



Transient Torsion During and After Saccades

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In five normal subjects, we analyzed uncalled for torsion (blips) during and after horizontal and vertical saccades. Torsion was defined as movement out of Listing's plane. During horizontal saccades in downward gaze the abducting eye extorted and the adducting eye intorted. The direction of the blips reversed in upward gaze. Peak torsional amplitudes (up to 1–2 deg) were always reached during saccades; drifts back to Listing's plane outlasted the saccades. Torsion of the extorting eye was larger than that of the intorting eye, producing a transient positive cyclovergence. Torsion and cyclovergence evoked by vertical saccades were also stereotyped in each eye, but showed idiosyncratic differences among subjects. We conclude that Listing's law is violated during saccades. Transient saccade-evoked torsion might reflect properties of the three-dimensional velocity-to-position integrator and/or the ocular plant.

Human Torsion Eye movements Three-dimensional Listing's law Blips

INTRODUCTION

A thorough understanding of the mechanical and neural factors influencing the dynamics and kinematics of saccades requires accurate analyses of so-called "second-order effects". These include transient changes in horizontal alignment (Collewijn, Erkelens & Steinman, 1988; Kapoula, Hain, Zee & Robinson, 1987) as well as translational and torsional movements of the globe (Enright, 1986). In this study we systematically investigated the direction and magnitude of torsion of both eyes during and after horizontal and vertical saccades.

The presence of saccade-evoked torsion has direct bearing on the validity of Listing's law for saccades. In its original formulation, Listing's law states that, with the head upright and stationary, all axes about which the eye would have to rotate from a given reference position to any other position approximately lie in a plane: the so-called Listing's plane (von Helmholtz, 1867). This can best be visualized by using head-fixed Cartesian coordinate systems like rotation vectors (Haustein, 1989) or quaternions (Westheimer, 1957; Tweed & Vilis, 1987): if the torsional axis, which points forward, coincides with primary gaze direction, all eye positions lie in Listing's plane defined by the horizontal and vertical coordinate axes.

Tweed and Vilis (1990) studied eye movements in humans and monkeys using the dual search coil technique

to determine whether Listing's law can be extended to include eye positions during saccades: on average, the standard deviation of eye positions from a best-fit plane during spontaneous saccades of different amplitudes and directions was 30% larger than during fixations. Based on this finding and the three-dimensional orientations of peak saccadic angular velocity vectors, the authors concluded that Listing's law indeed is valid during saccades. More recently, Minken, Van Opstal and Van Gisbergen (1993), reported that during saccades in response to double target jumps, in which case the trajectory of the eye movement may be curved, Listing's law is still obeyed.

In conflict with these results, using high-resolution video, Enright (1986) found torsional drifts of the eyes after centripetal saccades from different eccentricities along the horizontal meridian to straight-ahead gaze. These drifts, which suggest a rapid torsional eye displacement during the saccade, were usually intorsional after abducting saccades and extorsional after adducting saccades. After 8 deg saccades, drifts lasted up to 3–4 sec and peak torsional amplitudes were around 0.5–1 deg. Similarly, Ferman, Collewijn and Van den Berg (1987), using three-dimensional search coils, described torsional drifts in humans after saccades between tertiary positions.

Here, we reexamine the validity of Listing's law for saccades, with an additional emphasis on whether Listing's law holds for both eyes during saccades, i.e. is Listing's law conjugate? Torsion was defined as movement away from Listing's plane. We systematically analyzed the amount of transient torsion and cyclovergence evoked by horizontal and vertical saccades between different gaze positions. Our results will be discussed in relation to current

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models of the three-dimensional velocity-to-position integrator (Schnabolk & Raphan, 1994; Tweed, Misslisch & Fetter, 1994).

METHODS

Subjects

Five normal subjects (two female, three male, age 22–50 yr) were studied. Their visual acuities were 20/20 or better, with one subject (LE) wearing contact lenses (−3/−3 D, spherical correction). Informed consent was obtained after explanation of the experimental procedure.

Experimental setup

Movements of the eyes about all three cardinal axes were simultaneously recorded from both eyes using dual search coils (manufactured by Skalar, Delft, The Netherlands). The field coil is a modified Remmel system (Remmel, 1984), consisting of a cubic coil frame of welded aluminum with a side length of 1.02 m, which produces three orthogonal magnetic fields (frequencies: 55.5, 83.3, 42.6 kHz; intensity: 0.088 G). Amplitude-modulated signals are identified using synchronous detection. The bandwidth is 0–90 Hz.

Calibration procedure

The two dual search coils are calibrated *in vitro*, before each experiment. Inside the magnetic frame, an annulus yields two sensitivity vectors, one for the direction (horizontal–vertical) coil, the other for the figure-eight (torsion) coil. Each sensitivity vector is characterized by voltages induced by three orthogonal magnetic fields. The output of a dual search coil consists therefore of six signals. With the coils connected to the amplifier and the fields switched on, the annuli are placed in a metallic tube which completely shields the coils from the magnetic fields. In this setting, the measured voltages (offsets) do not originate from the search coils and therefore can be nulled. Hereafter, until the end of the experiment, offsets and gains are not changed.

Two right-handed orthogonal coordinate systems can be defined: one is given by the space-fixed frame of the magnetic field coils, the other is fixed to the eye. In both systems, the *x*-axis points forward, the *y*-axis leftward, and the *z*-axis upward. The dual coils are placed on a gimbal system in the center of the frame, and the coil sensitivity vectors are consecutively aligned with the three magnetic fields. Maximal voltages induced for each component are recorded. First, the sensitivity vector of the direction coil, which points straight ahead, is sequentially placed along the *x*-, *y*-, and *z*-axis of the magnetic frame. The two latter positions are reached from the first position by a leftward or upward rotation respectively, according to the right-hand rule. The sensitivity vector of the torsion coil, by definition, points

leftward. It is also sequentially placed along the *x*-, *y*- and *z*-axis of the magnetic frame. The first and the third position is reached from the second (default) position by a rightward or upward rotation of the sensitivity vector respectively.

After the experiment, the following off-line procedures are carried out on a personal computer using MATLAB™ (The MathWorks, Inc.): first, all data points of each channel are divided by the corresponding *in-vitro* calibration values. This normalizes the three-dimensional voltage vectors. Next, an orthogonal eye-fixed coordinate system is derived from the two coil sensitivity vectors. For this purpose, the torsional coil sensitivity vector, which may not be exactly orthogonal to the sensitivity vector of the direction coil, is projected onto the plane orthogonal to the direction coil sensitivity vector. The third axis of the eye-fixed coordinate system is given by the cross product between the direction coil and the orthogonalized torsion coil vector. All three orthogonal vectors are normalized for each data point (Hess, Van Opstal, Straumann & Hepp, 1992).

At the beginning of each trial, the subject has to fix upon the reference position straight ahead. All eye positions are described by a rotation of the eye coordinate system from this reference position. The rotation matrix R_{rc} describing this rotation is computed by:

$$R_{rc} = R_c^T * R_r$$

where R_r denotes the reference eye coordinate system and R_c the current eye coordinate system. Rotation vectors, which describe eye positions as single rotations from the reference position, are given by Van Opstal (1993)*:

torsional vector component:

$$r_x = (R_{rc}(3, 2) - R_{rc}(2, 3)) / (1 + R_{rc}(1, 1) + R_{rc}(2, 2) + R_{rc}(3, 3))$$

vertical vector component:

$$r_y = (R_{rc}(1, 3) - R_{rc}(3, 1)) / (1 + R_{rc}(1, 1) + R_{rc}(2, 2) + R_{rc}(3, 3))$$

horizontal vector component:

$$r_z = (R_{rc}(2, 1) - R_{rc}(1, 2)) / (1 + R_{rc}(1, 1) + R_{rc}(2, 2) + R_{rc}(3, 3))$$

Any eye position can be reached from the reference position by a single rotation. A rotation vector is oriented parallel to the axis of this rotation, i.e. orthogonal to the movement direction. The length of a rotation vector is given by $\tan(\rho/2)$, where ρ is the amount of rotation (Haustein, 1989). For the convenience of the reader, we shall describe ρ in deg for each vector component and usually refer to the direction of the associated movement. Leftward, downward, extorsion of the right eye and intorsion of the left eye are positive, according to the right-hand rule. During the saccades, elevation and azimuth denote the constant vertical and horizontal eye position component respectively, with positive values upward and rightward.

*Numbers in parentheses refer to rows and columns of the rotation matrix.

Experiments

Subjects sat inside the coil frame so that the center of the interpupillary line coincided with the center of the frame. During eye movement recordings, the head of the subject was immobilized with a bitebar. The position of the head was defined by the earth-horizontal orientation of the bitebar, which was checked by an inclinometer. After anesthetizing the conjunctiva with proparacaine HCl 0.5% (Ophthetic®), dual search coils were mounted on both eyes. During experiments, subjects were asked to fix upon light-emitting diodes (LEDs) at different locations on a tangent screen (distance 124 cm), which consecutively were switched on and off, such that only one LED was lit at any time in otherwise complete darkness. Voltages related to eye movements were digitized with a 12-bit A/D converter at 500 Hz and written to a hard disk. Data collection and visual stimuli were controlled by computer.

Subjects were tested with the following four paradigms, always with both eyes viewing.

Paradigm I. LEDs were switched on along the vertical meridian at 20, 10, 0, -10, and -20 deg elevation. After 2 sec the light jumped 20 deg horizontally, either to the right or left. Another 2 sec later, the light jumped back to its initial position and remained on for 2 sec. Each of the 10 possible horizontal jumps (two at each elevation) were

pseudorandomly displayed during the trial and appeared 10 times in total (Fig. 1).

Paradigm II. Analogous to paradigm I, lights appeared in the vertical directions from and to different positions on the horizontal meridian (azimuth).

Paradigm III. Along the horizontal meridian in both directions, lights were first switched on at zero position, then at 5, 10, 15, or 20 deg eccentricities, and finally at the zero position again. The duration of the fixation period was always 2 sec. Each step was presented ten times in pseudorandom order.

Paradigm IV. The lights consecutively appeared horizontally in 5 deg steps first to the right, then to the left, and back to the straight-ahead position. The maximal right and left eccentricities were 25 deg. The same procedure was repeated at different elevation (5 deg intervals) up to 20 deg above and below the zero position. The lights were always switched on for 0.8 sec. Data from this paradigm were used to characterize the Listing's planes of both eyes.

Artifacts

Noise levels of the system were checked with a dual search coil fixed in the center of the coil frame. Standard deviations were around 0.02 deg in the horizontal, vertical, and torsional direction. In our experiments we

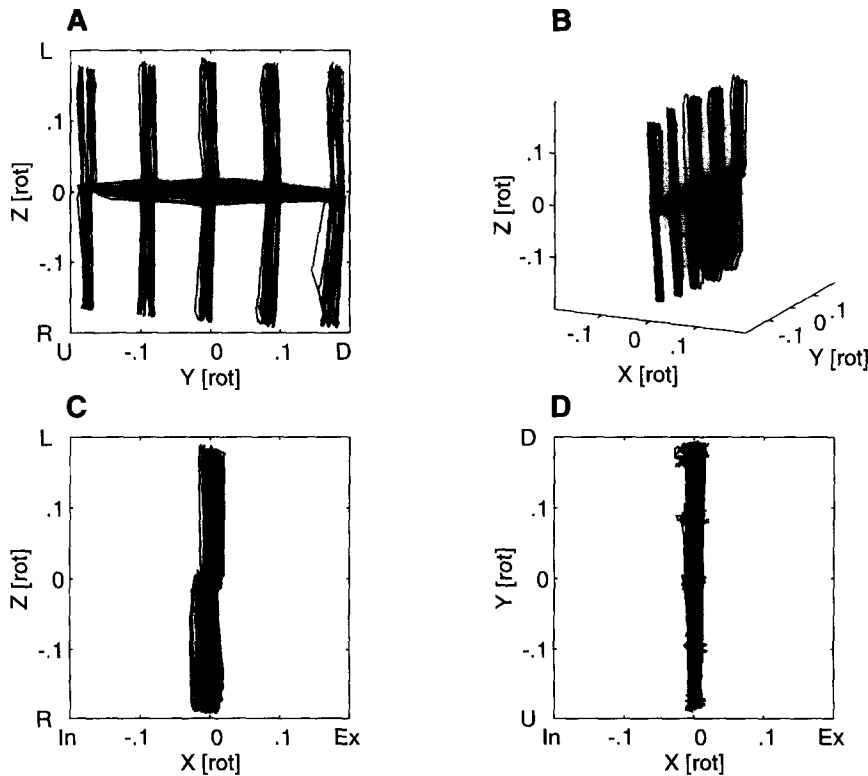


FIGURE 1. Example (subject DS) of three-dimensional eye rotation vectors during an entire trial with horizontal saccades at different elevations (Paradigm I). The data set is rotated and translated to align its best-fit plane with the Y-Z-plane of the coordinate system, and the reference position with the origin of the coordinate system, respectively. Capital letters describe the directions of movements. R, rightward; L, leftward; U, upward; D, downward; Ex, extorsional; In, intorsional. The standard deviation of all data points from the best-fit plane was 0.86 deg. (A) Frontal view with vertical (Z) and horizontal (Y) rotation vector components. (B) Three-dimensional plot with vertical (Z), horizontal (Y), and torsional (X) vector components. (C) Side view with vertical (Z) and torsional (X) vector components. (D) Top view with horizontal (Y) and torsional (X) vector components.

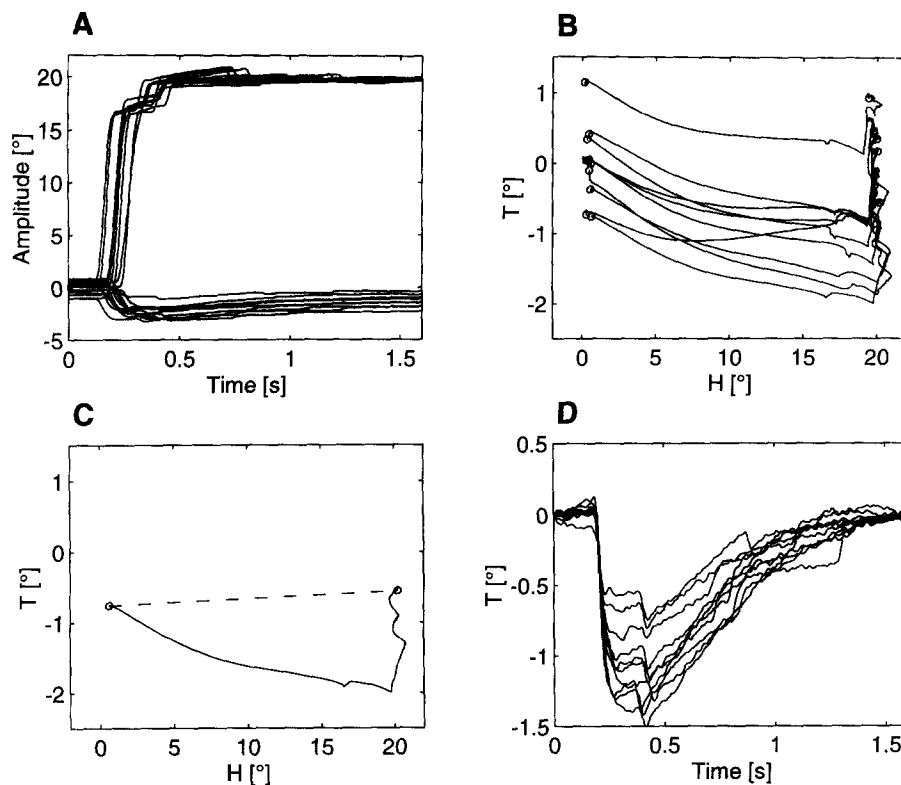


FIGURE 2. Steps to analyze torsional blips. Example of 10 centrifugal 20 deg leftward saccades of the left eye at an elevation of -10 deg (subject DS). (A) Torsional (lower traces) and horizontal (larger amplitudes) eye position components as a function of time. (B) Horizontal (H) vs torsional (T) position components from 200 msec before until 1500 msec after the beginning of saccades. \circ denote the starting and end points of the analysis window. (Before, the data of the entire trial was rotated as described in Fig. 1.) (C) Individual saccade of the saccade population in (B). The straight line (dashed) connecting start- and endpoint of the analysis window was considered to be the zero-torsion baseline. (D) Torsional blips (T) as a function of time after subtracting the zero-torsion baseline [as depicted in (C)]. The blips correspond to the same population of saccades displayed in (A) and (B).

did not observe significant (> 1 deg) long-term changes of the torsional baseline over an experimental period of about 30 min, implying that there was little coil slippage on the eye. Since we were interested in torsional eye position changes over a period of < 2 sec, any long-term changes would not affect our analysis.

Transient short-term torsional changes due to saccade-induced slippage of the annulus on the conjunctiva or movements of the conjunctiva with respect to the underlying sclera were our main methodological concern. We cannot completely rule out such artifacts. However, we have several indirect indicators that the torsional signal measured during and after saccades is not primarily due to artifacts: (1) Recordings in the same subjects on different days and with a different person mounting the coils showed identical results. (2) Transient torsional movements appeared consistent when evoked by saccades of equal onset and amplitude. (3) Measurements were not affected by whether the annuli were placed with the wires coming out nasally or temporally. (4) Simple visual inspection and video recordings revealed torsional postsaccadic drifts with directions that agreed with the search-coil data. (5) Enright's (1986) results with high-resolution video after centripetal saccades along the horizontal meridian were also in agreement with our data. A more detailed discussion on coil slippage can be found elsewhere (Van Rijn, Van der Steen & Collewijn, 1994).

RESULTS

Definition and characteristics of torsional blips

Our analysis was based on the existence of Listing's law for visual fixations (von Helmholtz, 1867). This law quantitatively describes the amount of eye torsion, during fixations and in the absence of vestibular stimulation, as a function of gaze direction. When expressed in rotation vectors (Haustein, 1989) or quaternions (Westheimer, 1957; Tweed & Vilis, 1987), the corresponding three-dimensional eye positions lie in a plane. We shall call them "Listing's positions". If two Listing's positions are connected by a straight line, all positions on this line are also in Listing's plane. However, if the connecting line is curved, eye positions can either stay in the plane—e.g. during an oblique movement in which the duration of the horizontal and vertical components are unequal—or temporarily leave the plane. Position trajectories with a component orthogonal to Listing's plane would violate Listing's law. It should be emphasized that our analysis was conducted with respect to eye positions. Eye position vectors should not be confused with angular eye velocity vectors, which—due to the non-commutativity of rotations—generally have to tilt out of Listing's plane even with eye positions restricted to Listing's plane (Tweed & Vilis, 1990; Minken *et al.*, 1993).

Listing's law is subject to biological noise: the standard deviation from zero torsion during fixation straight ahead

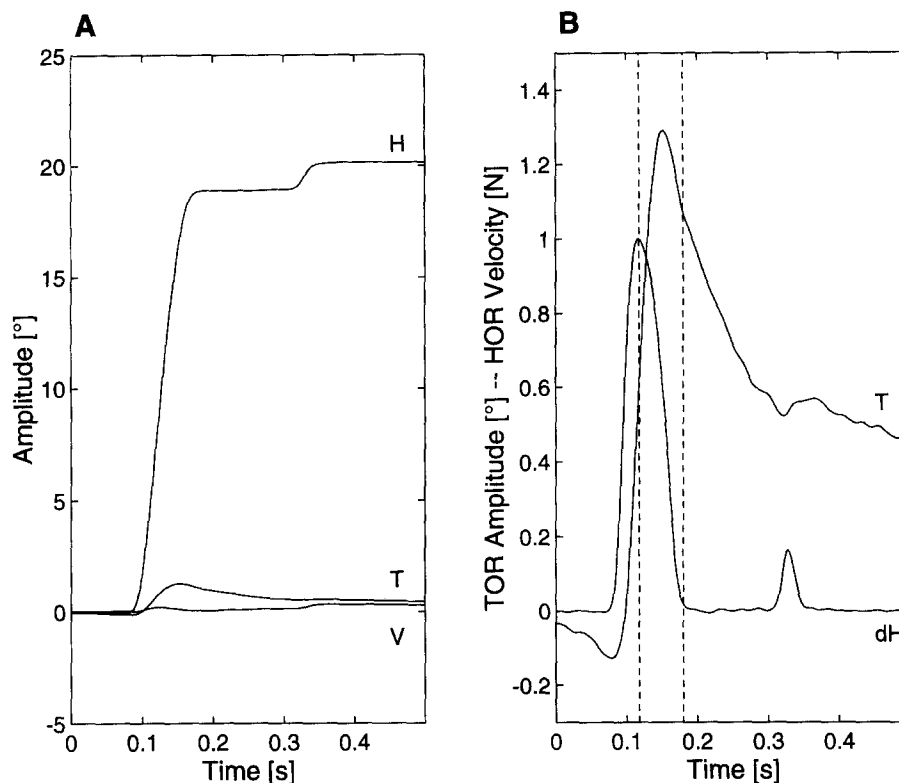


FIGURE 3. Movement components of a typical centrifugal 20 deg leftward saccade at 20 deg elevation plotted against time (right eye of subject DS). (A) Horizontal (H), vertical (V), and torsional (T) eye position components expressed in deg. (B) Same saccade as in (A), but the horizontal component was differentiated and normalized to 1 (dH). The torsional position component (T) in deg is enlarged. Torsional amplitude peaks between the time of saccade peak velocity (left dashed line) and the end of the saccade (right dashed line). The drift back to zero torsion appears biphasic with an initial fast component. The catch-up saccade produces a short interruption of the torsional drift with another small blip.

over a period of 30 sec is about 0.2 deg (Ott, Seidman & Leigh, 1992; Van Rijn *et al.*, 1994), and the standard deviation from a best-fit plane during spontaneous eye movements ranges around 1 deg (Tweed & Vilis, 1990; Straumann, Haslwanter, Hepp-Raymond & Hepp, 1991) (Fig. 1). To analyze the amount of transient torsion during and after each individual saccade, we defined two Listing's positions: the first, 200 msec before the onset of the saccade and the second, 1500 msec after the onset of the saccade. The *torsional deviation* of the saccade trajectory from a straight line between these two Listing's positions was termed "torsional blip" [Fig. 2(A-C)].* According to the right-hand rule, *extorsional blips of the right eye* and *intorsional blips of the left eye* were defined *positive*. Torsional components in single eyes evoked by identical visual stimuli appeared similar with respect to direction, peak amplitude, and profile [Fig. 2(D)].

Torsional blips usually outlasted the end of the horizontal or vertical saccade. The maximal torsional amplitude of the majority of blips was reached after saccadic velocity peaked, but before the end of the saccade (Fig. 3). Drifts back to Listing's plane typically lasted several hundred msec. Sometimes this drift was interrupted by catch-up saccades, when the primary saccade undershot the target. This usually caused another

small blip in the same direction as the primary blip. Because torsion was defined by a movement out of Listing's plane, as determined by eye positions before and after each saccade (see above), this paper does not address the question of torsional hysteresis (Enright, 1986; Ferman *et al.*, 1987).

To obtain representative profiles of torsional blips, we overlaid the 10 saccades evoked by identical visual stimuli and computed the median value for each data point [Fig. 4(A, B)]. This method of representing a population of saccades minimizes the effects of outliers, e.g. due to blinks, and allows one to perform the analysis without a subjective and arbitrary removal of atypical profiles.

Median blip profiles showed considerable differences in amplitude and temporal profile among subjects and sometimes, especially in vertical saccades, differences in the direction of torsional blips [Fig. 4(C, D)]. The extorsional drifts back to Listing's plane that followed intorsional blips tended to be slower than the intorsional drifts following extorsional blips. The peak torsional amplitudes of extorsional blips were usually larger than those of intorsional blips.

Several parameters of torsional blips were considered for correlation with the amplitude of the corresponding horizontal saccade. Parameters that need an independent definition of the end of the blip, like blip duration, area under the blip curve, or blip mean velocity, were not further investigated because, for methodological reasons

*This term was first used by Tweed *et al.* (1994) to stress the transient nature of these movements.

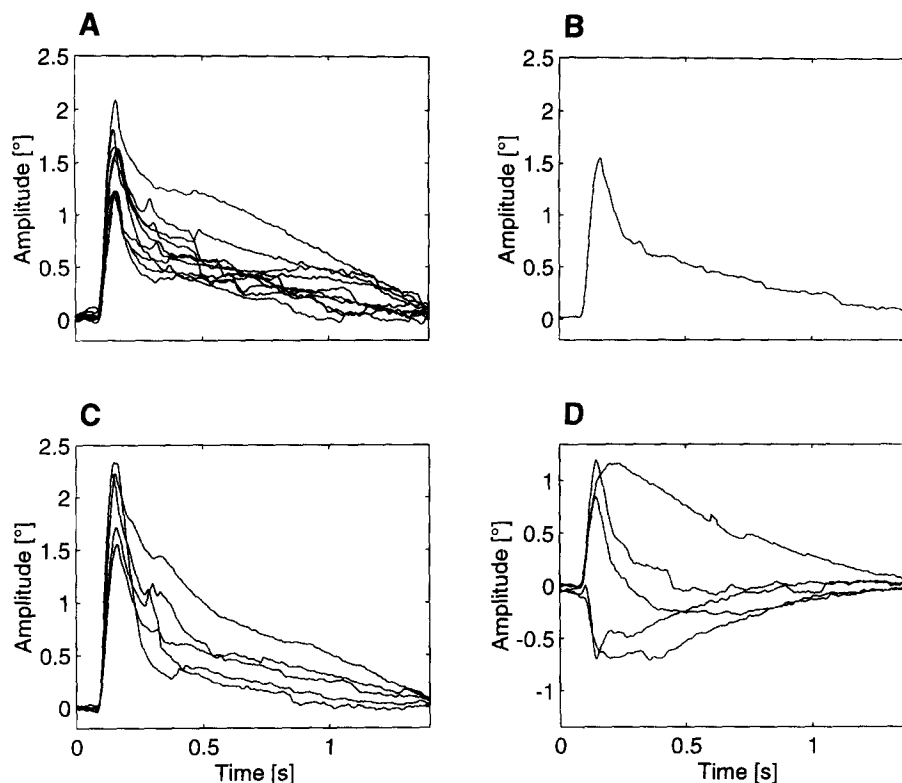


FIGURE 4. Blip overlays and median blips. (A) Example (subject DS): overlay of 10 blips of the right eye during and after horizontal centrifugal rightward saccades at -20 deg elevation, corresponding to 27 deg below primary position in this subject. Saccades were aligned with respect to their onset. (B) For each time interval (0.002 sec) the median of all overlaid saccades [in (A)] was computed. This resulted in the "median blip" depicted. (C) Median blips of all five subjects during and after horizontal centrifugal rightward saccades of the right eye at -20 deg elevation. Note the differences in peak amplitude and backward drift. (D) Median blips of all five subjects during and after 20 deg vertical saccades of the right eye from the horizontal meridian to the same end position as in (C), i.e. downward at 20 deg rightward gaze. Note the variations in blip direction.

(torsional noise during fixations, see above), the torsional curve was forced to zero 1500 msec after saccade onset.

Scatterplots of the peak torsion (ordinate) during centrifugal saccades along the horizontal meridian vs the saccade amplitude (abscissa) suggested an approximately linear relation up to 15 deg saccades with a slight tendency for saturation at larger saccade amplitudes [Paradigm III, e.g. Figure 5(A, B)]. Applying linear regressions to saccades up to 15 deg, y -intercepts were close to zero (range -0.22 to 0.19 deg), but slopes were variable (-0.03 to 0.10). r^2 values ranged between 0.42 and 0.72 .

Torsional blips evoked by horizontal saccades at different elevation

Saccade-evoked torsion. To determine whether the magnitude and direction of torsional blips depended on eye position and saccade direction, we first analyzed blips at different elevations associated with 20 deg horizontal saccades. Saccades were either centrifugal or centripetal with respect to the vertical meridian (Paradigm I). The parameter studied in each subject was the maximal torsional amplitude of the median blip.

For centrifugal horizontal saccades there was an intorsional/extorsional gradient of peak torsional position with changing gaze elevation in all subjects (e.g. Fig. 6; all subjects, Fig. 7). With 20 deg downward

gaze, blips were extorsional for the abducting and intorsional for the adducting eye. With elevation of the eyes, peak blip values of both eyes decreased. The majority of the gradients were such that there was a change of blip direction with further elevation of the eye, i.e. blips in 20 deg upward gaze were, on average, intorsional for the abducting and extorsional for the adducting eye. Torsional blips were generally larger in the hemifield below the straight-ahead position. There was a marked asymmetry between the extorting and intorting eye: the blip of the extorting eye was consistently larger. This finding will be further elaborated in the paragraph on cyclovergence (see below).

Centripetal horizontal saccades (not depicted) showed a similar pattern as centrifugal saccades, i.e. elevation and direction of saccades determined blip direction and magnitude. Peak blip amplitudes, however, were generally smaller for centripetal saccades ($68 \pm 22\%$ of peak amplitudes for centrifugal saccades, $N = 10$ eyes).

Saccade-evoked cyclovergence. Cyclovergence was defined as torsion of the right eye minus torsion of the left eye. Recently, an alternative definition has been proposed in which cyclovergence is the torsional component of the rotation that moves the left eye into the same position as the right eye (Minken, Gielen & Van Gisbergen, 1995). With far targets, however, the Listing's planes of both eyes are roughly parallel, so that both definitions of cyclovergence are equivalent. The patterns

of cyclovergence were similar in all subjects (e.g. Fig. 8; all subjects, Fig. 9). Since the amount of torsion of the extorting eye (positive torsion in the right, negative torsion in the left eye) was larger than the amount of torsion of the intorting eye (see Figs 6 and 7), cyclovergence was always positive. Cyclovergence was symmetric for rightward and leftward saccades (except in subject DS). The amount of cyclovergence varied gradually with vertical gaze; there was usually less cyclovergence in upward gaze. This gradient, however, was less steep than that for torsion of each eye alone. Only in one subject (LE) did cyclovergence change its direction for 20 deg elevation. The patterns associated with centripetal horizontal saccades (not illustrated) were similar, but the amount of cyclovergence was considerably smaller than that of centrifugal saccades ($25 \pm 16\%$ of peak amplitudes for centrifugal saccades, $N = 5$ eye pairs).

The relationship between peak cyclovergence and saccade amplitude for centrifugal saccades along the horizontal meridian (Paradigm III) was linear up to 20 deg amplitudes (r^2 values: 0.65–0.86), which suggests that the non-linearities in torsion that appeared in both eyes for saccades larger than 15 deg canceled each other [e.g. Fig. 5(C)].

Saccade-evoked cycloverision. Cycloverision, the average amount of torsion of both eyes, was also similar in all five subjects: just as the transient torsion of both eyes during and after horizontal saccades was in the same

direction, cycloverision showed the same intorsional/extorsional gradient (cf. Fig. 6). With downward gaze there was positive cycloverision for rightward centrifugal saccades and negative cycloverision for leftward centrifugal saccades. When gaze was further elevated, cycloverision approached zero and, in the majority of cases, changed direction, usually well above the reference position at zero elevation (except subject DS). Cycloverision associated with horizontal centripetal saccades was similar (not shown).

Torsional blips evoked by vertical saccades at different azimuth

The same analysis used for horizontal saccades was repeated for vertical 20 deg saccades away from and toward the horizontal meridian (Paradigm II, data not shown). Blips evoked by vertical saccades were consistent for identical visual stimuli, but showed considerable differences among subjects [Fig. 4(D)] and asymmetries between the right and left eye. Contrary to the results during horizontal saccades, vertical saccades did not produce a clear pattern of blips with changing azimuth. Ex- and intorsional gradients were inconstant. Centrifugal saccades and centripetal saccades in the same vertical direction, however, generally showed the same blip directions.

Like the patterns of peak torsion for individual eyes, cycloverision and cyclovergence during and after vertical saccades were rather idiosyncratic (not shown).

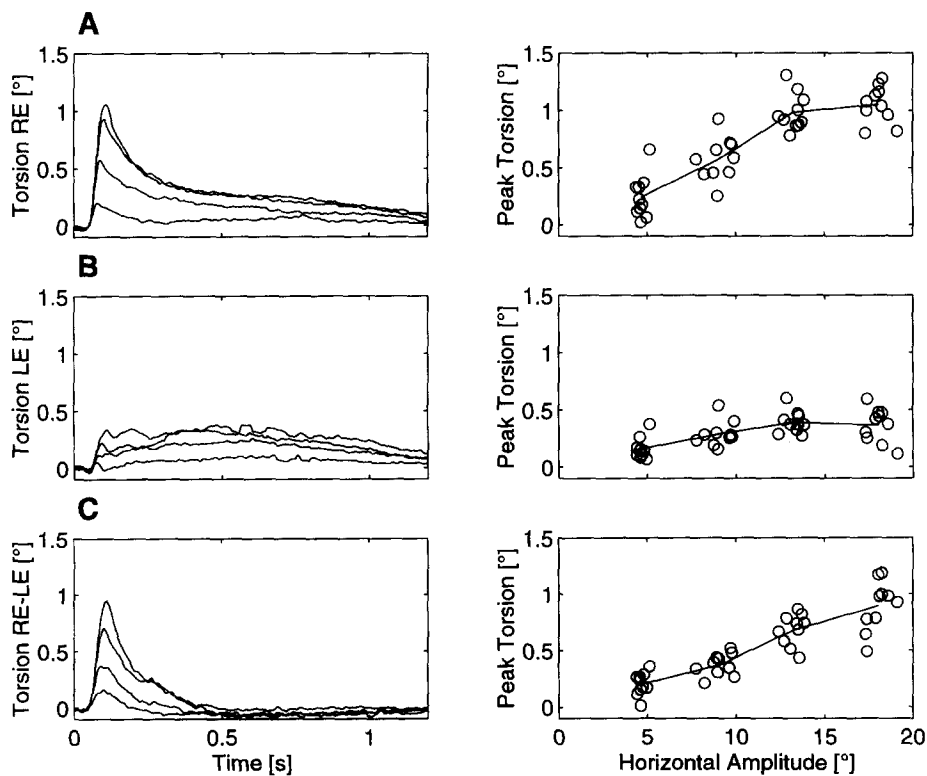


FIGURE 5. Median torsional blips and peak torsional amplitude-saccade amplitude relations. Typical example (subject DS). (A) Left: median blips of the *right eye* associated with rightward centrifugal saccades to 5, 10, 15, and 20 deg eccentric targets along the horizontal meridian. A majority of the saccades to the 20 deg targets undershot the target. Right: peak torsion during individual saccades as a function of saccade amplitude (same data as in the left panel). Mean peak blip amplitudes for the different stimuli are connected. (B) As in (A), but *left eye*. (C) As in (A), but *cyclovergence* (right eye minus left eye).

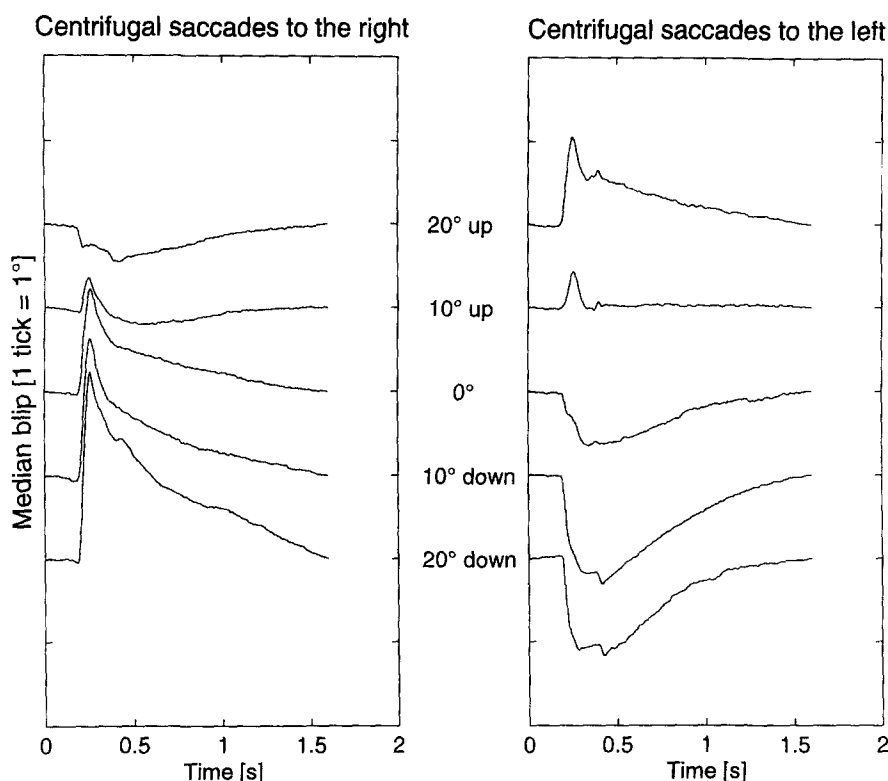


FIGURE 6. Example (subject DS) of median blips of the right eye evoked by 20 deg horizontal centrifugal saccades at different elevations to both sides of the vertical meridian.

For example, three subjects showed negative and two subjects showed positive cyclovergence with upward saccades. Centripetal vertical saccades showed similar idiosyncrasies.

Torsional blips and Listing's law

To statistically analyze whether a number of eye positions in three-dimensional space obey Listing's law, one usually computes the distance of each data point from a best-fit plane through the data cloud. The standard deviation of all distances is a quantitative measure of how well the eye positions are restricted to a plane. To demonstrate that saccade-evoked torsional blips lead to an increase of the standard deviation, we aligned all 200 centrifugal and centripetal saccades in Paradigm I with respect to their saccade onset for each subject [Fig. 10(A)]. For every time interval we then calculated the standard deviation of all 200 eye positions from the plane, which was defined by eye positions 200 msec before and 1500 msec after saccade onset [Fig. 10(B)]. Plotting standard deviations as a function of time showed a profile similar to a typical torsional blip, with a fast rise after saccade onset by about 20% of the baseline, a peak before the end of the saccade, and a slow postsaccadic drift. The postsaccadic standard deviation did not drop to its presaccadic value in all subjects. To test whether the saccade-evoked increase in standard deviation is due to increased scatter or to a transient reorientation of Listing's plane, we determined for each interval of the 200 onset-aligned saccades an individual Listing's plane and computed the corresponding standard deviation [Fig. 10(C)]. This analysis showed the same pattern as the

analysis with a fixation-defined Listing's plane, i.e. an increase of standard deviation during and after horizontal saccades. Hence the increased standard deviation was due to increased scatter.

We also asked whether or not the intorsional/extorsional gradients of blips associated with horizontal saccades at different elevation were related to primary direction as defined by Listing's plane. Specifically, we looked for a relation between the orientation of primary position in the sagittal plane (x - z -plane) and the point where the blip gradients of each eye for rightward and leftward saccades crossed each other (see Fig. 7): the elevation of primary position from the earth-horizontal plane was determined by multiplying the tilt of Listing's plane in the x - z -plane by 2 (Haustein, 1989). To compute the orientation of Listing's plane we took the points of fixation when subjects were sequentially looking at LEDs in the horizontal and vertical direction between fixations (Paradigm IV). LEDs were only 5 deg apart to avoid large torsional blips that would change the amount of torsion during the succeeding period of fixation and therefore could potentially change the determination of Listing's plane. There was no significant correlation between the elevation of primary position and the described blip parameter ($r^2 = 0.025$, $P = 0.66$). However, on average, both primary position and the crossing of blip gradients were above the reference position (straight-ahead gaze).

DISCUSSION

The systematic analysis of horizontal and vertical saccades at different elevation or azimuth respectively,

reveals that their trajectories are generally curved in the torsional direction and not restricted to Listing's plane. Based on visual inspection and video recordings, which show postsaccadic drifts opposite to the direction of saccade-evoked torsion with the dual search coil method, we are confident that our data are not primarily artifacts of annulus slip about the line of sight. Likewise, postsaccadic torsional drifts, recorded after horizontal centrifugal saccades by a high-resolution video system, are compatible with our search coil data (Enright, 1986).

Summary of results

For horizontal saccades we found in all five subjects (including the subject wearing contact lenses) a consistent pattern with the abducting eye extorting and the adducting eye intorting at downward gaze. On average, the maximum of peak torsional amplitudes was between 1 and 2 [Fig. 11(D)]. With increasing elevation of gaze, there was an intorsional/extorsional gradient for the maximal torsion in both eyes, with a tendency for the direction of the blips to reverse with gaze pointing

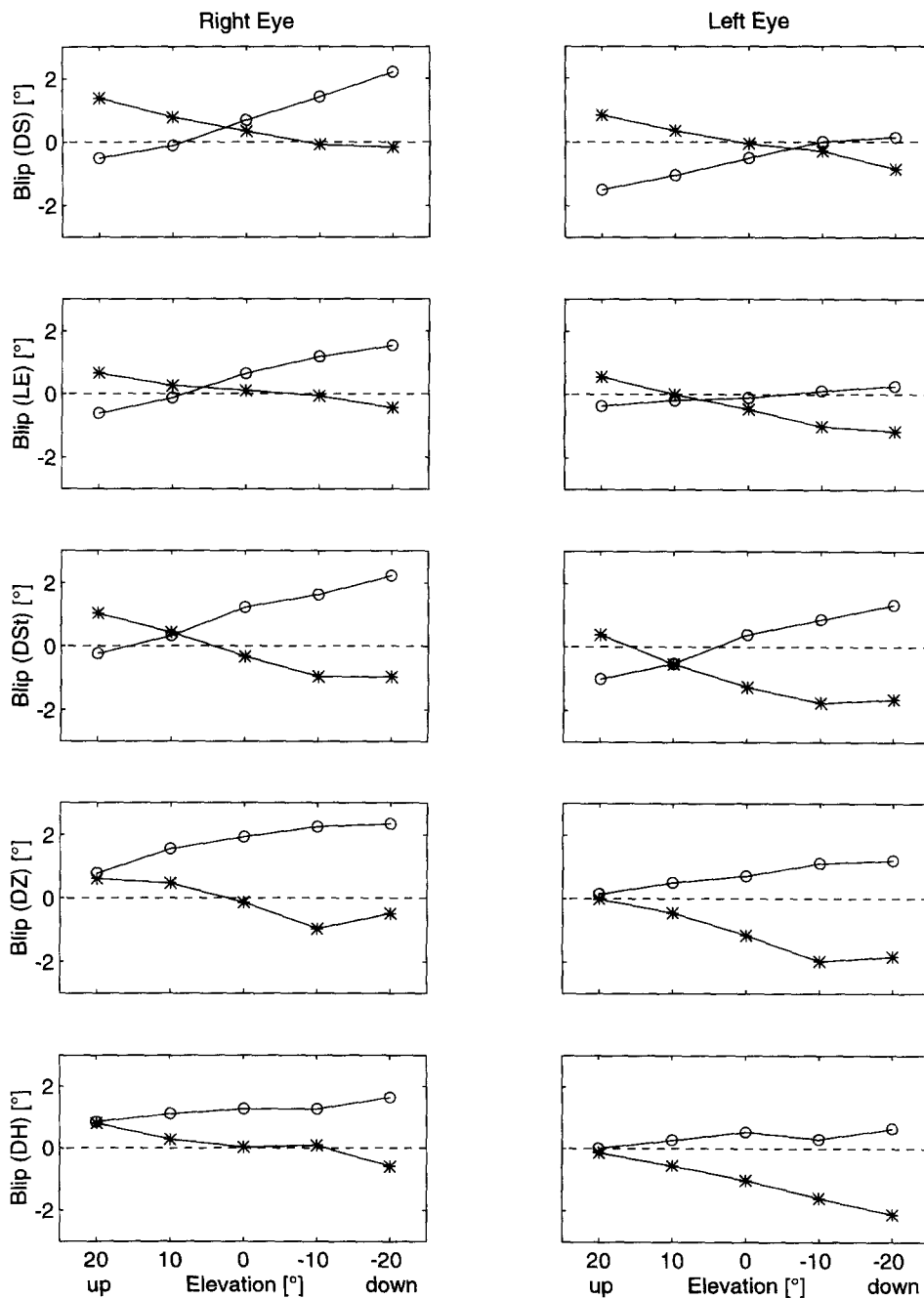


FIGURE 7. Peak values of median blips in degrees evoked by horizontal centrifugal saccades. Each row depicts a different subject. Left column: right eye. Right column: left eye. ○ Blips evoked by horizontal centrifugal saccades to the right. * Blips evoked by horizontal centrifugal saccades to the left. The abscissa denotes the different elevation (positive, upward gaze; negative, downward gaze).

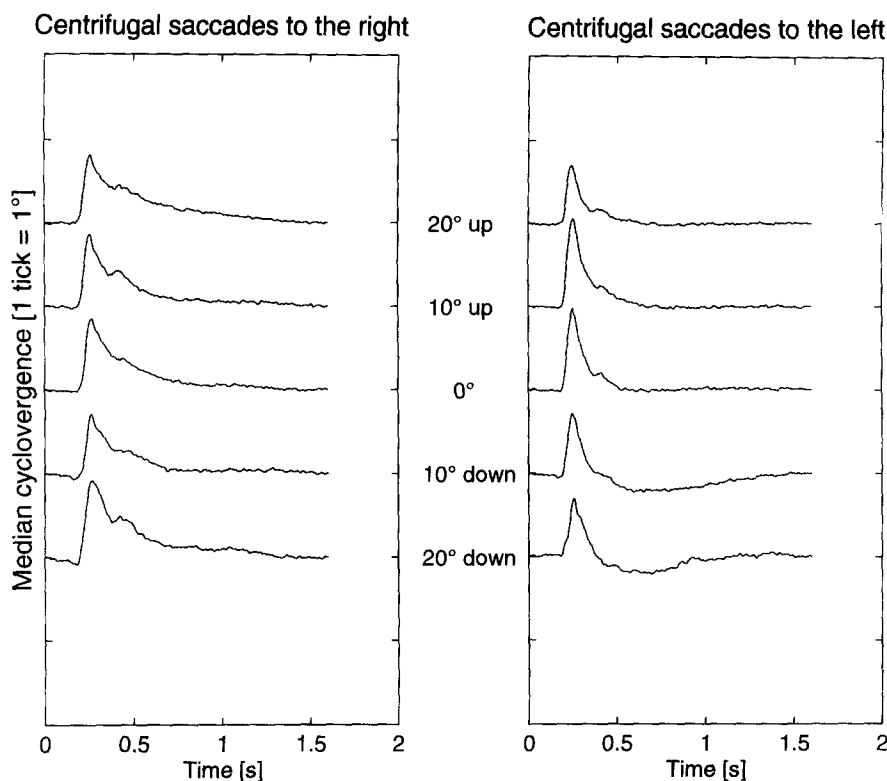


FIGURE 8. Example (subject DS) of median cyclovergence during blips evoked by 20 deg horizontal centrifugal saccades at different elevations to both sides of the vertical meridian. Data from the same saccades as in Fig. 6.

upward. The point of blip direction reversal was generally well above the horizontal meridian. This finding agrees with drift directions reported by Enright (1986) after centripetal saccades along the horizontal meridian to the straight-ahead position.

The torsional movement components were transient—therefore the name torsional blip—but outlasted the end of the saccade by up to several hundred msec. Maximal blip amplitudes increased as a function of saccade amplitude. This relation was roughly linear up to 15 deg amplitudes, but the slope decreased with 20 deg saccades. Since during horizontal saccades the amount of torsion of the extorting eye was always larger than the amount of torsion of the intorting eye, there was a consistent transient positive cyclovergence for saccades in both directions.

Quantitative analysis of how well Listing's law is obeyed during and after horizontal saccades, by computing the distance of data points from Listing's plane as measured during fixations, showed a rapid increase of the corresponding standard deviation after the saccade began. When the saccade finished, this increased standard deviation slowly decayed, but did not reach in all subjects its presaccadic value after 1.5 sec. Analogous analysis with computing individual Listing's planes for each time interval, showed similar time-dependent profiles of standard deviation, i.e. the increased standard deviation during and after saccades is not simply due to transient changes of the orientation of Listing's plane, but deviations of eye position trajectories from a plane.

Torsion evoked by vertical saccades was also stereotyped in each eye, but the magnitude and direction

of torsional blips showed large differences among subjects. Within subjects there were also differences between the paired eyes, with no regular pattern.

Current models of the three-dimensional velocity-to-position integrator

Recent controversies concerning three-dimensional ocular-motor control of saccades include the question whether or not the velocity-to-position integrator takes into account the non-commutativity of rotations in three-dimensional space. Two fundamentally different hypotheses have been proposed.

(1) Tweed and Vilis (1987) pointed out that in order to produce horizontal or vertical saccades that always lie in Listing's plane, the saccadic velocity signal has to be generated with a horizontal, vertical and torsional *angular velocity* component (TV-model). Since a three-dimensional displacement vector that moves the eyes from one position to another not only depends on the *difference vector* between the initial and final positions but also on the actual eye position, neural structures that integrate angular velocity to eye position in Listing's plane must have information on the current orientation of the eye in the orbit.

(2) The TV-model has recently been challenged by Schnabolk and Raphan (1994). Their model (SR-model) is an extension of the original one-dimensional model of Robinson (1975) to three dimensions. The authors propose that the saccadic system need not be concerned about the non-commutativity of three-dimensional rotations; horizontal and vertical pulse-step signals are simply translated into muscle torques, and the

three-dimensional eye position at any gaze direction is defined by the equilibrium of torques. As a consequence of the SR-model, when a saccade is made between two points not connected by a line passing through primary position (non-radial saccades), Listing's law is generally violated and the trajectory leaves Listing's plane. This torsional blip reflects a directional "error" of the saccadic pulse. The error occurs because, in the SR-model, pulse and step are always aligned and lie in Listing's plane. Therefore the angular velocity vector embedded in the pulse drives the eye into an "unwanted" torsional direction.

In an ocular motor plant that perfectly matches the applied pulse-step(-slide) control signal, the TV-model predicts that there should be no torsional blips at all. The appearance of blips, however, would not *a priori* negate

the TV-model since the brainstem could still encode saccades in Listing's plane with "correct" pulses reflecting the non-commutativity of three-dimensional rotations. Torsional blips might appear due to a central underestimation of torsional plant viscosity, e.g. Tweed *et al.* (1994).

In the SR-model, the directions and magnitudes of torsional blips show a specific pattern: they should only be evoked by non-radial saccades, increase in amplitude with increasing eccentricities of saccade on- and offset positions, and their sign should be diagonally symmetrical. For example, horizontal saccades to the temporal side during downward gaze and to the nasal side during upward gaze would always show extorsional blips. The dynamics of a blip out of Listing's plane in the SR-model

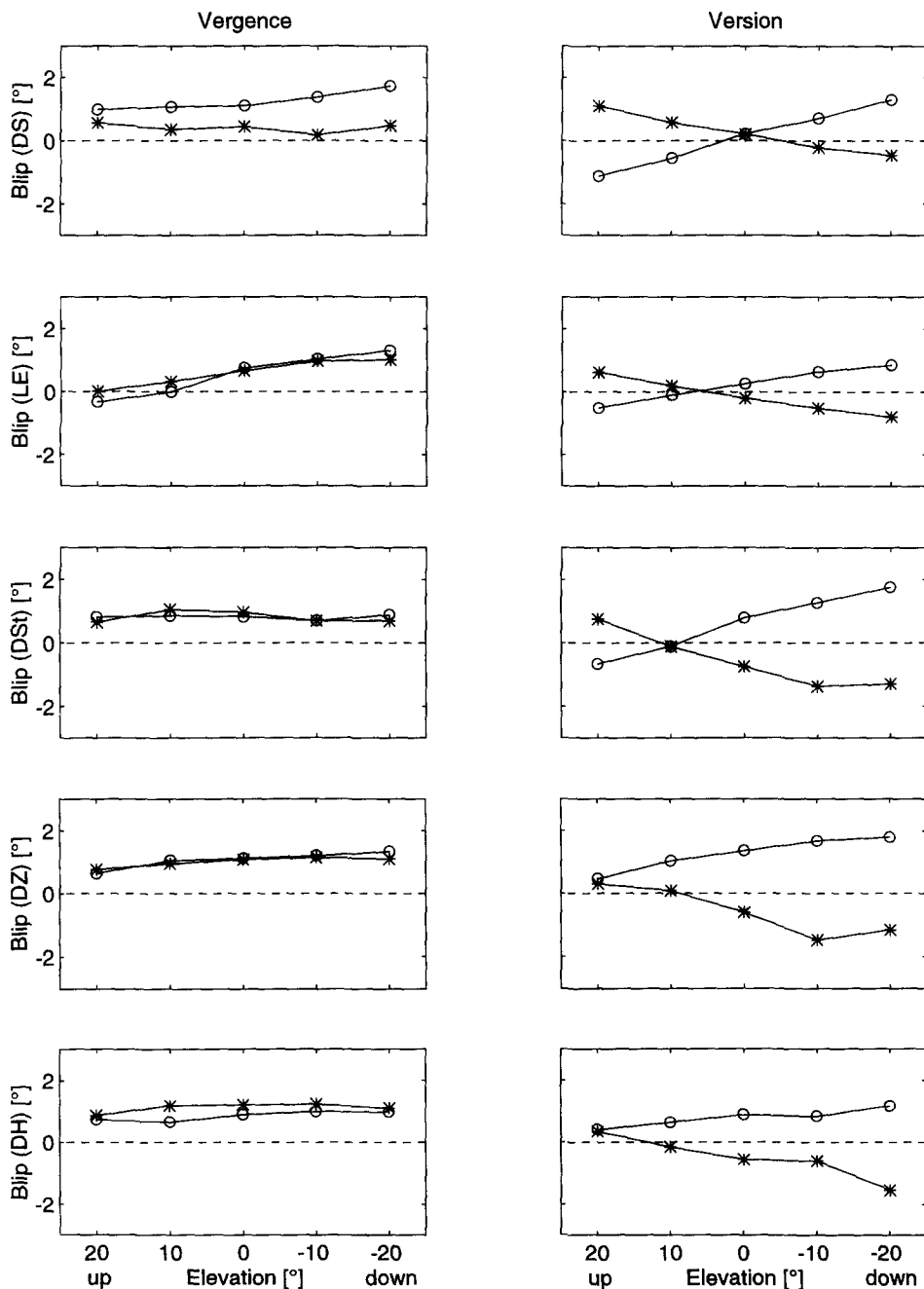


FIGURE 9. Same database as in Fig. 7. Corresponding peak cyclovergence (right eye torsion minus left eye torsion) and peak cyclovergence (average torsion) values during and after horizontal centrifugal saccades.

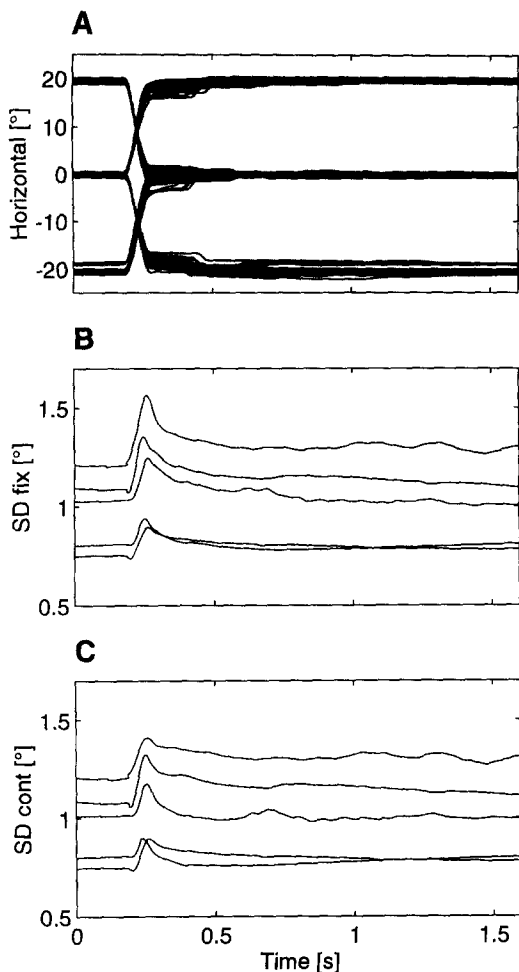


FIGURE 10. Standard deviation of the distance of eye positions from Listing's plane before, during, and after horizontal saccades (Paradigm I). (A) Example (subject LE): all 200 centrifugal and centripetal saccades are aligned at their onset. (B) Temporal profiles of standard deviation in all five subjects. The standard deviation is computed with respect to the best-fit plane of data points 200 msec before and 1500 msec after the saccades. (C) As in (B), but the standard deviation is computed with respect to the best-fit plane of data points in each individual time interval.

should reflect the missing torsional component of the pulse, filtered by the plant mechanics. Therefore the peak amplitude of the blip should be closely related to the gain of the premotor pulse component.

Compatibility of three-dimensional integrator models with torsional blip data

Our data are not perfectly compatible with either model. Judged on the bases of the original TV-model, saccades behave in a "kinematically incorrect" way, i.e. they generally leave Listing's plane. One could argue that the neural output correctly encodes saccades in Listing's plane but that a neuro-mechanical mismatch is responsible for the observed transient torsional movements. But why should the brain make the effort to perform a complicated vector multiplication at the level of the neural integrator if the effector (i.e. the mechanical plant) does not reflect the computed trajectories? For

example, why should the pulse underestimate (or overestimate) torsional plant viscosity?

The original SR-model correctly predicts the direction of torsional blips produced by horizontal saccades (see Figs 6 and 7). The predicted blips, though, are more than twice as large as those actually measured in our subjects. We conjecture that this shortcoming is mainly due to the dynamic parameters of the saccade model that the authors applied. They used a simplified linear burst command lasting 50 msec, a pulse-step neural integrator with a pulse gain of 0.1389, and a second-order plant with two poles but no zero (Table 1). We simulated the SR-model with a more realistic representation of the saccadic system's dynamic parameters using a non-linear burst generator, a pulse-slide-step input, and a second-order plant with one zero (Goldstein, 1983; Optican & Miles, 1985; Zee, Fitzgibbon & Optican, 1992) (Table 1). Since a second-order plant with one zero calls for a substantially lower pulse gain (in our simulation: 0.06), the peak amplitude of the torsional blip, which is closely related to the pulse gain, is approximately cut in half and falls in the range of our data for horizontal saccades (Fig. 11). If we apply the more realistic dynamic representation of the saccadic system, the SR-model also predicts a saturation tendency for the relation between peak torsion and saccade amplitude, which is in agreement with our data [Fig. 11(C), cf. Fig. 5]. This property reflects the non-linearity of the burst signal. The simplified linear burst signal of the original SR-model, however, produces a linear peak blip amplitude/saccade amplitude relation, which also does not conform with the data. In the simulation, we did not try to exactly match the time constants of the plant to actual durations of the postsaccadic torsional drifts. Its purpose was rather to show that the peak torsional deviations predicted by the SR-model critically depends on the model's dynamic representation of the saccadic system.

Two findings could not be simulated by changing the dynamic parameters of the saccadic system in the SR-model.

(1) We did not find a tight relation between the elevation at which the blip reverses direction and the primary position as defined by Listing's law. Likewise, there was no specific gaze elevation producing a minimal transient cyclovergence evoked by saccades to and from primary position. These findings raise the question whether the torsional blips evoked by horizontal saccades indeed reflect properties of the three-dimensional integrator or rather are due to changing pulling directions of the eye muscles related to different amounts of muscle sideslip with changing elevation of gaze (Miller & Demer, 1994). In addition, different distribution of saccadic innervation between agonists and antagonists for the pulse, step, and slide components might enhance geometrical gaze-dependent variations of muscle pulling directions.

(2) Magnitude and directions of blips evoked by *vertical saccades* were idiosyncratic and generally did not show an intorsional/extorsional gradient with changing azimuth. One reason for the latter result could be that vertical

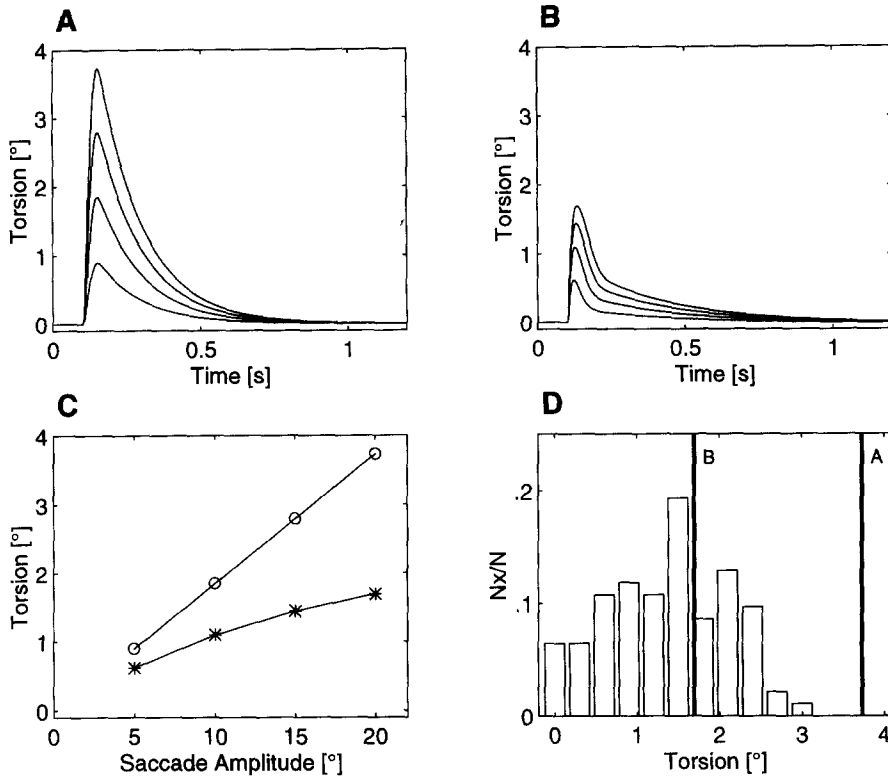


FIGURE 11. Simulations of torsional blips evoked by the SR-model with the two different sets of dynamic parameters listed in Table 1. Leftward horizontal 5, 10, 15, and 20 deg saccades at 30 deg downward gaze. (A) Simulations with the original dynamic parameters of the SR-model (see Table 1). (B) Simulations with the modified dynamic parameters (see Table 1). (C) Relation between peak torsional deviation and saccade amplitude. \circ Original parameters; \ast Modified parameters. (D) Frequency (Nx/N) of peak torsional deviations during horizontal abducting and adducting saccades at 30 deg downward gaze from the zero-crossing of the intorsional/extorsional gradient (see Fig. 7). Right eye data of the five subjects are pooled ($N = 100$). Vertical lines denote the prediction of the SR-model with the original (A) and the modified dynamic parameters (B). In the t -test, the data is significantly ($P < 0.01$) different from (A) but not from (B).

saccades are produced by two pairs of agonists/antagonists while for horizontal saccades only one pair of muscles is acting. Anatomical variations of the four vertical muscles, variations in the on-directions of vertical

motoneurons (Hepp & Henn, 1985), and small delays in innervation could also produce transient torsional eye movements that would mask or exaggerate torsional blips produced by the velocity-to-position integrator.

TABLE 1. Dynamic parameters of the saccadic system used in the simulation of the SR-model in Laplace notation

	Original parameters	Modified parameters
Burst	$t < t_0: x(t) = 0$ $t_0 \leq t < (t_0 + d): x(t) = \Delta C - (t - t_0) \cdot \frac{\Delta C}{d}$ $t \geq (t_0 + d): x(t) = 0$ $d = 0.05 \text{ s}$	 $SBN: yR = 400 \cdot (1 - e^{-(5+1)/10})$
Step	$\frac{30}{(30s + 1)}$	$\frac{20}{(20s + 1)}$
Pulse	0.1389	0.06
Slide		$\frac{0.165}{(0.08s + 1)}$
Plant	$\frac{1}{(0.15s + 1)} \cdot \frac{1}{(0.007s + 1)}$	$\frac{(0.08s + 1)}{(0.3s + 1)} \cdot \frac{1}{(0.01s + 1)}$

The left column lists the values used in the original SR-model (Schnabolk & Raphan, 1994). The right column shows the values with which the SR-model produced peak torsional blip amplitudes that resembled more closely the experimental data. SBN, short-lead burst neurons; ΔC , desired eye position change; d , burst duration; RI, resettable integrator.

Possible mechanisms of saccade-evoked cyclovergence

By introducing different mechanical time constants for in- and extorsion, with the time constant of return to zero torsion from extorsion being less than half that from intorsion, as described by Seidman, Leigh, Tomsak, Grant and Dell'Osso (1995), the SR-model produces transient cyclovergence with any plant model. We do not think, however, that this difference in torsional time constant is solely responsible for the transient cyclovergence: the gaze elevation at which blip directions change from intorsional to extorsional is different for abducting and abduction saccades, which also contributes to the difference in torsion between the right and left eye. Whether saccade-evoked cyclovergence has a special functional significance or is just an epiphenomenon of asymmetrical torsional blips of the abducting and adducting eyes remains unclear.

Conclusions

Based on these considerations and our ignorance of the fine but important anatomical and physiological details of the ocular motor plant, we do not yet know if the velocity-to-position integrator does or must mirror the non-commutativity of three-dimensional rotations. The occurrence of torsional blips cannot *a priori* falsify any of the current models since the blips could reflect geometrical properties of the plant, like gaze-dependent muscle sideslip, and not properties of the three-dimensional integrator. The crucial question is whether the burst neurons projecting to the integrator neurons encode angular velocity (compatible with the TV-model) or coordinate velocity, which is simply the derivative of eye position (compatible with the SR-model). This issue will probably only be settled on the bases of a careful statistical analysis of firing patterns for saccades of equal direction but different onset positions in large populations of burst neurons as found in the paramedian pontine reticular formation and the rostral interstitial nucleus of the MLF (Hepp, 1990).

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