OCULAR ORIENTATION DURING HEAD AND EYE MOVEMENTS: AN EVALUATION WITH A THREE DIMENSIONAL SCLERAL INDUCTION COIL TECHNIQUE

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(DE ORIENTATIE VAN HET OOG GEDURENDE HOOFD- EN OOGBEWEGINGEN: EEN ANALYSE MET BEHULP VAN EEN DRIE-DIMENSIONALE SCLERALE INDUCTIESPOEL TECHNIEK)

PROEFSCHRIFT

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AAN ELLEN

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Chapter I

General Introduction

In order to maintain proper fixation of a target which is of interest in the surrounding world a human being is required to change his eye orientation in space as he moves about or when the target itself moves relative to the eye. This seemingly effortless accomplishment is brought about by a complex system of (in)voluntary eye movements combined with cognitive processes, which aligns the target with an isoacuity area of some 50′ in diameter (Millodot, 1972) located in the foveal part of the retina, thus enabling visual perception with high resolution of the target. Compensatory eye movements generated by vestibulo-ocular and optokinetic reflexes, together with smooth pursuit, vergence and saccades constitute those elements of the oculomotor system which are used to bring about the required orientation of the eye-ball in its orbit, through the adequate excitation and inhibition of the appropriate extra-ocular eye muscles.

Visual pursuit of a moving target has generally been assumed to be possible up to frequencies not higher than about 1-2 Hz above which the visual image begins to blur. In recent work Martins et al. (1985), using stimuli with small amplitudes and recording with high resolution, found that the effectiveness of smooth pursuit already declined at target frequencies above 0.5 Hz. At frequencies above 3 Hz, smooth pursuit was totally ineffective in reducing retinal image speed. In contrast, fixation of a stationary target can be maintained during head movements of up to at least 5 Hz without disturbance of the visual perception which remains single, stable, clear and fused. Such head movements activate the vestibular organs and generate - by way of the canal-ocular reflexes - appropriate compensatory eye movements. Up to frequencies of about 0.1 Hz compensatory eye movements may in part be the result of the cervico-ocular reflex, originating from proprioceptors in the neck, although until this day its significance remains the subject of much controversy.

Since the visually perceived world remains single and fused during a wide frequency range of head and body movements, most oculomotor investigators had, until recently, interpreted this as the result of a unity gain brought about by compensatory eye movements.

In the last few years however, new measuring techniques have revealed the existence of conjugated residual retinal slip under natural conditions, corresponding to a gain of compensatory eye movements not better than about 0.9 (Skavenski et al., 1979). Moreover, disjunctive residual eye movements with vergence velocities up to 3 deg/sec were recorded (Steinman and Collewijn, 1980), despite the maintenance of a clear and stable world (for review see Steinman et al., 1982).

Skavenski et al. (1979) reported that with the head fixed on a bite-board, eye movements had a speed of about 14 min/sec; this speed increased to about 27 min/sec with the head off the bite-board and kept as still as possible. Collewijn et al. (1981) found retinal image slip speeds of about 1-2 deg/sec during passive or active head rotation (frequency range 0.33 - 1.33 Hz). As these accurate oculomotor recordings demonstrated, the physiological retinal image slip velocity is very likely to lie somewhere between 25-100 min/sec.

Such findings are easily reconciled with related psychophysical evidence on the viewing of moving retinal images: minimal retinal image slip velocities of at least 10-15 min/sec may be needed to achieve maximum contrast sensitivity (King-Smith and Riggs, 1978) and at the upper end, retinal image slip velocities of up to 100-150 min/sec do not impair visual acuity (Westheimer and McKee, 1975; Murphy, 1978; King-Smith and Riggs, 1978). Psychophysical measurements during head oscillation (Steinman et al., 1985) suggest that the associated retinal image slip is beneficial for visual acuity at low spatial frequencies and at the same time relatively harmless to contrast sensitivity at high spatial frequencies.

Although the existence of physiological retinal image slip could no longer be doubted, in view of the large body of evidence accumulated in recent years (for review see Steinman et al., 1982), the exact amount of retinal slip during natural head movements remained the subject of discussion. Duwaer (1982), using an afterimage method, measured retinal image displacement during active head rotation about a vertical axis at a frequency of 0.66 Hz and fixation of a point target. The S.D. of retinal image position and fixation disparity were much smaller, by a factor of 3 and 8 respectively, than the results reported previously by Steinman et al. (1982) for similar head rotations. Stark (1983) raised the possibility that this discrepancy may be due to kinematical cross-coupling artifacts leading to higher values.

The aim of the first part of this study (Chapter II) was twofold:
1) Since the existence of retinal image slip and its magnitude are of critical importance to the ultimate understanding of the visual process, it seemed opportune to further establish the amount of retinal slip as accurately as possible during natural conditions. The quality of oculomotor recordings was improved both in accuracy and dimension; a new

scleral coil measurement technique will be presented with which voluntary eye and head movements can be measured simultaneously in three dimensions: horizontal, vertical and torsion. A great effort was made to eliminate all potential artifacts (see also Collewijn et al., 1983), kinematical or otherwise.

2) In the past, virtually all oculomotor recordings were those of eye movements in the horizontal plane during passive or active head rotation around the vertical axis. Skavenski et al. (1979) and Duwaer (1982) measured both horizontal and vertical eye movements but also only during head oscillations in the horizontal plane. Oculomotor recordings were now extended to all three dimensions: eye movements were recorded while subjects actively oscillated their heads around the vertical, horizontal or sagittal axis at 0.33, 0.66 and 1.33 Hz and fixated a point target.

During voluntary head movements, the vestibulo-ocular reflex makes a major contribution to ocular compensation. Paradoxically, this reflex can only be measured accurately in the dark, thus depriving it of its function: gaze stability during head or body movements. However, in the dark a change of mental set can greatly influence the performance of the VOR (Barr et al., 1976; Baloh et al., 1984; McKinley and Peterson, 1985). In the literature on human VOR, there is a large amount of variability between the results. In recent experiments, random fluctuations of VOR gain in darkness by 10-20% and more were measured even though the subjects were highly motivated (Collewijn and Ferman, 1986). It must be concluded therefore, that measuring ocular compensation in the dark produces ambiguous results, at least in the frequency range 0.16-0.66 Hz used in this study. In view of the above, all experiments were conducted with a visual target present. Ocular compensation therefore, consisted of a contribution by both VOR and smooth pursuit.

Since active head movements are not only more natural (to the human being) than passive ones but also produce the highest gain (Collewijn et al., 1983) all subjects were required to perform voluntary head oscillations during target fixation. Active head movements possibly activate the cervico-ocular reflex (as stated above) but its contribution was probably not significant (see Collewijn et al., 1983).

As will be shown in the first part of this study (Chapter II), human gaze stability under more or less natural conditions is not perfect. In the second part of this study (Chapters III and IV) the gaze stability was examined with the head fixated, a relatively unnatural condition. In this situation, the laws of Listing and Donders could be examined. These laws provide kinematical descriptions of torsion and imply determinism in the programming of torsional eye movements, if they are valid. The measurement technique as previously mentioned was ideally suited for a critical test of both laws. In view of the results with the head unrestricted, it seemed unlikely that the eye would strictly obey rigid mathematical laws.

In the past, experimental verification of both laws has led to great confusion, in part because various methods were used and to some extent owing to different interpretations of the results. Human eye orientation was measured in this study directly and continuously in three dimensions, during sustained fixation in the primary, secondary and tertiary positions as well as during continuous or saccadic change of eye orientation from one tertiary position to another. Since the torsional dimension is the most important in this part of the study, the largest part of the presented results deals with the behaviour of the human eye around the visual axis under the various testing conditions.

The data acquired for sustained monocular fixation of the primary, secondary and tertiary positions demonstrate an only approximate validity of Listing's law and suggest that physiological eye movements show considerable stochastical as well as systematic deviations from this law. Oculomotor recordings representing the dynamic aspects of ocular torsion were made during fixation, blinking, smooth pursuit and saccades. Once again violations of Listing's law as well as Donders' law were seen, since torsion values varied with the direction and trajectory of pursuit; a clear hysteresis effect in conflict with the specifications of both laws.

It is concluded that the kinematical descriptions of human eye orientation by Listing and Donders, at least under these conditions, are only approximately followed. Finally, a hypothesis for the control of ocular torsion is suggested.

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Chapter II

Human gaze stability in the horizontal, vertical and torsional direction during voluntary head movements.

INTRODUCTION

In recent years evidence has accumulated that although fixation can be extremely precise in subjects with the head stabilized on a biteboard, much of this precision is lost when the head is not artificially supported and particularly when the head is moved. With the head on a biteboard, standard deviations of the position of the line of sight are typically smaller than 5 min arc and retinal image velocities are below 0.25 deg/sec (for reviews see Steinman et al., 1973; 1982). Skavenski et al. (1979) were the first to reliably record eye movements in subjects with the head free. They found that eye movements with the head fixed had a S.D. of about 6 min arc with a speed of about 14 min/sec whereas eye movements with the head free and kept as still as possible while the subjects were either sitting or standing had a S.D. of about 8 min arc and a speed of 27 min/sec. This made it clear that natural eye movements were not as stable as had been presumed.

With accurate scleral induction coil techniques allowing a large range of head motion substantial retinal image motion was found during active head motion (Steinman and Collewijn, 1980). In a more detailed analysis Collewijn et al. (1981; see also Steinman et al., 1982) estimated standard deviations of gaze position during passive or active head rotation (frequency range 0.33-1.33 Hz) as about 30 min arc. Retinal image speeds were in the order of 1-2 deg/sec.

Thus, oculomotor recordings with the head free indicate that the physiological velocity range of retinal images is at least 25-100 min arc/sec, and probably higher during more vigorous head movements. Psychophysical evidence obtained with the head stationary suggests that a non-zero retinal image velocity is optimal for visual perception. At the lower end, a retinal slip velocity of at least 10-15 min/sec may be needed to achieve maximum contrast sensitivity (King-Smith and Riggs, 1978). At the upper end, it has been found that slip velocities up to 100-150 min/sec do not impair visual acuity (Westheimer and McKee, 1975; Murphy, 1978; King-Smith and Riggs, 1978). Psychophysical measurements during head oscillation (Steinman et al., 1985) suggest that the associated natural retinal image motion is beneficial for the vision of low spatial frequencies and at the same time relatively harmless to contrast sensitivity at high spatial frequencies. However, the existence of significant retinal image slip during head motion has been contested. Duwaer (1982), using an afterimage technique, estimated the S.D. of retinal image position for fixation of a point target during active head oscillation at 0.66 Hz as no larger than about 9 min arc in the horizontal direction, whereas oculomotor recordings showed values of about 20-30 min arc (Steinman et al., 1982). Stark (1983) has asserted that these higher values may be due to kinematical cross-coupling artifacts.

Since the amount of physiological retinal image motion is fundamental to our understanding of the visual process, it was deemed important to further substantiate earlier findings (Steinman and Collewijn, 1980; Collewijn et al., 1981; Steinman et al., 1982), taking into account all sources of artifact that could be conceived of (see

Collewijn et al., 1983). Furthermore, it was important to extend oculo-motor recordings to vertical and torsional dimensions. Recently, a scleral induction coil was developed which transduces rotations in three dimensions. This made it possible to measure gaze stability simultaneously in the horizontal, vertical and torsional direction. Moreover, this three dimensional recording enabled a complete correction of any kinematical artifacts (see methods).

It will be shown that substantial retinal image slip does occur consistently during voluntary head oscillation. Horizontal and vertical smooth gaze movements amounted to about 2.5% of the amplitude of the head movements. In the torsional direction, retinal image motion was much larger due to a relatively low, frequency dependent gain of torsional compensatory eye movements (Collewijn et al., 1985).

METHODS

General Methodological Considerations

In the present experiments, rotations of the eye and the head in three dimensions were measured with respect to an earth-fixed magnetic field. In the case of unity gain of compensatory eye movements, the angles of rotation of the eye and head are exactly equal in magnitude and opposite in sign in all dimensions. This situation corresponds to a constant angular direction of gaze, i.e. no modulation of the eye-in-space direction by a change in head-in-space orientation.

For unity gain to be appropriate for constant fixation of a visual target, special, idealized conditions are required:

1. The target should be at optical infinity. When this is not the case, any translations of eye and head will change the angular direction of the target. Similarly, the spatial separations between the centres of rotation of the head and the eye and the non-coincidence of the nodal point of the eye with its centre of rotation will induce angular differences between eye and head rotation for constant fixation except for a target at infinity (see Steinman et al., 1982).
2. Spectacle corrections induce magnification factors that also dissociate the angular rotations of eye and head. Although a calibration procedure can be executed to correct for this effect (Collewijn et al., 1983) this extra complication can be avoided by using emmetropic subjects.
3. The recordings should be sensitive only to ocular rotations, and invariant for any translations. To achieve this, the magnetic fields have to be homogeneous in strength and direction over a space including any possible head position.

Recording Technique

The three dimensional scleral induction coil technique was applied using phase-locked amplitude detection as originally described by Robinson (1963), with two major modifications:

1. Homogeneous vertical and transverse a.c. magnetic fields were created in a cube of 125 cm on a side by arrays of field coils (250 cm on a side) as has been previously described (Rubens, 1945; Collewijn, 1977). The field frequency was 5000 Hz.

2. The scleral induction coils were not mounted on a suction-held hard contact lens, but embedded in a self-adhering silicone annulus. The type of annulus made several years ago (Collewijn et al., 1975) for the recording of horizontal and vertical eye movements was developed further. In addition to the traditional coil wound in the frontal plane the new annulus contained a second coil, wound effectively in the sagittal plane (Robinson, 1963). One turn of this coil follows first the outer (posterior) margin of the left half of the annulus, crosses at the vertical meridian to the inner (anterior) margin of the right half of the annulus, returns following its outer margin, recrosses to the inner margin of the left half of the annulus, and returns on its outer margin to complete the first turn. The combined annulus (shown in Fig. 1) turned out to be more flexible than the prototype recording torsion only (Collewijn et al., 1985) and adhered satisfactorily to all of the subjects' eyes.

An assembly of similarly oriented (frontal and sagittal) but larger coils was firmly strapped to the head to record head movements. The sensor coils were connected to high quality lock-in amplifiers (Princeton Applied Research, models 128 and 129A) to obtain the horizontal and

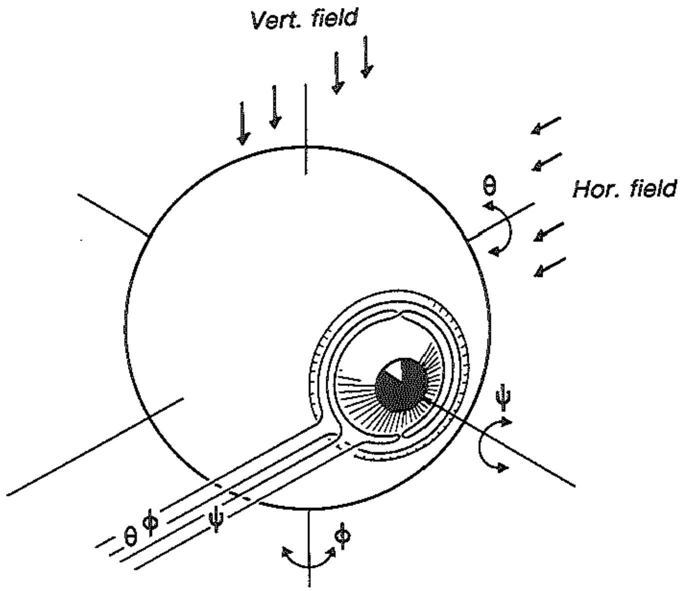

Fig. 1. Schematical diagram of the eyeball with the pupil (round and black part), the iris represented by the radial lines and the combined annulus as described in the text. The outer windings of the annulus record eye movements around the vertical and horizontal axis (ϕ and θ) and the inner part records eye movements around the visual axis (ψ). The orientations of the horizontal and vertical fields are also shown.

vertical positions (dual-phase detection) as well as the torsional positions (single phase detection). By suitable braiding and screening of connectors and leads their magnetic pick-up was effectively minimized so that with the coils in a frontal and upright position all output signals were zero. The sensitivity of the eye and head coils was calibrated prior to every experimental session with a calibration device made out of Lucite, with the axes of rotation organized according to Fick's coordinate system (see Alpern, 1962). With the coils mounted on the calibration device, the presence or the moving about of the experimenter in the magnetic field made no difference to the value of the output signals. It was concluded therefore that the bodies of the subjects wearing the coils did not significantly influence the induction in the coils. Recording sensitivities were standardized by adjusting instrument gains. The total recording range was set to about 25 deg in any direction from the midposition.

Visual Target

The target was a red spot formed by a laser beam on an opal glass screen, positioned in the focal plane of a large Fresnel lens (size 94 x 70 cm; focal length 118 cm). This lens was placed parallel to the subjects' frontal plane at a distance of about 180 cm. The diameter of the target was about 12 min arc. The calibration device contained a sight in which the target was exactly centered when all angular positions and electric outputs were zero. By sliding the calibration device sideways alongside a ruler, it was confirmed that pure translation affected neither the angular direction of the seen target nor the electric ouputs of the recording system.

Subjects and Recording Procedures

Horizontal, vertical and torsional eye and head positions were measured in 8 healthy subjects who had no known ocular or vestibular pathologies and were all emmetropes. All experiments were conducted in complete darkness, except for the point target. One eye of each subject (4 left and 4 right eyes) was measured with monocular vision: the coil was mounted on the viewing eye; the other eye was covered with a patch. The subject was first fitted with the previously calibrated head coils which were firmly strapped to the head. The subject was seated in the magnetic field viewing the target and with the head in that position which felt as the "natural zero position". If any large deviations from the zero position were seen (on the lock-in amplifiers) the position of the head coils on the head was changed to obtain an acceptable "zero" position. As the head was free to move this procedure was just an approximation, followed mainly to prevent head position values exceeding the recording range. Following the fitting of the head coils, the previously calibrated scleral coil was now fitted onto the subjects' eye and the other eye was patched. Any non-zero readings of eye position, caused by misalignment of the annulus on the eye, were <u>not</u> corrected at this time.

An experiment consisted of two parts:

<u>1. Static head positions</u>: the subject was verbally instructed to assume 4 different static head positions in either the horizontal, vertical or torsional direction while fixating the target. Measurements lasted for 4 seconds and the subject (after confirmation had been given by the experimenter that the head was in the desired position) tried to make as

few blinks as possible during the sampling period. When ready, the subject started each measurement by pressing a button. As an extra check each session started with 4 calibration measurements, in which targets at known eccentricities were fixated. In between the various head position measurements, 4 "zero" head position measurements were made. These measurements were done mainly to verify the constancy of gaze direction in various static head orientations.

2. Active head oscillations: the subject was now instructed to make sinusoidal head oscillations at the pace of an auditory signal emitted by a loudspeaker at 0.167 Hz and at the pace of metronome clicks at 0.333 and 0.667 Hz in either the horizontal, vertical or torsional direction while continuously fixating the target as well as he could. The subjects' head movement could be observed on a penrecorder and the subject was given verbal feedback until performance (amplitude and frequency) was satisfactory. Only then was the subject allowed to start the measurement (whenever he felt ready) by again pressing the button. These measurements lasted for 18 seconds during which subjects again tried hard to make as few blinks as possible. At regular intervals, zero measurements with the head stationary were interleaved with the dynamic trials. After completion, the whole sequence was repeated for static head positions as well as for active head oscillations. For analysis, that sequence (usually the first one) was used in which fewest blinks had been made by the subjects.

All data were digitized on line at a sample frequency of 170.67 Hz after low-pass filtering at 62.5 Hz and stored on disk by a PDP 11/73 computer for later off-line analysis. The overall resolution of the system including A/D conversion (12 bits precision) was about 3 min arc for the gaze signals and 2.5 min arc for the head signals.

Computation of Veridical Coordinates

Since the primary interest here is the orientation of the eye in space, eye and head position are described in Fick coordinates relative to the earth-fixated coil system. To obtain the veridical (effective) eye and head positions in Fick coordinates, the raw (nominal) data have to be submitted to two kinds of corrections:

1. The hierarchy of the vertical, horizontal and torsional axes in relation to the orientation of the magnetic fields implies certain goniometric relations between the angular rotations and the signals obtained (Robinson, 1963).

2. Any misalignment of the coil on the eye (i.e. non-zero outputs with the line of sight aimed at the target) induces cross-couplings due to rotation of the offset angles, with spurious changes in the gaze signals as a result (kinematical artifacts).

Both sources of error were eliminated by the following procedure: Analogous to Robinson's (1963) description a matrix M was derived relating a coordinate system moving with respect to the eye to a coordinate system fixed with respect to the magnetic field coils. Contrary to Robinson however, a right-handed coordinate system was used and ϕ and θ were used to describe horizontal and vertical eye rotations respectively.

M (ϕ,θ,ψ) is given by: (1)

$$M = \begin{matrix} \cos\phi\cos\theta & -\sin\phi\cos\psi-\sin\theta\cos\phi\sin\psi & \sin\phi\sin\psi-\sin\theta\cos\phi\cos\psi \\ \sin\phi\cos\theta & \cos\phi\cos\psi-\sin\theta\sin\phi\sin\psi & -\sin\psi\cos\phi-\sin\theta\sin\phi\cos\psi \\ \sin\theta & \cos\theta\sin\psi & \cos\theta\cos\psi \end{matrix}$$

Again analogous to Robinson's derivation it was found that phase-locked detection of the voltages induced in both coils of the annulus (which are in spatial quadrature) with reference to the driving signals of the two magnetic fields (which are in spatial and temporal quadrature) results in three voltages e_ϕ, e_θ and e_ψ related to M as follows: (2)

e_ϕ (:) M_{21}

e_θ (:) M_{31}

e_ψ (:) M_{32}

in which:

ϕ = angle of rotation around vertical axis

θ = angle of rotation around horizontal axis

ψ = angle of rotation around visual axis

(:) = proportional to

M_{ij} = element of the M matrix in the ith row and jth column.

The above equations only hold if the annulus with the coils is exactly perpendicular to the visual axis. In general, since the annulus (and thus also the coils) will show a misalignment with the visual axis the voltages e_ϕ, e_θ and e_ψ will depend on all three angles of rotation ϕ, θ and ψ; e.g. a horizontal misalignment of the coil combined with a torsional eye movement will result in an apparent vertical eye movement (as illustrated in the results section). It is therefore necessary to perform a correction to eliminate artifacts introduced by such a misalignment. This misalignment can be expressed as a rotation of the coil with respect to the visual axis over angles ϕ_0, θ_0 and ψ_0 with the concomitant transformation matrix $M_0 = M(\phi_0, \theta_0, \psi_0)$. It can then be shown that the following equations apply: (3)

e'_ϕ (:) $(MM_0)_{21}$

e'_θ (:) $(MM_0)_{31}$

e'_ψ (:) $(MM_0)_{32}$.

Under the assumption that ϕ_0, θ_0 and ψ_0 are constant during any one experiment they may be determined by the mean value of all samples during the very first measurement in which the subject fixated the target with the head kept still (the first "zero" measurement). ϕ, θ and ψ could then be calculated from the three equations (3) given above with ϕ_0, θ_0 and ψ_0 as the known parameters of the known equations.

Measuring with the amplitude detection method for angles larger than 20 degrees necessitates appropriate goniometric corrections of the raw data to obtain the veridical eye and head position angles (Robinson, 1963). These corrections were performed simultaneously along with the corrections for the annulus misalignment. Each sample taken for all 6 eye and head position signals and for all measurements was corrected off-line with a computer program using the above equations.

The corrections of all 6 "nominal" eye and head position angles thus produced the "effective" eye and head angles. The values of all 6 signals recorded during the very first zero position measurement (with the head held stationary) were automatically standardized to zero by the computer program. All values mentioned in this paper are effective values, unless stated otherwise. The validity of the correction procedure described above was verified by mounting an annulus on the calibration device with known angles of misalignment in all three directions with reference to the "visual axis" of the calibration device. Then the annulus was rotated in all three directions separately and in various combinations. It was established that after the correction procedure deviations from linearity and symmetry were less than 1-2% for all three signals up to angles of 20 degrees. There was no significant cross-talk between the channels. This result included slight angle reading errors and mechanical imperfections of the calibration device, imperfections of the magnetic fields and any distortions introduced by the hardware and software.

Further Data Processing

1. Static head positions: from the effective eye and head positions, means and SD's were calculated.

2. Active sinusoidal head oscillations: from the effective eye and head

positions, the SD of eye position in all measurements and the SD of head position in the zero position measurements were calculated. For the active head oscillation measurements the off-line analysis continued by removal of saccades from the gaze signals and interpolation to a cumulative smooth eye position. Eye-in-head position was computed by subtraction of gaze position from head position. Bias and trend were removed from eye and head position signals and the data were reduced by a factor 3 (by averaging each successive group of 3 samples) to 1024 samples, as appropriate for the subsequent transformation with a fast Fourier routine. The calculated fundamental frequency component was always the same as paced by the auditory signal and contained 60% - 95% of all the energy in the signal. Eye-in-Head/Head gain (ratio of peak-to-peak amplitudes of eye-in-head and head position) and phase were then calculated using standard techniques (including Bartlett window) for signals not containing a strictly integer number of cycles of all occurring frequencies. For the calculation of maximal retinal image velocity the gaze gain (ratio of peak-to-peak amplitudes of gaze and head position) and phase were also calculated with a Bartlett window (similar procedure as described above) and multiplied with head amplitude times $2\pi f$ to obtain gaze velocity attributable to non-compensated head oscillation. Finally, mean gaze (cumulative smooth eye position signals) and head speeds were calculated in the time domain by a sliding window technique with a window of 4 sample points (equivalent to about 70 ms since after the data reduction the sampling frequency was 56.89 Hz).

RESULTS

The Effect of the Correction Procedure

First, the extent to which the off-line correction procedure affected the gaze instability evident in the raw data shall be illustrated.

In the present experiments, the largest distortions of recorded gaze will result from horizontal and vertical misalignments of the annulus combined with ocular torsion. Since torsional eye movements are potentially much larger than either horizontal or vertical eye movements during fixation of a stationary point target, this effect could be substantial and would depend upon the amount of head torsion.

Annulus misalignments for all subjects, recorded during fixation with the head straight and stationary, ranged from 2.06 - 10.67 (mean 5.25) deg horizontally, 1.66 - 4.89 (mean 3.14) deg vertically and 0.25 - 12.57 (mean 5.19) deg in the torsional direction. Since horizontal annulus misalignments were systematically larger than those in the vertical direction, corrections had their largest effect on vertical gaze, especially in those measurements were torsional gaze movements were substantial.

The combined occurrence of misalignments and cross-coupling of head movements between the various planes could potentially introduce serious artifacts.

A systematic survey of cross-coupling of head movements in the different planes is shown in Table 1. During horizontal head oscillations cross-coupling to the torsional direction was about 11%; during vertical head oscillations it was about 5%. As torsional

Table 1. The cross-coupling of head movements during head oscillations are given as mean percentages (± S.D.) for pooled data of 8 subjects.

Main Plane of Head Osc.:	Horizontal		Vertical		Torsional	
Additional Planes of Head Osc.:	Vertical	Torsion	Horizontal	Torsion	Horizontal	Vertical
Cross-coupling % Mean:	4.6	11.1	3.4	5.4	49.1	6.6
(SD)	(2.5)	(6.9)	(1.7)	(4.0)	(29.9)	(5.4)

Table 2. Slopes (b) and correlation coefficients (r) of linear regressions of gaze position on head position for static horizontal or vertical head displacements (ranging between +15 and -15 deg) during fixation of a stationary point target at optical infinity. Subjects are shown in descending order of fixation accuracy.

Subject	Horizontal		Vertical	
	b	r	b	r
E.F.	-0.0012	-0.125	0.0026	0.161
M.P.	0.0029	0.400	0.0024	0.316
C.E.	-0.0010	-0.090	-0.0056	-0.933
H.S.	0.0016	0.113	0.0058	0.332
M.R.	0.0110	0.955	0.0048	0.935
D.T.	0.0110	0.858	0.0064	0.809
C.B.	0.0224	0.874	0.0101	0.765
K.V.	0.0281	0.949	0.0289	0.983
Mean (S.D.)	0.0094 ± 0.0110		0.0069 ± 0.0100	

compensatory eye movements have a low gain, the concomitant torsional eye rotations were also considerable (as will be shown later in this section). Table 1 also shows that subjects found it very difficult to make pure torsional head oscillations; these were accompanied by about 7% of vertical head movement and as much as 49% of horizontal head movement.

As it turned out, in most cases full correction of these effects had only modest consequences for the amount of gaze instability, except when large torsional head movements were deliberately made. In Fig. 2 an illustration of the effect of this correction is given for subject E.F. The misalignments of the annulus in this case were about 11, 3 and 13 deg, for respectively the horizontal, vertical and torsional directions. Horizontal, vertical and torsional gaze are shown for the cases of horizontal, vertical or torsional voluntary head movement at 0.333 Hz. The raw data are shown in the left column, the fully corrected (veridical) gaze positions in the right column. As can be seen in the figure, gaze corrections for horizontal and vertical head oscillations produced hardly any change in gaze instability. In this example the S.D. of vertical gaze position was changed from 7.28 to 5.89 min arc for horizontal head oscillation and from 13.15 to 13.64 min arc for vertical head oscillation. For torsional head oscillations, during which considerable torsional eye movements were seen, the correction procedure markedly reduced vertical gaze instability; the S.D. of vertical gaze position was reduced from 25.70 to 9.48 min arc. Horizontal and torsional gaze instabilities showed comparatively slight changes after correction.

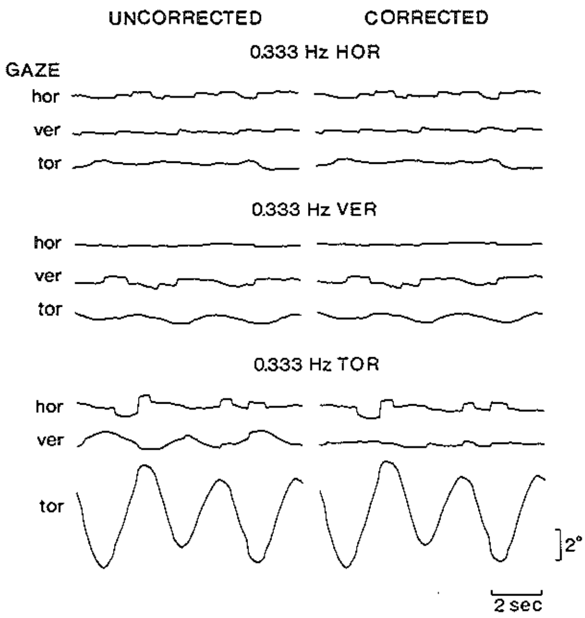

Fig. 2. Horizontal, vertical and torsional gaze are shown for subject E.F. during active head oscillations in the horizontal, vertical and torsional planes all at 0.333 Hz. The raw (uncorrected) data are shown in the left column, the veridical (fully corrected) gaze positions in the right column.

For accurate recording of torsion, it is obviously of vital importance that no significant slip of the annulus occurs around the visual axis. As Collewijn et al. (1985) reported earlier, any significant slip would be likely to show up as discontinuities in the recordings or irregular changes in the zero position. All measurements were plotted on paper and inspected; no evidence of this kind was observed in any of the recordings.

The instability of torsional gaze during the zero position measurement (lasting for 18 seconds) immediately preceding the torsional oscillation measurements was larger than that of horizontal and vertical gaze; effective torsional gaze (all subjects pooled) showed a mean S.D. of ±16.67 min arc in contrast to the horizontal and vertical gaze values which showed mean S.D.'s of ±6.86 and ±8.05 min arc respectively (values taken before horizontal or vertical oscillations, respectively). Variability of torsional gaze position between 4 zero position measurements interleaved with the active head oscillation measurements, expressed as the S.D. of the mean (all subjects pooled), was ±2.14 deg (concomitant horizontal and vertical gaze values were ±15.42 and ±36.05 min arc). This instability of torsional gaze is due to a rather pronounced drift, combined with saccades, of the eye around the visual axis; fluctuations of ocular torsion were observed in all subjects and varied idiosyncratically. Since torsional gaze values in the zero position measurements showed no particular trend and remained close to zero it was concluded that no substantial slip of the annulus occurred in any of the subjects. A more detailed analysis of torsional eye movements will follow in Chapters III and IV. One important point which will be reported there is that the marked torsional drift is not due to the open-loop nature of a point target with regard to torsion. Torsional instability is at least as high in the presence of a structured background.

Effects of Static Head Deviations on Gaze Stability

For a variety of different static eccentric head positions, one would expect an invariant gaze position in case of perfect fixation of a point target at optical infinity. In other words, a linear regression of static gaze position on static head position should have a slope (b) of zero. This part of the experiment served as an internal control on the quality of fixation as well as the overall insensitivity of the experimental procedure to translations.

It turned out that the accuracy of fixation differed between subjects. Table 2 gives a survey of the results. The slopes (b) represent the ratio's of gaze deviation/head deviation and can be considered as a gaze displacement gain, the ideal value of which is zero. Virtual independence of gaze direction from head direction was found in four subjects (E.F., M.P., C.E. and H.S.; top half of Table 2). In these 4 subjects b was on the order of a few parts on a thousand in both dimensions and correlation coefficients were mostly very low.

The other four subjects (M.R., D.T., C.B. and K.V.) showed slopes above 0.01 in one or both dimensions, with high correlations between head and gaze displacements. In the worst subject (K.V.) gaze displacement amounted to nearly 3% of head displacement in both directions. There was no correlation between the accuracy of fixation and the amount of experience of the subject; only C.E. and H.S. had worn scleral coils extensively before. All other subjects wore a coil for the first or second time.

Static head tilt angles between about 15 deg to the left and 15 deg to the right were accompanied by varying amounts of ocular compensation (counter-roll) within and between the subjects. From the pooled data of all subjects, a mean gain of compensation (ratio between eye-in-head and head position) of 0.26 ±0.24 (S.D.) was calculated. This counterroll, although insignificant in terms of stabilization, is rather large compared to earlier measurements (see Collewijn et al., 1985).

Effects of Active Head Oscillations on Gaze Stability

A number of calculated parameters of gaze and head movements are shown in Tables 3-5. Table 3 shows horizontal gaze movement associated with intended horizontal head motions; Table 4 shows vertical gaze movement during intended vertical head movements and Table 5 similarly shows the gaze/head relations in the torsional plane. Data are given for each frequency and subject as well as pooled over all 8 subjects. Data for the stationary head are labeled 0 Hz. For the stationary case, only the S.D. of head and gaze positions (over a period of 18 seconds) are shown. For the sinusoidal oscillations are given the calculated amplitude of the head motion, the S.D. of gaze position (including saccades), the gain of the smooth, compensatory eye movements (excluding saccades; Eye/Head), the gain of the gaze (Gaze/Head) and the maximal velocity of the smooth gaze changes (Gaze Vmax). The use of the standard deviation to characterize the distribution of gaze is justified because examination of these distributions showed that they had in general a pseudo-normal shape. The last 3 parameters (the 3 columns to the right

Table 3. Parameters of horizontal head and gaze movements with the head held stationary and voluntary oscillations in the horizontal plane.

Subj	Eye	Freq. (Hz)	SD Head (min)	Head Amp (deg)	SD Gaze (min)	Eye/Head Gain	Gaze/Head Gain	Gaze Vmax (min/s)
E.F.	R	0	11.06		4.87			
		0.167		13.860	10.36	0.993	0.015	13.09
		0.333		10.415	10.74	0.996	0.008	10.46
		0.667		8.567	13.28	0.999	0.001	2.15
M.P.	L	0	8.88		2.92			
		0.167		14.540	6.86	1.000	0.009	8.24
		0.333		13.921	7.15	0.992	0.011	19.22
		0.667		14.576	10.17	0.996	0.010	36.65
C.E.	R	0	3.88		4.54			
		0.167		8.254	9.38	0.989	0.012	6.24
		0.333		10.301	12.01	0.988	0.012	15.52
		0.667		5.855	12.17	0.979	0.027	39.75
H.S.	R	0	11.27		7.96			
		0.167		9.298	15.47	1.020	0.029	16.98
		0.333		9.709	18.52	1.003	0.018	21.94
		0.667		7.968	13.70	0.995	0.011	22.04
M.R.	L	0	5.78		5.93			
		0.167		4.984	25.25	0.966	0.040	12.55
		0.333		5.416	18.59	0.979	0.040	27.20
		0.667		9.067	20.47	0.974	0.030	68.40
D.T.	L	0	2.75		8.54			
		0.167		7.359	13.45	0.970	0.031	14.36
		0.333		8.838	17.88	0.979	0.026	28.85
		0.667		6.067	13.20	0.979	0.024	36.61
C.B.	L	0	6.32		15.08			
		0.167		9.953	30.92	0.956	0.043	26.94
		0.333		8.453	22.27	0.940	0.061	64.73
		0.667		6.344	26.50	0.951	0.050	79.76
K.V.	L	0	6.35		5.07			
		0.167		9.816	20.58	0.972	0.029	17.92
		0.333		8.469	16.78	0.968	0.043	45.72
		0.667		7.506	19.43	0.957	0.048	90.60
Mean (SD)		0	7.04 (3.13)		6.86 (3.79)			
		0.167		9.758 (3.179)	16.53 (8.39)	0.983 (0.021)	0.026 (0.013)	14.54 (6.39)
		0.333		9.440 (2.400)	15.49 (5.02)	0.981 (0.020)	0.027 (0.019)	29.21 (17.85)
		0.667		8.244 (2.817)	16.12 (5.49)	0.979 (0.018)	0.025 (0.018)	47.00 (30.08)

Table 4. Parameters of vertical head and gaze movements with the head held stationary (0 Hz) and voluntary oscillations in the vertical plane.

Subj	Eye	Freq. (Hz)	SD Head (min)	Head Amp (deg)	SD Gaze (min)	Eye/Head Gain	Gaze/Head Gain	Gaze Vmax (min/s)
E.F.	R	0	7.95		5.87			
		0.167		9.028	10.85	0.989	0.019	10.80
		0.333		9.288	13.64	0.987	0.017	19.82
		0.667		10.063	13.42	0.994	0.014	35.43
M.P.	R	0	8.77		5.97			
		0.167		15.226	6.71	1.002	0.003	2.88
		0.333		10.752	5.89	0.999	0.004	5.40
		0.667		11.616	8.50	1.000	0.010	29.21
C.E.	R	0	7.38		4.39			
		0.167		5.322	9.09	0.987	0.030	10.05
		0.333		5.428	9.30	0.993	0.017	11.58
		0.667		4.791	11.08	0.988	0.025	30.12
H.S.	R	0	11.15		13.13			
		0.167		6.760	17.26	0.992	0.027	11.49
		0.333		5.456	27.72	0.963	0.042	28.77
		0.667		5.865	22.61	0.982	0.019	28.02
M.R.	L	0	8.53		5.03			
		0.167		6.632	12.17	0.997	0.053	22.13
		0.333		6.404	13.04	0.991	0.012	9.65
		0.667		9.275	24.41	0.978	0.026	60.64
D.T.	L	0	12.77		10.70			
		0.167		6.289	16.55	0.966	0.036	14.25
		0.333		5.977	36.10	0.959	0.051	38.27
		0.667		10.575	41.35	0.980	0.027	71.80
C.B.	L	0	4.48		9.01			
		0.167		10.935	12.71	1.001	0.008	5.51
		0.333		7.658	13.37	0.994	0.026	25.00
		0.667		8.266	19.60	0.982	0.025	51.96
K.V.	L	0	32.54		10.26			
		0.167		6.643	13.50	0.978	0.029	12.13
		0.333		6.613	16.07	0.966	0.042	34.87
		0.667		5.714	18.50	0.957	0.049	70.40
Mean		0	11.70		8.05			
(SD)			(8.78)		(3.17)			
		0.167		8.354	12.36	0.989	0.026	11.16
				(3.300)	(3.54)	(0.012)	(0.016)	(5.77)
		0.333		7.197	16.89	0.982	0.026	21.67
				(1.921)	(10.02)	(0.016)	(0.017)	(12.11)
		0.667		8.271	19.93	0.983	0.024	47.20
				(2.540)	(10.28)	(0.013)	(0.012)	(18.78)

Table 5. Parameters of head and gaze stability in the torsional plane. Similar to Tables 3 and 4 except that all units are in degrees.

Subj	Eye	Freq. (Hz)	SD Head (deg)	Head Amp (deg)	SD Gaze (deg)	Eye/Head Gain	Gaze/Head Gain	Gaze Vmax (deg/s)
E.F.	R	0	0.3327		0.3270			
		0.167		7.360	2.4978	0.580	0.425	3.282
		0.333		8.268	2.1679	0.673	0.327	5.657
		0.667		7.104	1.5775	0.737	0.263	7.830
M.P.	R	0	0.0812		0.1242			
		0.167		20.459	11.9307	0.318	0.705	15.135
		0.333		17.163	8.4007	0.470	0.542	19.463
		0.667		13.023	5.1046	0.596	0.415	22.650
C.E.	R	0	0.0564		0.2213			
		0.167		8.919	3.4518	0.491	0.515	4.820
		0.333		9.384	3.4368	0.697	0.303	5.949
		0.667		5.267	1.6215	0.751	0.251	5.540
H.S.	R	0	0.2841		0.5044			
		0.167		6.140	3.6373	0.284	0.716	4.613
		0.333		4.667	2.8181	0.319	0.682	6.660
		0.667		5.688	2.8680	0.528	0.473	11.275
M.R.	L	0	0.1515		0.2630			
		0.167		16.521	10.1833	0.306	0.705	12.221
		0.333		11.077	6.4974	0.379	0.622	14.416
		0.667		9.408	4.7217	0.643	0.358	14.115
D.T.	L	0	0.0820		0.1749			
		0.167		9.167	6.4624	0.379	0.641	6.166
		0.333		8.275	5.2362	0.484	0.520	9.003
		0.667		8.735	5.3514	0.576	0.425	15.558
C.B.	L	0	0.0825		0.3540			
		0.167		11.128	5.1772	0.478	0.529	6.177
		0.333		11.312	4.7142	0.547	0.453	10.722
		0.667		7.869	2.7072	0.631	0.369	12.169
K.V.	L	0	0.1454		0.2539			
		0.167		9.880	4.6767	0.506	0.510	5.287
		0.333		9.420	4.3346	0.593	0.418	8.239
		0.667		6.654	2.2436	0.645	0.374	10.429
Mean (SD)		0	0.1520 (0.1028)		0.2778 (0.1182)			
		0.167		11.197 (4.862)	6.0022 (3.3733)	0.418 (0.110)	0.593 (0.112)	7.213 (4.169)
		0.333		9.946 (3.572)	4.7007 (2.0317)	0.520 (0.134)	0.483 (0.134)	10.014 (4.782)
		0.667		7.969 (2.484)	3.2744 (1.5547)	0.638 (0.076)	0.366 (0.077)	12.446 (5.225)

in Tables 3-5) were calculated from the amplitude of the fundamental frequency of the head oscillation penetrating into the gaze signals. The Eye-in-Head movements were approximately, but not exactly 180 deg out of phase with respect to the head movements. Due to small phase errors, the Eye/Head and Gaze/Head gains do not add up to unity; in fact the gaze movements are larger than the difference between the Eye/Head gain and unity. Notice that gaze changes are measured directly by the recording technique and not derived as a difference between head and eye-in-head movements. This makes the fluctuations of gaze reliable even though they are small; they would be also quite insensitive to minor errors of calibration.

Horizontal Oscillation

With the head held stationary, the standard deviations of head position pooled over 8 subjects had a mean value of 7.04 ±3.13 (S.D.) min arc. For gaze this value was 6.86 ±3.79 (S.D.) min arc. The active head oscillations at 0.167, 0.333 and 0.667 Hz had mean amplitudes of almost 10 deg. Independently of frequency, head oscillation caused the mean S.D. of gaze to increase to about 16 min arc. The gain of the smooth compensatory eye movements was about 0.98; the mean phase lag was 0.7 ±0.7 (S.D.) deg with respect to ideal compensation. Although this phase error seems very small, it contributed to the instability of gaze and made that the gaze/head gain and eye/head gain did not simply add up to unity. They did so, however, when the vectors (including phase) were added correctly. As a result, smooth gaze movements amounted to an average of 2.5% of head movement, which is slightly larger than the difference between eye/head gain and unity (2.0%). The corresponding gaze velocities were of course proportional to frequency and rose from 15 min arc/sec at 0.167 Hz to 47 min arc/sec at 0.667 Hz.

An example of the decline of gaze stability with increasing frequency is given in Fig. 3. In this figure, fully corrected gaze and head positions of subject K.V., who had a representative amount of dynamic gaze instability, are shown at 0 Hz and during horizontal head oscillations at 0.167, 0.333 and 0.667 Hz. At 0 Hz, all 3 gaze traces form more or less straight lines, except for a slight drift in torsional gaze: almost perfect gaze stability. At 0.167 and 0.333 Hz however, fluctuations of horizontal and torsional gaze are apparent, while vertical gaze still shows very good stability. Torsional gaze fluctuations are the result of accompanying torsional head movements (which are much smaller than the horizontal head movements and not very apparent in all traces since the scale for head traces is 10 times smaller than that for gaze traces). They are relatively large due to the low gain of torsional compensatory eye movements. Horizontal oscillations at 0.667 Hz, show considerable gaze fluctuations for horizontal and torsional gaze and even for vertical gaze.

Comparison of the Gaze/Head gain values in Table 3 with the slopes of gaze errors for static head deviations in Table 2 confirms that dynamic gaze instabilities were substantially larger than static errors for all individuals. The four most stable "fixators" in the static conditions also had the best dynamic stability; nevertheless their instability was augmented considerably by head oscillation.

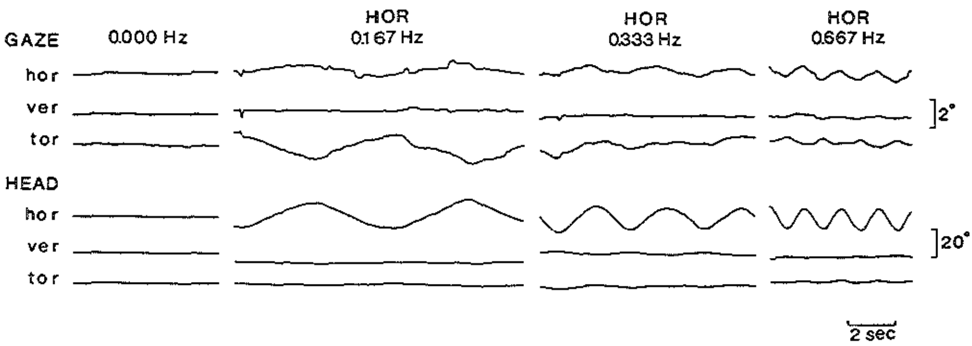

Fig. 3. Fully corrected horizontal, vertical and torsional gaze and head positions are shown for subject K.V. with the head stationary (0 Hz) and during active head oscillations in the horizontal plane at 0.167, 0.333 and 0.667 Hz.

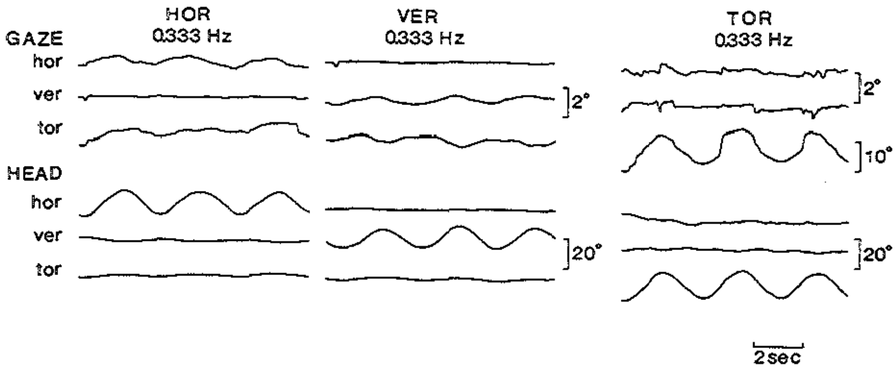

Fig. 4. Fully corrected horizontal, vertical and torsional gaze and head positions are shown for subject K.V. during active head oscillations in the horizontal, vertical and torsional planes all at 0.333 Hz.

Vertical Oscillation

Comparison of Table 4 to Table 3 shows that the mean amount of gaze instability in the vertical plane during vertical head movement is almost exactly similar to horizontal instability during horizontal head oscillation. Mean phase lag of the compensatory eye movements was 0.6 $\pm$1.0 deg with respect to ideal compensation. The average gaze motion was about 2.5% of the head motion. The two best performing subjects in the horizontal direction (E.F. and M.P.) showed the least gaze instability also in the vertical plane. For all individuals, dynamic instability (Table 4) was larger than static gaze error (Table 2) in the vertical plane.

Torsional Oscillation

Head oscillations in the torsional direction showed different results (Table 5). The most striking difference from the horizontal and vertical head oscillations were the Eye-in-Head/Head gain values, which were much lower, although they rose with the frequency of head oscillation from 0.418 at 0.167 Hz to 0.638 at 0.667 Hz. The Gaze/Head gains of course show an opposite trend. The mean phase lag of the torsional compensatory eye movements was 4.6$\pm$5.9 (S.D.) deg. The mean SD of torsional gaze position decreased with frequency (as Eye-in-Head/Head gain rose) from about 6 deg at 0.167 Hz to about 3 deg at 0.667 Hz. Maximal torsional gaze velocity showed a modest increase with frequency from about 7 to 12 deg/sec. These results are in agreement with those of Collewijn et al. (1985) who also showed that the presence of horizontal and vertical contours in addition to the point target improved the compensatory torsional eye movements somewhat, but not to a large extent.

In Fig. 4, typical examples of gaze instability during horizontal, vertical and torsional head oscillations at 0.333 Hz are shown for subject K.V., whose horizontal oscillations have already been described above (Fig. 3). Vertical oscillations showed almost perfect stability for horizontal gaze, but in the vertical and torsional gaze traces fluctuations are apparent. The vertical Eye-in-Head/Head gain during vertical oscillation was 0.966 (Table 4), with a corresponding gaze modulation of 4.2% of the head movement. Again, torsional gaze fluctuations were caused by accompanying torsional head movements. During torsional head oscillations, very large torsional gaze movements can be seen, moving in phase with the head. These reflect the low gain (Eye-in-Head/Head) of 0.593 in this condition. Horizontal and vertical gaze stability was much better, although not entirely perfect.

Remarkably, subject E.F. showed the highest amount of stabilization also in torsion and was therefore the most stable subject in all dimensions. For the other subjects, stability in torsion did not correlate with stability in horizontal and vertical direction.

Mean Retinal Image Speeds

Shown in Tables 3-5 (columns on the far right) are maximal retinal image speeds as related to the amplitude of the smooth gaze movements at the fundamental frequency of the head oscillation. These values therefore represent the velocities contributed by the specific component induced by head oscillation. However, in addition there is gaze instability unrelated to the oscillation frequency, due to erratic head movements and drift of the eye in the head.

Table 6. Mean speeds of gaze and head position (calculated in the time domain) during head oscillations in the horizontal, vertical and torsional directions with values of all subjects pooled together for the different frequencies.

Mean Speeds During Horizontal Head Oscillations

Freq. (Hz)	Horizontal Gaze (SD) (min/s)		Horizontal Head (SD) (deg/s)	
0	23.17	(5.18)	0.54	(0.20)
0.167	33.62	(7.87)	7.08	(1.98)
0.333	42.32	(11.63)	13.04	(3.10)
0.667	55.60	(21.50)	22.42	(7.61)

Mean Speeds During Vertical Head Oscillations

Freq. (Hz)	Vertical Gaze (SD) (min/s)		Vertical Head (SD) (deg/s)	
0	29.81	(12.46)	0.69	(0.19)
0.167	42.36	(14.81)	6.21	(2.21)
0.333	46.71	(20.53)	9.64	(2.51)
0.667	72.88	(23.57)	22.64	(7.09)

Mean Speeds During Torsional Head Oscillations

Freq. (Hz)	Torsional Gaze (SD) (deg/s)		Torsional Head (SD) (deg/s)	
0	0.76	(0.15)	0.55	(0.13)
0.167	4.96	(2.77)	8.09	(3.37)
0.333	6.63	(2.92)	13.54	(4.65)
0.667	8.57	(3.47)	21.87	(6.59)

The mean gaze and head speeds (absolute values of velocities) were calculated for the stationary and oscillating head from moment to moment with a sliding window technique in the time domain. The results are shown in Table 6.

They reflect mean head and retinal image speeds, the latter with exclusion of saccades, but including drifts unrelated to head motion. Thus, horizontal image speeds were about 23 min/sec with the head stationary; they increased with oscillation frequency of the head to about 56 min/sec at 0.667 Hz (amplitude of head oscillation about 10 deg). In the vertical direction, speeds were slightly larger. In the torsional direction slip speeds were very large, with a mean value of about 0.8 deg/sec even with the head held stationary.

It can be shown that the mean retinal image speeds in Table 6 in the horizontal and vertical dimensions consist indeed of the sum of the specific oscillation induced motion and a basic component which is always present with the head free. In Table 7, the left columns show mean maximal gaze velocities for 3 frequencies, copied from Table 3 and 4 (columns on the far right). In the second column of Table 7, these maximal values of a sinusoidal component have been converted to mean speeds by dividing them by the square root of 2. The third column shows mean gaze speeds, copied from Table 6. In the column at the far right of Table 7, the gaze speed with the head stationary (23.17 min/sec horizontally and 29.81 min/sec vertically) has been subtracted from the gaze speeds during oscillation. It can be seen that the resulting values agree in most cases satisfactorily with the values in the second column.

Table 7. Relations between maximal velocities of gaze contributed by the head oscillation, calculated in the frequency domain (column 1); the mean speeds of these components (column 2); the mean gaze speeds calculated in the time domain (column 3) and the mean speeds during head oscillation diminished by the gaze speed with the head stationary (column 4). Notice the correspondence between columns 2 and 4. All values in min/sec.

	V max Gaze	V max Gaze/√2	Mean Gaze Speed	Mean Gaze Speed - Base Values
Horizontal Osc. (Hz)				
0			23.17	
0.167	14.54	10.28	33.62	10.45
0.333	29.21	20.65	42.32	19.15
0.667	47.00	33.23	55.60	32.43
Vertical Osc. (Hz)				
0			29.81	
0.167	11.16	7.89	42.36	12.55
0.333	21.67	15.32	46.71	16.90
0.667	47.20	33.38	72.88	43.07

DISCUSSION

The present data on natural retinal image motion, with the corrections applied, can be considered essentially free of artifacts. They extend earlier observations (Collewijn et al., 1981, 1983; Steinman et al., 1982) on the imperfection of the compensatory eye movements and confirm that gaze instability during voluntary head motion is real, and not a measuring artifact as has been asserted by Stark (1983).

Gaze stability measured while the head was held as still as possible formed the baseline for these experiments.

With the head held stationary and straight, the mean S.D.'s of horizontal and vertical gaze were 6.86 and 8.05 min arc respectively with corresponding mean speeds of 23.17 and 29.81 min/sec. Skavenski et al. (1979) reported that eye movements with the head free but kept as still as possible while the subjects were sitting had a SD of about 6 min arc and a speed of 23 min/sec in the horizontal and vertical directions. The results presented here are virtually identical. Mean S.D.'s of horizontal and vertical head position (with the head stationary) were 7.04 and 11.70 min arc respectively with corresponding mean speeds of 0.54 and 0.69 deg/sec, again very much in agreement with Skavenski et al. (1979) who recorded a mean S.D. of head position (head free and subjects sitting) of about 11 min arc with a mean speed of 0.52 deg/sec in both horizontal and vertical directions.

Torsional eye position during a single zero measurement showed a mean S.D. of about 17 min arc; at least twice as high as the typical values in the horizontal and vertical plane. The variability between 4 zero measurements was ±2.14 deg (S.D. of the mean). No evidence was found that these fluctuations might be attributed to slip of the annulus on the eye-ball. Collewijn et al. (1985) using a torsion-sensitive scleral induction coil, found fluctuations of ocular torsion of ±1 deg in the zero position during static head tilt measurements and fluctuations up to 3 deg in the zero position during active torsional head oscillations. Diamond and Markham (1983) reported continuous and random fluctuations of ocular torsion up to 4 deg, although these fluctuations were not examined in detail for the upright position. In their experiments, measurements (by a photographic method) had an accuracy of 0.25 deg. In previous experiments by Diamond et al. (1982) variations of torsion in the upright position were studied more extensively (photographs taken every 10 seconds for 10 minutes) and peak-to-peak fluctuations of only 1.5 deg were found (for 2 normal subjects). The accuracy of these experiments was between 15 and 30 min. Fender (1955), Miller (1962) and Nelson (1971) reported torsional fluctuations ranging from 8 min arc to 1 deg, unfortunately without giving a clear indication of the sampling period during which measurements had been made or the number of measurements. The results presented here are more consistent with later findings than with earlier ones. The main reason is probably an improvement of recording technique; ocular torsion was constantly and directly measured and not intermittently and indirectly by for instance a photographic method. The recordings suggest that random and continuous drift of torsional eye position, resulting in values of up to 4-5 deg and reflecting a substantial torsional gaze instability, may be regarded as a normal physiological phenomenon.

The second step was the exclusion of static distortions as a source of artifact in the measurements by showing that gaze was not or minimally affected by sustained horizontal or vertical head deviations. An effect of horizontal and vertical static head deviations on horizontal and vertical gaze displacements was virtually absent in 4 out of 8 subjects. High correlations between head and gaze displacements were found in the other 4 subjects although gaze displacement only occasionally exceeded 1% of head displacement in either direction. This suggests that subjects may have some difficulty in maintaining precise fixation when the head as well as the eye are kept in an eccentric position, with a tendency for the ocular deviation to fall short of the target. The precision of eccentric fixation with or without deviation deserves closer scrutiny in future work.

In contrast, static head roll between angles of +15 and -15 deg produced ocular counter-roll which varied idiosyncratically and had a mean gain of 0.26 ±0.24 (S.D.). Collewijn et al. (1985), using a similar recording technique and with subjects also viewing a single laser spot, found a lower mean gain of ocular torsion: 0.096 with a SD of 0.012 for static head tilts up to 20 deg. Large variability of ocular counter-roll within and between subjects is quite probably the cause of this difference. Since the results shown here represent data of 8 subjects and Collewijn's those of only 2, it seems likely that torsional variability would manifest itself more clearly in the present experiments.

In all individuals, dynamic head oscillation in the horizontal and vertical plane produced a larger fluctuation of gaze than was seen during static deviations of the head.

Active horizontal and vertical head oscillations at 0.167, 0.333 and 0.667 Hz produced mean maximal horizontal and vertical gaze velocities (calculated in the frequency domain) rising with frequency up to about 47 min/sec; mean gaze speeds (calculated in the time domain) were not larger than about 1 deg/sec. It was demonstrated that the mean retinal image speeds in the horizontal and vertical direction consisted of two parts: a basic component present also with the head stationary and a component specifically related to the oscillation frequency. Subtraction of this basic component from the mean gaze speeds obtained during the oscillations provided the components specific for the oscillation (Table 7). A similar procedure has been reported earlier by Martins et al. (1985) who subtracted a constant (mean retinal image speed during fixation of a stationary target) from eye speed during fixation of a moving target.

About 2.5% of the head velocity penetrated into horizontal and vertical gaze, i.e. about 1 deg/sec for a head motion of 10 deg amplitude at 0.66 Hz which has a maximal velocity of about 40 deg/sec. The head movements in these experiments were relatively modest; head velocities could easily be increased by a factor 5 which may be expected to cause retinal image slip velocities exceeding 5 deg/sec. Such velocities have indeed been recorded elsewhere (Steinman, personal communication).

Mean S.D.'s of gaze (including saccades) in the horizontal and vertical direction during active oscillations in the respective horizontal and vertical planes were all smaller than 20 min arc. This result concurs with the values reported earlier by Collewijn et al. (1981) and Steinman et al. (1982). Duwaer (1982) found smaller values however: during active head oscillations at 0.66 Hz in the horizontal plane the mean S.D. of retinal image slip in the horizontal direction was about 9 min arc; the corresponding value here was about 16 min arc (mean S.D.) which is almost twice as high. The reason for this discrepancy may be potentially quite interesting: since Duwaer used an afterimage technique influences of central processing cannot be discounted and one might speculate that retinal image slip is reduced by higher order processes. In other words not only retinal image slip but also cortical processing and representation was measured. Experiments taking the contribution of the central nervous system into account might be of interest.

Horizontal compensatory eye movements during horizontal oscillations resulted in mean Eye-in-Head/Head gains which varied between 0.979 and 0.983; vertical compensatory eye movements during active oscillations in the vertical plane showed mean Eye-in-Head/Head gains between 0.982 and 0.989. Ocular compensation in the horizontal and vertical planes was thus 1-2% smaller than unity. Due to additional phase errors, the associated gaze movements amounted to a mean of 2.5% of the head movements. Skavenski et al. (1979) found a best average gain value of 0.95 with large amplitudes during passive horizontal rotation in the light at 2.5 Hz. In 1981, Collewijn et al. reported a mean Eye-in-Head/Head gain of 0.95 for active as well as passive horizontal rotations in the light at frequencies of 0.33, 0.66 and 1.33 Hz. Collewijn et al. (1983) found a gain of 1.01 ±0.03 (S.D.) for active horizontal head oscillations in the light (averaged over 5 subjects, 3 frequencies and 2 eyes). They reported that gain was never precisely unity and showed idiosyncratic variability. The results presented here are in close agreement with the results of these papers.

Gaze instability in the torsional plane was much larger than in the horizontal and vertical planes and increased further by active head oscillations in the torsional direction. The mean S.D. of torsional gaze decreased with frequency from about 6 deg at 0.167 Hz to little more than 3 deg at 0.667 Hz; maximal torsional gaze velocity increased with frequency from about 7 deg/sec to 12.5 deg/sec. The mean Eye-in-Head/Head gain values remained well below unity despite an increase with frequency from 0.418 at 0.167 Hz to 0.638 at 0.667 Hz. These gain values are slightly higher than those reported by Collewijn et al. (1985) but the trend is similar.

In contrast to the horizontal and vertical directions, dynamic torsional gaze stability is much better than static stabilization by counterroll. Naturally, horizontal and vertical static fixation is entirely controlled by vision. Static counterroll is mainly controlled by the otoliths; a single point provides obviously no visual reference for torsion but even the presence of a structured pattern improves static counterroll only marginally, if at all (Collewijn et al., 1985). Remarkably, dynamic counterroll is better with a single point target than in darkness (Collewijn et al., 1985), which suggests a visuo-vestibular interaction of a different nature than additivity of visual and vestibular motion information. A structured background improves dynamic counterroll somewhat further, but compensation remains very incomplete.

It has to be concluded that retinal images undergo considerable and continuous motion during natural head movements. Clearly this raises important problems for visual processing. Psychophysical work (Steinman et al., 1985) is beginning to reveal how vision tolerates and may even benefit from retinal image motion. Earlier work (Steinman and Collewijn, 1980; Collewijn et al., 1981, 1983) has shown that binocular retinal image motion contains a significant disjunctive (non-conjugate) component. Although the present work was done monocularly, the generally modest changes resulting from the elaborate corrections make it most likely that also this disjunctive component is real and not artifactual. As a result continuous fluctuations in disparity occur. Recent experiments (Erkelens and Collewijn, 1985a,b; Collewijn et al., 1986; Regan et al., 1986) have shown that fluctuations in absolute disparity up to 1-2 deg do not interfere with stereopsis or fusion, nor do they induce any perception of motion in depth. Only changes in relative disparity between different parts of retinal image lead to perception of relative depth. These observations fit very well with the findings of retinal image instability shown here and strongly suggest that the design of the visual system is such that considerable fluctuation of the position of the whole retinal image is well tolerated, not perceived and possibly even beneficial to vision.

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Chapter III

A direct test of Listing's law: I. Human ocular torsion measured in static tertiary positions.

INTRODUCTION

For more than a century, the kinematics of the eye have been the subject of many theoretical and some experimental analyses. The basic issues in this respect have been: (1) the number of degrees of freedom required to describe the rotations of the eye-ball; (2) the choice of a coordinate system to provide a frame of reference for such rotations; (3) the occurrence of so-called "false torsion" and its experimental proof.

If one regards the eye as rotating about a point fixed within the globe and also within the head, it has three rotational degrees of freedom (Westheimer, 1957) and in order to describe any position of the eye it is sufficient to specify its angle around three unambiguously defined axes. In Fick's (1854) coordinate system, horizontal eye movements are described around an earth-fixed vertical axis. Vertical movements are made around an axis in the horizontal plane, which rotates with the horizontal eye movements around the vertical axis. Finally, the eye can rotate around the visual axis (torsion or cyclorotation), which moves with the horizontal as well as the vertical eye movements. In this coordinate system the horizontal eye movements (projected on a sphere, not a flat plane) occur parallel to the horizon and vertical eye movements in a plane containing the objective vertical (the direction of gravity). No combination of horizontal and vertical displacements to tertiary positions does by itself introduce tilt of the eye with respect to the objective vertical. A practical difficulty arises in determining the vertical head position in which the vertical axis of rotation of the eye is objectively vertical; the absence of any indisputable criterion for this induced Helmholtz (1962) to introduce his own coordinate system, less affected by this difficulty. This system consists of a fixed horizontal axis of rotation coinciding with the line through the centres of rotation of both eyes and a vertical axis which moves about this horizontal axis; torsion is made around the visual axis as in Fick's system. In Helmholtz's system horizontal eye movements, projected on a sphere, are in general not parallel to the horizon and the meridian of the eye which is parallel to the objective vertical in the primary position will be tilted with respect to the objective vertical in any tertiary position. The true difference between the coordinate systems of Fick and Helmholtz is not the sequence of eye movements but the hierarchy of the nesting of the axes involved.

Listing proposed a simplified kinematic description, mainly propagated by Helmholtz (1962), in which only two degrees of freedom are needed to describe any eye position in a given frame of reference. Each position of the eye, according to "Listing's law", can be described as though it had been reached from the primary position by rotation about a single axis in the equatorial plane (Alpern, 1962). The tilt of this axis and the angle of rotation around it are the two degrees of freedom. A consequence of this description is that the meridian of the eye which is earth-vertical in the primary position is systematically tilted with respect to gravity in any tertiary position. Donders' law (1875) stated that the angle of this tilt is always identical regardless of the way the eye reaches that position. Listing's law also specified the magnitude of the tilt which is smaller than that reached in Helmholtz's sytem for the same tertiary position; in Fick's system there is of course no tilt with respect to the objective vertical. In order to reach the same tertiary eye positions as predicted by Listing, both the systems of Fick and Helmholtz would require a rotation around the visual axis but the direction of these rotations would be opposite to one another. This rotation has been called "false torsion", or cyclorotation with respect to the corresponding objective vertical (Boeder, 1957). Although Listing's law has gained acceptance as a valid description of tertiary end positions, it has been verified only approximately by direct observation (Quereau, 1954) and with indirect methods using afterimages (Helmholtz, 1962), photography (Moses, 1950) or the blind spot of the eye (Quereau, 1955). More recently, the validity of Listing's law was verified with an afterimage method by Nakayama and Balliet (1977). The concept of false torsion has elicited controversy and confusion, often aggravated by the use of Cartesian (flat) instead of spherical coordinate systems. In this case the laws of kinematics can easily be mixed up with those of perspective.

With the recently developed scleral induction coil (see Chapter II) horizontal, vertical and torsional movements of a single eye could be measured simultaneously with enough reliability for a critical test of Listing's law. In this chapter ocular torsion under static conditions shall be described; the dynamic aspects of torsion will be described in Chapter IV.

METHODS

Measuring Technique

Angular positions of the eye around the earth-fixed vertical axis and the subsequent horizontal and visual axes according to Fick's coordinate system were simultaneously measured with the scleral induction coil as previously described in Chapter II (methods section). The generation of the appropriate magnetic field, consisting of a vertical and transverse component in spatial and phase quadrature (frequency 20.000 Hz), and the subsequent measurement of eye position with the amplitude detection method (Robinson, 1963) was performed by an Eye Position Meter (type 3000) made by Skalar Instruments, Delft.

Procedure

Vertical, horizontal and torsional eye positions were measured in 4 healthy subjects. Both eyes of each subject were measured successively with monocular vision without any spectacle corrections. The coil was mounted on the viewing eye; the other eye was covered with a patch. Visual acuity was in all subjects good enough to fixate the presented targets properly. Calibration and evaluation of crosstalk were done with a calibration device. This was made of Lucite and included a sight following the visual axis upon which the coil could be mounted. The coil could be rotated with calibrated angles around the three Fick axes while the coil remained in the same centred position in the magnetic field, i.e. the same place were the subject's eye would be (ocular centre of rotation). The only significant crosstalk was induced by vertical motion into the torsion channel; it amounted to less than 2% (worst case) which is an order of magnitude lower than the tilts predicted by Listing's law.

Subjects viewed a row of 7 round targets (diameter 0.5 deg) placed at 10 deg intervals along a circle segment coinciding with a vertical meridian in Fick's coordinate system, against a dark background. Target distance from the ocular centre of rotation was constant at 60 cm. The row of targets could be displaced horizontally from 30 deg to the right to 30 deg to the left at 10 deg intervals around a vertical axis passing through the ocular centre of rotation. In this way a matrix of 49 target positions was presented to the subject. The accurate positioning of all 49 target positions was confirmed with the sight of the calibration device. The central target was positioned straight ahead of the centre of the magnetic field; this was defined as the zero position of all angles. The subject was seated in the magnetic field wearing the previously calibrated coil. The eye was centred in the field by means of a second sight, attached to the field coils, and the head was fixed with frontal, occipital and chin supports in an upright and straight ahead position. Unfortunately, no rigid criterion for the vertical head position representing the primary eye-in-head position for the straight ahead gaze direction is available. As a best approximation, the head was fixed in an upright position experienced as "natural" by the subject and allowing him to fixate targets 30 deg above and below the central target without exceeding the oculomotor range. The sight was then removed. Any non-zero readings of eye position (offsets), caused by misalignment of the annulus on the eye, were not corrected for at this time. Subjects fixated each designated target for 4 sec., making as few blinks as possible. When ready, they started each measurement themselves by pressing a button. During a single experiment a subject monocularly fixated a target in the 49 different positions, after which the sequence was repeated. The subject viewed the central target every few measurements (11 times all together) to check for any slip of the annulus (change of offset). For the analysis, the data from the sequence with the smallest offset changes were used. All data were digitized on line at a sample frequency of 250 Hz and stored on disk by a PDP 11/10 minicomputer for later off-line analysis. The overall resolution of the system including A/D conversion was about 2 minutes of arc in all dimensions.

Data analysis

Each sample taken for all 3 "nominal" eye positions (raw data) and for all measurements (1048 samples per signal per measurement) was corrected off-line as described in Chapter II (methods section) in order to obtain the "effective" (veridical) eye position angles. Following this correction the mean and S.D. were calculated for all 3 effective eye positions during each measurement. After obtaining the effective eye positions, the eye torsion values were compared to those which Listing's law would have predicted, expressed as "false torsion" in Fick's coordinate system. The following equation (Robinson, 1975) was used to calculate this false torsion (ψ; rotation of the upper pole of the eye to the right side of the subject positive)

$$\sin \psi = \frac{-\sin\phi\sin\theta}{1 + \cos\phi\cos\theta}$$

The measured horizontal (ϕ, leftward positive) and vertical (θ, upward positive) effective mean eye positions were substituted in this equation and the computer calculated the predicted false torsion. These results were then compared with the measured effective mean ocular torsion positions.

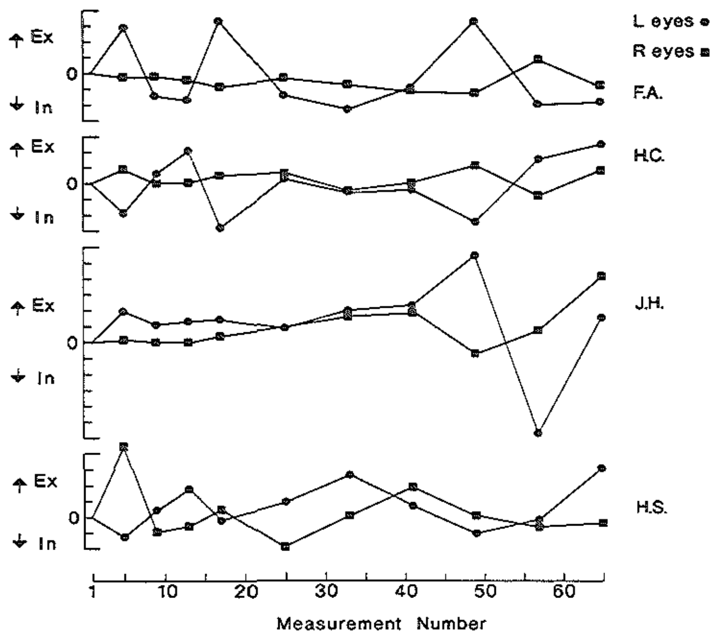

Fig. 1. Effective eye torsion values (ordinate, divided in degrees) in the 11 consecutive primary positions of both eyes of the 4 subjects. First measurements are normalized to zero. Black dots: left eyes; black squares: right eyes. Upward deflections represent extorsion; downward deflections represent intorsion.

RESULTS

Torsion in consecutive primary positions

The effective values of recorded torsional eye positions in the 11 zero position measurements (during which subjects viewed the central target) are shown in Fig. 1 for both eyes of all 4 subjects. Fluctuation of eye torsion in the consecutive zero position measurements is apparent in all eyes. Subject F.A.'s left eye showed several 3-4 deg displacements of extorsion (upper pole of the eye rotated in the temporal direction); however, these displacements were preceded and followed by intorsional values. More than 4 deg of extorsion was seen in subject H.S.'s right eye but only on a single occasion. The left eye of subject J.H. reached a value of more than 5 deg of extorsion in the 9th zero position measurement and an identical value of intorsion (upper pole of the eye rotated in the nasal direction) in the following one. These fluctuations were large but in opposite directions and furthermore the last zero position measurement showed a value of only about 1.5 deg of extorsion. In subject J.H.'s right eye, the last zero position measurement showed a value of slightly more than 4 deg of extorsion but it was preceded in all the other measurements by values much closer to zero.

The standard deviation of the mean torsion values in the 11 subsequent primary positions (in 4 subjects) was 2.07 and 1.20 deg for the left and right eyes, respectively. This long-term variability contrasts with the mean of the standard deviations of torsion within each measurement of 4 sec, which was much smaller: 0.12 deg and 0.15 deg for the left and right eyes. Thus, long-term fluctuation (over a session) was an order of magnitude larger than short-term variability (over a 4 sec measurement). This result may be expected if torsion undergoes substantial long-term drift and changes associated with large horizontal and vertical eye movements. The long-term fluctuations were random in character, and showed no systematic trend; they were different for each eye and subject and unrelated to the (standard) sequence of eye positions in a session. It seems therefore unlikely that these fluctuations are an artifact of slip of the annulus of the eye ball, although only frequent photography of a marked annulus' relation to fixed landmarks on the eye could prove the absence of long-term slip. Evidence against significant slip associated with saccades or blinks will be discussed in Chapter IV.

Torsion in secondary positions

The means (and S.D.) of effective torsional positions for both eyes of all 4 subjects as a function of only horizontal or vertical displacement of the eye from the primary position are shown in Fig. 2 and 3 respectively. As can be seen in Fig. 2, torsional values in the horizontal secondary eye positions showed no particular trend for either eye and were close to zero. Torsional values of the left eyes in the vertical secondary positions (Fig. 3) were also close to zero but the right eyes showed a trend of extorsion increasing with downward positions and a slight trend of intorsion increasing with upward positions. Assuming the validity of Listing's law, both trends might very well be explained by a systematical bias of the chosen primary position in the nasal direction with respect to the true primary position; secondary positions then becoming tertiary ones with corresponding values of ocular torsion. In the discussion section this possibility is developed further

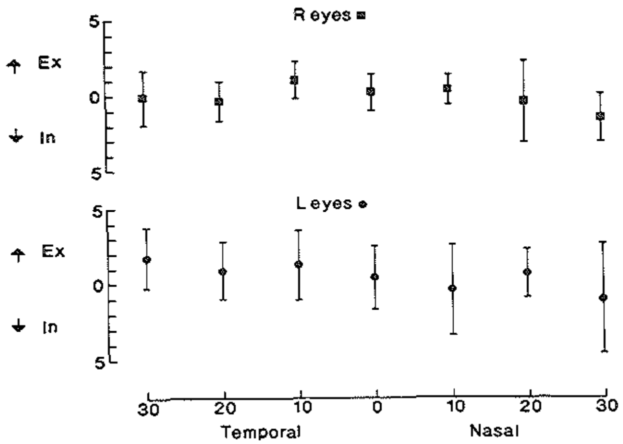

Fig. 2. Means of effective eye torsion values for both eyes of all 4 subjects' eyes in the horizontal (temporal and nasal) secondary positions and the primary position (n = 44). The bars indicate one S.D. Top: right eyes (black squares); bottom: left eyes (black dots). Upward deflections represent extorsion; downward deflections intorsion. All values in degrees.

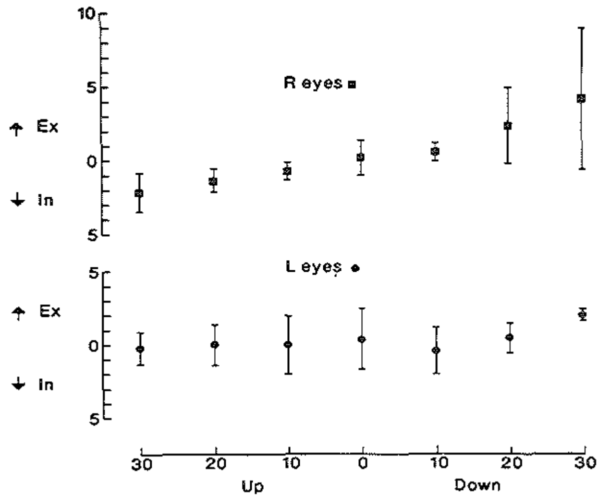

Fig. 3. Means of effective eye torsion values for both eyes of all 4 subjects' eyes in the vertical (up and down) secondary positions and the primary position (same values as in fig. 2). As in fig. 2.

for the ocular torsion values measured in the tertiary positions. Included in both figures are the means (and S.D.) of effective torsion in the primary position (n = 44) for both the left and right eyes. As can be seen, these values are very close to zero.

Tertiary positions

Fig. 4 and 5 show the means of the effective torsional eye positions corresponding to all the 49 target positions for the left and right eyes of the 4 subjects respectively. Both eyes showed extorsion in the upper temporal and lower nasal quadrants and intorsion in the lower temporal and upper nasal quadrants. Values of torsion increased with horizontal and vertical eccentricity as predicted by Listing's law; the direction of torsion was also in accordance with Listing.

Crosstalk induced by vertical eye positions into the torsion channel could have caused only a small fraction of the torsion measured; crosstalk during combined vertical and horizontal excursions each with angles of 10, 20 and 30 deg may have produced maximally about 15, 8 and 6% of the effective torsion respectively (worst case estimates based on calibration procedures). Crosstalk thus potentially produced less than one sixth of effective torsion at eccentricities of 10 deg and its effect on torsion at eccentrities of 20 or 30 deg was even less. In addition, effective torsional values at 10 deg angles were quite small anyway so the overall effect of crosstalk does not seem to have a disturbing influence on the general outcome.

A comparison between the actual "false torsion" which Listing's law predicts and the effective torsional values is shown in Fig. 6. The curves in this figure represent the values predicted by Listing's law for

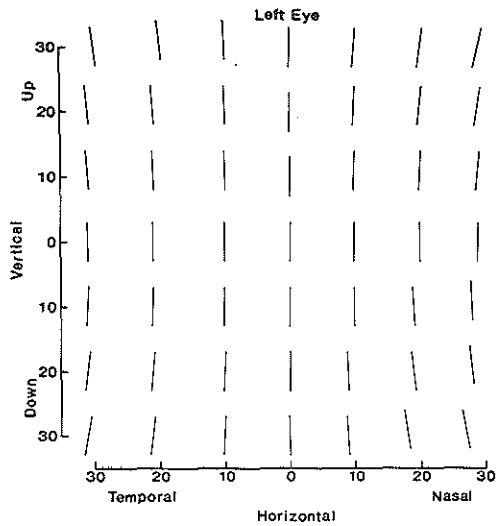

Fig. 4. Plotted lines in the figure represent the means of effective torsion values of the left eye of all subjects corresponding to all 49 target positions at the various horizontal and vertical eccentricities. Angles with the vertical made by the lines are actual torsion angles. Upper pole of line tilted clockwise: intorsion; upper pole of line tilted anti-clockwise: extorsion. All values in degrees.

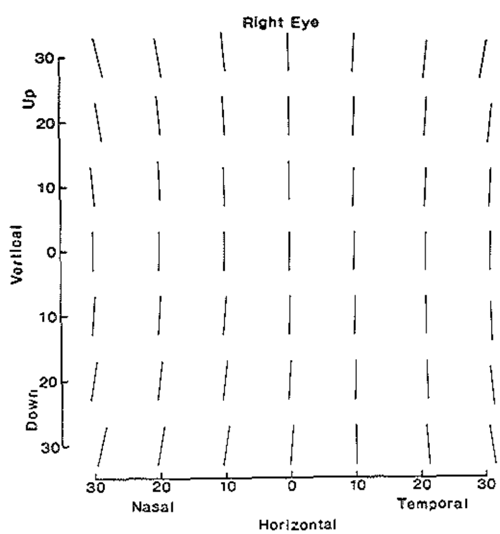

Fig. 5. As in fig. 4 for the right eye of all subjects. Upper pole of line tilted clockwise: extorsion; upper pole of line tilted anti-clockwise; intorsion.

the various eccentricities. Plotted in the figure are the means (S.D.) of effective torsion for both eyes of the 4 subjects in 12 diagonal tertiary positions; the points selected are combinations of 10, 20 and 30 deg horizontally with 10, 20 and 30 deg vertically for all 4 quadrants. This figure shows that effective torsional values in the upper and lower nasal quadrants were systematically larger than those predicted by Listing for both eyes in all 6 positions. The difference increased with eccentricity. Effective torsional values in both temporal quadrants however, were very close to those predicted by Listing and remained so with increasing eccentricity. Torsional values in the most eccentric positions (30 deg horizontal and 30 deg vertical) varied between about 10.5-13.5 deg in the nasal quadrants but only between about 8-9 deg (approximately the value Listing predicted) in the temporal quadrants; the naso-temporal differences amounted thus to more than 50%.

This trend was confirmed for the individual sets of tertiary positions for each measured eye, though more strongly for the right than for the left eyes. The means of the effective torsional values in all tertiary positions for the 4 left and 4 right eyes respectively were compared to the torsional values predicted by Listing. For the left and right eyes all 18 tertiary positions in the nasal quadrants showed larger mean values of effective torsion than those predicted by Listing; differences amounted to more than 5 deg. In the temporal quadrants mean values of effective torsion were larger than those predicted by Listing in 13 and 4 out of 18 tertiary positions for the left and right eyes respectively; differences however were slight and amounted to no more than 2 deg.

Using the effective values of eye torsion (y) obtained in the

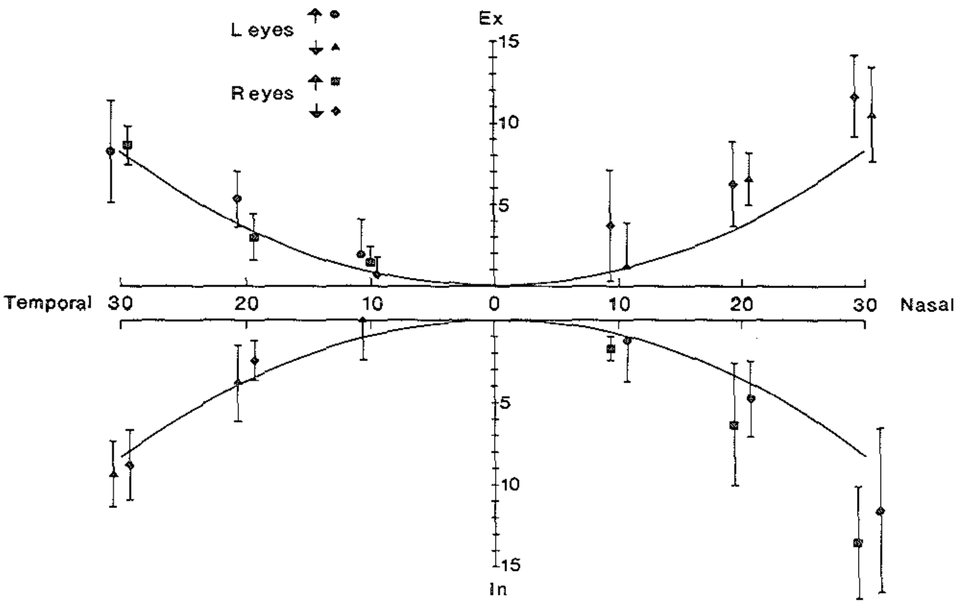

Fig. 6. The drawn curves in the figure represent the theoretical torsion values as predicted by Listing for the tertiary eye positions in diagonal directions. Plotted in the figure are the means (bars indicate one S.D.) of effective eye torsion values for both eyes of all subjects in 6 tertiary positions in both temporal quadrants and the 6 corresponding tertiary positions in both nasal quadrants as a function of combined, equal, horizontal and vertical eccentricity. Abscissa: horizontal and (similar) vertical eccentricity; ordinate: the upper part corresponds with extorsion and the lower part with intorsion. Left eyes: black dots indicate eye torsion values for upper temporal and nasal quadrants; black triangles indicate eye torsion values for lower temporal and nasal quadrants. Right eyes: black squares and black diamonds as the black dots and black triangles for the left eyes respectively. All values in degrees.

tertiary eye positions and the corresponding calculated "false torsion" values (x) predicted by Listing, regression lines (y = a + bx) were calculated for both the nasally and temporally oriented tertiary eye positions separately for each eye of the 4 subjects.

The results are shown in Table 1, in which it can be seen that in all cases the slopes (b) of the nasally oriented eye positions were higher than those obtained in the temporally oriented eye positions; the differences between slope values showed large variations however: from a very small difference in subject F.A.'s left eye to a very large one in subject H.C.'s right eye. Values differed idiosyncratically between subjects and between left and right eyes of any one subject. The coefficients of determination (squared coefficients of correlation, r^2) are included to show the good approximation of the relation by a linear regression.

An example of these calculated regression lines is shown for subject J.H.'s right eye in Fig. 7, in which effective torsional values are plotted as a function of Listing's predicted false torsion. As can also be seen in Table 1, the slope of the regression line was larger for the nasally than for the temporally oriented eye positions.

Since it was of critical importance to see whether the naso-temporal asymmetry could be statistically substantiated, two-tailed paired t-tests were done on the data of each eye of all subjects. Values used for these tests were the 18 corresponding pairs of effective torsion (absolute values) obtained in the symmetrical nasal and temporal tertiary eye positions at identical vertical angles. The significances of difference (shown as p values) obtained in this fashion are shown in Table 2. As can be seen only 4 out of 8 individual eyes showed a significant ($p<0.01$)

difference between torsional values for nasal and temporal tertiary eye positions.

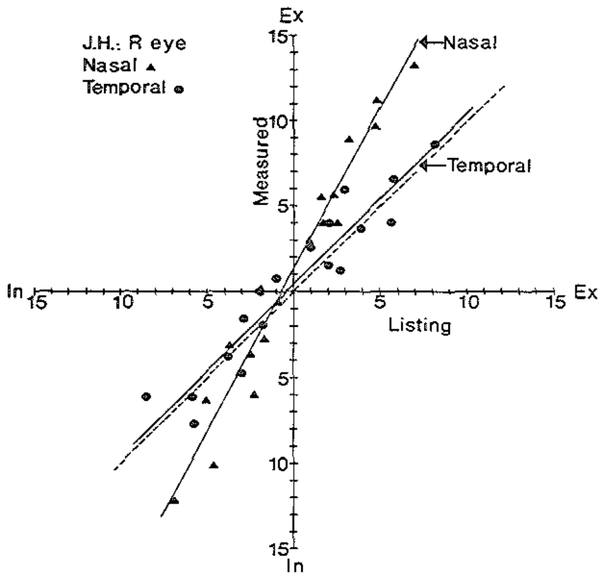

Fig. 7. Example of calculated linear regression (subject J.H.'s right eye) of effective eye torsion values for all tertiary positions on theoretical torsion values predicted by Listing. The calculated regression line for the nasal positions has a slope larger than unity (interrupted line); for the temporal positions the slope is about unity. Right part of abscissa and upper part of ordinate: extorsion; left part of abscissa and lower part of ordinate: intorsion. Black dots: temporal tertiary positions; black triangles: nasal tertiary positions. All values in degrees.

Table 1. Linear regressions of effective ocular torsion values on theoretical values predicted by Listing's law, with slopes b and coefficients of determination r^2. Values for each eye were based on 18 nasal and 18 temporal tertiary positions.

		L eye		R eye	
Subject		nasal	temporal	nasal	temporal
F.A.	b	1.3657	1.3625	1.3725	1.1108
	r^2	0.9490	0.9098	0.9660	0.9799
H.C.	b	1.7523	1.2701	2.2047	0.8911
	r^2	0.9615	0.9247	0.9673	0.8529
J.H.	b	1.6216	1.1155	1.8640	0.9914
	r^2	0.9667	0.8926	0.9524	0.8983
H.S.	b	1.4282	0.6790	1.5541	0.6940
	r^2	0.9701	0.8863	0.7895	0.6878

Table 2. Statistical significance of naso-temporal asymmetry of torsion, calculated with a two-tailed paired t-test for all eyes separately (18 pairs of temporal and nasal ocular torsion values). NS: non significant

Subject	L eye	R eye
F.A.	NS	NS
H.C.	NS	$p<0.001$
J.H.	NS	$p<0.01$
H.S.	$p<0.001$	$p<0.001$

DISCUSSION

The importance of using a spherical coordinate system as also emphasized in the introduction was recognized earlier by Quereau (1954, 1955). Unfortunately, almost all other investigators in the past used Cartesian coordinates or indirect methods which makes correct interpretation of their results difficult and comparison with those presented here almost impossible. Moreover, different definitions of torsion and false torsion were used. In an attempt to resolve some of the confusion which existed in the past a spherical coordinate system, an accurate direct method of measurement and clear definitions of torsion and false torsion were used in order to test the validity of Listing's law.

In these experiments considerable fluctuation of torsion was found among repeated measurements in the primary position. This is consistent with earlier findings of Collewijn et al. (1985) and with those in Chapter II. It suggests that random and continuous long-term fluctuations of torsion up to about 5 deg may be regarded as a normal physiological phenomenon. Such variability will of course diminish considerably the precision with which Listing's law applies to single measurements, but in a large sample of data it will probably average out.

Effective values of ocular torsion in the primary position and in the horizontal secondary positions were on average in accordance with Listing's law. In the vertical secondary positions the left eyes also showed values of ocular torsion in agreement with Listing; the right eyes showed a trend of torsional values which could be explained by a systematic shift of the primary position in the nasal direction. In the tertiary positions torsional values increased with eccentricity; extorsion was seen in the upper temporal and lower nasal quadrants and intorsion in the other two quadrants; these results are all in agreement with Listing's law.

The reason for the occurrence of eye torsion in tertiary positions is not clear apart from being the adventitious result of combined horizontal and vertical eye displacements involving complex relations between all six extra-ocular eye muscles. Nakayama (1978) introduced a "ball and membrane" model, in which the "eye" is attached to a tightly stretched elastic membrane which is equally taut in all directions. Forces which act only in (combinations of) the horizontal and vertical directions will let the model eye move in agreement with Listing's law. The analogy is illuminating, but at the same time it is unlikely that a real eye will behave exactly in this way. Elasticity is unlikely to be constant either in all directions or in time, as it will vary with muscular activity.

Quereau (1955), using a blind spot localization technique, qualitatively confirmed Listing's law but found a difference between nasal and temporal eye torsion; at extreme eccentricities both temporal quadrants showed 3-5 deg of torsion in excess of Listing's prediction. Torsion values in both nasal quadrants were not systematically different from Listing's law but these were measured at less extreme eccentricities. Although Quereau (1955) measured 8 subjects, he reported that results were nearly identical in all of them. This finding does not concur with the results presented here since they show substantial idiosyncratic variability between and within subjects.

The consequence of a difference between nasal and temporal eye torsion would be that binocular viewing of a target in a tertiary position could induce a cyclo-disparity between the two retinal images since one eye would be in a nasal and the other in a temporal tertiary position. This cyclo-disparity would then be expected to increase with eccentricity. Whether such disparity occurs and if it affects stereopsis or is influenced by the amount of provided visual information is unknown at present.

However, it is known that changes in cyclophoria are associated with the near reflex. The target distance of 60 cm used in these experiments would require 6 deg of convergence for binocular foveation. According to data of Landolt converted to Fick's axial system (Allen and Carter, 1967, Table 3), this would cause an excyclophoria of 1.7 deg at 0 deg elevation, decreasing to 0 deg at 25 deg elevation and increasing to 4.3 deg at 30 deg depression. Presumably, the excyclophoria is distributed systematically, causing each eye to be extorted by half of the values quoted. If these values apply, and torsion in the primary position is arbitrarily set at zero, it could be expected that this would result in about 1.1 deg intorsion at 30 deg elevation and 1.3 deg extorsion at 30 deg depression. A trend in this direction is visible in Fig. 3 for the right eyes, not for the left eyes. However, the effect of the near reflexes on the torsion measurements shown here is likely to be only a fraction of the values just quoted: (1) the average cyclophoria found by Allen and Carter (1967) in a large number of subjects was about half of Landolt's values; (2) measurements were done with monocular vision and therefore convergence was probably substantially less than 6 deg.

While eye torsion in temporal positions was about as large as predicted, corresponding nasal positions showed larger values and this

Table 3. Means (and S.D.) of theoretical primary positions, calculated from torsion in tertiary positions for each eye separately (n=9). N = nasal, T = temporal, U = up, D = down.

Subject		Horizontal	Vertical
F.A.	L eye	0.18 N (4.42)	5.31 D (6.32)
	R eye	3.67 T (1.60)	3.86 D (1.05)
H.C.	L eye	3.10 T (3.64)	5.34 D (1.96)
	R eye	14.53 T (3.27)	7.18 D (2.86)
J.H.	L eye	3.29 T (2.16)	5.32 U (3.28)
	R eye	6.43 T (4.41)	2.61 U (4.33)
H.S.	L eye	7.70 T (2.27)	2.17 U (2.25)
	R eye	16.62 T (8.02)	5.98 U (3.79)
Grand mean		6.90 T (6.81)	0.70 D (6.02)

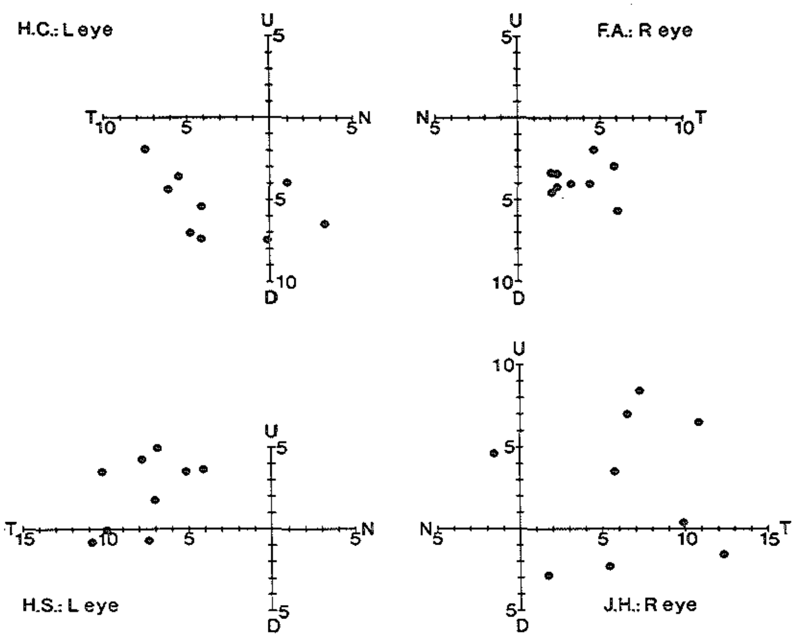

Fig. 8. Theoretical primary positions, calculated from torsion in tertiary positions (see text). Nine calculated primary positions are shown for one eye of every subject (black dots). Abscissa: horizontal eye position (N = nasal, T = temporal); ordinate: vertical eye position (U = up, D = down). All values in degrees.

difference in magnitude increased with eccentricity to more than 50%. Statistical analysis however, showed that the naso-temporal asymmetry was significant in only 4 out of 8 eyes. No specific anatomical or physiological explanation is immediately apparent for this naso-temporal asymmetry, which is obviously related to the choice of the primary position. Remarkably, the uncertainty concerns the horizontal rather than the vertical primary gaze direction. Whereas the latter one has to be chosen somewhat arbitrarily, the horizontal primary gaze direction is traditionally considered to be parallel to the mid-sagittal plane. Assuming that Listing's law is valid in all its respects the primary position can be calculated from the values of eye torsion measured in tertiary positions as described by Nakayama (1978). This method uses pairs of direction circles, each connecting two fixation positions and intersecting at the occipital pole. Once this point has been calculated, the primary position can be easily determined since it lies directly opposite the occipital pole.

Since the subjects in these experiments fixated targets in 36 tertiary positions the primary position could be calculated 9 times for each eye using 2 pairs of fixation positions on direction circles at right angles to each other. The means and S.D.'s of these calculated primary positions are given in Table 3 for each eye separately.

All eyes, except subject F.A.'s left eye, show more temporally oriented primary positions (grand mean: 6.9 deg temporally). The eyes of those subjects with the largest shift of the calculated primary position in the temporal direction are the same ones which showed a significant naso-temporal asymmetry in Table 2. The significant asymmetry found in these eyes might thus be explained by a relatively large shift of the chosen primary position other than coincidence in the nasal direction. A reason for this bias of choice of the primary position, other than coincidence is not immediately apparent. The grand mean of calculated primary positions showed virtually no vertical offset. The variability between and within the individual calculated primary positions apparent in Table 3 can also be seen in Fig. 8 in which the 9 calculated primary positions for one eye of every subject are shown. Obviously, the 9 points do not cluster tightly but show wide scattering. This variability is probably caused by two important factors:

1. random fluctuations of eye torsion;
2. Listing's law not being rigidly followed.

If the primary position were to be shifted in the temporal direction so that temporal and nasal eye torsion values would become equal to one another (as Listing's law predicts) all eye torsion values would become higher (at least in the extreme eccentricities) than those predicted by Listing since the temporal torsion values were already about equal to the predicted magnitude. Thus, a perfect fitting of these data to Listing's law cannot be obtained by manipulating the primary position.

In conclusion, the results with static, monocular fixation suggest that Listing's law is only approximately valid and that physiological eye movements show considerable stochastical as well as systematic deviations from this law.

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Chapter IV

A direct test of Listing's law: II. Human ocular torsion measured under dynamic conditions.

INTRODUCTION

In the preceding chapter, human ocular torsion reached in sustained tertiary positions was systematically explored. It was concluded that Listing's law is only qualitatively valid: torsion occurred in the right direction, but was on average too large. Moreover, torsion fluctuated considerably in time. In the analysis, general trends obtained by averaging data over time and subjects were emphasized.

In this chapter, the dynamic aspects of ocular torsion shall be described. The main interest here is in the behaviour of torsion as a function of time during steady fixation and during changes in gaze direction. Results of experiments in which subjects monocularly pursued a moving target enabled the evaluation of the validity of Listing's law under dynamic conditions and in addition, perhaps more interestingly, Donders' (1875) law which states that ocular torsion in any specified tertiary position has a constant value (and direction) regardless of the trajectory followed by the eye to reach that position. It will be shown that also under dynamic conditions, ocular torsion is specified only approximately by Listing's law. Furthermore, ocular torsion showed hysteresis effects and Donders' law therefore was violated.

METHODS

The measuring technique, procedure and data analysis were identical to those described in the preceding chapter apart from the following changes.

Horizontal, vertical and torsional eye positions were measured in 5 healthy subjects (including the 4 subjects of the previous chapter) with the head fixed. Only the right eye was measured; the left eye was patched. Subjects fixated a laserspot (diameter about 0.25 deg) back-projected on a translucent screen at a distance of 1.43 m in front of the eye of the subject. In addition to the spot, a stationary background pattern (consisting of randomly distributed black and white elements of 5 x 5 deg), covering the whole visual field, could be projected on the screen. Measurements lasted 16.4 or 32.8 seconds and were made with the target following different trajectories and under various conditions. After the target movement had been started, subjects started data collection themselves by pressing a button when they felt ready. They tried to make as few blinks as possible during the measurements. The sample frequency was 250 Hz.

Target in the primary position

Subjects fixated the spot target which remained stationary in the primary position and also with the stationary background added to the spot. In addition, measurements were made with the subjects in darkness while they attempted to fixate the imagined target in the primary position.

These measurements lasted for 32.8 sec with a sample frequency of

250 Hz resulting in 8192 samples per signal. After removal of saccades (and a sample reduction by a factor of 4 to 2048 samples) the torsional gaze position signal was transformed off-line by a computer program to a cumulative smooth eye position signal. Mean speeds of torsional smooth eye position were calculated by a sliding window technique with a window of 4 sample points (equivalent to 64 msec since the original sample frequency of 250 Hz was now reduced by a factor of 4 to 62.5 Hz).

Voluntary Blinks

Subjects were instructed to make voluntary blinks during fixation of the spot target. These measurements also lasted 32.8 sec with a sample frequency of 250 Hz.

Target in secondary positions

The target moved in steps at 4 second intervals between the zero position and the horizontal secondary positions at 20 deg nasally and 20 deg temporally as well as the vertical secondary positions at 20 deg upwards and downwards. Measurements lasted 16.4 sec (4096 samples) and each position was fixated twice for about 4 sec during each measurement.

Target in tertiary positions

Diagonal trajectory of target

Steps between the primary - tertiary position: the target followed a diagonal trajectory and stepped (at 4 sec intervals) between the primary position and any of 4 tertiary positions coinciding with the four corners of a square situated at eccentricities of 20 deg horizontally and vertically in both nasal and temporal quadrants. Measurements lasted 16.4 sec and the target was fixated twice in both positions for about 4 sec.

Steps between tertiary positions: the target moved in steps between diagonally opposite corners of the same square. Each tertiary position was fixated twice for about 4 sec (measurements lasted 16.4 sec).

Sinusoidal motion between tertiary positions: this condition was similar to the one above but now the target moved sinusoidally at 0.125 Hz. Each tertiary position was fixated twice (measurements lasted 16.4 sec).

Target stepping around a square

The target was moved in steps at 4 sec intervals from one corner of a square (same square as in diagonal conditions) to the next in either the clockwise or counter-clockwise direction. Measurements lasted 32.8 sec and every one of the 4 tertiary positions was fixated twice for about 4 sec.

Circular trajectory of target

The target followed a circular trajectory with a radius of 20 deg and its center in the primary position. Thus, it traversed through tertiary positions with maximal eccentricities of about 14 deg horizontally and vertically in all 4 quadrants. The target moved in either clockwise or counter-clockwise direction with a constant velocity of either 16 deg/sec (measurements lasting 16.4 sec) or 8 deg/sec (measurements lasting 32.8 sec). Every tertiary position was fixated twice during all measurements. Measurements were also made with the stationary background added to the spot.

For all secondary and tertiary position measurements torsional gaze position was displayed off-line on a computer terminal and with a cross-hair technique any desired sampling period could be defined one or more times during each measurement. The mean ocular torsion value during these periods was then calculated and in this way torsional gaze values in every fixated secondary and tertiary position were calculated twice during each measurement. During step trajectories the defined sampling period was usually about 4 sec for each position but during sinusoidal and circular trajectories this period was obviously shorter; great care was taken to define torsional gaze position only at maximal or minimal excursions of the eye, or during zero crossing of the horizontal and vertical eye position. Ocular torsion values predicted by Listing for the respective tertiary positions were calculated in the same way as described in the previous chapter.

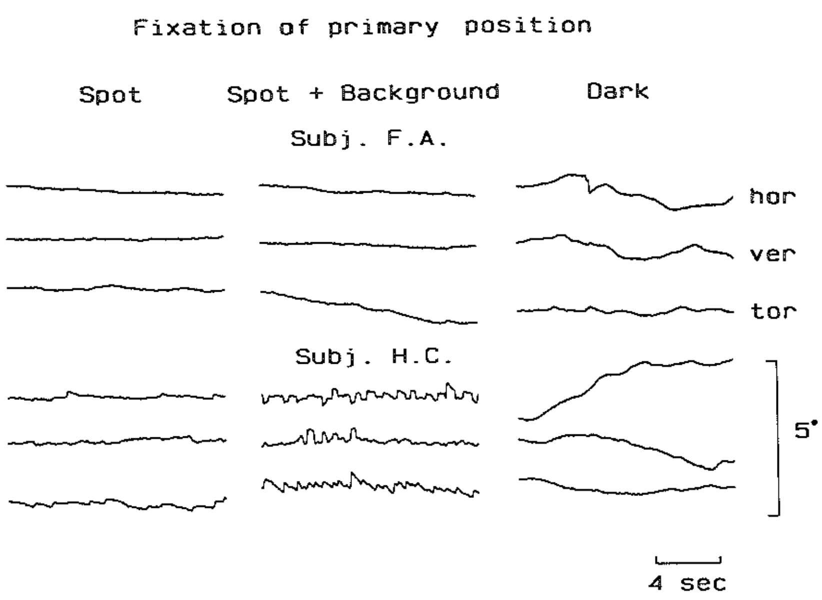

Fig. 1 Representative recordings of horizontal, vertical and torsional eye position during fixation of a single spot, a spot with a structured background, or the imagined spot in darkness. Two subjects are shown: F.A. and H.C. For all figures, upward deflection represents horizontal movement to the left, vertical movement upward and extorsion.

Table 1.
Mean speeds (min arc/sec) of torsional drift (excluding saccades) under three conditions: 1. subjects fixated the spot in the zero position; 2. a background was added to the spot; 3. subjects fixated the imagined spot in the dark.

Mean speeds of torsional gaze

Subj.	Target conditions		
	spot	spot + background	dark
F.A.	11.53	12.67	13.13
C.E.	13.67	13.01	15.58
J.H.	18.60	17.83	18.31
H.C.	15.33	24.41	12.41
H.S.	18.22	23.22	16.67
Mean (S.D.)	15.47 (3.01)	18.23 (5.51)	15.22 (2.45)

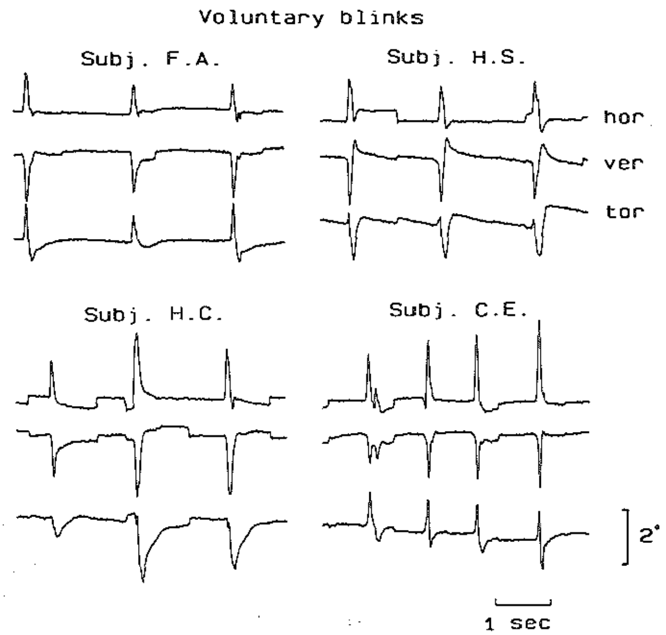

Fig. 2 Horizontal, vertical and torsional eye movements associated with voluntary blinks during fixation of a single point. Four subjects are shown.

RESULTS

Primary Position

Examples of fixation in the primary position are plotted with high resolution in Fig. 1 for two subjects in the three conditions used: spot only, spot plus structured background and darkness. The horizontal and vertical traces show the well known mixture of drift and microsaccades in the light, and uncontrolled drift in the dark. In the light, torsional gaze positions were relatively unstable. Fixation of the spot only resulted in a mean standard deviation of 0.23 deg within individual measurements lasting 16.4 or 32.8 sec (mean of 5 measurements x 5 subjects). However, the long term variability among successive measurements spread through a session was much larger: the S.D. of the mean (all subjects taken together) was 2.80 deg. As in the preceding chapter, no particular trend could be discerned and ocular torsion values remained close to zero, so once again it seemed justified to ascribe the long-term torsional fluctuations to natural drift of the eye around the visual axis. However, the absence of any slip of the lens was not checked by an independent method.

The possibility that this relatively large variability was due to a lack of cyclorotational visual reference during the fixation of a single point target was not supported by the results of adding a structured background. On the contrary, instability of torsion had the tendency to increase in the latter condition. In two out of the five subjects (HC and HS) the addition of a background converted the irregular torsional drift into a regular spontaneous torsional nystagmus (slow phase intorsional). The visual induction of this nystagmus is corroborated by

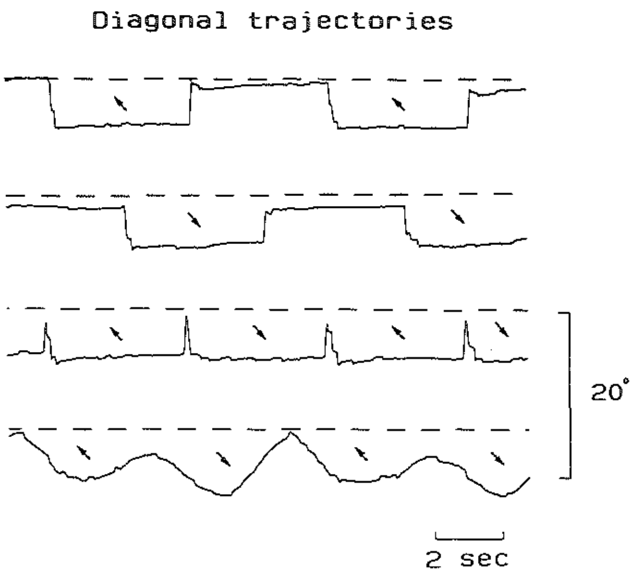

Fig. 3 Torsion associated with right eye movements to tertiary positions. Upper two traces: saccades between the primary position and the nasal-up position (first trace) or the temporal-down position (second trace). Third trace: saccades between the same two diagonally opposite tertiary positions, passing the primary position in midflight. Lower trace: torsion during smooth pursuit of a target oscillating sinusoidally between the same two tertiary positions. The tertiary positions had horizontal as well as vertical eccentricities of 20 deg; their position (as seen by the subject) is indicated by the arrows. Subject: J.H.

its total absence in darkness (Fig. 1), although HS showed a high-velocity vertical drift in darkness.

Mean torsional drift speeds (excluding saccades) for all 5 subjects under the 3 conditions are shown in Table 1. On average, drift velocities were on the order of 15 min arc/sec. This is about a factor 3 lower than was found under conditions with the head free (see Chapter II), in accordance with the general tendency for gaze instability to be substantially larger with the head free than with the head immobilized (see Steinman et al., 1982). In three subjects, torsional drift speeds were largely unaffected by visual conditions but the other two showed a nystagmus in the presence of a pattern, associated with an increase in the mean drift speed. This suggests again an enhancement of torsional instability by structured visual patterns in some subjects.

Voluntary Blinks

During fixation of the spot in the primary position subjects were instructed to make voluntary blinks; in Fig. 2 examples of these blinks are given showing horizontal, vertical and torsional gaze traces of 4 subjects (the fifth subject produced only very few blinks with a small amplitude and is therefore not shown). Horizontal and vertical gaze behaved quite similarly during blinks in all 4 subjects, showing nasal and downward deflections with amplitudes varying between 1-3 deg and durations of about 100-200 msec, in agreement with previous findings of Collewijn et al. (1985a). Torsional gaze deflections showed a larger variability between and within subjects. Although torsional gaze amplitudes during blinks were very similar to the horizontal and vertical ones and ranged between 1-3 deg, the deflections consisted of extorsion,

Table 2. Mean ocular torsion values (all subjects pooled) in 4 tertiary positions (eccentricities of 20 deg horizontally and vertically in all 4 quadrants) during diagonal target trajectories between primary and tertiary positions, and between two tertiary positions either in steps or sinusoidally. Also shown are the values reached in the primary position during these diagonal trajectories. All ocular torsion values in deg (+ = extorsion; - = intorsion).

Diagonal target trajectory

Target position	Target condition	
	steps primary-tertiary	steps tertiary-tertiary
nasal up	-4.11	-4.39
temp. down	-2.38	-2.40
primary	1.24	0.83
temp. up	6.38	7.00
nasal down	3.22	3.50
primary	1.03	0.79

Table 3. Mean ocular torsion values (all subjects pooled) in 4 tertiary positions located at the corners of a square (eccentricities of 20 deg horizontally and vertically in all 4 quadrants) during square step target trajectories in both the clockwise (CW) and counter-clockwise (CCW) direction. The results of a two-tailed paired t-test between the respective values in either direction are given in the right-hand column as the significance of difference of this test. All ocular torsion values in deg (+ = extorsion; - = intorsion).

Square step trajectory

Target position	Target condition		Significance of difference
	CW	CCW	
nasal up	-3.9937	-3.3689	$p<0.05$
temp. up	7.2115	7.9105	$p<0.05$
temp. down	-2.6392	-1.2537	$p<0.01$
nasal down	3.0392	5.0079	$p<0.001$

intorsion or a combination of both. The duration of blink-associated torsion showed a large variability. Fig. 2 shows several examples where blink-associated torsion had a rapid onset but a slow, exponential return by which the original position was on average gradually attained once more, but only after 300 - 800 msec. This sluggish behaviour was not seen in the associated horizontal and vertical deflections.

During a blink, the lids will close down on the wires coming out of the coil and may exert some pull on it. This would lead to erratic variations in torsion measured before and after blinks if the annulus were easily displaced on the eye. The recordings bear no evidence of this; the overall variability of torsional rest positions before and after blinks is only slightly larger than that of horizontal and vertical position. A slip of 0.16 mm in torsion corresponds to 1 deg; as there is a space of several mm between the opened lids it is inconceivable that a slipping annulus would return to the pre-blink position to within a fraction of a degree by some mechanical artifact. Thus, the recording of torsion during blinks provides fairly strong evidence against any significant short-term slip of the annulus.

Secondary Positions

These static measurements served primarily as a check on the correct choice of the primary position. In the ideal case, purely horizontal or vertical gaze displacements from the chosen central position should not cause any changes in torsion. Off-line analysis showed that this situation was closely approximated only in subject H.S. For the other four subjects it had to be concluded -assuming validity of Listing's law- that when subjects fixated the zero target position, their gaze was

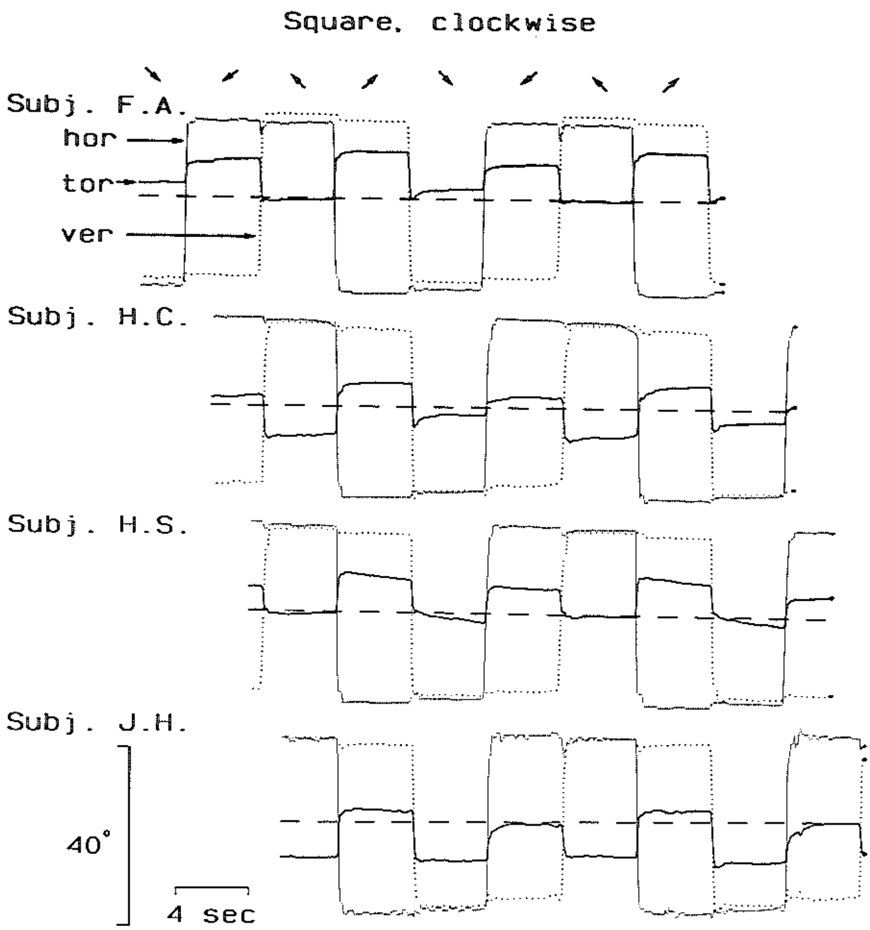

Fig. 4 Horizontal, vertical and torsional eye movements during saccadic stepping around the corners of a square (eccentricities of the corners: 20 deg horizontally and 20 deg vertically). Stepping was clockwise; four subjects are shown. Arrows indicate direction of tertiary positions as seen by subject.

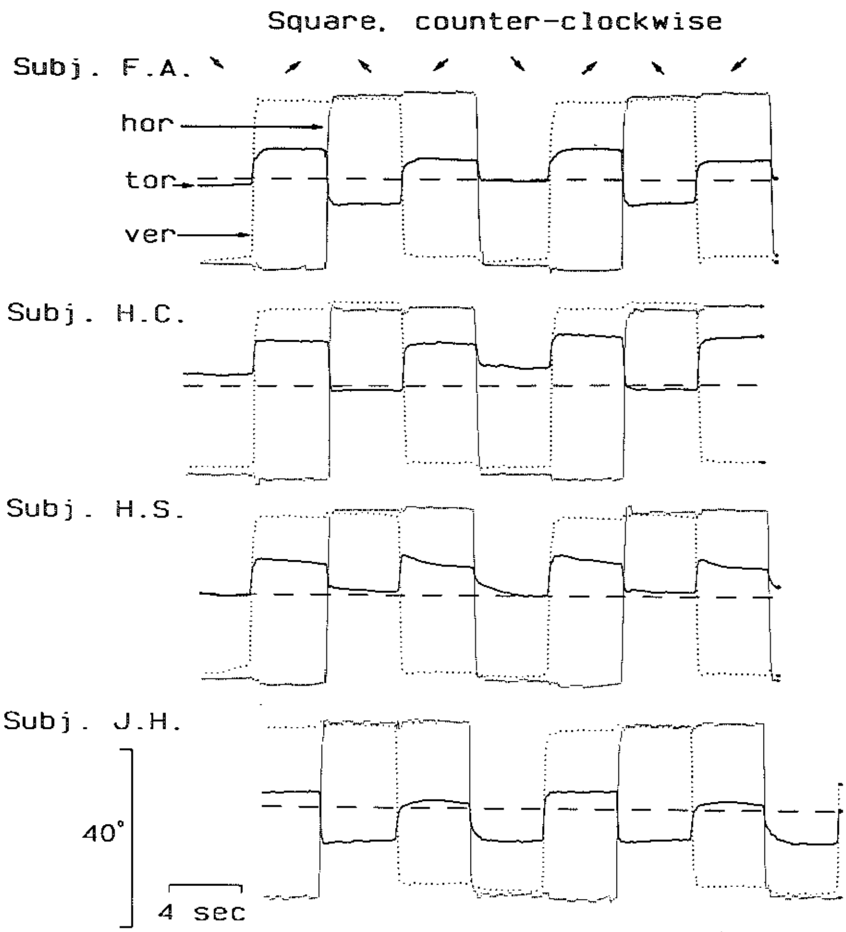

Fig. 5 Saccadic stepping around a square, as Fig. 4, but in counterclockwise direction.

elevated significantly above the primary position. Their eyes showed intorsion when looking to the left and extorsion when looking to the right. Two subjects (F.A. and H.C.) were in addition centered to the nasal side, and two others (J.H. and C.E.) to the temporal side of the primary position. These deviations from the true primary position as deduced from torsion can be expected to cause apparent violations of Listing's law, particularly disturbances of symmetry. Therefore, in this chapter attention shall be focused on the dynamic aspects of torsion and its absolute magnitude disregarded.

Tertiary Positions

Diagonal trajectories

Fig. 3 illustrates torsional gaze changes of subject J.H. while he made (1) saccadic steps between primary and tertiary positions; (2) saccadic steps between diagonally opposite tertiary positions; (3) smooth pursuit movements with the target moving sinusoidally between diagonally opposite tertiary positions. According to Listing's law, the torsion should be identical in size and direction for two opposite tertiary positions at the same absolute eccentricity; torsion should also reach the same "zero" value whenever the eye passes through the primary position irrespective whether it is attained statically (case 1), in saccadic midflight (case 2) or during smooth pursuit (case 3). Fig. 3 shows that this is approximately, although not precisely, the case. The upper two traces show that for repetitive steps between primary and tertiary positions the torsional values were largely reproducible, and reached in a saccadic mode. The saccades were often multiple.

The third trace of Fig. 3 shows that during saccades between tertiary positions torsion briefly reached a minimum relatively close to zero, while (at least in this subject) the pre- and post-saccadic torsional positions were indeed identical. These findings are shown quantitatively (all subjects pooled) in the left and right column of Table 2. The theoretical torsion expected in these tertiary positions according to Listing is about 3.5 deg. The actual changes relative to the torsion in the primary position were at the average slightly larger, reflecting a general trend in the results. The tertiary torsion values were virtually identical whether reached from the primary or the diagonally opposite tertiary position. Remarkably, torsional values in the primary position also differed very little - compared to the deviations in the tertiary positions - whether attained statically (left column) or transiently in midsaccadic flight (right column).

These results - which, incidentally, strongly argue against any significant slip of the annulus - suggest that at least certain aspects of Listing's law are fairly well obeyed. Interestingly, this appears to be less clear during smooth pursuit. As shown in Fig. 3, fourth trace, the minimal torsion values reached at the transition through the primary position depended strongly on the direction of pursuit: they varied with the side from which the primary position was reached. However, the results were reproducible from cycle to cycle. Although a slight directional asymmetry could be seen also during saccades (Fig. 3, trace 3), the asymmetry during smooth pursuit was stronger and opposite in sign. The case illustrated in Fig. 3 represents a general trend in the data: in 8 out of 10 recordings (5 subjects x 2 diagonal directions) torsion during crossing of the zero position appeared to be

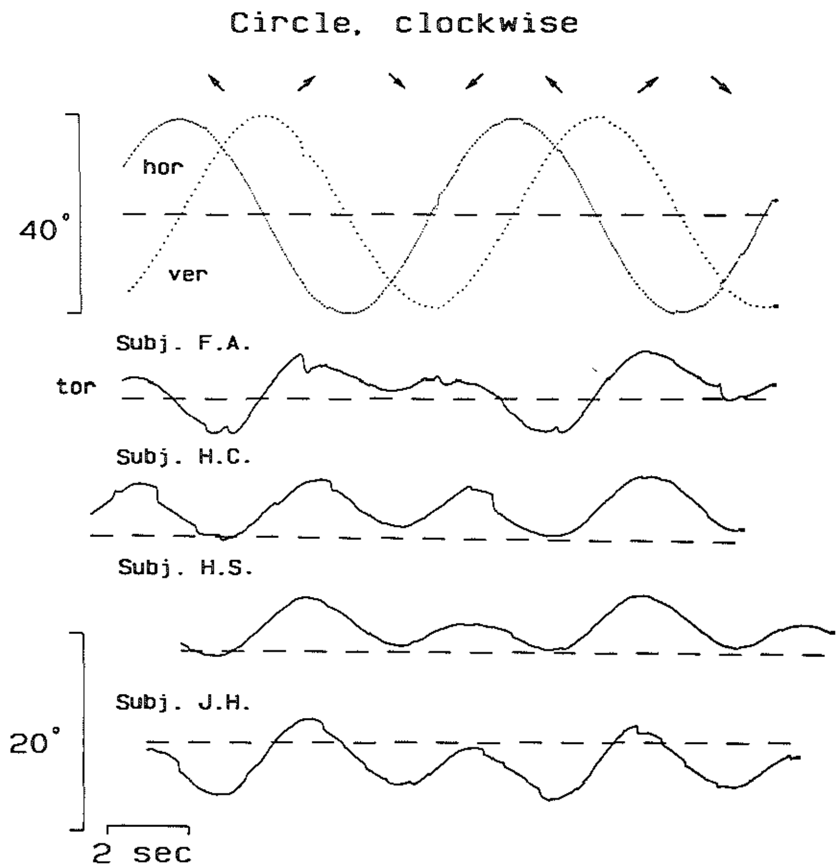

Fig. 6 Smooth pursuit of a spot, circling around the primary position with a radius of 20 deg and an angular velocity of 16 deg/sec. The top traces show the horizontal and vertical eye movements of subject F.A.; the lower four traces show torsion of 4 subjects, all correctly aligned in phase with the horizontal and vertical traces. Clockwise pursuit. Arrows indicate directions of tertiary positions.

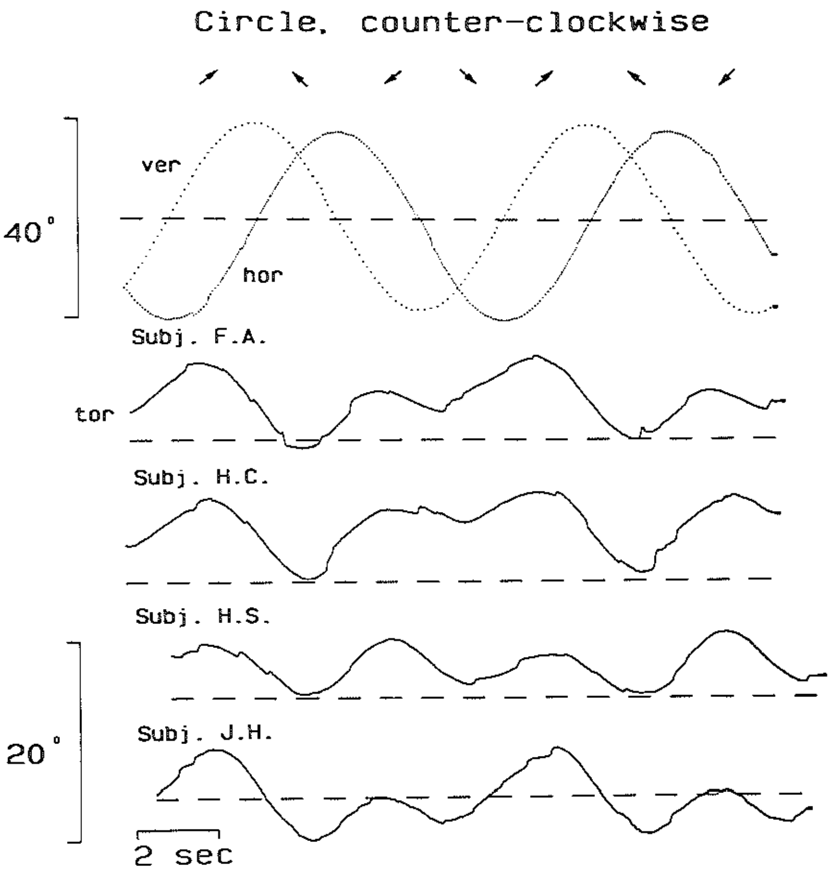

Fig. 7 Circular pursuit as in Fig. 6, for counterclockwise motion.

systematically larger for smooth pursuit in one direction than in the other direction. However, the sign and size of the difference varied unsystematically between the two diagonal trajectories and between subjects; therefore no statistically significant trend could be shown in the pooled data. On the whole, these data strongly suggest that during smooth pursuit Donders' law is frequently violated, in agreement with Westheimer and McKee (1973).

Saccadic stepping around a square

Fig. 4 shows examples of horizontal, vertical and torsional gaze during two cycles of stepping through a square in the clockwise direction, with the corners each having vertical and horizontal eccentricities of 20 deg, for 4 subjects. Fig. 5 shows similar recordings for stepping in the counterclockwise direction. All traces are aligned with regard to phase. According to Listing's law, in these cases a sequence of torsional steps of equal size and alternating in direction should be expected, distributed symmetrically around zero. However, deviations from this ideal situation should be expected due to the errors of primary position and also due to long-term torsional drift. In fact subjects showed considerable size-differences of the steps in torsion made between the different adjacent tertiary positions. These asymmetries were roughly in agreement with the errors in the primary positions as deduced from the static torsion values in the "secondary" positions. However, the behaviour of torsion during the stepping around the square showed several remarkable features unrelated to static misalignments.

Firstly, torsional drift was often very marked. Although the

Table 4. Mean ocular torsion values (all subjects pooled) in 4 tertiary positions located on a circle (eccentricities of about 14 deg horizontally and vertically in all 4 quadrants) during circular target (spot) trajectories in either the clockwise (CW) or counter-clockwise (CCW) directions at target velocities of 16 and 8 deg/sec, with or without an added background. In the right-hand column the results of a two-tailed paired t-test between the respective values under the various conditions are shown as the significance of difference of this test. All ocular torsion values in deg (+ = extorsion; - = intorsion). NS: non significant

Circular target trajectory

Target position	Target condition		Significance of difference
	CW	CCW	
	Spot at 16 deg/sec		
nasal up	-2.7989	-1.5030	p<0.01
temp. up	4.2961	6.2878	p<0.01
temp. down	-1.5604	0.3073	p<0.01
nasal down	1.3077	3.4388	p<0.001
	Spot at 8 deg/sec		
nasal up	-2.5857	-0.9332	p<0.01
temp. up	3.9939	6.0384	p<0.01
temp. down	-2.2263	0.0041	p<0.01
nasal down	0.7006	3.2271	p<0.001
	Spot + background at 16 deg/sec		
nasal up	-1.9189	-1.3337	NS
temp. up	4.8718	6.2503	p<0.02
temp. down	-1.6937	0.8591	p<0.001
nasal down	1.9079	3.7847	p<0.01
	Spot + background at 8 deg/sec		
nasal up	-2.0277	-1.6266	NS
temp.up	4.0266	5.8829	p<0.01
temp. down	-2.2118	-0.1323	p<0.01
nasal down	1.5881	3.7121	p<0.001

vertical and horizontal traces show stable intersaccadic intervals, this was much less the case for torsion. In several cases substantial intersaccadic torsional drift occurred, although in other cases this was absent.

Secondly, torsional saccades were often sluggish. In several subjects torsional saccades, particularly in certain idiosyncratic directions, showed extremely glissadic behaviour: they drifted more or less exponentially to an end position. This shape differed strongly from the concomitant vertical and horizontal saccades, which were crisp and sharp.

Thirdly, a hysteresis of torsion was noticed. Mean ocular torsion values (all subjects pooled) measured in the 4 tertiary positions during the square steps, for both the clockwise and counter-clockwise directions, are shown in Table 3.

Since theoretically, according to Listing, torsion should alternate between about + and - 3.5 deg for adjacent tertiary positions, the differences between the successive numbers in Table 3 should amount to about 7 deg. The mean difference is actually 8.44 $\pm$ 2.53 deg, suggesting that the average changes in torsion exceed Listing's predictions. This agrees with the findings in the preceding chapter but of course it reflects only an average trend, not individual eyes or tertiary positions.

Also shown in Table 3 are the results of a two-tailed paired t-test in which the 10 measured values (two values for 5 subjects) in each tertiary position reached in the clockwise and in the counter-clockwise direction were compared; they are shown in the right-hand column as the significance of difference. As is apparent from Table 3 both the nasal-up and temporal-down tertiary positions show significantly larger absolute values ($p<0.05$) for the clockwise direction and the other two tertiary positions show significantly larger values ($p<0.05$) for the counter-clockwise direction. Notice also, that the mean values in Table 3 do not deviate substantially from those shown in Table 2 for saccadic diagonal trajectories. The hysteresis effect constitutes a clear violation of Donders' law.

Smooth pursuit of circular trajectories

Fig. 6 shows 4 examples of torsional gaze position with subjects pursuing the spot rotating in the clockwise direction at a constant velocity of 16 deg/sec. At the top of Fig. 6 subject F.A.'s horizontal and vertical gaze position during the same measurement are shown for the sake of orientation, and to show that the target was properly pursued. All tracings are aligned with regard to phase. Once again the large variability of torsion between subjects and the asymmetries around the zero position may be due to the incorrect choice of the primary position. The reproducibility of torsion within any subject from cycle to cycle was very good. The frequency of torsional gaze modulation was twice that of either horizontal or vertical gaze, in agreement with Listing's law.

Examples of torsional gaze traces of the same subjects as in Fig. 6 are shown in Fig. 7 but now for the counter-clockwise direction also with a target velocity of 16 deg/sec. At the top of Fig. 7 subject H.C.'s horizontal and vertical gaze position traces have now been added as a phase reference. Comparison of Fig. 6 and 7 shows that ocular torsion values for any specific tertiary position differed within one subject depending upon the direction of the target trajectory. Especially in subjects F.A. and J.H. the mean value of ocular torsion during the whole measurement showed an overall shift when both directions where compared to each other; this can be seen when observing the torsional gaze position in relation to the zero-axis. The same features as described above for Fig. 6 can also be seen in Fig. 7.

The mean ocular torsion values (all subjects pooled) in the 4 diagonal tertiary positions (at eccentricities of about 14 deg horizontally and vertically) under the various conditions are listed in Table 4; both directions and both velocities for the spot alone as well as with the background added to the spot. Listing's law predicts about 1.75 deg of extorsion or intorsion (depending on the quadrant) for these tertiary positions; thus the change between adjacent values should be about 3.5 deg. The actual mean change was about 5 deg for all conditions; there was no effect of velocity or background.

Once more, however, there was a clear effect of direction of pursuit. Comparison between Fig. 6 and 7 already shows clear examples of this type of asymmetry. For instance, subject HC showed a reasonable regular sinusoidal modulation of torsion while pursuing in the clockwise direction (Fig. 6), whereas in the counterclockwise direction there was a strong distortion with changes in torsion enhanced between some, and reduced between other tertiary positions. Obviously, such directional effects (measured within one session) cannot be attributed to the choice of the primary position. Comparison of values measured in either the clockwise or counter-clockwise direction for any tertiary position shows that in nearly all cases there was a preferred direction leading to the largest values; for nasal-upward and temporal-downward it was the clockwise direction and for the other two tertiary positions the counter-clockwise direction. A two-tailed paired t-test for clockwise vs. counterclockwise was done for all the tertiary positions and under all 8 conditions; its results are shown in the right-hand column. In 14 out of 16 cases the directional effect was significant ($p<0.02$). Once more, this shows a clear violation of Donders' law.

DISCUSSION

The main conclusion from these experiments is that the control of ocular torsion is relatively imprecise. Even though the head was fixed and therefore vestibular input was constant, there was considerable short- and long term drift of torsion. Such short-term drift, in excess of the Listing-type torsion associated with horizontal and vertical drift, was already reported by Fender (1955). Furthermore, although the general tendencies of Listing's law are confirmed by the data presented here, particularly after averaging, it appears that this law is by no means strictly followed by every eye at every time during every oculomotor task. Donders' law was followed only when the eye reached a similar tertiary position by way of a similar trajectory. When different trajectories were followed, deviations up to several deg of torsion for similar horizontal and vertical positions were commonly observed. Since such violations were often reproduced remarkably well from cycle to cycle in a repetitive task, it follows that they were systematic and not just due to random fluctuation. Thus, in addition to considerable random fluctuation in torsion each eye shows consistent, idiosyncratic deviations from the classical rules for torsion.

Even though verification of the classical laws describing torsion has been attempted in the past mostly by indirect methods such as afterimage techniques, rather lacking in spatial and temporal resolution, clear exceptions to these laws have been noticed before. Listing's law is not obeyed as soon as the eyes converge (Allen and Carter, 1967). Westheimer and McKee (1973) showed that Donders' law was violated during smooth pursuit. When the eye passed transiently through the primary position, deviations up to several degrees from the torsion measured in the sustained primary position were detected. These deviations were unsystematic and varied idiosyncratically between subjects, right and left eyes, trajectories and even directions of pursuit.

The findings shown here confirm and provide further evidence for the imprecision of torsional control. This is in line with some earlier findings. Under natural conditions, with the head moving, human compensatory eye movements in torsion have a dynamic component much inferior in accuracy to similar horizontal and vertical movements, and only a rudimentary sustained component (see Collewijn et al., 1985b; Chapter II). The control of compensatory eye movements in torsion is largely vestibular; torsional optokinetic nystagmus in the human is very weak and inconsistent (Collewijn et al., 1985b). This suggests that control of torsion is imprecise in the human, probably because foveal viewing with high acuity restricted to an angle of a few degrees is only marginally affected by errors or fluctuations in torsion.

There was no evidence for any visual correction of torsion in the present (monocular) experiments. During fixation, torsional drift was not inhibited and in two subjects even enhanced by a large stationary background. During pursuit of a circular trajectory, torsion remained also unaffected by the presence or absence of a background.

All these experiments were done monocularly. In a binocular situation, the cyclovergence system may contribute much to the coordination of torsion in the two eyes (see Sullivan and Kertesz, 1978). However, the elimination of cyclodisparity would not require the eyes to follow Listing's law since this could be achieved in any torsional orientation.

A further example of imprecise torsional control was seen in saccadic displacements (Fig. 4 and 5). Although vertical and horizontal saccades were invariably crisp with sharp endings, the associated changes in torsion often showed very rounded terminations lasting for a second or even more.

Obviously, this raises the question whether Listing's and Donders' laws, in as far as they are followed, reflect a special effort and programming by the nervous system, or are just an adventitious consequence of the mechanics of the peripheral oculomotor plant. Although on the surface Listing's law simplifies ocular kinetics because it allows only two degrees of freedom, it is very clear that torsional movements can be actively produced, both as a reflex and voluntarily (Balliet and Nakayama, 1978). This would require the nervous system to, as it were, contain a "Listing's law box" (Nakayama, 1975; 1983) in order to make the eyes follow Listing's law whenever active torsion is not called for. Arguments for the intrinsic merits of following this law have been hard to provide (see Nakayama, 1983 for a discussion). Any advantage would have to be very slight, since vision functions perfectly well in conditions in which violations of the classical laws have been shown before: vergence and smooth pursuit.

An illuminating mechanical analogy was proposed by Nakayama (1978; 1983) which describes the eye as a ball, suspended in a tightly stretched elastic membrane, equally taut in all directions and attached to the edges of a cylinder. When only horizontal and vertical forces are exerted on this ball, it will exactly follow Listing's law; i.e. the ball will rotate around an axis in the elastic membrane (equivalent to

Listing's plane).

It is well established that the suspension of the eye in the orbit contains a significant elasticity, pulling the eye back to the midposition with a force of roughly 1 gram per deg of excursion in the horizontal and vertical dimensions (Robinson, 1965; Robinson et al., 1969). Remarkably, lower elastic forces around the torsional axis have been reported (Simonsz et al., 1984).

However, it is hard to relate Nakayama's rubber sheet model to the actions of the six muscles, which in combination can produce any type of eye movement, given the right commands. For instance, to produce a pure upward motion without torsion from the primary position, the ratio of innervation between the vertical recti and obliques must be just right. Therefore, an explanation of Listing's law in terms of plant mechanics alone (which in any case would vary with the state of activity of the various muscles) is not adequate, and compliance with this law must be the result of central programming. Why oculomotor programs, which in general show considerable functional adaptability, preferably follow Listing's law, at least largely, remains a mystery. Helmholtz's (1962) suggestion of a minimum energy condition remains a viable hypothesis in the absence of a more convincing argument.

It is well known that the oculomotor plant also possesses considerable viscosity, which will affect the velocity at which new positions are reached. The combination of elasticity and viscosity gives the plant a time constant of about 200 msec for horizontal eye movements (Skavenski and Robinson, 1973) and in fact the nervous system has developed special motor programs to overcome this viscosity. When saccadic eye movements are made, a pulse-step pattern of activation is generated (Robinson, 1970) to achieve high velocities with a sharp beginning and end. When the pulse component is absent or inadequate, saccades can become very slow and reach their endpoint more or less exponentially (Robinson, 1978). In fact many examples were recorded here where torsion associated with saccades or blinks reached its endpoint slowly (Figs. 2, 4, 5). This would suggest that "Listing" torsion is not always correctly programmed. Although the horizontal and vertical displacements are precisely controlled, the associated torsion, being of no consequence, may be left to the periphery.

Independent evidence for sluggish changes in torsion associated with saccades was recently provided by Enright (1986), who used video-recordings of the eye in the primary position, which was reached by 8 deg horizontal saccades from the nasal or temporal side. Transient torsion up to 1 deg, decaying with a time constant of about 1 sec was frequently observed, as well as residual static torsion with hysteresis, the end-position depending on the direction from which the saccade was made. These findings, which are obviously not liable to artifacts such as annulus slip, strongly support a sloppy control of torsion, dynamically as well as statically.

On the other hand torsion, including saccades, can be generated independently from horizontal and vertical saccades. Examples can be seen during fixation (Fig. 1) as well as during vestibular and optokinetic responses (Collewijn et al., 1985b). Even voluntary torsional saccades can be made. Such saccades have amplitude-maximal velocity relations which are not grossly different from horizontal saccades (Balliet and Nakayama, 1978) although they may be somewhat slower. This suggests that the nervous system is capable of programming fast and precise torsional eye movements, inclusive a pulse-step pattern for saccades, whenever they are relevant.

Marked torsional hysteresis was found in square and circular trajectories. During saccadic stepping around a square as well as during smooth pursuit of a circular trajectory marked effects of direction occurred, which were statistically significant in nearly all cases (Tables 3 and 4). There are two ways of looking at these very systematic differences. One general conclusion could be that the absolute value of torsion with respect to the vertical plane in any tertiary position is larger when it was reached through a vertical trajectory than when it was reached through a horizontal trajectory. For instance, in the nasal-up position torsion is larger when the previous eye position was nasal-down (CW trajectory) than when it was temporal-up (CCW trajectory). On the surface, this might suggest that changes in torsion are larger for vertical than for horizontal eye movements of similar magnitude.

Theoretically, values leading to such a distinction are feasible. However, it turns out that for all the sets of values found in the present experiments (Tables 3 and 4) the sum of the absolute values of changes in torsion for horizontal displacements is identical to the similar sum for the vertical displacements. In other words, if we call the values for torsion in the 4 sequential tertiary positions a, b, c and d, we find that:

$$|a-b| + |c-d| = |b-c| + |d-a|$$

This is not a property of any arbitrary set of numbers, but it is always true that:

$$(b-a) + (d-c) = (b-c) + (d-a)$$

Thus the general requirement is that all of these terms in brackets be positive. This is the case when:

$$a<b \wedge b>c \wedge c<d \wedge d>a$$

This minimal requirement is equivalent to stating that changes in tertiary positions should produce changes in torsion that occur at least in the direction implied by Listing's law, irrespective of the size of the changes.

It is satisfied by all experimental values; as a consequence it is proven that no systematic differences can exist between the average amounts of change in torsion during successive vertical and horizontal gaze displacements following a closed trajectory.

The second way to summarize the directional differences in Tables 3 and 4 is to state that the values in the CCW column are always larger (more positive) than the corresponding values in the CW column. This means that during clockwise pursuit the eye is relatively rotated in the intorsional direction, and during counterclockwise pursuit in the extorsional direction. Actually, these overall shifts are easily recognized by comparing Figs. 6 and 7. For the circular pursuit, the average difference (all subjects and conditions pooled) between CCW and CW tracking amounts to a mean of 1.79 $\pm$ 0.61 (S.D.) deg of torsion. A possible cause for this phenomenon could be the viscous drag exerted by the orbital structures upon the eye. Such drag could lead to intorsion of the right eye during clockwise pursuit, and vice versa. Given enough slack or tolerance in the control of torsional eye position, part of this torsion could be retained even in the intersaccadic periods of the square trajectory; a similar hysteresis was found by Enright (1986).

The findings as a whole lead to the hypothesis of the following scheme for the control of ocular torsion:

(1) In many cases, the precise orientation of the eye in torsion is not important to vision. Only vertical and horizontal positioning of the visual axis will then need to be optimally controlled by the nervous system. Torsion will be specified only loosely and show considerable variability and poor dynamic control.

(2) Under certain conditions, the nervous system controls torsion with greater precision and generates crisp saccades with an appropriate pulse-step innervation. The reason why torsion is controlled precisely in some cases and not in others is unclear at this time.

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Chapter V

Concluding Remarks

The results of the new scleral coil measurement technique and the elaborate correction procedure of oculomotor recordings as described in Chapter II can be considered veridical and thus representing the actual ocular orientation. The results confirm that a significant amount of retinal image slip exists during voluntary head motion, indicating imperfect ocular compensation in close agreement with the previous reports by Skavenski et al. (1979) and Collewijn et al. (1981, 1983) as far as horizontal and vertical gaze displacements are concerned with the mean S.D.'s during active head oscillation never exceeding 20 min arc. Binocular oculomotor recordings by Steinman and Collewijn (1980) and Collewijn et al. (1981, 1983) demonstrated the existence of a disjunctive component between both eyes during head movement leading to considerable vergence velocities. Although the results presented here were obtained monocularly, the correction procedure led to only modest changes indicating that also this disjunctive component could hardly be artifactual.

The mean S.D. of retinal image slip in the horizontal direction during active head oscillation at 0.66 Hz in the horizontal plane reported here is almost a factor 2 higher than reported by Duwaer (1982), but since he used an afterimage technique the reduction of retinal image slip by higher order processes can not be ruled out, as discussed in Chapter II. This makes a comparison with our results perhaps somewhat precarious.

All individuals showed a significant increase in gaze instability during active head rotation in the horizontal and vertical planes, as compared to the static situation. Ocular compensation was 1-2% smaller than unity and a mean of 2.5% of head velocity penetrated in horizontal and vertical gaze velocities even at these moderate head velocities of maximally about 40 deg/sec. Once again, these results concur with Skavenski et al. (1979) and Collewijn et al. (1981, 1983).

Recordings of torsional eye position in the stationary, straight ahead position suggest random and continuous long-term drift of torsional eye position; fluctuations of up to 4-5 deg reflected a substantial torsional gaze instability. This instability under static conditions was much larger than that of horizontal or vertical gaze and increased further during active head oscillations around the sagittal axis, although instability decreased with frequency; gain of torsional compensatory eye movements (counterroll), increased from about 0.4 at 0.16 Hz to about 0.6 at 0.66 Hz. A similar trend was seen earlier by Collewijn et al. (1985). Although torsional gaze instability decreased with frequency, it still remained much larger than horizontal and vertical gaze instability under identical conditions. Obviously the point target provided no visual reference for torsion, in contrast to horizontal and vertical gaze, so the increase in gain with the increase in frequency must be due entirely to increased stimulation of the canal-ocular reflexes.

Of immediate interest is the extent to which gaze instability in the horizontal and vertical planes, and to a lesser extent in the torsional plane, during natural head movements, causes problems with regard to the visual process. As shown by Steinman et al. (1985) vision not only tolerates but perhaps even benefits from natural retinal image slip.

Westheimer and McKee (1975) reported that visual acuity was unimpaired by retinal image motion up to about 2 deg/sec. This was confirmed by Murphy (1978) who also found that visual acuity was determined only by retinal image motion and was not reduced by smooth pursuit eye movements, although their velocity did not match that of the target. Erkelens and Collewijn (1985) reported that fluctuations in absolute disparity up to 2 deg do not interfere with stereopsis or fusion nor did they induce any perception of motion in depth. Only changes in relative disparity between different parts of retinal image lead to perception of relative depth.

In conclusion, retinal image instability commonly occurs in various oculomotor tasks and suggests a practical and efficient framework with which the visual system is well equipped to meet routine demands. Less sophisticated and extensive neuronal circuitry is required than otherwise would be needed in an attempt to meet all demands with 100% precision. On top of this framework an adaptation mechanism would then deal with naturally occurring circumstances such as ageing, disease or trauma. That such an adaptation mechanism exists can be demonstrated by the mere wearing of or changing to a new pair of spectacles. Collewijn et al. (1983) demonstrated the ability of the visual system to almost instantaneously adapt itself to new demands; a capacity reported earlier in the classical experiments by Gonshor and Melvill Jones (1976). In the adaptation experiments reported by Collewijn et al. (1983) there is another aspect of the adaptation capacity of the visual system meriting special interest. Under normal visual conditions, all subjects had gains which were close but never equal to unity. With the addition of magnifying glasses, gains easily adapted to values much larger than 1.0, indicating that the visual system is perfectly capable of achieving such a unity gain. It was concluded that the visual system apparently had a preference for a non-unity gain, resulting in retinal image slip.

Thus one might envisage relatively imprecise but fast and efficient oculomotor subsystems such as ocular compensatory movements, smooth pursuit and vergence, to be adjusted whenever required by the circumstances.

In Chapters III and IV, the experiments were primarily designed for the precise recording of ocular torsion in the sustained primary, secondary and tertiary positions, as well as during saccade-like steps and various trajectories followed in smooth pursuit along these positions. In the latter experiments, the effect on torsion of changing pursuit velocity and its direction, was examined as well as the effect of a large background. With the previously described recording technique and using a spherical coordinate system with clear definitions of (false) torsion, a direct test of Listing's and Donders' law was possible.

The existence of short-term and long-term drift of ocular torsion was already noticed in Chapter II and confirmed in Chapters III and IV. The mean S.D. of ocular torsion in the zero position increased more than two-fold with an increase in measuring time; it rose from about ± 8 min arc (Chapter III, 4 second measurements) to about ± 17 minarc (Chapter II, 18 second measurements). In Chapter IV, zero position measurements lasted either 16 or 32 seconds and showed a mean S.D. of torsion of about ± 14 min arc (about ± 13 minarc and ± 15 minarc for 16 and 32 second measurements respectively), indicating that short-term drift did not rise further with an increased sampling period. Long-term drift was expressed as the S.D. of the mean of ocular torsion in the zero position measurements interleaved with the other measurements during a particular session. It varied from about ± 1.64 deg (Chapter III, total session time about 15 min) to about ± 2.80 deg (Chapter IV, total session time about 30 min).

These results indicate that control of torsional gaze is relatively imprecise even though the head is fixed (Chapters III and IV) providing a constant vestibular input. Long-term drift among repeated measurements in the primary position is consistent with earlier findings by Collewijn et al. (1985). Short-term drift was also reported by Fender (1955). The results presented here, strongly suggest that random and continuous long-term fluctuations of torsion up to about 5 deg may be regarded as a normal physiological phenomenon.

In Chapter III the results were to a certain extent in accordance with Listing's law. Ocular torsion increased with eccentricity, extorsion was found in the upper temporal and lower nasal quadrants and intorsion in the remaining two quadrants. The effective values of torsion in the primary position and in most secondary positions were on average also in agreement with Listing. Another finding involving the choice of the primary position, was the naso-temporal asymmetry between torsion values in the tertiary positions, amounting to a difference of more than 50% at the largest eccentricities, although the difference was significant in only 4 out of 8 eyes.

The veridical primary position (assuming a validity of Listing's law in all its respects) was calculated as described by Nakayama (1978) by using torsion values obtained in tertiary positions and it was found that 7 out of 8 eyes had indeed been located in a more nasally oriented primary position and required a shift in the temporal direction; the largest shift was for those 4 eyes for which a significant naso-temporal asymmetry had been found. This shift might explain the asymmetry but the question remains why this bias of choice occurred, other than by coincidence. Moreover, a large variability was seen within individual calculated primary positions; this could be well explained by random fluctuations of torsion and Listing's law not being rigidly followed. Since torsion values in the extreme temporal positions were already equal to those predicted by Listing, a shift of the primary position in the temporal direction in order to achieve complete symmetry in all 4 quadrants would result in all torsion values (at least in extreme eccentricities) becoming higher than Listing's prediction. Manipulation of the primary position does not result in a perfect fit of measured values with those predicted by Listing.

Although Nakayama's (1978) ball and membrane model shows that forces acting only in horizontal or vertical directions (or combinations of both) result in a movement of the model eye exactly as predicted by Listing, it does not seem probable that a real eye will behave exactly in this fashion. Eye torsion in tertiary positions involves complex relations between all 6 extra-ocular muscles and muscle elasticity is not likely to be constant at all times. The suspension of the eye in the orbit provides an elastic force of about 1 gram/deg of excursion in the horizontal and vertical directions which pulls the eye back to the midposition (Robinson, 1965; Robinson et al., 1969). It is difficult to envisage a pure horizontal or vertical movement with no torsional component, demanding exactly the appropriate amount of excitation and inhibition in all extra-ocular muscles simultaneously, in terms of plant mechanics alone. For such a restricted movement to occur, Nakayama's model seems insufficient and would have to be supplemented by an oculomotor program of central origin.

In Chapter IV it was shown that during horizontal and vertical saccades, the associated torsion component often demonstrated sluggish behaviour as also independently found by Enright (1986) with a video-recording method. These findings could very well be the adventitious result of plant mechanics.

Since the oculomotor plant possesses considerable viscosity, affecting the velocity of the eye while it is moving to a new position, the nervous system apparently has developed special oculomotor programs to overcome this problem by the generation of a pulse-step pattern of activation during saccades (Robinson, 1970). However, if this pulse-step is absent, saccades can become slow and reach their end-position more or less exponentially (Robinson, 1978).

In the experiments reported here, torsion associated with horizontal or vertical saccades was often sluggish and did not seem to be controlled by any oculomotor program. On the other hand, torsional saccades could be generated during fixation. Independent torsional saccades were reported earlier by Collewijn et al. (1985), as a part of either vestibular or optokinetic responses. Balliet and Nakayama (1978) demonstrated that torsional saccades can even be made voluntarily indicating the capacity of the central nervous system to execute a certain oculomotor program resulting in fast and precise torsional movements.

Repeated demonstrations of hysteresis (Chapter IV), and therefore violations of Donders' law, were seen during pursuit along different trajectories resulting in the same horizontal and vertical end positions, but showing idiosyncratic deviations up to several degrees of torsion. These violations of Donders' law were often very reproducible and systematic; therefore they were independent of random torsional fluctuations. Donders' law was only followed if a certain end position was reached by way of a similar trajectory. Hysteresis of torsion values occurred during the square-step and circular trajectories and was statistically significant in nearly all cases. Changes in tertiary position resulted in changes of torsion in the direction (in- or extorsion) as predicted by Listing and it was shown that no systematic difference existed between the average amounts of change in torsion during either horizontal or vertical gaze displacements between equally eccentric positions in the diagonal meridians. Since absolute values of torsion obtained during clockwise pursuit were always smaller than those in counter-clockwise pursuit, indicating a relative rotation in intorsional direction during clockwise and a relative rotation in extorsional direction during counter-clockwise pursuit, it was postulated that this might be caused by viscous drag exerted by orbital structures upon the eye. Since part of this (in- or ex)torsion could be retained even in the intersaccadic intervals during the square step trajectories, the orbital structures showed slack as well.

In the light of the previous evidence, it was concluded that during static and dynamic monocular fixation Listing's and Donders' laws are only approximately valid and that physiological eye movements show considerable stochastical as well as systematic deviations; in summary, our findings confirm and provide further evidence for imprecision of torsional control.

Exceptions to both laws were reported earlier:

1. Allen and Carter (1967) using data of Landolt converted to Fick's axial system noted that Listing's law was not obeyed during convergence of the eyes;

2. Westheimer and McKee (1973) found that Donders' law was violated during smooth pursuit;

3. Balliet and Nakayama (1978) demonstrated that torsion can be actively produced, both as a reflex and voluntarily.

Torsional control is not only imprecise with respect to the classical laws. Vestibular input, through the canal-ocular reflexes, produces relatively small torsional compensatory eye movements during natural head movements resulting in very low gains. This fact was already reported by Collewijn et al. (1985) and is corroborated in Chapter II. Visual stimuli produced weak and inconstant effects on ocular torsion. Collewijn et al. (1985) found only a weak and inconsistent torsional optokinetic nystagmus. As was seen in Chapter IV, the introduction of a large stationary background did not inhibit torsional drift and in some cases it was even enhanced. During pursuit along circular trajectories absolute torsional values remained unaffected by the addition of a background.

Since foveal viewing with high acuity in humans is restricted to an angle of only a few degrees and will be only marginally affected by errors or fluctuations in torsion, and in addition vision functions perfectly well under conditions in which violations of classical laws occur, such as vergence and smooth pursuit, precise torsional control is not required for the proper functioning of vision, at least under normal circumstances. Finally the following hypothesis was suggested for control of ocular torsion:

1. When precise ocular orientation in the torsional direction is not important to vision only the horizontal and vertical positioning of the visual axis will need to be optimally controlled by the nervous system. Torsion will then only be loosely specified and show considerable variability and poor dynamic control.

2. Under certain conditions, the nervous system controls torsion with greater precision and generates crisp saccades with an appropriate pulse-step innervation.

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SUMMARY

This thesis presents the results of oculomotor recordings obtained with a new type of scleral induction coil with which horizontal, vertical and torsional eye movements were measured simultaneously. In Chapter II, the stability of gaze in these three dimensions was measured in eight emmetropic observers. Subjects held the head still or oscillated it at 0.16-0.67 Hz (amplitude about 10 deg) in the horizontal, vertical or torsional plane while fixating a point target at optical infinity. Veridical gaze and head coordinates were calculated with full correction for non-linear goniometric relations and for cross-coupling artifacts due to misalignments of the coil on the eye. The amount of gaze instability in the horizontal and vertical direction was virtually identical. With the head still, in either of these directions the mean standard deviation of gaze position (inclusive saccades) was about 7 min arc; mean non-saccadic retinal image speeds were 20-30 min arc/sec. During head oscillation these values increased to about 16 min arc and 1 deg/sec; a mean of about 2.5% of the head motion remained uncorrected by the compensatory eye movements. Gaze stability in the torsional plane was considerably inferior to that in the horizontal and vertical plane. With the head held still, the mean S.D. (short-term drift) of torsional gaze position was about 17 min arc; mean torsional non-saccadic retinal image speed was about 46 min arc/sec. Long-term drift, expressed as the S.D. of the mean of torsional gaze position in consecutive zero position measurements, was 2.14 deg. Gain of the torsional compensatory eye movements was frequency dependent and rose from about

0.26 in static conditions (0 Hz) to about 0.42 at 0.16 Hz and 0.64 at 0.67 Hz.

The validity of Listing's law was reinvestigated in Chapter III by means of a direct test. Either eye of 4 subjects was measured monocularly. Eye positions were measured in Fick coordinates and ocular torsion values were compared to the theoretical ones predicted by Listing's law. During consecutive measurements in the primary position torsion values were close to zero although considerable fluctuations of torsion were seen. Short-term drift was about 8 min arc and long-term drift about 1.64 deg. Torsion values in the secondary positions were also close to zero. In the tertiary positions torsion in the direction as predicted by Listing's law and increasing with eccentricity was recorded. In the temporal quadrants mean torsion was quantitatively in agreement with Listing's law; torsion values in the nasal quadrants however showed systematically larger values and this discrepancy increased with eccentricity to more than 50%. Statistical support for this finding however, was seen only in 4 out of 8 eyes. Symmetry could be obtained by shifting the chosen horizontal primary position (gaze parallel to the midplane) in the temporal direction; as a consequence all measured torsion values would exceed the ones specified by Listing's law. Torsion values varied idiosyncratically among subjects and among the left and right eyes of any one subject. It is concluded that Listing's law specifies ocular torsion only approximately: physiological eye movements show considerable stochastical as well as systematical deviations from this law.

In Chapter IV, the dynamic aspects of torsion were investigated during monocular fixation, blinking, smooth pursuit and saccades in five normal subjects. Torsion in the primary position showed a short-term drift of about 14 min arc and a long-term drift of about 2.80 deg. During saccades between diagonally opposite tertiary positions torsion transiently reached values approximating those in the sustained primary position. During smooth pursuit across the primary position, the minimal values of torsion varied with the direction and the trajectory of pursuit, in violation of Donders' law. Changes in torsion associated with horizontal and vertical saccades and during the aftermath of blinks often had a sluggish, exponential time course. During eye movements around a circular or square trajectory torsion showed hysteresis. During clockwise pursuit the right eye showed relative intorsion compared to counterclockwise pursuit. It is proposed that central nervous control of torsion is usually imprecise, and that the eye follows Listing's and Donders' laws only approximately.

SAMENVATTING

Talloze malen per dag zal ieder gezond individu zijn ogen richten op een of ander voorwerp welk op dat moment van belang is. Om het voorwerp scherp te kunnen zien, is het noodzakelijk dat het beeld daarvan binnen een bepaald deel van het netvlies valt. Dit deel van het netvlies - van nog geen booggraad in doorsnede - maakt deel uit van de fovea of gele vlek en bevat de grootste dichtheid van fotoreceptoren. Het oog wordt op de juiste plaats gebracht en gehouden door zes uitwendige oogspieren. Het bewust volgen van een bewegend voorwerp met het oog is mogelijk tot frequenties van ten hoogste 3 Hz (b.v. een slinger die per seconde drie maal heen en weer beweegt); bij hogere frequenties wordt het beeld onscherp. Een stilstaand voorwerp kan echter scherp worden waargenomen tijdens hoofd en/of lichaamsbewegingen van tenminste 5 Hz. Dergelijke hoofdbewegingen activeren beide evenwichtsorganen die via een reflex een adequate compensatoire oogbeweging tot stand brengen. Een hoofdbeweging naar links zal zo resulteren in een oogbeweging (in het hoofd) naar rechts. Het oog in de ruimte blijft dan stilstaan. Aangezien het beeld tijdens hoofdbewegingen subjectief steeds scherp blijft, ging men er tot voor kort van uit dat de compensatoire oogbeweging zo precies werd uitgevoerd, dat het oog in de ruimte volkomen stabiel bleef. Door meer nauwkeurige meettechnieken is het de laatste jaren echter duidelijk geworden dat dit niet het geval is. Anders gezegd: de stabiliteit van het oog in de ruimte is niet 100%. Dit impliceert dat er tijdens hoofdbewegingen ook een beweging van het beeld op het netvlies moet bestaan: retinale slip. Deze bevinding heeft grote consequenties, want blijkbaar is ons visuele systeem in staat om ondanks deze retinale slip een subjectief scherpe waarneming te bewerkstelligen. In een poging de retinale slip zo nauwkeurig mogelijk te meten, werd er een speciale kunststof ring ontwikkeld, die op eenvoudige wijze op het oog kan worden geplaatst. Binnen de kunststof ring zijn enkele koperdraadwindingen aangebracht en wanneer deze zg. sclerale inductiespoel in een magnetisch veld wordt gebracht, zal er een electrisch stroompje worden opgewekt in de koperdraadwindingen. De grootte van het stroompje hangt af van de stand van de sclerale inductiespoel - en dus van het oog - binnen het magnetisch veld. Door het koperdraad op speciale wijze te wikkelen bleek het mogelijk om niet alleen horizontale en verticale oogbewegingen te meten maar ook draaiingen van het oog rond de visuele as: oogtorsie. De oogpositie kon in drie dimensies tegelijk worden gemeten tot op honderdsten van een graad nauwkeurig. Zoals in hoofdstuk II wordt beschreven bestaat er retinale slip in alle drie de dimensies, niet alleen tijdens hoofdbewegingen, maar ook wanneer het hoofd zo stil mogelijk wordt gehouden, ook al is de slip in het laatste geval veel kleiner. Onder alle omstandigheden bleek de retinale slip in horizontale en verticale richting ongeveer gelijk aan elkaar te zijn en die rond de visuele as het grootst.

In hoofdstuk III en IV wordt vooral nader ingegaan op de beweging van het oog rond de visuele as: oogtorsie. Meer dan 100 jaar geleden formuleerden zowel Listing als Donders een eigen wet volgens welke de richting en grootte van oogtorsie konden worden voorspeld voor elke willekeurige stand van het oog. Het blijkt dat beide wetten slechts een globaal juiste beschrijving geven van oogbewegingen rond de visuele as. Het oog gedraagt zich niet geheel conform deze wetten en er worden zowel systematische als individuele verschillen gevonden. Ook deze bevindingen wijzen erop dat onder gewone omstandigheden het visuele systeem er blijkbaar geen hinder van ondervindt als het beeld op het netvlies niet precies de juiste ruimtelijke orientatie weergeeft.

CURRICULUM VITAE AUCTORIS

The author was born in The Hague in 1952. After obtaining his HBS-B diploma he worked in a bank and fulfilled his military service in the Royal Dutch Army. He qualified in medicine in 1982, after which he worked as a research assistant in the vascular laboratory (head: Dr. T.J. Bast) of the St. Antonius Hospital in Utrecht (now in Nieuwegein) and the ENT department (head: Prof.Dr. N.A.M. Urbanus) of the University Hospital of Amsterdam. From 1983 to 1986 he worked on the present doctoral thesis at the department of Physiology I (head: Prof.Dr. M.W. van Hof) in Rotterdam (Medical Faculty, Erasmus University) with Prof.Dr. H. Collewijn as supervisor. In 1986 he started training as an ENT surgeon at the ENT department (head: Prof.Dr. C.D.A. Verwoerd) of the University Hospital Dijkzigt in Rotterdam. The author is married and lives in Rotterdam.