The kinematics of far-near re-fixation saccades

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Abstract

We have analyzed the three-dimensional spatio-temporal characteristics of saccadic re-fixations between far and near targets in three behaviorally trained rhesus monkeys. The kinematics underlying these rapid eye movements can be accurately described by rotations of the eyes in four different planes, namely first dis-conjugate rotations in the horizontal plane of regard converging the eyes towards the near target followed by rotations in each eye’s vertical direction-plane and finally dis-conjugate rotations in a common fronto-parallel plane. This compounded rotation of the eye was underlying an initially fast rising variable torsion that typically overshot the final torsion, which the eyes attained at the time of target acquisition. The torsion consisted of a coarse widely varying component of opposite polarity in the two eyes, which contained a more robust much smaller modulation that sharply increased towards the end of saccades. The reorientation of the eyes in torsion depended on each eye’s azimuth, elevation and target distance. We conclude that re-fixation saccades are generated by motor commands that control ocular torsion in concert with the saccade-generator, which operates in Donders-Listing kinematics underlying Listings law.

Key words:

Eye movements, Donders’ law, Listing’s law, dis-conjugate saccades, stereoscopic vision
Introduction

For orientation in space our eyes constantly scan the visual surround by saccades, which are rapid, highly coordinated binocular movements. To direct gaze on objects located at different depths in space, the two eyes must rotate by different amounts. Specifically in the horizontal plane of regard the eyes move towards near targets by rotating through different angles in opposite directions until the visual lines cross at the target of interest. Moreover, near targets in the peripheral visual field off the horizontal plane of regard require different combinations of movements in the horizontal and vertical plane. Under these circumstances, the eyes rotate also in the frontal plane for some still not fully understood reasons. Originally, this latter motion has been described as torsion of the eyes about the lines of sight (Enright 1980, Helmholtz 1867, Nakayama 1983). When looking for example at objects on the ground that require our attention during walking the fixation eye movements are accompanied by small rotations such that the vertical retinal meridians move away from the head’s mid-sagittal plane, which is called ex-torsion. Conversely, fixation of targets in the upper visual field for example for catching or hitting an approaching small ball requires small rotations that move the vertical retinal meridians towards the head’s mid-sagittal plane, called in-torsion. Although it has long been known that these small adjustments of eye position, which are symmetric for targets in the head’s mid-sagittal plane depend on both the vergence angle as well as the amount of elevation of the eyes (Mok et al 1992, Porill et al 1999), its purpose remained largely obscure. Here we provide evidence suggesting that these movements, although small in amplitude specifically serve stereoscopic vision.

Originally the torsion of the eyes in near vision has been interpreted as a violation of Listing’s law, according to which visually guided eye movements are controlled by two rather than three degrees of freedom of motion (for a review, Hepp 1994; Hepp et al 1997). Mok and colleagues (1992) however found that under iso-vergence conditions fixation eye movements still obeyed Listing’s law but now with respect to torsional and vertical movement planes that were rotated in each eye in the horizontal plane of regard away from the head’s mid-sagittal plane. The modulation of the eye’s torsion in near vision thus appeared merely as an extension rather than a violation of Listing’s law (Mok et al 1992; Tweed 1997).

The experimental verification of the amount of rotation of the torsional and vertical movement planes of each eye turned out to be unexpectedly difficult. In the original study of Mok and colleagues (1992) the estimated angles were too small compared to the theoretical prediction of one half of the half-vergence angle for symmetric vergence, whereas in the
study of Van Rijn and Van den Berg (1993) it was too large. In subsequent studies, Minken
and van Gisbergen (1994, 1996) reported values that were generally closer to the theoretical
prediction although they differed from each other due to different fitting models. Although
these authors used in their first study various visual conditions they could not resolve the
discrepancy of their results with the earlier results of Van Rijn and van den Berg (1993).

From a kinematic standpoint the torsion of the eyes must change if horizontal and vertical
rotations occur in mutually orthogonal planes. For example, a horizontal-vertical
compounded rotation generates torsions of the right and left eye relative to a head-fixed
frame, whose directions are compatible with the experimentally observed torsions
accompanying vertical rotations during vergence. In the following we will refer to this fact as
the Helmholtz kinematic model because it suggests that the observed torsion in near vision
simply arises as a mechanical consequence of the horizontal and vertical rotations of the eyes.
Indeed the Helmholtz kinematic model could explain the kinematics of binocular fixations of
targets located in as well as off the horizontal plane of regard. First we notice that the locus of
binocular targets is a circle located in a vertical plane for targets at distances smaller than
(optical) infinity, which is obtained by intersecting two imaginary shells around each eye with
the respective eye-to-target distances as radius (Fig. 1). This circle, which may be called
Helmholtz-circle for short, contains all potentially binocularly visible targets at the given
distances relative to the two eyes. Its location depends on the distance between the two eyes’
rotation centers (O_a and O_b in Fig. 1) and the respective eye-to-target distances (a, b in Fig. 1).

The alternative to pure kinematic torsion is an oculomotor system that operates in default
mode in a Donders-Listing mode for generating saccades across the whole visual space
irrespective of changes in depth. In far vision, binocular fixations are made possible because
the gaze lines and associated direction-planes in which the eyes rotate are parallel to each
other. This parallelism brakes down, however, when the depth plane of fixation changes
relative to optical infinity. Specifically, when the eyes converge in the horizontal plane of
regard, the vertical direction-planes rotate towards each other (Fig. 1, white circles). For
geometric reasons, the rotated planes of the right and left eye meet the Helmholtz-circle of
binocular positions at just one single position. Saccades that typically move the gaze lines
from one fixation position to the next along direction-circles will therefore no longer allow
binocular fixation in near space (for far vision, see Hess 2013). Here we will show that for
pure geometric reasons the eyes must rotate under these circumstances also in a frontal plane
to fuse the dichoptic retinal target images. We will call this model the Donders-Listing model.
To test the Helmholtz kinematic versus the Donders-Listing model we analyzed saccades between far and near targets in the upper and lower visual half-space in three behaviorally trained Rhesus monkeys. We show that the eyes redirect the gaze lines by combining rotations in horizontal and vertical direction-planes with active torsion in the frontal plane. The modulation of torsion during such re-fixation saccades consisted of a rapidly developing, overshooting coarse torsion followed by a smaller fine-tuned torsion at delayed-onsets. Although the Helmholtz kinematic model perfectly could explain the horizontal and vertical rotations of the eyes it failed to predict the torsion.
Materials and Methods

The experimental data used in this study were obtained in the context of a larger project requiring three-dimensional (3D) eye movement records in non-human primates. We used rhesus monkeys because of the physiological proximity of the organization of their visual and oculomotor system to humans. The animals had a chronic acrylic head implant for restraining the head in the experimental sessions. Three-dimensional eye movements were recorded with the magnetic search coil technique (Robinson 1963) using a dual search coil that was implanted on both eyes under the conjunctiva as previously described (Hess 1990, Mandelli et al 2005). All surgery was performed under aseptic conditions and general anesthesia, and postoperative pain treatment was applied for at least three consecutive days. All procedures were in accordance with the recommendations in the Guide for the Care and Use of Laboratory Animals of the US National Institutes of Health. The housing, husbandry and experimental procedures were reviewed, approved and supervised by the Veterinary Office of the Canton of Zurich.

Experimental procedures

3D eye movement records were analyzed in three female rhesus monkeys (Macaca mulatta), which had been trained to re-fixate between a far and a near light-emitting diode. The far target was located at eye level 0.8 m straight ahead (horizontal vergence ~2°, vertical eye position ~0°). In most experiments, the near target was located 10° down at a distance of 0.1 m (horizontal vergence 17°). In a few experiments, it was also presented at 10° up at the same distance. To examine a larger range of azimuth and elevation angles including asymmetric vergence effects we analyzed all saccades that landed on or in the vicinity of the near target (Table 1). All experiments were performed in dimmed light, i.e. with a background illumination inside an opaque sphere where the animal was seated upright, with the head restrained in a primate chair, which completely surrounded the animal. The inner
wall of the sphere was covered with randomly arranged black dots about 1 to 5 cm in size on a white background. Three-dimensional eye positions were recorded with an Eye Position Meter 3000 (Skalar, Delft, The Netherlands), calibrated as described in Hess et al. (1992), digitized at a sampling rate of 833.33 Hz, and stored on a computer for off-line analysis. To express eye positions as rotation vectors (Haustein 1989), the zero or reference positions were defined to be the eye’s orientations while the monkey fixated a target 0.8 m straight ahead. In two animals (M1, M2), Listing’s plane tilted less than -2° vertically (that is backwards) and -1° horizontally (that is leftwards), in one animal it tilted vertically about -6° and horizontally 0° (M3). We did not correct eye positions for these deviations from primary position (see Hess and Thomassen 2014). The on- and offset of saccades were isolated by a semiautomatic procedure based on the magnitude of the jerk (derivative of angular eye acceleration), followed by applying an empirically adjusted position threshold based on the change in magnitude of the eye position vector. Specifically, after choosing a position threshold in the one-figure percent range the time course of the coarsely delimited saccadic events was narrowed down to stay within these provisional limits (where they exceeded the threshold). To further refine the saccade window, we computed the mean +SD of the initial rising phase up to the point of exceeding the threshold, which determined the final onset-threshold. Likewise we computed the mean +SD of the falling phase below threshold, which defined the final offset-threshold of the saccade. This procedure avoids noise problems inherent with velocity or acceleration thresholds and isolates saccades by preserving their typically asymmetric time course. Saccades with amplitudes < 1° were discarded.

Vectors will be denoted by bold characters, unit vectors by regular fonts with caret. When referring to components, we write vectors for convenience as row vectors within round parentheses, separating the components by commas.

Gaze movements and representation of 3D eye position
3D eye positions were represented in the convenient axis-angle representation of rotation vectors, where the magnitude of rotation is expressed as tangent of half the angle of rotation \( \rho \), and the axis as a vector of unity length orthogonal to the plane of rotation (denoted \( \hat{n} \)):

\[
E = \langle E_{\omega x}, E_{\omega y}, E_{\omega z} \rangle = \tan(\rho/2)\hat{n} \quad \text{(Haustein 1989)}.
\]

Torsional eye position, \( E_{\text{tor}} \), is the rotation of the eye in the head’s frontal plane (clockwise positive), vertical eye position, \( E_{\text{ver}} \), is the rotation in the vertical plane (downward positive), and horizontal eye position, \( E_{\text{hor}} \), is the rotation in the horizontal plane of regard containing the reference position straight ahead (leftward positive). A rotation (saccade) from straight ahead position O to position B via the intermediate position A, denoted \( E_{\text{BAO}} \), is the composition of a rotation from O to A, followed by a rotation from A to B:

\[
E_{\text{BAO}} = E_{\text{BA}}E_{\text{AO}} := \left( E_{\text{BA}} + E_{\text{AO}} + E_{\text{BA}} \times E_{\text{AO}} \right)/(1 - E_{\text{BA}} \cdot E_{\text{AO}}) \quad \text{("\times": vector product, "\cdot": dot product; Haustein 1989)}.
\]

To relate gaze shifts in visual space to the underlying rotations of the eye, we represented the gaze line by a unity vector, \( \hat{g} = \sum_{i=1}^{3} g_i \hat{e}_i \) in the spherical field of fixations with coefficients \( g_1 = \cos \varepsilon \), \( g_2 = -\sin \varepsilon \sin \psi \) and \( g_3 = \sin \varepsilon \cos \psi \) using the polar coordinate \( \varepsilon \), that is the angular eccentricity relative to straight ahead and \( \psi \), the signed dihedral angle between the plane \( \hat{e}_i \times \hat{g} \) and the frontal plane represented by \( \hat{e}_i \times \hat{e}_3 \) (right side down positive)\(^1\). The unit vectors \( \hat{e}_i \) (\( i = 1, 2 \) and 3) represented a right-handed, head-fixed Cartesian coordinate system with \( \hat{e}_i \) pointing in direction straight ahead, \( \hat{e}_i \) pointing along the inter-ocular line from right to left, and \( \hat{e}_i \) pointing upward. A general rotation of the eye was described by a rotation operator \( R = R(\hat{n}, \rho) \), where the unit vector describes the orientation of the rotation.

\(^1\) In geometric terms the cross product of two unit vectors, \( \hat{e}_i \times \hat{e}_j \) (\( i \neq j \)) represents an oriented unit plane. Indeed the exterior product (bivector) \( \hat{e}_i \times \hat{e}_j \) is related to the cross product by \( \hat{e}_i \times \hat{e}_j = -(\hat{e}_i \wedge \hat{e}_j)\hat{e}_{123} \), using the 3-dimensional pseudo-scalar \( \hat{e}_{123} = \hat{e}_1 \hat{e}_2 \hat{e}_3 \).
plane and $\rho$ the angle of rotation. A rotation of the gaze vector from A to B in the plane $\hat{n}$ through the angle $\rho$ is obtained by the operation $\hat{G}_{BA} = R_{BA} R_{BA}^{-1}$, where $R_{BA}^{-1}$ is the inverse of $R_{BA}$.

Definition of normed target space

In the following we represent the eye movements by their rotation centers, separated by the inter-ocular distance, and the two gaze lines pointing at the target of interest. In a spherical visual field, the distances of a single target to two rotation centers are related to the azimuth angles and the distance between the rotation centers by the following relations: $a/b = \cos \beta / \cos \alpha$ and $a \sin \alpha - b \sin \beta = k$ where $a$, $b$ are the distances, $\alpha$ and $\beta$ the azimuth angles and $k$ the inter-ocular distance (Figs. 1, 2). From these relations one derives $a = k \cos \beta / \sin (\alpha - \beta)$ for the right and $b = k \cos \alpha / \sin (\alpha - \beta)$ for the left eye-to-target distance, which simplify to $a = b = k / (2 \sin \alpha)$ for equal azimuth angles. In the horizontal plane of regard the triangle formed by the rotation centers and the point of fixation scales for fixed azimuths $\alpha$ and $\beta$ with the inter-ocular distance (see triangle $O_a O_b A$ in Fig. 2). In the following we set $k = 1$ without loss of generality. By this convention, target distances scale in terms of multiples of the inter-ocular distance. In our rhesus monkeys the inter-ocular distances were about 3.0 cm.

Geometry of vertical direction-circles and Helmholtz-circles in near vision

In order to determine the rotation of the eye during saccadic re-fixations from far to near targets, we decomposed the rotation into a first rotation in the horizontal plane of regard. In the Helmholtz kinematic model, this moved the gaze lines towards a point on the line of intersection of the horizontal plane of regard with the Helmholtz plane, i.e. the vertical plane of intersection of the associated target shells. A subsequent vertical rotation of the eyes in this plane then moved the gaze lines towards the brain’s estimated target location.

In the alternative Donders-Listing model the vertical rotations occurred in each eye’s direction-plane that intersected with the Helmholtz plane and the horizontal plane of regard in a single point (Fig. 3, position A). Thereby the gaze lines moved along the respective vertical
direction-circles up to slightly divergent positions that shared the same depth plane as the
final target position (Fig. 3, positions A, B_a, and B_b for a target in the upper hemi-field). We
then calculated the torsion of the right and left eye that was required to move the gaze lines to
their intersection at the binocular target position (Fig. 3, position C). Geometrically this
position is the intersection of the two circles centered at the respective directions straight
ahead and passing through the Listing positions B_a and B_b that share the same fronto-parallel
plane with the binocular target position C.

To determine the geometric relation between binocular Helmholtz-positions, denoted by C
and the associated Listing-positions B_a of the right and B_b left eye, we first note that the y-
coordinates are functions of the horizontal disparities of these positions and the azimuth of
the respective eye (q and α in Fig. 4). Specifically, for the right eye we have the relations

\[ [B_a]y = -a \sin \psi_b \sin \epsilon_b = -a (q/a - \sin \alpha) \]  
and \[ [C^{(a)}]y = -a \sin \psi_c \sin \epsilon_c = a \sin \alpha. \]

From these we obtained the trigonometric relation

\[ \sin \psi_b \sin \epsilon_b = \sin (\psi_b + \omega_a) \sin \epsilon_b + q/a (\text{Fig. 4}), \]

accounting for the condition that B_a and C^{(a)} have the same eccentricity relative to the
direction of straight ahead, namely \[ \epsilon_c = \epsilon_b = \sin^{-1} \left( r_a/a \right) \], where \( r_a \) is the radius of the circle
through B_a, B_a' and C (Fig. 4). Thus \[ \omega_a = \sin^{-1} \left\{ \sin \psi_b - (q/a)/\sin \epsilon_b \right\} - \psi_b \]. An analogous
formula holds for \( \omega_b \). Second, we determined the horizontal disparity q by

\[ q/a = (p/a) \sin \alpha/2, \]  

where \( p/a = (\cos \alpha - \cos \epsilon_c)/(\cos \alpha/2) \) noting that \( \| A'O \| = 2a \sin^2 \alpha/2 \)

and \( \| O_a'O_a' \| = a \cos \epsilon_c \). And finally, the vertical rotation angle subtended by the line segments

\( O_{DL}A \) and \( O_{DL}B_a \) in the direction-plane (Fig. 4C) was calculated as a function of the ratio p/a

with \( \eta_a = \cos^{-1} \left\{ 1 - (p/a)/\cos \alpha/2 \right\} \). Similarly, \( \eta_b \) of the left eye was computed. In brief, the

2 Superscripts ‘a’ and ‘b’ enter parentheses indicate that the coordinates of a particular binocular position C are
taken relative to the rotation center O_a or O_b, respectively.
two Listing-positions $B_a$ and $B_b$ in the neighborhood of the target position $C$ were obtained from the estimates of $C^{(a)}$ and $C^{(b)}$ relative to the respective rotation centers $O_a$ and $O_b$. For simulating the trajectories of far-near re-fixation saccades, we applied the equation

$$\hat{g}_A = R_{AO} \hat{g}_O R_{AO}^{-1},$$

which moved the gaze line from its initial position parallel to straight ahead to the line intersecting the intermediate target position $A$ in the horizontal plane of regard. In the Helmholtz kinematic model, this motion was followed by a vertical rotation moving the tip of the gaze vector $\hat{g}_A = \overrightarrow{OA}$ from position $A$ to the estimated final target position $C$,

according to $\hat{g}_C = R_{CA} \hat{g}_A R_{CA}^{-1}$. The compound action that moves the tip of the gaze line from $O$ to $A$ to $C$ thus was obtained by computing $\hat{g}_C = R_{CA} \left( R_{AO} \hat{g}_O R_{AO}^{-1} \right) R_{CA}^{-1}$. In the Donders-Listing model, the vertical rotation was computed in each of the direction-planes, which subtended the angle $\alpha/2$ in the right and $\beta/2$ in the left eye relative to the vertical plane. We simulated this motion by $\hat{g}_B = R_{BA} \hat{g}_B R_{BA}^{-1}$, where $R_{BA}$ is a rotation operator associated to the respective eye’s vertical-direction plane. Finally, we computed $\hat{g}_C = R_{CB} \hat{g}_B R_{CB}^{-1}$ for each eye, where $R_{CB}$ mediated a rotation of the gaze line in the common fronto-parallel plane from $B_a$ to $C$. For details about the rotation operators $R_{AO}$ and $R_{CA}$ used in the Helmholtz kinematic model and $R_{AO}, R_{BA}$ and $R_{CB}$ used in the Donders-Listing model see Appendix. In the following we refer to the compounded rotation operator $R_H = R_{CA} R_{AO}$ as Helmholtz operator (Helmholtz kinematics) and $R_{DL} = R_{BA} R_{AO}$ as Donders-Listing operator (Donders-Listing kinematics),

Root-mean square errors were computed by evaluating the expression

$$rms_X^\mu = \sqrt{\frac{\sum_{k=1}^N (\hat{X}_k^\mu - X_k^\mu)^2}{\sum_{k=1}^N (X_k^\mu)^2}},$$

where $\hat{X}_k^\mu$ and $X_k^\mu$ are the $k^{th}$ sample of the $\mu^{th}$ component of the experimental and reconstructed eye position, respectively ($\mu = \text{“tor”, “ver”, or “hor”}, N = \text{number of samples}$). In the exponential least-squares fits of torsion, we
computed the generalized $R^2$-values based on the residual sum of squares of the fit and the reduced model consisting of average torsion (Anderson-Sprecher 1994).

Results

Reconstruction of three-dimensional eye positions during far-near re-fixation saccades

Fixation of near targets requires in general a compound rotation of the eyes consisting of a vergence movement and adjustments of the elevation of the eyes relative to the horizontal plane of regard. Such compound rotations generate torsion of the eyes except in the case where the eyes rotate in horizontal and vertical direction-planes. In earlier studies we have described the suppression of ocular counter-roll during fixations of near targets in tilted head positions and also compared counter-roll before and after convergent or divergent saccades. We also reported average latencies, showing that in far to near re-fixation saccades they were shortest for the horizontal and longest for the torsional rotation component (Misslisch et al 2001; Mandelli et al 2005). In the following paragraphs we describe specifically the kinematics of far-near re-fixation saccades obtained in the same animals by comparing the Helmholtz-kinematic model with the Donders-Listing model.

Using the azimuth and elevation derived from the recorded eye movement data (see Methods) first we estimated the torsional variation underlying the Donders-Listing kinematics. For this we estimated the rotation angles in the respective direction-planes and evaluated the Donders-Listing kinematics $R_{DL} = R_{BA} R_{AO}$ for each eye (see Methods, Fig. 4 and Appendix). We found small modulations in torsion of each eye in the range of about $\pm 0.5^\circ$ during the re-fixation trajectory. Next we removed this torsion from the saccade trajectory in order to estimate the ocular torsion caused by the active, not kinematics-related torsion of the eye. Assuming that the experimentally measured rotation was a compounded rotation based
on Donders-Listing kinematics and active torsion, we evaluated the rotation quotient

\[ R_{NL} = R_{exp} R_{DL}^{-1}, \]

to obtain the non-Listing-rotation, from which we computed the angle of ocular torsion \( \xi = 2 \tan^{-1} \left[ R_{NL} \right] \), for each eye. Finally, we estimated the experimentally observed rotation of each eye by compounding the active rotation in the frontal plane through the angle \( \xi \) and the Donders-Listing rotation \( R_{\text{eye}} = R_{F} R_{DL}, \) where \( R_{F} = R_{F}(\xi) \) and

\[ R_{DL} = R_{DL}(\eta, \vartheta) \]

with the appropriate torsion \( \xi \), elevation \( \eta \) and azimuth angles for the right \( (\vartheta = \alpha; \xi = \xi_a; \eta = \eta_a) \) and left eye \( (\vartheta = \beta; \xi = \xi_b; \eta = \eta_b) \), respectively. We found a close match between the experimentally measured rotations of the eyes and the so reconstructed rotations in all components (Fig. 5A to C, reconstructed eye position in black superimposed on experimental eye position in gray). To highlight the spatial characteristics we analyzed the torsional modulation that evolved during far-near re-fixation saccades also in the spatial domain. We found a consistent slow built up as the gaze lines approached the near target (Fig. 5D, right eye torsion in black, left eye torsion in gray). Typically the eyes torsion increased in magnitude reaching amplitudes up to about 2.5° shortly before hitting the estimated target location. Subsequently torsion abruptly diminished such that the difference between right and left eye torsion settled to a steady position in a range of about 1° to 2°. To characterize the torsion of the eyes more specifically we measured peak torsion defined as the maximum torsion of the right and the minimum torsion of the left eye during the saccade and compared it with the respective final torsion, which was defined as the torsion reached when the horizontal vergence movements ceased. In the three animals, we found an average maximal torsion (±SD) of the right eye of 0.9° (±0.6), 1.7° (±1.1) and 0.5° (±0.5) and an average minimal torsion (±SD) of the left eye of -0.9° (±0.9), -0.7° (±0.6) and -1.9° (±0.8). Similarly we found an average final torsion (±SD) of the right eye of 0.7° (±0.9), 1.6° (±1.1) and 0.3° (±0.7) and an average final torsion (±SD) of the left eye of -0.4° (±1.1), 0.1° (±0.8) and -1.8°.
(±0.8) \((N = 65, 297, 202)\). Although on average peak and final torsion in the three animals were fairly close together, this was not necessarily the case for individual saccades (Fig. 5).

**Orientation of rotation planes as a function of azimuth and elevation**

Comparing the estimated rotation of the eyes based on the Helmholtz kinematics and the Donders-Listing model, we found that the two approaches yielded very similar predictions of the vertical and horizontal gaze trajectories yet drastically different predictions regarding the time-evolution of the spatial orientation of the rotation planes. Viewed in a frontal projection, the instantaneous horizontal and vertical rotation planes of the two models had similar orientations along the trajectory (Fig. 6C, top and bottom panel). In projections orthogonal to the frontal plane the orientation of the vertical and horizontal rotation planes remained constant after an initial change early in the trajectory in the Helmholtz kinematic model. In contrast both rotation planes changed continuously their orientation along the saccade trajectory in the Donders-Listing model (compare top and side views in Fig. 6A, B top and bottom panels). While the torsion generated by the Helmholtz kinematics did not match the experimentally observed torsion, the Donders-Listing model reproduced the experimentally observed modulation of torsion during re-fixation saccades within error margins of a few percent (Table 2). Most interestingly, the rotation trajectories often made an abrupt turn towards pure torsion towards the end, which was faithfully reproduced by the Donders-Listing but not by the Helmholtz kinematic model (compare top and bottom panel in Fig. 6A).

To quantify the observed torsion we estimated the tilt of the instantaneous rotation plane of the eyes during re-fixation saccades as well as the average orientation over the last 50ms at the end of saccades. The Donders-Listing model predicted the following angular ratio between the instantaneous orientation of the torsional plane and the orientation of the vertical-horizontal rotation plane, given by \(\hat{n}_{hv} = \left(n_2^\xi \hat{\xi} + n_3^\eta \hat{\eta} \right) \left(n_2^\xi + n_3^\eta \right)\) (see Appendix):

\[
\tan \tau_{hv} = \left( n_1 \sqrt{n_2^2 + n_3^2} \right) = \left(\sin \xi/2 \cos \eta/2 \cos \phi/2\right) / \sqrt{1 - \cos^2 \eta/2 \cos^2 \phi/2},
\]

where the unit
vector $\mathbf{n} = (n_1, n_2, n_3)$ represents the normal on the rotation plane, $\eta$ the elevation, $\varphi$ the azimuth, and $\xi$ the angular excursion of the eye due to active torsion. According to this relation, the orientation of the horizontal-vertical rotation plane modulates relative to the frontal plane mainly with the torsion angle and much less with the azimuth and elevation of the eye. Indeed, re-fixation saccades exhibited large dynamic modulations of the orientation of the horizontal-vertical rotation plane relative to the frontal plane. Specifically, we found large transient tilts shortly before the gaze lines hit the estimated target location, which were little dependent on the azimuth and elevation of the eyes (Fig. 7). The large torsional excursions rapidly decayed to a few degrees around the equilibrium torsion at target acquisition. The formula for $\tau_{DL}$ also shows that there exists no functional relation between torsion and elevation at constant vergence or between torsion and azimuth at constant elevation. In fact, the Donders-Listing model implies that the torsion also depends on target distance (for details, see Discussion).

Fine-tuned torsional modulation

Although it has long been known that binocular fixations require dis-conjugate rotations of the eyes about the lines of sight, the quantitative aspects in terms of rotations in the frontal plane have been less clear. In contrast to the Helmholtz kinematic model, which predicts torsion as a function of azimuth and elevation, the Donders-Listing kinematics does not alter the torsion of the eyes. In this latter model the final torsion required for binocular fusion at the time of target acquisition is determined by the geometric configuration between the Helmholtz-plane and the rotations of each eye in the vertical direction-planes. Evaluating the disparity between the vertical positions and the finally acquired binocular target position (see Methods, Fig. 4) we found small but robust torsions of each eye in opposite directions in the range of 0.1° to 0.6°. These torsional rotations were often delayed by a few tens of milliseconds compared to the saccade onset (Fig. 8A, C and Fig. 9). To quantify these delays we compared the points in time, where the torsion and $\omega$-torsion of the eyes increased in absolute terms by more than 0.01° relative to saccade onset. In the three animals we found average delays (±SD) of 4.9ms (±3.3), 4.2ms (±2.5) and 16.2ms (±9.5) for torsion and average delays (±SD) of 35.4ms (±10.3), 33.6ms (±14.2), and 48.2ms (±7.4) for $\omega$-torsion of
the right eye. Similarly we found average delays (±SD) of 7.1ms (±4.3), 3.7ms (±2.0) and
10.8ms (±6.3) for torsion and average delays (±SD) of 41.8ms (±11.5), 37.5ms (±16.0) and
45.3ms (±8.3) for ω-torsion of the left eye (N =65, 297, 202). The torsional rotations sharply
increased in both eyes when the eye-to-target distance was less than about ten inter-ocular
distances (Fig. 8D). To distinguish it from the overall torsion of the eyes we refer to it as ω-
torsion.

Modulation of coarse and fine-tuned cyclo-vergence

The temporal evolution of cyclo-vergence, computed as difference of right minus left eye
torsion, exhibited in all three animals a more or less pronounced under-dumped oscillation
(Fig. 9, black traces). In frontal projection the retinal images thus rotated relative to each
other thereby modulating the torsional disparities. These out-of-phase rotations are likely to
support the visual system’s search for corresponding images in the two eyes, thereby
enhancing stereopsis (see Discussion). The fine-tuned cyclo-vergence, obtained as difference
between ω-torsion of the right minus left eye set on with a delay of about 25 to 50 ms relative
to the onset of the coarse cyclo-vergence. In contrast to the coarse cyclo-vergence its time
evolution showed over-dumped characteristics (Fig. 9, gray traces).

The Donders-Listing model implies that torsion modulates with respect to both eye’s
azimuth and elevation, an implication that follows by right-multiplication of the equation
\[ R_{\text{eye}} = R_{R} R_{DL} \text{ with } R_{DL}^{-1} \]. Since the ω-torsion was obtained as part of the overall torsion, we
expected a similar angular dependency. Indeed, we found that the ω-torsion of each eye
depended on both the azimuth and elevation of the eye as well as target distance. To evaluate
the dependency of ω-torsion on these parameters, we pooled all saccades obtained in several
experimental sessions, irrespective of whether the animal perfectly hit the near target and
evaluated the ω-torsion averaged across 12 milliseconds at the end of the saccades. In one
animal we had collected enough data to be able to single out two clusters with respect to the
saccades’ azimuth that covered also a reasonable large range in vertical direction as well as
eye-to-target distance. The two clusters showed the expected exponential dependency of ω-
torsion as a function of elevation and eye-to-target distance with little or no overlap on average (Fig. 10).

Discussion

We have studied the 3D kinematics of saccadic re-fixations between far and near targets. We found that ocular torsion modulated in flight in a specific manner: First it increased by about 1° to 2° relative to saccade onset before it sharply decreased again around the time of target acquisition to reach constant post-saccadic values. The widely varying torsion of the eyes included a robust but much smaller component, emerging at a delay before sharply increasing up to peak values at the time of target acquisition. A detailed analysis of the underlying ocular kinematics revealed three different rotations of the eyes: one rotation in the horizontal plane of regard converging towards the near target followed by a rotation in each eye’s vertical direction-plane and finally a rotation in the fronto-parallel plane common to both eyes. Reconstruction of these rotations based on the eye excursions predicted the time course of re-fixation saccades in all three dimensions within error margins of a few percent. While the first two rotations conformed to Listing’s law, the third rotation clearly violated Listing’s law even so in a very limited torsional amplitude range. In the following paragraphs first we will discuss these findings in the light of previous studies then address the kinematical implications in terms of binocular motor control and binocular vision.

Attempting to uncover a functional relation between ocular torsion, elevation and vergence of the eyes, previous studies have reported conflicting results about the role of Listing’s law during re-fixation saccades or steady fixations under iso-vergence conditions (Mok et al 1992, Van Rijn and van den Berg 1992, Minken and van Gisbergen 1994, 1996, Minken et al 1995, Tweed 1997). Although it has been found that the horizontal-vertical plane of ocular rotation tilted relative to the frontal plane, a phenomenon called “binocular extension of Listing’s law”, the amount of tilt varied largely between the different studies. The reasons for these discrepancies have been sought in different visual conditions but could not be clarified up to date. This was in fact not surprising as it has been known since the time of Helmholtz that there is no single visual criterion that could define the 3D orientation of the eyes providing optimal retinal correspondences in near vision (Helmholtz 1867; Van Rijn and van den Berg 1992; Hepp 1995). At the level of single targets, however, it is possible to define the optimal orientation of the eyes for single binocular vision. From a visuo-motor standpoint it is Donders’ and Listing’s law that guarantee the existence of retinal
correspondences in far vision by laying down the relations between azimuth, elevation and
torsion of each eye. Although the same kinematic principles do allow for binocular vision of
near targets in the horizontal plane of regard they fail for targets off the horizontal plane. In
these circumstances the optimal binocular kinematics turns out to be more complex because
of the emergence of two-dimensional disparities in the binocular field of fixations. A key
difference of the here proposed kinematics and the more simple Helmholtz kinematics is that
in a binocular setting the Donders-Listing kinematics entails torsional rather than horizontal-
vertical disparities for targets off the horizontal plane of regard. Such torsional disparities
arise even under the condition of symmetric ocular vergence, which is in line with the
experimentally well-established observations of disjunctive torsion of the eyes in near vision
(Fig. 11).

A crucial property of torsional disparities is that they can be locally eliminated by
modulating ocular torsion without affecting the intrinsic geometry of the retinal projection
images. The torsion required for binocular fusion of the disjunctive Listing-positions in the
binocular visual field is prima facie a simple function of the estimated binocular target
position and the associated Listing-positions of each eye. However, the azimuth and elevation
of these positions relative to each eye are linked to each other via the eye-to-target distances
and the anatomically fixed inter-ocular distance. As illustrated by the concept of normed
target-space (Figs. 1 and 2) and verified by experimental reconstructions (Fig. 10), four of
these parameters suffice in conjunction with the anatomical inter-ocular distance to control
binocular saccades in near vision: Each point in the normed binocular space is determined by
the two azimuths and the elevation of the estimated binocular target relative to either eye plus
the anatomical inter-ocular distance. Similarly, the $\omega$-torsion required for target fusion
depends on any two of the three parameters azimuth, elevation and eye-to-target distance in a
non-linear way. Generally the two eyes must torque by different amounts depending on the
respective eye-to target distance. More specifically, the torsion required for fusion depends
exponentially on target distance. At constant vergence it depends linearly on elevation in the
intermediate and large distances range (Fig. 12).

Does ocular torsion facilitate stereoscopic depth perception?

A striking observation was the steadily increasing torsion of the eyes during re-fixation
saccades, which abruptly stopped and returned to smaller values at the time of target
acquisition (Fig. 5C, D). This behavior was observed consistently in all three animals. It has
recently been found that ocular torsion may enhance or oppose stereoscopic vision suggesting
that the search zones for detecting corresponding features on the retinas are retina-fixed (Schreiber et al 2001). Disparity-selective neurons in the visual cortex V1 on the other hand have been shown to encode a larger range of horizontal than vertical disparities (Barlow et al 1967; Cumming 2002). On the oculo-motor side we found that horizontal and vertical disparities in peripheral viewing in fact are taken as torsional disparities driving torsional adjustments of the eyes (Figs. 3 and 11, \( \omega \)-torsion Figs. 8 to 10). Taken together this suggests that torsional disparity represents a crucial stimulus in stereoscopic vision. If so it is plausible that the brain actively modulates ocular torsion in search for corresponding features during re-fixation saccades: In fact, ocular torsion sweeps the epipolar lines (relative to either eye) across the frontal projection of the retinas with the result that the two retinal projection images can be correlated with each other without affecting their intrinsic geometry. Thereby the predominantly horizontally organized disparity zones acquire a vertical dimension. In this view, the observed active modulation of ocular torsion might represent an important mechanism that helps searching for corresponding retinal features localizing a small target in near space. Although we have studied re-fixation saccades in a restricted field of view the principals of ocular kinematics outlined here may also shed some new light on the debate about the role of vertical disparity detection in stereoscopic depth perception (Read et al 2006; for a review, see DeAngelis 2000).

**Donders’ law in binocular fixation space**

Donders’ law states that the ocular orientation of each eye during fixation of a target does not depend on the location of the previously fixated target whatever path the eye may take in the configuration space of rotations. In far vision this fundamental law in oculo-motor control holds in the monocular as well as in the binocular visual fixation space due to the normally strong yoking of saccades. In near visual space, the question arises how Donders’ law might be realized because now the ocular motion required for fixation of a binocular target is a compounded rotation in three rather than just two rotation planes. What does the third rotational degree of motion freedom determine when the eye saccades between binocular targets in near visual space? The answer lies in the particular geometry of disjunctive eye positions on the vertical direction-circles in relation to the neighboring binocular positions on the associated Helmholtz-circle. For fusion of the dichoptic target images these positions must share the same fronto-parallel depth plane, which guarantees that there is one and only one path in the configuration space of rotations that connects those disjunctive positions with the binocular position in question. Because the two possible points of intersection of the respective vertical direction-circle and the Helmholtz-circle are in symmetric position relative
to the horizontal plane of regard (Fig. 3), there is no ambiguity about which path to choose.

For saccades between the monocular and binocular field or outside the binocular field of fixations this singular connectivity does obviously not exist because the Helmholtz-circle of binocular positions is not a direction-circle for eye movements. Saccade thus may start from or land on a Listing-position in near vision that cannot be fused for physical reasons, in which case Donders’ law just holds for each eye separately. In contrast to far vision, the binocular extension of Donders’ law requires an extra effort of the brain to fuse the images of the two eyes to establish stereoscopic vision.

Possible role of Donders-Listing kinematics on binocular perception

The Donders-Listing kinematics of the eyes implies that vertical rotations typically occur in planes that are tilted about the vertical axis towards the Helmholtz plane of binocular positions in the visual field. Viewed in frontal projection, the tangential lines to Listing-positions on the vertical direction-circles thus increasingly incline towards the Helmholtz-circle with increasing eccentricity of visual lines (Fig. 3), thus describing a systematic torsional gradient of disparities that ultimately drives the torsion of the eyes. Since ocular torsion can only locally eliminate these disparities, the fusion of the disparate monocular target images in near vision is bound to interfere with the perception of the visual field in specific ways. One well-studied example is the perception of verticality, which has been shown to deviate from the physical vertical in near vision as might be expected from the distribution of torsional disparities along the Helmholtz-circle in symmetric vergence (Fig. 11). The possible influence of torsional disparity gradients across the binocular visual field on perception remains to be investigated (for a review on binocular vision, see Howard and Rogers 1995).

Appendix

For computing rotations in three-dimensional Euclidean space we used the associated Clifford algebra that is generated by the three numbers \( \hat{\gamma}_1, \hat{\gamma}_2, \hat{\gamma}_3 \) and unity I, which are defined by the properties \( (\hat{\gamma}_j^2) = 1 \) (identity) and \( \hat{\gamma}_j \hat{\gamma}_k \hat{\gamma}_j = 2\delta_{jk}I \) with \( \delta_{jk} = 1 \) for \( j = k \) and

\[ \delta_{jk} = 0 \] for \( j \neq k \].
\[ \delta_{jk} = 0 \text{ if } j \neq k \text{ (Snygg 1997).} \]

Using these numbers, we represented the unit gaze vector \( \hat{\mathbf{g}} \) by replacing the Cartesian basis vectors \( \mathbf{e}_i \) with the basis 1-vectors \( \hat{\mathbf{y}}_i \), which can be conveniently represented by 4x4 Dirac matrices. In this basis the 2-vectors \( \hat{\mathbf{y}}_{23} = \hat{\mathbf{y}}_2 \hat{\mathbf{y}}_3 \), \( \hat{\mathbf{y}}_{31} = \hat{\mathbf{y}}_3 \hat{\mathbf{y}}_1 \), and \( \hat{\mathbf{y}}_{12} = \hat{\mathbf{y}}_1 \hat{\mathbf{y}}_2 \) represent the frontal, vertical and the horizontal plane, respectively.

A rotation of a 1-vector \( x \) through angle \( \chi \) in the plane \( \hat{\mathbf{A}} = \hat{\mathbf{y}}_{\alpha\beta} \) spanned by the two 1-vectors \( \hat{\mathbf{y}}_{\alpha} \) and \( \hat{\mathbf{y}}_{\beta} \) with \( \| \hat{\mathbf{A}} \| = 1 \) is obtained by the conjugation \( R_{\hat{\mathbf{A}}} (\chi) x R_{\hat{\mathbf{A}}}^{-1} (\chi) = x' \) with the operator

\[ R_{\hat{\mathbf{A}}} (\chi) = I \cos(\chi / 2) - \sin(\chi / 2) \hat{\mathbf{y}}_{\alpha\beta} \].

The inverse of \( R_{\hat{\mathbf{A}}} \) is \( R_{\hat{\mathbf{A}}}^{-1} (\chi) = R_{\hat{\mathbf{A}}} (-\chi) \).

**Helmholtz kinematic model**

The Helmholtz kinematic model as defined in this study consisted of a compounded rotation of the eye, which moved in case of the right eye the gaze line in the horizontal plane of regard from \( \overline{O_aO} \) to \( \overline{O_aA} \) through the azimuth \( \alpha \) (denoted \( R_{\alpha\theta} \)) and subsequently in the vertical plane from \( \overline{O_aA} \) to \( \overline{O_aC} \), where \( C \) is a binocular position on the Helmholtz-circle, through the elevation angle \( \eta_a \) (denoted \( R_{\eta\alpha} \)). An analogous compounded rotation was used for the left eye (see Figs. 1 to 4). Gaze trajectories were reconstructed step by step using the compounded rotation operator \( R_{\eta\alpha\theta} \) (for notational simplicity we write in the following formulas ‘\( \eta \)’ instead of ‘\( \eta_a \)’):

\[
R_{\eta\alpha\theta} = R_{\eta\alpha} (\eta) R_{\alpha\theta} (\alpha) = (I \cos \eta / 2 - \sin \eta / 2 \hat{\mathbf{y}}_{31}) (I \cos \alpha / 2 - \sin \alpha / 2 \hat{\mathbf{y}}_{12})
\]

\[
= I \cos \eta / 2 \cos \alpha / 2 - \sin \eta / 2 \sin \alpha / 2 \hat{\mathbf{y}}_{23} - \sin \eta / 2 \cos \alpha / 2 \hat{\mathbf{y}}_{31} - \cos \eta / 2 \sin \alpha / 2 \hat{\mathbf{y}}_{12}.
\]

With the rotation angle \( \chi / 2 = \cos^{-1} (\cos \eta / 2 \cos \alpha / 2) \), we can write this compounded rotation in standard format \( R_{\eta\alpha\theta} = I \cos \chi / 2 - \sin \chi / 2 \hat{\mathbf{y}}_{\eta\alpha\theta} \), where \( \hat{\mathbf{y}}_{\eta\alpha\theta} = \sum_i \eta_i \hat{\mathbf{y}}_{jk} \) is the rotation plane.

The unit vector

\[
\hat{\mathbf{g}} = \sum_{i=1}^{3} g_i \hat{\mathbf{e}}_i
\]

represents the unit gaze vector in the Cartesian basis.
\[ \hat{n} = \frac{1}{\sqrt{1 - \cos^2 \eta/2 \cos^2 \alpha/2}} \{ \sin \eta/2 \sin \alpha/2 \hat{e}_1 + \sin \eta/2 \cos \alpha/2 \hat{e}_2 + \cos \eta/2 \sin \alpha/2 \hat{e}_3 \} \]

describes the orientation of the rotation plane in the Cartesian frame \( \hat{e}_1 \) (straight ahead), \( \hat{e}_2 \) (leftward, parallel to the inter-ocular line), and \( \hat{e}_3 \) (upward). Note that in this model torsion is generated proportional to \( \sin \eta/2 \sin \alpha/2 \). Analogous formulas hold for the left eye with azimuth \( \beta \) and elevation \( \eta = \eta_b \).

**Donders-Listing kinematics**

The Donders-Listing kinematics used in this study consisted of a rotation in the horizontal plane of regard, exerted by a rotation operator \( R_{AO} \), followed by a rotation in the vertical direction-plane, exerted by a rotation operator denoted \( R_{BA} \). The direction-planes of the eye, denoted by \( \hat{\gamma}_{DL} \), in the following, are in general linear combinations of the frontal plane (\( \hat{\gamma}_{23} \)), the vertical plane (\( \hat{\gamma}_{31} \)) and the horizontal plane of regard (\( \hat{\gamma}_{12} \)), that is \( \hat{\gamma}_{DL} = \sum_i d_i \hat{\gamma}_i \) (\( i \neq j \neq k \)).

In the horizontal plane of regard we have for the right eye with azimuth \( \alpha \) (Fig. 4)

\[
\hat{\gamma}_{DL} = R_{AO} \hat{\gamma}_{31} R_{AO}^{-1} = (I \cos \alpha/4 - \sin \alpha/4 \hat{\gamma}_{12}) (I \cos \alpha/4 + \sin \alpha/4 \hat{\gamma}_{12}) = -\hat{\gamma}_{23} \sin \alpha/2 + \hat{\gamma}_{31} \cos \alpha/2
\]

An analogous relation holds for the left eye with azimuth \( \beta \).

Rotations of the right eye (and similarly of the left eye) moving the gaze line in the horizontal plane of regard from \( \overrightarrow{O_aO} \) to \( \overrightarrow{O_aA} \) through the azimuth \( \alpha \) and further in the vertical direction-plane from \( \overrightarrow{O_aA} \) to \( \overrightarrow{O_aB_a} \) through the elevation angle \( \eta_a \) were simulated with the compound rotation operator \( R_{BAO} \) (for notional simplicity we use ‘B’ instead of ‘Ba’ and ‘\( \eta \)’ instead of ‘\( \eta_a \)’ for the right eye as shown in Fig. 4):

\[
R_{BAO} = R_{B_3} (\eta) R_{AO} (\alpha) = (I \cos \eta/2 - \sin \eta/2 \hat{\gamma}_{DL}) (I \cos \alpha/2 - \sin \alpha/2 \hat{\gamma}_{12})
\]

\[
= I \cos \eta/2 \cos \alpha/2 - (\sin \eta/2 \hat{\gamma}_{31} + \cos \eta/2 \sin \alpha/2 \hat{\gamma}_{12})
\]

With the rotation angle \( \chi/2 = \cos^{-1} (\cos \eta/2 \cos \alpha/2) \), we can write this compound rotation in standard format \( R_{BAO} = I \cos \chi/2 - \sin \chi/2 \hat{\gamma}_{BAO} \), where \( \hat{\gamma}_{BAO} = \sum_i \eta_i \hat{\gamma}_i \) is the rotation plane.
The unit vector \( \hat{n} = \frac{1}{ \sqrt{1 - \cos^2 \eta/2 \cos^2 \alpha/2}} \{ \sin \eta/2 \hat{e}_2 + \cos \eta/2 \sin \alpha/2 \hat{e}_3 \} \) describes the orientation of the rotation plane in the Cartesian frame \( \hat{e}_1 \) (straight ahead), \( \hat{e}_2 \) (leftward, parallel to the inter-ocular line), and \( \hat{e}_3 \) (upward). Note that \( R_{\text{BAO}} \) does not generate torsion.

**Donders-Listing model**

The Donders-Listing model combines the Donders-Listing kinematics with rotations of the eye in a common fronto-parallel plane, which fuse the disparate target images of the right and left eye. The rotation that moves the gaze line of the right eye through the angle \( \omega_a \) from \( \overrightarrow{OB} \) to \( \overrightarrow{OC} \) is 

\[
R_{\text{CB}}(\omega_a) = (I \cos \omega_a/2 - \sin \omega_a/2 \hat{y}_{21}) (I \cos \eta/2 - \sin \eta/2 \hat{y}_{DE}) (I \cos \alpha/2 - \sin \alpha/2 \hat{y}_{12})
\]

\[
= I \cos \chi_{\omega_a}/2 - \sin \chi_{\omega_a}/2 \hat{y}_{\text{CBAO}}
\]

where \( \chi_{\omega_a}/2 = \cos^{-1} (\cos \omega_a/2 \cos \eta/2 \cos \alpha/2) \) is the rotation angle and \( \hat{y}_{\text{CBAO}} = \sum n_i \hat{y}_i \) rotation plane. The unit vector \( \hat{n}_{\omega_a} = \frac{1}{ \sqrt{1 - \cos^2 \omega_a/2 \cos^2 \eta/2 \cos^2 \alpha/2}} \sum n_i \hat{e}_i \) has the Cartesian coefficients \( n_1 = \sin \omega_a/2 \cos \eta/2 \cos \alpha/2 \), \( n_2 = \cos \omega_a/2 \sin \eta/2 - \sin \omega_a/2 \cos \eta/2 \sin \alpha/2 \) and \( n_3 = \cos \omega_a/2 \cos \eta/2 \sin \alpha/2 + \sin \omega_a/2 \sin \eta/2 \). The tilt angle of the rotation plane relative to the vertical-horizontal rotation plane is

\[
\tan \tau_{\omega_a} = \left( \frac{n_1^2 + n_3^2}{n_2^2} \right) = \left( \frac{\sin \omega_a/2 \cos \eta/2 \cos \alpha/2}{\sqrt{1 - \cos^2 \omega_a/2 \cos^2 \eta/2 \cos^2 \alpha/2}} \right) / \sqrt{1 - \cos^2 \eta/2 \cos^2 \alpha/2} \]

Note that the tilt is zero for zero elevation because the torsion required for binocular vision vanishes as the elevation approaches zero. The same is true for version movements in far vision where \( \alpha = \beta \).
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Figure Captions

Figure 1: Locus of visual targets at constant distances relative to the centers of rotation of the right and left eye. Binocular targets at constant distances ‘a’ and ‘b’ relative to the two centers of rotation O_a and O_b are located on the circle of intersection of the two imaginary shells drawn around O_a and O_b with radius ‘a’ and ‘b’. We call this circle Helmholz-circle for short (indicated by arrow heads). It intersects the horizontal plane of regard at the two antipodal positions A and A’’ (gray line segment AA’’). The forward position A also determines the azimuth of the vertical direction-circles associated to O_a and O_b (shown in white). Abbreviations: R, right; L, left; N, north; O, fixation point straight ahead of the right eye.

Figure 2: Locus of visual targets at constant distances relative to the eyes’ centers of rotation. A: Front view of a binocular target (C’’) located on the Helmholz-circle (thick gray line indicated by arrow heads). B: Top view onto the horizontal plane of regard. The Helmholz-circle intersects with this plane at the two positions A and A’’ (thick gray line segment AA’’). Binocular targets on the Helmholz-circle have constant distances ‘a’ and ‘b’ from the two centers of rotation O_a and O_b, respectively. The gaze lines to these binocular targets all subtend a constant vergence angle γ. Abbreviations: C’, C’’, projections of C onto the frontal and horizontal plane of regard; k, inter-ocular distance; α, β, azimuth angles relative to O_a and O_b; a, b, target distances to O_a, O_b; γ =α-β, vergence angle; R, right; L, left; N, north; O, fixation point straight ahead of the right eye; F, rear fixation point of right eye.

Figure 3: Binocular target- and neighboring Listing-positions at constant distances from each eye (rotation centers O_a and O_b). A, 3D view: Binocular target C on the Helmholz circle (black circle indicated by arrow head) through A in the horizontal plane of regard (plane through R, A and, L). The associated Listing-positions B_a and B_b are located at the intersection of the fronto-parallel plane through C and the respective vertical direction-circles through A (white circles). B, frontal view: The four Listing-positions B_a, B_b, B_a’, B_b’ are located at the intersections of the vertical direction-circles (here appearing as ellipses) with circles concentric with straight ahead that intersect with each other at the binocular position C (not labelled in this projection). Abbreviations: R, right; L, left; N, north. For more detailed explanations, see Methods.

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4 Since the nodal point of the eye does not coincide with the center of rotation, gaze lines passing through the center of rotation as defined here differ from visual lines that by definition pass through the nodal point.
Figure 4: Donders-Listing model of far-near re-fixation saccades in the spherical field of
fixations. Any rotation that moves the gaze line to a binocular positions on the Helmholtz-
circle (thick gray line) can be compounded by a horizontal rotation moving the gaze line from
its initial position OaO through the angle $\alpha$ to OaA in the horizontal plane of regard (panel A),
followed by a vertical rotation of the gaze line in the vertical direction-plane $F_aAB_a$ through
the angle $\eta_a$ to position $B_a$ (panel C), and finally a rotation in a fronto-parallel plane $N_aB_aC$
through the angle $\omega_a$ moving the tip of the gaze line from $B_a$ to $C$ (panel B). The motion
parameters for these rotations are obtained from the intersection of the Helmholtz-circle with
the horizontal plane of regard and the fronto-parallel plane through the intermediate position
$B_a$ and the target $C$ (for more details, see text).

Figure 5: Reconstructing the horizontal, vertical and torsional components of far-near re-
fixation saccades. A to C: Experimental data represented in gray are superimposed by black
traces obtained by solving the equation $R_{eye} = R_F R_{DL}$ using the horizontal, vertical and
torsional excursion of each eye. Torsion of the right eye was initially always increasing,
peaking at about 0.1 s before settling to smaller final values. Similarly, torsion of the left eye
was initially always decreasing, reaching a minimum at about 0.1 s before increasing towards
final less negative values. Positive (negative) horizontal movements are from the right (left)
eye. Vertical movements are shown only for the right eye because of the largely overlapping
right and left vertical excursions. D: Same experimental torsion as in C plotted against
normed target distance. Note the slow build-up of and abrupt change in torsion direction
shortly before the gaze lines hit the target. Data from monkey M1 (mean vergence 15.5\degree
$\pm 0.4\degree$, $N = 10$); RE, right eye; LE, left eye.

Figure 6: Spatial orientation of rotation planes according to the Helmholtz kinematic model
and the Donders-Listing model during far-near re-fixation saccades. A to C, top panels:
Simulations of the Donders-Listing model (black traces) superimposed on experimental data
(gray traces). A (top panel), The torsion of the right eye increased up to a peak value where it
started abruptly to decrease (right bundle of traces in A with sharp left turns on top). The
opposite is true for the left eye torsion (left bundle of traces with sharp right turns on top). B,
C (top panels): Right eye traces with positive-going, left eye traces with negative-going
horizontal amplitudes. A to C, bottom panels: Simulations of the Helmholtz kinematic model.
A, B (bottom panels), Traces shift in torsion but here is no modulation during the simulated
saccades (black traces for right, gray traces for left eye). C (bottom panel), Simulations in
frontal projection (black traces) approximately match experimental data (gray traces). Same
experimental data set as in Fig. 5; RE, right eye; LE, left eye.
Figure 7: Top: Orientation of the horizontal-vertical rotation plane relative to the frontal plane as a function of target distance (right eye, black traces; left eye, gray traces). Time flows from right to left. Bottom: Average time from saccade onset to end plotted against normed target distance (mean, black trace; ±SD, gray traces); same experimental data as in Figs. 5 and 6; RE, right eye; LE, left eye.

Figure 8: Azimuth and ω-torsion of the right (black traces) and left eye (gray traces) in the time-and space-domain. In comparison to the modulation of vergence of the eyes (panel A, B), the ω-torsion typically emerged with a delay of a few tens of milliseconds (compare arrow heads), built up rapidly and remained stable in the post-saccadic interval (panel C, D). Same experimental data set as in Figs. 5 to 7. The average delay (±SD) for crossing the levels of ±0.01° relative to saccade onset was 10.6ms (±5.2) and 5.9ms (±2.9) for the azimuth and 44.4ms (±5.8) and 39.1ms (±5.8) for the ω-torsion of the right and left eye, respectively (N =25) ; RE, right eye; LE, left eye.

Figure 9: Time-course of coarse and fine-tuned cyclo-vergence showing data from all three animals. Note the delayed onset of fine-tuned versus coarse cyclo-vergence (compare arrow heads). The average delay (±SD) for crossing the level 0.01° relative to saccade onset was 3.3ms (±1.2), 2.7ms (±1.2), and 8.3ms (±1.7) for cyclo-vergence and 32.8ms (±5.4), 45.8ms (±18.3), and 36.6ms (±6.1) for the ω-cyclo-vergence. Mean vergence (±1SD) of re-fixation saccades 13.9°±0.72° (N =19) in A (M3), 16.2°±0.30° (N =16) in B (M2), 18.5°±0.42° (N =26) in C (M1, same animal as in Figs. 5 to 8 but different set of saccades).

Figure 10: Spatial characteristics of ω-torsion. A, Normed target space (x, y, z) with eye-to-target distance (x), horizontal direction (leftward positive, y), and vertical direction (upward positive, z) displaying two clusters of saccade end positions located in overlapping depth planes but segregated in horizontal direction. Rotation center of right eye located at origin (x, y, z) = (0, 0, 0), of left eye located at (x, y, z) = (0, 1, 0); target distance in units of inter-ocular distance. B, ω-torsion (positive: right; negative: left eye) increased in magnitude exponentially with depression and shifted with the eye’s azimuth. C, ω-torsion (positive: right, negative: left eye) decreased exponentially in magnitude as a function of target distance and shifted with the eye’s azimuth. Data from monkey M1 (N =204); exponential fits of ω-torsion as a function of distance, ω =ω0 exp (-d/λ) and elevation, ω =ωoff exp (-η/k). Cluster 1 (black), right eye: (ω0, λ) = (0.41°,-1.8), r² =0.62; (ωoff, k) = (0.1°,6.6), r² =0.75; left eye: (ω0, λ) = (-0.51°,-1.3), r² =0.71; (ωoff, k) = (-0.1°,6.1), r² =0.94. Cluster 2 (gray), right eye: (ω0, λ)
Figure 11: Comparison of two-dimensional disparities of single targets created by the Helmholtz kinematic model and the Donders-Listing model. 

**A.** Helmholtz kinematic model with $\alpha = 5^\circ$, $\beta = -20^\circ$ (H1), $\alpha = -\beta = 10^\circ$ (H0), and $\alpha = 20^\circ$, $\beta = -7.5^\circ$ (H2). The target images align on the Helmholtz-circle H0, H1 and H2, irrespective of the eyes’ vertical position, which was varied between $0^\circ$, $15^\circ$, $30^\circ$ and $45^\circ$ down. Symmetric vergence $20^\circ$: open circles, target images from the right and left eye on H0; asymmetric vergence $25^\circ$ (H1), and $27.5^\circ$ (H2): black dots, target images from right eye; gray dots, target images from left eye. Note zero disparity of projected targets in the horizontal plane of regard.

**B.** Donders-Listing model with same angular parameters. Target images fall to either side of the respective Helmholtz-circle, depending on the eye-to-target distance, except for targets in the horizontal plane of regard with zero disparity. Note the symmetric torsional disparities for symmetric vergence. After torsional fusion, targets images align with the respective Helmholtz-circles (white dots).

Normed planar projection map of right and left retina: right center of rotation at horizontal meridian 0, left center of rotation at 1; iso-eccentricity circles relative to right center in black, relative to left center in gray.

Figure 12: Simulation of $\omega$-torsion required for target fusion in the Donders-Listing model. The array of exponential curves are iso-elevation curves showing the $\omega$-torsion as a function of normed target distance for viewing $0^\circ$ (straight ahead) to $30^\circ$ down in $5^\circ$ steps. The vertical-oriented array of curves represents iso-azimuth curves connecting points of equal azimuth from $15^\circ$ at the closest distance down to $2^\circ$ at the largest distance in $1^\circ$ steps.
Table Captions

Table 1: Parameter ranges of re-fixation saccades. In monkey 2 re-fixation saccades were tested to a near target in the lower (M2, first row) and the upper visual hemi-field (M2, second row). Abbreviations: $\alpha, \beta$, azimuth of the right, left eye; $\eta = \eta_a$ or $\eta_b$, depression of the right, left eye.

Table 2: A, Root-mean square errors of Donders-Listing model showing mean values ±SD. B, Root-mean square errors of Helmholtz kinematic model showing mean values ±SD. Note the large root-mean square error in torsion. In monkey 2 re-fixation saccades were tested to a near target in the lower (M2, first row) and the upper visual hemi-field (M2, second row).

Footnotes

1. In geometric terms the cross product of two unit vectors $e_i \times e_j$, ($i \neq j$) represents an oriented unit plane. Indeed the exterior product $\hat{e}_p = \hat{e}_i \wedge \hat{e}_j$ (bivector) is related to the cross product by $\hat{e}_i \times \hat{e}_j = -(\hat{e}_i \wedge \hat{e}_j)\hat{e}_{123}$, using the 3-dimensional pseudo-scalar $\hat{e}_{123} = \hat{e}_1 \hat{e}_2 \hat{e}_3$.

2. Since the nodal point of the eye does not coincide with the center of rotation, gaze lines passing through the center of rotation as defined here differ from visual lines that by definition pass through the nodal point.

3. Superscripts ‘a’ and ‘b’ enter parentheses indicate that the coordinates of a particular binocular position $C$ are taken relative to the rotation center $O_a$ or $O_b$, respectively.

4. There is a pair of Listing-positions that share the same fronto-parallel depth plane with a binocular target of interest, one in the upper and one in the lower visual plane. Only one of these positions is close to the target.
A

Target shell around $O_b$

Helmholtz circle

$N_a$

Target shell around $O_a$

B

$N_a$

$N_b$

$O_b$

$B_b$

$B_b'$

$a$

$k$

$b$
A: Horizontal plane of regard

B: Fronto-parallel plane

C: Vertical direction-plane
distance to target-shells (interocular units)
Table 1: Parameter ranges of re-fixation saccades

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Table 2: A. Root-mean square errors of the Donders-Listing model

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Table 2: B. Root-mean square errors of the Helmholtz kinematic model

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