Three-dimensional visuo-motor control of saccades

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Hess BJ. Three-dimensional visuo-motor control of saccades. J Neurophysiol 109: 183–192, 2013. First published October 10, 2012; doi:10.1152/jn.00513.2012.—Although the motion of the line of sight is a straightforward consequence of a particular rotation of the eye, it is much trickier to predict the rotation underlying a particular motion of the line of sight in accordance with Listing’s law. Helmholtz’s notion of the direction-circle together with the notion of primary and secondary reference directions in visual space provide an elegant solution to this reverse engineering problem, which the brain is faced with whenever generating a saccade. To test whether these notions indeed apply for saccades, we analyzed three-dimensional eye movements recorded in four rhesus monkeys. We found that on average saccade trajectories closely matched with the associated direction-circles. Torsional, vertical, and horizontal eye position of saccades scattered around the position predicted by the associated direction-circles with standard deviations of 0.5°, 0.3°, and 0.4°, respectively. Comparison of saccade trajectories with the likewise predicted fixed-axis rotations yielded mean coefficients of determinations (±SD) of 0.72 (±0.26) for torsion, 0.97 (±0.10) for vertical, and 0.96 (±0.11) for horizontal eye position. Reverse engineering of three-dimensional saccadic rotations based on visual information suggests that motor control of saccades, compatible with Listing’s law, not only uses information on the fixation directions at saccade onset and offset but also relies on the computation of secondary reference positions that vary from saccade to saccade.

eye movements; Listing’s law; reference positions; motor error; computational model

SACCADE EYE MOVEMENTS quickly redirect the line of sight from one visual target to the next by transforming visual information into precise motor commands. After each saccade, the actual ocular orientation at the newly acquired fixation position must be known to the brain to keep track of self-orientation in space and for controlling coordinated visually guided movements. The actual orientation at the end of each saccade is also important for proper object perception. Although the underlying mechanisms are probably primarily mediated by corollary discharge of the motor commands to the ocular plant (Duhamel et al. 1992; Guthrie et al. 1983; Sommer and Wurtz 2008), there is to date little information about the nature of these signals. Since each of the three rotational degrees of freedom of the eye ultimately affects visual spatial orientation, corollary discharge likely must mediate information about three-dimensional (3D) eye position relative to space (Ghasia et al. 2008). As saccades typically occur in sequences, updating mechanisms must be not only fast but also robust in the face of error accumulation. In contrast to premotor control, eye position representations in higher cortical centers down to the level of the superior colliculus operate in 2D visual rather than 3D motor coordinates (Hepp et al. 1993; Klier et al. 2003; Van Opstal et al. 1991). There is, however, a well-founded “motor” theorem due to H. von Helmholtz, which he established in his famous study of visual afterimages (von Helmholtz 1867), that may shed new light on the visuo-motor side of eye position updating: “The prolongation of all circular arcs in the spherical field of fixations, which are described by the line of fixation in turning around a fixed axis according to Listing’s law, will pass through the occipital point of fixation.” Helmholtz called these lines of fixation direction-circles, a notion that in fact provides the missing link between Listing’s law in motor control and vision. In motor terms, Listing’s law can be dissected into two conditions as follows: First in primary position, the axis of rotation to any other eye position must be perpendicular to primary gaze direction. Second, the axis of any further rotation into a different direction must lie in the plane perpendicular to the first one and be tilted by half the angle of eccentricity reached after the first rotation. Translated into visual terms, the first condition means that the line of sight must follow a great circle in the spherical field of fixations whose plane includes primary gaze direction (e.g., saccade from O to A in Fig. 1). The second condition means that, further, it must follow a direction-circle whose plane is normal to the great circle plane containing primary gaze direction in order to reach the next target in fixation space (saccade from A to B in Fig. 1). Although these two conditions unequivocally specify Listing’s coordinates in visual space, they have the following, at first sight paradoxical, consequence: In a sequence of saccades starting from primary position, the two Listing conditions seem to implicate that among the infinitively many potential targets only a vanishing fraction can directly be reached without violating Listing’s law, namely, those lying on the direction-circle in the plane normal to the great circle arc that connects saccade onset with primary gaze direction (e.g., saccade from A to B but not from A to B’, Fig. 1). Conceiving the rotation from A to B’ as the result of composing the rotation from A to O and the rotation from O to B’ does not really resolve the paradox (although it preserves Listing’s law) because it leads to the absurd consequence that motions of the line of sight, even along the same single direction-circle, require a complex computation of a series of rotations back and forth between positions on the direction-circle and the primary position.

Here we show by analyzing 3D eye movements recorded in rhesus monkeys that sequences of saccades indeed closely follow the direction-circles associated with their respective onset and offset positions. However, in order to reach targets that do not fall on the respective normal direction-circles (e.g., target B’ in Fig. 1), we provide evidence that motor control refers the actual rotation of the eye to the ocular orientation at specific positions on the direction-circles that serve as secondary reference positions next to the primary position (e.g.,...
star-labeled position in Fig. 1). The benefit of this increased computational load is that updating 3D eye position at the end of each saccade can be achieved by a simple algorithm. The resulting control principles bear on the neural mechanisms, which implement visuo-motor transformations in Listing coordinates.

Glossary

\( \hat{e}_i \)  
Head-fixed Cartesian coordinates \((i = 1, 2, 3)\)

\( \hat{e}_\alpha \)  
Head-fixed spherical polar coordinates \((\alpha = r, \theta, \phi)\)

\( \hat{g} \)  
Unit vector parallel to the line of sight (specifying the current fixation point)

\( \hat{n} \)  
Unit vector parallel to rotation axis

\( \hat{\gamma}_i \)  
1-Vectors (Dirac), expressed in Cartesian coordinates \((i = 1, 2, 3)\)

\( \hat{\gamma}_\alpha \)  
1-Vectors (Dirac), expressed in spherical polar coordinates \((\alpha = r, \theta, \phi)\)

\( \hat{\gamma}_k \)  
2-Vectors, expressed in Cartesian coordinates \((i, k = 1, 2, 3)\)

\( \hat{\gamma}_{\alpha \beta} = \hat{\gamma}_\alpha \hat{\gamma}_\beta \)  
2-Vectors, expressed in spherical polar coordinates \((\alpha, \beta = r, \theta, \phi; \alpha \neq \beta)\)

\( O \)  
Fixation point in primary gaze direction

\( A, B \)  
Arbitrary fixation positions (in nonprimary directions)

\( N \)  
Normal position on direction-circle

\( \rho \)  
Rotation angle (used in single-axis rotations)

\( \eta \)  
Rotation angle subtended by the great circle arc connecting \( O \) to \( A \)

\( \xi \)  
Rotation angle subtended by the direction-circle arc connecting \( A \) or \( N \) to \( B \)

\( \varepsilon = \eta/2 \)  
Half-angle rule

MATERIALS AND METHODS

Subjects. Four female rhesus monkeys (Macaca mulatta) were chronically implanted with skull bolts for head restraint and dual search coils implanted under the conjunctiva for 3D eye movement recording as described previously (Hess 1990). All procedures conformed to the National Institutes of Health Guide for the Care and Use of Laboratory Animals and were approved by the Veterinary Office of the Canton of Zurich.

Recording and representation of 3D eye position. Spontaneous eye movements were recorded in four female Rhesus monkeys, while they were looking around, sitting in a primate chair with the head restrained. To evoke movements in all directions, the experimenter was standing ~1.8 m in front of the animal, facing away from it and trying to attract its attention by waving with a stick and tapping on the wall at various locations for up to 3 min. 3D eye positions were recorded by the magnetic search coil method (Robinson 1993) with an Eye Position Meter 3000 (Skalar). Eye position was calibrated as previously described (Hess et al. 1992), digitized at a sampling rate of 833.33 Hz (Cambridge Electronic Design 1401plus), and stored on a computer for off-line data analysis. All eye positions were expressed in Listing coordinates based on the best fit plane through spontaneous eye movements recorded in each experimental session. The onset and offset of saccades were isolated by a semiautomatic procedure based on the magnitude of the jerk (derivative of angular eye acceleration), followed by application of an empirically adjusted position threshold based on the relative change in magnitude of the eye position vector. Saccades with amplitudes <1° were discarded.

3D eye positions\(^1\) 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 unit length parallel to the axis of rotation \( \hat{E} \) (Hausen 1989). Torsional eye position, \( \hat{E}_{\hat{n}} \), is the rotation of the eye about an axis \( \hat{e} \) normal to the head’s frontal plane (clockwise positive), vertical eye position, \( \hat{E}_{\hat{N}} \), is the rotation about an axis \( \hat{e}_N \) normal to the sagittal plane (downward positive), and horizontal eye position, \( \hat{E}_{\hat{A}} \), is the rotation about an axis normal to both \( \hat{e}_N \) and \( \hat{e}_V \) (leftward positive). A rotation (saccade) from position \( A \) to \( B \) relative to primary position \( O \), denoted \( \hat{E}_{\hat{BA}} \), is the composition of a rotation from \( O \) to \( A \), followed by a rotation from \( A \) to \( B \): \( \hat{E}_{\hat{BA}} = \hat{E}_{\hat{AO}} \hat{E}_{\hat{BA}} := (\hat{E}_{\hat{BA}} \cdot \hat{E}_{\hat{AO}})/(1 - \hat{E}_{\hat{BA}} \cdot \hat{E}_{\hat{AO}}) \times \) vector product, dot product (Hausen 1989).

In the following, we refer to the three parameters (angle of rotation, direction cosines of rotation axis) that are required to define rotation vectors (or unit quaternions; Tweed et al. 1990) in 3D space as motor coordinates. For studying saccades in visual space we use Clifford numbers to represent rotations, with the advantage that they can easily be used to describe rotations on a curved surface like the spherical field of fixations. We refer to the two parameters needed to determine the location of a fixation point (or direction) in 2D visual space as visual coordinates. Note that the two coordinate systems can be thought of sharing the same origin (head-fixed and orbit-centered to the eye) as indicated in Fig. 1. The distinction between motor and visual coordinates, however, is not strict because they may share the same polar coordinates to define the line of sight and the direction cosines of rotation axes as outlined in the next section.

Motion of the line of sight associated to 3D ocular rotations. The Clifford algebra of rotations (Clifford 1882; Snygg 1997) uses a multiplicative unit, denoted \( \theta \), and so-called 1-vectors or Dirac vec-

\(^1\) We denote vectors as bold letters and represent the components for convenience as row vectors. Entities marked with a caret denote unit vectors. Estimated and reverse-computed entities are marked with a tilde.
tors, denoted \( \hat{\gamma}_1, \hat{\gamma}_2, \) and \( \hat{\gamma}_3. \) Using these basic entities one derives the 2-vectors (or bivectors) \( \hat{\gamma}_a, \) defined as \( \hat{\gamma}_a = \hat{\gamma}_a \hat{\gamma}_a, \) according to the rules \( \langle \hat{\gamma}_a \hat{\gamma}_b \rangle = I \) (unity) and \( \hat{\gamma}_a \hat{\gamma}_b = -\hat{\gamma}_b \hat{\gamma}_a \) (for \( i \neq k; i, k = 1, 2, \) or 3).

To relate gaze shifts in visual space to the underlying rotations of the eye, we use a unity gaze vector, \( \hat{g} = \sum_{i=1}^{3} g_i \hat{e}_i, \) to represent the line of sight. Replacing the Cartesian basis vectors \( \hat{e}_i \) by the Dirac vectors \( \hat{\gamma}_i, \) we write \( \hat{g} = \sum_{i=1}^{3} g_i \hat{\gamma}_i \) with the same components \( g_1 = \cos \phi, \) \( g_2 = -\sin \phi \sin \theta, \) and \( g_3 = \sin \phi \cos \theta. \) A rotation of the gaze vector through the angle \( \rho \) about the \( \hat{n} \) axis is obtained by the operation \( \hat{g}' = R \hat{g} R^{-1}, \) where \( R = 1 \cos(\rho/2) - \sin(\rho/2)(n_1 \hat{\gamma}_23 + n_2 \hat{\gamma}_31 + n_3 \hat{\gamma}_12) \) and \( R^{-1} = R(n, -\rho). \) In the quaternion formalism, the same rotation operator would write \( R = 1 \cos(\rho/2) + \sin(\rho/2)(n_1 i + n_2 j + n_3 k), \) using the correspondences \( i \hat{=} -\hat{\gamma}_{23}, j \hat{=} -\hat{\gamma}_{31}, \) and \( k \hat{=} -\hat{\gamma}_{12}. \) For sequences of two rotations, the rotation operation writes in the order from right to left \( R_{BAO}(\hat{g}, \eta) = R_{BA}(\hat{g}) R_{AO}(\eta): \) The first operator, \( R_{AO}(\eta), \) would rotate the gaze vector through the angle \( \eta \) from \( A \) to \( O \) about an axis, \( \hat{n}_{AO}, \) whereby \( O \) is the reference position (usually primary position). The second, \( R_{BA}(\xi), \) would rotate it further from \( A \) to \( B \) about an axis, \( \hat{n}_{BA}, \) through the angle \( \xi. \) More explicitly, this 2-rotation sequence writes:

\[
R_{BAO}(\xi, \eta) = (I \cos(\xi/2) - \sin(\xi/2) \hat{\gamma}_\theta)(I \cos(\eta/2) - \sin(\eta/2) \hat{\gamma}_\phi)
\]

(1)

thus providing the gaze direction \( \hat{g}' = R_{BAO} \hat{g} R_{BAO}^{-1} = R_{BA} R_{AO} R_{AO}^{-1} R_{BA}^{-1}. \)

Here \( \gamma_\theta = \gamma_\phi \hat{\gamma}_3, \) and \( \gamma_\phi = \hat{\gamma}_3 \hat{\gamma}_\phi, \) with the tangent vectors \( \hat{\gamma}_i = \partial \tilde{g}/\partial \hat{\gamma}_i = \hat{g}, \) \( \hat{\gamma}_e = \partial \tilde{g}/\partial \hat{\gamma}_e = \hat{g}, \) and \( \gamma_\phi = \partial \tilde{g}/\partial \hat{\gamma}_\phi \) that point along the polar coordinate axes \( \hat{e}_r, \hat{e}_\theta, \) and \( \hat{e}_\phi \) in the direction of increasing \( r, \theta, \) and \( \phi. \) Note that \( \hat{e}_\phi \) is taken parallel to the line of sight, \( \hat{g}. \) Using the multiplication rules, \( \hat{\gamma}_\theta \hat{\gamma}_i \) and \( \hat{\gamma}_\phi \hat{\gamma}_i \) can be expressed in terms of the basic \( \hat{\gamma}_a. \) To conform to Listing’s law, the first rotation implied by \( R_{BAO} \) must be about an axis \( \hat{n}_{AO}, \) that is perpendicular to primary gaze direction. The second rotation must fulfill the following two conditions in terms of axis orientation: First, \( \phi = \eta/2 \) (i.e., half the rotation angle of the first rotation) and second, \( \psi = \phi_0 \) (i.e., mutual orthogonal rotation axes).

Under these two conditions, Eq. 1 becomes

\[
R_{BAO}(\xi, \eta) = \cos(\xi/2) \cos(\phi/2) + \sum_{i=1}^{3} n_i \hat{\gamma}_a \hat{\gamma}_a \sin(\xi/2) \sin(\phi/2)
\]

(2)

It involves no torsion since the axis \( n_{BAO} \) has no torsion component (although the axis of the second rotation from \( A \) to \( B \) has a nonzero torsion component, see Eq. 4). The coordinates \( \alpha \) and \( \nu \) are functions of the rotation angle \( \angle \) and the polar angles \( \phi = \eta/2 \) and \( \psi. \) For a proof that Eq. 1 indeed represents a rotation operator in standard format, see APPENDIX.

Secondary reference positions in visual fixation space. Although \( R_{BAO} \) (Eq. 1) provides an accurate description of eye movements in Listing coordinates, it only describes saccades from \( A \) to \( B \) on the direction-circle that is tangential to the Thales circle passing through \( O \) and \( A \) with center at the midpoint of the line segment \( OA. \) More generally, position \( A \) can be characterized as the unique position where the associated direction-circle intersects the great circle through

Fig. 2. Parameterization of gaze directions in the spherical field of fixations. A: the polar angle \( \phi \) (subtending the arc \( OA \) in the direction-circle) describes the eccentricity of the line of sight, relative to primary gaze direction (line segment \( EO \)); the polar angle \( \psi \) (subtending the arc \( PM \)) describes the roll angle of the plane through \( E, O, \) and \( A \) relative to the plane through \( E, O, \) and \( P. \) B: saccade trajectory from position \( A \) to \( B. \) According to Helmholtz’s theorem, the line of sight moves along the common direction-circle (outlined in white), defined by the positions \( A \) and \( B \) and the occipital point \( F. \) C: front view: the secondary reference position associated to the saccade from \( A \) to \( B \) is the position on the direction-circle, where the great circle plane through primary position intersects the direction-circle plane at a right angle. The focus of all these positions is the Thales circle through the positions \( O, A, \) and \( C. \) A. D: side view onto the great circle plane through \( O, N, \) and \( F. \) The angle subtended by the line segments \( FO \) and \( FN \) is half the angle subtended by the line segments \( EO \) and \( EN \) that parallel the respective gaze directions. The axis \( \hat{n}_{BAO} \) is normal to the line segment \( FN \) (half-angle rule). \( M_A, M_N, \) great circles associated with onset and secondary reference position of the saccade from \( A \) to \( B; P, \) north.
O and A at equal angles on either side. In the following, we describe this property in short as “A is in normal position” or “A is a normal position.” For all other saccades with onset at A, the normal positions dissociate from A. They are the points of intersection of the associated direction-circles with the Thales circle through O and A (for a geometrical proof, see APPENDIX). As the direction of a saccade starting from A approaches the great circle are OA or as the eccentricity of the fixation position A converges to zero, the associated normal positions converge toward one single point, the fixation position in primary gaze direction. In the subsequent paragraph we prove that, next to the primary position, normal positions are the reference positions for rotations of the line of sight in accordance with Listing’s law. We call the normal position associated with a saccade the secondary reference position.

Consider a normal position, labeled N, on the direction-circle of a saccade from A to B so that A ≠ N. Then one can write for the compound rotation from O to B in the order from right to left (as indicated by subscripted position labels): $R_{BANO} = R_{BA}R_{AN}R_{NO}$, where $R_{NO}$ corresponds to the rotation of the line of sight from primary position to the normal position N, $R_{AN}$ to the rotation from the normal position N to the saccade onset position A, and $R_{BA}$ to the rotation from the saccade onset position A to the offset position B. Note that the two rotation operators $R_{AN}$ and $R_{BA}$ share the same rotation axis. Therefore, we can simplify the expression by writing $R_{BANO} = R_{BN}R_{SN}$, where $R_{BN}$ is a single-axis rotation defined by $R_{BN} := R_{BA}R_{AN}$. The remaining two rotations $R_{BN}$ and $R_{NO}$ have axes perpendicular to each other, in conformity with the second Listing condition (and the prerequisites of Eq. 2). Altogether, programming a saccade from any position A to any other position B implies computing the following compound rotation operator (denoting the inverse of $R_{BA}$ by $R_{BA}^{-1}$):

$$R_{BA} = R_{BANO}[R_{AN}R_{NO}]^{-1} = R_{BN}R_{NO}R_{ON}R_{KA} = R_{BN}R_{NA} \ (3)$$

The final expression on the right-hand side shows that $R_{BANO}$ is in fact a single-axis rotation since the axes of $R_{BN}$ and $R_{NA}$ are parallel. To compute this rotation, primary position O and the normal position N need to be known. Thus normal positions associated to an eccentric fixation position serve in fact, next to primary position, as reference positions for programming the planned saccade: The axis orientation of the underlying single-axis rotation depends on the location of both the primary and the respective secondary reference position. Equation 3 also includes the special cases 1) that the saccade onset position is in normal position, i.e., $A = N$, reducing $R_{BANO}$ to $R_{AN}$ (see Eq. 2), and 2) that the normal position is identical with primary position, i.e., $N = O$, in which case A, O, and B lie on a great circle. Altogether, this analysis shows that knowledge about the coordinates of the four positions O, A, B, and N in visual fixation space suffices to program saccades in Listing coordinates. It implies controlling just 8 parameters in visual space.

Experimentally, the position vector of the secondary reference position was obtained from the gaze directions at onset $\hat{g}_A$ and at offset $\hat{g}_O$, primary gaze direction $\hat{g}_O$ and the axis of the direction-circle $\hat{f}_A = (f_A \times f_{OA}) \parallel f_{OA}$, where $f_A = \hat{g}_O + \hat{g}_A$ and $f_{OB} = \hat{g}_O + \hat{g}_B$ (see line segments $FA$, $FB$, and $EO$ in Fig. 2, A and B). While the secondary gaze direction shares the $\psi$-coordinate with this axis, the $\epsilon$-coordinate is $\epsilon = 2\cos^{-1}(\hat{g}_O \cdot \hat{f}_A - \pi/2)$ (Fig. 2, C and D). Finally, to reverse compute the onset and offset positions A and B, we used Eq. 1 and expressed the result in rotation-vector format $\hat{E}_A = \tan(\rho/2)\hat{f}_O \times \hat{g}_A$ and $\hat{E}_B = \tan(\rho/2)\hat{f}_O \parallel \hat{g}_B$ (re primary position). From these calculations,

2 Because of the spherical geometry, these angles can be greater than $\pi/2$.
3 According to Euler’s rotation theorem, any rotation of a rigid body in 3D space is equivalent to a single-axis rotation about some axis through the fixed point. Here we use the notion “single-axis rotation” if the rotation results from composing two or more rotations about one and the same axis. In this case the composition is commutative, justifying the notion “single-axis rotation” for the compound rotation.

$R_{BA}$ can be written explicitly in terms of the polar angles $\epsilon$ and $\psi$ of the respective gaze directions. Specifically, rewriting Eq. 2 in the form of $R_{BA} = R_{BAO}[R_{NO}]^{-1}$, one arrives after a few algebraic manipulations at the following equation (using the half-angle rule $\epsilon = \eta/2$):

$$\tilde{R}_{BA} = \cos(\eta/2) - \sin(\eta/2)\hat{g}_A \times \hat{g}_B$$

The angle $\xi$ is the angle required to rotate the eye from A to B about the tilted axis $\hat{g}_A$. At onset position, gaze direction is $\hat{g}_A$ = (cos 2$\xi$, −sin 2$\xi$ sin 2$\psi$, cos($\psi$)). For all other saccades with onset at $A$, the normal position $N$ is normal to the rotation axis, i.e., $R_{BA}f_A = 0$. If the angle $\eta$ remains fixed during the rotation, i.e., if $d\theta/dt$($\eta$) = 0, also the subsequent positions $f_i = \hat{g}_O + \hat{g}_i$ along the trajectory from A to B will be normal to the rotation axis. Furthermore, if the rotation is in Listing coordinates, the angular velocity is parallel to the rotation axis, i.e., $d\theta/dt$($\eta$) = 1/2$d\theta/dt$($\eta$). Thus fixed-axis-rotation saccades move the line of sight under the action of $R_{BA}$ along the associated direction-circle. Conversely, if the line of sight moves along a direction-circle, it is possible to recompute the underlying rotation $R_{BA}$ based on the trajectory in fixation space, which is independent of the actual dynamics.

Estimation of saccade trajectories along the associated direction-circles.

To test Helmholtz’s theorem for saccade trajectories, first we expressed each experimentally recorded saccade as a rotation vector relative to saccade onset. We then replaced the implicit rotation axis of $E_{BA}$ by a fixed axis obtained from the two gaze directions at saccade onset ($\hat{g}_A$) and offset ($\hat{g}_O$). This axis is $\hat{g}_{BA} = f_A \times f_B / ||f_A \times f_B||$, where we bused the vectors $f_A = \hat{g}_O + \hat{g}_A$ and $f_B = \hat{g}_O + \hat{g}_B$ on the fixed primary position $\hat{g}_O$, determined from the spontaneous eye movements. Under the same hypothesis, the dynamics and spatial characteristics of the saccade should be independent of each other. Thus we used also the angular increments of the experimentally recorded saccades, $\theta_{BA}(\eta/2)$ = tan$^{-1}(\theta_EBA/||\hat{g}_B||)$ to compute a fixed-axis rotation $E_{BA} = (E_{BA})^{i=1\ldots N} E_{BA} = \tan(\rho_{BA})/||\hat{g}_B||$ (i = 1 ... N) exhibiting comparable dynamics. For statistical comparison of the spatial characteristics of the constructed fixed-axis rotation saccade ($E_{BA}$) with the experimentally recorded saccade ($E_{BA}$), we computed the coefficients of determination for each movement component k,

$$R_k = 1 - \sum (\Delta E_k)^2 ||\Delta E_k||^2$$

where $\Delta E_k = E_{BA} - E_{BA}$ and $\Delta E_k = E_{BA} - E_{BA}$ (for i = 1 ... N) are the residual of the full and reduced model, respectively, and $E_{BA} = \sum E_{BA}$ (Anderson-Sprecher 1994).

RESULTS

Geometric properties of gaze movements across the field of fixation positions.

According to Helmholtz’s theorem, eye movements conforming to Listing’s law should fall on direction-circles in the spherical field of fixations. We thus expressed saccades in visual coordinates as motions of a point in the field of fixations, represented by the tip of the gaze vector. Representing the field of fixations as a spherical surface with the eye in the sphere’s center, we characterized saccade trajectories by the eccentricity ($\epsilon$) and the roll angle ($\psi$) with respect to primary position (Fig. 2A). Helmholtz’s theorem applied to saccades means that the trajectory from a position A to a new position B should follow the direction-circle through A, B, and F, F being the occipital fixation position opposite to primary position O (Fig. 2B). An illustration of this prediction is provided in Fig. 3, which depicts a sequence of three saccades both in motor space, outlined in gray in Fig. 3A, and
in fixation space, outlined as black arcs on top of the associated direction-circles in Fig. 3C. Although this example demonstrates somewhat unsurprisingly that Listing’s law holds not only in motor but also in visual coordinates, it raises the intriguing question of how such sequences of saccades are actually programmed. For example, to generate the actual saccade from position 2 to 3, the rotation of the eye must occur with reference to the associated normal position rather than the actual onset position on the direction-circle. For reasons explained in MATERIALS AND METHODS (Eqs. 2 and 3), normal positions are the secondary reference positions next to the primary (reference) position. Note that in none of the three highlighted saccades in Fig. 3, A and C, did the onset positions coincide with the secondary reference positions that are defined as the points of intersection of a great circle through the primary position and the respective direction-circles at equal angles on either side (see star-labeled positions, Fig. 3C).

To determine the secondary reference positions, we searched for the great circles (through F and O) that intersected the saccade-associated direction-circles at equal angles on either side. Since these positions determined the axis tilt of the rotation, we analyzed the eccentricity, i.e., the polar angle $\epsilon$ subtending the arc ON, as a function of the angular deviation of the secondary reference position from saccade onset, given by the polar angle $\delta_{AN} = \psi_N - \psi_A$ (Fig. 2C). For a given saccade onset position A, the locus of all associated normal positions is a Thales circle through O and A, centered at $\hat{OA}/2$ (Fig. 2C). This suggests that the relation $||\hat{ON}|| = ||\hat{OA}||\cos \delta_{AN}$ must hold true. Hence we binned saccades of equal onset eccentricities, using bin widths of 1° and fitted the data in each bin with the linear equation $k = h \cdot \cos(\delta_{AN}) + h_0$, where $k$ is the length of the line segment $\hat{ON}$, i.e., $k := 2 \sin(\epsilon/2)$ (Fig. 2D), and the slope $h$ is the length of the line segment $\hat{OA}$, i.e., $h = 2 \sin(\epsilon/2)$ (Fig. 2A). The mean coefficient of determination ($\pm SD$) of these fits across all experiments was 1 (1.000, $n = 285$ fits, $N = 2,750$ saccades), thus corroborating the Thales circle relation (Fig. 4). The location of secondary reference positions covered the whole range of directions in fixation space, as did the rotations in motor space (Fig. 3A). This is shown by lumping together the normalized line segments $\hat{OA}$ to represent a common x-axis and plotting the secondary reference positions as a function of the polar angle $2\delta_{AN}$ relative to this axis on the unit circle (Fig. 4, inset).

Fig. 3. Spontaneous eye movements after transformation to Listing-coordinates. A and B: 3D oculomotor space representing eye positions in angle-axis format in front (A) and side (B) view. Highlighted in gray is a sequence of 3 consecutive saccades. C: 2D spherical field of fixations showing the same sequence of saccades from position 1 to 2, 2 to 3, and 3 to 4 in visual coordinates. Note that the trajectories lie on top of circles that pass through position F, i.e., on direction-circles. $D_{12}, D_{23}, D_{34}$: direction-circles associated, respectively, with the saccades from 1 to 2, 2 to 3, and 3 to 4. $M_{12}, M_{23}, M_{34}$: great circle arcs whose planes intersect the respective direction-circle planes at right angles, thus determining the secondary reference positions of the respective saccades (labeled with stars). $EO$: primary direction; $E$: center of fixation sphere (location of eye); $F$: occipital fixation point; $P$: north.

Fig. 4. Angular eccentricity ($\epsilon_N$) of saccade-associated secondary reference positions as a function of angular deviations ($\delta_{AN}$) from saccade onset positions. Solid lines (spaced at 5°): dependence predicted from Thales circle geometry. Inset: angular distribution of secondary reference positions lumped together by normalizing the onset eccentricities. $\epsilon_N$, angle subtended by the gaze directions $EO$ and $EN$; $\delta_{AN}$, angle subtended by the great circle planes through O and A and O and N, respectively.

\[ h = 2 \sin(\epsilon/2) \]
Table 1. Torsional eye positions at saccade onset and offset

<table>
<thead>
<tr>
<th></th>
<th>(\mathbf{E}) at Onset, °</th>
<th>(\mathbf{E}) at Onset, °</th>
<th>(\mathbf{E}) at Offset, °</th>
<th>(\mathbf{E}) at Offset, °</th>
<th>LP SD, °</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>-0.001 (0.002)</td>
<td>0.002 (0.63)</td>
<td>0.034 (0.76)</td>
<td>0.040 (0.63)</td>
<td>0.64</td>
</tr>
<tr>
<td>2</td>
<td>0.001 (0.002)</td>
<td>-0.032 (0.69)</td>
<td>-0.007 (0.79)</td>
<td>-0.035 (0.62)</td>
<td>0.66</td>
</tr>
<tr>
<td>3</td>
<td>0.0004 (0.001)</td>
<td>-0.056 (0.70)</td>
<td>-0.030 (0.86)</td>
<td>-0.065 (0.69)</td>
<td>0.74</td>
</tr>
<tr>
<td>4</td>
<td>0.0002 (0.001)</td>
<td>0.116 (0.70)</td>
<td>-0.001 (0.68)</td>
<td>0.11 (0.70)</td>
<td>0.79</td>
</tr>
</tbody>
</table>

Mean (SD) data of 2 sessions from monkeys 1–4. The estimated torsional eye positions (\(\mathbf{E}\)) were obtained by reverse-computing the rotation of the eye based on the fixation directions at saccade onset and offset and the direction of primary position. Note the small SD of the torsion estimates at saccade onset due to referencing the rotation to a fixed (average) primary position. \(\mathbf{E}\) at onset, experimentally measured torsional eye position; LP SD, thickness of Listing’s plane expressed as 1 SD relative to the best-fit plane.

Updating postsaccadic eye position based on saccade onset and offset positions. Using secondary reference positions, saccades can be programmed as single-axis rotations between any positions in the visual field in concordance with Listing’s law (see Eqs. 2 and 3 in MATERIALS AND METHODS). Moreover, the 3D orientation of the eye at each new fixation position can directly be estimated from the information on the gaze directions at saccade onset and offset. To verify these predictions, we first computed for each saccade the axes and angles of 3D eye positions, associated with the onset, offset, and secondary reference position, and compared the results with the experimentally determined eye positions. Since the secondary reference positions can be located up- or downstream from the fixation point rather than the center of the eye. Also, the rotation angles involved were easily obtained relative to these positions.

The mean ocular torsion at saccade onset and offset positions of both the estimated and experimentally measured positions tightly scattered about zero. Although the reverse-computed onset positions often scattered less about zero than the experimentally measured positions (Table 1), the standard deviations of the torsion estimates at saccade offsets were statistically not different from the standard deviations of primary position based on the Listing’s plane fits \([F(1,14) = 1.1, P = 0.29]\). The mean signed deviations (±SD) of the estimated and experimentally measured onset and offset positions across all saccades were & -0.02° (±0.64°), 0.09° (±0.34°), and -0.12° (±0.31°) for onset torsional, vertical, and horizontal positions, respectively, and -0.02° (±0.64°), 0.08° (±0.31°), and -0.12° (±0.31°) for offset torsional, vertical, and horizontal positions, respectively (\(N = 2,570\)). Thus, although the saccades covered a large oculomotor range, the reverse-computed saccade on- and offset positions did not differ significantly from the experimentally measured positions (Table 2).

A one-way ANOVA analysis (Kruskal-Wallis) of estimated versus measured positions yielded values of 0.45 and larger except for torsion, where in half of the experiments \(P \leq 0.05\) for saccade onset positions were obtained. This difference reflected the significantly smaller scatter of the simulated versus the experimentally measured torsion, most likely due to the fixed primary position used for the estimation.

Estimating 3D rotations from gaze trajectories in 2D visual fixation space. As predicted by Helmholtz’s theorem, saccades moved the line of sight in general rather precisely along the respective position vectors were taken relative to the occipital fixation point rather than the center of the eye.

Table 2. Differences in vertical and horizontal eye positions at saccade onset and offset

<table>
<thead>
<tr>
<th></th>
<th>(\Delta E) at Onset, °</th>
<th>(\Delta E) at Offset, °</th>
<th>(\Delta E) at Onset, °</th>
<th>(\Delta E) at Offset, °</th>
<th>(N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.10 (0.27)</td>
<td>0.09 (0.26)</td>
<td>-0.09 (0.28)</td>
<td>-0.08 (0.27)</td>
<td>355</td>
</tr>
<tr>
<td>2</td>
<td>0.67 (0.91)</td>
<td>0.63 (0.81)</td>
<td>-0.07 (0.29)</td>
<td>-0.06 (0.28)</td>
<td>330</td>
</tr>
<tr>
<td>3</td>
<td>0.17 (0.37)</td>
<td>0.15 (0.33)</td>
<td>0.00 (0.31)</td>
<td>0.00 (0.31)</td>
<td>401</td>
</tr>
<tr>
<td>4</td>
<td>-0.40 (0.59)</td>
<td>-0.38 (0.57)</td>
<td>-0.19 (0.41)</td>
<td>-0.19 (0.40)</td>
<td>250</td>
</tr>
<tr>
<td>1</td>
<td>-0.14 (0.37)</td>
<td>-0.14 (0.31)</td>
<td>-0.18 (0.28)</td>
<td>-0.18 (0.29)</td>
<td>213</td>
</tr>
<tr>
<td>2</td>
<td>0.11 (0.27)</td>
<td>0.11 (0.25)</td>
<td>-0.15 (0.28)</td>
<td>-0.14 (0.28)</td>
<td>373</td>
</tr>
<tr>
<td>3</td>
<td>0.04 (0.23)</td>
<td>0.04 (0.23)</td>
<td>-0.18 (0.29)</td>
<td>-0.17 (0.28)</td>
<td>315</td>
</tr>
</tbody>
</table>

Mean (SD) estimated vs. measured differences of vertical (\(\Delta E\)) and horizontal (\(\Delta E\)) eye positions at saccade onsets and offsets; \(N\), number of saccades. Same computational procedure as used for torsion shown in Table 1. Because eye positions varied across the whole oculomotor range, only differences are shown. Data from the same sessions as in Table 1.
associated direction-circles in fixation space (e.g., examples in Fig. 3C and Fig. 5). To analyze the underlying geometry, we reverse computed the rotation trajectory in motor space, using saccade onset and offset directions and the associated direction-circle arc in visual fixation space. In contrast to the usual representation of 3D eye position relative to primary position, we referenced the rotation of each saccade relative to its onset position. Thus for each saccade from A to B we obtained the rotation vector \( E_{RA} = \tan(\rho/2)\hat{n} \), where \( \hat{n} \) denotes the rotation axis and \( \rho \) the rotation angle. The respective reverse-computed rotation, denoted \( E_{BA} \), was calculated as \( E_{BA} = \tan(\rho/2)\hat{f} \), using the same rotation angle \( \rho \) as a function of time (i.e., the same saccade dynamics) but a rotation axis, defined by the saccade-associated direction-circle (denoted \( \hat{f} \)). The rationale for this was to make it possible to compare the time courses of \( E_{BA} \) and \( E_{RA} \), the latter moving the line of sight along the direction-circle arc \( AB \) about a fixed rotation axis.

We found that the experimentally measured trajectories of individual saccades in general closely matched the reverse-computed trajectories. In terms of coefficients of determination, more than half of the evaluated saccades were strictly fixed-axis rotations, providing positive \( R^2 \) values for all movement components. Specifically, 60.4% (±7.8), 90.2% (±1.3), and 96.8% (±1.0) of all analyzed saccades provided positive \( R^2 \) values for the torsional, vertical, and horizontal components, respectively \( (N = 2,570) \). The mean coefficients of variation (±SD) were 0.72 (±0.26) for torsion, 0.97 (±0.10) for vertical position, and 0.96 (±0.11) for horizontal position. In contrast to the vertical and horizontal components, the \( R^2 \) values were relatively often negative for torsion. Visual inspection showed that in these cases torsion under- or overshot the position predicted by the associated direction-circle arc or oscillated about it, which happened rarely for vertical or horizontal eye position (Fig. 5). Across all experiments and saccades, the mean differences (±SD) were –0.01° (±0.45°) for torsion and 0.04° (±0.29°) for the vertical and 0.03° (±0.36°) for the horizontal component \( (N = 2,562) \). Taking only saccade trajectories with negative \( R^2 \) values in torsion \( (N = 1,031) \), the differences were –0.02° (±0.59°) for torsion and 0.05° (±0.31°) for the vertical and 0.03° (±0.36°) for the horizontal component.

**DISCUSSION**

We have shown that saccades in far viewing sweep the line of sight from one fixation point to the next along a circular path that joins the saccade onset and offset positions in the spherical field of fixations to a point, called the occipital fixation point opposite to primary gaze direction (Fig. 1). H. von Helmholtz (1867) called these circles direction-circles and showed by analyzing visual afterimages that they emerge as a consequence of Listing’s law. Motion of the line of sight along a direction-circle, however, is only a necessary and not a sufficient condition for a Listing reveals that saccades, starting from eccentric fixation positions, can reach only those targets (by a single fixed-axis rotation of the eye without violating Listing’s law). A detailed geometric analysis of this conjecture further reveals that saccades, starting from eccentric fixation positions, can reach only those targets (by a single fixed-axis rotation of the eye without violating Listing’s law). We have shown in fact that rotations from eccentric fixation positions are closely matched the reverse-computed rotation trajectory in motor space, using saccade onset and offset directions and the associated direction-circle arc in visual fixation space. In contrast to the usual representation of 3D eye position relative to primary position, we referenced the rotation of each saccade relative to its onset position. Thus for each saccade from A to B we obtained the rotation vector \( E_{RA} = \tan(\rho/2)\hat{n} \), where \( \hat{n} \) denotes the rotation axis and \( \rho \) the rotation angle. The respective reverse-computed rotation, denoted \( E_{BA} \), was calculated as \( E_{BA} = \tan(\rho/2)\hat{f} \), using the same rotation angle \( \rho \) as a function of time (i.e., the same saccade dynamics) but a rotation axis, defined by the saccade-associated direction-circle (denoted \( \hat{f} \)). The rationale for this was to make it possible to compare the time courses of \( E_{BA} \) and \( E_{RA} \), the latter moving the line of sight along the direction-circle arc \( AB \) about a fixed rotation axis.

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**Sequential acquisition of fixation targets.** Starting from a global reference such as primary gaze direction straight ahead, any target in the field of fixations can easily be reached by a single rotation of the eye without violating Listing’s law. However, saccades usually start from fixation positions away from the primary direction and more often than not the primary position is not in the center of the oculomotor range. Nevertheless, the brain manages with apparent ease to generate sequential saccades from one target to the next. To study the kinematics of such sequences it is convenient to represent the rotations of the eye (relative to the head) in terms of trajectories of actual or virtual fixation points in a normed spherical visual field. According to Helmholtz’s analyses of the motion of afterimages, saccadic trajectories should follow arcs of direction-circles in the visual field of fixations if Listing’s law is obeyed. A detailed geometric analysis of this conjecture further reveals that saccades, starting from eccentric fixation positions, can reach only those targets (by a single fixed-axis rotation of the eye with reference to the current ocular orientation at the onset position) that are located on the direction-circle whose plane is either parallel or normal to the great circle plane through primary and saccade onset positions. In all other cases the motor commands must implement an additional computational step to determine the associated secondary reference position, as it does not coincide with the onset position.

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**Fig. 5.** Examples of 3 saccades expressed in motor coordinates compared with the predicted fixed-axis rotations according to the associated direction-circles. A: example of saccade performing a fixed-axis rotation, displacing the eye from \( E_A = (-0.2°,22.2°,9.4°) \) to \( E_B = (-0.06°,29.8°,33.3°) \) relative to primary position. B: example of saccade where the rotation axis deviates in torsion, displacing the eye from \( E_A = (-1.6°,42.5°,6.9°) \) to \( E_B = (-0.2°,23.8°,8.1°) \) relative to primary position. Note the negative \( R^2 \) value and undershooting of torsion. C: example of saccade where the rotation axis oscillates in horizontal direction, displacing the eye from \( E_A = (-0.1°,16.0°,-27.1°) \) to \( E_B = (-0.4°,34.6°,-26.5°) \) relative to primary position. Note the negative \( R^2 \) value, the oscillation, and the final undershooting of the horizontal component relative to the rotation predicted by the direction-circle arc. Eye positions are in gray and rotation components according to associated direction-circle arcs in black. Primary position at 15° up and 6.5° left from straight ahead.
From Listing coordinates in the 2D field of fixations to motor coordinates in the space of 3D rotations. In the context of saccades, Helmholtz’s notion of direction-circles can shed new light on three major issues in oculomotor research: First, although the geometric relationships between eye movements and the associated motions of the line of sight are visually intuitive, the inverse geometric relationship is much less intuitive: What are the criteria that guarantee that a rotation of the eye underlying a particular motion of the line of sight in fixation space follows Listing’s law? According to Helmholtz’s theorem the answer is this: The line of sight must follow a direction-circle in fixation space. This is a necessary but not a sufficient condition. Second, the transformation of retinal signals into motor commands can indeed be achieved by simple recursive algorithms. Various algorithms relating 2D retinal errors to 3D motor errors controlling saccades have been used by different research groups (Crawford and Guitton 1997; Glasauer et al. 2001; Hepp et al. 1993; Tweed 1997; Tweed and Vilis 1987). Here we showed that these algorithms, sometimes summarized as Listing’s operator, have a simple visual basis, using the concept of direction-circles in fixation space and the notion of secondary reference positions. Based on this, the required transformations can be expressed by simple algorithms in the position domain. They depend on the specific secondary reference positions that need to be determined with respect to the planned saccade direction and the chosen primary reference direction. Together they provide the reference for the rotation of the eye in two ways: First, their location on the direction-circle determines the axis tilt. Second, updating 3D eye position at the end of the each saccade simply requires information about the angular offset of the saccade onset position relative to this reference. This offset can be positive (downstream from the onset position), zero, or negative (upstream from the onset position; see examples in Fig. 3C). In case the onset position is already in normal position with respect to the desired target, the underlying rotation is a single fixed-axis rotation (see MATERIALS AND METHODS: Eq. 3 with \( R_{AN} = 1 \) suffices for updating, as in this case \( A = N \)). In contrast, if the onset position is upstream or downstream from the respective secondary reference position, updating requires referencing the rotation to the ocular orientation at the secondary reference position (Eq. 3 with \( R_{AN} \neq 1 \) for referencing the saccade to the preceding orientation of the eye). In either case, the updating mechanism requires only information on the primary reference position, the saccade onset and offset positions, and the location of the secondary reference position on the direction circle. Thereby, we make the implicit assumption that, in flight, the saccade actually follows the direction-circle arc between onset and targeted offset position. If this is not the case, as for example in curved saccades, the proposed updating mechanism still provides the correct Listing position at the landing position of the saccade, thus providing the basis for a correction saccade that moves the eye back to Listing’s plane.

Dual oculomotor control of saccades and ocular attitude.

The close correlation of saccade trajectories and direction-circles in visual fixation space supports the concept of dual oculomotor control (Hess and Thomsen 2011): On one side there is the extensively studied gaze control system, which moves the line of sight in visual space by operating in a 2D nonlinear parameter space, at least as far viewing in head-restrained conditions is concerned (Sparks and Mays 1990; Wurtz and Goldberg 1989). On the other side, there is a 3D eye position control system located in the brain stem and cerebellum that controls the torsional degree of freedom of the eye in coordination with the movements of the line of sight (Crawford et al. 2003; Hepp 1994; Tweed et al. 1998; Van Opstal et al. 1996). In visually guided eye movements, Listing’s law facilitates neural control of 3D eye position and central updating mechanisms at least in two ways: First, it tends to constrain the eye movement to fixed-axis rotations by forcing the line of sight to move as accurately as possible along direction-circles. Note, however, that these trajectories do often not exactly follow geodesics (i.e., the shortest connections between 2 positions in the field of fixations) because they rarely coincide with great circles (for geodesics in motor space, see Hepp 1990). Second, as the eye rotates in a fixed-axis mode, the temporal and spatial characteristics of ocular motion decouple from each other, rendering indistinguishable the rate of change of eye position and angular eye velocity \( (dR_{BA}/dt \sim df/dt; \text{see MATERIALS AND METHODS}) \). As a consequence, postsaccadic maintenance of eye position can be managed by simple mathematical integration of the neural pulse that generates the rapid ocular motion at saccade onset (Hestenes 1994). Altogether this guarantees optimal pulse-step matching.

It should also be noted that the rotation mediated by \( R_{BA} \) (Eq. 4) requires knowledge about absolute eye position, namely, the ocular orientation at the associated secondary reference position. Assuming fixed-axis rotations, this information can be obtained from visual information on saccade onset, planned saccade direction, and primary position. In fact, most spontaneous saccades in this study were close to fixed-axis rotations that followed the associated direction-circles in fixation space. In the light of these findings, it appears easier than earlier suggested to extend Robinson’s model of saccade control (1975) or its modification by Scudder (1988) from one to three dimensions (Quaia and Optican 1998; Tweed and Vilis 1987; but also see Tweed et al. 1994). These two prototypical approaches base on desired eye position as described by \( R_{BAO} \) (Eq. 2) and desired rotation (or motor error) as described by \( R_{BA} \) (Eq. 4), respectively. The two rotation measures are separated from each other by just one single rotation and may share the same visual and motor parameters if Listing’s law holds [see equation \( R_{BAO}(\xi, \eta) = R_{BA}(\xi)R_{AO}(\eta) \) and assume \( \xi = \eta/2 \) as outlined in MATERIALS AND METHODS]. In models of spatial orientation, it is the rotation mediated by the operator \( R_{BAO} \) that presumably matters, whereas in modeling motor control at the level of local brain stem and cerebellar networks it is rather the operator \( R_{BA} \).

At the motor output, ocular motion along direction-circles facilitates sensorimotor integration: Since saccades sharing the same direction-circle possess the same single secondary reference position as well as axis orientation, the required muscle innervation patterns for generating these saccades must all be similar. In particular, the tonic innervation that generates the axis tilt will always be the same for saccades along the same direction-circle, irrespective of the planned amplitude or direction, which depend on the phasic command signals. A much debated question is how tonic innervation patterns generate the axis tilt. The recently proposed “active pulley hypothesis” of Demer and colleagues (1997, 2000) suggests that ocular torsion of visually guided eye movements is controlled in the periphery by specific neuromechanical structures, so-called muscle pulleys (De-
mer et al. 1995; Miller 1989; Miller et al. 2003). These structures are supposed to generate the appropriate tilt of the eye’s rotation axis (re Listing’s plane) based on the horizontal and vertical motor command signals, including some additional not further specified neural innervation. Although it is likely that such mechanisms facilitate the generation of eye movements in Listing coordinates, it is the central programs upon which the direction, the effective trajectory relative to the actual onset position, and the location of the particular secondary reference position of the envisaged saccade depend. All this information must be known to issue appropriate rotation commands to the ocular plant.

APPENDIX

Derivation of Listing’s conditions. To evaluate the compound rotation \( R_{BAO} \) from primary position \( O \) (direction straight ahead) to \( A \) about an axis \( n_{AO} \) in the frontal plane, followed by a rotation from \( A \) to \( B \) about an axis \( n_{BA} \) (Eq. 1 in MATERIALS AND METHODS), we first evaluate the expressions \( \hat{\gamma}_{\text{BAO}} = \sum n_{BA, i} \hat{\gamma}_{jk} \) with \( n_{BA} = (0, -\cos \psi_0, -\sin \psi_0, v_0) \), \( \hat{\gamma}_{\text{A0}} = \sum n_{AO, i} \hat{\gamma}_{jk} \) and the product \( \hat{\gamma}_{\text{A0}} \hat{\gamma}_{\text{BAO}} = \hat{\gamma}_{\text{A0}} \). In the polar coordinates \( \epsilon \) and \( \psi \) we obtain (see Fig. 2A)

\[
\hat{\gamma}_{\epsilon \psi} = \sum n_{AO, i} \hat{\gamma}_{jk} \quad \text{with} \quad n_{AO} = (0, -\cos \psi_0, -\sin \psi_0, v_0) = (0, 0, 0, 0)
\]

With these expressions, Eq. 1 expands to

\[
R_{BAO}(\epsilon, \psi) = I(\cos(\epsilon/2)\cos(\psi/2) - \sin(\epsilon/2)\sin(\psi/2)) \cos \psi (\epsilon - \psi_0) + \sin(\epsilon/2) \cos(\psi/2) - \sin(\psi/2)\sin(\epsilon/2)) \quad (A1)
\]

\[
+ \left( \sin(\epsilon/2)(\cos(\psi/2)\cos(\psi/2) - \sin(\psi/2)\sin(\psi/2)) \sin \psi (\epsilon - \psi_0) + \cos(\epsilon/2)\sin(\psi/2) \sin(\psi/2) \right) \quad (A1)
\]

\[
+ \left( \sin(\epsilon/2)(\cos(\psi/2)\cos(\psi/2) - \sin(\psi/2)\sin(\psi/2)) \sin \psi (\epsilon - \psi_0) - \cos(\epsilon/2)\sin(\psi/2) \sin(\psi/2) \right) \quad (A1)
\]

Note that 1) if the angle of rotation from primary position \( O \) to \( A \) is \( \epsilon = 2\pi \) and 2) if \( \cos(\psi - \psi_0) = 1 \), then the coefficient of \( \hat{\gamma}_{23} \) disappears. The first condition is the so-called half-angle rule. The second condition means that \( \psi = \psi_0 (\pm 2\pi) \), that is, the two axes \( n_{AO} \) and \( n_{BA} \) of the compound rotation \( R_{BAO} \) must be normal to each other, \( n_{AO} \cdot n_{BA} = 0 \). Under these two conditions, the compound rotation is

\[
R_{BAO}(\epsilon, \psi)_{\epsilon=\psi=2\pi} = R_{BO}(\epsilon, \psi) = uI + v \hat{\gamma}_{31} + w \hat{\gamma}_{12},
\]

\[
\hat{R}_{BA} = \hat{R}_{BAO} = (0, v, w) \quad (A2)
\]

with \( u = \cos(\epsilon/2)\cos(\psi), v = \sin(\epsilon/2)\sin \psi + \cos(\epsilon/2)\sin(\psi) \cos \psi, \) and \( w = -\sin(\epsilon/2)\cos \psi + \cos(\epsilon/2)\sin( \psi) \sin \psi. \) Note that \( \sqrt{u^2 + v^2 + w^2} = 1 \). Therefore, defining \( u = \cos(\epsilon/2), \sqrt{v^2 + w^2} = \sin(\epsilon/2) \) with \( \epsilon = (0, v, w)/\sqrt{v^2 + w^2} \) (A2’).

Thus the format of Eq. A2 is indeed equivalent to the standard format of rotation in the Clifford algebra. Note that the rotation axis and the associated angle are functions of the angular position and rotation angles \( \psi \) and \( \epsilon \) and \( \psi \). Equations A2 and A2’ represent rotations relative to primary position \( O \).

Locus of normal positions associated with eccentric saccade onset positions. We conjectured that the locus of normal positions associated with an eccentric fixation position is a Thales circle centered at the midpoint of the chord joining this position to primary position (Fig. 1). For a geometric proof, pick an arbitrary eccentric fixation position \( A \) and consider the set of all associated iso-eccentric positions (Fig. 6A). Then there are three geometrically distinct ways to move to another position along an associated direction-circle: 1) The motion follows the direction-circle through \( A \) and \( O \), which is also a great circle. In this case, the primary and secondary reference positions are identical. 2) The motion follows the unique direction-circle that is tangential to the circle of iso-eccentric positions at \( A \). Then \( A \) is the secondary reference position of this motion (see Eq. 2 in MATERIALS AND METHODS). 3) The motion follows one of the infinitely many direction-circles that intersect the iso-eccentric circle twice without passing through the primary position. If so, consider the unique plane through \( F \) and \( O \) that intersects the direction-circle plane through \( F, A \), and \( A \) at a right angle (F: occipital fixation position, opposite to \( O; A: \) mirror-symmetric position to \( A \)). The intersection of these two planes

Fig. 6: A: front view onto the spherical field of fixations illustrating a direction-circle through an eccentric fixation position (labeled \( A \)) that intersects the circle of iso-eccentric fixation positions at positions \( A \) and \( \hat{A} \). The associated points of symmetry are the occipital fixation position \( F \) (not visible in \( A \)) and the point labeled \( N \) where the great circle through occipital fixation point \( F \) and primary position \( O \) intersects the direction circle at equal angles on either side. The 3 positions \( O, N, \) and \( A \) lie on a Thales circle (shown in gray) centered at the midpoint of line segment \( OA \). B: side view on the great circle through \( F, O, \) and \( A \). Superimposed on this is the great circle through \( F, O, \) and \( N \) (see A). Also shown are line segments \( FA \) and \( FN \) as well as \( OA \) and \( ON \). Since the 2 great circles represent Thales circles through \( F \) and \( O \) with center at \( E \), the angles \( \angle FAO \) and \( \angle FNO \) are right angles. But segment \( ON \) is also orthogonal to the direction-circle plane through \( F, N, \) and \( A \) (see A), and thus also to \( \hat{AN} \). E, position of the observer’s eye; \( P, \) north.
defines two points on the direction-circle that are at equal distance from both $A$ and $\bar{A}$, namely, $N$ and $\bar{F}$ (Fig. 6, $A$ and $B$). The line segment $\overline{ON}$, joining $O$ to $N$, is orthogonal to the line segment $\overline{FN}$ and, by symmetry, also orthogonal to the respective direction-circle plane (Fig. 6B). The line segment $\overline{AN}$, on the other hand, lies in the direction-circle plane. Thus the two segments $\overline{ON}$ and $\overline{AN}$ must be orthogonal to each other, implying that $N$ lies on the Thales circle through $O$ and $A$ with center at the midpoint of the line segment $\overline{OA}$.

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AUTHOR CONTRIBUTIONS

Author contributions: B.J.H. conception and design of research; B.J.H. performed experiments; B.J.H. analyzed data; B.J.H. interpreted results of experiments; B.J.H. prepared figures; B.J.H. drafted manuscript; B.J.H. edited and revised manuscript; B.J.H. approved final version of manuscript.

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