of horizontal and vertical movements. The movements that will be considered in this paper belong to the latter category. Cyclorotation in response to vestibular input (counterroll) has been demonstrated initially for static tilt (e.g. Nagel, 1896; Diamond, Markham and Furuya, 1982; Collewijn, Van der Steen, Ferman and Jansen, 1985), but its gain has been consistently found to be low (about 0.1). Dynamic counterroll, in response to head oscillation about a sagittal axis, has a gain which is higher, but still substantially lower than the gain of the horizontal and vertical VOR (Collewijn *et al.*, 1985; Ferman, Collewijn, Jansen and Van den Berg, 1987a; Seidman and Leigh, 1989).

Cyclorotation in response to visual input has a low gain as well. One can distinguish between two types of visually induced cyclorotation, namely cycloversion and cyclovergence. Cycloversion is conjugate cyclorotation in response to tilt of a visual stimulus in the frontal plane. Such tilt can be presented either statically or dynamically. Stimuli that are tilted statically (with respect to the objective vertical) induce at most a slight sustained cyclorotation (about 1 deg in amplitude; Crone, 1975, but see Howard and Templeton, 1964 and Goodenough, Sigman, Oltman, Rosso and Metz, 1979). The response to dynamic tilt (oscillation or rotation at constant velocity of a visual stimulus around the line of sight) is larger. Its gain is highest for low stimulus velocities and decreases with increasing frequency, amplitude and velocity (e.g. Brecher, 1934; Collewijn *et al.*, 1985; Cheung and Howard, 1991).

Cyclovergence is disjunctive cyclorotation in response to static or dynamic cyclodisparity. This response has also been generally found to be incomplete, its gain being lower than 0.6, though improving with increasing stimulus size (Kertesz and Sullivan, 1978). However, recently Howard and Zacher (1991) demonstrated that, with a full-field visual stimulus, cyclovergence gain approached unity when stimulus frequency and amplitude decreased to close to zero. They postulated on this basis that the function of cyclovergence lies in the long-term preservation of retinal correspondence.

Thus, previous studies have clearly demonstrated visually induced cycloversion and cyclovergence, but these have rarely been directly compared in a single study. Therefore it remains unclear in how far these responses have essentially different properties.

Furthermore, it is unclear whether different stimulus attributes contribute differently to the two types of cyclorotation. Demonstrations of slight optostatic cyclorotation (Crone, 1975) suggest that in cycloversion the presence of a vertical contour might be a significant factor, while Crone (1975) also hypothesized that stimulus "complexity" contributes to cyclovergence. On the other hand it has been proposed that vertical disparities contribute more to cyclovergence than horizontal disparities (Crone and Everhard-Halm, 1975), although in this latter study no objective measurements of cyclorotation were performed.

The present study was conducted to answer some of these questions by directly comparing cycloversion and cyclovergence under identical conditions and by comparing the responses to stimulus types that were different with respect to the presence of continuous contours (such as gratings vs. randomly distributed dots). The question whether cyclovergence is a truly binocular process was investigated by comparing the responses to fusible and non-fusible stimulus patterns. We conclude that cycloversion and cyclovergence are essentially different processes. Their gains are similar (and low), but they differ with respect to phase-lag and stimulus dependency. Furthermore, cyclovergence can only be elicited by binocular (fusible) stimuli, contrary to cycloversion. Related data, focusing on the relation between torsional eye movements and slant perception, have been published previously (Collewijn, Van der Steen and Van Rijn, 1991). Some of the present findings have been presented at the 1991 meeting of the European Neuroscience Association in Cambridge.

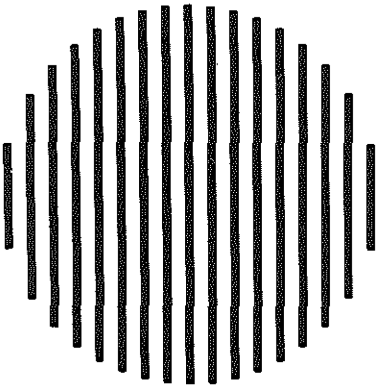
3.3 Methods

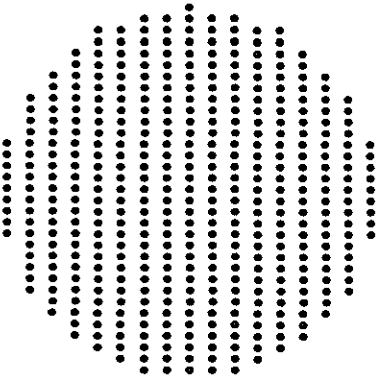
Subjects

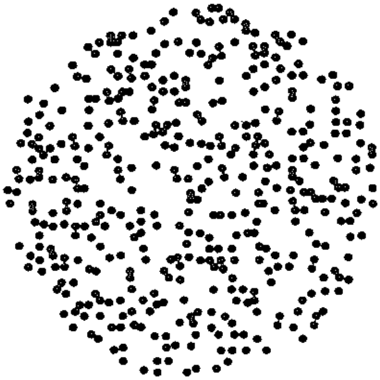
Seven human subjects (1 female, 6 males; age range 28 - 55 year) participated in the experiments. Their visual acuity was measured with a Snellen letter chart, while the subjects wore their normal spectacle correction. Each subject had a visual acuity of at least 1.0 in each eye. All subjects had stereopsis, with a disparity threshold not exceeding 60 sec of arc in the TNO test for stereoscopic vision (Medical Workshop, Groningen, Holland).

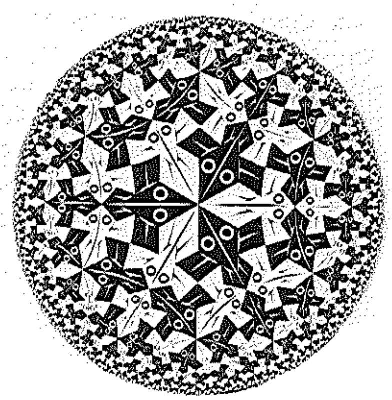
Visual stimuli

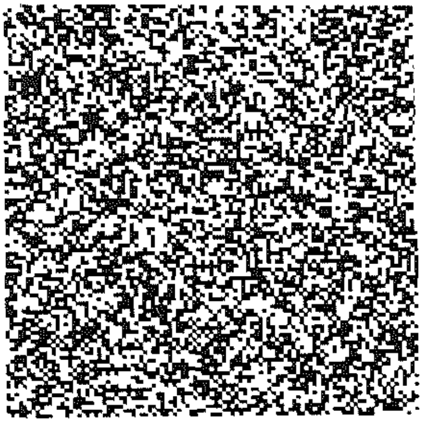
Subjects were seated with their heads supported on a chin rest, at 1.45 m from a translucent screen on which the stimuli were back-projected. The images presented to the left and right eye were generated by two slide-projectors and separated by red and green filters, placed in the light-pathways of the projectors and on goggles. The slides could be rotated around the optical axes of the projectors (in cyclorotation) by galvanometers (General Scanning, Watertown, Massachusetts, model MG350D). In this way, the image for either eye could be rotated independently by computer-generated control signals with an overall bandwidth of about 3 Hz. Throughout the experiments the room was darkened,

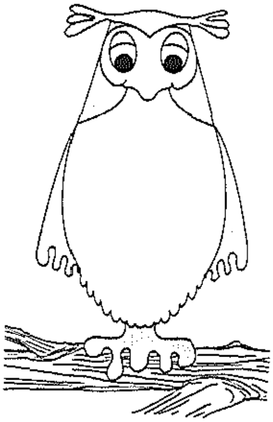












so that the projected stimuli were viewed in the absence of visual references.

The visual stimuli that were used are depicted in Fig. 3.1. The stimuli *grating* (presented horizontally or vertically), *rows of dots* and *random dots* contained progressively less explicit orientation cues. In the latter two patterns, this information was only available by imaginary interpolation of lines between the dots. The distance between the dots was approximately 1.3 deg for the *random dots*; for the *rows of dots* it amounted to 0.28 deg between two vertical dots and 1.1 deg between two horizontal ones. The *Julesz stereogram* was a truly binocular object; it contained a central square (diameter 10 deg) at a crossed disparity of 30 min arc. The *single line* was the most simple oriented stimulus. All circular stimuli, as well as the *single line*, subtended about 28 deg of visual angle. The *Julesz stereogram* measured 29 x 29 deg, the owl had a height of 33 deg and a width of about 20 deg. (Stimuli of about 28 deg were the largest that could be presented on the screen. We considered this large enough, since we were particularly interested in differences between stimulus types.)

In order to investigate the influence of stimulus-correspondence, in one session the *grating* and *Julesz stereogram* were presented with the image to one eye rotated by 90 deg, so that a non-corresponding, non-fusible image was obtained.

Because the previous stimuli all represent rather abstract images, we also included some images with a pictorial meaning: an *owl* caricature (Crone, 1973) and a plate ("Circle limit I") by M.C. Escher (1959) ("*Escher*").

Recording of eye positions

Eye positions were measured in three dimensions with scleral induction coils of the combination-type (supplied by Skalar, Delft, The Netherlands). These annuli contain one coil in the frontal plane for registration of horizontal and vertical movements and another coil, wound effectively in the sagittal plane, for registration of cyclorotation (Robinson, 1963; Ferman et. al., 1987a). Angular positions of the coils were measured with a phase-locked amplitude-detection technique (Robinson, 1963). The analog eye movement signals were low-pass filtered at 62.5 Hz and sampled at 125 Hz. Together with feedback signals from the servo-controlled stimulus cyclorotation angles, these samples were stored on disk by a minicomputer (DEC PDP 11/73), for off-line analysis.

Data analysis

Gain and zero position of each coil were objectively calibrated prior to an experiment, using a protractor device. At the start of an experiment, two calibration measurements were performed to determine the straight-ahead position. A mirror was placed in a frontal

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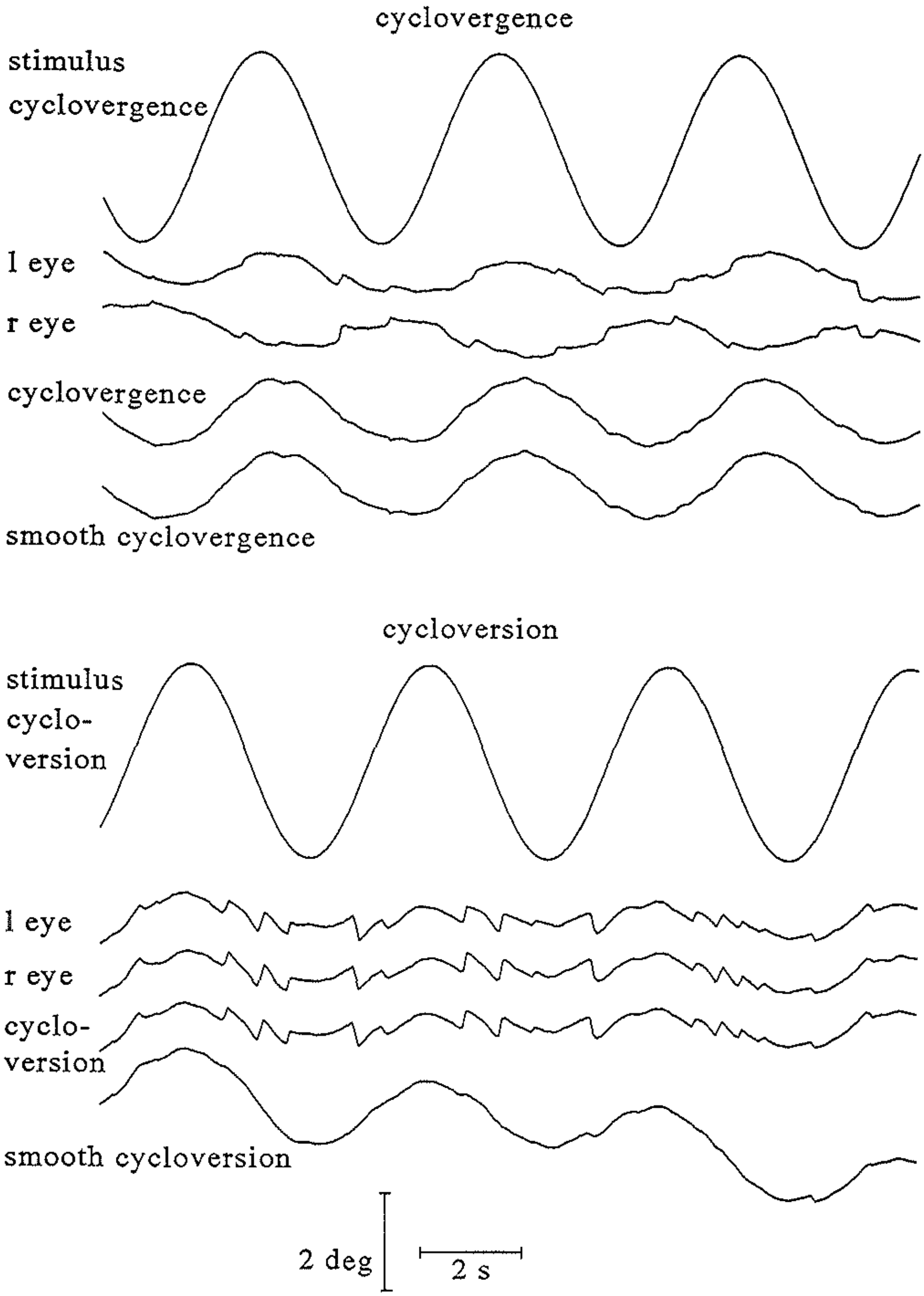
← FIGURE 3.1. The optic stimuli that were used: *gratings, single line, rows of dots, random dots, Escher, Julesz stereogram* and *owl*.


cyclovergence
stimulus cyclovergence
l eye
r eye
cyclovergence
smooth cyclovergence
cycloversion
stimulus cyclo-version
l eye
r eye
cyclo-version
smooth cycloversion
2 deg
2 s

plane, and subjects fixated the centre of the pupil of their own left or right eye monocularly. The steady offset values in this position, representing the misalignment of the coil relative to the line of sight, were used to recalculate all data from original coil-rotation to actual eye-rotation. This was done using a matrix transformation described earlier (Ferman *et al.*, 1987a). In this way we obtained signals that 1) represented the veridical eye position in an earth-fixed (Fick's) coordinate system and 2) were free of cross-coupling between rotational axes due to misalignment of the coil. All signals shown have been corrected with this procedure. After correction, the overall noise-level of the signals was less than 0.1 deg and the remaining cross-talk (due to small distortions of the coil) was less than 5% for vertical deviations to cyclorotation and less than 1% for horizontal deviations to cyclorotation.

Ocular cyclovergence was calculated as left eye cyclorotation minus right eye cyclorotation for each pair of data samples, and ocular cycloversion as the mean of left and right eye cyclorotation. Stimulus cyclovergence was calculated as left minus right stimulus cyclorotation, whereas stimulus cycloversion was taken as one of the stimulus signals, since they were identical for both half-images. Saccades and blink-related eye movements were removed from the cyclovergence and cycloversion signals by a computer program. The correctness of these removals was checked by visual inspection for all measurements. Measurements containing frequent blinks (11% of cyclovergence and 16% of cycloversion measurements) were excluded from further analysis. The data from one subject (HS) were excluded altogether because frequent blinks occurred in nearly all of his measurements.

Eye and stimulus signals were transformed by a fast Fourier routine and the gain and phase of eye cyclovergence relative to stimulus vergence and of eye cycloversion relative to stimulus cycloversion were computed from the components obtained from this transformation.

Procedures

The data-recording for each subject was divided between two sessions. A session consisted of 3 series of 12 measurements and 1 series of 6 measurements. Each series was preceded by 2 calibration measurements. Each measurement lasted 16 seconds. During 6 consecutive measurements, one stimulus pattern was tested under different conditions. The phase shift between left and right image movement was zero deg (for measurement of cycloversion) or 180 deg (for measurement of cyclovergence). The amplitude of stimulus cycloversion was 2, 4 or 8 deg peak-to-peak. For cyclovergence,

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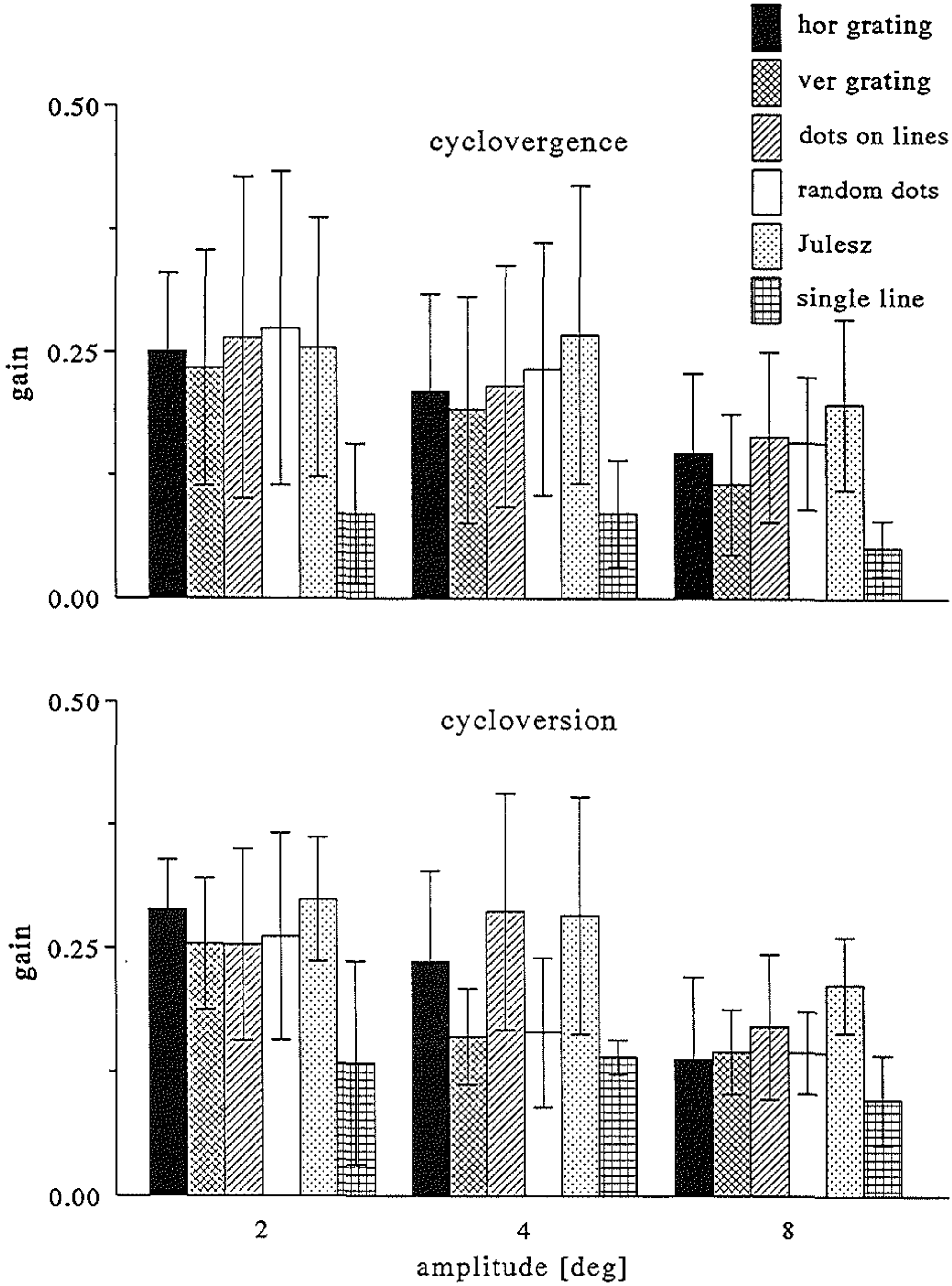
← FIGURE 3.2. Examples of recordings. (subject, AL; stimulus pattern, *Julesz stereogram*; stimulus amplitude, 4 deg). Cyclovergence response: gain 0.330; phase-lag 37 deg. Cycloversion response: gain 0.310; phase-lag 4 deg.


hor grating
ver grating
dots on lines
random dots
Julesz
single line
cyclovergence
cycloversion
gain
0.50
0.25
0.00
gain
0.50
0.25
0.00
2
4
8
amplitude [deg]

the amplitude for each half-image was 1, 2 or 4 deg peak-to-peak, resulting in stimulus cyclodisparities varying between 1, 2 or 4 deg crossed and uncrossed, i.e. a total range of 2, 4 or 8 deg. These 6 conditions were presented in a pseudo-random order. The stimulus frequency was always 0.2 Hz. During the first session, the stimuli of Fig. 3.1 were presented. During the second session, the *grating* was tested at different orientations (horizontal, vertical and crossed), as was the *Julesz stereogram*, presented either in a normal or non-corresponding way.

Subjects were instructed to look at the central part of the stimulus, and to reproduce any perceived movement (slant or tilt) with a two-dimensional joy-stick to keep their attention to the stimulus. No fixation point was presented because selective focal attention to such a point may cause a reduction in gain (Van der Steen, unpublished results).

After each cyclovergence trial the subjects reported whether or not they had been seeing a single, fused image. Loss of fusion was easily noticed as 1) motion at the periphery of the image (When the image was fused, hardly any motion could be detected in cyclovergence trials.) and 2) colour separation: a fused image appeared yellowish. With loss of fusion red and green areas appeared in the periphery of the image.

Statistical procedures

A two-factor analysis of variance was used to determine the role of stimulus pattern and amplitude in cyclovergence and cycloversion separately. Because of missing values (see Data analysis section) we entered the data in the BMDP 5V computer programme (BMDP Statistical Software Inc, Los Angeles, Cal., USA), which uses a maximum-likelihood approach. In this analysis, each subject was treated as one case. Differences between pairs were assessed with the calculated estimates and their standard errors. P-values of differences between pairs were calculated, assuming two-sided alternative hypotheses. Differences between cyclovergence and cycloversion responses were assessed with a three-factor analysis of variance using the same computer program. In order to obtain data with a (pseudo-)normal distribution, gain was log-transformed prior to analysis.

3.4 Results

General

Fig. 3.2 shows examples of recordings obtained from measurements with stimulus

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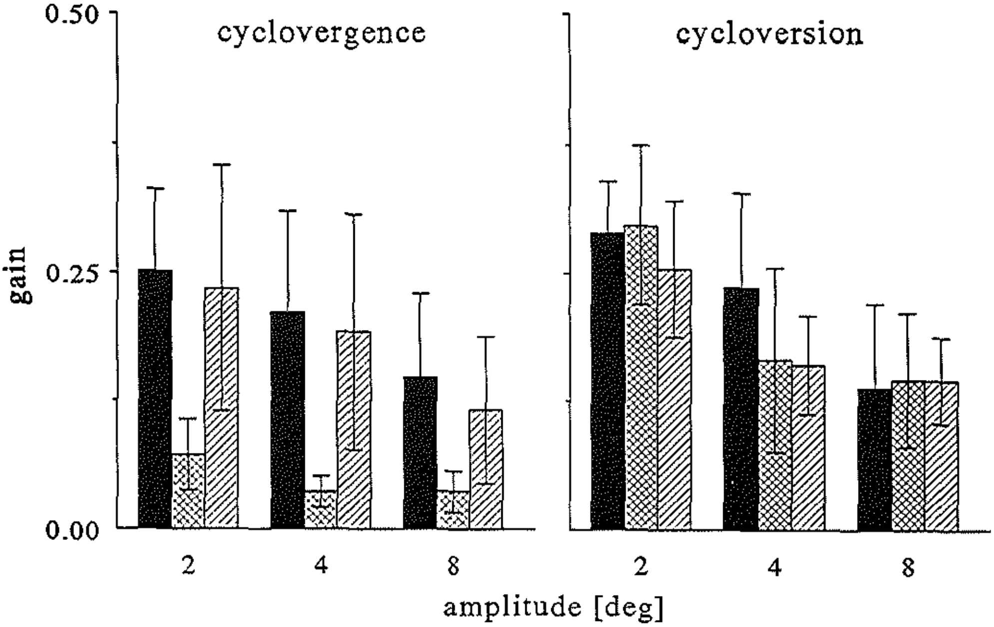
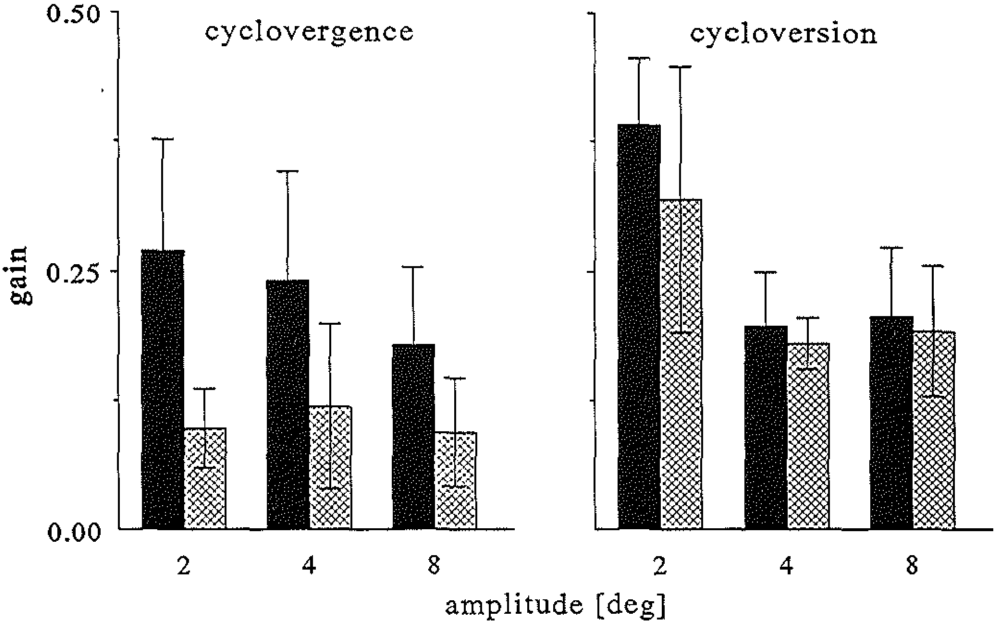
← FIGURE 3.3. Response to stimulus patterns at the amplitudes that were used, displayed as mean ± S.D. averaged across 6 subjects.


0.50
0.25
0.00
gain
cyclovergence
cycloversion
2
4
8
2
4
8
amplitude [deg]


0.50
0.25
0.00
gain
cyclovergence
cycloversion
2
4
8
2
4
8
amplitude [deg]

cyclovergence and cycloversion. In most cases, the recordings of each eye contained frequent saccades, which were largely conjugate. Therefore, saccades were eliminated almost completely by the mere subtraction of the eye signals to obtain cyclovergence. Cycloversion, the mean of the two cyclorotatory eye positions, still contained the saccades, which were removed by the computer routine. For uniformity, both cycloversion and cyclovergence were treated with this routine, which in addition eliminated blink artifacts.

Effects of different stimulus patterns on gain

The gain of the responses to the stimulus patterns *vertical grating, horizontal grating, rows of dots, random dots, Julesz stereogram* and *single line* are shown in Fig. 3.3. The response to the *single line* was lower than the responses to all other stimuli in both cyclovergence and cycloversion trials (gain 0.073 ± 0.053 for cyclovergence and 0.122 ± 0.063 for cycloversion). The size and contour length of this stimulus was much smaller than that of the other stimuli and this lower response confirms the previous literature (Crone and Everhard-Halm, 1975; Kertesz and Sullivan, 1978).

The stimuli other than the *single line*, had about the same size and black-to-white ratio; therefore they were compared in a statistical analysis. The overall gain, averaged across stimulus patterns, amplitudes and subjects (excluding *single line*) was 0.212 ± 0.114 (S.D.) for cyclovergence and 0.220 ± 0.094 for cycloversion. These values were not significantly different (P = 0.13).

To assess the influence of the orientation of image elements, the stimulus patterns *horizontal grating, vertical grating, rows of dots and random dots* were compared in a separate statistical analysis. The results are shown in Table 3.1, which gives the P values without corrections for multiple comparisons. After such a correction by a Bonferoni adjustment, only the outcome of the comparison of *random dots* vs *horizontal grating* changed (i.e. from *significant* to *not significant*).

For cyclovergence, the *vertical grating* elicited a lower response than either the *horizontal grating, random dots* and *rows of dots*. It should be noted that, though significant, these differences were very small. For example, the difference between

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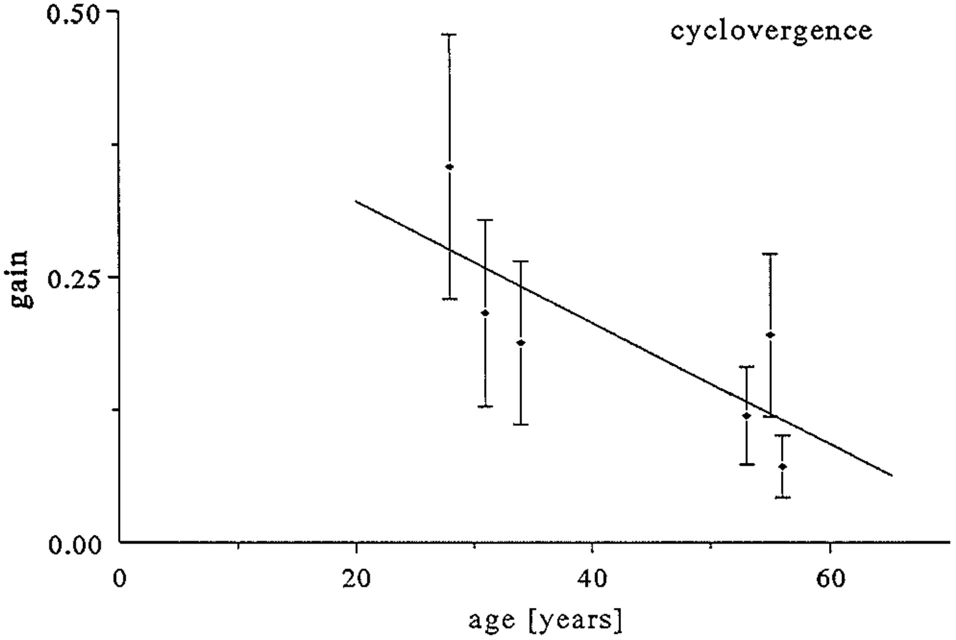
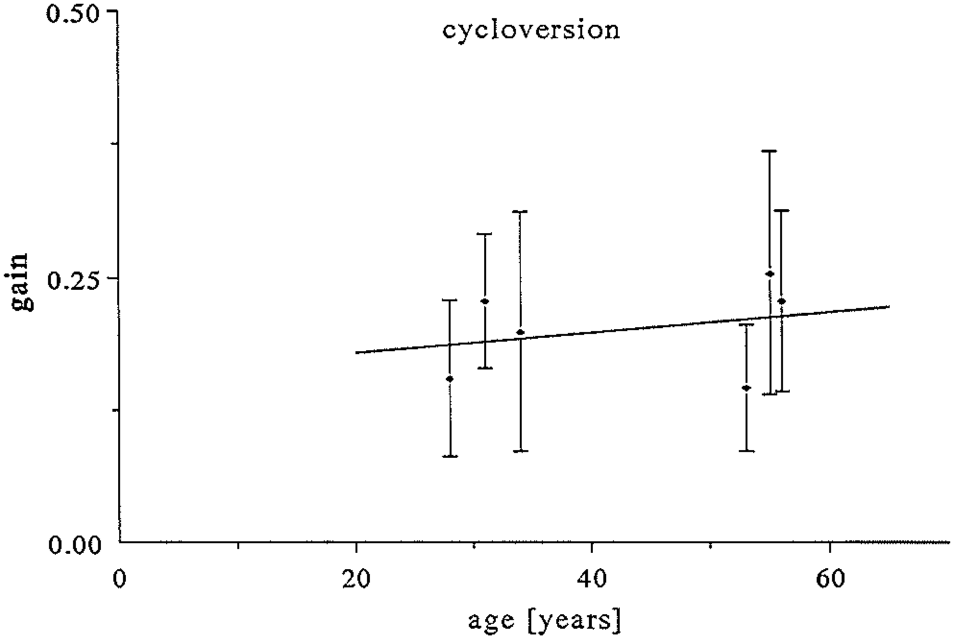
↖ Fig. 3.4. Response to the *grating* at different orientations. Black: horizontal grating, crossed: non-corresponding grating (ie horizontal to one eye and vertical to the other eye), hatched: vertical grating.

← Fig. 3.5. Response to the *Julesz stereogram* displayed in a normal and non-corresponding way. To obtain the non-corresponding stimulus, the Julesz pattern to one eye was rotated over 45 deg with respect to the pattern to the other eye. Black: normal presentation, crossed: non-corresponding presentation.


cyclovergence
gain
0.50
0.25
0.00
0
20
40
60
age [years]


cycloversion
gain
0.50
0.25
0.00
0
20
40
60
age [years]

Stimulus patterns	P-values	
	Cyclovergence	Cycloversion
Horizontal vs. vertical grating	P < 0.0019 (ver. grating smaller)	P < 0.31
Random dots vs. horizontal grating	P < 0.035 (hor. grating smaller)	P < 0.35
Random dots vs. vertical grating	P < 0.0000026 (ver. grating smaller)	P < 0.92
Random dots vs. rows of dots	P < 0.29	P < 0.080
Rows of dots vs. vertical grating	P < 0.00022 (ver. grating smaller)	P < 0.069

TABLE 3.1. Results of statistical analysis of differences between stimulus patterns of Fig. 3.3. Values are not corrected for multiple comparisons.

horizontal grating and *vertical grating* was only 30 % of their mean response. The differences between *random dots* vs *rows of dots* and *random dots* vs *horizontal lines* were not significant. For cycloversion, none of the comparisons revealed a significant difference, as can be seen in Table 3.1.

The stimuli *random dots* and *Julesz stereogram* differed with respect to the shape of the outline (circular versus rectangular) and also in the fact that in the *Julesz stereogram* there was a relative disparity, in such a way that a square appeared in front of the screen. Also, the *Julesz stereogram* contained explicit horizontal and vertical contours, which were absent in the *random dots* pattern. Therefore, one might expect the *Julesz stereogram* to induce cyclorotatory responses with a higher gain than the *random dots* pattern. There was, however, no significant difference between the responses to these stimuli ($P < 0.69$). It should be noted that all subjects continuously perceived the central square of the *Julesz stereogram* in front of the background under all conditions. For cycloversion, the difference between these two patterns was not significant either ($P < 0.11$).

Effect of correspondence of stimulus pattern

Fig. 3.4 shows the results of a comparison of the responses to a *horizontal*, *vertical* and *crossed grating* (i.e. presentation of a *horizontal grating* to one eye and a *vertical grating* to the other eye). In the cyclovergence trials, the response to the *crossed grating* was much lower than the response to corresponding *vertical* or *horizontal grating* ($p < 0.0001$). In cycloversion trials there was no difference between these 3 stimulus patterns.

← FIGURE 3.6. Overall response as function of age of subjects. Responses are displayed as mean ± S.D., averaged across stimulus patterns and amplitudes. Results of the first measurement session only.

The same effect observed for the *crossed grating* was found for the *Julesz stereogram*. In Fig. 3.5 a comparison is shown between the responses to the *Julesz stereogram* presented in a corresponding and non-corresponding way. Also in this case, the cyclovergence response was lower to the non-corresponding presentation ($p < 0.0001$), whereas there was no difference between cycloversion responses.

Effect of pictorial content

The responses to the two pictures with a pictorial content were in the same range as those to the abstract stimuli (for cyclovergence: a gain of 0.199 and 0.234; for cycloversion: a gain of 0.181 and 0.218 for *owl* and *Escher*, respectively).

Differences between subjects

Fig. 3.6 shows the gain as function of age of the subjects. Responses per subject are averaged across stimulus patterns and amplitudes. Stimulus patterns are those of Fig. 3.3 (again excluding the *single line*). It can be seen that there is a strong tendency for cyclovergence to decrease as age increases. However, correlation coefficients were not significant (r for cyclovergence was -0.77 ($P = 0.072$, two tailed); r for cycloversion was 0.283 ($P = 0.59$)). In addition to the large inter-subject differences, there were also considerable intra-subject differences between cycloversion and cyclovergence. Actually, the inter-subject differences were much larger than most of the differences between stimulus patterns, but as the latter differences were consistent among subjects, they were nevertheless significant.

Reproducibility of results

The stimuli *vertical grating* and *Julesz stereogram* were both presented in each of the two different measurement sessions (on different days). The responses were reproducible: the mean difference between the cyclovergence gains was less than 0.5% ($P < 0.86$) and the mean difference between the cycloversion gains was less than 2.7% ($P < 0.44$).

Effect of amplitude

In Fig. 3.7 the mean gain is shown (averaged across stimuli and subjects), for the stimuli *vertical grating, horizontal grating, rows of dots, random dots* and *Julesz stereogram*. Gain decreased with increasing amplitude. As was mentioned before, the difference between cycloversion and cyclovergence was not significant. Also, there was no significant interaction between type of movement (cycloversion vs cyclovergence) and amplitude ($P < 0.92$); thus, it appears that cycloversion and cyclovergence responses decreased in a similar way with increasing amplitude.

Effects on phase

In Fig. 3.8 the phase is shown for the stimuli from Fig. 3.3. Overall phase-lag for cyclovergence was 43 ± 9 deg, equivalent to 597 ± 125 ms, for cycloversion there was a phase-*lead* of 4 ± 13 deg, equivalent to 56 ± 181 ms. For neither cycloversion nor cyclovergence could a significant effect on phase be demonstrated of either stimulus

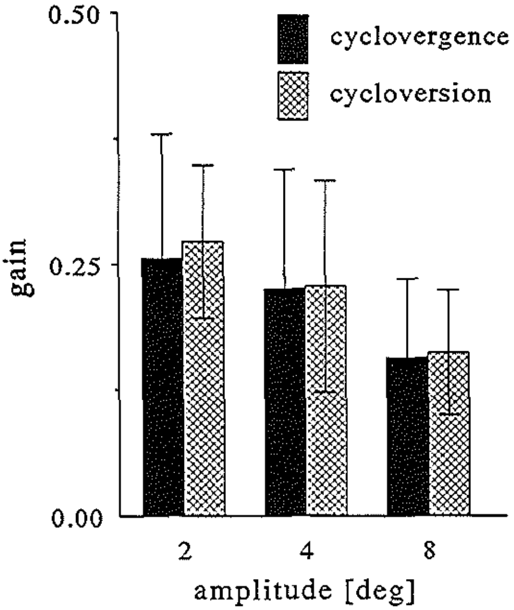


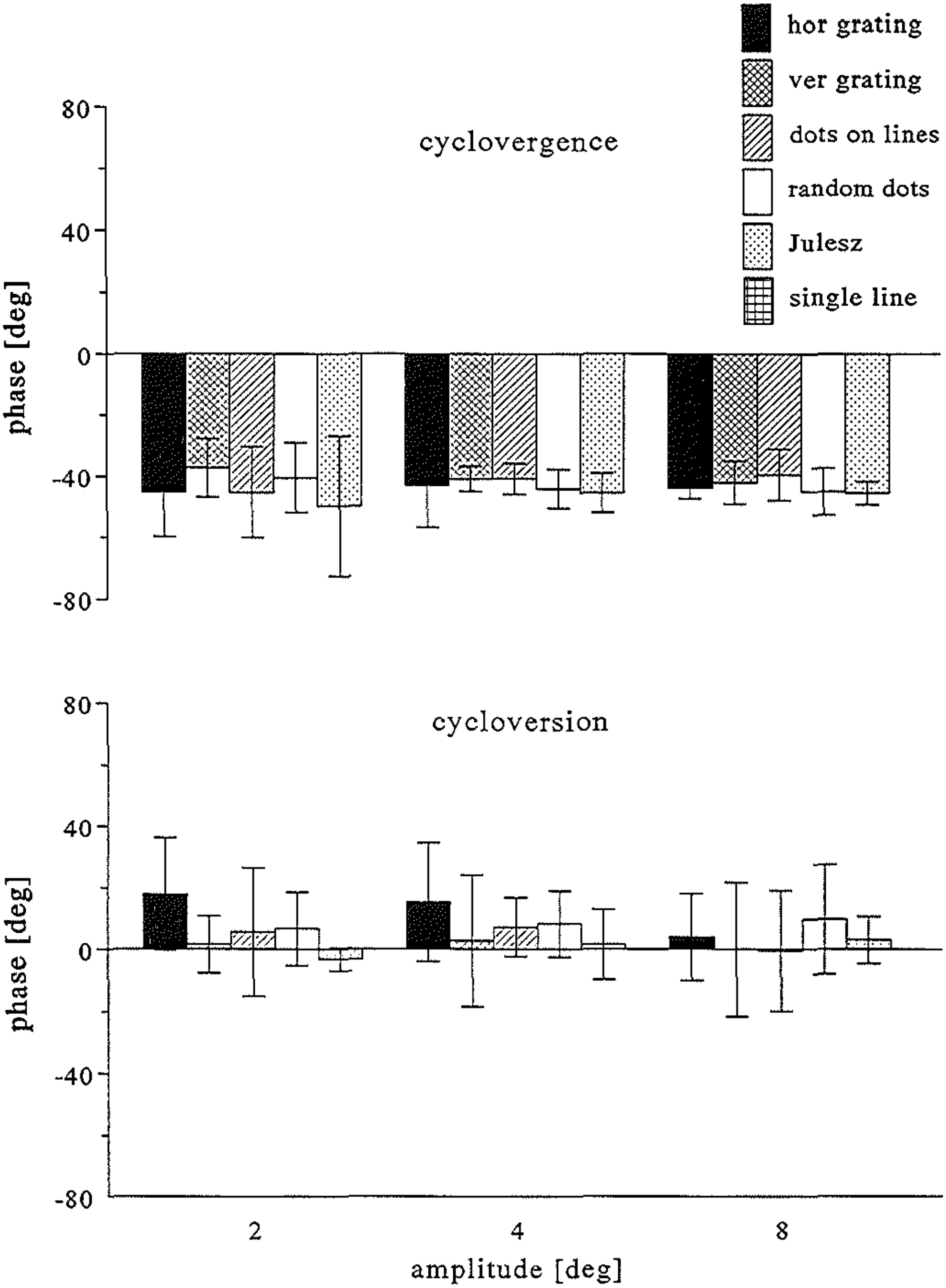
FIGURE 3.7. Overall response for cyclovergence and cycloversion at the amplitudes that were used, displayed as mean ± S.D. averaged across stimulus patterns (those of which the results are displayed in Fig. 3, except for the single line) and subjects. Black: cyclovergence, crossed: cycloversion.

pattern or amplitude. The stimuli that are not shown displayed similar behaviour. It should be noted that only the trials with gain greater than 0.1 were considered in the computation of phase, in order to avoid large effects of noise at low energy-levels. (Therefore, the *single line* is omitted in Fig. 3.8.)

3.5 Discussion

General

The present results confirm that cyclorotatory eye movements compensate partly for optically induced cyclodisparities and lateral tilt motion. Neither cyclovergence nor cycloversion did compensate fully for the presented stimulus cyclorotation. In the case of cyclovergence, this implies that a major part of the disparity was absorbed by central fusional mechanisms, since under our experimental conditions fusion was never lost. Erkelens and Collewijn (1985) have shown that, for visual patterns rather similar to ours, horizontal disparities of 1-2 deg do not interfere with fusion. Of course, our stimuli did not contain foveal disparities. The maximum horizontal disparity, occurring in the


hor grating
ver grating
dots on lines
random dots
Julesz
single line
cyclovergence
cycloversion
phase [deg]
phase [deg]
80
40
0
-40
-80
80
40
0
-40
-80
2
4
8
amplitude [deg]

periphery of the stimulus, amounted in our experiments to approximately arctan[(tan 14)*(tan 8)] = 2 deg at 14 deg above and below the fovea. Therefore, at least in the horizontal dimension, no loss of fusion was to be expected indeed, even if gains were zero. Kertesz (1981) demonstrated that for vertical disparities, fusional amplitudes also lay between 1 and 2 deg, although their experimental conditions differed from ours.

Effect of stimulus pattern
In our data, differences between the responses to various stimulus patterns were very small (except for the *single line*), for cyclovergence as well as cycloversion. However, for cyclovergence the response to the *vertical grating* was slightly but significantly lower than the response to the other stimuli. The direction of this difference is qualitatively in agreement with the (subjective) data of Crone and Everhard-Halm (1975), who attributed this difference to the fact that vertical contours elicit stereoscopic phenomena (slant), and therefore would not demand correction through cyclovergence. Crone and Everhard-Halm (1975) reported that the response to a horizontal grating may be up to 4 times as large as the response to a vertical grating (as estimated from their figure). Recently, Howard (1991) reported that stimuli undergoing horizontal shear elicit cyclovergence which is up to 5 times as big as cyclovergence elicited by stimuli undergoing vertical shear. Although we confirm the direction of this difference, we found it to be much smaller. Actually, the cyclovergence responses to the *horizontal* and *vertical gratings* differed only by about 30%, casting doubt on the hypothesis of Crone and Everhard-Halm (1975) with respect to the origin of this phenomenon. The discrepancy between the results of Howard (1991) and ours is puzzling, since we used rather similar techniques. There were some differences: in stimulus size: Howard used larger stimuli, in correction procedure: we corrected our signals for coil misalignment, and in image separation: we used red and green filters to obtain dichoptic image presentation. It seems unlikely that any of these factors could explain the difference in results. This issue will be further elaborated in Van Rijn, Van der Steen and Collewijn, 1994.

In our experiments, the representation of orientation information did not affect either cyclovergence or cycloversion responses. At the cortical (area 17) level, cells have been described whose response is a function of the orientation of the visual stimulus (Hubel and Wiesel, 1959). The spatial frequency-selectivity of these cells is a measure for their receptive field size. This aspect has been investigated in the macaque monkey by De Valois, Albrecht and Thorell (1982). They showed that the majority of foveal and parafoveal (3-5 deg peripherally) simple and complex cells responded maximally to a spatial frequency of more than 5 cycles per degree, implying a receptive field size of no more than 12 min arc. This population of cells included the orientation-selective ones. It

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← FIGURE 3.8. Phases to stimulus patterns at the amplitudes that were used, displayed as mean ± S.D. averaged across 6 subjects. Negative values imply phase lags.

appears that, because of larger inter-dot distances, our *random dots* and *rows of dots* stimuli would excite only a minority of those cells. Since we did not find a difference in response between *random dots*, *horizontal grating* or *rows of dots*, we might assume that the orientation-tuned cells in area 17 are not involved in either cycloversion or cyclovergence. We cannot, however, exclude the possibility that cells with lower spatial frequencies are involved preferentially.

Differences between cyclovergence and cycloversion

We also demonstrated that correspondence of image elements presented to both eyes is a necessary condition for a cyclovergence response to occur at all. The trials including the *crossed grating* and *non-corresponding Julesz stereogram* demonstrate clearly that out-of-phase cyclorotation of retinal images *per se* does not induce cyclovergence. From this result the conclusion emerges that cyclovergence is a truly binocular process, controlled by cyclodisparity occurring in a pattern that otherwise corresponds for both eyes. Such correspondence is not important in the control of cycloversion. Also, there is a marked difference in phase-lag: cyclovergence shows a phase-lag, contrary to cycloversion, even though the gain was similar. Finally, within subjects there is no relation between cyclovergence response and cycloversion response. This suggests that cyclovergence and cycloversion are mediated through different central mechanisms.

Comparison with previous data on cyclovergence

Our data reveal cyclovergence responses that are in the same range as those of static responses, reported previously. Crone and Everhard-Halm (1975) presented subjects with static cyclodisparities up to 7 deg, using a stimulus pattern subtending 25 deg of visual angle. They found a cyclovergence response of up to 5 deg. Sullivan and Kertesz (1978) presented subjects with static cyclodisparities of between 2 and 10 deg, and found that cyclovergence compensated for 48 to 75% of these disparities. The stimulus pattern consisted of horizontally segmented lines, and had a size of 50 deg. Kertesz and Sullivan (1978) demonstrated that the cyclovergence response decreased when the stimulus size decreased. When the stimulus diameter was 30 deg (comparable to ours), in-cyclorotation compensated for 66% of the 5 deg (step-) stimulus disparity, whereas ex-cyclorotation compensated 32%. Our results, when compared with these static data, suggest that cyclovergence responses are not enhanced, but rather reduced, under dynamic conditions. This fits in well with the recent results of Howard and Zacher (1991), who reported that the gain of cyclovergence decreased both with increasing frequency and increasing stimulus amplitude. The smaller magnitude of our responses compared to those of Howard and Zacher (1991) at comparable frequency and amplitude (gain 0.6 - 0.7 at 0.2 Hz and 2 deg of amplitude) may be due to the fact that they used a larger stimulus. In the experiments of Howard and Zacher (1991), the two younger subjects had higher cyclovergence responses than the one older subject. We demonstrate that there is indeed a strong (albeit not significant) tendency for cyclovergence responses to decrease as age increases.

Comparison with previous data on cycloversion
In the literature, several reports are available on optostatic tilt. From these it appears that optostatic tilt is either absent (Howard and Templeton, 1964), virtually absent (Goodenough *et al.*, 1979) or amounts at most to 1 deg (Crone, 1975; optostatic tilt in response to a grating, tilted at various angles). Collewijn *et al.*, (1985) found that visual information hardly enhances cyclorotation (counterroll) in response to static head tilt. The dynamic cycloversion responses that we found are, on the whole, much larger than the static responses in the experiments discussed above. It seems feasible that cycloversion, contrary to cyclovergence, is a typical velocity response, with a low optimal velocity. This would be in agreement with results of Cheung and Howard (1991), who measured monocular cyclorotation (other eye patched) in response to an oscillating, near full-field visual stimulus. They found that the gain decreased when either stimulus frequency increased from 0.2 to 2 Hz, or stimulus amplitude increased from 10 to 80 deg. It should be noted that they calculated gain as slow-phase velocity relative to stimulus velocity. Cheung and Howard (1991) found a phase-lag of about zero at stimulus frequencies of 0.2 and 0.5 Hz, about 73 deg at 1 Hz, and about 90 deg at 1.5 and 2 Hz. Our measurements at 0.2 Hz confirm their results.

Comparison with horizontal eye movements
Erkelens and Collewijn (1985) measured horizontal vergence and version responses to in-phase and out-of-phase oscillations of the half-images of a Julesz stereogram similar to ours. For the nearest corresponding stimulus motion parameters (0.25 Hz, amplitude up to 5 deg) we may contrast their horizontal responses to our cyclorotatory responses. Horizontal version has a much higher gain (close to unity) than cycloversion, but for both types of version phase-lag is nearly zero. Horizontal vergence also has a much higher gain (about 0.9) than cyclovergence, while the phase-lag of horizontal vergence could be accounted for by a constant time lag of 210 ms (independent of frequency and amplitude). Furthermore, horizontal vergence, like cyclovergence is abolished by the use of non-fusible half-images. We may conclude that, for similar stimulus conditions, cyclorotatory responses are much smaller than horizontal responses, and that cyclovergence is further characterized by a long delay (about 600 ms).

3.6 References

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CHAPTER 4

EYE TORSION ELICITED BY OSCILLATING GRATINGS: EFFECTS OF ORIENTATION, WAVELENGTH AND STATIONARY CONTOURS

4.1 Summary

We studied binocular cyclorotatory (torsional) eye movements in response to gratings that oscillated sinusoidally in a frontal plane. The square-wave gratings viewed by the right and left eye were presented and controlled separately to induce cycloversion and cyclovergence by oscillation in phase and out of phase. Eye movements were recorded with scleral induction coils. Stimulus oscillation frequency ranged from 0.125 to 1 Hz and the wavelength of the gratings ranged from 0.92 to 25.75 deg of visual angle.

Cycloversion and cyclovergence gain were, on average, comparable in magnitude and decreased with increasing oscillation frequency. There was no consistent effect of the wavelength on the magnitude of the responses. In general, responses were considerably higher to gratings that were oriented horizontally than to those oriented vertically. This anisotropy was present both in cycloversion and cyclovergence. It was enhanced in a larger sized stimulus and by presenting stationary, orthogonal contours (mimicking a

"shear" movement), but it was not consistently influenced by wavelength. Cyclovergence showed a phase lag, which increased with oscillation frequency but which was independent of wavelength. In contrast, cycloversion showed a slight phase lead which was independent of both oscillation frequency and wavelength.

4.2 Introduction

Binocular cyclorotatory eye movements in response to visual stimuli can be divided into conjugate cycloversion and disjunctive cyclovergence movements, analogous to horizontal and vertical version and vergence movements. During cycloversion the eyes rotate in parallel about their optical axes; during cyclovergence they rotate in opposite directions. The most obvious potential function of cyclovergence is to promote retinal correspondence. Dynamic cycloversion has been considered (since Brecher, 1934) as a torsional optokinetic response, serving to reduce retinal slip in torsional direction. In this paper we describe some properties of cyclovergence and cycloversion induced by visual gratings.

The first goal of this study was to resolve apparent controversies between our previous results and reports from other investigators. Several authors have reported that stimuli containing horizontal contours elicit much larger cyclovergence responses than stimuli containing vertical contours (Crone and Everhard-Halm, 1975; Howard, 1991). In a previous experiment (Van Rijn, Van der Steen and Collewijn, 1992b) we also found such a difference, but it was much smaller than reported by the other authors, cited above. Our measurement technique and that of Howard were similar, but some differences existed between his and our experiments. The size and density of the stimulus gratings were different and, moreover, Howard used composite ('shear') stimuli, i.e., stimuli consisting of both a horizontal and a vertical grating, of which only one was oscillating. In the present study we investigated the effect of stimulus configuration on the anisotropy of cyclovergence responses. In addition we investigated whether a similar anisotropy was present for cycloversion.

To further elucidate the function and mechanism of cyclovergence and cycloversion, these response types were compared with each other under various stimulus conditions. We recently reported that at an oscillation frequency of 0.2 Hz the magnitude of the responses of cycloversion and cyclovergence, averaged across subjects, were about similar (Van Rijn *et al.*, 1992b). Within subjects, however, these response magnitudes were uncorrelated. Also, cyclovergence and cycloversion showed marked differences in phase lag. Both cycloversion and cyclovergence have been previously studied as a function of oscillation frequency of the stimulus (cycloversion: Cheung and Howard (1991); cyclovergence: Howard and Zacher (1991)), but because of differences in experimental conditions, the results of most prior work cannot be directly compared. We investigated, as a second goal of this study, the behaviour of cyclovergence and cycloversion in one single experiment and at various (low) stimulus oscillation frequencies.

We found that the predominance of the response to horizontal contours over that to vertical contours occurred in cycloversion as well as cyclovergence. The magnitude of this anisotropy was influenced both by the presence of stationary contours and by the size of the stimulus but was unaffected by stimulus wavelength or oscillation frequency.

4.3 Methods

Subjects
Eight human subjects (1 female, 7 males; age range 23 - 55 year) participated in the experiments after giving informed consent. Their visual acuity, measured with a Snellen letter chart while the subjects wore their normal spectacle correction, was at least 1.0 in each eye. All subjects had normal binocular vision, with stereoacuities not worse than 60 sec of arc in the TNO test for stereopsis (Medical Workshop, Groningen, The Netherlands).

Recording of eye-positions
The experimental design was identical to that described in Van Rijn *et al.* (1992b). Subjects were seated at the centre of the magnetic field of a scleral-coil eye-position recording system. Their heads were supported by a chin rest. Visual stimuli were backprojected on a translucent, frontoparallel screen at 145 cm distance. The images were presented dichoptically. Separation of the images for the left and right eye was achieved by red and green filters mounted on the slide projectors and on goggles. The slides could be oscillated about their optical axes by galvanometers (General Scanning, Watertown, MA), either in phase (cycloversion) or out of phase (cyclovergence). Eye movements were measured in three dimensions (horizontal, vertical and torsion) by scleral induction coils of the combination type (Skalar, Delft, The Netherlands). Eye-position signals were low-pass filtered at a cut-off frequency of 62.5 Hz, sampled at 125 Hz and stored by a minicomputer for off-line analysis, together with the position signals of the galvanometers. All data were corrected for coil misalignment by a matrix transformation, in order to obtain eye-positions relative to an earth-fixed (Fick type) coordinate system and free of cross-coupling artifacts (Ferman, Collewijn, Jansen and Van den Berg, 1987). Cyclovergence and cycloversion were calculated for each sample as the difference between and the mean of the torsional positions of the left and right eyes. Saccades and blink-related eye movements were removed from the cyclovergence and cycloversion tracings by a computer routine. This routine removed all sections of the tracings in which eye velocity exceeded 15 deg/s. The correctness of this procedure was verified in all measurements by visual inspection. After removal of trends and biasses, eye and stimulus signals were Fast Fourier transformed and gain and phase were calculated from the components. Gain was computed as eye cyclovergence/stimulus

cyclovergence and eye cycloversion/stimulus cycloversion in cyclovergence and cycloversion trials, respectively. Of all the raw data, a fraction of 5.6% was rejected because of excessive blinks. If in any trial the gain was below 0.05, we did not calculate the phase lag to avoid unreliable results at low energy levels. For this reason, 20.0% of the (non-rejected) trials from the first experiment (see further) and 9.8% of those from the second experiment were excluded from phase calculations.

Visual stimuli

Gratings were oscillated in cyclovergence or cycloversion and presented to the subject in a number of configurations (Fig. 4.1). The order of presentation of these configurations was pseudo-random.

In *Experiment I*, the following configurations were tested: 1) the orientation of the oscillating grating was either horizontal or vertical; 2) the frequency of oscillation was 0.125, 0.25, 0.5 or 1 Hz.; 3) in half of the measurements a secondary, stationary grating, oriented orthogonally to the average orientation of the moving grating was superimposed, to mimic a shear-stimulus as used by Howard (1991). All possible combinations of these conditions were presented to each subject, both for cyclovergence and for cycloversion. The wavelength of the grating, i.e. the width of one black plus one white bar, was 3.00 deg of visual angle. Seven subjects participated in this experiment.

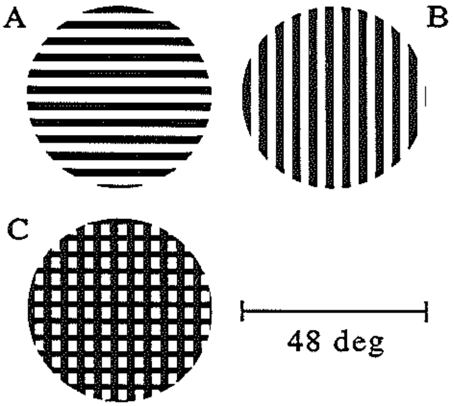


FIGURE 4.1. The stimulus patterns that were used in these experiments were isolated horizontal (A) or vertical (B) gratings or a combination of both (C). Of these combined ("composite") gratings either the horizontal or the vertical component was oscillating. In experiment I all stimulus types were used. In experiment II only isolated gratings were used, of which the wavelength was varied. (Wavelength was the width of one black + one white bar in deg of visual angle.)

In *Experiment II*, we elaborated on the role of wavelength. In this experiment we used gratings with wavelengths of 0.92, 2.03, 4.73, 8.65, 16,55 or 25.75 deg of visual angle. All gratings were presented horizontally as well as vertically. The oscillation frequency was always 0.25 Hz and no stationary gratings were superimposed. This experiment was performed on 4 subjects. Each condition was measured twice within each subject.

In both experiments, the shape of the stimulus was circular with a diameter of 48 deg of visual angle. The amplitude of the stimulus cyclovergence or cycloversion was 4 deg peak to peak. Hence in the cyclovergence measurements the amplitude of the stimulus oscillation to each eye was half of that in the cycloversion measurements.

Statistical procedures

Data were analyzed with univariate analysis of variance, linear regression, paired or grouped t-tests or a Student-Newman-Keuls test, using the SPSS-PC statistical software. Reported P-values of t-tests were calculated assuming two-sided alternative hypotheses. In order to normalize data distributions, all gain values were log-transformed prior to statistical testing.

4.4 Results

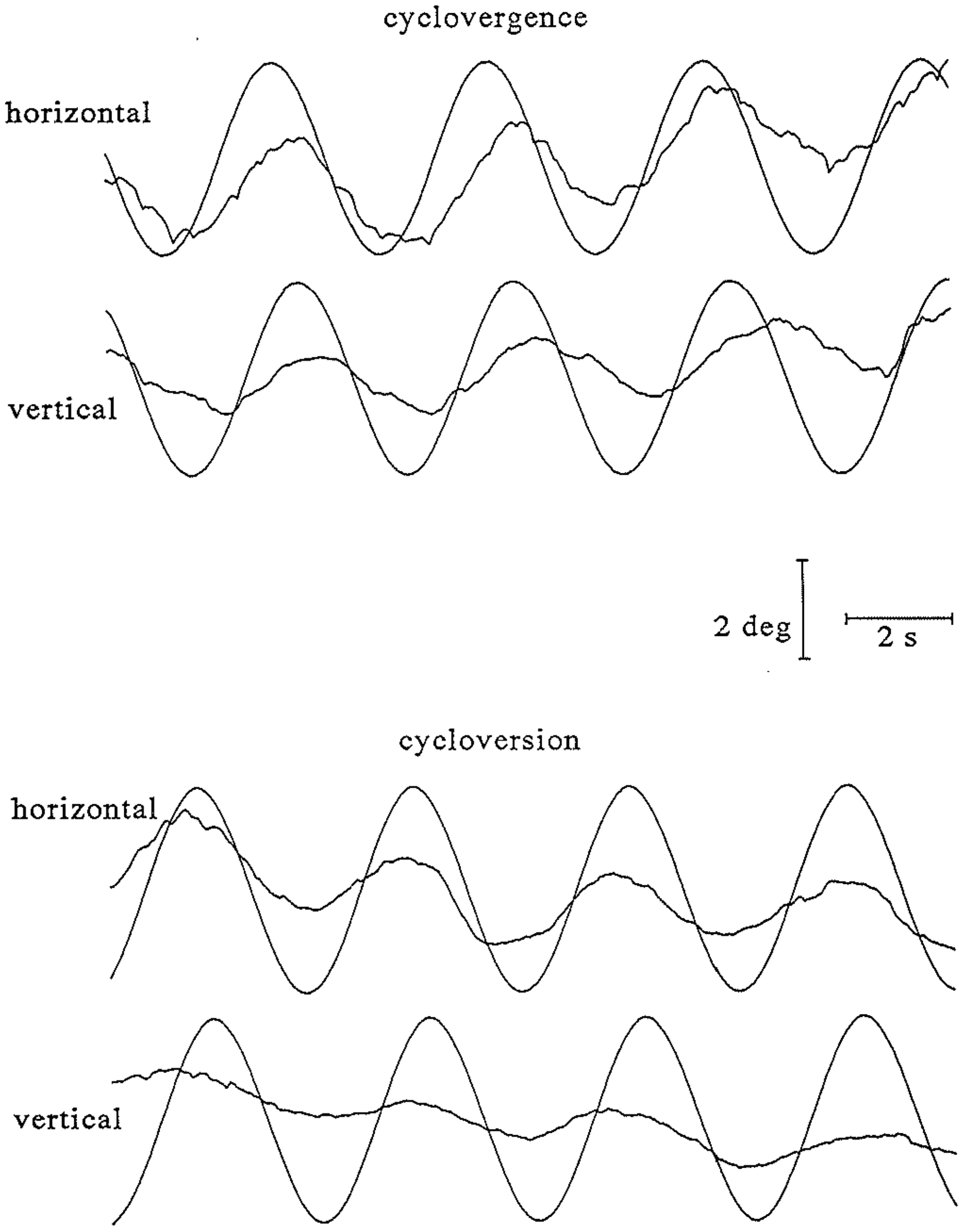
Experiment I

Effects of oscillation frequency, moving-grating orientation and presence of a stationary grating

All stimuli elicited distinct sinusoidal cyclorotation responses under all conditions. Horizontal moving gratings always elicited higher responses than vertical moving gratings and, in general, the addition of a stationary grating inhibited the responses. Gain decreased with increasing oscillation frequency. Fig. 4.2 shows some examples of recordings obtained from cyclovergence and cycloversion measurements, illustrating the effect of grating orientation.

Fig. 4.3 shows an overall gain and phase diagram for the first experiment. The upper panels show gain for cyclovergence (left) and cycloversion (right).

We compared the response magnitudes (gain) in an analysis of variance. Both for cyclovergence and cycloversion, the effects of the orientation of the moving grating, the presence of an additional stationary grating, and the oscillation frequency were all significant. All interactions between these factors were not significant, except for the interaction between the orientation of the moving grating and the presence of a stationary grating. In order to further examine the effects of these latter two factors, we compared the four groups formed by the different combinations of the factors "orientation of the


cyclovergence
horizontal
vertical
2 deg
2 s
cycloversion
horizontal
vertical

moving grating" and "presence of a stationary grating", in a Student-Newman-Keuls test (significance level 0.05). The differences between the responses to the moving horizontal grating and to the moving vertical grating were significant, both in the presence and in absence of a stationary grating. A stationary grating inhibited the response significantly only when a stationary horizontal grating was added to an oscillating vertical grating; the addition of a stationary vertical grating to an oscillating horizontal grating did not significantly inhibit the response. Thus, oscillating horizontal gratings elicited higher responses than oscillating vertical gratings; also, stationary horizontal gratings were more effective in inhibiting responses. This applied to both cyclovergence and cycloversion.

The lower panels in Fig 4.3 show the phase lags of the responses in Experiment I. Cyclovergence, in general, showed a phase lag (overall mean ± SD: -62.6 ± 31.0 deg). For three stimulus conditions (isolated horizontal grating, isolated vertical grating, horizontal moving + vertical stationary grating) the relations between phase lag and stimulus frequency were similar. For these conditions phase lag increased with increasing frequency, until a plateau was reached at about -90 deg. The fourth stimulus (vertical moving + horizontal stationary) displayed large variability. This may well be due to a low gain in response to this stimulus, which cause phase measurements to be less reliable.

For cycloversion, phase was generally close to zero, but variability was large (overall mean ± SD: 7.2 ± 52.5 deg), despite the fact that the overall gain was of similar magnitude as that of cyclovergence (see Discussion).

Experiment II

Effects of wavelength of grating

Fig. 4.4 shows the results of Experiment II, in which the wavelength of the grating was varied. No stationary gratings were added in this experiment. The wavelength of the stimulus pattern had no systematic effect on either cyclovergence or cycloversion. This was confirmed by linear regression; the slope of the regression line was not significantly different from zero for either cycloversion or cyclovergence, irrespective whether the gratings were horizontal or vertical. (All slopes were smaller than 0.031 log unit/deg of wavelength; all P-values were greater than 0.12.) The rather high standard deviations in Fig. 4.4 were mainly due to differences between subjects. Experiment II further confirmed the difference between responses to horizontal and vertical gratings that was

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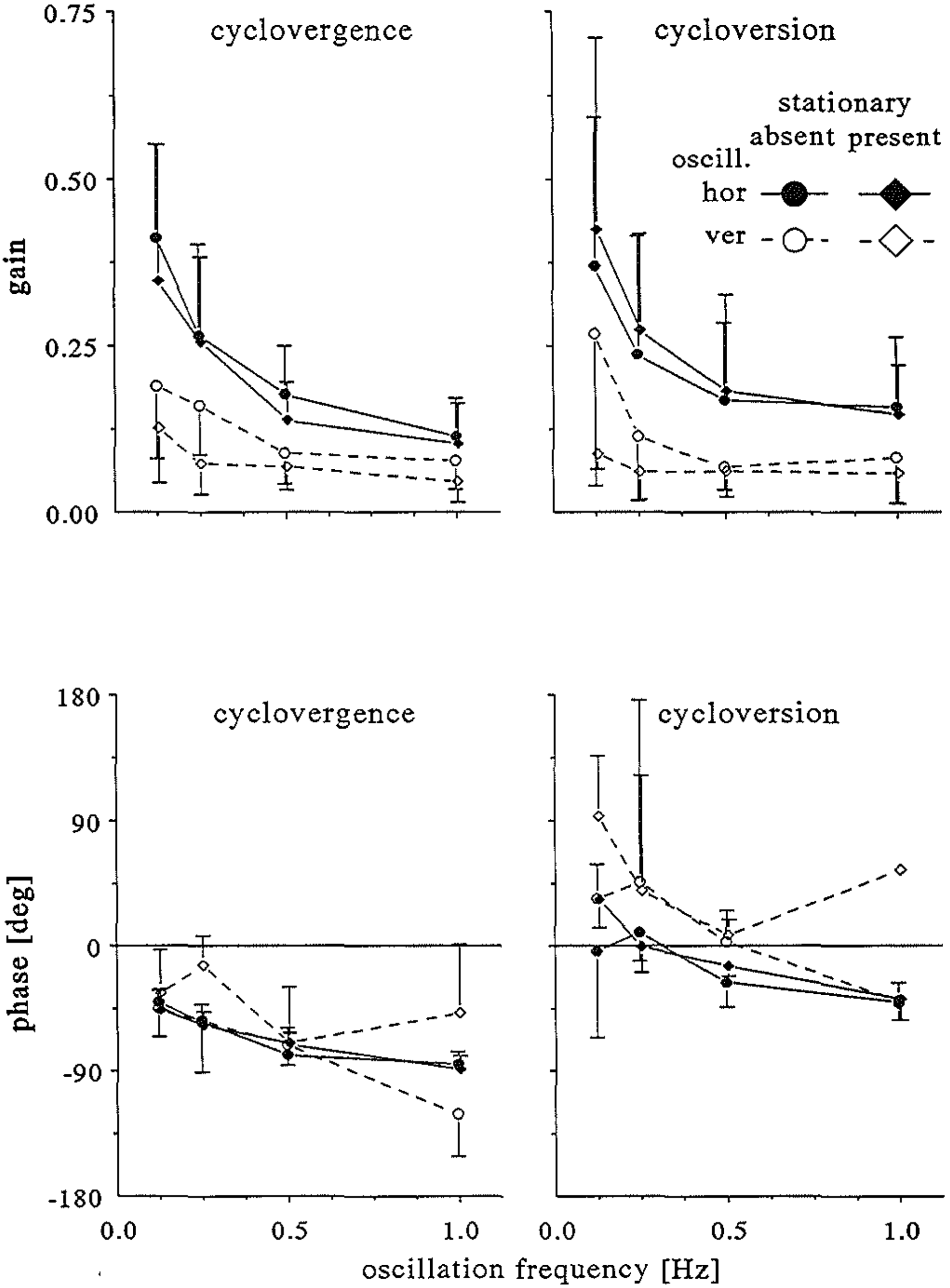
← FIGURE 4.2. Examples of tracings obtained in experiment I, demonstrating the effect of grating orientation. Isolated gratings, either horizontal or vertical, were presented at an oscillation frequency of 0.25 Hz. The regular sine wave reflects the (cyclovergence or cycloversion) movement of the stimulus. Gain values of cyclovergence were 0.50 and 0.30; gain values of cycloversion were 0.27 and 0.16, for horizontal and vertical gratings, respectively.


0.75
0.50
0.25
0.00
gain
cyclovergence
cycloversion
stationary
absent
present
oscill.
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ver
180
90
0
-90
-180
phase [deg]
cyclovergence
cycloversion
0.0
0.5
1.0
0.0
0.5
1.0
oscillation frequency [Hz]

found in Experiment I.

The phase lags of the responses in Experiment II are shown in Fig. 4.4, lower panels. They are in agreement with the cyclovergence - cycloversion difference found in Experiment I. Average phase showed a lag for cyclovergence (-52.1 ± 14.5 deg for horizontal and -66.6 ± 41.9 deg for vertical gratings), while a lead was found for cycloversion (24.0 ± 27.2 deg for horizontal and 29.0 ± 40.7 deg for vertical gratings). The difference between the phase of the responses to horizontal and vertical gratings was significant for cyclovergence ($P = 0.027$), but not for cycloversion ($P = 0.306$). There was no effect of stimulus wavelength on phase of either cyclovergence or cycloversion, either for horizontal or for vertical gratings (all P-values greater than 0.38).

Role of movement type

In the analysis, up to this point, cyclovergence and cycloversion were treated separately. At this stage we compare overall response magnitudes of cyclovergence and cycloversion.

In the first experiment gain values of cyclovergence and cycloversion were not significantly different (paired t-test: $P = 0.693$). In the second experiment, gain values were slightly lower for cyclovergence than cycloversion, particularly so for the vertical grating. The differences were, however, small (gain for horizontal gratings: 0.247 ± 0.153 and 0.253 ± 0.067; for vertical gratings: 0.127 ± 0.082 and 0.163 ± 0.066 for cyclovergence and cycloversion, respectively).

In both experiment I and II analysis of variance showed no interaction between the effects of movement type (cyclovergence or cycloversion) and either oscillation frequency (experiment I, $P = 0.360$) or presence of stationary contours (experiment II, $P = 0.610$). Hence the decrease in gain due to the addition of stationary contours was similar for cyclovergence and cycloversion. The interaction between movement type and subject was significant in both experiments ($P = 0.003$). This means that cyclovergence-cycloversion differences were subject dependent. It confirms our earlier observations

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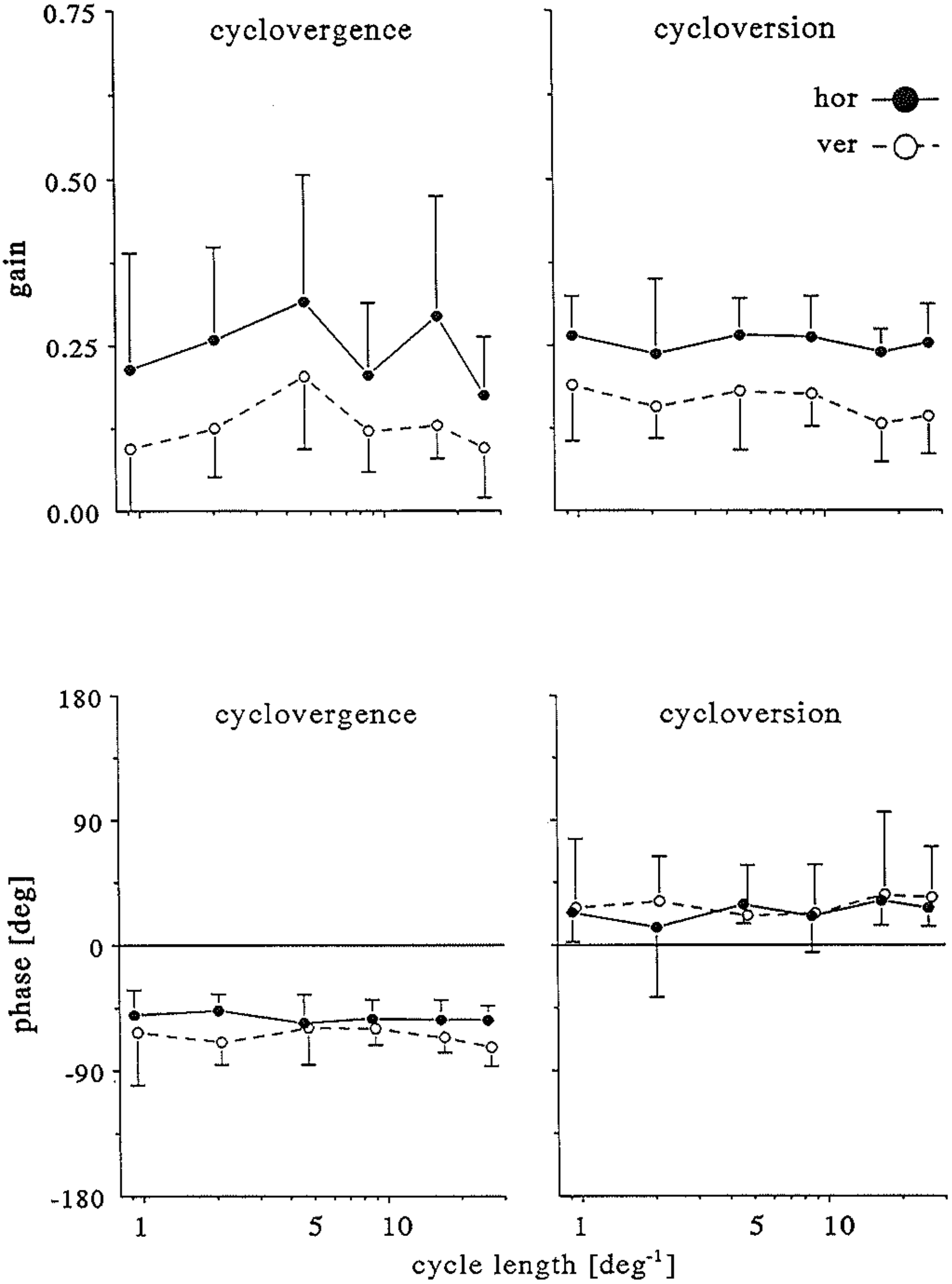
← FIGURE 4.3. Gain and phase of cyclovergence and cycloversion as function of oscillation frequency of the stimulus. Plotted are the means ± SD's of all 7 subjects. The *gain* of both cyclovergence and cycloversion (upper panels) was higher in response to horizontal gratings than in response to vertical gratings. Both response types were inhibited when a horizontal stationary grating was added to an oscillating vertical grating, but the inhibition of the response to an oscillating horizontal grating by the addition of a stationary vertical grating was not significant. Decrease in gain with increasing stimulus oscillation frequency was similar for both movement types. The *phases* of cyclovergence and cycloversion (lower panels) were clearly different. In general, cyclovergence displayed a phase lag which depended on the oscillation frequency of the stimulus. Cycloversion displayed a slight phase lead which was unrelated to oscillation frequency. Markers have been plotted slightly left and right to the actual oscillation frequencies to enhance readability of the figure.


cyclovergence
cycloversion
hor
ver
gain
0.75
0.50
0.25
0.00
cyclovergence
cycloversion
phase [deg]
180
90
0
-90
-180
1
5
10
1
5
10
cycle length [deg-1]

(Van Rijn *et al.*, 1992b). There was no significant interaction between movement type and oscillation frequency.

4.5 Discussion

In a previous investigation (Van Rijn *et al.*, 1992b) we found that horizontal contours were only slightly more effective than vertical contours in eliciting cyclovergence. That result seemed at odds with the findings of Howard (1991) and Crone and Everhard-Halm (1975), who found that horizontal gratings were 4 to 5 times and 2 to 3 times, respectively, more effective than vertical gratings. In this study, we investigated a number of stimulus variables that may be at the basis of this discrepancy: 1) the presence or absence of stationary contours, resulting in shear or real rotational stimuli; 2) the oscillation frequency; and 3) the wavelength of the grating. We will add the size of the stimulus as a fourth variable, by comparing the present results to those from our previous experiment.

In addition, we compared horizontal contours to vertical contours as stimuli for cyclorotation for both cyclovergence and cycloversion.

Rotation vs. shear
We found that the response to an oscillating vertical grating was inhibited by a stationary horizontal grating. In contrast, the inhibitory effect of a vertical stationary grating on the response to an oscillating horizontal grating was not significant. This difference in inhibition is in agreement with the difference between the responses to both grating orientations: a stimulus eliciting a large response, when moving, should be expected to also exert a large inhibitory effect, when stationary. As a consequence, stimuli that are composed of a horizontal and vertical grating display a large difference between responses elicited by oscillations of the horizontal and vertical components. The responses to vertical shear are much larger than the responses to horizontal shear. This difference is larger than the difference between the responses elicited by horizontal and vertical gratings alone. Our composite stimulus closely resembled the shear stimulus that was used by Howard (1991). Since in our previous study we only used purely horizontal or vertical gratings, this accounts for (part of) the discrepancy. It does not explain the

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← FIGURE 4.4. Gain and phase of cyclovergence and cycloversion as functions of the wavelength of the stimulus. Plotted are the means ± SD's of all 4 subjects. The *gain* (upper panels) of neither cyclovergence nor cycloversion displayed a systematic dependence on stimulus wavelength. The variability was larger for cyclovergence than cycloversion, but overall response magnitudes were similar. The *phases* are shown in the lower panels. Cyclovergence displayed a phase lag; cycloversion showed a phase lead. Both were independent of the wavelength. Markers have been plotted slightly left and right of the actual oscillation frequencies to enhance readability of the figure.

discrepancy between our results and those of Crone and Everhard-Halm (1975), who also did not add stationary gratings. However, they performed objective measurements in one subject only.

In our reasoning we implicitly assumed that the cyclovergence and cycloversion systems respond to the separate oriented elements of the stimulus. A different approach would be to assume that these systems respond to the stimulus as a whole. As stated above, our composite stimulus has the character of a shear stimulus. Shear can be decomposed in distortion and rotation (for example Feynman, Leighton and Sands, 1964). The rotation component of a shear stimulus equals half the angle of shear. Therefore, if the oculomotor system were to respond to this rotation component of the shear stimulus as a whole, our effective stimulus amplitude would be only half as large as stated in the Methods. The gain would therefore be twice as high. This interpretation would make the responses to shear stimuli much larger than the responses to horizontal or vertical gratings alone, and therefore this mechanism is unlikely. Another argument against this hypothesis is that the rotation component of the horizontal shear stimulus (i.e. vertical grating oscillating + horizontal grating stationary) is as high as that of the vertical shear stimulus, while the responses to these two "shear types" were very different. Thus, we conclude that the differently oriented components of the stimuli were initially processed by separate channels, being relayed with a different gain to the oculomotor system.

Oscillation frequency
We found that the difference between responses to horizontal and vertical contours did not depend on the oscillation frequency: there was no interaction between oscillation frequency and grating orientation, either for cycloversion or cyclovergence. For cyclovergence, this lack of interaction is in agreement with the figure presented in Howard (1991).

Wavelength
Another possible origin of the discrepancy with previous authors could have been the wavelength of the stimulus grating. From the figures in Crone and Everhard-Halm (1975) and in Howard (1991), it can be inferred that in those studies the predominant wavelengths were approximately 5 deg and 3 deg of visual angle. In the first experiment of the present study it was 2.5 deg of visual angle. In our previous study, wavelength was smaller: 1.7 deg. However, this possible source of the discrepancy is made unlikely by our findings from the second experiment of this study. It appears that there is no systematic dependence of cyclovergence or cycloversion on stimulus wavelength, either for horizontal or for vertical gratings.

Stimulus size
Stimulus size may also lie at the basis of the discrepancy. Howard (1991) used a stimulus that subtended about 80 deg of visual angle; in our previous experiment the stimulus size was about 28 deg. In the present experiment, the stimulus size was

Experiment	type of experiment	cyclovergence response	cycloversion response	size
1a.	variation of oscillation frequency, stationary grating absent	2.28 ± 1.80 (n = 56)	3.00 ± 3.30 (n = 56)	48 deg
1b.	variation of oscillation frequency, stationary grating present	-3.54 ± 3.19 (n = 56)	5.23 ± 4.62 (n = 56)	48 deg
2.	variation of wavelength of grating, stationary grating absent	2.49 ± 1.78 (n = 96)	1.77 ± 0.98 (n = 96)	48 deg
3. Van Rijn *et al.*, 1992b	variation of amplitude, stationary grating absent	1.30 ± 0.41 (n = 36)	1.25 ± 0.54 (n = 36)	28 deg

TABLE 4.1. Mean ± S.D. of ratios of responses to horizontal grating / responses to vertical grating in the different experiments. "Stationary present" indicates that superimposed on the oscillating horizontal grating (numerator) there was a stationary vertical grating and superimposed on the vertical grating (denominator) there was a stationary horizontal one. Data are pooled over subjects, grating orientations (i.e. horizontal or vertical) and over the factor that was varied in the considered experiment (see second column). Comparing rows 1a and 2 with row 3 by grouped t-test revealed that differences were significant, both for cycloversion and cyclovergence (all 4 p-values <0.013). The differences between row 1a and 2 were not significant).

intermediate (48 deg). These latter two experiments cannot be compared directly because response magnitudes also depended on other factors, which were varied in the present and previous experiments (present experiment: oscillation frequency; previous experiment: oscillation amplitude). To circumvent this problem we calculated the ratio of responses to horizontal gratings to those to vertical gratings. With analysis of variance we could not demonstrate that this ratio depended either on oscillation frequency or on oscillation amplitude. Also, there was no dependence on wavelength. Therefore, this ratio could be compared across these experiments. Table 4.1 lists the ratios for the different stimulus conditions in the present experiment and for our previous experiment. Ratios in the previous experiment, with its smaller stimulus size, were significantly lower than all ratios in the present experiments (grouped t-test: all P-values <0.013). Since measurement techniques, data analysis and even most of the subjects were identical in these two studies, this strongly suggests that for large stimuli the predominance of horizontal over vertical contours is stronger than for small stimuli. Howard, using a large stimulus found a ratio of about 4.5 (as estimated from his figure) and we conclude that the difference in stimulus size may explain (part of) the discrepancy.

We did not use this response ratio as a primary parameter in the analysis because the scatter in response ratios was larger than in response magnitudes, particularly when responses were low.

Horizontal vs. vertical contours in cycloversion
The present experiments demonstrate that the predominance of the effect of horizontal stimulus contours is present in cycloversion as well. For cyclovergence the "explanation" for this phenomenon has been teleologic: cyclodisparities of vertical contours may be caused by slant of the observed object and do, therefore, not require compensation by eye-cyclovergence, while cyclodisparities of horizontal contours always indicate cyclovergence errors and therefore do need correction (Crone and Everhard-Halm, 1975). This explanation is plausible indeed. However, the presence of the same phenomenon in cycloversion cannot be fitted into this hypothesis since cycloversion stimuli do not contain disparities. One may think of a teleologic explanation that is slightly different: in an outdoor setting, the most prominent horizontal contour is the horizon. This is a reliable reference for calibrating one's cycloversion state, much more so than vertical (or oblique) contours. If, then, the cycloversion mechanism would "try" to stabilize the eyes relative to the outside world, horizontal contours would be the best candidates for reference marks.

An alternative explanation for the predominance of horizontal contours in cycloversion is that the same neurophysiological mechanism mediates both cycloversion and cyclovergence. Differences and similarities between cycloversion and cyclovergence response types are discussed below.

Cyclovergence vs. cycloversion responses
For all oscillation frequencies we found the cyclovergence and cycloversion responses (gain) to be in a similar range of magnitude. This confirms our earlier findings that at an oscillation frequency of 0.2 Hz responses were largely similar. We found no dependence of either cyclovergence or cycloversion response magnitude on the wavelength of the stimulus. It must be noted though, that the variation was larger for cyclovergence than for cycloversion (Fig. 4.4). (The possibility of a very weak dependence of cyclovergence on the wavelength of the stimulus cannot be ruled out completely on the basis of our results.) From these results one is tempted to conclude that cycloversion and cyclovergence are essentially similar. This is supported by our finding that the predominant role of horizontal contours is similar in both movement types. Previously (Van Rijn *et al.*, 1992b) we found distinct differences between cyclovergence and cycloversion responses: within subjects the response magnitudes of cycloversion and cyclovergence did not correlate; the phases of both movement types were very much different and both movement types did show different behaviour in response to non-corresponding stimuli. All these findings are in favour of different mechanisms for cycloversion and cyclovergence. The different phases of cycloversion and cyclovergence, as well as the poor correlation between cyclovergence and cycloversion responses within subjects, were confirmed in the present results. In view of the differences and similarities that we found, it seems best to assume that cyclovergence and cycloversion are different

processes, but part of their pathways may be in common.

Our results suggest that cyclovergence must be interpreted as a truly static response. This is in agreement with reports on static cyclovergence from the literature (Kertesz, 1983) and with the results and interpretation of Howard and Zacher (1991). The stimulus for cyclovergence is a disturbance of retinal correspondence of (especially) horizontal contours. In the literature, dynamic cycloversion has been interpreted as torsional optokinetic nystagmus (Brecher, 1934; Cheung and Howard, 1991), serving to reduce retinal slip. If this would be the single function of cycloversion, one should not expect the presence of any static cycloversion response. However, static cycloversion (i.e. cycloversion in response to a static tilted visual stimulus) has been found by different investigators (Crone, 1975; Goodenough, Sigman, Oltman, Rosso and Metz, 1979), although its magnitude was small. Its interpretation has been in terms of a visual analogue of the otolith response (Crone, 1975).

The apparent difference between the nature of dynamic and static cycloversion disappears if one assumes that cycloversion is a truly static response as well, just as cyclovergence. The difference is that the stimulus for cyclovergence is a disturbance of retinal correspondence of (especially) horizontal contours, whereas for cycloversion, as we pointed out above, it may be the alignment of the horizontal ocular meridian with the real world horizon. This hypothesis would also explain our finding that the gain steadily increases with decreasing stimulus oscillation frequency. Strong support for this hypothesis would come from an experiment demonstrating a continuum between static and dynamic cycloversion responses. However, it is difficult to measure at still lower oscillation frequencies than we did because of the presence of a slow, spontaneous drift on cycloversion (Van Rijn and Van der Steen, 1992a). This drift was less consistently present and of smaller magnitude in cyclovergence. This is in agreement with Enright's (1990) results, demonstrating that, within periods of fixation, the variation of cyclovergence is less than that of cycloversion. Static cycloversion responses and dynamic responses at low oscillation frequencies require cautious interpretation.

Phase relations

Previously (Van Rijn *et al.*, 1992b) we reported that at a frequency of 0.2 Hz, cyclovergence displays a phase lag, contrary to cycloversion. Howard and Zacher (1991) reported that the phase lag of cyclovergence increases with the frequency of movement, while Cheung and Howard (1991) found that cycloversion does not display a phase lag up to a frequency of 1 Hz. Our present data are in agreement with these previous reports. There is one difference between our results on phase and those of Howard and Zacher: the relation between oscillation frequency and phase in their results was a curve that was convex upward. The maximum phase lag was -100 deg. We found that the convexity was pointing downward and that there was a plateau at -90 deg. In order to interpret their findings, Howard and Zacher referred to a non-linear model proposed by Buizza and Schmidt (1985). In this model, the phase curve has both concave and convex parts, depending on the frequency. Both our results and those of Howard and Zacher may be in agreement with this model, but the maximum phase lag would be expected to be similar.

Conclusions

The present results confirm earlier reports (Crone and Everhard-Halm, 1975; Howard, 1991) that horizontal contours are much more effective in eliciting cyclovergence than are vertical contours. This predominance of horizontal contours appeared to be present in cycloversion as well. We showed that this predominance was enhanced by the presence of stationary contours rotated by 90 deg with respect to the oscillating contours. The predominance was less for smaller sized stimuli, but there was no consistent effect of oscillation frequency or the wavelength of the grating that was used as stimulus.

Furthermore we found that the decrease of responses with increasing stimulus oscillation frequency was similar for cyclovergence and cycloversion and that the response magnitude of neither cyclovergence nor cycloversion depended on the wavelength of the stimulus.

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CHAPTER 5

BINOCULAR EYE ORIENTATION DURING FIXATION: LISTING'S LAW EXTENDED TO INCLUDE EYE VERGENCE

5.1 Summary

Any eye position can be reached from a position called the primary position by rotation about a single axis. Listing's law states that for targets at optical infinity all rotation axes form a plane; the so-called Listing plane. Listing's law is not valid for fixation of nearby targets. To document these deviations of Listing's law we studied binocular eye positions during fixations of point targets in the dark. We tested both symmetric (targets in a sagittal plane) and asymmetric vergence conditions. For upward fixation both eyes showed intorsion relative to the position that would have been taken if each eye followed Listing's law. For downward fixation we found extorsion. The in- or extorsion increased approximately linearly with the vergence angle.

The direction of the Listing axis and the turn angle about this axis can be decribed by rotation vectors (Haustein, 1989). Our observations indicate that for fixation of nearby targets the rotation vectors of the two eyes become different and are no longer located in

a single plane. However, we find that it is possible to decompose the rotation vector of each eye into the sum of a symmetric and an anti-symmetric part, each with its own properties: (1) The symmetric part is associated with eye version. This component of the rotation vector is *identical* for both eyes and lies in Listing's plane. In contrast to the classical form of Listing's law, this part of the rotation vector lies in Listing's plane *irrespective* of the fixation distance. (2) The anti-symmetric part of the rotation vector is related to eye vergence. This component is of equal magnitude but *oppositely* directed in each eye. The anti-symmetric part lies in the mid-sagittal plane, also irrespective of fixation distance. For fixation of targets at optical infinity the anti-symmetric part equals zero and the eye positions obey the classical form of Listing's law. Thus, the symmetric and anti-symmetric parts of the rotation vectors are restricted to two perpendicular planes.

Combining these restrictions in a model, with the additional restriction that the vertical vergence equals zero during fixation of point targets, we arrive at the prediction that the cyclovergence is proportional to the product of elevation and horizontal vergence angles. This was well born out by the data. The model allows to describe the binocular eye position for fixation of *any* target position in terms of the bipolar coordinates of the target *only* (i.e. using only three degrees of freedom instead of the six needed for two eyes).

5.2 Introduction

Until recently most studies on oculomotor control restricted the analysis to the horizontal and vertical dimensions. Sufficient as such studies may be for a description of human performance for binocular foveation of a target of interest, they are of little use when one is interested in the normal range of retinal disparities with which the visual system has to cope during natural eye movements. Such questions require an analysis of the spatial relation between the retinae and the images of objects in a three dimensional lay-out. Ocular torsion cannot be ignored in those cases.

The development of a precise and stable recording technique for the measurement of ocular torsion (Robinson, 1963; Collewijn, Van der Steen, Ferman and Jansen, 1985) and the introduction in the oculomotor literature of mathematical tools appropriate to the analysis of rotating bodies (Westheimer, 1957; Tweed and Vilis, 1987; Haustein, 1989) have created a good starting point for a thorough investigation of ocular torsion.

Much research on ocular torsion has concentrated on Listing's law. This law states that there exists a special eye position (the primary position) from which any normal eye orientation can be reached by rotation about a single axis which lies in a plane perpendicular to the primary direction. This plane is called the Listing plane.

Listing's law holds to a good approximation during monocular fixation (Ferman, Collewijn and Van den Berg, 1987b; Tweed, Cadera and Vilis, 1990). The Listing plane is usually not exactly aligned with the fronto-parallel plane but may be tilted by several degrees about a horizontal axis through the eyes. Even during saccades eye positions roughly follow Listing's law (Tweed and Vilis, 1990), as well as during smooth pursuit (Ferman, Collewijn and Van den Berg, 1987c; Haslwanter, Straumann, Hepp, Hess and Henn, 1991; Tweed, Fetter, Andreadaki, Koenig and Dichans, 1992).

During convergence, however, eye positions violate Listing's law. Nakayama (1983) reported that the torsion of the non-verging eye depended on the vergence of the other eye. Several other deviations have been described; for instance Listing's law is also violated during sleep (Nakayama, 1975) and extensive training enables some subjects to make voluntary torsional eye movements (Balliet and Nakayama, 1978). Together, these violations indicate that Listing's law is the result of central control rather than a side effect of mechanical properties of the orbit or eye muscle geometry.

We interpret the deviations from Listing's law during vergence as pointing to the law's incompleteness rather than posing a limit on the law's validity. We aim to extend Listing's law in such a way that it applies to binocular eye orientations for fixation of any position in head-space. For the development of the theory we assume that each spatial position with respect to the head is fixated with a unique pair of eye orientations. In this sense the theory is the binocular analogue of Listing's law. Thus, we propose that the neural control reduces the number of degrees of freedom for binocular eye positions from 6 (3 for each eye) to 3 (the dimension of head-space). The derivation will be in the spirit of Hering's law of equal innervation (Hering, 1868); eye positions are not independently controlled but are the sum of version and vergence. We will give a novel three dimensional interpretation of these concepts.

After a broad description of the theory predictions concerning eye orientations will be presented. Subsequently, binocular three-dimensional eye-position data, collected with the search-coil technique, will be presented in support of the theory. The detailed mathematical derivations are postponed to the appendices at the end of this chapter.

Extending Listing's law

In an intuitive way one may quantify eye rotations by specification of the axis of rotation and the angle of the turn about this axis. For any two orientations of a body the axis' direction and the turn angle, required to reorient the body from the first into the second position are uniquely determined. Such a representation of body rotation treats all directions of rotation equally. It thereby captures in a natural way the fact that the axis of eye rotation may have any direction. Because eye movements are brought about by the simultaneous activation of three muscle pairs, the orientation of the resultant rotation axis is continuously variable and depends on the relative activation of the muscle pairs. In formal descriptions the axis direction and the turn angle are combined in one three-component rotation vector with a direction parallel to the axis of rotation and a length related to the turn angle. One may find excellent introductions to the mathematical properties of the rotation vector or the related quaternion in Haustein (1989) and Tweed and Vilis (1987), respectively.

It should be noted that the rotation vector is related to changes in orientation of the eye and thus would seem appropriate for descriptions of, for instance, eye velocity. To use the rotation vector for descriptions of eye positions one selects a reference eye orientation to which all possible eye orientations are to be related by single turns. For a given reference position each rotation vector then specifies a unique eye orientation. We stress here that rotation vectors give a description of eye position in a head-fixed reference frame because the components of the rotation vector equal the tangent of half the turn angles about three axes that are fixed in the head.

In terms of rotation vectors Listing's law takes a very simple form: the rotation vectors during natural eye fixations of distant targets with the head upright lie in a plane (the displacement plane). The orientation of the plane relative to the head depends on the choice of the reference eye position (Tweed and Vilis, 1987; Haustein, 1989). The planar arrangement of the rotation vectors, however, is preserved irrespective of the chosen reference position. There is one unique reference position (the primary position) for which the line of sight in the reference position is perpendicular to the displacement plane, which is then called the Listing plane.

We give a precise meaning to Hering's law of equal innervation by proposing that the rotation vectors of the right eye ($\mathbf{r}_r$) and the left eye ($\mathbf{r}_\ell$) are each composed of two parts; one part of the rotation vector reflects the activity of the ver<u>g</u>ence system (g) the other that of the ver<u>s</u>ion system (s). The version part is identical for both eyes. The vergence part is anti-symmetrical[1]. Its magnitude is identical but its direction is opposite for the two eyes. By definition, the contribution of vergence is nil for pure conjugate eye-movements ($\mathbf{g} = 0$). In vector notation we may thus write:

$$\mathbf{r}_r = \mathbf{s} - \mathbf{g} \tag{1}$$

$$\mathbf{r}_\ell = \mathbf{s} + \mathbf{g} \tag{2}$$

---

[1] The two eyes can be thought of to be displaced equally relative to the ego-centre, but in opposite directions. The symmetric part takes identical values in the rotation vectors of the eyes. This is reminiscent of a symmetric function like the *cosine*, which takes identical values for positive and negative angles of equal magnitude. Similarly, the opposite direction of the anti-symmetric part in the rotation vectors resembles an anti-symmetric function like the *sine*, which has its sign reversed when the sign of the angle reverses.

It follows from this proposal that Listing's law is a property of the version system as defined above, because we know that the rotation vectors of the eyes obey Listing's law in the absence of vergence ($g = 0$). Thus, the version part s must lie in Listing's plane. We immediately remark that this proposal predicts that the *average* rotation vector of the two eyes ($(\mathbf{r}_\ell + \mathbf{r}_r)/2 = s$) should satisfy Listing's law *irrespective of the vergence of the eyes.*

This proposal implies that the primary directions of both eyes should be identically directed. Reports by Ferman *et al.* (1987b) and Tweed and Vilis (1990) of a slight lateral displacement of the primary direction for each eye seem at variance with this proposal. However, these authors did not use targets at optical infinity. Monocular stimulation as used by these authors does not preclude eye vergence, which may have affected the results (Nakayama, 1983; Mays, Zhang, Thorstad and Gamlin, 1991; Enright, 1980). In fact, the model predicts a temporal rotation of the displacement plane of each eye as a result of eye vergence (see below). Therefore, the mentioned reports do not provide decisive evidence against the first proposal.

Secondly, we propose that for normal eye fixations the vergence part (g) of the eye rotation vector is restricted to the median plane in the head. To understand this, consider what happens if g is directed parallel to the interocular axis. Because g is anti-symmetrical, it would result in upward rotation of one eye and downward rotation of the other. Consequently, the lines of sight would no longer intersect. This is obviously detrimental to foveal vision and should be prevented by the oculomotor system. Thus, we assume that the *difference of the rotation vectors* of the eyes (which equals 2g) lies in the median plane of the head *irrespective of the spatial location that is fixated.*

It is customary to express Listing's law in a coordinate system with its origin located at the centre of rotation of the eye. Because we aim at a binocular description of eye movements it is more appropriate to choose angles of target position relative to the ego-centre. The ego-centre is located midway between the eyes on the interocular axis.
Fig. 5.1 shows the bipolar coordinate system which is used. Rotation vectors are expressed with respect to a cartesian reference frame with its origin at the ego-centre. The positive x-axis points straight ahead from the ego-centre, the positive y-axis is directed leftward. The z-axis is directed upward. Eye torsions are rotations about the x-axis. Vertical eye movements are rotations about the y-axis, while horizontal eye movements result from rotations about the z-axis.

The target position relative to the ego-centre is specified by three angles: (1) positive elevation is the downward rotation about the interocular axis (θ). This rotation alters the orientation of the plane of regard which contains the target point and the two centres of rotation of the eyes, (2) positive azimuth (α) is leftward rotation within the plane of regard of the line through the ego-centre and the target point, (3) the vergence angle (v) is the angle at the target between the lines connecting target with the centres of rotation

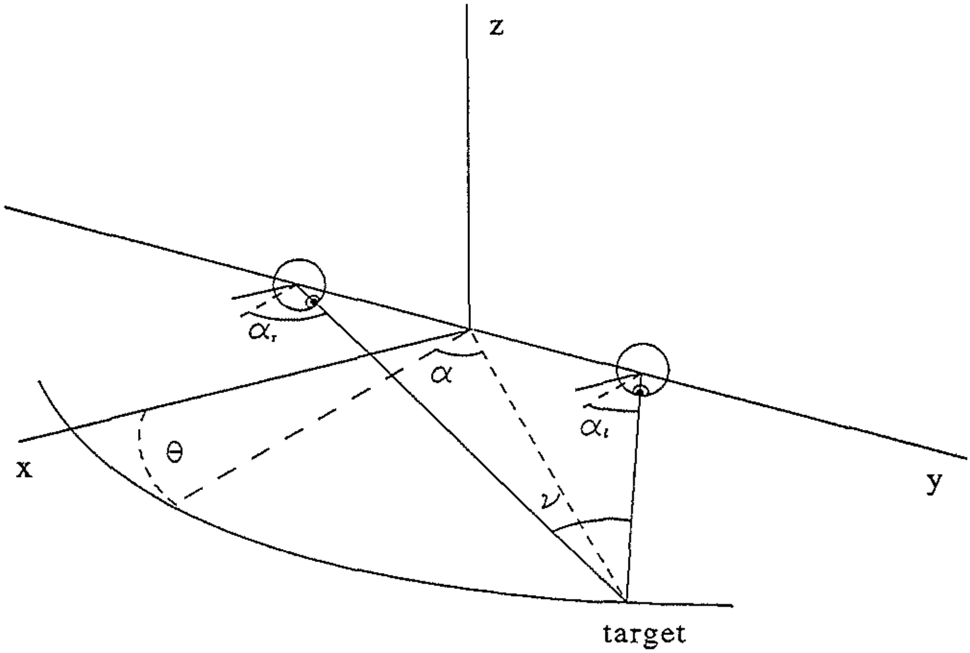

FIGURE 5.1. The eye positions are expressed either in Helmholtz coordinates or in rotation vectors. Both are relative to the ego-centre which is located at the origin of the cartesian reference frame. Indicated are the version angles α (azimuth) and θ (elevation) and the horizontal vergence angle ν. Components of the rotation vectors ($\mathbf{r} = r_1, r_2, r_3$) are the projections on the x, y and z axes, respectively. In the Helmholtz coordinate system (Carpenter, 1988), the horizontal axis is fixed in the head and the vertical axis rotates with the eye. The major advantage over the Fick system is that intersecting lines of sight imply equal angles of elevation in both eyes (i.e. $d\theta = 0$).

of the eyes (by convention this angle is negative for convergence). In these coordinates the primary position is specified by $\alpha = \theta = \nu = 0$. It can be conceived of as the primary direction of Hering's 'double eye' or the Julesz' cyclopean eye. In the primary position the line of sight of the double eye is directed along the positive x-axis.

As shown in App. A the (x,y,z) components of the rotation vectors of the eyes can be expressed as functions of the Helmholtz angles (Carpenter, 1988) relative to the ego-centre, as is the case for the target, provided that small angles occur ($|\alpha|$, $|\theta|$, $|\nu| <$ 30 deg). In addition, a full specification of the rotation vectors of the eyes requires three more angles: (4) the conjugate torsion of the eyes (ψ) and the vertical ($d\theta$) and torsional ($d\psi$) vergence angles. Positive torsion results in rightward motion of the upper pole of the eye, i.e towards the negative y-axis (see Fig. 5.1). The difference between the torsion of the left (ψ_l) and the right eye (ψ_r) equals the torsional vergence.

The assumed restrictions on the orientations of s and g can be formulated with respect to the above reference system as:

$$s_1 = 0 \tag{3}$$

i.e. the component of s in the primary direction is zero.

$$g_2 = 0 \tag{4}$$

i.e. the component of g parallel to the inter-ocular axis is zero.

By itself the restriction on the orientation of g does not guarantee that the lines of sight intersect. The requirement that the lines of sight should intersect is equivalent to:

$$d\theta = 0 \tag{5}$$

This is not a model prediction but a requirement for binocular foveal fixation. This requirement together with the above restrictions on g and s form the core of the model. They lead to the following prediction for the rotation vectors of the left ($\mathbf{r}_\ell$) and right ($\mathbf{r}_r$) eye (ignoring higher order terms):

$$\mathbf{r}_\ell = \begin{bmatrix} \theta v/4 \\ \theta/2 \\ \alpha/2+v/4 \end{bmatrix} \qquad \mathbf{r}_r = \begin{bmatrix} -\theta v/4 \\ \theta/2 \\ \alpha/2-v/4 \end{bmatrix} \tag{6}$$

The torsion component of the rotation vectors of the eyes is fully determined by the anti-symmetric part g because the symmetric part s has no component in the primary direction ($s_1 = 0$). Thus, the torsional components of the rotation vectors of the eyes should be of equal magnitude but of opposite signs:

$$r_{\ell,1} = -r_{r,1} = g_1 = (\theta\ v)/4 \tag{7}$$

The left eye intorts for upward ($\theta<0$) fixations during convergence ($v<0$) because $r_{\ell,1}$ is positive. The right eye also intorts relative to the Listing orientation, because its torsion component is negative for upward fixation. For downward fixation both eyes extort.

Alternatively, we may consider eye torsion as in the Helmholtz system, i.e. as rotation about the visual axis. In Helmholtz coordinates we find for cyclovergence:

$$d\psi = \psi_\ell - \psi_r = (\theta\ v)/2 \tag{8}$$

i.e. the eyes show positive cyclovergence (intorsion) for fixation of upward target positions ($\theta < 0$ and $v < 0$) and negative cyclovergence (extorsions) for downward target positions ($\theta > 0$ and $v < 0$). The amount of in- or ex-torsion is proportional to the vergence angle. Cyclovergence does not depend on the azimuth.

$$\psi = -(\theta\ \alpha\ )/2 \tag{9}$$

i.e. the average (or conjugate) eye torsion depends on target elevation and target azimuth[2]. Negative conjugate torsion occurs for left-downward and right-upward target positions relative to the ego-centre. This prediction corresponds to equation (3), only it is now expressed in Helmholtz coordinates.

One implication of this model is that the rotation vectors of the eyes during fixation of targets on an iso-vergence plane lie in non-parallel planes. These displacement planes are rotated laterally by $|v/2|$ degrees, i.e. in a top view the displacement plane of the right eye is rotated clockwise and the displacement plane of the left eye is rotated anti-clockwise.

We tested the above relations (Eq. 3-9) during fixation of targets having different viewing directions and distances. We found that in general they were well supported by the data.

5.3 Methods

Subjects
Five human subjects participated in the experiments. Three of them were emmetropic, two (BB and RR) were myopic. Their correction was about –3 and –2 D, respectively and the difference between left and right eye corrections was 0.5 D or less. They wore their glasses during the experiment. All subjects had a visual acuity of at least 20/20 (with correction) in each eye. Their disparity threshold did not exceed 60 sec of arc in the TNO test for stereoscopic vision (Medical Workshop, Groningen, Holland).

Recording of eye positions
Eye positions were measured in three dimensions with two dual search-coils (supplied by Skalar, Delft, The Netherlands) (Robinson, 1963; Ferman, Collewijn, Jansen and Van den Berg, 1987a). These devices consist of a silicone annulus that contains two induction

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[2] The equation (9) is a close analogue of the equation for 'false torsion'(ψ_c), i.e. the torsion of one eye that is found in Helmholtz coordinates if the eye followes Listing's law ($\tan(\psi_c) = -\sin(\theta_c)\sin(\alpha_c)/(\cos(\theta_c)+\cos(\alpha_c))$), which reduces to $\psi_c = -\theta_c\ \alpha_c\ /2$ for small elevation (θ_c) and azimuth (α_c) angles of the eye. Note that in Eq. (9) the angles are relative to the ego-centre and not to the centre of the eye. Also, Eq. (9) is expected to hold for any fixation distance; the formula for false torsion holds only for targets at optical infinity.

coils: one (horizontal/vertical) coil is wound in the plane of the annulus. The other (torsion) coil's windings effectively enclose a surface perpendicular to that of the annulus.

Angular positions of the coils were measured with a phase-locked amplitude detection technique (Robinson, 1963). The analogue eye position signals (horizontal, vertical and torsional position for each eye) were low-pass filtered with a cut-off frequency of 125 Hz. and sampled at 250 Hz. The data were stored on disk by a minicomputer (DEC PDP 11/73) for off line analysis. Prior to each experiment, gain and offset of the amplifiers were precalibrated with the coils in reference position. In this reference position, the horizontal/vertical coil is oriented parallel to the revolving magnetic field (the transversal plane) and the torsion coil is located in the sagittal plane.

Procedures

Subjects were seated with the bridge of the nose in the centre of the magnetic field. The head was restraint by a biteboard containing a silicone mould of the dental impression. The room was darkened. One small fixation point (Light emitting diode (LED), diameter 4 mm) was presented at a time, for binocular fixation. These LED's were mounted on three frames positioned parallel to the transversal plane, either at 20, 40 or 200 cm distance from the frontal surfaces of the subject's eyes. During measurements, only one frame at a time was mounted. In each frame 15 LED's were mounted in a matrix of 3 horizontal positions (azimuth: −15, 0 or 15 deg) and 5 vertical positions (elevation: −15, −10, 0, 10, or 15 deg) We took care that no other visual references were present besides the one LED. In addition, we payed much attention to minimizing offsets of jaw and roll angles of the head with respect to the earth-fixed straight ahead. To this end, each eye was inspected through a sighting device from both the left and the right. The position of the biteboard was manipulated until the front surfaces of both corneae were located in a transversal plane and at identical heights. We estimate that after this procedure, jaw and roll angles were within 0.5 deg from zero. An objective zero position of the pitch angle cannot be established with the help of head reference marks (Carpenter, 1988), so the subjects positioned their heads in what they felt to be their most 'natural' upright position. After a LED was turned on at either one of the 3x3x5 possible positions the subjects started the measurement when they felt ready. One measurement lasted 4 seconds. In between every 7 or 8 measurements 2 calibration measurements were included. In these calibration measurements, a LED was presented at 2 m distance in the reference direction with respect to left and right eye, respectively; the other eye was covered (see Data analysis section). One data set thus consisted of 45 measurements plus 6 sets of calibrations. During an experiment we either collected one (subjects JW and DB) or two (HS, BB and RR) data sets.

Data analysis

The data from the calibration measurements were used in a matrix transformation described by Ferman *et al.* (1987a) for correction of coil misalignment and of non-

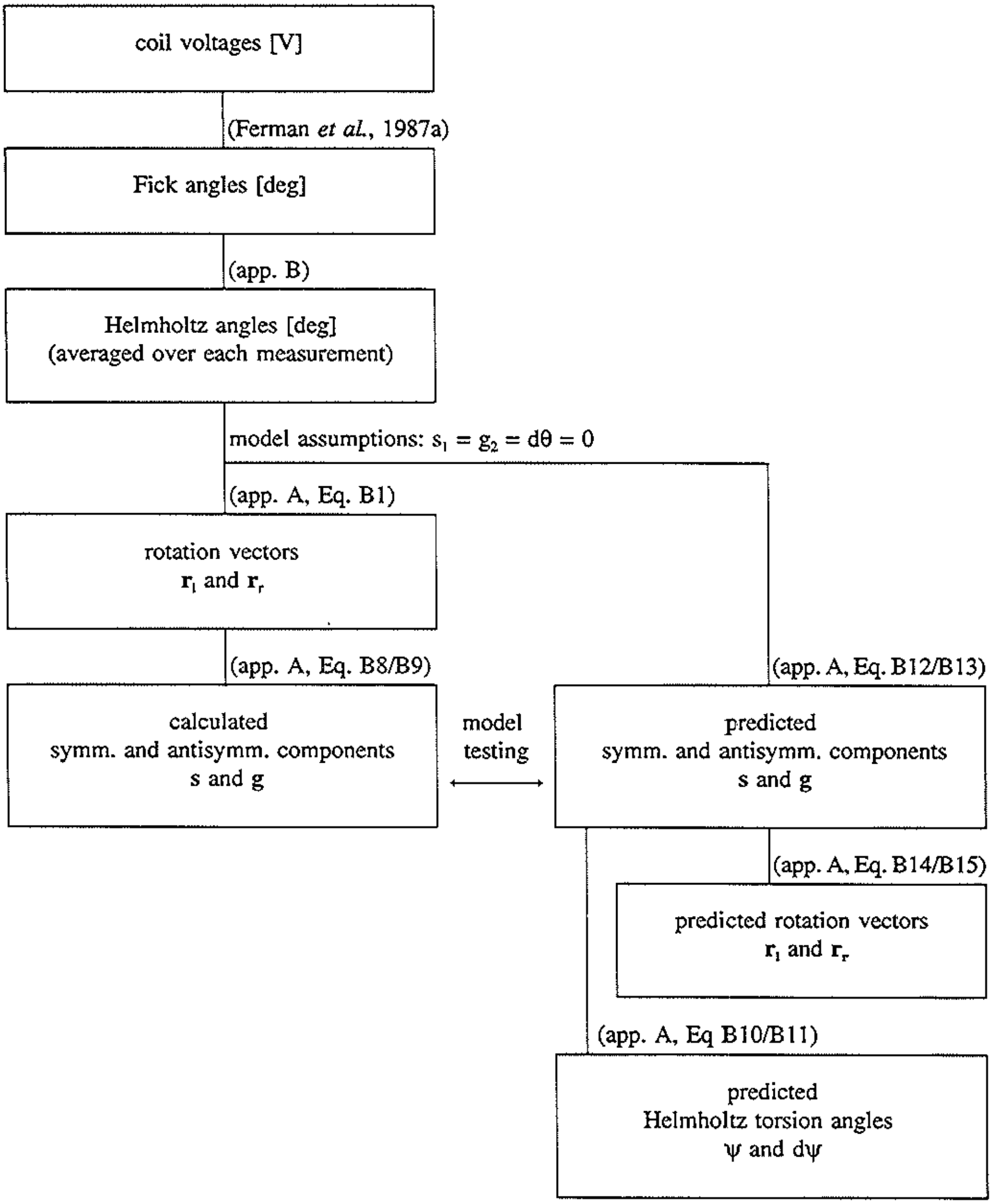

FIGURE 2. The sequential steps in the data analysis and model testing. The boxes on the left side indicate experimental data; those on the right side indicate model predictions.

linearities between coil voltages and rotation angles. In contrast to Ferman, we define downward angles of elevation (θ) as positive and the θ-terms of the matrix were inverted correspondingly. Because of the frequent calibrations we were able to keep track of possible coil slippage during the experiment. One data set was rejected because coil position showed a systematic drift in torsional direction. In the included data (of 5 subjects), the SD of subsequent calibrations within one session was 0.081 ± 0.031[3] deg in horizontal and vertical directions and 0.58 ± 0.27 deg in torsional direction. The variation is composed of the effects of veridical fixation instability and of possible coil slippage. (Enright (1990) measured eye position photographically and showed that fixation instability of torsion is in the range of 0.25 deg (SD).) The influence of coil slippage was minimized by correcting each measurement, using the values of the temporally closest calibration measurements.

From the matrix transformation we obtained data in Fick coordinates, relative to the (precalibrated) reference direction. These data were transformed to Helmholtz coordinates (azimuth: α, elevation: θ and torsion: ψ) by a computer routine (App. B). For each measurement the means of α, θ and ψ were calculated for each eye. These means were entered in a spreadsheet program (Quattro pro™) on a personal computer for calculation of rotation vectors of the left and right eye ($\mathbf{r}_\ell$ and $\mathbf{r}_r$), symmetrical and anti-symmetrical parts (s and g) and testing of model predictions. The successive steps of the data analysis are summarized in Fig. 5.2.

Statistical analysis (regression of rotation vector parts for determination of the primary direction of s) was performed using the SPSS statistical program.

5.4 Results

The duplicate data sets of subjects BB, HS and RR did not display major differences. Therefore the first and second data sets of these subjects were combined. In Fig. 5.3a-e, the upper panels show the results of the mean rotation vector (i.e. the symmetrical part s) for all subjects individually. All parts s form a plane that includes the interocular axis. For all subjects this plane is rotated so that the primary direction is pointing upward. Similarly, Fig. 5.3a-e (lower panels) show the results for the anti-symmetrical part g, ie half the difference of rotation vectors ($(\mathbf{r}_\ell - \mathbf{r}_r)/2$). As is the case for s, the parts g form a plane that in this case lies close to the sagittal plane.

The next step in the analysis involved a change of the frame of reference. Initially, Helmholtz angles and rotation vectors were referred to the precalibrated reference orientation. We derived the primary direction relative to the reference direction from the

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[3] The second value indicates the variation between subjects.

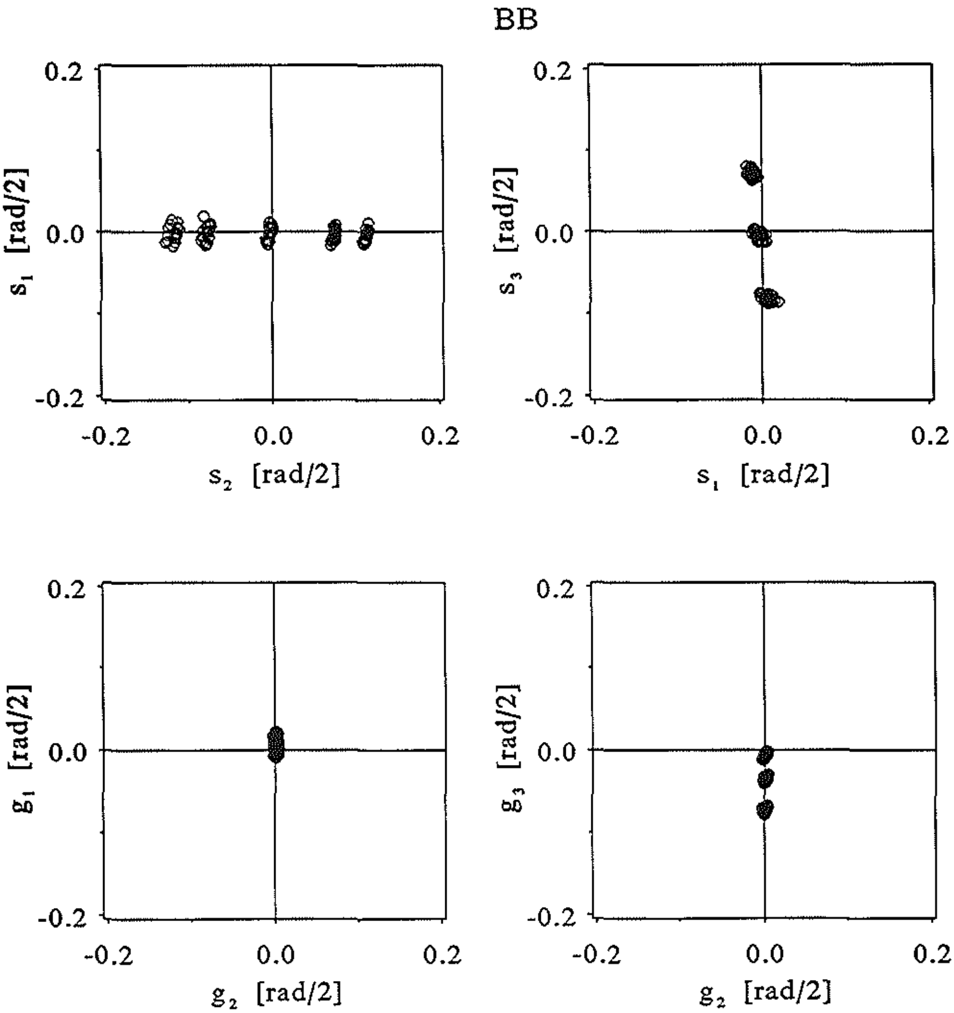


FIGURE 5.3a. The orientation of the symmetric (s) and anti-symmetric (g) parts of the rotation vectors of the left ($\mathbf{r}_l$) and right ($\mathbf{r}_r$) eye in subject BB. s was found by averaging $\mathbf{r}_l$ and $\mathbf{r}_r$; g was found by taking half the difference of $\mathbf{r}_l$ and $\mathbf{r}_r$. Left panels show top views (x and y components) of s (s_1 and s_2) and g (g_1 and g_2), respectively. The right panels show side views (y and z components) of s (s_2 and s_3) and g (g_2 and g_3), respectively. It can be seen that s is restricted to the fronto-parallel (y-z) plane, because s_1 is close to zero, whereas g lies in a mid-sagittal (x-z) plane, because g_2 is close to zero. The standard deviations of s_1 and g_2 are listed in Table 5.1. The data were obtained at three fixation distances, 5 different elevation- and 3 different azimuth angles.

observed orientation of the plane of parts s, using the fact that the normal to the plane of rotation vectors bisects the angle between the primary direction and the reference

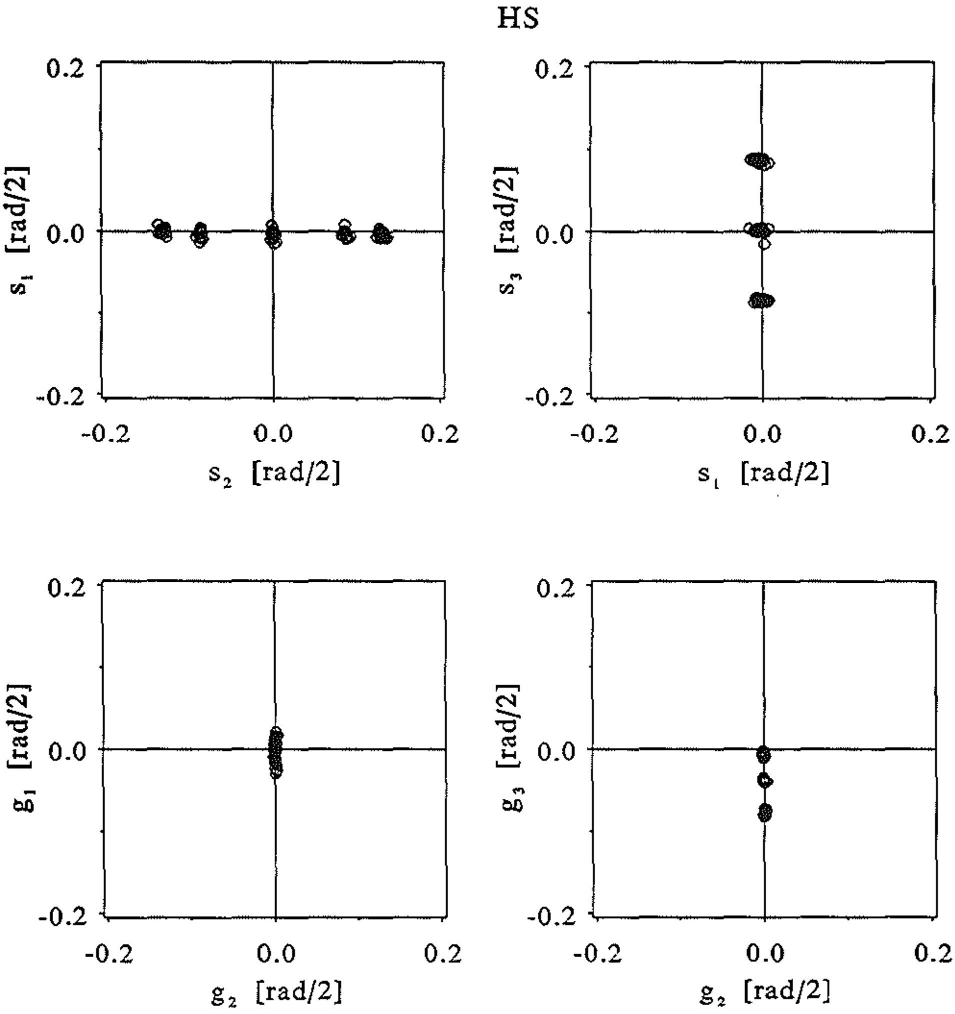


FIGURE 5.3b. Positions of s and g in subject HS. For explanation see Fig. 5.3a.

direction (Tweed *et al.*, 1990). The angle of rotation of this plane was calculated by means of linear regression of s_1 on s_2 and s_3. Subsequently, all Helmholtz angles were offset with the primary direction and the rotation vectors were recalculated using these corrected angles. With this transformation we obtained rotation vectors relative to the primary direction of s. Because effectively only the elevation angle was altered by this procedure, there was no influence on the position of the plane of parts g.

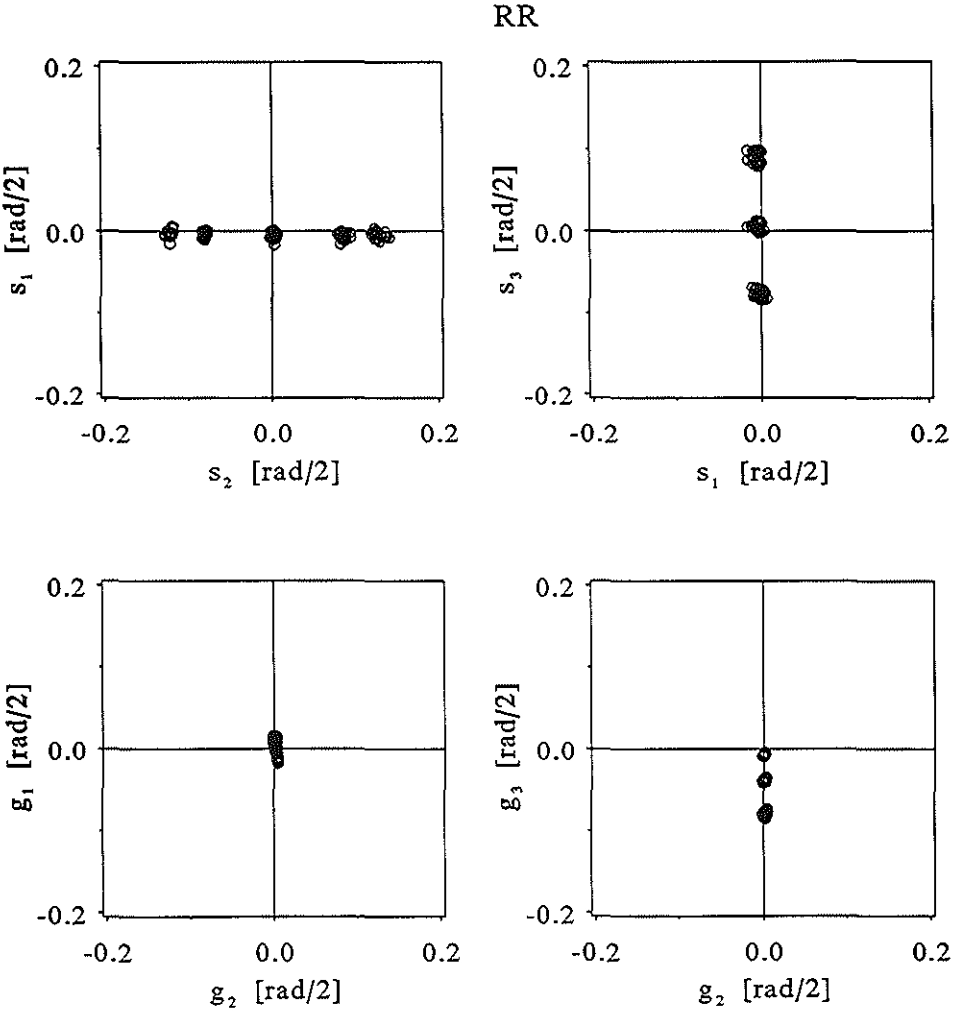


FIGURE 5.3c. Positions of s and g in subject RR. For explanation see Fig. 5.3a.

Model assumptions

The decomposition of the rotation vectors into symmetric and anti-symmetric parts implies that s should lie in the Listing plane *irrespective of the fixation distance.* As shown in Fig. 5.3a-e, the pooled data for each subject are located in a narrow plane. In order to show this distance independence more directly, we calculated mean and SD of the components perpendicular to the plane (ie s_1 and g_2) separated according to fixation distance. The results are shown in Table 5.1. For s_1, the SD's at the different fixation distances have the same range. In addition, there is no systematic dependency of the

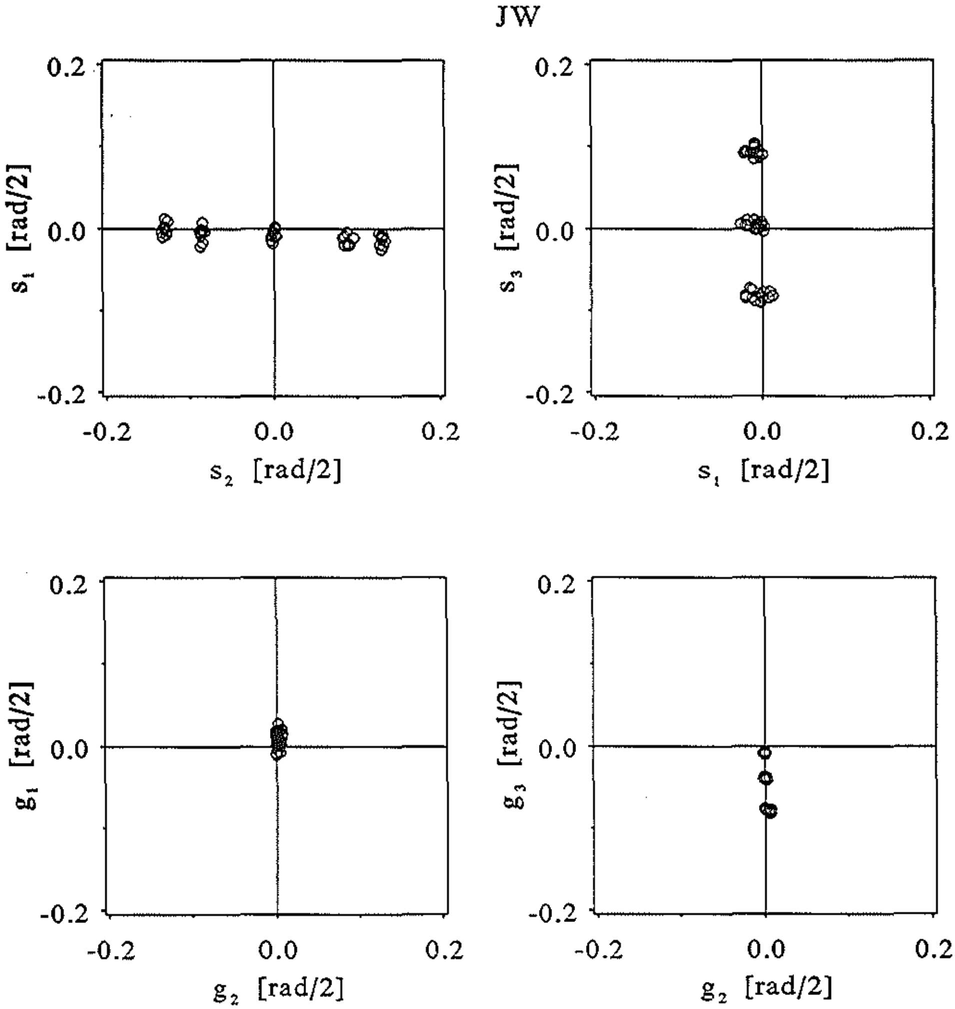


FIGURE 5.3d. Positions of s and g in subject JW. For explanation see Fig. 5.3a.

mean s_1 on fixation distance. The same applies to both means and SD's of g_2. Apparently, there is no systematic relation between either position or thickness of the planes of rotation vector parts and viewing distance. We consider these results as direct evidence for our assumptions that Listing's law is a property of the version system and that the orientation of the axes of the anti-symmetric vergence part are similarly restricted to a plane.

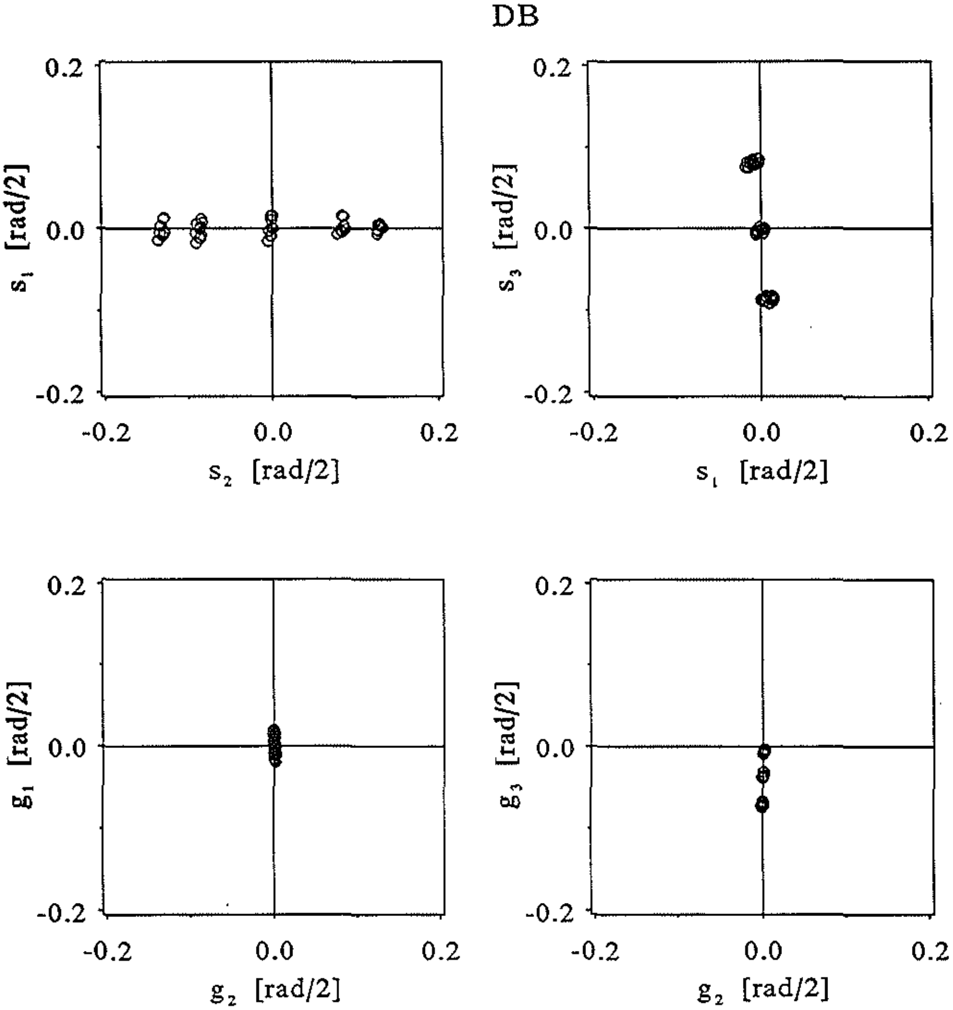


FIGURE 5.3e. Positions of s and g in subject DB. For explanation see Fig. 5.3a.

fixation distance	s_1	g_2
2 m	0.00377 ± 0.00114	0.00118 ± 0.00064
40 cm	0.00491 ± 0.00150	0.00123 ± 0.00051
20 cm	0.00433 ± 0.00106	0.00155 ± 0.00072
overall	0.00476 ± 0.00107	0.00161 ± 0.00060

TABLE 5.1. Variation of s_1 and g_2, separated according to fixation distance. Reported values are SD's, expressed as mean ± SD, averaged over 5 subjects.

As was mentioned before, the requirement that the lines of sight intersect implies that they should be confined to the plane of regard, i.e. the vertical vergence angle ($d\theta$) in Helmholtz coordinates should be zero. In fact, in our experiments $d\theta$ displayed some variation (SD = 0.301 ± $0.112^{3)}$ deg). However, if these non-zero $d\theta$'s would reflect a property of oculomotor control, we would anticipate a systematic relation of $d\theta$ with either α, θ and/or v. We did not find such relations and we suggest that random variation of $d\theta$'s are caused by head-movements in the course of the experiment. Note that an offset of the head in roll causes a difference in elevation between the eyes, since head roll raises one eye and lowers the other relative to the earth-fixed coordinate system.

Predictions for s and g

Having established that the main assumptions are roughly valid, it is of interest to investigate whether the data for the remaining components of s and g (i.e. s_2, s_3, g_1, and g_3) are in agreement with the predicted values (App. A, Eq. B12 and B13.) For s_2, s_3 and g_3 these predictions hold very well (see Table 5.2). They appear not to be very sensitive to our model assumptions. This is not surprising, since the first-order components of s_2 and s_3 are $\theta/2$ and $\alpha/2$, respectively (App. A, Eq. B9). These are input to the model. ψ and $d\psi$, which do follow from model assumptions, affect s_2 and s_3 only through second order terms. In addition, ψ is always much smaller than θ and α. The same holds for the prediction concerning g_3 (App. A, Eq. B8). Here, $v/4$ is the first-order term.

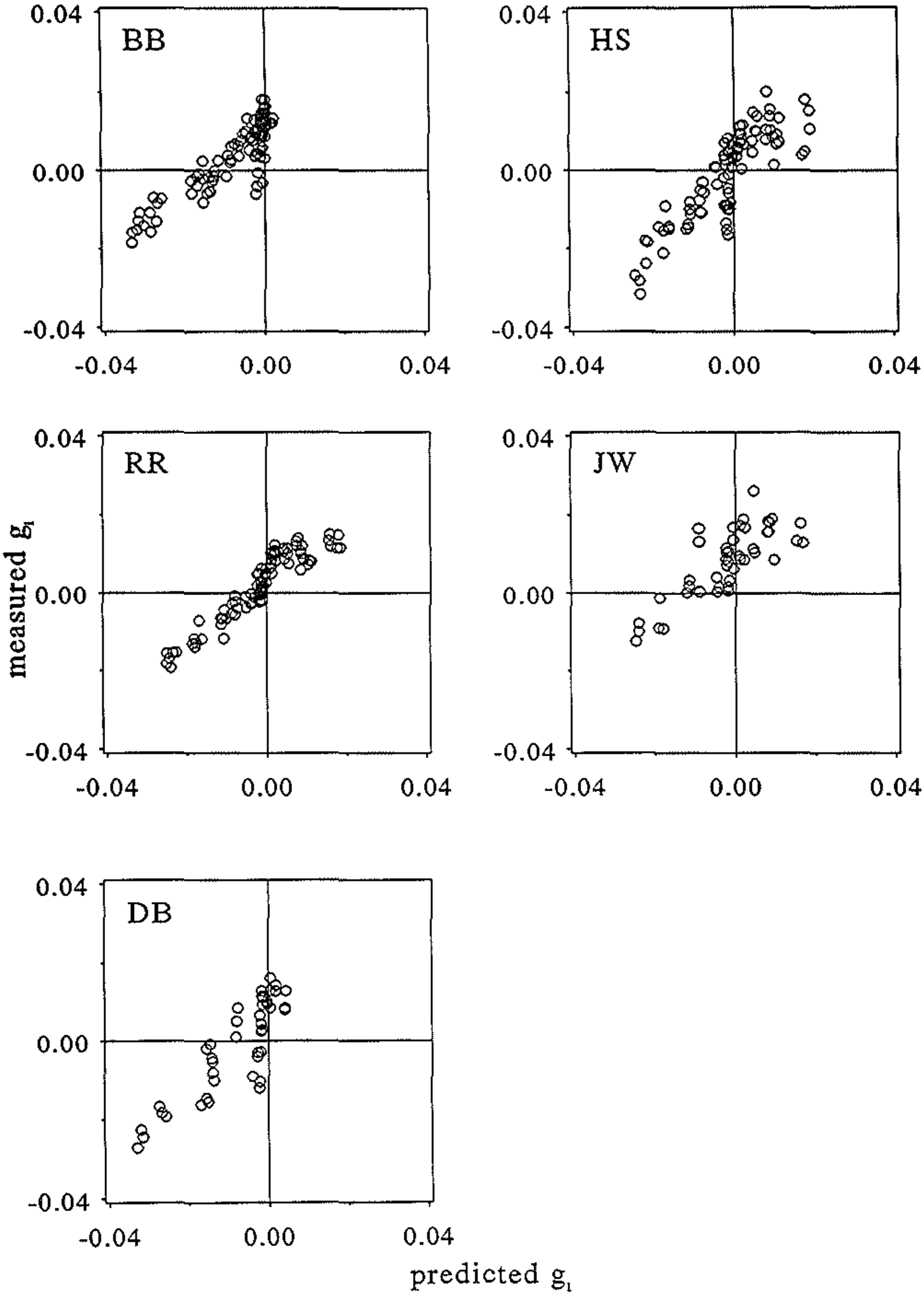
curve	offset	slope	corr. coeff r
measured s_2 - predicted s_2	– 0.0002	0.9996	0.9998
measured s_3 - predicted s_3	0.0002	1.0037	1.0000
measured g_3 - predicted g_3	– 0.0000	1.0173	0.9993

TABLE 5.2. Curve-fit coefficients of the plots of the measured vs. predicted s_2, s_3 and g_3. It shows that in our measurements these parameters are virtually insensitive to the model assumptions.

The most interesting prediction is that for g_1:

$$g_1 = \theta v/4$$

(App. A, Eq. B13). This component determines eye torsion, the magnitude of which is strongly dependent on the model assumptions. The relation between the predicted and calculated values of g_1 is shown in Fig. 5.4. This prediction is particularly interesting when one compares our model with possible alternatives, e.g. 'Listing applies to both


BB
HS
RR
JW
DB
0.04
0.00
-0.04
-0.04
0.00
0.04
measured g_l
predicted g_l

eyes separately' (see Discussion). It shows that the slope is somewhat less than, but close to unity (0.855 ± 0.124, averaged over the 5 subjects), although sometimes there is a slight offset (see below). Note that for most subjects negative g_1's predominate. In these subjects the primary direction was pointing upward (Fig. 5.3a-e, upper right panels). Therefore, fixation of most targets resulted in positive (i.e. downward) elevation relative to the primary direction. In line with the prediction, g_1 is negative for positive elevation during convergence.

Offsets

As was mentioned above, the measured value of g_1 follows the predicted value very well, apart from an offset in some subjects. As will be shown below (paragraph on ψ and $d\psi$), these offset were associated with offsets on $d\psi$. The magnitude of the offsets in $d\psi$ are shown in Table 5.3. In our opinion they represent artifacts introduced by the nature of the calibration procedure (see Discussion). We removed the offsets before we continued with the next steps of the data analysis. We subsequently pooled the data of the different subjects since the offset was the only systematic difference between them.

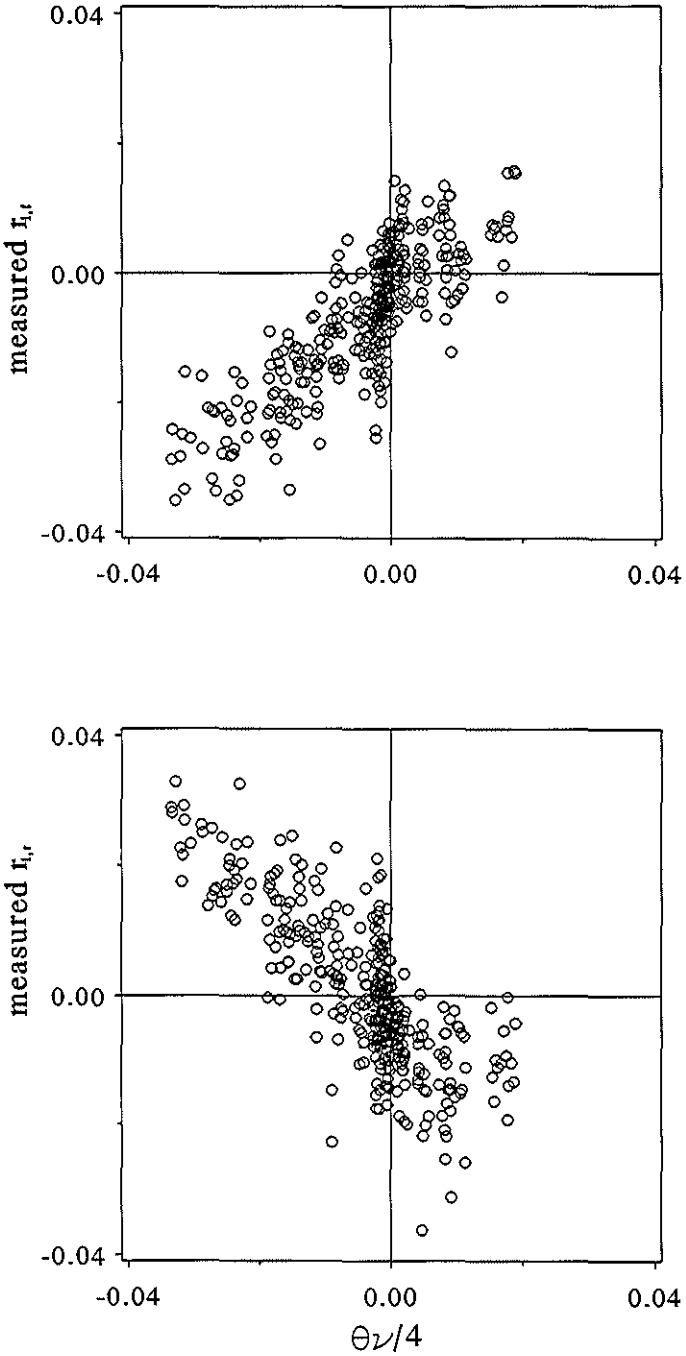
Predictions for r_ℓ and r_r

From the predicted symmetrical and anti-symmetrical parts s and g, we may now calculate predictions for the rotation vectors of the left and right eye's separately. Again the interesting prediction is the one concerning the first (torsion) components (i.e. $r_{\ell,1}$ and $r_{r,1}$). They are critically dependent on g_1 and s_1. The model assertion that g is anti-symmetric is directly tested here because the torsional components of the rotation

subject	$d\psi$ offset [deg]
BB	2.37
HS	0.14
RR	0.76
JW	2.16
DA	1.57

TABLE 5.3. Values of the offsets on $d\psi$, separated according to subject, that can account for the offsets in the prediction for g_1 (Fig. 5.4).

← FIGURE 5.4. The prediction for the torsion component of the anti-symmetric part (g_1) is $\theta v/4$. The measured values roughly support the prediction: the slope is 0.855 on average and the range of the correlation coefficients r is 0.804-0.934. The cyclovergence angles that could account for the offsets on the measured values are listed in Table 5.3.


0.04
0.00
-0.04
measured $r_{l,l}$
-0.04
0.00
0.04
0.04
0.00
-0.04
measured $r_{l,r}$
-0.04
0.00
0.04
$\Theta\nu/4$

vectors of the left and right eye should be equal in magnitude but oppositely directed:

$$r_{\ell,1} = (\theta\ v)/4$$

and:

$$r_{r,1} = -(\theta\ v)/4$$

Indeed, as is shown in Fig. 5.5, $r_{\ell,1}$ and $r_{r,1}$ are linearly related to g_1, but with opposite signs. In addition, this is another confirmation of the model assumption that the symmetric part has no component in the torsional direction (i.e. $s_1 = 0$).

Predictions for ψ and $d\psi$

Until now we have expressed our model assumptions and predictions in terms of rotation vectors (apart from "$d\theta = 0$"). The formulation of the model also allows expression in Helmholtz coordinates. The assumption that s_1 equals zero is equivalent to s obeying Listing's law. In terms of Helmholtz coordinates this can be formulated as:

$$\psi = -(\alpha\ \theta)/2$$

(App. A, Eq. B10). In Fig. 5.6 this prediction is shown for the pooled data of all subjects. It can be seen that it holds very well.

The assumption that g_2 equals zero leads to a prediction of $d\psi$:

$$d\psi = (\theta\ v)/2$$

(App. A, Eq. B11). In Fig. 5.7, this prediction is shown, again for the pooled data of all subjects. This prediction holds less well than the prediction for cyclovergence expressed in g_1. To gain some insight into the origin of the discrepancy between these predictions, we looked at the relation between the deviation from the predicted g_1 and the deviation

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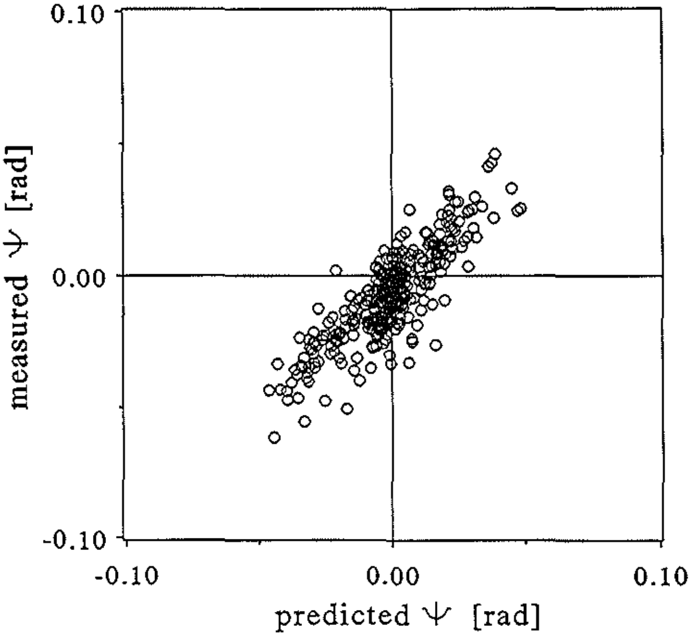
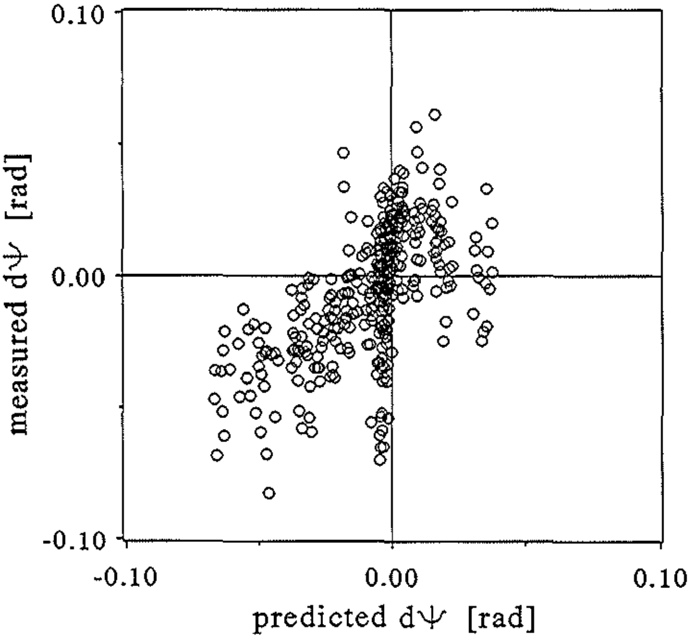
↖ FIGURE 5.5a. The predicted torsion component of the left eye ($r_{\ell,1}$) equals $\theta v/4$. The slope of the relation between measured and predicted values is 0.836 and the correlation coefficient r is 0.817. Data have been corrected for the offsets in Fig. 5.4 (see Table 5.3) and are pooled over 5 subjects and all fixation conditions.

← FIGURE 5.5b. The predicted torsion component of the right eye ($r_{r,1}$) equals $-\theta v/4$, hence the opposite of that of the left eye. The slope of the relation is -0.876 and the correlation coefficient r is -0.778. Data have been corrected for the offsets in Fig. 5.4 (see Table 5.3) and are pooled over 5 subjects and all fixation conditions.


0.10
0.00
-0.10
-0.10
0.00
0.10
measured Ψ [rad]
predicted Ψ [rad]


0.10
0.00
-0.10
-0.10
0.00
0.10
measured dΨ [rad]
predicted dΨ [rad]

from the predicted $d\psi$ (i.e. measured g_l – predicted g_l (Fig. 5.4) vs. measured $d\psi$ – predicted $d\psi$ (Fig. 5.7)). These deviations appeared to be highly correlated (r= 0.999). This was also the case when the data were not corrected for offsets (see above). Notably, there was no correlation between $d\theta$ and the deviation of either $d\psi$ or g_l from their predicted values. It appears that both the random variation and the offsets in Fig. 5.4 and Fig. 5.7 have a common origin in variations in $d\psi$. The prediction for $d\psi$ is much more sensitive to these variations than the prediction for g_l.

5.5 Discussion

In this study we have presented a model for predicting the 3-dimensional binocular eye position as one fixates a point in 3-dimensional space. In this model we use for the description of eye coordinates rotation vectors that are expressed in terms of Helmholtz coordinates. The asset of this approach is that Helmholtz angles lend themselves to a simple description of the retinal correspondence of the target images. On the other hand, rotation vectors allow efficient description of motor properties like Listing's law. In the current description, both coordinate systems are combined, which allows us to describe in a simple way the effect of Listing's law and of our current extension of Listing's law on retinal correspondence.

Listing's law classically applies only to monocular fixations of targets at optical infinity (Nakayama, 1983; Carpenter, 1988). Our extension includes a description of binocular eye positions for fixations of targets at all distances. When the target distance approaches infinity, our model becomes equal to Listing's law in its classical form.

We demonstrate that binocular eye positions can be described by two vectors s and g, representing the symmetrical and anti-symmetrical parts of the rotation vectors of the left and right eyes. Irrespective of the fixation distance, s is located in the transversal plane

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↖ FIGURE 5.6. The predicted Helmholtz torsion angle ψ equals $-\alpha\theta/2$. This equation is a close analogue of the equation for 'false torsion', i.e. the torsion of one eye that is found in Helmholtz coordinates if the eye follows Listing's law (see footnote 2). Contrary to the formula for false torsion, this equation holds for any fixation distance. The relation between measured and predicted values has a slope of 0.881; the correlation coefficient r is 0.843. Data have been corrected for the offsets in Fig. 4 (see Table 3) and are pooled over 5 subjects and all fixation conditions (which include 5 different elevation angles and 3 azimuth angles at each of the three fixation distances: 20, 40 and 200 cm).

← FIGURE 5.7. The predicted Helmholtz cyclovergence angle $d\psi$ equals $\theta v/2$. The relation between measured and predicted values has a slope of 0.698; the correlation coefficient r is 0.594. Data have been corrected for the offsets in Fig. 5.4 (see Table 5.3) and are pooled over 5 subjects and all fixation conditions.

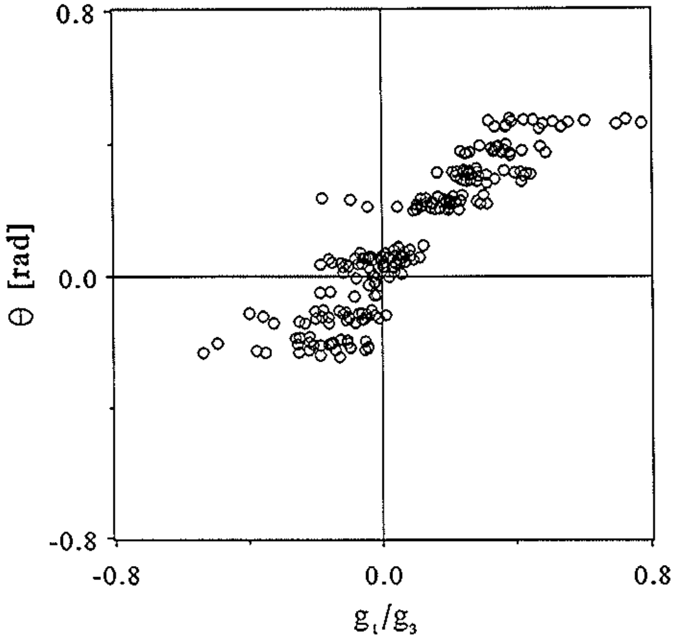

FIGURE 5.8. Measured elevation angle θ vs. quotient of predicted g_t/g_3. This relation shows that g is approximately perpendicular to the plane of regard. (slope 0.840 and correlation coefficient r 0.908) Data have been corrected for the offsets in Fig. 5.4 (see Table 5.3) and are pooled over 5 subjects. Data for fixations of targets at 200 cm distance are not included because of unreliable quotients caused by small g_3's.

and g in the sagittal plane, i.e. perpendicular to the interocular axis. When target distance is infinity, g equals zero. s obeys Listing's law irrespective of target distance.

For any fixation direction from the ego-centre, s is perpendicular to the plane through this fixation direction and the primary direction. On the other hand, g is perpendicular to the plane of regard because:

$$g_t/g_3 = \theta(1-\theta^2/4) \approx \theta$$

(see Fig. 5.8 and App. A, Eq. B13).

The decomposition of rotation vectors into symmetric and anti-symmetric parts complies with Hering's concept of equal innervations. Contrary to classical elaborations of Hering's law in Helmholtz or Fick angles, in our extension arbitrary rotations of the eye cannot be equated to a combination of rotations about the symmetric and the anti-symmetric parts in isolation[4]. Also, the symmetric and anti-symmetric parts each depend on version as well as vergence (Helmholtz-) angles (App. A, Eq B8 and B9). Thus, the symmetric and anti-symmetric parts should be considered no more than analogues of the classical concept of version and vergence.

Hering's law by itself is a tautology. This holds for the Helmholtz version and vergence angles as well as our symmetric and anti-symmetric parts, in the sense that the movements of the two eyes can always be decomposed in the sum of a conjugate and a disconjugate movement. However, this law has been interpreted to imply that a binocular eye position results from the action of independent version and vergence subsystems. Support for this interpretation comes from various experiments. For instance, when a prism is suddenly introduced in front of one eye while the subject is fixating a target, a saccadic version movement (i.e. similar in both eyes), followed by a slow vergence movement (opposite in both eyes) is observed (Alpern, 1957), although for sustained foveation of the target only one eye needed to move. Erkelens and Collewijn (1985) presented subjects with stereograms, the half-images of which could be moved independently. When only one half-image moved, response movements occurred in both eyes. The dynamic characteristics (gain and phase lag) of the version and vergence components were similar to those observed with isolated vergence or version.

These experiments suggest the existence of different subsystems for vergence and version because of more sluggish dynamic behaviour of vergence compared to version. On the other hand, saccades have properties that do not seem to comply with independence of version and vergence. Enright (1984, 1986) and Erkelens, Steinman and Collewijn (1989) investigated binocular eye movements between targets that required pure vergence or combinations of vergence and version movements. They observed that for a combination of vergence and version the larger part of the eye vergence was carried out during the saccade. This vergence component was much faster than that observed for refixation between targets that required pure vergence, suggesting that version and vergence are not independent subsystems during saccades.

Our elaboration of Hering's law stresses the different geometric properties of the analogues of version and vergence. The symmetric part obeys Listing's law. Similarly, the anti-symmetric part is restricted in its orientations to the mid-sagittal plane. Static eye positions which require version, vergence or combinations of them can be described adequately by this model. It is a matter of speculation whether these properties are maintained for the instantaneous eye positions during saccades and smooth eye movements. If so, this would support independence of version and vergence in this geometric sense.

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[4] A rotation about s followed by a rotation about g is equivalent to a rotation about $(s + g - s \times g)/(1 - s \cdot g)$ (Haustein 1989).

Offsets on the predictions

As can be seen in Fig. 5.4 and Fig. 5.7, both g_l and $d\psi$ have an offset on their predicted values. These offsets have a common origin. Torsion by nature has no objective zero, therefore every calibration procedure has some arbitrary element. We have assumed that torsion equals zero during monocular fixation of a point straight ahead. We do not know whether this was a correct assumption. There may be a problem, as is indicated by the following observation. One may anticipate that during the calibrations the covered eye also assumes a torsion angle of zero. However, in the covered eye we often measured a torsion angle that was different from the angle that was measured when this eye was the viewing one. Possibly torsion should be calibrated in relation to the experimental task. With hindsight a better choice for calibration in our experiment would have been binocular fixation of a point target at optical infinity.

Comparison with another (hypothetical) scheme for 3D binocular eye positions

During fixation of near targets Listing's law is violated. In our description of eye positions, the violation is represented by the term g_l. If this term is set to zero, the classical Listing's eye positions appear. In line with the model predictions, we observe that during convergence ($v < 0$) the right and left eye show intorsion when the target is above the primary direction and extorsion when it is below.

A model for oculomotor control that could be anticipated from a theoretical point of view is one in which the eyes 'try' to maintain optimal retinal correspondence of the fixated objects under all conditions. If one looks at 3-dimensional targets, full correspondence can in general not be achieved, even for small objects, because of self-occlusion of the object that is different for the two eyes. Therefore, we can merely define optimal correspondence. For targets perpendicular to the plane of regard this condition is easily defined in the Helmholtz coordinate system as: $d\theta = d\psi = 0$. If these constraints were implemented by the oculomotor system, such an 'optimal correspondence' model would lead to the following expression for g_l:

$$g_l = \theta v/8$$

Our model, based on the presumptions $d\psi = g_2 = 0$, leads to the prediction $g_l = \theta v/4$. Thus, our model predicts twice as large angles of cyclovergence as would be obtained if retinal correspondence would be optimized. Our data (Fig. 5.4) can be fitted by the relation $g_l = 0.855(\theta v/4)$. This is close to our model prediction, but there is a slight deviation in the direction of the prediction resulting from a control system subserving 'optimal correspondence'. Possibly the observed binocular torsions reflect a compromise between efficient motor control and optimal support of retinal correspondence.

Comparison with other data on 3D eye positions with fixation of nearby targets

In the past several investigators have used subjective techniques to study the eye torsion that accompanies horizontal vergence movements (see Helmholtz, 1867; Donders, 1876;

Allen 1954). For example, it was observed that dichoptically presented vertical (Helmholtz) or horizontal (Donders) contours lose their parallelism during convergence in the horizontal plane, in a way that is consistent with extorsion of the eyes. These extorsions did not occur during convergence in downward gaze. From this, these investigators concluded that the primary position shifts downward during convergence. Our findings do not confirm these observations; we find no significant differences in primary positions determined from data obtained at different fixation distances. From Table 5.1 it can be observed that the thickness of the plane of vectors s is independent of fixation distance. This implies that the primary position has a similar direction for all distances. We have no clear explanation for the discrepancy between these results and our findings, but we remark that even these classic studies do not agree on the magnitude of the phenomenon (Helmholtz, 1867). Possibly, it is partially caused by the large angles of convergence that were used in these studies. Another factor may be the presence of a visible surround during these experiments (see below).

Later investigators used objective techniques for studying monocular torsion as a result of a change in fixation distance. Nakayama (1983) took photographs of one eye while the subject binocularly fixated points at different distances on a line between the camera and the photographed eye. He repeated this experiment with 3 different gaze elevation angles. For elevation angles of zero and of 20 deg down he reported an extorsion up to 3 deg when the vergence angle was changed from 3 to 27 deg (as estimated from his figure). For an elevation angle of 20 deg up, there was less than 1 deg extorsion. It is not clear whether or not these results were obtained in one single experiment. Using an analogous design in monkeys, Mays *et al.* (1991) found an extorsion of about 1 deg as the vergence angle changed from 2.2 to 18.2 deg. Enright (1980) reported that either an intorsion or an extorsion of up to 2.5 deg may occur during monocular fixations as fixation distance changes from 4 m to 15 cm (i.e. when the vergence angle changes from 1 deg to 26 deg).

One possible explanation for the conflicting outcomes of these studies with objective techniques may be that these data may be obtained at different elevation angles relative to the primary direction. One may observe from Fig. 5.3 (upper right panels) that the head often has an offset in pitch (i.e. rotation about the y-axis) of up to 10 deg (twice the amount of rotation of the plane; Tweed *et al.*, 1990). This occurred even though all subjects were explicitly asked to assume a natural upright position. Our model predicts that both the magnitude and the direction of torsion in the non-verging eye depend on both elevation and horizontal vergence angles. Suppose that only the right eye is verging ($\alpha = -v/2$), then the torsion of the left eye (ψ_ℓ) would equal:

$$\psi_\ell = \psi + (d\psi)/2 = -(\theta\ \alpha)/2 + (\theta\ v)/4 = (\theta\ v)/2$$

For example, if one mistakenly assumes that θ equals zero whereas in fact it is +10 deg (down) and the horizontal vergence angle (v) changes from zero to −30 deg, one finds that the left eye extorts by 2.6 deg. This is in the same range as found by most authors. We conclude that it is essential to determine the orientation of the Listing plane for studies of cyclovergence in relation to horizontal vergence.

Recently, Mok and co-workers (Mok, Ro, Cadera, Crawford, Tweed and Vilis, 1992) studied three-dimensional binocular eye positions during fixation of point targets on an iso-vergence surface. In their study, eye positions were expressed as quaternions, which are equivalent to the rotation vectors used by us in the sense that the torsion component of the quaternion relates to rotation about a head-fixed axis (x-axis).

For 30 deg of vergence and 30 deg of elevation, they reported torsion of about 3 deg for each eye, but in opposite directions. They further reported that with 30 of vergence, the displacement plane was rotated over 5 deg in the temporal direction. This is *qualitatively* consistent with our model which predicts that with increasing vergence angles, the displacement plane of each eye rotates in the temporal direction[5]. However, on the basis of our model, with 30 deg of vergence and 30 deg of elevation, we would expect the torsion component of the rotation vector to be about 0.14 radians or 8 deg (from equation (6) we find: $\mathbf{r}_{\ell,1} = -\mathbf{r}_{r,1} = \theta v/4$; θ and v in radians) i.e. nearly 3 times as large as observed by these authors. Consistent with these larger torsion angles, our model predicts that the displacement plane would be rotated temporally by about 15 deg instead of 5 deg. Because our data generally support our model there is a conflict in the reported torsion angles.

Possibly, the smaller torsion angles observed by these authors reflect the influence of visual stimuli other than the fixated target, which may have caused visually induced cyclovergence (e.g. Van Rijn, Van der steen and Collewijn, 1992). We used point targets in a darkened room, which provide a minor - if any - stimulus for visually induced cyclovergence. In contrast, Mok *et al.* arranged their targets on an isovergence surface which was continuously visible throughout the experiment. Suppose that the presence of the visual surround as used by Mok *et al.* induced cyclovergence so as to bring the images of the target configuration in optimal correspondence. As shown above, the 'optimal correspondence' hypothesis predicts g_1 components which are half as large as found by us. If, then, we assume that the difference between our data and those of Mok *et al.* were caused by visually induced cyclovergence, we can account for about 70% of this difference.

Functional organization

We demonstrate that the binocular eye position during fixation of isolated point-targets in space can be described by a model using only three degrees of freedom: target elevation,

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[5] If in equations (6) v is constant, the equations are those of planes that are rotated over $v/2$ and $-v/2$ for the left and right eye respectively with respect to the frontal plane. (Note that v is less than zero for convergence.)

azimuth and vergence angles. In response to specific stimuli the system is capable of using all six possible degrees of freedom. Isolated cycloversion and cyclovergence can be made in response to visual stimuli rotating about the optical axis (Crone, 1975; Crone and Everhard-Halm, 1975; Van Rijn *et al.*, 1992). The presentation of vertical disparate stimuli elicits vertical vergence movements (Perlmutter and Kertesz, 1982). How then should we interpret our result that these 3 parameters are sufficient? Crawford and Vilis (1991) rotated monkeys about axes with varying orientations in space, and measured monocular eye positions. When the required VOR had a torsion component, they found that the quick-phases of the VOR moved the eyes out of the Listing plane so as to keep the average eye position during the quick-slow phase cycle close to this plane. They suggested that Listing's law dictates an optimum and that the system uses all 3 (monocular) degrees of freedom in order to minimize the deviations from this optimum. We speculate that this also applies to the binocular situation: The system may use 6 degrees of freedom to keep the binocular eye position confined to an optimum described by the three parameters of our model. The visual configuration of targets may influence the location of this optimum.

5.6 Conclusions

We have presented evidence for a model which describes the binocular eye position during fixation of any point in 3-dimensional space. The rotation vector of each eye is a composition of a symmetrical part s and an anti-symmetrical part g. These components form an analogue to Hering's (1868) version and vergence components of gaze. We demonstrated that s lies in a frontal plane and obeys Listing's law, whereas g lies in a sagittal plane and is perpendicular to the plane of regard.

In addition, the vertical vergence angle $d\theta$ is close to zero. This observation, together with the restrictions on s and g allowed us to express the binocular eye position in terms of azimuth angle α, elevation angle θ and horizontal vergence angle v of the target. This implies that during fixation of any target in three-dimensional space, the binocular eye position can be described by three parameters in a simple fashion. Our model was developed and tested for fixation of point targets in the dark, which put very little demands on the achievement of retinal correspondence. In that sense our model may not fully capture the geometry of oculo-motor control, because we feel that richer visual stimuli as normally encountered may add to or modify the constraints which determine the final set of possible eye positions.

5.7 References

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5.8 Appendices

A. Mathematical derivation of the model predictions

To derive a set of predictions on the possible eye orientations during fixation of nearby and distant targets we make three assumptions concerning eye position control:

(A1) Eye version obeys Listing's law; the axes of rotation are confined to a plane that is approximately fronto-parallel.
(A2) A similar law applies to the eye vergence; the rotation axes of vergence are confined to the mid-sagittal plane.
(A3) The visual axes intersect at the fixated target.

For the derivations the following coordinates are used. Fig. 5.1 shows a cartesian reference frame with its origin located at a point midway between the centres of rotation of the eyes. This point is called the ego-centre. The right-handed coordinate system of Fig. 5.1 shows forward, leftward and upward directions as the positive x, y and z directions, respectively. For a fixed interocular distance, the target position with respect to the ego-centre is uniquely specified by the three angles of a bipolar coordinate system.

Headcentric target coordinates

Direction lines connect the ego-centre with the target. To describe any target direction relative to the head the following pair of nested rotations is used:

(1) The angle of elevation (θ_t) is the rotation about the interocular axis. Positive rotation about this axis turns the plane of regard in front of the eyes downward. The plane of regard contains the target and the centres of rotation of the eyes.

(2) The angle of azimuth (α_t) is positive for leftward rotation about an axis perpendicular to the plane of regard. The direction-line in the plane of regard, that is perpendicular to the inter-ocular axis corresponds to $\alpha_t = 0$.

The reference direction-line with $\alpha_t = \theta_t = 0$ coincides with the positive x-axis.

Target distance is specified by,

(3) The vergence angle (v_t), which the visual axes subtend in the plane of regard at the target point.

Oculocentric eye coordinates

In addition to the headcentric coordinates, we need a coordinate system that is centred at the eye for the description of the eye's orientation during fixation of the target. We use Helmholtz coordinates. Azimuth (α_ℓ , α_r) and elevation (θ_ℓ , θ_r) are defined as above. However, direction lines towards the target now emanate from the centre of rotation of the eye. Thus, the origin of the coordinate system is located at the centre of the eye. For each eye looking straight ahead (α_ℓ, $\alpha_r = 0$), positive torsion (ψ_ℓ , ψ_r) displaces the upper pole of the eye in the negative y-direction, that is *to the right*. All these oculocentric coordinates are indexed with 'ℓ' or 'r' for the left or the right eye, respectively. The reference orientation of the eye is characterized by ($\alpha_i = \theta_i = \psi_i = 0$), with 'i' taking values 'ℓ' or 'r'. Thus in reference orientation, the eye looks straight ahead into the positive x-direction.

To relate these coordinates to the headcentric coordinates it is useful to introduce version and vergence angles. The horizontal vergence angle is related to the azimuthal directions of the eyes as $v = \alpha_\ell - \alpha_r$. The vertical vergence angle is indicated by $d\theta = \theta_\ell - \theta_r$. To denote cyclovergence, the symbol $d\psi$ ($= \psi_\ell - \psi_r$) is used. The version angles are defined as the means of the corresponding angles of the left and the right eye,

$$\alpha = (\alpha_\ell + \alpha_r)/2$$
$$\theta = (\theta_\ell + \theta_r)/2$$
$$\psi = (\psi_\ell + \psi_r)/2$$

The horizontal version angle (α), the vertical version angle (θ) and the horizontal vergence angle (v) together determine the desired fixation point relative to the ego-centre. During fixation these angles should equal the corresponding target angles (α_t , θ_t , v_t). We stress here that the version and vergence angles defined above are not meant to imply properties of the oculomotor system. The above coordinates are merely useful for a description of the eye position in relation to the position of the fixated target. We believe that they only partially allow for a concise description of the restraints on eye position control. To that end, rotation vectors, as defined below, are more appropriate.

The rotation vector (**r**) quantifies the single rotation that carries the eye from the reference position into the eye position which it characterizes. More specifically:

$$\mathbf{r} = \tan(\varepsilon/2)\mathbf{n}$$

where **n** denotes the normalized direction vector of the rotation axis and ε denotes the turn angle about this axis. For a given rotation vector $\mathbf{r} = (r_1 , r_2 , r_3)$, the components indicate the projections of the vector on the head-fixed x, y and z axis, respectively. The length of the rotation vector,

$$|\mathbf{r}| = \sqrt{(r_1^2 + r_2^2 + r_3^2)}$$

is equal to the tangent of half the angle of rotation about the axis that has the same orientation as the vector **r**. Thus, the eye position relative to the reference position is defined by the direction of the rotation axis and the turn angle about this axis. When the reference orientation for the rotation vectors is the same as that for the Helmholtz coordinates above there is a simple relation between the eye orientation in Helmholtz coordinates and its corresponding rotation vector:

$$\text{(B1)} \qquad \mathbf{r}_i = \begin{bmatrix} \tan(\psi_i/2) + \tan(\alpha_i/2)\tan(\theta_i/2) \\ \tan(\theta_i/2) + \tan(\alpha_i/2)\tan(\psi_i/2) \\ \tan(\alpha_i/2) - \tan(\theta_i/2)\tan(\psi_i/2) \end{bmatrix} / \, (1-\tan(\alpha_i/2)\tan(\theta_i/2)\tan(\psi_i/2))$$

The subscript 'i' can take the values 'ℓ' and 'r' to indicate the rotation vector and the Helmholtz angles of the left and right eyes, respectively. The above expression quantifies the single turn which carries the eye from the reference position ($\alpha_i = \theta_i = \psi_i = 0$, that is: the eye looks into the direction of the positive x-axis, with zero torsion) to the current eye position (α_i , θ_i , ψ_i).

One may obtain an intuitive justification of expression (B1) by consideration of the *headcentric* direction of the 'nested' rotation axes of the Helmholtz system. The components of the first term of **r**, for instance, tell us that positive rotation about the x-axis ($r_1 > 0$) occurs for a positive Helmholtz torsion, that is, a rotation about the torsion axis (ψ_i) when the eye looks into the reference direction ($\alpha_i = \theta_i = 0$). Positive rotation about the same headcentric axis occurs also for positive rotation about the azimuthal axis (the axis perpendicular to the plane of regard; $\alpha_i > 0$) when the plane of regard is turned 90 degrees downward ($\theta_i = 90$). This illustrates the meaning of the second term of the x-component of $\mathbf{r}_i$. Notice that this argumentation is only valid, because in the Helmholtz system the azimuthal axis is oriented perpendicular to the plane of regard and thus turns about the interocular axis when the elevation changes. Interchanging the azimuthal and the elevation coordinates in the above reasoning is therefore not possible. Similar reasoning applies to the relation of the other components of **r** to the Helmholtz angles.

For small angles ($|\alpha|, |\theta|, |\psi| < 30$) Eq. B1 can be simplified by replacing the tangent of the angle by the angle itself, in radians. For these conditions the angular term in the denominator on the right hand side of Eq. B1 can be neglected. This approximation introduces errors of the order of 2.5% or less.

(B2)
$$\mathbf{r}_i \approx \begin{pmatrix} \psi_i/2 + \alpha_i/2\ \theta_i/2 \\ \theta_i/2 + \alpha_i/2\ \psi_i/2 \\ \alpha_i/2 - \theta_i/2\ \psi_i/2 \end{pmatrix}$$

Following Hering's principle, eye positions are represented by the sum of a symmetric and an anti-symmetric component. In this context, version may be identified with the symmetric component of the rotation vectors of the eyes (s) and the vergence component with the anti-symmetric component (g) with the proviso that both s and g depend on a combination of the vergence and version angles, as shown below.

(B3)
$$\mathbf{r}_\ell = s + g$$

(B4)
$$\mathbf{r}_r = s - g$$

We are now in a position to express the restrictions (A1) and (A2) in a more quantitative manner. Suppose that the coordinate system is chosen such that the positive x-axis of Fig. 5.1 is directed perpendicular to the Listing plane. In that case (A1) may be expressed as:

(B5)
$$s_1 = 0$$

That is, the x-component of s equals zero.

Similarly, (A2) implies the following constraint:

(B6)
$$g_2 = 0$$

This means that the y-component of g equals zero. The third assumption (A3) states that the lines of sight must intersect, which implies that the elevation of the two eyes is identical: $\theta_\ell = \theta_r$ or,

(B7)
$$d\theta = 0$$

These three constraints on eye position enable us to formulate the components of the rotation vectors of both eyes as a function of the coordinates of the desired fixation position (α, θ, v) only. These expressions are the goal of our derivations because they tell us the orientation of the eyes during fixation of a target, which may be located at any point in front of the subjects head.

Taking the difference of the rotation vectors of the left and right eye and replacing the oculocentric angles by the version and vergence angles[6] we obtain,

(B8) $$g = (\mathbf{r}_\ell - \mathbf{r}_r)/2 = 0.5 \begin{bmatrix} d\psi/2 + \alpha\, d\theta/4 + \theta\, v/4 \\ d\theta/2 + \alpha\, d\psi/4 + \psi\, v/4 \\ v/2 - \psi\, d\theta/4 - \theta\, d\psi/4 \end{bmatrix}$$

Similarly, taking the sum of the rotation vectors of the left and the right eye and replacing the oculocentric angles by the version and vergence angles[6] we obtain,

(B9) $$s = (\mathbf{r}_\ell + \mathbf{r}_r)/2 = 0.5 \begin{bmatrix} \psi + \alpha\, \theta/2 + d\theta\, v/8 \\ \theta + \alpha\, \psi/2 + d\psi\, v/8 \\ \alpha - \psi\, \theta/2 - d\theta\, d\psi/8 \end{bmatrix}$$

Combining equations B9, B7 and B5 we obtain,

(B10) $$\psi = -\alpha\theta/2$$

Combining equations B10, B8, B7 and B6 we obtain,

(B11) $$d\psi = \theta v/2$$

Finally, by substitution of B7, B10 and B11 in B8 and B9 we obtain explicit expressions of the symmetric and anti-symmetric components of the rotation vectors:

(B12) $$s = \begin{bmatrix} 0 \\ \theta/2\,(1 + \alpha^2/4 - v^2/16) \\ \alpha/2\,(1 + \theta^2/4) \end{bmatrix}$$

(B13) $$g = \begin{bmatrix} \theta\, v/4 \\ 0 \\ v/4\,(1 - \theta^2/4) \end{bmatrix}$$

Using Eq. B3 and B4 it is straightforward to derive expressions of the rotation vectors of both eyes. Fig. 5.9 shows the major results of the theory in a scheme.

For the left eye the rotation vector is give by,

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[6] $\alpha = (\alpha_\ell + \alpha_r)/2$ $d\alpha = (\alpha_\ell - \alpha_r)$
$\theta = (\theta_\ell + \theta_r)/2$ $d\theta = (\theta_\ell - \theta_r)$
$\psi = (\psi_\ell + \psi_r)/2$ $d\psi = (\psi_\ell - \psi_r)$

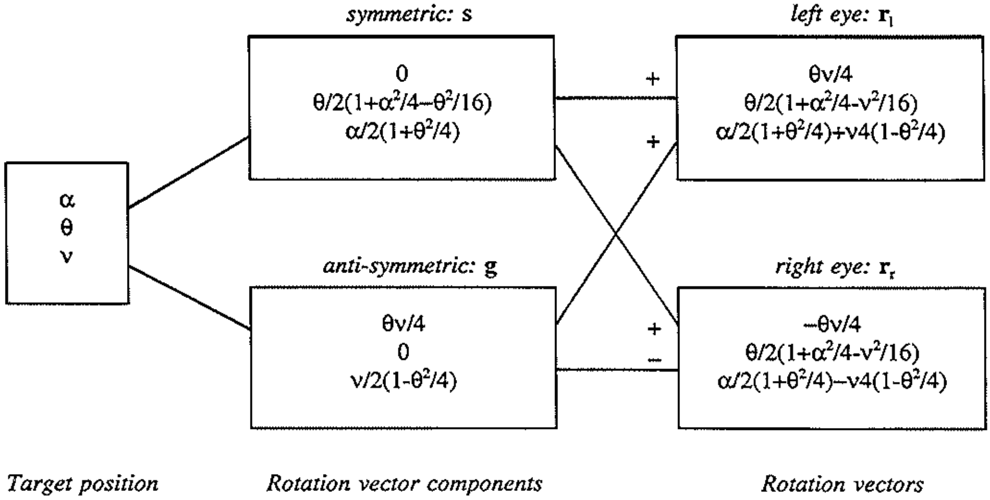

FIGURE 5.9. The main results of the theory. The symmetric part s and the anti-symmetric part g are expressed in terms of the target angles (α, θ, v) α denotes the azimuth angle, θ the elevation angle and v the horizontal vergence angle. These angles are relative to a Helmholtz coordinate system. s is analogous to traditional version and g to traditional vergence. $\mathbf{r}_\ell$ and $\mathbf{r}_r$ denote the rotation vectors of the left and right eyes (Eq. B3 and B4). In the vectors s, g, $\mathbf{r}_\ell$ and $\mathbf{r}_r$, the first, second and third components indicate rotation about the x,y and z axes. respectively.

(B14)
$$\mathbf{r}_\ell = \begin{bmatrix} \theta\, v/4 \\ \theta/2\,(1 + \alpha^2/4 - v^2/16) \\ \alpha/2\,(1 + \theta^2/4) + v/4\,(1 - \theta^2/4) \end{bmatrix}$$

and for the right eye we obtain,

(B15)
$$\mathbf{r}_\ell = \begin{bmatrix} -\theta\, v/4 \\ \theta/2\,(1 + \alpha^2/4 - v^2/16) \\ \alpha/2\,(1 + \theta^2/4) - v/4\,(1 - \theta^2/4) \end{bmatrix}$$

These expressions, then, specify for each eye the torsion position (as rotation about the x-axis), the vertical eye position (as rotation about the y-axis) and the horizontal eye position (as rotation about the z-axis) in that order.

Finally, we remark that it is possible to derive more accurate expressions for ψ and dψ when we refrain from replacing the tangent of the angles by the angles themselves, as was done for the derivations of Eqs. B10 and B11. In that case, the following equations (B10b and B11b) apply. In this derivation the only approximations are replacement of the cos(ψ) and cos(dψ) by cos(5 degrees). This approximation holds to an accuracy of better than 2%, provided that the torsion angles of the eyes do not exceed 10 degrees.

(B10b) $$\sin(\psi) = \frac{-1.97\sin(\alpha)\tan(\theta/2)}{\cos(\alpha) + \cos(v/2)}$$

and,

(B11b) $$\sin(d\psi) = \frac{1.97\sin(v)\tan(\theta/2)}{\cos(\alpha)\,(\cos(\alpha) + \cos(v/2))}$$

B. Transformation from Fick- into Helmholtz coordinates

In the Helmholtz system we define α as the azimuth angle, θ as the elevation angle and ψ as the torsion angle. In the Fick system these definitions are μ for azimuth angle, δ for elevation angle and λ for torsion angle. It can be shown that:

$$\alpha = \arcsin(\ \cos(\delta)\sin(\mu)\ )$$

$$\theta = \arctan(\ \tan(\delta)/\cos(\mu)\ )$$

$$\psi = \lambda - \arcsin(\ \sin(\delta)\sin(\mu)/(1+\cos(\delta)\cos(\mu))\ ) - \arcsin(\ \sin(\alpha)\sin(\theta)/(1+\cos(\alpha)\cos(\theta))\ )$$

(Lemij, 1990) The two arcsin components of ψ represent the 'false torsion' angles that are found in the Fick and Helmholtz system respectively when the eye obeys Listing's law (Ferman *et al.*, 1989b).

CHAPTER 6

EYE TORSION ASSOCIATED WITH DISPARITY-INDUCED VERTICAL VERGENCE IN HUMANS

6.1 Summary

Recently, Enright described an unexpected association between disparity-induced vertical vergence and cycloversion (conjugate eye torsion) (Enright, JT *Vision Research 415,* 279 (1992)). The present experiments were performed to verify these findings and investigate the nature of this association. We presented subjects with a dichoptic image of concentric circles in which a step in vertical disparity of 1 deg was introduced. After 4 s the disparity was eliminated. Eye movements were measured with scleral coils. We confirmed Enright's findings in that a left-over-right vertical vergence was associated with levo-cycloversion (upper poles towards left shoulder) and vice versa. The size of the cycloversion and the vertical vergence were in the same range. In addition we found that part of the cycloversion response was in the form of a torsional nystagmus and that the relative contribution of the left and right eyes was independent of the horizontal gaze angle. These additional findings are in conflict with the hypothesis, offered by Enright, that the association is caused by a bilateral activity of the superior oblique muscles.

6.2 Introduction

Binocular, single vision requires optimal correspondence between the images on the retina's of the two eyes. Such correspondence is achieved by horizontal and vertical alignment of the two lines of sight, such that they intersect in a single binocular fixation point, as well as by correct orientation of each eye around the axis formed by its line of sight. The horizontal distance between the eyes, combined with the variable distance of objects, necessitates a large degree of freedom in the horizontal angle between the eyes, which is manifest as a large range of horizontal vergence eye movements. In natural conditions, horizontal convergence is associated with accommodation and pupillary constriction (the near triad); the functional significance of this association is obvious.

Recently, we (Van Rijn and Van den Berg, 1993) described the association of cyclovergence with horizontal vergence and elevation (vertical gaze angle), and argued that this linkage, formally described as a 3-D extension of Listing's law, serves to optimize torsional correspondence. Accordingly, only limited independent control of cyclovergence by cyclodisparity has been demonstrated (Kertesz, 1983; Howard and Zacher, 1991; Van Rijn, Van der Steen and Collewijn, 1992).

In a similar vein, the vertical alignment of the eyes is usually constrained by the need to keep both lines of sight within a single plane of regard. Accordingly, independent control of vertical gaze angles (vertical vergence) is limited (Kertesz, 1981). The limited range and dynamics of vertical vergence and cyclovergence (as far as the latter is independent of horizontal vergence and elevation) suggest that they are mainly involved in the slow reduction of vertical and cyclo-disparities, resulting from imperfections in binocular motor control, rather than in a moment-to-moment control of binocular gaze.

Recently, Enright (1992) described an association between two movement directions which seems less readily interpretable in functional terms such as sketched above. He reported that disparity-induced vertical vergence was associated with conjugate eye torsion, i.e. cycloversion. Left-over-right (L/R) vertical vergence (i.e., elevation of the left eye above the right eye) was associated with counter-clockwise torsion in both eyes, i.e. rotation of both upper poles towards the left shoulder[1]; right-over-left vertical vergence (R/L) with clockwise torsion. Enright also found vertical vergence to be combined with slight lateral translations of the eyes. Therefore, he hypothesized that this torsion was caused by the fact that vertical vergence was mediated predominantly by the superior oblique muscles. This would indicate a mechanical constraint rather than a functional significance as the basis for this linkage.

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[1] We define all eye rotations with respect to the subject. See Methods.

Enright obtained his results using video-oculography, which offers a very limited temporal resolution. The first purpose of the present study was to reproduce these unanticipated results with scleral coils. After we confirmed Enright's findings we tried, as a second goal, to gain insight in the mechanism of this phenomenon. For this purpose, we investigated the dynamic relation between the vertical vergence and cycloversion. The superior-oblique hypothesis of Enright predicts this relation to be very tight. Secondly, according to this hypothesis one should expect that an abducted eye displays more torsion than an adducted eye because in the latter, the primary action of the superior oblique muscle is depression and not torsion. We tested this prediction by measuring the gaze dependency of the contribution of the left and right eyes to the cycloversion response.

The results indicate that the association between vertical vergence and cycloversion is indeed present, at least, this was the case in 4 out of our 6 subjects. However, in some of these subjects the torsional responses were partly in the form of a cycloversional nystagmus. The contribution of the left and right eyes was independent of horizontal gaze angle. These findings are in conflict with the superior-oblique hypothesis of Enright.

6.3 Methods

Subjects

Six human subjects (3 females and 3 males) participated in these experiments after giving informed consent. Their age ranged from 26 to 44 years. One of them (subject 5) wore spectacles (S -2.5 D, ODS). All had a visual acuity of at least 20/20 in each eye (with spectacle correction) and a stereo-acuity of at least 60 sec of arc, as measured with the TNO fly-test (Medical Workshop, Groningen). Phorias were determined in horizontal and vertical directions using a Maddox cross. The test was performed with the subject at 145 cm distance from the cross since this was the distance of the visual stimulus during the experiment. Horizontal and vertical phorias were small: vertical phorias were less than 0.6 deg (see table 1); horizontal phorias ranged from 1.32 deg *eso* to 0.06 deg *exo*.

Recording of eye positions

Eye positions were measured with scleral induction coils of the combination type (Ferman, Collewijn, Jansen and Van den Berg, 1987) according to the technique of Robinson (1963). Eye position signals were amplified, low-pass filtered, digitized at 125 Hz and stored on disk by a PDP 11/73 minicomputer, for off-line analysis. Prior to each experiment, all channels were calibrated with the coils mounted on a protractor device, near the centre of the magnetic field. During the first measurement of each session subjects fixated a small dot that was straight ahead with respect to the coil system. The steady offset values from this measurement represented coil misalignment. Correction for this misalignment was performed by a matrix transformation (Ferman *et al.*, 1987) using these steady offset values. (We neglected the small adduction of each visual axis (about 1.3 deg) due to the finite distance (145 cm) of the target.) All eye rotations were expressed in Fick coordinates (see e.g. Robinson, 1963; Carpenter, 1988). Therefore, torsion is expressed as rotation about the line of sight. All eye deviations are defined with respect to the subject. Hence, levo-cycloversion means that the upper poles of the eyes rotate towards the subject's left side.

Protocol and visual stimulus

Subjects were seated with their eyes near the centre of the magnetic field of the eye position measurement system. Their heads were supported by chin and forehead rests. The visual stimulus was backprojected on a translucent screen at 145 cm distance in front of the subject. This stimulus, subtending 43 deg of visual angle, consisted of 5 concentric circular rings, each about 2 deg wide (see Fig. 1). It was presented to the subjects dichoptically; two images were presented by separate slide projectors with red and green filters. Filters of the same material were mounted on a pair of spectacles worn by the subject. The position of the images of the left and right eyes could be controlled by mirrors, attached to scanners (General Scanning, Watertown, Mass., Model MG 350D). This stimulus configuration was designed to enable control of vertical disparity without providing any reference for eye torsion.

Each experiment consisted of 16 trials (plus calibrations). Each trial lasted 12 seconds. At the start of a trial, no disparity was present; after 4 s a vertical disparity was introduced, either left-over-right (L/R) or right-over-left (R/L). Again 4 s later this disparity was eliminated. Introduction and elimination of the disparities were step-like. The size of the disparity was 1 deg. This appears to be about the maximum vertical disparity that can be fused when presented in a step (Perlmutter and Kertesz, 1978). The presentation of the disparity was symmetric in the sense that the displacements of the images to the left and right eyes were equal but opposite in magnitude (+/- 0.5 deg). The duration of the disparity presentation was limited to 4 s in order to restrict the contamination of cycloversion by spontaneous variation (Van Rijn, Van der Steen and Collewijn, 1993). Subjects were instructed to fixate the centre of the visual stimulus, but, if possible, to appreciate the stimulus as a whole and to achieve a single, fused image. Subjects were asked to abstain from blinking during trials. Throughout the experiment, the room was darkened.

An additional experiment in subject 6 was performed using the same protocol, except that the head was fixated by a bite-board. An additional experiment in subject 2 consisted of 36 trials (plus calibrations). The protocol was identical except that the stimulus was presented either straight ahead or 20 deg left or right from the straight ahead.

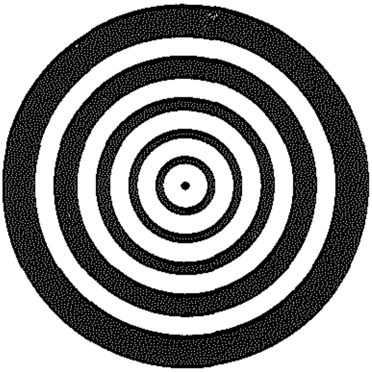


FIGURE 6.1. The stimulus pattern used in these experiments. Concentric circles were used so as to be able to present vertical disparities and leave torsion free. The width of each white annulus was about 2 deg. The width of the black annuli increased in the visual periphery, to compensate for decreased visual acuity. The outer border of the peripheral black circle could not be perceived in the dark room; the stimulus size (43 deg of visual angle) is measured as the diameter of the outer border of the outer white annulus.

Data analysis

Prior to analysis, all data were inspected for the occurrence of blinks; 13% of the trials were excluded on this ground.

After correction for coil misalignment (see above), vertical vergence, cyclovergence and cycloversion were calculated for each data sample. Vergence was calculated as left eye position minus right eye position (hence cyclovergence = left eye torsion − right eye torsion) and version as the mean of the position of the left and right eye. Data shown in Fig. 2 are typical examples of recordings for all subjects obtained in this way.

Saccades were removed from the cycloversion traces by a computer routine. A saccade was defined as any period during which torsional eye velocity exceeded 3 deg/s. This criterium proved to remove the majority of small torsional saccades without affecting slow torsional eye movements. Cycloversion with saccades removed will be denoted as 'smooth cycloversion'.

For the purpose of averaging, sample numbers were reduced by a factor 12, i.e. every 12 consecutive samples were replaced by one sample that represented the mean of these 12 samples. Subsequently, samples were averaged across all trials with a similar disparity direction in one session. Averaged responses are shown in Fig. 3.

Statistical analysis

Exponential curve-fits of vertical vergence responses were performed using the program Slide-Write 5.0 (Advanced Graphics Software Inc., Carlsbad CA). In this program, curves are fitted by an iterative process, minimizing the value of X^2 (chi squared). Curve-fit parameters were tested for differences with the MANOVA routine from the SPSS-PC statistical package.

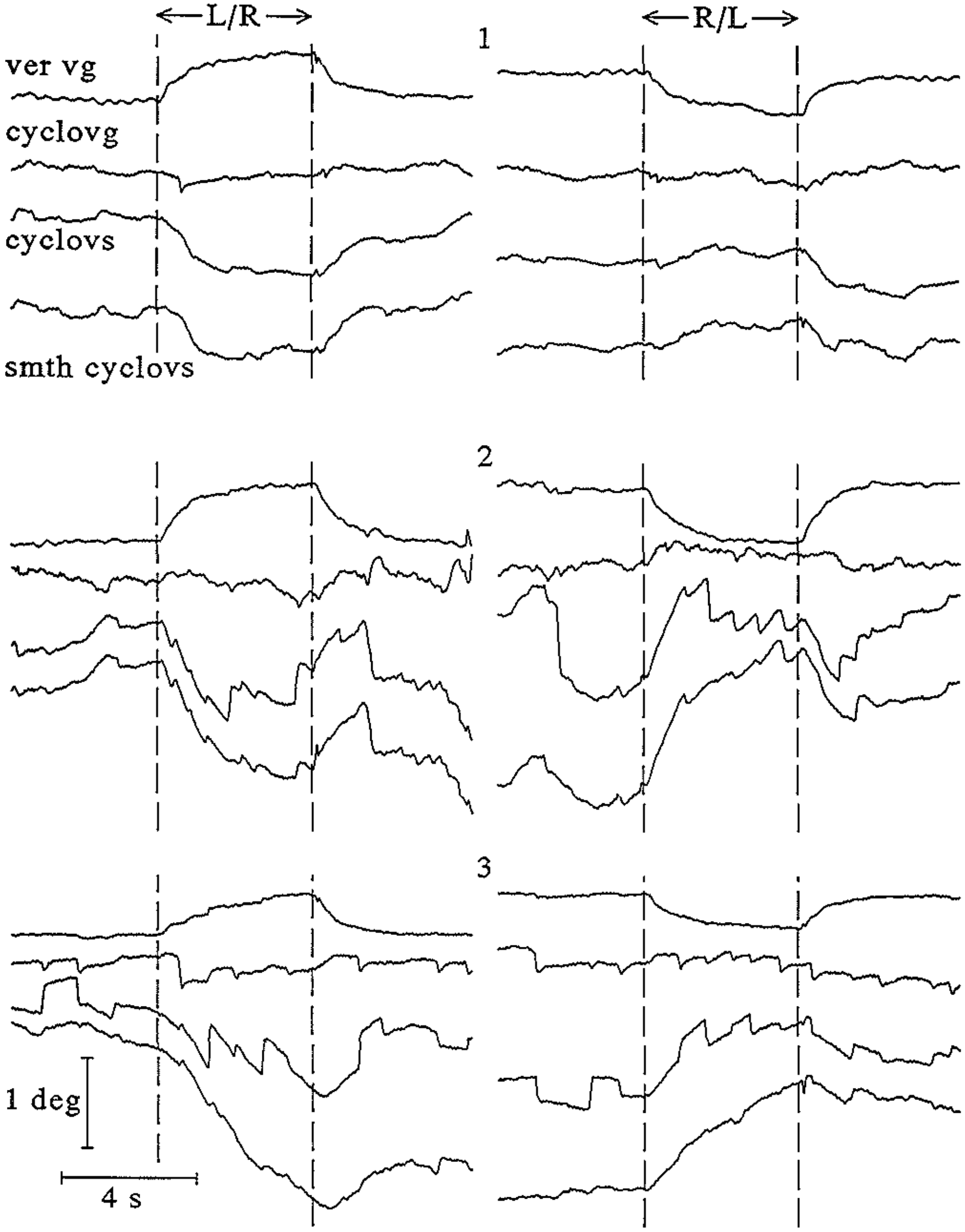
6.4 Results

Vertical vergence

Vertical eye movements were recorded in 5 of our 6 subjects. (Due to technical problems, in subject 4 only torsional movements were recorded.) All of them displayed clear vertical vergence responses to the vertical disparity-stimulus in either direction (L/R or R/L). Examples of individual trials, for all subjects, are shown in Fig. 2. Averaged responses are shown in Fig. 3.

We computed the gain and time constant of the responses by fitting to these average curves an exponential curve of the type $(a_0*(1-\exp(-t/\tau))$ for the response to the introduction of the disparity and $(a_0*\exp(-t/\tau))$ for the response to its elimination. In these fits, t is the elapsed time after the disparity step, a_0 is the asymptote of the response and τ is the time constant. In general the curve fit quality was good: r^2 was 0.984 ± 0.021 (mean ± SD of all 20 fits). a_0 was 0.55 ± 0.11 (mean ± SD) and not significantly different between disparity introduction and elimination or between positive and negative disparities. Since the disparity step was 1 deg, this value of 0.55 equals the gain of the vertical vergence movement. τ was significantly shorter for disparity elimination as compared to introduction: 0.60 ± 0.12 s as compared to 0.94 ± 0.48 s. (ANOVA: $P = 0.030$). Time constants for positive and negative disparities were not significantly different.

→ and →→ FIGURE 6.2. Individual responses of all subjects to the 1 deg stimulus disparity. In each panel, the first and second interrupted vertical lines indicate introduction and elimination of the disparity, respectively. In the left panels the disparity was left-over-right (L/R); in the right panels, right-over-left (R/L). L/R vertical vergence is signed positive, as well as *in*-cyclovergence and *dextro*-cycloversion. Vertical vergence responses (not measured in subject 4) are roughly exponential. In subjects 1 through 4 the induction of a left over right vertical vergence by a step in stimulus disparity is associated with levo-cycloversion (left panels) and vice versa (right panels). Responses were partly in the form of a cycloversional nystagmus, particularly in subjects 2 and 3. Cyclovergence hardly showed any variation, indicating that the cycloversion was evenly distributed over the left and right eyes. Subject 5 shows dextro-cycloversion, both after the introduction and after the elimination of the disparity; subject 6 does not show torsion in relation to the vertical disparity.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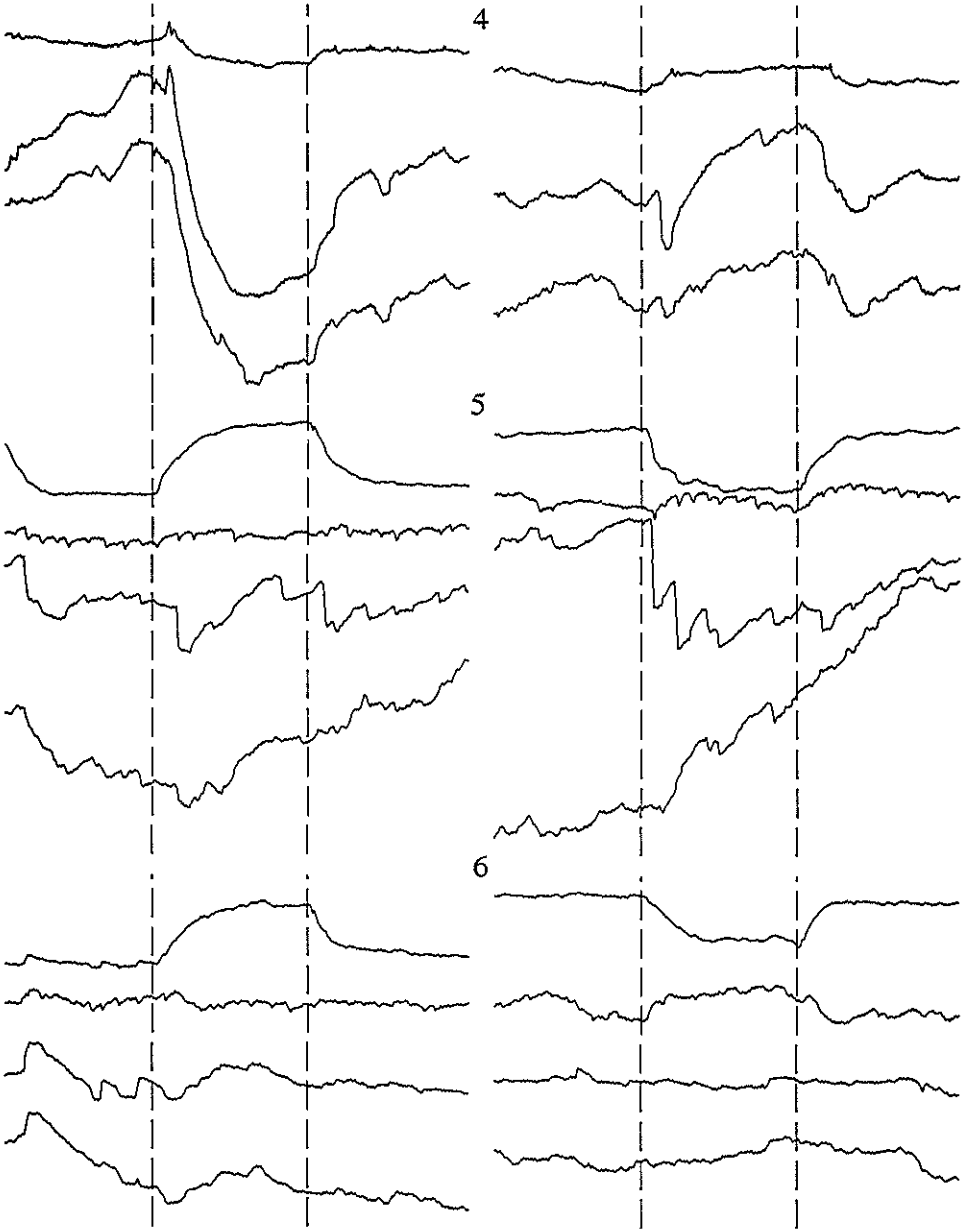
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6

Cycloversion

Fig. 2 and 3, lower tracings, show the 'raw' and 'smooth' cycloversion responses, prior to, during and after the elimination of the vertical disparity. Fig. 2 shows individual responses, Fig. 3 depicts averaged responses.

Spontaneous cycloversion

Prior to the introduction of the vertical disparity, subjects 2 and 4 showed a systematic drift of spontaneous cycloversion. This is best appreciated from the averaged smooth cycloversion tracings (Fig. 3). Both in subjects 2 and 4 this drift was in dextro-cycloversional direction.

Disparity introduction

The introduction of a vertical disparity was associated with vertical vergence and, in 4 of our 6 subjects (1 through 4), with conjugate eye torsion or cycloversion. Left-over-right (L/R) vertical disparity was associated with levo-cycloversion; right-over-left (R/L) vertical disparity with dextro-cycloversion. A variable part of the cycloversion was in the form of a cycloversional nystagmus (with the slow phase in the indicated direction) rather than a tonic response. The magnitude of this nystagmoid part can be deduced from the difference between the 'raw' and cumulative 'smooth' cycloversion tracings in Fig. 3. In subjects 1 and 4 the response was almost exclusively tonic; in subjects 2 and 3 the responses were roughly half tonic and half nystagmoid. The averaged responses, shown in Fig. 3, demonstrate, in addition to the effects shown in Fig. 2, that cycloversion responses were exponential or linear, depending on the subject and the disparity direction. Because of this variability, curve fits were not performed on cycloversion data. Subject 5 displayed a dextro-cycloversional nystagmus, independent of the direction of the vertical disparity step (see Fig. 2 and 3, fifth panels). Only during a very short time interval after a L/R disparity step (or after the reversal of a R/L disparity step) did this subject display a nystagmus with the slow phases in levo-cycloversional direction (indicated by asterisks in Fig. 3). The sixth subject failed to show any torsion in association with vertical vergence (Fig. 2 and 3, sixth panels).

Disparity elimination

In subjects 1 through 4, the elimination of the stimulus disparity led to a reversal of the cycloversion, independent of whether the disparity was left-over-right (left panels) or right-over-left (right panels). In subjects 2 and 4 this reversal was only transient. This may be caused by the rapid takeover of the 'normal' cycloversional nystagmus that was observed prior to disparity introduction in these two subjects (see above). Subject 5 continued to show a dextro-cycloversional nystagmus, independent of the direction of the

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← FIGURE 6.2, subjects 4, 5 and 6. Legends see previous page.

preceding vertical disparity. Only after elimination of a right-over-left disparity the cycloversion was, transiently, in levo-cycloversional direction. As was the case for disparity introduction, in subject 6 the elimination of the disparity did not elicit eye torsion.

Association with horizontal and vertical version

The cycloversional nystagmus movements that were described above did not occur, altogether, in isolation. Cycloversional fast phases were accompanied by microsaccades in horizontal and vertical direction. Subjects 2 and 3 displayed a small vertical nystagmus that was upbeat and downbeat in these two subjects, respectively. The fast phases of this vertical nystagmus coincided with the fast phases of the cycloversional nystagmus and the amplitudes of the vertical and cycloversional nystagmus were in the same order of magnitude. Subject 6 also displayed a small vertical (upbeat) nystagmus, although in this subject there was no cycloversional nystagmus. Notably, in subjects 2, 3 and 6 this vertical nystagmus was also present in the (calibration) measurements in which no vertical disparity was presented.

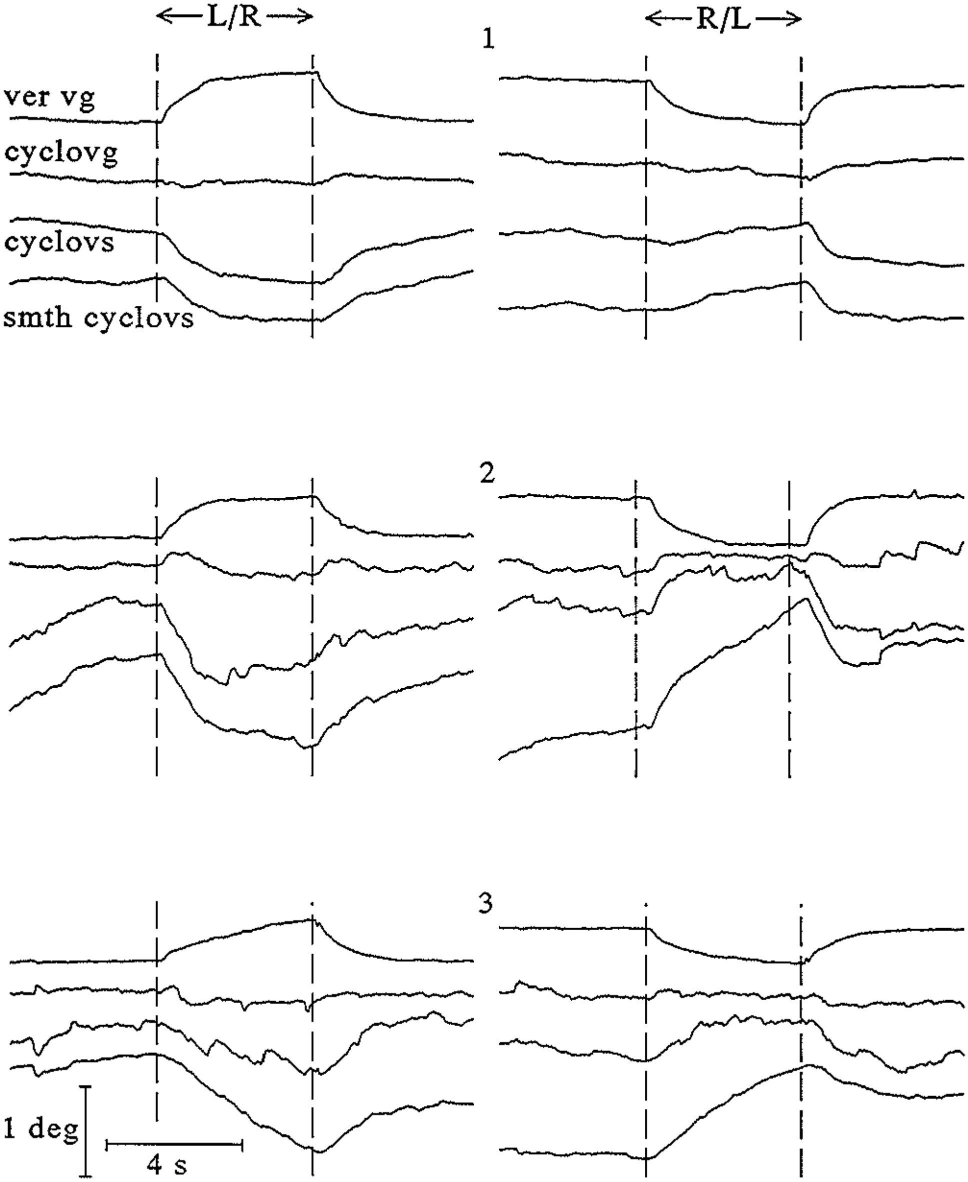
Head fixation in subject 6

The absence of any cycloversion in association with vertical vergence in one subject (subject 6) is a strong argument against the superior oblique hypothesis of Enright (see Discussion). In theory, however, this absence may be caused by compensatory torsional head movements. In order to exclude this latter possibility, we repeated the experiment in subject 6, but fixated the subject's head by a bite-board. The results were identical: neither the introduction of the disparity nor its elimination elicited cycloversion.

Role of gaze direction

In abduction the superior oblique muscle will act more as a cyclorotator than in adduction. Therefore, if one postulates (as Enright) that vertical vergence is mediated predominantly by the superior oblique muscles, one should expect that an abducted eye will cyclorotate more than an adducted eye.

→ and →→ FIGURE 6.3. Averaged tracings, separated according to disparity direction (L/R or R/L). Tracings are averages of 6 to 8 trials. Conventions are as in Fig. 2. In subjects 1 through 4 the induction of a left over right vertical vergence by a step stimulus disparity is associated with levo-cycloversion (left panels) and vice versa (right panels). The reversal of the vertical vergence generally also leads to a reversal of the cycloversional response. Subject 5 shows dextro-cycloversion on all occasions. However, a small transient levo-cycloversion (indicated by asterisks) was found after introduction of the L/R- or elimination of the R/L disparity. Subject 6 does not show any torsion in relation to the vertical disparity. In all subjects, cyclovergence shows little variation, indicating that the torsion was about equal in both eyes.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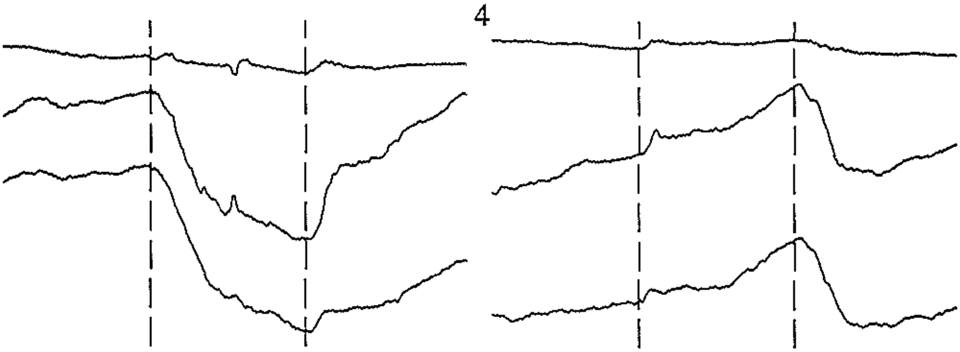

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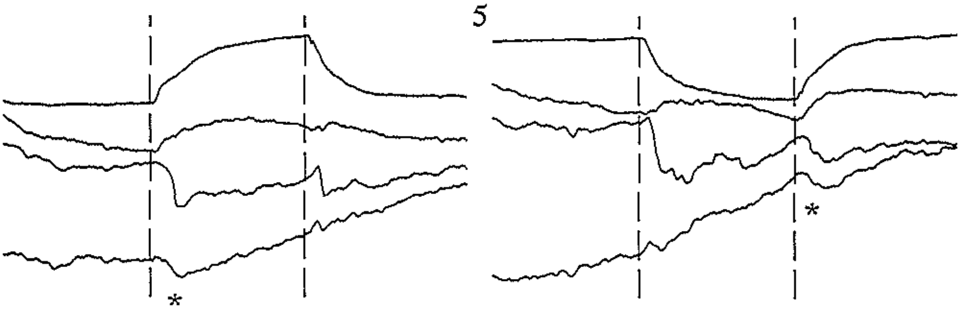

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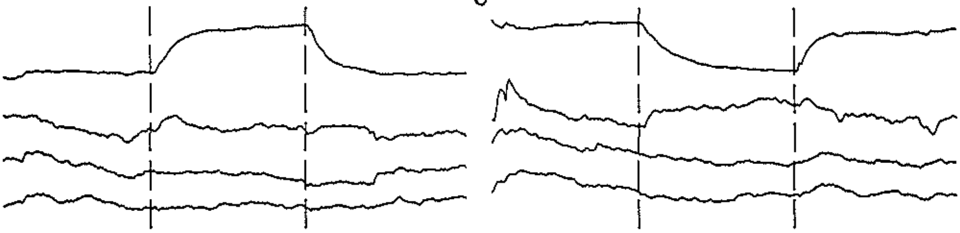

We tested this prediction in subject 2, who showed the vertical vergence - cycloversion association very markedly. We presented to this subject the stimulus at various azimuth angles: 20 deg left, straight ahead and 20 deg right. One should expect *ex*-cyclovergence when looking at a L/R disparity that is presented *rightward* with respect to the straight ahead. A R/L disparity should induce *in*-cyclovergence when presented in this direction. Disparities presented leftward from the straight ahead should induce cyclovergence with opposite sign.

If the superior oblique muscle would act as a string attached to the globe, the ratio between torsion and elevation should equal the sine of the insertion angle. Since in straight ahead direction the insertion angle equals about 51 deg (Von Noorden, 1990), one may calculate that in 20 deg lateral gaze, cyclovergence should be about 60% of cycloversion[2]. The pulling direction may rotate, to some extent, along with rotations of the globe (the 'no-pully' model proposed by Miller and Robbins, 1987; see Miller, 1989). Therefore the torsion / elevation ratio may be less dependent on the insertion angle and cyclovergence may be considerably smaller. However, it should still be in the indicated direction.

The results from our experiment, shown in Fig. 4 (averaged responses), demonstrate that cyclovergence varied hardly at all. Moreover, cyclovergence did not systematically depend on either the horizontal gaze direction or the direction of the vertical disparity. In contrast, cycloversion was elicited in all three horizontal gaze directions, in a way that was similar to that found in the first experiment.

6.5 Discussion

A primary purpose of these experiments was to try to reproduce the results of Enright (1992), who found that disparity-induced vertical vergence is associated with cycloversion. We largely confirmed his results, but found that the response was partly in the form of a cycloversional nystagmus rather than a tonic response. In a specific experiment we tested and rejected the hypothesis offered by Enright to explain his findings. Furthermore, our present results may relate to the spontaneous torsional nystagmus that was observed in this and earlier experiments. In the final section of this discussion we will compare the characteristics of our vertical vergence responses to findings reported in the literature.

← FIGURE 6.3, subjects 4, 5 and 6. Legends see previous page.

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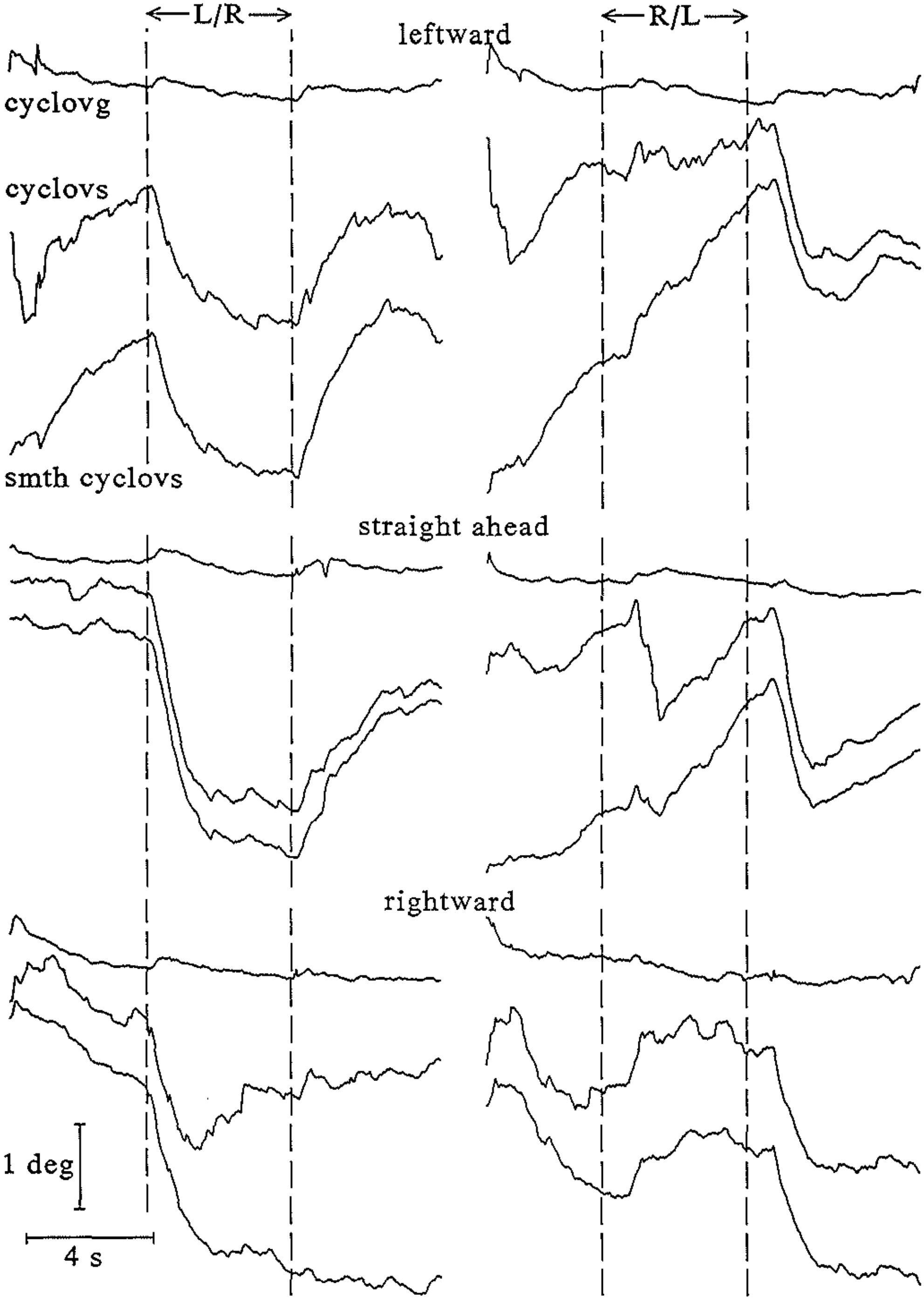
[2] The advantage of using cyclovergence rather than torsion of the individual eyes is that the former is less contaminated by spontaneous variation. See Van Rijn *et al.*, 1994.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Vertical vergence vs. cycloversion

In the present experiments we confirm, in 4 of our 6 subjects, the findings of Enright that cycloversion is coupled to vertical vergence. However, we found that vertical vergence partly induced a cycloversional nystagmus rather than an exclusively tonic cycloversion. This cycloversion was rightward for R/L vertical disparities and leftward for L/R disparities. The slow phase velocity of the cycloversional nystagmus either decreased exponentially or was constant, depending on subject and disparity direction.

Enright found that the cycloversion responses were about 40% of the vertical disparity size (which was 0.86 deg). We found the size of the tonic components of the cycloversion responses to be about equal to that of the vertical vergence (Fig. 2, saccades present). If we take into consideration that the gain of the vertical vergence was about 0.55, our response magnitudes are in agreement with those of Enright.

Mechanism

The hypothesis offered by Enright to explain his findings is that vertical vergence is mediated predominantly by the superior oblique muscles. Contraction of this muscle produces eye depression and also intorsion. Relaxation produces the opposite effects. Enright found support for this hypothesis in his findings that vertical vergence was associated with a slight lateral displacement of the eye, in a direction that was in agreement with expected contraction or relaxation of the superior oblique muscle.

Our findings are in conflict with this hypothesis in three ways. Firstly, according to this hypothesis one should anticipate a tonic cycloversion rather than a cycloversional nystagmus since the tonic vertical vergence requires a tonic contraction of the superior oblique muscle. The fact that in our experiment the cycloversion was often nystagmic in nature strongly suggests that the origin is central and not peripheral. Secondly, a mechanical coupling, as proposed by Enright, predicts a firm relation between vertical vergence and cycloversion in all subjects. However, we find this relation to be idiosyncratic: in subject 5 we only found dextrocycloversion, independent of the direction of the vertical vergence; in subject 6 there was no cycloversion at all. In a repeated experiment in subject 6 we fixated the head by a bite-board and demonstrated that this lack of cycloversion was not caused by compensatory torsional head movements

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← FIGURE 6.4. Cycloversion and cyclovergence responses in different horizontal gaze directions: "leftward" and "rightward" indicate gaze angles that are rotated 20 deg with respect to the straight ahead. Tracings are averages of 3 to 6 trials. Conventions are as in Fig. 2.
Cyclovergence does not systematically depend on either horizontal gaze angle or the direction of the disparity. Although cycloversion responses were variable, the pattern largely corresponds to that found in the earlier experiment (see Fig. 2 and 3). The transient ex-cyclovergence at the beginning of most tracings is an aftereffect of blinking during inter-trial intervals. Due to technical problems, vertical vergence was not recored in this experiment.

(i.e. eye-in-head torsion and head-in-space torsion adding to zero eye-in-space torsion). Thirdly, Enright's hypothesis leads to the prediction that the relative contribution of the left and right eyes to the cycloversion response should depend on the horizontal gaze angle. Hence, one should expect that cyclovergence shows typical changes depending on the gaze direction in which the vertical vergence is elicited. Contrary to this prediction, our second experiment in subject 2 (Fig. 4) demonstrates that cyclovergence does not depend on either horizontal gaze direction or direction of vertical disparity. In our view this second argument may be weakened but certainly not overthrown by the uncertainty about the exact relation between torsion and elevation in various horizontal gaze angles (no-pully model of ocular muscles, see Miller, 1989).

Another association between vertical vergence and cycloversion exists in the so-called ocular tilt reaction. In this reaction, head tilt, vertical vergence and cycloversion are elicited by stimulation of various brain stem parts. It was first described by Westheimer and Blair (1975), who stimulated, in a monkey, a brain stem area that included the interstitial nucleus of Cajal (INC). Later investigators reported similar associations between vertical vergence and cycloversion in a human patient after stimulation of this nucleus (Lueck, Hamlyn, Crawford, Levy, Brindley, Watkins, and Kennard, 1991) and in patients with central (Lopez, Bronstein, Gresty, Rudge, and Du Boulay, 1992) and peripheral (Halmagyi, Gresty, and Gibson, 1979) vestibular lesions. In all these reports, the direction of the association is reversed with respect to our results. In the ocular tilt reaction, left over right vertical vergence is associated with dextro-cycloversion, i.e. a rotation of the upper poles towards the right shoulder. It has been suggested that the ocular tilt reaction may be related to the vestibulo-ocular reflex for roll head movements in animals with lateral eyes (Lopez *et al.*, 1992). Because of the reversed association it is unlikely that the relation between disparity induced vertical vergence and cycloversion that we report is an epiphenomenon of this ocular tilt reaction.

Despite the questions on the physiological meaning of the association the occurrence of a cycloversional nystagmus does strongly suggest a central rather than peripheral origin. Vertical and torsional eye movements are mediated by the same premotor nuclei in the brain stem: the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF) mediates fast eye movements and the INC serves as the neural integrator for these movement types. Independently of the physiological role, the observed association may have its origin in some coupling at the level of these premotor nuclei.

Association of cycloversion with horizontal and vertical version

We found that the fast phases of the cycloversional nystagmus in our subjects coincided with horizontal and/or vertical microsaccades or with the fast phases of a small vertical nystagmus. This vertical nystagmus appeared not to be related to the presentation of the vertical disparities since it was present in the calibration measurements as well. Both the occurrence of spontaneous microsaccades and the small vertical nystagmus have been documented in the literature (microsaccades, see for example, Steinman, Haddad, Skavenski and Wyman, 1973; Ditchburn, 1980; Kowler and Steinman, 1980; vertical nystagmus see Van Rijn *et al.*, 1994). Our results demonstrate that the cycloversional nystagmus is, in a way, superimposed on these movements in horizontal and vertical directions. The fact that the cycloversional fast phases coincide with these horizontal and vertical saccades does not corroborate our findings with respect to the association between vertical vergence and torsion, nor does it disqualify our hypotheses with respect to its origin. It merely demonstrates that saccadic control occurs for the three movement dimensions simultaneously (see, for example, Crawford and Vilis, 1991). A discussion of this issue falls, however, outside the realm of these experiments.

Relation to vertical phoria

In subjects 2 and 4 we observed a systematic drift of spontaneous cycloversion. In subject 5 there was a preference for dextrocycloversion after introduction as well as elimination of the vertical disparity. The relation between vertical vergence and cycloversion that we found in the present experiment gives rise to the hypothesis that this directional preponderance of cycloversion may be caused by a vertical phoria that requires continuous vertical disparity vergence. This might also explain the spontaneous torsional (cycloversional) nystagmus that we observed in a previous experiment (Van Rijn *et al.*, 1994). This torsional nystagmus was enhanced by a rich visual background. This may fit in this hypothesis since a rich background is more compelling for fusion and therefore also for disparity vergence.

In order to get an indication of the answer to this question we compared vertical phorias in our subjects with the directional preponderance of the cycloversion as estimated from Fig. 2 and 3. Results are listed in Table 1. The vertical phorias, when present, were left-over-right and preponderances of cycloversion, when present, were in dextro-cycloversional direction. Since a left-over-right phoria requires a right-over-left vertical vergence (in absence of disparity), the direction of the association between cycloversion and vertical vergence is similar to that found during disparity presentations. At first sight this seems to support a relation between vertical phoria and cycloversional direction preponderance.

A complicating factor is that disparity vergence appears to have a fast and a tonic component (Ellerbrock, 1950; Ludvigh, Mckinnon and Zaitzeff, 1964; Carter, 1965; Schor, 1979, Sethi and Henson, 1984). The fast component may be stimulated directly by the disparity whereas the slow component may be affected by the duration of the fast vergence presence. These fast and slow components may be distinguished by the time course of their relaxation. The slow component, which predominates when the disparity is presented during a longer time interval, may persist during several hours after monocular occlusion (Alpern, 1946). It seems possible that these fast and slow components of vertical disparity vergence are related differently to cycloversion. The fast component of vertical vergence most likely has a direct relation to cycloversion. This may be observed in Fig. 2 and 3. Upon elimination of the vertical disparity there is, in all 5 subject that show torsion responses, at least a temporary reversal of the

subject	vertical phoria	cycloversional (slow phase) directional preponderance
1	0.0	none
2	0.2 L/R	dextro–cycloversion
3	0.2 L/R	none
4	0.0	dextro–cycloversion
5	0.7 L/R	dextro–cycloversion
6	0.3 L/R	none

TABLE 6.1. Vertical phorias and cycloversional directional preponderances in our subjects. Vertical phoria values were obtained with a Maddox cross at 1.45 m distance (coinciding with the distance of the stimulus during the experiment) and represent averages of three measurements. If values were different for left and right eye coverage, the maximum of these values is listed. The directional preponderances of cycloversion are estimated from Fig. 3.

cycloversion response along with the reversal of vertical vergence. It must be noted that disparity elimination (Fig. 2 and 3) is not identical to vergence relaxation (Schor, 1979) since in the former a zero disparity is presented and in the latter, one eye is covered. However, since the presentation time of the disparity was short (only 4 s) it seems unlikely that the slow vergence system is involved to a large extent.

In the correction of vertical phoria the slow vergence system is much more important than the fast system since, obviously, the duration of the disparity presentation is much longer. The question therefore is whether slow vertical vergence is also is associated with cycloversion. This question cannot be directly answered from our data since all our measurements were short term.

Vertical vergence

These results will be discussed only briefly since a study of the vertical vergence system was not the main purpose of this experiment. We found that a step vertical disparity induced a vertical vergence response with a gain of about 0.55 and a time constant of about 0.94 s (on establishment of the disparity). In general, subjects obtained a single, fused image. Kertesz (1981), investigating the maximum disparity that could be fused, found gain values of 0.63 and 0.75 in his two subjects. Our value seems low in relation to those of Kertesz, but we note that Kertesz used randomly segmented horizontal lines as a stimulus, which may be more compelling for vertical vergence than our concentric circles. The rationale behind our stimulus choice has been explained in the Method section. We note that Perlmutter and Kertesz (1978) found gain values between 0.80 and 1.00 percent for the vertical vergence response to a step disparity of 1 deg in a single horizontal line. This result seems in disagreement with ours, although we cannot exclude the possibility that even a single horizontal line is more compelling for vertical vergence than our stimulus.

For the return movement (after disparity elimination) we found a time constant of about 0.60 s. In the literature, much longer values have been reported. Houtman, Roze and Scheper (1977) found time constants of between 3 and 5s. Henson and North (1980) and Ellerbrock (1950) found values of about 1 and several minutes, respectively, as estimated from their figures. In all these investigations, disparity presentation times were much longer than in ours, which may explain, though differences in tonic parts of the responses, the differences in the time constants.

6.6 References

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SUMMARY

This thesis reports on a series of experiments on torsional eye movements. Torsional eye movements can be defined as rotations about the visual axis. Of all possible functions of eye movements in general, two may be especially important in relation to torsion: stabilisation of the retinal image and correspondence of the retinal images in the left and right eye. Stabilisation of the retinal image may prevent motion blur; correspondence avoids the perception of double images. The experiments in this thesis were aimed at the elucidation of the torsional regulatory systems. The basic question was how these two functions of torsion are implemented.

The torsional eye movements of the left and right eye can be decomposed in a component that is directed similarly in both eyes, namely *cycloversion* and a component that is directed oppositely, *cyclovergence*. Instability of retinal images is, in general, caused by head movements. This results in retinal image motion that is similar in the left and right eye. Therefore, compensation for these head movements must also be equal in both eyes and, thus, needs to be performed through cycloversion. Cyclovergence, in

contrast, is more important in relation to retinal image correspondence. The experiments were aimed at the description of different aspects of cycloversion and cyclovergence eye movements.

Chapters 2, 3 and 4 give a description of torsion in absence of horizontal and vertical eye rotations. In chapter 2, the spontaneous variation of cycloversion and cyclovergence is being described. Chapter 3 and 4 handle with torsion in response to visual stimuli. From the experiments in these chapters it appears that cycloversion and cyclovergence are mediated through different (sub-) systems, each with its own characteristics. Cycloversion has a relatively large spontaneous variability and a short response latency. Cyclovergence is more stable and has a longer latency. The gain of both movement types is similar.

An unexpected finding (chapter 4) is that both cycloversion and cyclovergence respond better to stimuli that are oriented horizontally than to vertically oriented stimuli. This seems to indicate that both systems function, partly, through maintenance of a stable eye orientation relative to the horizon, rather than through maintenance of correspondence and stability alone.

Chapter 5 handles with torsion as function of horizontal and vertical eye rotations. In this chapter the torsional positions of both eyes simultaneously are being described. This description formes an extension of the monocular description that was known from the literature. The results of this extended description indicate that the binocular torsion related to horizontal and vertical eye movements formes a compromise between optimal retinal correspondence and eye position control with a plain geometry.

Chapter 6 reports about torsion that is associated with vertical vergence. Vertical vergence is a vertical eye movement that is directed oppositely in the left and right eye. Such movement appears associated with cycloversion. This association seems not to serve any physiological purpose. It may be a 'side effect' of the organisation of eye movement control in the brain stem.

SAMENVATTING

In dit proefschrift wordt een serie van experimenten beschreven aan torsie-oogbewegingen. Torsie-oogbewegingen kunnen worden gedefinieerd als bewegingen van het oog rond de visuele as. Van de diverse functies die door oogbewegingen worden uitgevoerd zijn er twee met name belangrijk in verband met bewegingen in torsierichting: stabilisatie van het netvliesbeeld en correspondentie van de netvliesbeelden in de beide ogen. Stabilisatie van het beeld is nodig ter voorkoming van bewegings-onscherpte, correspondentie is nodig ter voorkoming van dubbelzien. De experimenten waren erop gericht de regelsystemen voor torsie te beschrijven met als onderliggende vraag hoe deze beide functies worden uitgeoefend.

Van belang in deze beschrijving is dat de torsiebewegingen van beide ogen kunnen worden ontbonden in een component die gelijkgericht is in beide ogen, namelijk *cycloversie* en een component die tegengesteld gericht is, *cyclovergentie*. Instabiliteit van netvliesbeelden wordt in het algemeen veroorzaakt door hoofdbewegingen. De resulterende netvliesbeeld-beweging is dan ook ongeveer gelijk in linker en rechter oog.

Compensatie voor torsie-hoofdbewegingen moet derhalve ook gelijk zijn in beide ogen en vindt dus (al dan niet) plaats door cycloversie. In tegenstelling hiermee is cyclovergentie met name belangrijk voor correspondentie. De experimenten waren er dan ook op gericht om de diverse eigenschappen van cycloversie- en cyclovergentiebewegingen te beschrijven.

De hoofdstukken 2, 3 en 4 geven een beschrijving van torsie in afwezigheid van horizontale en verticale oogrotaties. In hoofstuk 2 wordt de spontane variatie van cycloversie en cyclovergentie beschreven, in de hoofdstukken 3 en 4 de torsie in respons op visuele stimuli. Uit deze experimenten blijkt dat aan cycloversie en cyclovergentie verschillende deel-regelsystemen ten grondslag liggen, elk met hun eigen karakteristieken. Cycloversie heeft een relatief grote spontane variabiliteit en een korte latentietijd voor de respons op veranderingen. Cyclovergentie is relatief stabiel en heeft een langere latentietijd. De accuraatheid, uitgedrukt in *gain*, is voor beide systemen vergelijkbaar.

Een verrassende vinding (hoofdstuk 4) is dat beide systemen beter reageren op horizontaal dan op verticaal georienteerde stimuli. Dit lijkt erop te duiden dat deze systemen deels functioneren door sturing van de orientatie van de ogen ten opzichte van de visuele wereld en niet alleen door het handhaven van stabiliteit en correspondentie.

Hoofdstuk 5 behandelt een ander aspect van torsie, namelijk die als functie van horizontale en verticale oogbewegingen. De in dit hoofdstuk gepresenteerde simultane beschrijving van de posities van beide ogen vormt een uitbreiding op de beschrijving die voor de ogen afzonderlijk bekend was. De resultaten verkregen met deze uitgebreide beschrijving duiden erop dat de gemaakte torsie een compromis vormt tussen geometrisch eenvoudige sturing enerzijds en optimale correspondentie anderzijds.

Hoofdstuk 6 behandelt torsie die gerelateerd is aan verticale vergentie. Verticale vergentie is een verticale oogbeweging die tegengesteld gericht is in beide ogen. Verrasenderwijze gaat een dergelijke beweging gepaard met een cycloversie beweging. Deze koppeling, die geen fysiologisch doel lijkt te dienen, kan een 'bijwerking' zijn van de wijze waarop de sturing van ooggewegingen in de hersenstam georganiseerd is.

CURRICULUM VITAE EN LIJST VAN PUBLICATIES

Curriculum vitae

Laurentius Johannes (René) van Rijn werd geboren op 12 november 1962 te Leiden. Vanaf 1975 volgde hij in deze stad atheneum-onderwijs aan het Bonaventuracollege, hetgeen in 1981 werd afgesloten met het diploma 'ongedeeld VWO'. In hetzelfde jaar ving hij aan met de geneeskunde studie aan de Rijksuniversiteit te Leiden. In 1987 behaalde hij het kandidaatsexamen en in 1989 het artsexamen. Tijdens zijn studieperiode was hij assistent bij diverse studenten-practica van de vakgroep fysiologie van deze universiteit. Daarnaast bedreef hij gedurende enkele perioden onderzoek in diverse laboratoria. In 1984 gedurende drie maanden in het Laboratorium voor Experimentele Gerontologie van TNO in Rijswijk. Het onderzoek betrof het verminderde levermetabolisme bij veroudering. In 1985 verrichtte hij gedurende drie maanden onderzoek aan een diermodel voor anti-psychotische geneesmiddelen. Dit onderzoek vond plaats bij Wander AG te Bern, Zwitserland. In 1987 verrichtte hij gedurende een half jaar onderzoek aan de rol van bloedvat-elasticiteit bij de distributie van bloed over de verschillende lagen van de hartspier. Dit onderzoek deed hij in het CardioVascular Research Institute, aan de University of California at San Francisco, U.S.A. Na zijn geneeskundestudie werkte hij, in 1989, gedurende vijf maanden als 'Junior House Officer' op de afdeling Interne Geneeskunde van het Royal Shrewsbury Hospital in Shrewsbury, Engeland. Van 1991 tot medio 1993 verrichtte hij het onderzoek aan torsieoogbewegingen op de afdeling Fysiologie van de Erasmus Universiteit, onder begeleiding van Prof. H. Collewijn. Van de werkzaamheden uit deze periode doet hij in dit proefschrift verslag. Sinds oktober 1993 werkt hij als arts-assistent in het Oogziekenhuis te Rotterdam. Daarnaast verricht hij, in samenwerking met de oogarts J-Tj.H.N. de Faber, onderzoek, onder meer aan oogbewegingsstoornissen bij patienten met scheelzien.

Lijst van publicaties

1. L.J. van Rijn, J. van der Steen and H. Collewijn (1994) Instability of ocular torsion during fixation: Cyclovergence is more stable than cycloversion. *Vision Research,* in press.
2. L.J. van Rijn, J. van der Steen and H. Collewijn (1992) Visually induced cycloversion and cyclovergence. *Vision Research, 32,* 1875-1883.
3. L.J. van Rijn, J. van der Steen and H. Collewijn (1994) Eye torsion elicited by scillating gratings: role of grating orientation, cycle length and stationary contours. *Vision Research,* in press.
4. L.J. van Rijn and A.V van den Berg (1993) Binocular eye orientation during fixations: Listing's law extended to include eye vergence. *Vision Research, 33,* 691-708.
5. L.J. van Rijn and H. Collewijn (1994) Eye torsion associated with disparity induced vertical vergence in humans *Vision Research,* in press.
6. L.J. van Rijn, J. van der Steen and H. Collewijn (1991) Binocular torsional eye movements in response to dichoptically presented oscillating optic stimuli. *European Journal of Neuroscience (Suppl), 4,* 308.
7. L.J. van Rijn, J. van der Steen and H. Collewijn (1991) Torsional eye movements elicited by oscillating optic stimuli. *Pflügers Archiv (Suppl), 418,* R150.
8. L.J. van Rijn and J. van der Steen (1992) Stability of the human eyes in torsional direction: Short term spontaneous torsional eye movements are conjugate. *Pflügers Archiv (Suppl), 420,* R42.
9. L.J. van Rijn, A.V van den Berg and J.Tj.H.N. de Faber (1993) Intermittent exotropia can be interpreted as peripheral offset on eye position and unchanged central control. *Investigative Ophthalmology and Visual Science (Suppl), 34,* 1309.

De publicaties genummerd 1 tot en met 5 zijn, vrijwel onveranderd, in dit proefschrift opgenomen als de hoofdstukken 2 tot en met 6.

DANKWOORD

Op deze plaats wil ik graag alle personen bedanken die op de een of andere wijze hebben bijgedragen aan de totstandkoming van dit proefschrift.

Allereerst mijn promotor, Prof. Dr H. Collewijn. Beste Han, gedurende de afgelopen 3.5 jaar heb ik grote waardering gekregen voor je manier van werken en voor de wijze waarop je mijn promotie begeleidde. Jouw wetenschappelijke inzichten, in combinatie met je efficiente, op resultaat gerichte aanpak waren onmisbaar voor het slagen van mijn onderzoeksprojecten. Bovendien heb ik er persoonlijk veel van geleerd.

Mijn 'dagelijkse begeleider', Dr H. van der Steen. Beste Hans, vooral in mijn beginperiode op de afdeling heb je veel geïnvesteerd in mijn onderzoek. Ik heb grote bewondering voor het geduld dat je telkens weer had bij het helpen oplossen van de problemen met de meetkast en de computer.

Dr A.V. van den Berg. Beste Bert, je vervulde een grote rol bij de totstandkoming van ons '3D-Listing'-artikel (hoofdst. 5). Ik wil je bedanken voor je grote tijdsinvestering hierin. Onze uitgebreide discussies waardeer ik erg en ik heb hier veel van opgestoken. Bovendien wil ik je bedanken voor je bereidheid als paranimf op te treden.

Alle proefpersonen wil ik bedanken voor hun bereidheid tijd en moeite in mijn onderzoek te investeren. Mijn speciale waardering is voor PS en JW die, van buiten de afdeling en belangeloos, meerdere keren hun medewerking hebben verleend.

Prof. Dr P.V.T.M. de Jong, Prof. Dr C.J. Erkelens en Dr J.A.M. van Gisbergen. wil ik bedanken voor het kritisch doorlezen van het manuscript en de bereidheid in de promotiecommissie plaatst te nemen. Dr van Gisbergen, beste Jan, bovendien bedankt voor de leerzame en interessante wetenschappelijke discussies.

Prof. Dr F.G.A. van der Meché en Prof. Dr H.F.M. Busch, hartelijk dank voor het plaatsnemen in de promotiecommissie.

Dr J.J. Simpson. Jerry, many thanks for your comments on the paper of Bert and me on the 3D-extension of Listing's law (chapter 5). Your comments were of great value and contributed a lot to the readiblity of the paper.

Dr J.T. Enright, many thanks for your efforts in reviewing the 'vertical vergence vs. cycloversion' paper (chapter 6). Your extensive comments greatly improved the logic of the paper.

Drs J.G.E. Janzing. Beste Joost, het 'promotiemonster' was onze gemeenschappelijke vijand en daardoor beter te bestrijden. Bedankt voor je bereidheid als paranimf op te treden.

Mw S. Markestijn, Suzanne, bedankt voor je werk aan de omslag-figuur van dit proefschrift.

De Stichting voor Ooglijders, de Rotterdamse Vereniging Blindenbelangen, de Prof. Dr H.J. Flieringa Stichting, de Prof. Dr Flieringa-Houët Stichting en Skalar Medical B.V., hartelijk bedankt voor de financiele steun bij de verspreiding van dit proefschrift.

Tot slot: alle medewerkers van de afdeling Fysiologie van de Erasmus Universiteit, hartelijk bedankt voor de leuke en leerzame tijd die ik er heb doorgebracht.