RESEARCH ARTICLE

P. Bruno · A.V. Van den Berg

Torsion during saccades between tertiary positions

Abstract We systematically studied the effect of saccade direction and saccade starting position on the velocity profile of the saccade. Saccades were made between targets placed at optical infinity by dichoptic presentation. This arrangement was chosen to evoke conjugate eye movements. Eye movements were recorded binocularly, including torsion. Horizontal and vertical movements of the eyes are strongly correlated ($r \geq 0.95$) during the saccade, torsional movements are much less so ($r \simeq 0.67$). Listing's law would predict that the three-dimensional versional velocity of the eye would be located in a plane that is tilted out of Listing's plane by an amount that depends on the saccade's starting position (half angle rule). Taking together all saccades that started from the same initial position a plane could be fitted through the velocity vectors. However, this plane was tilted less relative to Listing's plane than predicted by the half angle rule. The deviation was especially large for the yaw component of the tilt (56% of predicted). For the pitch component the prediction was better (81% of predicted). In addition, we find that the torsional velocity during the fast "intrasaccadic" part of the motion can be unequal in the two eyes. The implications for three-dimensional models of saccadic control are discussed.

Key words Ocular torsion · Angular velocity · Saccades · Version · Velocity planes

Introduction

Eye movements are much more restricted in the torsional than in the horizontal and vertical directions. At least for

P. Bruno · A.V. Van den Berg
Department of Physiology I, Faculty of Medicine,
Erasmus University Rotterdam,
Rotterdam, The Netherlands

P. Bruno (✉)
Dipartimento di Elettrotecnica, Elettronica ed Informatica,
University of Trieste, Via Valerio 10,
I-34127 Trieste, Italy
Tel.: +39-40-6767120, Fax: +39-40-6763460,
e-mail: bruno@gnbts.univ.trieste.it

voluntary fixations of distant targets with the head upright, ocular torsion depends on the gaze direction. This constraint is known as Listing's law (Helmholtz 1867). Listing's law states that the eye rotates about axes that are located in a plane when a single starting (or reference) position is considered. This plane is called the displacement plane and its orientation depends on the reference position. That reference position for which the displacement plane is perpendicular to the gaze direction is called the primary position, and the associated plane is called Listing's plane. Listing's constraint on eye orientation implies a similar constraint for the angular velocity of the eye. In this case all the eye velocity vectors that carry the eye away from the same starting position are located in a plane: the velocity plane (Tweed et al. 1990). Its orientation depends on the eye position (Helmholz 1867; Tweed and Vilis 1987, 1990; Van den Berg 1995). The velocity vectors tilt out of Listing's plane by an angle equal to half the angle of eccentricity of the starting position; thus, all saccades starting from the same eye position carry a "signature" (in the torsional velocity) that is determined by that starting position. This result is also known as the half angle rule.

Saccadic eye movements are the most demanding movements in terms of neural control since they need to overcome the plant's dynamic limitations (Robinson 1973). Their control originates in a possibly two-dimensional (Van Opstal et al. 1991) signal for desired gaze displacement, which is converted into a velocity like neural (burst) activity. Because Listing's law prescribes a direct relation between the torsional and the horizontal and vertical components of the eye velocity, the most demanding test of that law would require that the instantaneous torsional velocity during a saccade depends linearly on the other velocity components. To date such an analysis has not been done. Previous studies have established that the half angle rule holds to a good approximation at the instant of the peak velocity of the saccade (Tweed and Vilis 1990). Here we wish to go one step further and analyse the relation between the velocity components throughout the saccadic trajectory. In addition, we extended previous

studies by recording the saccades binocularly. We used dichoptic stimuli to simulate targets at optical infinity. Primary directions for fixation of such targets are not always parallel and may be exodeviated by 9 deg (Bruno and Van den Berg 1997). This means that in many cases the torsional states of the eyes are not identical although the lines of sight are parallel. Transient cyclovergence during the saccade has been reported by Straumann et al. (1995). Thus, it seems possible that horizontal and vertical components of the saccades are strongly correlated (as found by Bains et al. 1992) but not the torsional movements. A second objective of this study, then, was to describe the three-dimensional (3D) correlation of the eyes' velocities during saccades.

Recently, several studies have investigated the validity of Listing's law when the eyes converge (Mok et al. 1992; Van Rijn and Van den Berg 1993; Minken et al. 1995; Bruno and Van den Berg 1997). All studies agree that during convergence the eyes intort in upgaze and extort in down gaze and that cyclovergence is linearly related to the product of convergence and elevation of the eyes, but different amounts of cyclovergence have been reported. A recently proposed kinematic scheme (Van den Berg 1995) for eye displacements can handle such variation in the amount of convergence-linked cyclovergence. This kinematic scheme was the starting point of our study. Following Hering (1868) the control of the eye displacements can be split into two components: version (the average of the two eyes' positions) and vergence (the difference). Each component is subject to certain restrictions. According to this scheme the versional component of the velocity vectors would follow the half angle rule even when the primary positions of the two eyes are not aligned. Deviations from Listing's law can possibly be captured by parametric adjustments of the scheme. If so, this may provide valuable information on the implementation of Listing's law. Such a result might, for example, be taken to mean that the torsional component of the saccade is a (possibly neural) derivative of the horizontal and vertical bursters' activity and that it is not independently controlled.

Part of this work has been published in abstract form (Bruno and Van den Berg 1995).

Methods

Procedures

The 3D positions of both eyes were recorded at 500 Hz with the search coil technique (Robinson 1963; Collewijn et al. 1975; Ferman et al. 1987a), using a two-magnetic-field system from Skalar. Subjects were seated at the centre of the coil frame (a cube of 70 cm) with the head upright and facing forward, restrained by a biteboard. Each eye's position relative to the projection screen was measured by means of a computerised trigonometric procedure (Van den Berg 1996). This allows one to determine the angle between the interocular axis and the projection screen. We assumed that the head pointing direction (the head antero-posterior axis) was orthogonal to the interocular axis. We tried to keep the head pointing close to the centre of the screen by correcting head position on the basis of the estimated orientation of the interocular axis. Small differences between the left and right eye's distance to the screen have not been corrected, allowing the head to point a few degrees out of centre. The trigonometric procedure also gave us the lateral displacement of each eye relative to the screen centre. We used these distances to set the visual (dichoptic) stimulation at optical infinity.

Experimental paradigms

Visual stimuli were back-projected (Sony VPH1270) onto a translucent flat screen placed at 1.5 m in front of the subject and parallel with the coil frame. Alternate frames generated by the graphics computer (SGI IRIS 4D/210 GTX) were presented to the left and to the right eye by means of shutter spectacles. The frame rate for each eye was 60 Hz. The dichoptic presentation allowed us to show targets at optical infinity by shifting the left and right eye images relative to one another by the interocular distance. The target's direction was thus identical for the two eyes. Each target consisted of a red disc (2 deg diameter) on a dark background. On each disc a vertical and a horizontal line (0.1 deg width) were superimposed forming a black cross. The targets were presented in the dark.

The subjects were seated in the coil frame and faced the screen (more than 60 deg wide in the horizontal and vertical directions) in an otherwise dark room. Each recording session started with a sequence of brief (2-s) eccentric fixations (eight targets arranged on a square of 20 deg) at optical infinity. These fixations were used to estimate the primary position. We divided the screen into four quadrants: right-up (RU), right-down (RD), left-up (LU) and left-down (LD). For each quadrant nine targets were used, arranged as a hub with eight spokes. The hub was always located at 22.6 deg eccentricity (16 deg up or down and 16 deg left or right) of the screen's centre and the other eight targets were located at the circumference of a circle with a radius of 12 deg. The eight targets were arranged at 45-deg intervals along the circle and included vertical and horizontal directions (Fig. 1 shows this arrangement for the RU quadrant). In every trial only the hub and one of the eccentric targets were visible (Fig. 1, target pair 2). Saccades were made between these two targets at a fixed rate (0.6 Hz), which was indicated to the subject by a metronome. About 20 saccades were collected in each 40 s trial. We collected about 640 saccades for each subject: 320 outward saccades (movements that started from the hub) and 320 inward saccades (movements towards the hub). Data were usually collected in two experimental sessions. For one subject (HS) we obtained the data for only three quadrants. To counter the effects of coil slip, each saccadic sequence was preceded by a brief fixation of a dichoptically presented target straight ahead (Fig. 1, target 1). Each dichoptic image of this central target was located just in front of each eye in a direction perpendicular to the revolving magnetic field.

Subjects

We tested four volunteers with normal stereoscopic vision. One myopic (WD) subject wore contact lenses during the experiment. Subject PB showed a small esophoria on clinical tests.

Data analysis

Before each experiment we performed an in vitro calibration to determine the sensitivity of each coil and the relative orientation of the direction and torsion coils for each composite annulus. Care was taken to place the annuli onto the eyes with minimal offset when the subject was gazing straight ahead. We recorded eye position in Fick's coordinates with the following convention: positive rotations were left, down and clockwise (upper pole of the right eye towards the right) rotations. The torsional signals were corrected for pseudo-torsion related to vertical movements due to the non-orthogonality of the torsional and directional coils (Bruno and Van den Berg 1997).

All the signals were linearised and converted into rotation vectors (Haustein 1989). The rotation vector $\mathbf{r} = |r_x, r_y, r_z|$ is a 3D vector

Fig. 1 The experimental paradigm. Targets were dichoptically presented on the screen. The left and the right eye images were horizontally shifted on the screen according to the interocular distance. In this figure the targets for the left eye are shown as *dark targets* and the targets for the right eye as *white targets*. The real stimuli consisted of red discs on a dark background for both eyes. On each disc a cross was superimposed. For calibration purposes initially only the central target (labelled *1*) appeared [in front of the left (*L*) and the right (*R*) eyes]. After a 2-s fixation of this target it was switched off and two (for each eye) eccentric targets (labelled *2*) appeared. They were both located within one quadrant of the screen and elicited saccades along one of the eight principal directions (as indicated by the *triangles*). For each quadrant we selected one eccentric position (at 16 deg up or down and left or right from the screen's centre). From that position we measured saccades along eight different directions and fixed amplitude (12 deg)
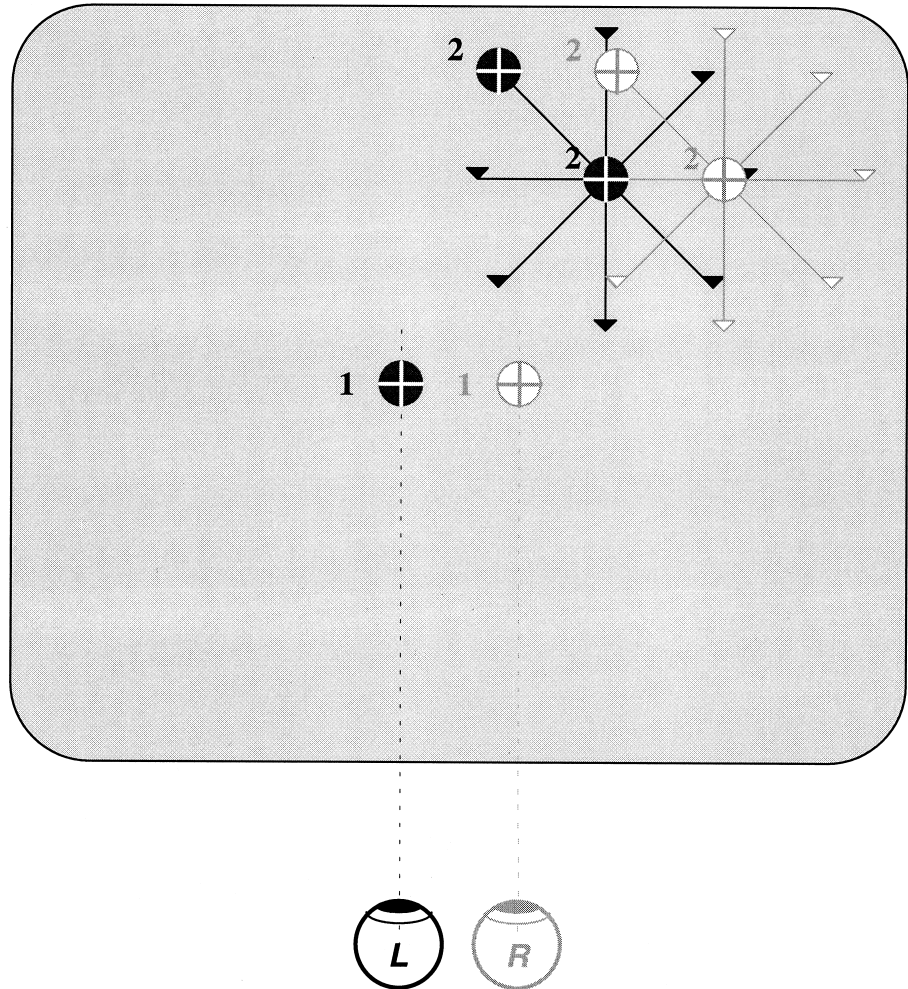
to characterise the eye's orientation. It does so by specification of the direction of the rotation axis and the amount of rotation about that axis that is required to carry the eye from the reference orientation to the eye orientation to be specified. The rotation vector's forward component or the component perpendicular to the magnetic field (r_x) specifies eye torsion, r_y or the horizontal component parallel to the screen specifies the vertical eye position while r_z (perpendicular to r_x and r_y) specifies the horizontal eye position. The rotation vector is aligned with the axis of rotation. Its magnitude equals the tangent of half the turn angle about the axis. The reference orientation is determined at the outset by the measurement system and corresponds to the direction perpendicular to the revolving magnetic field (and zero output for the torsion coil). At later stages in the analysis we changed the reference frame (Haslwanter 1995) so that the reference direction corresponded to the primary direction.

From the fixation of the reference target we determined the coil's misalignment. We mathematically corrected for the offset orientation of the coil using a procedure (3D counter-rotation) described in Haslwanter (1995). Conceptually the procedure does not differ from the one used by Ferman et al. (1987a). Moreover, from the fixation data we estimated the displacement planes and the primary direction (PP) (see, for example, Haslwanter 1995) for each eye as well as for the versional signal: the average of the left and right eye rotation vectors. We expressed the rotation vector of each eye relative to the versional primary position by rotation of the reference frame. This was done because the versional primary position is invariant for vergence state (Van Rijn and Van den Berg 1993).

Subsequently, we evaluated the angular velocity vector by means of the following discrete symmetric filter:

$$\Omega_t \simeq \frac{\dfrac{(\mathbf{r}_{t+\Delta t} - \mathbf{r}_{t-\Delta t} + \mathbf{r}_{t-\Delta t} \times \mathbf{r}_{t+\Delta t})}{1 + \mathbf{r}_{t-\Delta t} \cdot \mathbf{r}_{t+\Delta t}}}{2 \cdot \Delta t}.$$

where **r** is the rotation vector describing eye position at the time t, Ω is the angular velocity, $\times$ the vector cross product, "·" the inner product and Δt the sampling interval. Subsequently, we computed the vergence and the versional components of eye rotations in terms of position and velocity. The vergence is half the difference between left and right eye vectors. The versional component is the average vector of left and right eye vectors (Van Rijn and Van den Berg 1993).

Saccades were detected on the basis of an angular velocity criterion (those samples were selected for which the magnitude of the eye velocity vector exceeded 10 deg/s). For each trial we split the saccades in two groups according to the direction (away or towards the hub). We computed the mean trace (average) and the variability (standard deviations) for both groups. Summary data refer to these average signals. Position and velocity signals are presented in terms of vector components after conversion to degrees. Rotations expressed in degrees are positive to the right, up and for extorsion (intorsion) of the right (left) eye.

The kinematic description

For a given rotation $\mathbf{r} = |r_x, r_y, r_z|$ Listing's law (LL) imposes $r_x = 0$. (Haustein 1989). Following the extension of LL proposed by Van Rijn and Van den Berg (1993) the left ($\mathbf{r}^l$) and the right ($\mathbf{r}^r$) eye rotation can be expressed in terms of vergence ($\mathbf{g} = (\mathbf{r}^l - \mathbf{r}^r)/2$) and ver-
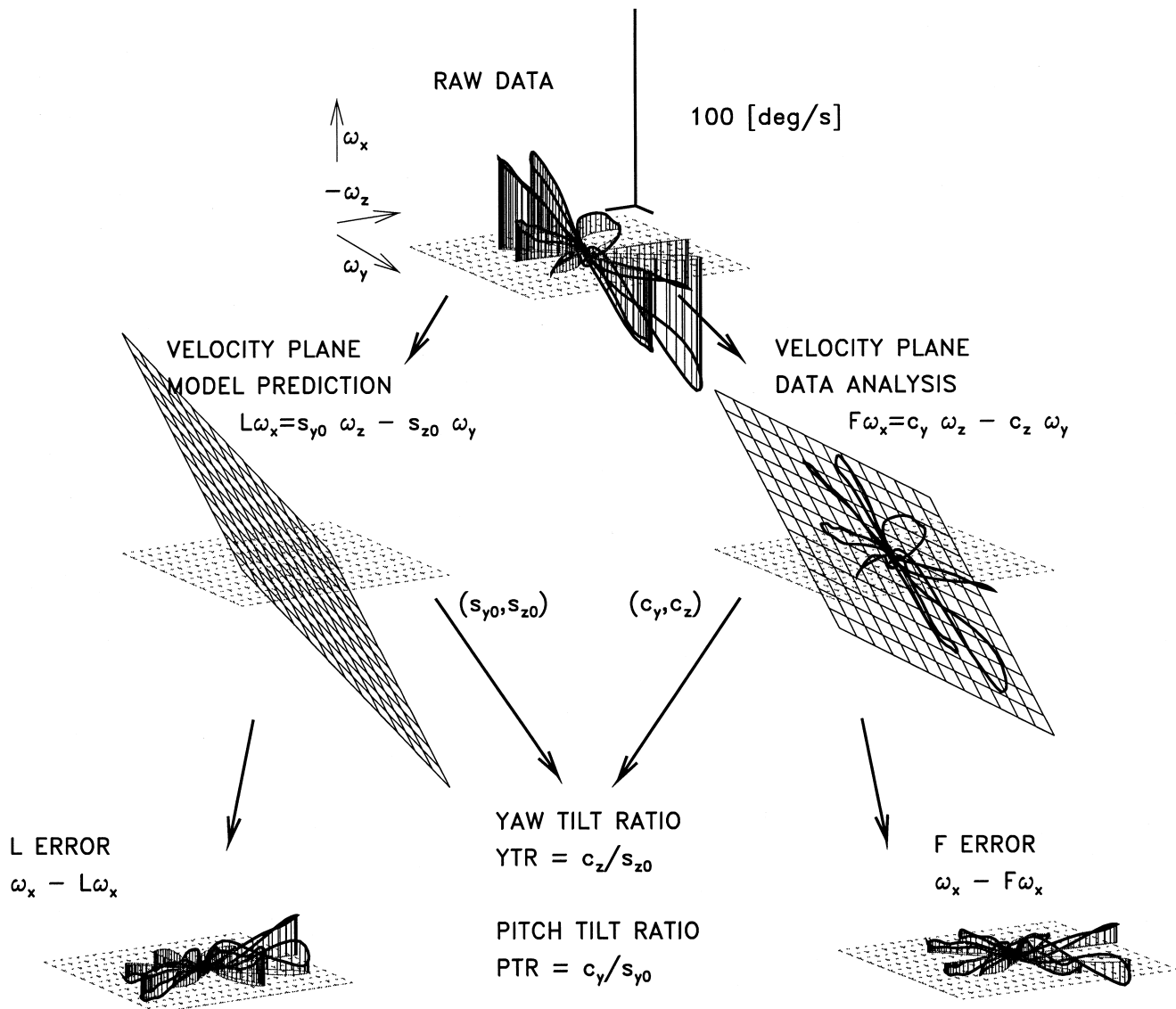
Fig. 2 Data analysis for one quadrant. The *uppermost panel* shows the relationship among the three components – torsional (ω_x), vertical (ω_y) and horizontal (ω_z) – of the versional angular velocity during saccades. The data set consists of saccades of eight different directions but starting from the same tertiary position (left-down quadrant) of subject WD. In all panels torsion is magnified as indicated by the tripod length (100 deg/s for all directions). The torsional component of the angular velocity vector (ω_x) was compared with the torsional velocity predicted by Listing's law. This prediction specifies a linear relationship between torsion and the other two angular velocity components. Thus, the motion trajectories of these saccades should lie in a plane (the velocity plane, $L\omega_x$, with the planes linear coefficients determined by that starting position (s_{y0}, s_{z0}). The *middle panel on the left* shows $L\omega_x$. The data analysis confirmed a planar distribution ($F\omega_x$) of torsion (*middle panel on the right*) by linear regression of the torsional velocity components versus horizontal and vertical velocity components. The orientation of the plane $F\omega_x$ (given by c_y and c_z) was compared with the orientation of $L\omega_x$ (s_{y0}, s_{z0}) to derive the YTR (c_z/s_{z0}) and PTR (c_y/s_{y0}) parameters. The *bottom two graphs* show the errors that remain between the observed data and the linear fits ($L\omega_x$ or $F\omega_x$)

sion ($\mathbf{s} = (\mathbf{r}^l + \mathbf{r}^r)/2$) in the following way: $\mathbf{r}^{l,r} = \mathbf{s} \pm \mathbf{g}$. Of the $2 \times 3 = 6$ components of version and vergence 3 are constrained [$g_x = f(s_y, g_z)$, and $s_x = g_y = 0$] and 3 are free (s_y, s_z and g_z). When the eye movement starts from a position other than the primary position, the axis about which the eye turns is not generally located in Listing's plane. The change in eye position can be described by a displacement vector Δr. The displacement vector is linked to the initial ($\mathbf{r}_1$) and final ($\mathbf{r}_2$) eye position as follows:

$$\Delta \mathbf{r} = \frac{\mathbf{r}_2 - \mathbf{r}_1 + \mathbf{r}_1 \times \mathbf{r}_2}{1 + \mathbf{r}_1 \cdot \mathbf{r}_2}.$$

Also the displacement vectors for the left ($\Delta \mathbf{r}^l$) and right ($\Delta \mathbf{r}^r$) eye can be described by version ($\Delta \mathbf{s}$) and vergence ($\Delta \mathbf{g}$): $\Delta \mathbf{r}^{l,r} = \Delta \mathbf{s} \pm \Delta \mathbf{g}$. The dependent components are Δg_x, Δs_x and Δg_y; the independent components are Δs_y, Δs_z and Δg_z. The following formula restricts eye displacements in such a way that eye positions follow Van Rijn and Van den Berg's extension of LL (Van den Berg 1995). The equation is derived neglecting third- and higher-order terms.

$$\Delta \mathbf{r}^{l,r} = \begin{vmatrix} s_y \Delta s_z - s_z \Delta s_y \\ \Delta s_y \\ \Delta s_z \end{vmatrix} \pm \begin{vmatrix} \Delta g_z \begin{pmatrix} 3 s_y + 2 \Delta s_y \\ 0 \\ 1 \end{pmatrix} + \begin{pmatrix} \Delta s_y g_z \\ -2 s_y g_z \Delta s_z \\ 0 \end{pmatrix} \end{vmatrix}.$$

where Δ indicates the difference between final and initial value of the given vector component. This equation can be transformed into

the velocity domain considering initial and final positions that are separated by an infinitesimally small time interval and evaluating the incremental ratio. Then, the angular velocity of each eye can be described by version (Ωs) and vergence (Ωg) velocities as follow: $\Omega l, r = \Omega s \pm \Omega g$. For the versional term we get the expression:

$$\Omega s = \begin{vmatrix} s_y \omega_z - s_z \omega_y \\ \omega_y \\ \omega_z \end{vmatrix}.$$

Of the three components of the versional velocity vector Ωs the second ω_y (vertical velocity) and the third ω_z (horizontal velocity) are independent and the first ω_x (torsional velocity) is constrained

$$\omega_x = s_y \cdot \omega_z - s_z \cdot \omega_y \tag{1}$$

and depends on both position (s) and velocity (ω) terms. Equation 1 says that the torsional component is a linear combination of the horizontal and vertical velocity components (ω_z, ω_y). The linear coefficients coincide with the two gaze components (s_z horizontal position and s_y vertical position) of the actual versional position vectors. For small saccades (and confined within one quadrant) one can replace s_y and s_z with their presaccadic value (s_{y0} and s_{z0} respectively). Then, we get a relation with time-independent coefficients (which we call the Listing machine). We applied Eq. 2 to our data to compute the (Listing's) prediction of torsion ($L\omega_x$):

$$L\omega_x = s_{y0} \cdot \omega_z - s_{z0} \cdot \omega_y. \tag{2}$$

We compared the (kinematic) Listing's prediction with the observed torsional velocity (ω_x). In addition, we determined the linear regression of ω_x on the vertical (ω_y) and the horizontal (ω_z) versional velocities:

$$F\omega_x = c_y \cdot \omega_z - c_z \cdot \omega_y. \tag{3}$$

Comparing Eqs. 3 and 2 one may observe that the fit parameters (c_y, c_z) correspond to the initial eye position parameters (s_{y0}, s_{z0}) in Eq. 2. Thus we interpreted c_y and c_z as specifying a "virtual starting position" for the saccade's torsional velocity. For each quadrant we summarised the difference between the Listing's prediction and the best fit using ratios: the yaw tilt ratio (YTR) = c_z/s_{z0} and the pitch tilt ratio (PTR) = c_y/s_{y0} or differences: $d_y = s_{y0} - c_y$ and $d_z = s_{z0} - c_z$. The procedure is described in Fig. 2.

Finally, to evaluate a possible contribution of the change in the eye's position during the saccade (and to get rid of the approximation of Eq. 2) we also performed the best fit in a slightly different way:

$$F\omega_x = c_y \cdot s_y \cdot \omega_z - c_z \cdot s_z \cdot \omega_y. \tag{4}$$

In this case s_y, ω_z, s_z and ω_y are time-dependent functions and the corrective terms d_y and d_z can be redefined as $d_y = s_{y0} \cdot (1-c_y)$ and $d_z = s_{z0} \cdot (1-c_z)$.

Results

Position

Figure 3 shows a typical set of saccades (subject WD). Each trace shows the mean ($n \leq 10$) saccade profile plus or minus 1 standard deviation. Clearly, the mean trace of the versional component of eye positions remains close to Listing's plane even during saccades. Oblique saccades are curved idiosyncratically. In spite of the large horizontal and vertical range (more than 50 deg) the versional torsion remains close to zero. In this example, the planar fit, which relates torsion to the direction components of the rotation vector during saccades, is rotated less than 0.4 deg out of Listing's plane as found for fixations.

Table 1 Standard deviation (deg) of torsion. *Version* Average signal left+right eye rotations. *Left* Left eye torsion. *Right* Right eye torsion. The reference for both eyes is the versional primary position (PP). The larger standard deviation for individual eyes in comparison with the versional signal is also due to relative rotation of each eye's PP. During saccades the mean yaw tilt difference (of PP) was 10.7 deg and the mean pitch tilt difference was 0.9 deg

Subject	Version	Left	Right
AL	0.61	1.51	1.73
HS	0.97	1.00	1.29
PB	0.76	1.27	1.06
WD	0.60	0.63	0.92

The side view shows that the most eccentric saccades tend to tilt out of the plane. Torsion for each eye separately is larger, as shown in the lower right panels, in part because the two displacement planes are not aligned. Standard deviations of torsion for version and for each eye separately are reported in Table 1.

In Fig. 3 an asymmetry appears: the four groups of saccades are not symmetric around zero. This is caused by the non-alignment of the direction toward the screen's centre and the primary direction of this subject. Nevertheless each group of saccades remains almost completely (see Fig. 3, behind view) confined within one quadrant.

Saccadic velocity profiles

Figure 4 shows an example of binocular oblique saccades between two tertiary positions. Only the fast phase of the motion is shown. Even for these saccades between targets at optical infinity a transient intrasaccadic divergence occurs. This means that transiently the lines of sight intersect behind the subject. The vertical traces of the two eyes superimpose; thus vertical vergence during the saccade is negligible. Torsional signals show small differences in the two eyes. Occasionally, torsion is less similar in the two eyes than shown in this example.

Correlation of left and right eye velocity

For the fixation data we find an exorotation of about 5 deg of the eyes' displacement planes on average. This implies that the torsion of the two eyes differs as fixation shifts vertically. If saccades are purely versional movements one would expect identical velocity for the two eyes also in the torsional direction, and a post-saccadic drift could account for the difference. Alternatively, part of the cyclovergence could occur during the saccade. As a first step to test this we evaluated the correlation between the angular velocities of the two eyes.

(1) For each eye we joined the velocity traces of all the saccades of one quadrant component-wise. Then we evaluated the correlation between corresponding components of the left and right eye's angular velocities. We performed the analysis on such "multidirectional" velocity

Fig. 3 Saccadic movements of subject WD. Rotation vectors describing eye positions have been converted to degrees and are shown with the following conventions: right, up and extorsion of the right eye are positive. All the data refer to the versional primary position (the *fat dot* at 0,0). Each *data trace* indicates mean values. The *vertical bars* indicate 1 standard deviation. The *axis labels* indicate the names of the rotation vector components (TOR = r_x; VER = r_y; HOR = r_z). All the graphs show versional traces except the two (monocular) *lower right panels*. In the *behind view* an asymmetry appears: the four groups of saccades are not symmetric around zero. This is caused by the non-perfect alignment of the interocular axis of this subject and the screen
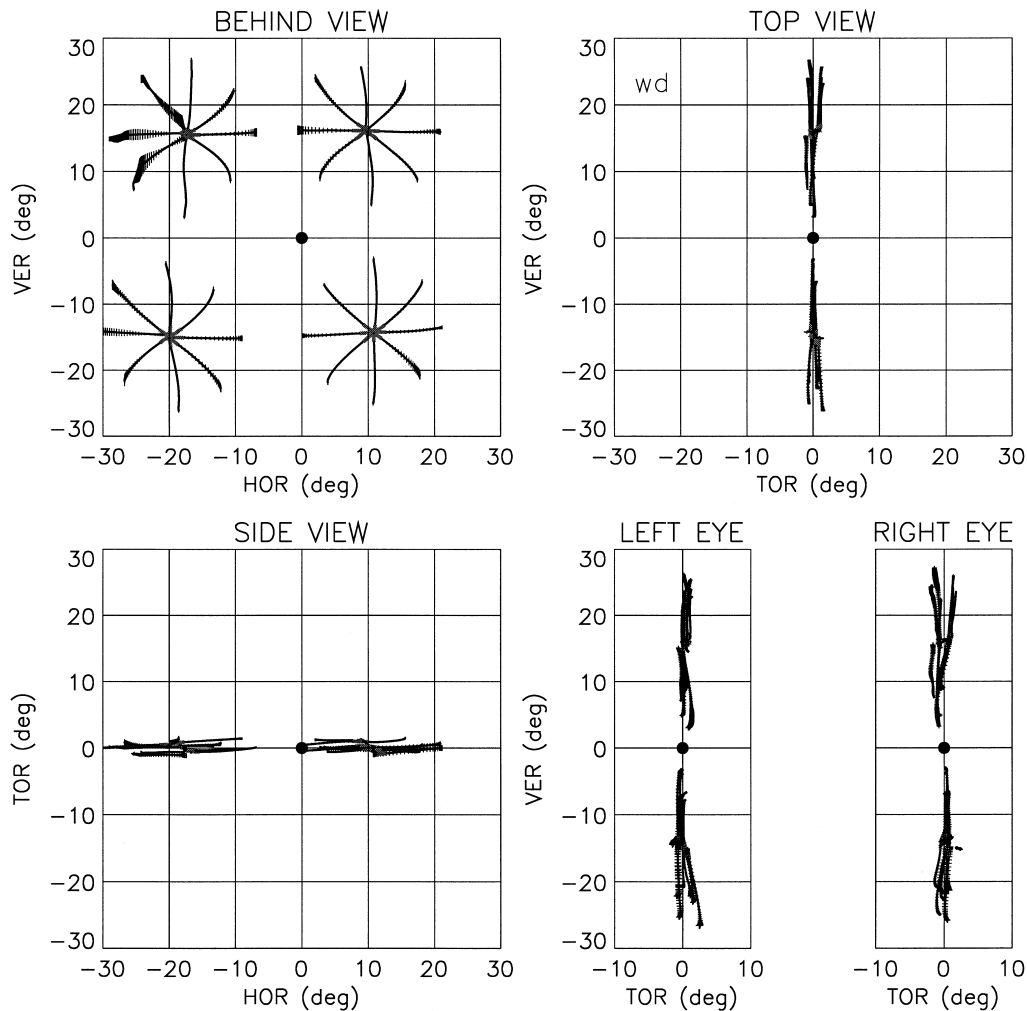

vectors to normalise the expected components' correlation. An example may explain this: the correlation between horizontal velocity components is not independent of the saccade's direction; it is very high during horizontal saccades but very poor during vertical movements when this velocity component approaches zero. A similar reasoning holds (but for different rotation directions) for vertical as well as torsional components (if Listing's law is obeyed). Therefore, only one specific saccade direction (depending upon starting direction) could provide maximal velocity, and therefore the most reliable estimate of the correlation, for each velocity component. Since (a) this direction may not be part of the directional set we measured, (b) this direction does not need be the same for both eyes, and (c) its selection implies an a priori assumption of the validity of Listing's law, such a procedure could give biased results. To overcome this problem we simply considered all the available directions for any given starting position. Thus, for all three components we equally considered the more and the less favourable conditions and estimated a mean correlation across directions.

Figure 5 shows instantaneous angular velocity of left and right eyes plotted against one another, pooled

for all saccades in one quadrant for one subject. In this example the correlation coefficient was about 0.99 for both horizontal and vertical velocities but 0.67 between the two torsional velocities. The average value, across subjects and quadrants, was 0.996 between the vertical components, 0.988 for the horizontal and 0.668 (min 0.1, max 0.93) between the two torsional velocities.

(2) To establish whether the correlation coefficient of the torsional components showed any relation with direction, we repeated the correlation estimation for each single saccade. The observed correlation coefficient ranged from –1 to +1. For only 25% of the saccades was a negative torsional correlation found. One subset of strongly correlated saccades emerged. This subset, of which an example is shown in Fig. 4, has positive correlation (> 0.5), but we observed also some saccades with a strong (–0.9) negative correlation (opposite torsion in the two eyes). We could not identify either a subject, or an experimental session, a direction or a position for which these non-conjugate saccades clustered. Such disjunctive saccades occurred only occasionally (about 4% of the mean traces; five of these movements were vertical saccades).

Fig. 4 Diagonal saccades back and forth between two same targets are shown for subject PB. *Top panels* show position trajectories (behind views; horizontal eye position on abscissa) of version. *Right-hand panels* show vergence velocity of *A* (right-down) and *B* (left-up) movements. *Arrows* indicate the angular velocity components: *T* torsion; *H* horizontal; *V* vertical. Binocular eye velocity components are compared in the *lower graphs*. *Conventions* are as in Fig. 3 and apply to both velocity and position traces. A clear transient divergence occurred during the saccade. Vertical eye velocity was very similar for the two eyes. Torsional components were also very similar in this condition
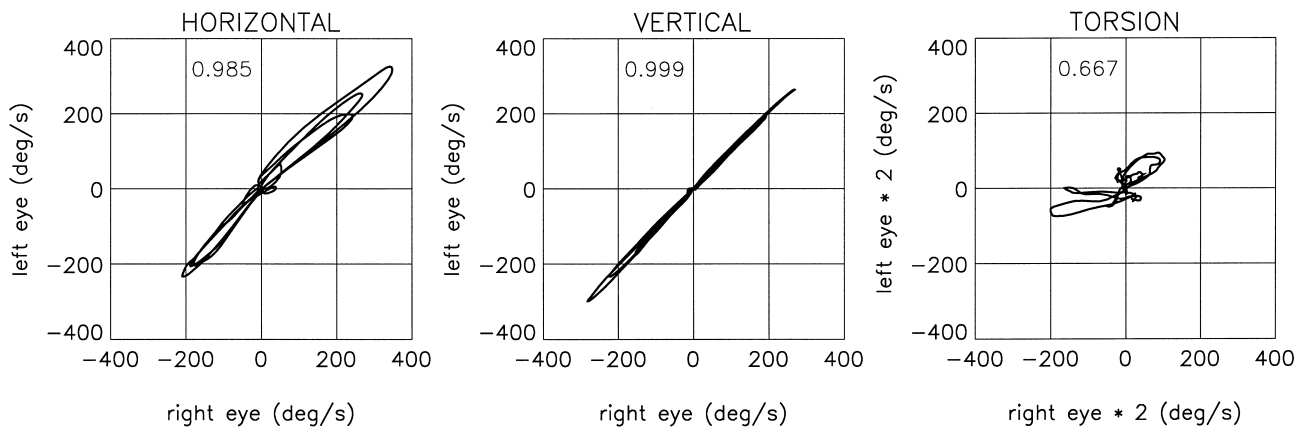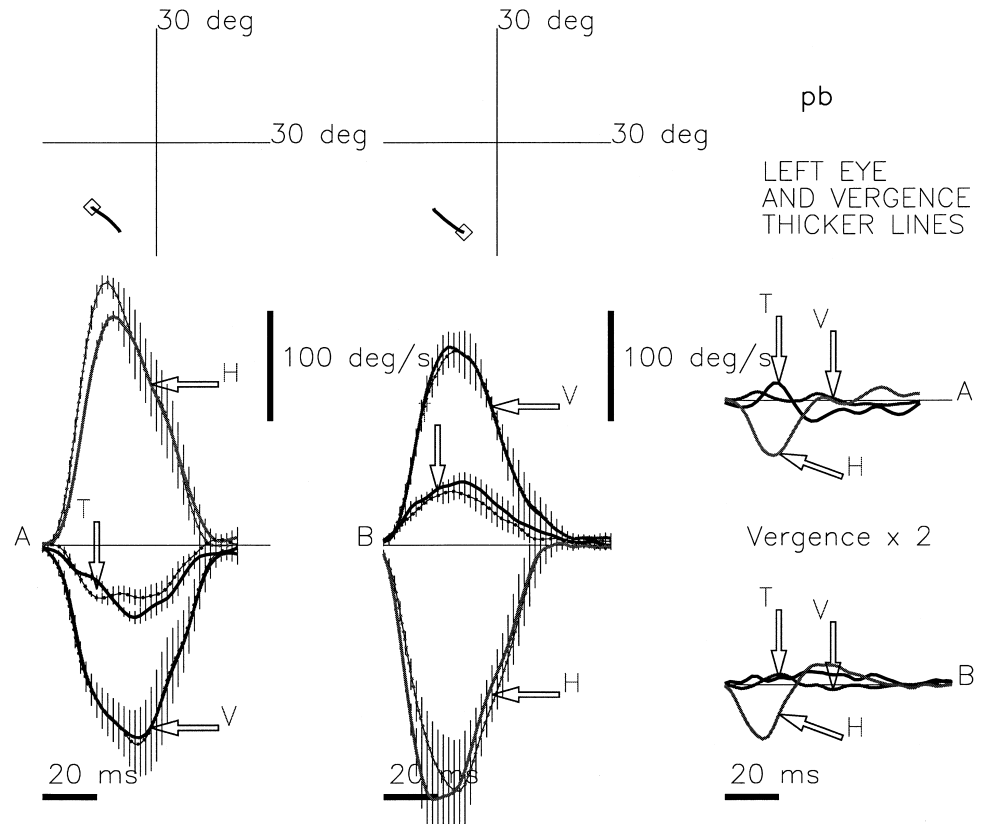
Fig. 5 A comparison of the angular velocities of left and right eyes during the saccade. *Conventions* are as for Fig. 3. The figure shows data from one quadrant of one subject (PB). The different components of the velocity vector are shown in different panels. The *number inside each panel* indicates the correlation coefficient between the velocity components of the left and right eyes. Vertical and horizontal components were highly correlated, the torsion much less so. Note that torsional traces have been magnified 2 times. The loops in the *left-hand panel* reflect the transient divergence during the saccade

Traces of the eight outward saccades are shown in the lower-right panel. Loops are evident in the behind view of the velocity traces; horizontal and vertical accelerations have a different temporal structures. Also, directional asymmetries of the peak velocity occur, particularly in this example. The other two views show the relation between torsion and vertical (top view) and horizontal (side view) components. Loops are present also in these two views. The loops were wider for the side view (horizontal and torsional components) than for the top view (vertical and torsion). The looping direction is constant. In the side view torsion is initially slow (close to zero during acceleration), then it reaches a peak (roughly as the horizontal component peaks) and finally it returns to zero during the horizontal deceleration. Next, we evaluated the orienta-

Velocity planes

Listing's law states that torsional velocity should depend on the initial eye position. Thus, we grouped saccades by starting position. An example of such a subset of movements is shown in Fig. 6.

Fig. 6 An example of the directional dependency of the relationship between versional velocity components (mean traces). The *lower-right panel* (position panel) shows the position trajectories of the saccades. The *diamond* identifies the common starting position. *Numbers* identify the directions. The *other three panels* show behind, side and top views of the velocity vectors (TOR = ω_x; VER = ω_y; HOR = ω_z). The torsional component is magnified by a factor of 2. Vectors have been converted into degrees. The initial part of the velocity trace is thicker. Loops of the velocity traces are evident in all views. Clearly wider loops are present in the side view than in the top view
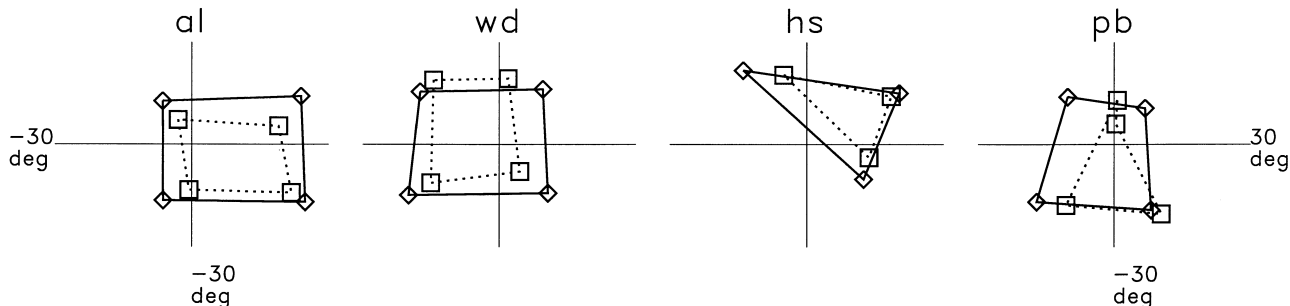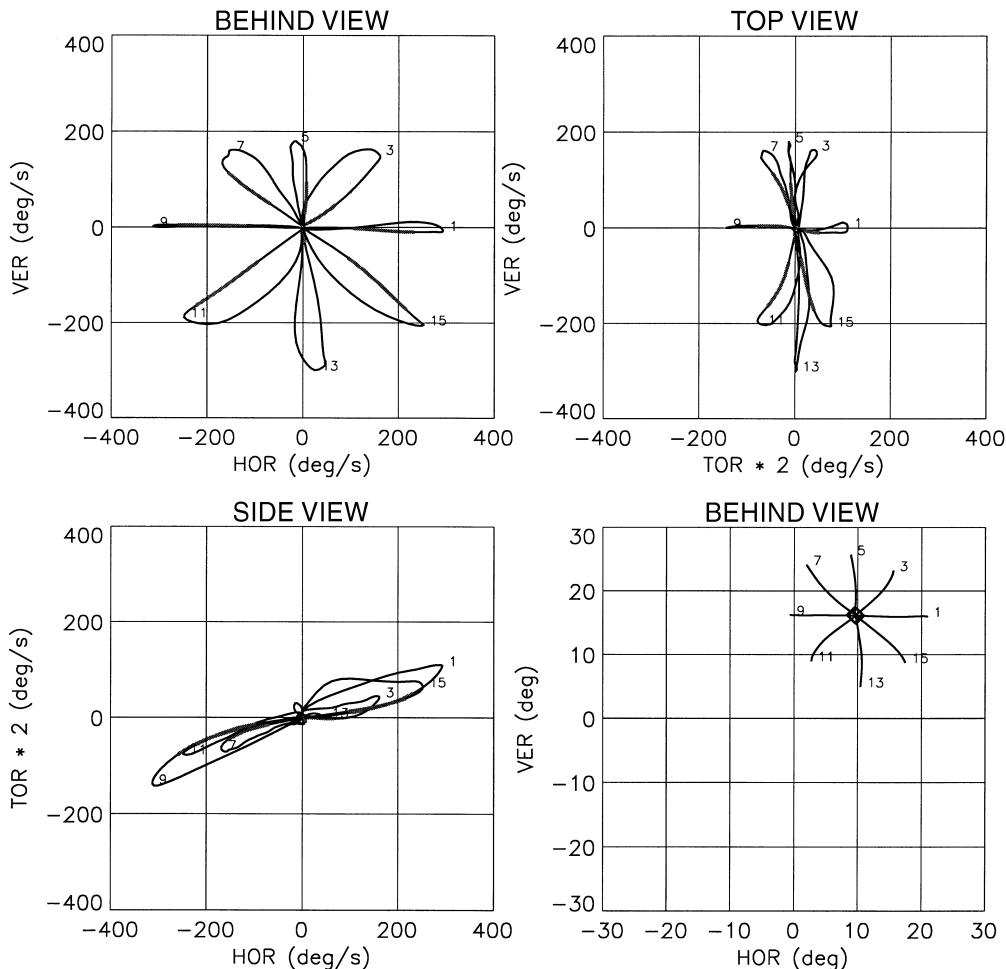
Fig. 7 Interpretation of the orientation coefficients of the velocity planes as virtual starting positions. The actual orientation of the velocity plane can be regarded as a virtual initial position of the saccades (i.e. an internal representation of the actual starting position used to attach weights to the contribution of horizontal and vertical bursters) that determines the torsional velocity profile of version. *Diamonds connected by continuous lines* are the actual versional starting positions relative to the primary position. These points are not always located on a square because the data for the different quadrants were usually collected in different sessions; the primary position could vary in relation to the screen across sessions. *Squares, connected by dotted lines*, are the "virtual positions". The *panels* refer to the four subjects (AL, WD, HS and PB). Rotation vectors components have been transformed into degrees (up and right are positive). Vertical position is along the vertical axis, horizontal position is along the horizontal axis

tion of the velocity plane for each quadrant, again using only the outward saccades. The coefficients of the planar fit ($F\omega_x$) were compared with the Listing's prediction ($L\omega_x$). We postpone a description of the errors to the end of the Results section. The dependency of torsion on the horizontal velocity component (ω_z) was very close to Listing's prediction: the PTR was about 1 (PTR = 0.83 ± 0.25 on average across subjects). Much more scatter appeared in the YTR distribution; the YTR was 0.56 ± 0.38 on average. This indicates that the relation between torsion and vertical velocity (ω_y) deviated most from Listing's law.

The two components of the rotation vector s_{y0} and s_{z0} are equal to the coefficients of the linear combination im-
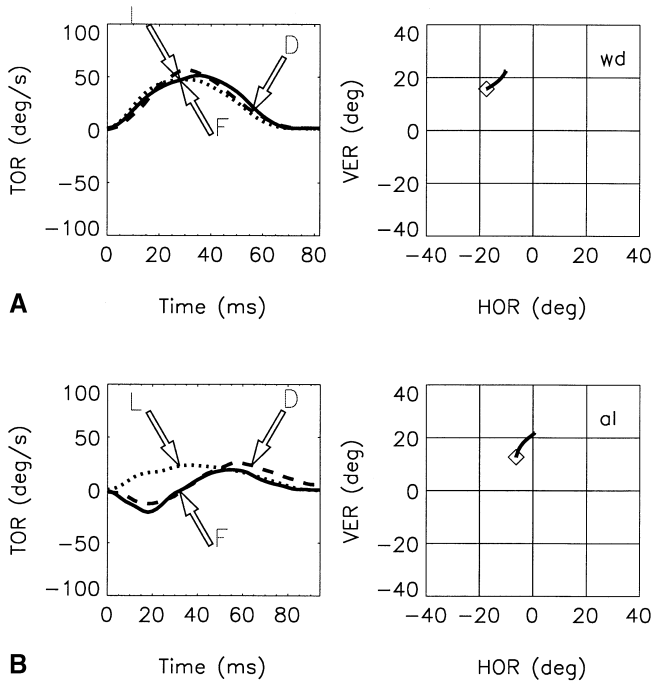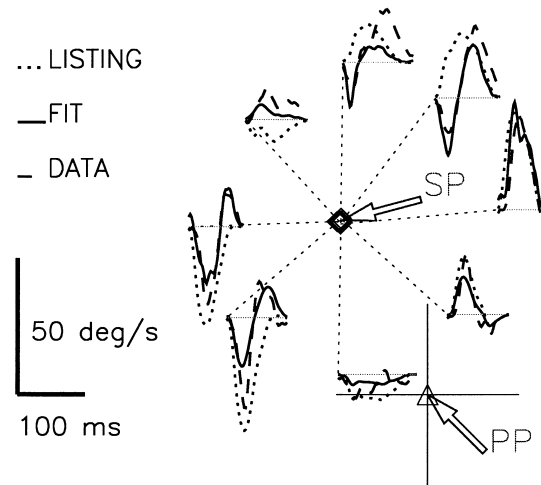
Fig. 8 A, B Examples of the time course of torsional velocity components during diagonal saccades between tertiary positions (*panels on the left*). **A** (WD) and **B** (AL) show saccades of two different subjects for the same targets. *Panels on the right* show position traces. The *diamonds* indicate the starting positions. Rotation vector components have been transformed into degrees, up and right are positive. In the velocity plots (*left side*) three traces are superimposed as indicated by *arrows*. *Dashed line* actual torsional velocity (*D*), *dotted line* prediction of the Listing machine (*L*), *continuous line* best estimation of torsional velocity on the basis of a linear combination of the two gaze components of the velocity (*F*). **A** is an example of a Listing-like movement. **B** is an example of a significant deviation from Listing's prediction. Nevertheless a different linear combination of the gaze components (F) can account quite well for the deviation from Listing's law


Fig. 9 Examples (subject AL) of the variety of torsional velocity profiles of saccades starting from the same tertiary starting position (*SP*). In this example SP was displaced left and up with respect to the primary position (*PP*). The predicted torsional velocity according to Listing's law and the linear fit are superimposed. The *thin straight dotted lines* indicate the saccade directions. The predicted (*LISTING*) traces never show double peaking (negative-positive) as observed for the data (*DATA*). Sometimes the Listing's prediction is in the wrong direction (saccade toward left-up). The fitting procedure (*FIT*) can also accommodate the "less regular profiles". Other subjects did not have such a varied pattern of torsional velocity profiles. This example was chosen to indicate the descriptive power of the scheme we applied

plemented by the Listing machine but at the same time denote the versional starting position of the saccades. Hence, the coefficients of the linear regression (c_y, c_z) can be interpreted as a "virtual" initial position. Figure 7 shows our results from this point of view, showing actual (continuous lines) and virtual (dotted lines) starting positions of each group of saccades.

This recoding (actual to virtual) characterises the saccades; it indicates how the basic Listing's prediction for saccade velocity has to be corrected to obtain the best fit to the actual torsional velocity. The recoding involves a transformation that cannot be reduced either to a pure scaling (gain factor) or to pure shifts (offset) or their combination. Nevertheless, our data show that the dependency on orbital position, postulated by Listing's law, although deformed, is present.

We wondered whether the deformation could be due to different dynamics of the vertical and horizontal components (which is manifest already in the looping as shown in Fig. 6). To assess this we split the saccades into acceleration (before the peak velocity) and deceleration (following the peak velocity) parts. We then applied the same

linear regression procedure to the acceleration and deceleration samples separately. Again we compared the parameters of the planes in relation to the Listing's prediction using the PTR and YTR. Dynamic differences should appear as systematic differences between the parameters for acceleration and deceleration. The results indicate that both the YTR and the PTR parameters are higher during deceleration than acceleration. The difference was 0.20 ± 0.28 for the YTR and 0.25 ± 0.18 for the PTR. The larger difference, but in particular the smaller standard deviation, shows that the PTR showed the dynamic effect most clearly. Thus, for the same horizontal velocity the torsional velocity is higher during deceleration than during acceleration.

The YTR parameter (torsion vs vertical velocities) indicates that not all the saccades are well approximated by the Listing machine. We show in Fig. 8 two examples of the torsional velocity for oblique saccades. Figure 8A shows one example of "Listing's behaviour" and Fig. 8B shows one of "non-Listing's behaviour". Clearly, the prediction of the Listing machine (dotted line) closely resembles the observed torsion (heavy continuous line) only in Fig. 8A.

We wondered to what extent directional variability could account for the remaining error and for the observed variability of YTR. Thus we analysed single movements. We fitted the torsional traces, again, by means of linear regression between torsion and horizontal and vertical components of the angular velocity. We
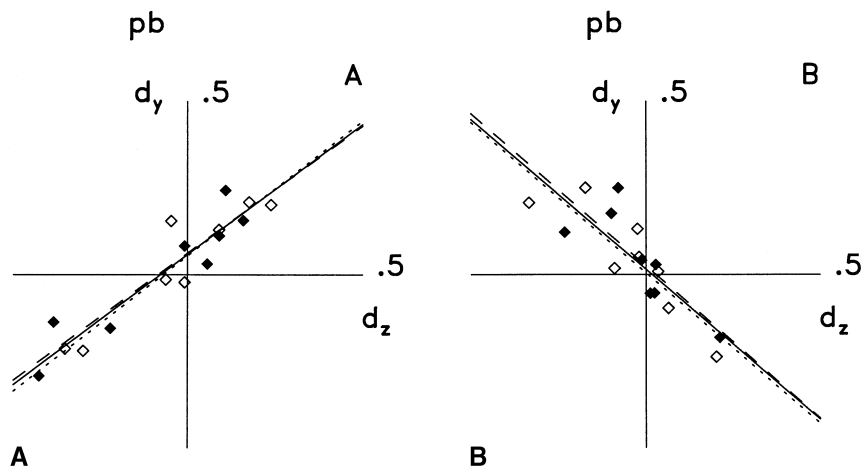
Fig. 10 A, B Typical directional distribution of the d_y and d_z terms (subject PB). For each saccade the torsional versional velocity has been fitted by a linear combination of the two gaze components of angular velocity (linear regression). d_z and d_y are the differences between the coefficient of the Listing machine and the corresponding coefficients of the linear regression. **A** Data for left-down → right-up or right-up → left-down saccades. **B** Data for left-up → right down or right down → left up saccades. In both panels *open symbols* indicate outward saccades (starting from the quadrant's centre) and *filled symbols* indicate inward saccades (in this case each saccade has a different starting position). Independent of the starting position the two parameters d_y and d_z appear to be linearly related. The relation depends on the diagonal direction. *Dotted lines* (inward saccades) and *continuous lines* (outward saccades) represent the linear regressions of d_y and d_z

Table 2 Correlation (r) and linear regression $d_y = p*d_z+q$ parameters (p and q) between the two corrective terms (d_y, d_z) of the two-dimensional fits (eq 3) interpreted as deviation from presaccadic position. $LD \leftrightarrow RU$ indicates saccades along the first diagonal: left-down to/from right-up. $LU \leftrightarrow RD$ indicates saccades along the other diagonal direction left-up to/from right-down

Direction		AL	WD	HS	PB
LD↔RU	r	0.875	0.867	0.928	0.934
LD↔RU	q	0.021	–0.030	–0.092	0.058
LD↔RU	p	0.635	0.671	1.105	0.751
LU↔RD	r	–0.852	–0.937	–0.932	–0.841
LU↔RD	q	0.044	0.004	0.014	0.015
LU↔RD	p	–0.902	–0.943	–0.695	–0.866

found that the torsional component of the angular velocity can be quite accurately described as a linear combination of the vertical and horizontal velocity components during the saccade. This can be seen in Fig. 8 by comparing the observed and reproduced torsional traces. A more complete picture of the approximations of the torsional component of the velocity by means of this linear fitting is reported in Fig. 9. In Fig. 9 the eight saccades along different directions are compared with the linear best fit and with the prediction of the Listing machine (dotted line). This example (showing the data of one quadrant of one subject) was particularly "rich" in terms of qualitatively different torsional velocity profiles: negligible, bell-shaped, double-peaked with initial positive or negative torsional velocity, or a peak followed by a plateau.

The coefficients of these linear best fits varied for different saccade directions, starting positions and subjects. We express this variability as the difference between the coefficients of the Listing machine and the best fit coefficients ($d_y = s_{y0}-c_y$ and $d_z = s_{z0}-c_z$). The differences d_y and d_z (corrective terms) turned out to be linearly dependent. An example is reported in Fig. 10; Table 2 reports the correlation and regression coefficients between d_y and d_z for all subjects.

From these observations we concluded that the deviation of torsional velocity from Listing's law has two components, governed by: (1) the difference between the "virtual position" and the actual starting position of the sac-

cade and (2) saccade direction. Because the coefficients d_y and d_z are linearly related it would seem that the effect of saccade direction is essentially one-dimensional. This provided the rationale to attempt a simpler fitting procedure to describe the effect of saccade direction. The PTR was less variable and closer to 1 than the YTR. Thus most of the variability was related to the vertical eye velocity (through position parameter c_z; YTR = c_z/s_{z0}) and the parameter d_z is most important. These considerations led us to the following equation:

$$F\omega_x = c_y \cdot \omega_z - c_z \cdot \omega_y - d_{dz} \cdot \omega_y. \tag{5}$$

We took for c_y and c_z the virtual positions, as shown in Fig. 7, to obtain d_{dz} for each oblique saccade direction. We selected the oblique saccades (four outward and four inward) because non-zero horizontal and vertical velocity components are best suited for the fitting procedure. Remarkably, the pattern of d_{dz} as a function of the saccade direction was very similar for the four quadrants in two subjects (Fig. 11). In the other subjects the contribution of d_{dz} was usually relatively small. Thus, the effect of saccade direction was independent of the effect of starting position in most cases. The dependency of d_{dz} on starting position can be seen by averaging the d_{dz} estimate for saccades with different direction but equal starting position, i.e. for each subject, the four data points marked with the same symbol in Fig. 11. These averages (one for each quadrant and subject) were always close to zero and pro-
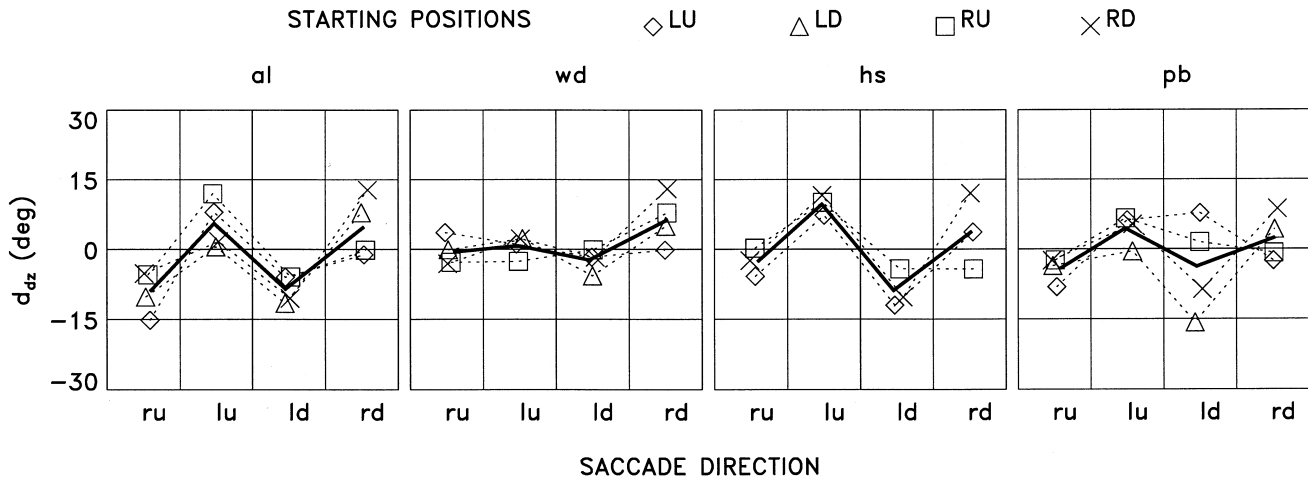
Fig. 11 Directional dependency of the corrective term d_{dz} (see text for a definition). Data from different subjects are shown in different panels. Labels along the horizontal axes identify the four saccade directions considered for this analysis (*LU* left-up, *RU* right-up, *RD* right-down, *LD* left-down). Different *symbols* indicate the different quadrants (see *key* above figure). Values estimated for the same starting position have also been connected by *dotted lines*. For each subject the *continuous line* is the mean (across starting positions) directional corrective term

vided correction terms for the initial virtual positions of less than 3 deg. On the other hand when the averages were evaluated across saccades equally directed but starting from different positions a clear modulation (up to 15 deg) of d_{dz} appeared (continuous heavy line in Fig. 11).

Finally we quantified to what extent the starting position and the saccade direction contributed to the improved fit of the torsional velocity. We quantified this parameter by the mean absolute errors. We computed the error between the observed torsional velocity and the fit. We compared for each quadrant the mean absolute error (Fig. 12) using the four oblique outwards saccades in that quadrant. Only for this dataset could all the different fitting procedures could be applied. Thus this set was the only one suitable for a comparative error analysis.

There was a monotonic reduction (Fig. 12) of the error modifying the Listing's prediction (LS) with positional correction (FT) and with both positional and directional corrections (1D and 2D). The largest error reduction is achieved by the positional corrections c_y and c_z [from 7 deg/s (LS) to 5 deg/s (FT) on average]. One-dimensional estimation of the directional coefficients' dependency (d_{dz}) further reduces the error to 4.5 deg/s (1D). A somewhat larger improvement is achieved with two-dimensional estimation of the directional corrective terms d_y and d_z (2D).

We wondered whether the assumption of fixed coefficients for the fitting could be responsible for the directional modulation. If one interprets these coefficients as some form of the brain's attempt to maintain Donders' law by taking into account the eye position, one could argue that, since the eye positions vary during the saccade, constant coefficients (be it the actual or the virtual starting position of the saccade) are not appropriate. To establish
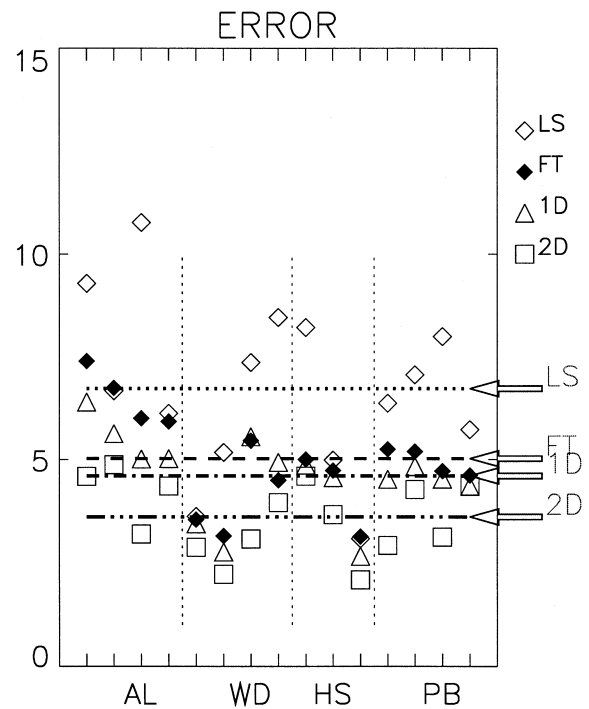
Fig. 12 Error reduction achieved by the various fitting procedures. For each subject (*horizontal axis*) and for each quadrant (indicated by four *markers* on the horizontal axis per subject) the difference between the predicted and the observed torsional velocity was computed. We obtained the mean absolute error (for the diagonal saccades) taking differences of the following measures: *LS* actual data and Listing's prediction (*open diamonds*); Eq. 2. *FT* actual data and the direction-independent linear fit. Saccades are pooled by starting position and analysed as one data set: velocity plane (*filled diamonds*); Eq. 3. *1D* actual data and the direction-independent linear fit adjusted by d_{dz} (one-dimensional fit; *open triangles*); Eq. 5. *2D* actual data and the direction-dependent linear fit (two-dimensional fit for each saccade; *open squares*); Eq. 3 applied on a single movement data set. *Lines* are the mean values of the error across quadrants and subjects for the indicated predictions. Values are in degrees per second

the validity of this argument we repeated the fitting procedure to take into account the change in eye position during the saccade (see Methods). The results of this analysis are shown in Table 3 and Fig. 13. Applying the two-dimensional fit (Eq. 4) the two corrective terms exhibited, as they did using Eq. 3, a direction-dependent linear correlation (compare Tables 2 and 3). Moreover, we found similar results (compare Figs. 13 and 11) re-evaluating the d_{dz} parameter with the following equation:

$$F\omega_x = c_y \cdot s_y \cdot \omega_z - c_z \cdot s_z \cdot \omega_y - d_{dz} \cdot \omega_y \qquad (6)$$

which differs from Eq. 5 by the presence of time-dependent terms (s_y and s_z). As for Eq. 5 the c_y and c_z parameters were fixed as previously estimated from the sets of saccades from each quadrant.

Table 3 Correlation (r) and linear regression $d_y = p*d_z+q$ parameters (p and q) between the two corrective terms (d_y, d_z) of the two-dimensional fits (eq 4) interpreted as deviation from presaccadic position. The procedure allowed continuous updating of eye position data during saccadic fit. $LD\leftrightarrow RU$ indicates saccades along the first diagonal: left-down to/from right-up. $LU\leftrightarrow RD$ indicates saccades along the other diagonal direction left-up to/from right-down

Direction		AL	WD	HS	PB
LD↔RU	r	0.894	0.908	0.926	0.945
LD↔RU	q	0.026	−0.031	0.094	0.056
LD↔RU	p	0.598	0.722	1.070	0.747
LU↔RD	r	−0.833	−0.922	−0.916	−0.850
LU↔RD	q	0.061	0.005	0.020	0.015
LU↔RD	p	−0.944	−0.948	−0.688	−0.871

Fig. 13 This figure is similar to Fig. 11 but, to build torsion, a time-dependent combination of velocity components has been considered. The corrective term d_{dz} has been computed by Eq. 6 (see text). Data from different subjects are shown in different panels. *Labels* along the horizontal axes identify the four saccade directions considered for this analysis (*LU* left-up, *RU* right-up, *RD* right-down, *LD* left-down). Different *symbols* indicate the different quadrants (see *key* above figure). Values estimated for the same starting position have also been connected by *dotted lines*. The *continuous lines* are the mean (across starting positions) directional corrective terms
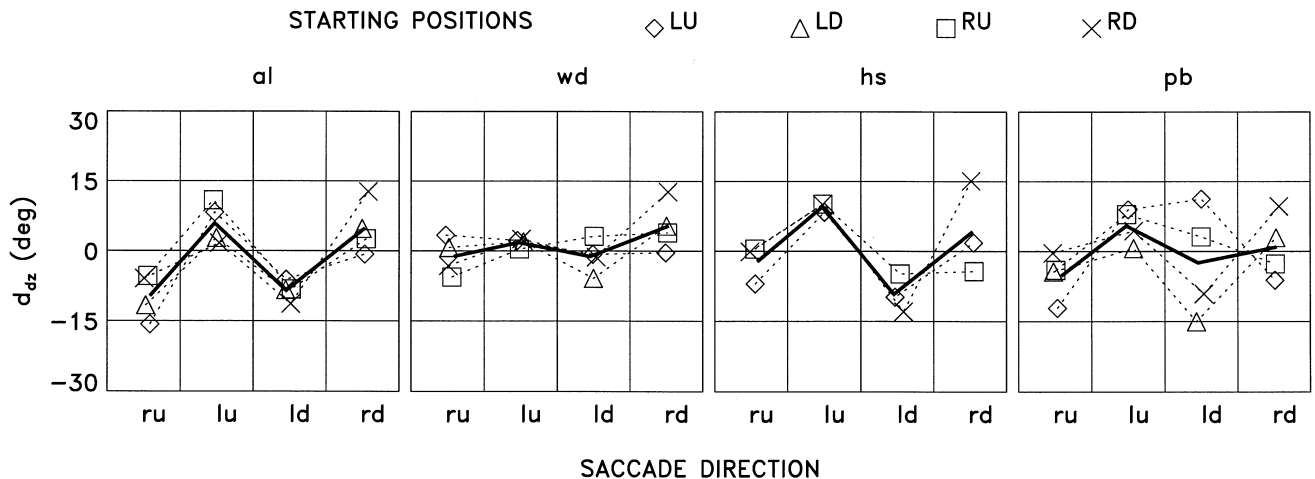
Discussion

We made a systematic study of the effect of saccade direction and saccade starting position on the angular velocity profile of the saccade. We used targets at optical infinity to provide optimal targets for a conjugate controller. We compared the relation between velocity (position) components (to test Listing's law) as well as the time course of torsion during the saccades. The latter aspect has received little attention. In line with some previous studies we found that the torsional velocity, during the fast "intrasaccadic" part of the motion can be variable, unequal in the two eyes, and can deviate transiently from Listing's law. The deviations from Listing's law for the versional component showed a systematic influence of starting position and saccade direction.

A binocular description of the saccades was mandatory because we observed that for fixations of targets at optical infinity the eyes did not attain fully conjugate positions (Bruno and Van den Berg 1997). To evaluate our observations on saccades we used a recently proposed binocular extension of Listing's law (Van Rijn and Van den Berg 1993; Van den Berg 1995) to predict the version component of the eye velocity (Eq. 1). This analysis uses certain approximations to derive closed form expressions for the eye velocity vectors and rotation vectors. In addition, this analysis treats the rotation vectors of the eyes as a simple summation (subtraction) of versional and vergence vectors. In this approach the version and vergence parts cannot be associated with rotations from the reference position but rather with symmetric and anti-symmetric components of torque that are needed to keep each eye in an eccentric position. Minken et al. (1995) preferred a separation of the rotation vectors into versional and vergence parts using rotational kinematics. The associated components then can be associated with a rotation from the reference position (the version component) and a rotation to turn each eye relative to the other in opposite directions (the vergence component). Using the same math-

STARTING POSITIONS ◇ LU △ LD □ RU ✕ RD

ematical constraints on version and vergence components of eye position these two studies derived different predictions for the amount of cyclovergence as a function of horizontal vergence and elevation. One could wonder to what extent our conclusion that eye velocities differ from those predicted by Listing's law is dependent on our choice of analysis. We think such concern is not justified. First, we used targets at optical infinity: this means that the lines of sight were parallel (or very nearly so). For such conditions the difference between the eye orientations predicted by Minken et al. (1995) and Van Rijn and Van den Berg (1993) is negligible, and the same eye velocities are predicted. Thus, the deviations that we find would also occur relative to a prediction based on the scheme by Minken et al. (1995). Secondly, Van den Berg (1995) showed that, by a simple parametric adjustment of the vergence component of the predicted eye velocity, eye orientations corresponding to the scheme by Minken et al. (1995), corresponding to Van Rijn and Van den Berg (1993) or intermediate could be obtained. The versional component of the eye velocity was, however, not adjusted. This indicates that the predicted versional component of the eye velocity is robust with respect to the choice of the particular model for the constraints on eye vergence. Thus, we believe that the deviations from Listing's law of saccadic eye velocities are real and not an artefact of the data analysis that we performed.

Correlation between angular velocity components of the two eyes

Bains et al. (1992), analysed the correlation between the horizontal and vertical velocity components of the two eyes. They found a high correlation, and concluded that both eyes were controlled by a common, versional saccadic system. We applied here the correlation technique in a slightly different way. (a) We took into account the torsional component considering the angular velocity vector instead of the derivative of horizontal and vertical eye position. (Hereafter we will refer always to angular velocity vector components unless otherwise specified.) (b) We based the correlation on the entire saccadic motion and not just the peak velocities. (c) We worked on individual movements and on groups of saccades starting from the same tertiary position. We found a high correlation (> 0.98) between direction components but a clearly lower value for torsion (0.67 on average) when we pooled the saccades of one quadrant. The single-movements analysis revealed that there was a small subset of saccades with a disjunctive torsional component (correlation about -0.9) but that the majority of the saccades were positively correlated. A fully versional control would imply for torsion also a correlation always close to 1. On the other hand, if the saccades had reflected the fixation data (opposite torsion in the two eyes associated with vertical gaze shifts; Bruno and Van den Berg 1996) a negative correlation for the torsional components would be expected for the majority of the movements.

To distinguish between these hypotheses we can divide our data in three groups:

(1) pure horizontal saccades (25% of the data) that are expected to be positively correlated for either hypothesis.
(2) Saccades towards or away from the primary position. The movements of this subset (another 25%) that should have no torsional velocity at all, are less reliable as they are sensitive to noise. Their correlation may be positive or negative.
(3) The remaining saccades (50%) that are expected to be positively or negatively correlated depending on the hypothesis.

In short, the two hypotheses can be tested by checking the percentage of saccades with positive/negative correlation. Positive correlation for more than 75% of the cases (group 1 and 3) would confirm the versional nature of torsion. Negative correlation for at least 50% of the saccades (group 2) would point to the second hypothesis (monocular implementation of the half angle rule). We found that 75% of the saccades were positively correlated. However, not all the movements with negative correlation have the expected directions (i.e. towards or away from the primary position). Thus, the versional control hypothesis is most consistent with the data but an effect of the different torsional positions of the two eyes seems to be present. Also, positive correlation does not imply that the torsional velocities are identical; some cyclovergence may build up during the saccade. Nevertheless, a post-saccadic (drift) torsional drift is probably required to account for the changes in cyclovergence for changes in vertical fixation. This conclusion is in agreement with the observation of Mok et al. (1992) who reported that during convergence velocity planes of the two eyes do not rotate as much as the displacement planes.

The torsional component of the versional angular velocity

Grouping saccades by starting position we found a basically planar distribution of the angular velocity vectors for each of the four tertiary positions. However, the vertical (pitch tilt) and the temporal (yaw tilt) rotations of the plane were not equal to the vertical (s_y) and horizontal (s_z) components respectively of the rotation vector describing the saccade's starting position. Comparing the starting positions with the virtual starting positions that were derived from the fitting procedure we found a deformation (shift + compression) of the basic Listing's prediction (Fig. 7). The temporal rotation of the velocity plane was more variable than the vertical rotation across subject and starting position. Only the pitch tilt showed values close to the prediction (ratio 0.83). The pitch tilt ratio differed rather systematically between the acceleration and deceleration phases (difference 0.25). This indicates that torsion is underestimated during deceleration and overestimated during acceleration by the fit. The pitch tilt of the plane links horizontal velocity (reflecting horizontal rectus activity) and torsional velocity (that is mainly imposed

by the action of the other four extraocular muscles). The difference in pitch tilt during acceleration and deceleration points to different dynamics (or dynamic compensation) of the horizontal and vertical-torsional muscles. The looping of the velocity components and the curvature of the saccade trajectory that we observed in our data is consistent with this view. Looping was observed also for the vertical and the torsional components but it was less evident (an example is shown in Fig. 6). Therefore, we suggest that part of the transient deviations from the kinematic prediction is due to the different dynamics of the different muscles. Indirect evidence for different dynamic behaviour can be found in the different post-saccadic drift observed in association with horizontal or vertical saccades (Collewijn et al. 1988a, b).

Remarkably, the torsional velocity profiles can vary qualitatively in relation to the saccadic direction, changing from bell-shaped to double-peaked. Yet the linear combination of ω_z, ω_y can account for almost all the torsional velocity profiles we observed (Fig. 9). Most of the variability could be explained as a direction-dependent variation of just one of the planar fit parameters (the coefficient that links torsional velocity to vertical eye velocity).

Implications for models

Recently, the implementation of Listing's law by the oculomotor system has been the cause of controversy. The debate focused on the functional structure of the velocity-to-position integration in the brainstem. On the one hand Tweed and Vilis (1987, 1990) have argued that to follow Listing's law the oculomotor integrator should reflect rotational kinematics; i.e. it should combine 3D velocity commands and current eye position multiplicatively to correctly update the integrator. Only in this way would the integrator provide the right signals to keep the eye in an eccentric position that conforms to Listing's law. In contrast, Schnabolk and Raphan (1994) argued that simple linear integration of horizontal and vertical signals is sufficient. In their view Listing's law is caused by elastic orbital forces that drive the eye back towards a position of minimal eccentricity; i.e. the eye's 3D orientation reflects a balance of horizontal and vertical torques, but no torsional torque is generated by the integrator. This concept has received some anatomical support (Demer et al. 1995) through the finding of fibrous structures that keep the eye muscles from moving freely within the orbit. It would seem that this model runs into trouble when fixation of nearby targets is considered. In such cases the eyes intort or extort relative to Listing's orientations depending on the amount of convergence and elevation; this requires additional torque in the torsional direction that is not included in the model by Schnabolk and Raphan (1994).

For static eye positions or slow movements the difference between the two proposals is minimal. For saccades, however, Tweed and Vilis' scheme predicts trajectories that keep the eye in Listing's plane throughout the saccade, whereas Schnabolk and Raphan's model predicts transient deviations from Listing's law that are related to the amount of clockwise or counterclockwise rotation of the eye about the primary direction. The deviations that according to this model build up during the saccade, are slowly reduced by a post-saccadic drift. Such phenomena (post-saccadic torsional drift or torsional "blips") have been found by some investigators (Enright 1986; Ferman et al. 1987b; Strauman et al. 1995) but not by others (Tweed et al. 1994). To what extent do our data fit one or the other model? Our saccades were quite small (12 deg) and started from eye positions of moderate eccentricity. Even Schnabolk and Raphan's model would predict small torsional blips. Thus, our data do not allow for a strong test of these models. The largest deviation we found between the predicted and the fitted velocity plane concerned the yaw component. In most subjects the yaw tilt of the velocity plane was only half of the predicted value. This means that for vertical saccades torsional velocity was about half the predicted value. For a 30-deg vertical saccade starting at 16 deg eccentricity (11 deg up, 11 deg right) this deviation would carry the eye out of Listing's plane by about 1.5 deg. This is not unlike the peak torsion during a blip as reported by Strauman et al. (1995). Note, however, that our computation is an overestimate because corrective drift during the saccade is ignored in the computation. We agree with the latter authors that such data do not argue decisively against one or the other model, because either modifications of the plant model in Schnabolk and Raphan's scheme or parametric adjustments in Tweed and Vilis' proposal can bring about transient torsion during a saccade that needs to be corrected by drift.

Van den Berg's (1995) description of eye displacements suggests a rather simple scheme to implement the half-angle rule for version at the level of the burster activity. The velocity-to-position is non-commutative and is similar to what Tweed and Vilis (1987) proposed in terms of quaternions but based on vector algebra. Such an implementation relies on multiplicative feedback of eye position signals in combination with the two gaze components of the bursters. Mathematically speaking the torsional velocity is described as a linear combination of the two gaze velocities. The coefficients of the combination are proportional to the two gaze components of eye position. This scheme is particularly attractive for its simplicity. However, it suffers, as do all the other commutative formulations of the control, from an intrinsic weakness: the knowledge of absolute eye position. Current eye position is required to build the torsional component of the burst (the angular velocity), from 2D desired eye displacement signals. The absence of eye position signals in the brainstem poses a problem that had suggested models (one- and two-dimensional) of the saccadic system based on displacement (Jürgens et al. 1981) and velocity feedback (Lefèvre and Galiana 1992; Lefèvre 1993). From this point of view, the non-commutative schemes of saccade control in 3D, go back to the original idea of

Robinson (1975), without having proven either the existence of the required signals or the accuracy required in such a coding. Our findings are compatible with the idea of a non-accurate representation of eye position. At least one of the two positional feedback signals would convey a signal that differs from the actual eye position.

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