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A DIRECT TEST OF LISTING'S LAW—II. HUMAN OCULAR TORSION MEASURED UNDER DYNAMIC CONDITIONS

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Abstract—Ocular torsion was recorded with a scleral search coil technique in five normal subjects. The dynamic aspects of torsion were investigated during monocular fixation, blinking, smooth pursuit and saccades. Torsion near the primary position showed considerable short-term (SD about 0.25 deg) and a much larger long-term fluctuation (SD about 2.3 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.

Listing's law   Donders' law   Eye torsion   Tertiary eye positions   Dynamic condition   Human

INTRODUCTION

In the preceding paper (Ferman *et al.*, 1987b) 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, we emphasized general trends obtained by averaging data over time and subjects.

In the present paper, we shall describe the dynamic aspects of ocular torsion. Our 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 us to evaluate 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 paper (Ferman *et al.*, 1987b) apart from the following changes.

Horizontal, vertical and torsional eye positions were measured in 5 healthy subjects (including the 4 subjects of the previous paper) 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 × 5 deg), covering the whole visual field, could be projected on the screen. Measurements lasted 16.4 or 32.8 sec 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/sec.

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/sec 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 at 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 positions 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 paper (Ferman *et al.*, 1987b).

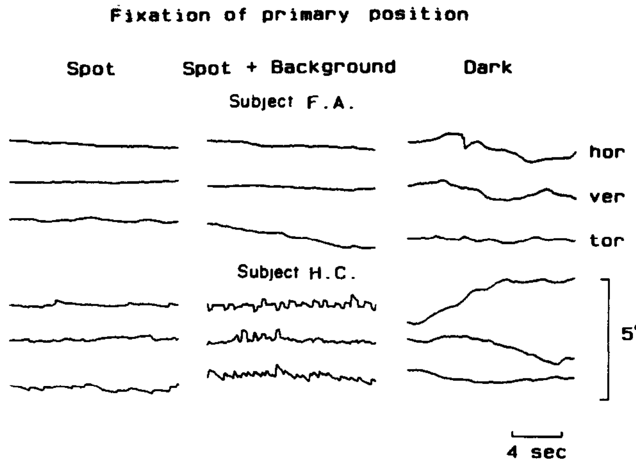

Fig. 1. Representative recordings of horizontal, vertical and torsional eye position during fixation of a single spot, a spot with a structured background, or the imagined spot in darkness. Two subjects are shown; F.A. and H.C. For all figures, upward deflection represents horizontal movement to the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

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 × 5 subjects). However, the long term variability among successive measurements spread through a session was much larger: the mean SD of the variation (all subjects taken together) was 2.80 deg. As in the preceding paper (Ferman *et al.*, 1987b), no particular trend could be discerned and ocular torsion values remained close to zero, so once again we felt justified in ascribing 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 (H.C. and H.S.) 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 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 we found under conditions with the head free (Ferman *et al.*, 1987a), in accordance with the general tendency for gaze instability to be substantially larger with the head free than the head immobilized (see Steinman *et al.*, 1982). In

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		
	Target conditions		
Subject	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	15.47	18.23	15.22
(S.D.)	(3.01)	(5.51)	(2.45)

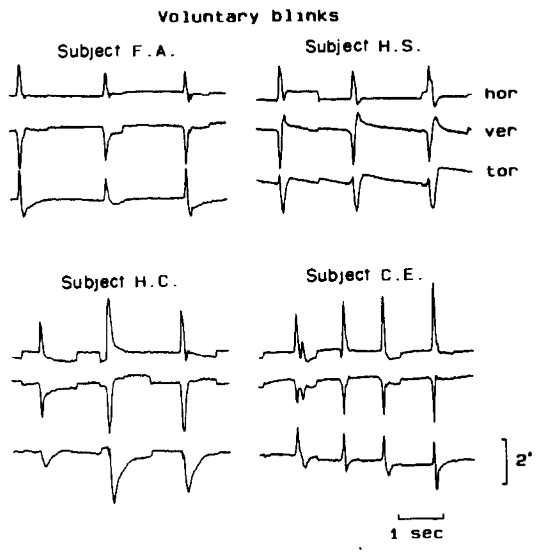

Fig. 2. Horizontal, vertical and torsional eye movements associated with voluntary blinks during fixation of a single point. Four subjects are shown.

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 structural 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 and 3 deg and durations of about 100–200 msec, in agreement with our previous findings (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, intorsion or a combination of both. The duration of blink-associated torsion showed a large variability. Figure 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 positon. 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

The 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 we had to conclude—assuming validity of Listing's law—that when subjects fixated the zero target position, their gaze was 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 paper we shall concentrate on the dynamic aspects of torsion and disregard its absolute magnitude.

Tertiary positions

Diagonal trajectories. Figure 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

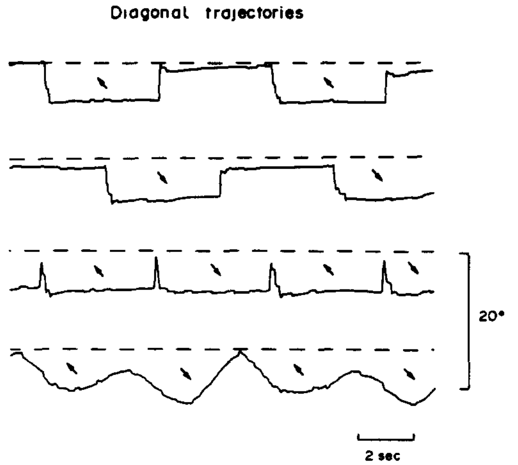

Fig. 3. Torsion associated with right eye movements to tertiary positions. Upper two traces: saccades between the primary position and the nasal-up position (first trace) or the temporal-down position (second trace). Third trace: saccades between the same two diagonally opposite tertiary positions, passing 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.

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

	Diagonal target trajectory Target condition	
Target position	Steps primary–tertiary	Steps tertiary–tertiary
Nasal up	−4.11	−4.39
Temporal down	−2.38	−2.40
Primary	1.24	0.83
Temporal up	6.38	7.00
Nasal down	3.22	3.50
Primary	1.03	0.79

Also shown are the values reached in the primary position during these diagonal trajectories. All ocular torsion values in deg (+ = extorsion; − = intorsion).

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). Figure 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 our 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 persuit. 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 for 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 our data: in 8 out of 10 recordings (5 subjects × 2 diagonal directions) torsion during crossing of the zero position appeared to be 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).

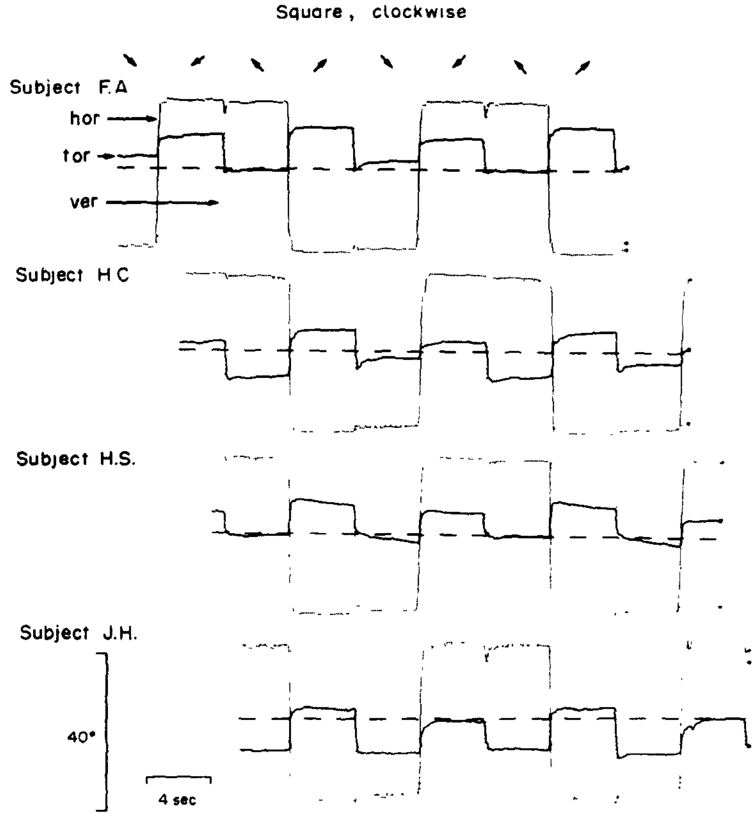

Fig. 4. Horizontal, vertical and torsional eye movements during saccadic stepping around the corners of a square (eccentricities of the corners: 20 deg horizontally and 20 deg vertically). Stepping was clockwise; four subjects are shown. Arrows indicate direction of tertiary positions as seen by subject.

Saccadic stepping around a square. Figure 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. Figure 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 we should expect a sequence of torsional steps of equal size and alternating in direction, 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 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 ± 3.5 deg

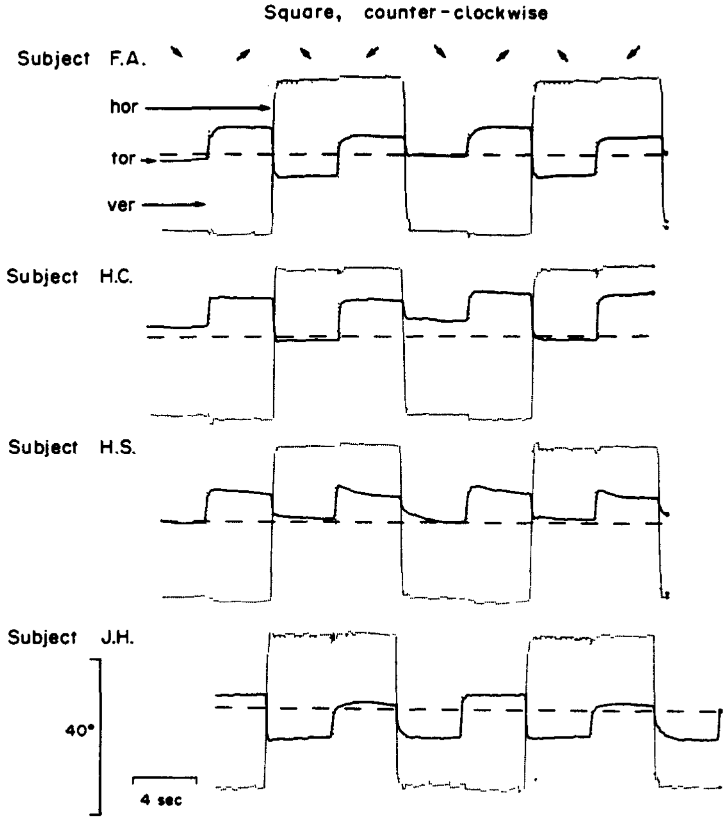

Fig. 5. Saccadic stepping around a square, as Fig. 4, but in counterclockwise direction.

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 ± 2.53 deg, suggesting that the average changes in torsion exceed Listing's predictions. This agrees with our findings in the preceding paper (Ferman *et al.*, 1987b) 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 higher 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. Figure 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

Table 3. Mean ocular torsion values (all subjects pooled) in 4 tertiary positions located at the corner 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

Target position	Square step trajectory Target conditions CW	CCW	Significance of difference
Nasal up	−3.9937	−3.3689	$P < 0.05$
Temporal up	7.2115	7.9105	$P < 0.05$
Temporal down	−2.6392	−1.2537	$P < 0.01$
Nasal down	3.0392	5.0079	$P < 0.001$

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).

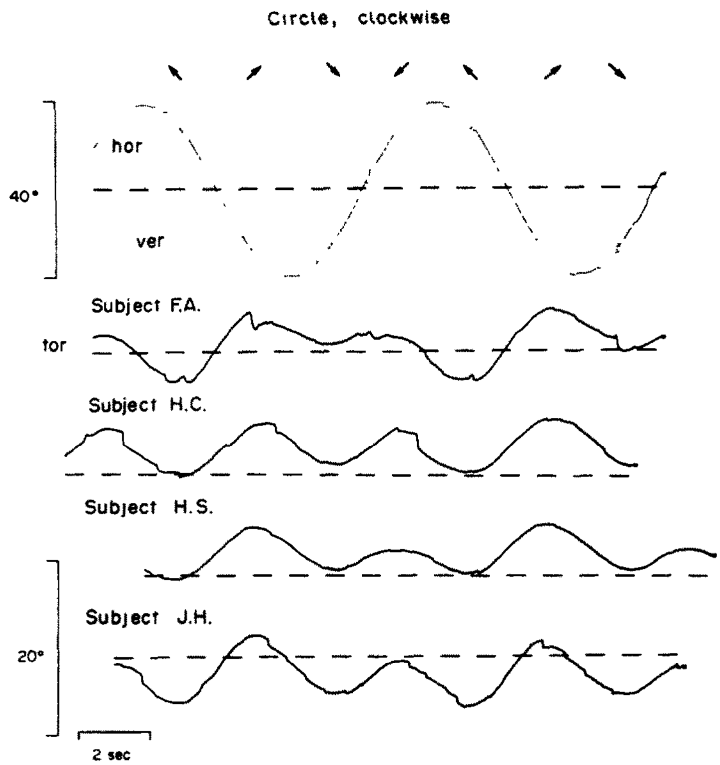

Fig. 6. Smooth pursuit of a spot, circling around the primary position with a radius of 20 deg and an angular velocity of 16 deg/sec. The top traces show the horizontal and vertical eye movements of subject F.A.; the lower four traces show torsion of 4 subjects, all correctly aligned in phase with the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

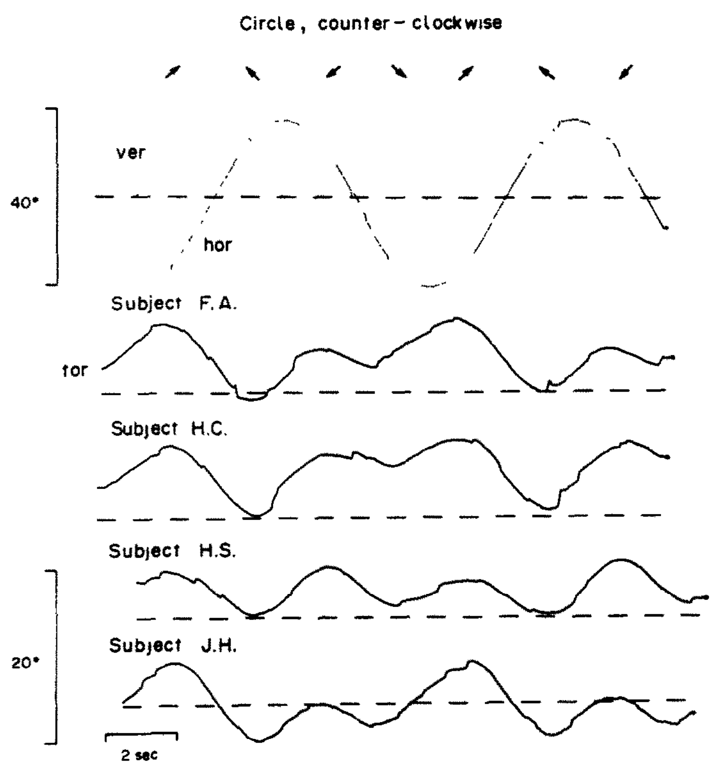

Fig. 7. Circular pursuit as in Fig. 6, for counterclockwise motion.

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

Target position	Circular target trajectory Target condition CW	CCW	Significance of difference
	Spot at 16 deg/sec		
Nasal up	−2.7989	−1.5030	$P < 0.01$
Temporal up	4.2961	6.2878	$P < 0.01$
Temporal 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	$P < 0.01$
Temporal up	3.9939	6.0384	$P < 0.01$
Temporal 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
Temporal up	4.8718	6.2503	$P < 0.02$
Temporal 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
Temporal up	4.0266	5.8829	$P < 0.01$
Temporal down	−2.2118	−0.1323	$P < 0.01$
Nasal down	1.5881	3.7121	$P < 0.001$

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.

same measurement are shown for the sake of orientation, and to show that the target was properly pursued. All tracing 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 reproducibitity 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 Figs 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 direction 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 not effect of velocity or background.

Once more, however, there was a clear effect of direction of pursuit. Comparison between Figs 6 and 7 already shows clear examples of this type of asymmetry. For instance, subject H.C. showed a reasonable regular sinusoidal modulation of torsion while pursuing in the clockwise direction (Fig. 6), where 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 ($P \ll 0.02$). Once more, this shows a clear violation of Donders' law.

DISCUSSION

The main conclusion from the current 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 our data, 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 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 after-image techniques, rather lacking in spatial and temporal resolution, clear exceptions to these laws have been noticed before. There appears to be a consensus that Listing's and Donders' law are not obeyed as soon as the eyes converge (Allen, 1954). Furthermore, 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.

Our findings 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; Ferman *et al.*, 1987a). 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 of fluctuations in torsion.

There was no evidence for any visual correction of torsion in our present (monocular) experiments. During fixation, torsional drift was not inhibited and in two of our 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.

Our experiments were all 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 (Figs 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 the 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 elsatic 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 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 we recorded many examples where torsion associated with saccades or blinks reached its endpoint slowly (Figs 2, 4 and 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 videorecordings 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 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 our experiments (Table 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 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 our 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 ± 0.61 (SD) 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).

Our findings as a whole lead us to hypothesize 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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