Quick phases control ocular torsion during smooth pursuit

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One of the open questions in oculomotor control of visually-guided eye movements is whether it is possible to smoothly track a target along a curvilinear path across the visual field without changing the torsional stance of the eye. Here we show in an experimental study of three-dimensional eye movements in subhuman primates (*Macaca mulatta*) that although the pursuit system is able to smoothly change the orbital orientation of the eye’s rotation axis, the smooth ocular motion was interrupted every few hundred milliseconds by a small quick phase with amplitude <1.5° while the animal tracked a target along a circle or ellipse. Specifically, during circular pursuit of targets moving at different angular eccentricities (5°, 10° and 15°) relative to straight ahead at spatial frequencies of 0.067 Hz and 0.1 Hz, the torsional amplitude of the intervening quick phases was typically around 1° or smaller and changed direction for clockwise versus counterclockwise tracking. Reverse computations of the eye rotation based on the recorded angular eye velocity showed that the quick phases facilitate the overall control of ocular orientation in the roll plane, thereby minimizing torsional disturbances of the visual field. Based on a detailed kinematic analysis, we suggest that quick phases during curvilinear smooth tracking serve to minimize deviations from Donders’ law, which are inevitable due to the spherical configuration space of smooth eye movements.

Key words: eye movements, three-dimensional rotations, Listing’s law, Donders’ law, vision
INTRODUCTION

Although the eye can rotate in multiple ways, the kinematics of many eye movements simply corresponds to a fixed-axis rotation of the eye with respect to the bony orbit. This is true for the vestibulo-ocular reflexes, where the rotation axis of the eye parallels the axis of head rotation. As a result these reflexes move the fovea along the shortest path from one position to the next in retino-centric coordinates. Even though saccades are typically also encoded as fixed-axis rotations, they do not always follow the shortest path from one target to the next. They are characterized by a principle of minimal cost of rotations: they minimize the total angular excursion of the eye (Nakayama 1983; Hepp et al 1997) or, equivalently, the extent of ocular torsion (Listing’s law: Helmholtz 1867; Tweed and Vilis 1990). In contrast, the evolutionary young pursuit system deploys a much richer kinematic repertoire enabling it to track targets along straight but also curvilinear paths. Indeed, if a target moves off to one side along a curved path it could not be tracked by a fixed-axis rotation without generating a distortion of the entire visual space. To avoid such disturbances the pursuit system might choose among the infinitely many non-fixed axis rotations those corresponding to a minimal torsion of the visual space, a strategy first proposed by von Helmholtz (1867) as basis of Listing’s law (Hepp 1995; Hepp et al 1997). Although there is experimental evidence suggesting that Listing’s law is obeyed under such circumstances, it has been overlooked that the brain faces in fact an intractable problem when trying to generate perfectly smooth tracking movements requiring non-fixed-axis rotations. Consider for example an observer that tracks a fly along a curvilinear path (Fig. 1). First, he intercepts the fly’s track with a saccade and subsequently manages supposedly to track it smoothly. When saccading back to the starting position after a while of smooth tracking he might
find that the world has appreciably rotated opposite to the direction of path rotation. Thus, smooth tracking bears the risk of violating a fundamental law, due to Donders (1848), which states that the eyes always return exactly back to its original angular orientation in three dimensions after a closed path motion. The question thus is what strategy the oculomotor system employs to minimize violations of Donders’ law during curvilinear target tracking.

To this time there exist a fair number of studies on two-dimensional, curvilinear smooth pursuit focusing on questions of predictive mechanisms and other aspects of response dynamics (Kettner et al 1996; Leung and Kettner 1997; De’Sperati and Viviani 1997; Engel et al 1999; Soechting et al 2005; Mrotek et al 2006; Mrotek and Soechting 2007a, b). One important outcome of these studies is the finding that the performance of two-dimensional pursuit cannot be predicted from the system’s performance during horizontal and vertical tracking (De’Sperati and Viviani 1997; Leung and Kettner 1997; Engel, Anderson and Soechting 1999, Schwartz and Lisberger 1994). It has been noted also that the system is able to smoothly change not only the velocity (Lisberger and Westbrook 1985) but also the direction of tracking, suggesting that angular target velocity might be an important input for the neural control mechanism (Engel et al 1999). In contrast, saccades, triggered by directional position errors, have been reported to have no appreciable effect on the direction of tracking and considered to contribute insignificantly to the input of the pursuit system (Engel et al 1999).

To address the Donders’ problem of smooth curvilinear tracking, we first investigated how target motion in space can be generally encoded in terms of three-dimensional angular eye velocity during steady-state smooth pursuit. We then show experimentally that eye movements during curvilinear pursuit consist of smooth tracking phases interrupted by small amplitude quick phases with significant torsional components, a strategy that minimizes the expected violation of Donders’ law.
Thus, while the system keeps the fovea close to the target it also controls the orientation of the eye to avoid accumulation of torsion. We show that this dual control of the eye’s torsional orientation and gaze velocity can not be achieved by velocity feedback alone but must be supplemented by quick phases to correct torsional position errors.
MATERIALS AND METHODS

Four female rhesus monkeys (*Macaca mulatta*) were used in these experiments. The animals were chronically prepared during sterile surgery under isoflurane anesthesia with skull bolts for head restraint. Dual search coils were implanted on one eye under the conjunctiva for eye movement recording as described previously (Hess 1990). All procedures accorded with the NIH Guide for the Care and Use of Laboratory Animals and were approved by the Veterinary Office of the Canton of Zurich.

**Recording and representation eye positions.** Three-dimensional eye positions were measured using the magnetic search coil technique (Robinson 1963) with an Eye Position Meter 3000 (Skalar, Delft, The Netherlands). Eye position was calibrated as described in Hess et al. (1992), digitized at a sampling rate of 833.3 Hz and stored on a computer for off-line data 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 all four animals Listing’s plane tilted, respectively, less than 4° vertically and 1° horizontally from the frontal plane.

During the behavioral tasks, the animal was seated upright, with the head restrained in a primate chair that was mounted within an opaque sphere 1.6 m across. The animals were trained to track a small laser spot (0.35°), which was projected onto the inner wall of the sphere describing circular (0.067 or 0.1 Hz, radius 5°, 10°, and 15°) or moderate elliptic paths (major axis 20°, minor axis 15°, 0.1Hz) on a structured background. The quality of smooth tracking was controlled with behavioral windows of 1-2° across. During successful tracking the animal received fluid rewards. Experiments were performed in light, i.e. with a background illumination inside the opaque sphere, which completely surrounded the animal.

**Data analysis**

All tracking responses were analyzed cycle per cycle. Saccades, quick phases and blink artifacts were detected and marked by applying time and amplitude windows to the time derivative of eye acceleration (jerk). Cycles with saccades or blink artifacts were eliminated by visual inspection. To
facilitate identification of quick phase events in terms of magnitude, duration and peak velocity eye position traces were rectified by subtracting the sinusoidal modulation determined by least squares fitting. Three-dimensional angular eye velocity was computed in two fundamentally different ways: In the first conventional approach, we eliminated also all the small step-like shifts in horizontal and vertical eye position, which obviously are components of quick phases that reposition torsional eye position (see Results, Fig. 3). Then we computed the angular eye velocity ($\boldsymbol{\Omega}$) with the formula

$$\boldsymbol{\Omega} = 2(d\boldsymbol{E}/dt + \boldsymbol{E} \times d\boldsymbol{E}/dt) / (1+\|\boldsymbol{E}\|^2)$$ (Hepp, 1990), where $d\boldsymbol{E}/dt$ is the time derivative of eye positions, expressed as rotation vector ($\boldsymbol{E} = \tan(\rho/2)\hat{e}$), closely related to the eye position quaternion $E_q = \cos(\rho/2) + \hat{e}\sin(\rho/2)$; $\hat{e}$: rotation axis; $\rho$: rotation angle). Finally we fitted each of the three components of the angular eye velocity ($\Omega_{tor}$: torsional, $\Omega_{ver}$: vertical, and $\Omega_{hor}$: horizontal) with a sum of sinusoids up to the $3^{rd}$ harmonic of the spatial stimulus frequency using the Levenberg-Marquardt algorithm (Matlab, the MathWorks Inc). This procedure accurately estimated the actual slope of the slow phase segments in between quick phases. The resulting angular velocity or fits are traditionally called slow phase or slow phase-related angular eye velocity (SPV). In a variant of this approach we fitted a generic Listing model, calling the resulting fits Listing law-based slow phase-related angular eye velocity (LSPV). This procedure is described in more detail below. In the second approach, we fitted three-dimensional eye position with the same sum of sinusoids without removing the small step-like changes in eye position due to quick phases. Based on these position-related fits, we estimated the angular eye velocity using the same formula as above. We refer to this angular eye velocity (fits) in the following as eye position-related angular eye velocity (EPV).

**Notational remarks:** Here and in the following, we denote vectors by bold letters and represent the components as column or, for convenience, also as row vectors within the text. Identities marked with a caret denote unit vectors. Identities marked with a tilde represent control parameters (vectors, scalars) that ultimately base on the brain’s estimate of target motion. For example, eye position reflecting estimated target position in space is represented as $\hat{\boldsymbol{E}}$; it is a 2-dimensional vector that, however, may also be written $\hat{\boldsymbol{E}} = (0, \hat{E}_{ver}, \hat{E}_{hor})$. For simplicity, we do not accumulate cares and tildes on the same identity.
**Extended generic Listing model:** To describe steady-state smooth pursuit eye movements in a generic way in three-dimensions (3D) we started from the general formulas that express 3D angular eye velocity as a function of 3D eye position and velocity, namely

\[ \mathbf{\Omega} = 2(d\mathbf{E} / dt + \mathbf{E} \times d\mathbf{E} / dt) / (1+ \| \mathbf{E} \|^2) \]

and its inverse \( d\mathbf{E} / dt = (\mathbf{\Omega} + \mathbf{\Omega} \times \mathbf{E} + (\mathbf{\Omega} \cdot \mathbf{E}) \mathbf{E}) / 2 \) (\( \times \) stands for cross vector product, “\( \cdot \)” stand for scalar product; Hepp 1990, 1994). In the following we refer to these two vector equations, respectively, by \( \mathbf{\Omega} = \mathbf{\Omega}(d\mathbf{E}/dt, \mathbf{E}) \) and \( d\mathbf{E}/dt = d\mathbf{E}/dt (\mathbf{\Omega}, \mathbf{E}) \). For successful tracking of a far target, the angular eye position and velocity must approximately equal target angular position and velocity taken relative to the eyes (see also Mays and Sparks 1980). In the simple case of straight line pursuit, the angular velocity of the target is a vector in the observer’s frontal plane. Thus, by substituting \( \mathbf{E} \) and \( d\mathbf{E}/dt \) on the right hand sight of \( \mathbf{\Omega} = \mathbf{\Omega}(d\mathbf{E}/dt, \mathbf{E}) \) by the brain’s estimate of target angular position \( \mathbf{\tilde{E}} \) and angular velocity \( \mathbf{\tilde{\Omega}} \) in space, this equation suggests in fact that the angular velocity of the eye (as measured at the motor output) is proportional to the estimated target velocity plus a non-linear target-position and velocity dependent term, i.e.

\[ \mathbf{\Omega}_{\text{eye}} \approx (\mathbf{\tilde{\Omega}} + \mathbf{\tilde{E}} \times \mathbf{\tilde{\Omega}}) / (1+ \| \mathbf{\tilde{E}} \|^2) \tag{1} \]

In deriving this equation, we used the relation \( \mathbf{\tilde{\Omega}} = 2d\mathbf{\tilde{E}} / dt \) that accounts for \( \mathbf{\tilde{E}} \) and \( \mathbf{\tilde{\Omega}} \) being confined to the y-z or frontal plane. Equation (1) predicts a non-zero torsional angular eye velocity component at the motor output due to the cross vector product on the right hand sight. How and where this cross vector product is implemented in the brain is beyond the scope of this study. Although this simple heuristic approach is sufficient to explain steady-state straight line pursuit responses as a function of eye position it poses serious problems if the target’s angular velocity is not confined to the horizontal-vertical plane (see example in Fig. 1: the angular velocity component “\( d\psi/dt \)” is not in the observer’s y-z plane). In that case, the predicted angular velocity of the eye would violate Listing’s law as a consequence of the implied (eye-position independent) non-zero torsional eye velocity. How can the brain then encode a general target angular velocity in oculomotor commands without violating Listing’s law? The most efficient solution is to make use of the rotational degree of freedom of the eye about the gaze line. Specifically, by counter-rotating at a certain velocity about the gaze line, the eye can encode the torsional component of the estimated
target angular velocity. Thus, we define *ocular counter roll* as angular velocity of the eye about the current gaze direction and devise the following necessary condition for a tracking strategy compatible with Listing’s law: First, we express the estimated target angular velocity in terms of a magnitude \( \tilde{\omega}_{\text{target}} \) times a unit direction (in space), i.e. \( \tilde{\Omega}_{\text{target}} = \tilde{\omega}_{\text{target}} \hat{n} \) and assume that a certain fraction of its magnitude is encoded by ocular counter roll, say \( \tilde{\omega}_{\text{CR}} = \lambda \tilde{\omega}_{\text{target}} \). Second, we assume that the motor system encodes the estimated target angular velocity in form of a linear combination of target angular velocity and ocular counter roll velocity, i.e. \( \tilde{\Omega}' = \tilde{\Omega}_{\text{target}} + \tilde{\Omega}_{\text{CR}} = \tilde{\omega}_{\text{target}} (\hat{n} + \lambda \hat{g}) \), where \( \lambda \) is a certain fraction of ocular counter roll velocity and \( \hat{g} \) denotes current gaze direction. We express this relation more concisely in terms of the two direction vectors by writing:

\[
f = \tilde{\omega}' / \tilde{\omega}_{\text{target}} = \hat{n} + \lambda \hat{g}
\]  

(2)

Intuitively it is clear that for coherence with Listing’s law the parameter \( \lambda \) in equation (1) has to be chosen such that the forward component of the estimated target angular velocity cancels out, resulting in \( [f]_x = 0 \). Thus, a necessary condition for encoding angular target velocity compatible with Listing’s law is that the ratio of counter roll velocity to the estimated target velocity, \( \tilde{\omega}_{\text{CR}} / \tilde{\omega}_{\text{target}} = \lambda \), compensates the forward directional component of target angular velocity, \( [\tilde{\Omega}_{\text{target}}]_x / \tilde{\omega}_{\text{target}} = \hat{n}_x \). If there is no such forward component, Listing’s law can be satisfied without any counter roll. Using this constraint, the generic equation for eye velocity at the premotor level is:

\[
d\tilde{E} / dt = \left( \tilde{\omega}_{\text{target}} / 2 \right) f, \quad \text{where } f = (0, f_y, f_z),
\]  

(3)

This relation encodes the estimated target angular velocity according to the first, linear term of the above mentioned equation \( d\tilde{E}/dt = \tilde{E}/dt(\Omega, E) \). As previously noted, \( \tilde{\omega}_{\text{target}} \) is the brain’s best estimate of instantaneous target angular velocity. The complexity of this vector equation lies in the vector \( f \), which changes from moment to moment as a function of gaze direction (equation 2). Note that this eye velocity is not yet the angular velocity measured at the motor output. To obtain the angular velocity at the motor output, denoted by \( \Omega_{\text{eye}} \), a second, non-linear transformation must be postulated, which follows from the above mentioned kinematical equation \( \Omega = \Omega (d\tilde{E}/dt, E) \). Inserting
the estimated horizontal and vertical target position ($\mathbf{E}$) and velocity ($d\mathbf{E}/dt$ as defined in (3)) it
yields:

$$\Omega_{\text{eye}} = \frac{\partial \omega_{\text{target}}}{1+\|\mathbf{E}\|^2} \left( \begin{array}{c} f_x \mathbf{E}_{\text{ver}} - f_y \mathbf{E}_{\text{hor}} \\ f_y \\ f_z \end{array} \right),$$

where $\|\mathbf{E}\|$ is the magnitude of $\mathbf{E}$ given by $\|\mathbf{E}\| = \sqrt{\mathbf{E}_{\text{ver}}^2 + \mathbf{E}_{\text{hor}}^2}$. From this equation, we see that the
axis of angular eye velocity $\hat{\mathbf{f}} = \Omega_{\text{eye}}/\|\Omega_{\text{eye}}\|$, measured at the motor output, is a function of
horizontal and vertical eye position. This equation together with the implicit condition $f_x = 0$ in
equation (2) is not only an accurate implementation of the half-angle rule of Listing’s law, when the
eye rotates about a fixed axis but also a good approximation when it performs a more complex form
of rotation. Specifically, during straight-line tracking the eye movement is a fixed-axis rotation
(i.e. $\hat{n}_x = 0$: $\hat{f} = \hat{n}$, $\lambda = 0$: no counter rotation). For example, during horizontal tracking the target
rotates about the head vertical axis (i.e. $\hat{n}_x = \hat{n}_y = 0$, $\hat{n}_z = 1$) whereas the eye rotates about an axis that
tilts by half the angle of vertical eccentricity ($\phi$), i.e. $\phi / 2 = \tan^{-1}\left(\frac{\mathbf{E}_z}{\sqrt{(\Omega_{\text{eye}})_y^2 + (\Omega_{\text{eye}})_z^2}}\right)$ (half-
angle rule, equivalent to Listing’s law). The same is true for vertical tracking (i.e. $\hat{n}_x = \hat{n}_z = 0$, $\hat{n}_y = 1$). During circular tracking, equation (4) approximates the half-angle rule with less
than 2% error for gaze eccentricities $\varepsilon \leq 16^\circ$. In this range, the angular eye velocity depends on
current gaze direction approximately as

$$\Omega_{\text{eye}} = \tilde{\omega} \tan(\varepsilon) \left(1 + \tan^2(\varepsilon/2)\right)\left(\tan(\varepsilon/2)\sin(\psi) - \cos(\psi)\right)$$

where $\psi$ is the angle and $\tilde{\omega} = d\psi / dt$ is the velocity of the target along the circular path (see Fig. 1; for computational details see Appendix A). The angular velocity tilts out of Listing’s plane by half the angle of gaze eccentricity ($\varepsilon$)
$\varepsilon / 2 = \tan^{-1}\left(\frac{\Omega_{\text{eye}}_y}{\sqrt{(\Omega_{\text{eye}})_y^2 + (\Omega_{\text{eye}})_z^2}}\right)$ whereas its projection on the frontal y-z plane
continuously changes orientation with $\tilde{\omega} = d\psi / dt$. Experimentally, we found that this prediction is
accurate only up to an additional eye position-independent torsional term $\partial \mathbf{O} = \partial_{\text{target}}(f_x, 0, 0)$ that
can capture the observed violation of Listing’s law during circular pursuit. We refer to this extension
of equation (4) as extended generic Listing model. The rationale for this extension is both theoretical
Listing law-based slow phase-related angular eye velocity (LSPV)

We used also the extended model (equation (4) + torsion term $\mathbf{\Omega} = \tilde{\omega}_\text{target} (f_x, 0, 0)$) to fit the circular pursuit responses. To estimate the magnitude $\tilde{\omega}_\text{target}$ we used the equation (Tchelidze and Hess 2007):

$$\tilde{\omega}_\text{target} = \left( \frac{dE_{\text{hor}}}{dt} - E_{\text{hor}} \frac{dE_{\text{ver}}}{dt} \right) \left( E_{\text{ver}}^2 + E_{\text{hor}}^2 \right),$$

which we evaluated by fitting independently eye position with a sum of sinusoids up to the third harmonic according to:

$$E_{\mu} = a_{\mu 0} + \sum_k a_{\mu k} \sin(2k \pi v t + \alpha_{\mu k})$$

The Fourier coefficients $a_{\mu k}$ and phase angles $\alpha_{\mu k}$ ($\mu$ for ”tor”, “ver”, and “hor”; $k = 1, \ldots, 3$). The directional vector $f = (f_x, f_y, f_z)$ was fitted component-wise with a similar sum of sinusoids. The second and higher harmonics of these fits were very small and could therefore be neglected, except for the second harmonics of torsional eye position and velocity (see Results). The spatial frequency parameter ($v$) was set equal to the spatial stimulus frequency. We determined the coefficient of determination of these fits by computing the generalized $R^2$ of the (extended) model versus a reduced model with $a_{\mu k} = 0$ and $\alpha_{\mu k} = 0$ ($\mu$ for “tor”, “ver”, and “hor”; $k = 1, 2, 3$), using the formula $R^2 = 1 - \text{RSS (full model)} / \text{RSS (reduced model)}$, where RSS stands for residual sum of squares (for details see Anderson-Sprecher 1994).

So far no use was made of equation (2) which formulates a necessary condition for Listing’s law whenever the angular velocity of the target has a non-vanishing $x$-component. To check the prediction that the counter rolling velocity increases as a function of target eccentricity $\varepsilon$, we estimated the counter roll velocity ratio $\lambda$ by solving the quadratic equation $\| \hat{n} \|^2 = || f - \lambda \hat{g} ||^2 = 1$, which leads to $\hat{n}_z = f \cdot \hat{g} \pm \sqrt{ (f \cdot \hat{g})^2 - f^2 + 1 }$ (the dot "\cdot" stands for the scalar product) and a stimulus direction $\hat{n}_z = f - \lambda \hat{g}$. We used this relation to test the prediction of equation (2) that $\lambda$ increases with target eccentricity $\varepsilon$ as $1/\cos(\varepsilon)$ for circular tracking. For this we fitted the curve $\lambda = a$
Compensation of torsion by ocular counter-roll:

To comply with Listing’s law, the eye must compensate the torsional velocity of the target by counter roll. Here we provide a geometrical argument showing that this compensation cannot be fully achieved by a smooth (i.e. non-saccadic) motion of the eye (for a quantitative argument see Appendix B and C). We will use this geometric argument in the following paragraph to back compute the 3D angular motion of the eye based on the experimentally measured eye angular position and velocity.

To estimate the required counter roll of the eye during circular or curvilinear tracking consider three mutually orthogonal vectors labeled $\mathbf{g}$, $\mathbf{h}$ and $\mathbf{v}$ associated with the gaze line. In the initial orientation (labeled with subscript zero), these vectors coincide with the x-, y- and z-axes, respectively. For tracking a target that moves in front of the subject along a circle, the eye needs to move first from primary position A straight up to intercept the target at B and then about the x-axis, which transports the gaze line from B towards C along a circular path (Fig. 2A, B). By this maneuver, the angular orientation of the eye changes as indicated by the respective orientations of the $\mathbf{g} - \mathbf{h} - \mathbf{v}$ frames in position A, B and C (see Fig. 2A and 2B; in primary position A the vectors $\mathbf{g}$, $\mathbf{h}$ and $\mathbf{v}$ coincide with the direction of the x-, y-, and z-coordinate axes). To keep the vertical retinal meridian invariant in space, the eye simultaneously counter rolls about the gaze line (Fig. 2B and C). By comparing the orientations of the vectors $\mathbf{v}$ in position B and $\mathbf{v'}$ in position C, it is obvious that the torsion of the globe, acquired by moving from B to C, can not be fully compensated by counter roll about the gaze line. This is possible only in the four cardinal positions where $\psi = k\pi/2$ ($k = 0, 1, 2$ and 3). Thus, if the eye would saccade back from C or from any other non-cardinal position to primary position A after perfect smooth tracking along the circular path, Donders’ law would be violated. For a quantitative proof, see Appendix B and C.
Reconstruction of ocular torsion: We used the three different definitions of angular velocity, SPV, LSPV and EPV to back compute the actual rotation of the eye. Since the angular velocity represents at each moment the direction of rotation of the eye, we took this information to reconstruct the motion of gaze in space. By normalizing the angular velocity we obtained the direction of the rotation axis \( \hat{f} = \| \Omega_{\text{eye}} \| \| \Omega_{\text{eye}} \| \) at any moment in time. Let us denote the time samples by superscripts, i.e. \( \hat{f}^k \) is the rotation axis computed from the data sample \( k \) that was recorded at the time \( t = k \cdot \Delta t \) (\( \Delta t \) = sampling interval). From this we calculated the rotation \( R^k \) for each sample \( k \), which we specify by the axis \( \hat{f}^k \) and angular increment \( \Delta \psi \) summarized as: \( R^k = R(\hat{f}^k, \Delta \psi) \). The time evolution of gaze direction \( \{ \hat{g}^k, k=1: N \} \) and its orthogonal vertical component \( \{ \hat{v}^k, k=1: N \} \) is thus obtained as follows:

\[
\hat{g}^{k+1} = R^k \hat{g}^k, \quad \text{with } \hat{g}^0 = \hat{g}(t = 0), \text{ i.e. gaze orientation at onset of tracking} \quad (7a)
\]

\[
\hat{v}^{k+1} = R^k \hat{v}^k, \quad \text{with } \hat{v}^0 = \hat{v}(t = 0) \quad (7b)
\]

Since the vectors \( \hat{v}^k, \hat{g}^k \) and \( \hat{h}^k = \hat{v}^k \times \hat{g}^k \) form an orthogonal triple of unit vectors it is straightforward to compute an estimate of 3D eye position \( \hat{E}^k = (\hat{E}_{\text{tor}}, \hat{E}_{\text{ver}}, \hat{E}_{\text{hor}}) \) from them. Using this approach, we were particularly interested in comparing the torsional component \( \hat{E}_{\text{tor}} \) based on the two different estimates of eye angular velocity, the eye position-related (EPV) and the slow phase angular eye velocity (SPV). Finally, we also computed \( \hat{E}^k \) based on a pure slow phase-based counter roll strategy with no intervening quick phases. The rationale for these procedures was to determine the influence of quick phases on the ocular torsion of the eye during curvilinear pursuit. For this, we postulated that the plane spanned by the current gaze direction and its orthogonal vertical component remained always vertical as the initial orientation at onset of the tracking. Using at each step in time the counter rotation \( \hat{R}^k = R(\hat{g}^k, \rho^k) \) about the momentary direction of gaze \( (\hat{g}^k) \), we computed the following sequence of orthogonal vertical gaze directions:

\[
\hat{u}^{k+1} = \hat{R}^k \hat{u}^k, \quad \text{with } \hat{u}^0 = \hat{u}(t = 0) \text{ and } \rho^k = -\tan^{-1}(\hat{g}^{k+1} \cdot \hat{u}^k) \quad (7c)
\]

From the vectors \( \hat{u}^k, \hat{g}^k \) and \( \hat{l}^k = \hat{u}^k \times \hat{g}^k \) that formed also an orthogonal triple of unit vectors we obtained a different estimate of 3D eye positions \( \hat{E}^k \), where we were particularly interested in comparing the torsional component with \( \hat{E}_{\text{tor}} \) from eye position vector \( \hat{E}^k \).
To evaluate the accuracy of the reconstructions, we computed the normalized root mean square error between the reconstructed and the actual least square fitted eye position:

\[
\frac{\text{rms} \tilde{E}_\mu}{\text{rms} \hat{E}_\mu} = \sqrt{\frac{\sum_{k=1}^{N} (\tilde{E}_\mu^k - \hat{E}_\mu^k)^2}{\sum_{k=1}^{N} (\hat{E}_\mu^k)^2}} \quad \text{for each eye position component } \mu = \text{"tor", "ver", and "hor".}
\]

Alternatively, we also computed the generalized R² values based on the residual sum of squares obtained from the fitted and reconstructed rotations by reverse computation.

RESULTS

Basic observations

Steady-state tracking eye movements consisted of smooth pursuit segments lasting about 100 to 300 ms separated by small quick phases with a torsional component. This pattern was observed most clearly during tracking of targets describing an elliptic path as illustrated in Fig. 3 but also during the simpler circular tracking. In the following, we first characterize the global properties of these quick phases before addressing the more intricate analyses of their interactions with slow phase segments. Since we did not find significant differences for circular and elliptic pursuit trials at the mentioned moderate ellipse eccentricity (e = 0.66) we focus our analyses on circular pursuit trials.

We analyzed quick phases during steady-state pursuit in two ways: First, we determined the frequency distribution of the amplitudes in terms of horizontal, vertical and torsional components. We found that these amplitude components were mostly confined to within less than ±1.5° relative to the sinusoidal least squares fit of the tracking response. Only rarely quick phases showed larger components in horizontal or vertical direction. Second, we analyzed the main sequence properties of these rapid eye movements. We found that the peak velocity was linearly correlated to the amplitude of quick phases (Fig. 4A and B). For example, linear fits of quick phase peak velocities during circular pursuit at 15° eccentricity and spatial frequency of 0.067 Hz (N = 155 distributed across 6 clockwise and 6 counterclockwise cycles) yielded offset \(a = 0.3 \pm 0.1°/s\) and slope \(b = 16 \pm 0.2 s^{-1}\) (\(R^2 = 0.83\)) for torsional components, \(a = -0.5 \pm 0.1°/s\) and \(b = 31 \pm 0.1 s^{-1}\) (\(R^2 = 0.97\)) for vertical
components, and \( a = -0.6 \pm 0.1 \, ^\circ / s \) and \( b = 26 \pm 0.2 \, s^{-1} \) \( (R^2 = 0.84) \) for horizontal components. Separately fitting these quick phases during clockwise and counterclockwise pursuit delivered significantly different values only for the torsional components (clockwise: \( a = 1.9 \pm 0.1 \, ^\circ / s \), \( b = 18 \pm 0.4 \, s^{-1} \) with \( R^2 = 0.88 \); counterclockwise: \( a = -2.3 \pm 0.2 \, ^\circ / s \), \( b = 22 \pm 0.5 \, s^{-1} \) with \( R^2 = 0.90 \)). The duration of these quick phases was approximately constant across the small amplitude range (Fig. 4C) whereas the peak velocity strongly decreased with increasing duration (Fig. 4D).

Impact of quick phases on ocular kinematics

To evaluate the impact of the quick phases during steady-state pursuit trials, in particular with respect to the torsional component, we analyzed the ocular kinematics as follows: First, we estimated angular eye velocity based on sinusoidal eye position fits up to second order without removing the small step-like position modulations due to quick phases. These fits perfectly matched the eye position modulation (Fig. 5, upper panels, dashed lines superimposed on eye position traces) and the angular velocity, EPV, derived from these fits also provided good estimates of the horizontal and vertical slow phase angular velocity, except for the torsional slow phase angular velocity (Fig. 5, lower panels, dashed lines superimposed on slow phase angular velocity traces). Thus, the angular velocity derived from the torsional eye position fit provided a relatively poor description of the admittedly rather small modulation of torsional slow phase angular velocity. The coefficients of determination \( (R^2) \) summarized in Table 1 under “Sinusoidal fits” emphasize this observation: the position fits predicted slow phase angular velocity with average \( R^2 \)-values >0.85 in vertical and horizontal direction compared to \( R^2 \)-values <0.15 in torsional direction. In a second approach we fitted the data using the extended generic Listing model, which included an eye position-independent torsional term (labeled \( \hat{\Omega}_{\text{tor}} = \hat{\omega}_{\text{target}} \hat{f}_x \) in Methods) in order to account for a torsional component violating Listing’s law (equations 4 to 6 in Methods). Note that the eye position-dependent torsional component of the (not extended) generic Listing model predicts no modulation at higher harmonics unless such modulation would be present in the horizontal and/or vertical component. We found that the extended generic Listing model provided superior fits of the torsional responses although there
was no significant non-linearity in the fits of the vertical and/or horizontal components as
documented below (see solid lines in second row of Fig. 5). A comparison of the coefficients of
determination ($R^2$) showed significant improvements of the $R^2$-values when fitting the extended
generic Listing model compared to the sinusoidal fits, which also included a second harmonic ($p$
$<0.001$, t-test). This was true in all animals (Table 1). In the remaining parts we further analyze the
torsional non-linearity based on the fits provided by the extended generic Listing model.

The potential impact of the torsional non-linearity can best be analyzed by characterizing the
relative power of the second and higher harmonic contributions in terms of that at the fundamental
frequency. From the sinusoidal fits to eye position, we computed the squared ratios $(a_{\mu i}/a_{\mu 1})^2$ of the
Fourier components $a_{\mu i}$ versus $a_{\mu 1}$ at the fundamental frequency for each eye movement component
(see Methods, equation 6). This approach takes into account that the total power is proportional to
the sum of squares of significant Fourier components. Since during circular pursuit the input signal is
a pure sine at the spatial frequency of target motion, these ratios are a measure of the amount of
harmonic distortion at each frequency. We found that the power, contributed by the second order
harmonics to the horizontal and vertical response component, amounted to less than 1‰ relative to
the power of the fundamental. In contrast, the mean relative power of the second harmonic of
torsional angular velocity was around 13% and 19% for clockwise and counter-clockwise circular
pursuit, respectively (Table 2). At higher Fourier frequency there was a strong roll-off in power.

Evaluation of the rotation axis of the eye during steady-state pursuit

The geometric relation between gaze direction and the estimated target rotation (see Methods,
equations (2)) can be used to reconstruct the actual rotation of the eye ball (relative to the head). To
analyze this motion, we first estimated the ocular rotation vector $\hat{f}$ as a function of time by fitting the
extended generic Listing model to 3D eye position and 3D slow phase angular velocity, both being
an essential input to the model. Second, we computed the rotation of the gaze vector $\hat{g}$ as a function
of time from the fits of 3D eye position. With these vector functions $\hat{f}(t)$ and $\hat{g}(t)$ at hand we
computed the associated parameter $\lambda(t)$ by solving the respective quadratic equation and computed
the underlying estimate of the axis of target rotation, represented by the unit vector \( \mathbf{n}(t) \). Plots in the
time domain showed that the gaze vector oscillated in the horizontal (z) and vertical (y) direction
with very little jitter across cycles (Fig. 6A). The estimated target rotation axis pointed in the
direction of the x-axis, exhibiting only small modulations in the y- and z-direction during a rotation
cycle (Fig. 6B). Most interestingly the angular velocity vector of the eye oscillated in the y-z-plane
with some jitter around zero in x-direction (Fig. 6C). The lambda parameter (equation (1)), which
relates the gaze vector to the estimated rotation axis modulated at negative levels exceeding -1 (Fig.
6D). The minus sign reflected the fact that counter rotation of the eye opposed the estimated angular
target velocity in x-direction, whereas the magnitude >1 accounted for the target eccentricity (see
further analysis of this point below). In the spatial domain, the angular velocity vector of the eye
traveled around a circle in the subject’s frontal plane (z-y-plane, Fig. 7A). Its projections onto the
yaw and pitch plane showed always some wobble of the circular trajectory due to the small
oscillations in x-direction (Fig. 7B, C). This wobble reflected the deviation of circular pursuit
responses from the ideal Listing’s law behavior. It is accounted for by the term \( \delta \dot{\omega} = \dot{\omega}_{\text{target}} \delta f \) in the
extended generic Listing model. As mentioned, this term significantly improved the fits of the small
torsional modulations. Despite the torsional wobble of the angular velocity vector, the gaze vector
showed virtually no distortion of its circular trajectory in the target plane. Similarly, the estimated
rotation axis of the target motion was often surprisingly stable in space. Variability in the y- and z-
direction was compensated for by corresponding modulations of \( \lambda \). To further corroborate the
validity of our approach, we tested the dependence of \( \lambda \) as a function of eccentricity as explained in
the next paragraph.

Estimating ocular counter rotation

We evaluated the dependence of \( \lambda \) as a function of gaze eccentricity for circular pursuit at gaze
eccentricities of \( \sim 5^\circ, \sim 10^\circ \) and \( \sim 15^\circ \). According to equation (2) in Methods, \( \lambda \) is expected to lie on
the graph \( 1/\cos(\varepsilon) \) where \( \varepsilon \) is the target eccentricity. A geometric explanation of this effect is
illustrated in Fig. 8B. Describing the target motion as a circle on a unit sphere (with the observer’s
eye in the center), the eccentricity $\varepsilon$ is related to the radius of target circle $r$ by $\varepsilon = \arcsine(r)$. This relation is exact if the observer’s frontal plane parallels the plane of target motion. Otherwise the target’s eccentricity will vary about an average value during circular tracking. Indeed, we found that $\lambda$ varied along each cycle suggesting that $\varepsilon$ was not perfectly constant throughout on tracking cycle (Fig. 8A). To verify the predicted $1/\cos(\varepsilon)$ behavior, we fitted the curve $\lambda = a + b/\cos(\varepsilon)$ to the $\lambda$-data, which we obtained from fitting the extended generic Listing model to the angular eye position and velocity data. Although the predicted increase of $|\lambda|$ is small in the tested range of eccentricities, we found an excellent correspondence of experimental data with prediction (Fig. 8A). $R^2$-values and fitted parameters $a$ and $b$ from experiments in three animals are summarized in Table 3.

Reconstruction of 3D ocular rotation from steady-state pursuit data

Having established the relation between target motion and ocular rotation in terms of how the brain might encode 3D target angular velocity (equations 1 to 4 in Methods), we finally tackled the question of whether it is possible to predict the angular eye position including its small but consistent second harmonic modulation in torsion from the angular velocity observed during circular pursuit. Motivated by the observation that quick phases appear to be an integral part during steady-state pursuit in primates, we reconstructed the ocular rotation based on the two different ways of estimating the angular velocity of the eye (see SVP versus EPV in Methods). In the first approach, we estimated angular eye velocity by fitting slow phase angular velocity obtained from eye position after removing all quick phases (SVP) or in a variant, by using the extended generic Listing model (LSVP, based on fits of eye position and slow phase eye velocity). Alternatively, we estimated angular eye velocity based on the best sinusoidal fits of the angular eye position traces (EPV), including the small quick phases (see Fig. 3A and B). We call this alternative eye position-related angular velocity. Using the axis-angle method for calculating rotations we used the thus estimated angular eye velocity to calculate the instantaneous direction of the eye’s rotation axis, and to reconstruct the rotation of the eye sample per sample by reverse computation. We found that the slow phase-related angular velocity (both variants) failed to reproduce the experimentally observed
torsional eye position modulation, despite the fact that it could predict the observed vertical and horizontal eye position modulation. More specifically, although torsional eye position initially changed in the correct direction (compared to the actual data), torsion soon accumulated in the same direction as the tracking (Fig. 9B). This meant that in these simulations torsional eye position ran off unbounded from cycle to cycle, since eye position at the end of one cycle equaled initial position of the following cycle. In these simulations, the normalized root mean square error was 2.7 ± 0.4 for torsion, 0.07 ± 0.02 for vertical, and 0.06 ± 0.009 for horizontal eye position in clockwise direction and 6.5 ± 1.5 for torsion, 0.05 ± 0.02 for vertical and 0.03 ± 0.01 in counter clockwise direction (data shown in Fig. 9B). In contrast, using the integral angular eye position-related angular velocity the reconstructed rotation of the eye consistently reproduced not only the vertical and horizontal eye position modulation but also the observed modulation of torsional eye position (Fig. 9C). Most importantly, torsional eye position did not run off because it returned at the end of one cycle to the value at which it started at the beginning. The normalized root mean square error was 0.11 ± 0.02 for torsion, 0.01 ± 0.003 for vertical, and 0.02 ± 0.004 for horizontal eye position in clockwise direction and 0.10 ± 0.04 for torsion, 0.008 ± 0.006 for vertical and 0.01 ± 0.003 in counter clockwise direction (same data as in Fig. 9C). Notice that although the normalized root mean square error for the reconstruction of torsion was roughly a factor 10 larger than that of vertical and horizontal eye position, it was not significantly larger in absolute terms because the peak-to-peak modulation of torsional eye position was about a factor 10 smaller than that of vertical or horizontal eye position. We also computed the average coefficient of determination ($R^2$) for the reconstructed ocular rotation as summarized in Table 4.

To compare these results with a smooth counter rolling strategy of the eye (i.e. without quick phases), we also reconstructed the rotation of the eye by using the angular velocity to reconstruct the rotation of the gaze vector and the principle of minimal torsion to compute the torsional position modulation as described in Methods. This procedure yielded the predicted modulation of ocular torsion at the second harmonic of the spatial tracking frequency (see Appendix B: equation B1 and
Fig. A3). The peak amplitudes of this modulation were comparable to the experimentally observed peak amplitudes (Fig. 9A, C).
DISCUSSION

To track target motion in space, the oculomotor system has to be able to generate motion patterns that are geometrically more complex than the relatively simple fixed-axis rotations underlying the vestibulo-ocular reflex movements or the ballistic movements of the eye during visually-guided saccades. A major challenge in motor control of smooth tracking movements are the restrictions that prevent the eyes to redirect gaze by using the most efficient shortest path rotation. This difficulty arises in particular during curvilinear tracking where the dual requirement of controlling the eye’s torsion orientation comes into conflict with the requirement of rotating the eye in the most efficient way to smoothly track the target. We have shown that this dual task requires that the rotation axis of the eye continuously changes its orientation relative to the orbit. This particular motion pattern results from two simultaneous rotations of the eye, one to keep gaze on the moving target and another one to control ocular orientation by counter rolling the eye about the instantaneous gaze direction. Although this particular motion strategy is needed to prevent accumulation of ocular torsion, we show that it also implies that Donders’ law is no longer automatically maintained. We suggest that the intervening small quick phases serve to minimize the inevitable deviations from this fundamental law during curvilinear smooth tracking.

Extended generic Listing model

It has been noted almost two decades ago that smooth pursuit is governed by Listing’s law (Haslwanter et al 1991; Tweed et al 1992). These studies reported that Listing’s law was followed with a precision of about ±1.5° in humans and about ± (<1°) in (rhesus) monkey (where slippage of the search coil can be excluded). Compared to the tested oculomotor range of about ± 50° and 40°, respectively, the conclusion that smooth pursuit obeys rather than violates Listing’s law (see Westheimer and McKee, 1973 and the pertinent Discussions in Haslwanter et al 1991 and Tweed et al 1992) seems well justified. In the present work, we focused our attention on the greatest challenge of Donders’ law during generation of curvilinear smooth pursuit. Without knowing the details about
how the brain might encode 3D target motion in space, we start from the simple assumption that this process depends on estimating and predicting the momentary target angular velocity and position relative to the observer’s eye (for saccades see Mays and Sparks 1980; Ghasia et al 2008; for a review see Crawford et al 2003). With this assumption in mind we used 3D rotation kinematics and a principle akin to Helmholtz’s principle of minimal torsion of the visual space as guiding principles (Helmholtz 1867; Hepp et al 1997). Assuming smooth target tracking it is possible to express the kinematics of the eye in terms of the 3D angular velocity and position of the target. For this one has to assume that the motor commands to the ocular plant implement, at least on average, a counter roll condition similar to the one described by equation (2) in order to maintain control of the ocular attitude. This implies that an observer who tries to track a target along a circular path must transform the estimated motion into a sequence of rotations of the eye in order to avoid accumulation of ocular torsion (see Fig. 2 and Fig. 10). The mentioned guiding principles lead to a generic expression of Listing’s law that accurately implements the half-angle rule (Helmholtz 1867) for straight line pursuit but also shows that it can only be approximately followed during circular or curvilinear pursuit (less than 0.5° deviation of the predicted tilt of angular eye velocity for gaze eccentricities ≤20°). Indeed, we found that the generic Listing model can not explain the finer experimental details of curvilinear tracking responses: During circular tracking, there is in fact a significant second harmonic in the modulation of torsional eye position, which is not predicted by the model. Specifically, there is no such second harmonic modulation of horizontal and vertical eye position, excluding the possibility that the observed second harmonic in ocular torsion reflects the multiplicative interaction of velocity and position signals predicted by the term \( \bar{\omega}_{\text{target}} \left( f_x \bar{E}_\text{ver} - f_y \bar{E}_\text{nor} \right) \) in the generic Listing model (equation 4). Straightforward calculations show that this term does not generate a second harmonic if none of its constituents includes such a harmonic. Consistent with this observation, the ad hoc addition of an extra term to the generic model that was free to modulate at the second harmonic independent of horizontal and vertical eye position led to a significant improvement of the model fits in torsional direction. This observation suggests that smooth tracking of curvilinear targets is not possible without violation of Listing’s law. An
independent kinematic analysis based on the counter roll condition (equation 2) without making use of any of the approximations leading to equation (4) supports this finding (see Appendix B and C). For reasons that will become clear in the following paragraph, the required additional torsion term, providing only a small but nevertheless significant correction of torsional angular velocity, most likely reflects the adjustments caused by quick phases to maintain ocular orientation during tracking.

**Functional role of quick phases during steady-state pursuit**

Since the experiments of Rashbass (1961) saccades or rapid eye movements have been recognized as an important part of pursuit eye movements. During steady-state pursuit they are in fact an integral part, alternating with portions of smooth tracking (Collewijn and Tamminga, 1984; Kettner et al 1996, De’Sperati and Viviani 1997). The typical role of rapid eye movements during tracking is to correct motor errors in eye position, keeping the fovea, which is far more sensitive to image motion than the periphery, close to the target (Dubois and Collewijn 1979). The rapid eye movement events observed in this study had amplitudes mostly below 1.5°. Their function is most likely not to catch up target position since they have a clear-cut repositioning phase in torsional direction. We therefore refer to them as quick phases. The torsional onset component of these quick phases typically drives the eye across the torsional equilibrium position (defined as average zero torsion position), either from clockwise to counterclockwise or vice versa. During the subsequent slow phase, 3D eye position drifts back towards the previous torsional offset position (see insets in Fig. 3). Thus, altogether angular eye velocity never quite matches target velocity, confirming earlier observations from other studies performed in 2D (Engel et al 1999; De’Sperati and Viviani 1997; Mrotek et al 2006).

What sort of motor error drives these small quick phases during curvilinear pursuit? As mentioned, it is unlikely a horizontal and/or vertical position error that causes these events in the sense of catch up saccades. Our animals were well trained to track targets during highly predictable paradigms, so that there is little reason to assume that velocity feedback signals were not sufficient to control pursuit (Engel et al 1999; Lisberger and Ferrara 1997; Mrotek et al 2006). There is however
an on-going debate about the role of position input during smooth pursuit (Noda and Warabi 1982; Polya and Wyatt 1980), which might reflect the fact that the system’s control of eye position and velocity is non-linearly interconnected. At the level of 2D oculomotor control, there seems to be growing evidence for such interaction (Blohm et al 2005; Carl and Gellmann, 1987; Morris and Lisberger, 1987). From the perspective of 3D control, the challenge of the oculomotor system during continuous tracking is twofold: one is to smoothly control gaze position and velocity in order to keep the retinal target image close to the fovea, the other is to control 3D ocular orientation which involves the holding function of all eye muscles while at the same time gaze is tracking the target. This task is much more complex in the case of circular pursuit than during straight line pursuit because it involves the activation of muscles or muscle compartments with mutually orthogonal pulling directions that smoothly change orientation in the roll plane. For the simple paradigm of circular tracking, the geometric analysis reveals that the required counter rolling of the eye is a trigonometric function of horizontal and vertical gaze direction (see Fig. 2 and Appendix B, C). Since this constraint can not be expressed in terms of target velocity alone (e.g., by transforming it into the velocity domain), it cannot be realized inside a simple velocity feedback loop, although velocity feedback represents the major drive during steady-state pursuit (Robinson 1965, Lisberger et al 1981, Robinson et al 1986, Goldreich et al 1992). Rather it is bound to involve independent position control, simultaneously or alternating with smooth tracking control. Our results suggest that the system uses a strategy where smooth tracking alternates with quick phases for correcting deviations from ocular torsion.

From a strategic point of view one might wonder why the ocular counter roll during pursuit is not fully parametrically controlled in a continuous smooth manner. One of the reasons is likely related to Donders’ law, which is not automatically warranted during smooth curvilinear tracking. The particular motion pattern required during circular tracking, which is a combination of tracking and counter rolling of the eye, undermines the premises on which Donders’ law are based (Hepp et al 1995, 1997). To minimize the inevitable torsion due to the spherical geometry of the eye’s configuration space, the system apparently invokes quick phase control. Another
related reason might be that quick phase control reduces the computational load since it can take advantage of existing neuronal hardware and might ultimately be more efficient. In fact, we found that the average modulation of torsional eye position only exhibited a fraction of the power at the second harmonic (Table 2) compared to that predicted by a full parametric control strategy (compare Fig. 2B and Fig. 9A). Furthermore, the peak-to-peak modulation was smaller than the predicted smooth modulation of ±1° at a target eccentricity of 15° (compare Fig. 9A and C).

Role of the oculomotor plant

Over the last two decades an increasing number of anatomical and theoretical studies have provided evidence converging on the idea that the half-angle rule of angular eye velocity might originate from an intricate neuro-mechanical control of the oculomotor plant (Demer 2004; Demer et al 1995, 2000; Miller 1989, 2007; Miller et al 2003; Kono et al 2002a, b; Quaia and Optican 1998; Raphan 1998). The theory was kindled by the observation that fibro-elastic sheaths, surrounding the extraocular muscles, could in fact change the pulling direction of eye muscles and mechanically produce the half-angle rule. This implies that both agonist and antagonist muscles change their action plane appropriately as a function of eye position (for a review see Angelaki and Hess 2004). Since not all eye movements, notably not the vestibulo-ocular eye reflexes follow the half-angle rule (Misslisch and Hess 2000; Misslisch and Tweed 2001; Misslisch et al 1994; Tchelidze and Hess 2008), the required coordinated changes of muscular action planes must necessarily be under some neuronal control, as in fact soon proposed in form of the so-called active pulley hypothesis (Demer et al 1997, 2000). In a recent study of smooth pursuit initiation, evidence has been presented suggesting that the oculomotor commands do undergo a reference frame transformations taking ocular torsion into account (Blohm and Lefèvre 2010). This finding supports the notion that the brain has access to 3D eye position signals coded in space coordinates, independent of whether the oculomotor plant be controlled by 2D or 3D motor commands (Blohm and Lefèvre 2010; Ghasia et al 2008; Green et al 2007). In recent electrophysiological studies, Klier and colleagues (2006, 2010) have shown that electrical stimulation of the abducens nerve in subhuman primates generates eye
movements whose angular velocity profiles approximately follow the half-angle rule, irrespective of static head orientation or orbital eye position. Since peripheral stimulation of motor nerves precludes the intervention of central processing, these observations emphasize the importance of the peripheral biomechanics in the implementation of the half-angle rule.

Listing’s law requires that the torsional component of the eye angular velocity at the output is numerically equivalent to a multiplicative interaction of current horizontal and vertical position and velocity signals (half-angle rule, see equation (4)). Although recent evidence suggests that this interaction does not happen at the premotor level (Ghasia and Angelaki 2005), its biomechanical implementation remains obscure. It has been pointed out that such implementation requires that the same muscles controlling eye velocity also must exert appropriate position control (Crawford and Guitton 1997; Raphan 1998; Optican and Quaia 1998, Smith and Crawford 1998). To illustrate the geometric complexity of the required muscle activation pattern, circular pursuit provides an ideal example. In the first place, one notices that the vectors of eye angular acceleration and velocity geometrically move in different planes, even though in phase quadrature: while the angular velocity tilts by half the angle of gaze eccentricity as predicted by $\Omega_{\text{tor}} = \text{o}_{\text{target}} (f_x \tilde{E}_{\text{ver}} - f_y \tilde{E}_{\text{hor}})$ in equation (4), the angular acceleration remains approximately confined to z-y plane because $d\Omega_{\text{tor}}/dt = 0$ while rotating about the x-axis (Fig. 10). At the same time, the gaze holding mechanisms must continuously change orientation in order to keep ocular torsion minimal and to maintain gaze at constant eccentricity during circular tracking. Altogether, this requires highly coordinated muscle activity patterns, encoding simultaneously the continuously changing tonic and phasic motor command signals by differential activation of phasic and tonic muscle fibers. Although it has been known for long that extraocular muscles contain different muscle types (Bach-y-Rita and Ito 1966; Hess and Pilar 1963; Kern 1965; Kono et al 2002b; Lim et al 2007; Oh et al 2001; Scott and Collins 1973) with different functional properties, our knowledge about their actual deployment in eye movement control is unfortunately still rather limited (Dieringer and Precht 1986; Davis-Lopez de Carrizosa 2011; Anderson et al 2009). Independent of how the details of a neuro-mechanical implementation of the half-angle rule during pursuit might look like, our analysis suggests that
circular or curvilinear pursuit requires intricate dual control of ocular orientation and gaze, involving a close interaction of slow and fast eye movement mechanisms at some premotor level of 3D oculomotor control.
APPENDIX A: LIMITED VALIDITY OF HALF-ANGLE RULE DURING CIRCULAR PURSUIT

Consider tracking a target that moves on a circle centered on straight ahead in a fronto-parallel plane at constant velocity. To evaluate the generic Listing model (equation 4 in Methods) we first compute the underlying premotor eye velocity command (equation 3) by evaluating the vector \( \mathbf{f} \) with \( \hat{\mathbf{n}} = (1, 0, 0) \) and \( \lambda = -1/\hat{g} \), (equation 2). In the polar coordinates \( \varepsilon \) and \( \psi \) (see Fig. A1), the gaze vector writes \( \mathbf{g} = (\cos(\varepsilon) \sin(\psi) \sin(\varepsilon) \cos(\psi)) \) such that \( \mathbf{f} = \tan(\varepsilon)(0 \sin(\psi) - \cos(\psi)) \). With this, we find \( \frac{d\tilde{E}}{dt} = \left(\frac{\hat{\omega}}{2}\right) \mathbf{f} \). To estimate the eye position rotation vector that moves the eye from straight ahead to the target and then along a circular path as illustrated in Fig. 2, we note that the time integral of the estimated eye velocity, \( \int d\tilde{E} = -(1/2) \tan(\varepsilon) \hat{e} \) with \( \hat{e} = (0 \cos(\psi) \sin(\psi)) \) is a close approximation of a rotation vector written as \( \mathbf{E} = -\tan(\varepsilon/2) \hat{e} \). For angular target eccentricities \( \varepsilon \leq 16^\circ \) the ratio \( \tan(\varepsilon)/2 : \tan(\varepsilon/2) \leq 1.02 \). This rotation vector describes every eye position along the circular path as an eye movement about axis \( \hat{e} = (0 \cos(\psi) \sin(\psi)) \) through the angle \( +\varepsilon \) or \( -\varepsilon \) for \( \psi \) varying in the interval \([0 \ \pi]\). With this approximation we can write the generic Listing equation for circular pursuit (equation 4 in Method):

\[
\mathbf{\Omega}_{\text{eye}} = \hat{\omega} - \frac{\tan(\varepsilon)}{\sqrt{1 + \tan^2(\varepsilon/2)}} \hat{f}, \quad \text{with} \quad \hat{f} = \frac{1}{\sqrt{1 + \tan^2(\varepsilon/2)}} \begin{pmatrix} \tan(\varepsilon/2) \\ \sin(\psi) \\ -\cos(\psi) \end{pmatrix} 
\]

(A1)

Thus, in a specified eccentricity range, the tilt of the angular eye velocity during smooth circular pursuit approximates the half-angle rule. In the next two paragraphs we show the limitations of this approximation. First we show that although the proposed counter roll condition (equation 2) guarantees no accumulation of torsion during circular tracking across cycles, zero ocular torsion is generally not maintained in secondary eye positions. Second, we show that these violations of Listing’s law are due to violations of Donders’ law, which does not hold in general during non-fixed axis rotations.
The optimal counter roll motion during curvilinear pursuit can be evaluated as follows: Consider the change in ocular orientation if during circular pursuit the eye would simply rotate about the forward pointing x-axis, say through an angle $\psi$ from position B to C as illustrated in Fig. 2. Using three mutually orthogonal unit vectors $\hat{g}$, $\hat{h}$ and $\hat{v}$ (defined in Methods), this change in orientation is the difference in angular orientation of the frame $\hat{g}'$, $\hat{h}'$, $\hat{v}'$ relative to $\hat{g}$, $\hat{h}$, $\hat{v}$ in the respective positions (see Fig. 2A, B). Let $R = R(\hat{e}, \rho)$ represent the usual rotation operator with rotation axis $\hat{e}$ and rotation angle $\rho$. Applied to the vectors $\hat{g}$, $\hat{h}$ and $\hat{v}$ with axis $\hat{e} \equiv \hat{g}$, we find their new orientation $\hat{h}' = \hat{v}' \times \hat{g}'$ and $\hat{v}'$ with $\hat{v}' = R\hat{v} = \sin(\rho) \hat{g} \times \hat{v} - \cos(\rho) \hat{g} \times (\hat{g} \times \hat{v})$. Since the vectors $\hat{g}$, $\hat{h}$, $\hat{v}$ represent a right-handed orthogonal triple, we can use $\hat{g} \times \hat{v} = -\hat{h}$ and $\hat{g} \times (\hat{g} \times \hat{v}) = -\hat{v}$ to simplify the equation for $\hat{v}'$ to $\hat{v}' = -\sin(\rho) \hat{h} + \cos(\rho) \hat{v}$. To find the counter roll angle $\rho$ that keeps the vector $\hat{v}'$ in a vertical plane through the new gaze direction $\hat{g}'$, one has to require that the projection of $\hat{v}'$ onto a vector parallel to the z-axis, $\hat{e}_z$ is minimal (compare $\hat{v}$ and $\hat{v}'$ in Fig. 2C). Taking the scalar product of $\hat{v}'$ and $\hat{e}_z$ we find the relation $f(\rho) = \hat{v}' \cdot \hat{e}_z = -\sin(\rho) \sin(\psi) - \cos(\rho) \cos(\psi) \cos(\epsilon)$ and evaluate the angles $\rho$ for which the slope $\partial f(\rho)/\partial \rho = 0$. We find that for $\psi = \pi/2$, $\pi$, $3\pi/2$, and $2\pi$ the eye has to counter rotate through $\rho = -\pi/2$, $-\pi$, $-3\pi/2$ and $-2\pi$ at which angles $f(\rho)$ is minimal (i.e., $\partial^2 f(\rho)/\partial \rho^2 > 0$). However for angles in between the eye has to counter rotate through slightly larger angles. Specifically, one finds the remaining minima of $f(\rho)$ for $\rho = -\tan^{-1}(\tan(\psi) / \cos(\epsilon))$ for $\psi \neq k\pi/2$, $k = 1, 2$ and 3. Thus during circular pursuit ocular counter roll does not completely compensate the ocular roll for rotation angles in between the four quadrants (i.e., for $\psi \neq k\pi/2$, $k = 1, 2$ and 3). If there are no intervening torsional quick phases the residual torsion of the eye in these quadrants should follow the relation

$$\delta \rho = \psi - \tan^{-1}(\tan(\psi) / \cos(\epsilon)) \quad (B1)$$

for all angles $\psi \neq k\pi/2$, $k = 1$ to 3. The residual torsion $\delta \rho$ modulates at twice the frequency of $\psi$ (Fig. A3B).
APPENDIX C: OCULAR ROTATION DURING SMOOTH CIRCULAR PURSUIT EYE MOVEMENTS

To compute 3D-eye position during curvilinear pursuit, we represent gaze direction \( \hat{g} \) in spherical polar coordinates \( \vartheta \) (horizontal gaze deviation, positive leftward) and \( \phi \) (vertical gaze deviation, positive downward, Fig. A2):

\[
\hat{g} = x\hat{e}_x + y\hat{e}_y + z\hat{e}_z = \cos(\vartheta)\cos(\phi)\hat{e}_x + \cos(\vartheta)\sin(\vartheta)\hat{e}_y - \sin(\vartheta)\hat{e}_z
\]

(C1)

In Cartesian coordinates, the three basis vectors \( \hat{e}_x, \hat{e}_y, \) and \( \hat{e}_z \) can be represented by 3x1 matrices \( \hat{e}_x = (1 0 0)^T, \hat{e}_y = (0 1 0)^T, \) and \( \hat{e}_z = (0 0 1)^T \) (superscript T for transpose), pointing, respectively, along the x-, y-, and z-axis. For the following calculations, it is advantageous to use an alternative basis represented by the four Clifford numbers \( \hat{1}, \hat{2}, \hat{3}, \) and \( I \), the multiplicative unit, with the following two properties:

\[
(\hat{1})^2 = (\hat{2})^2 = (\hat{3})^2 = I \text{ and } \hat{1}\hat{2}\hat{1} + \hat{2}\hat{1}\hat{2} = \hat{1}\hat{3}\hat{1} + \hat{3}\hat{1}\hat{3} = \hat{2}\hat{3}\hat{2} + \hat{3}\hat{2}\hat{3} = 0.
\]

This Clifford basis can be represented by real 4x4 matrices also called Dirac matrices (Snygg 1997):

\[
\hat{1} = \begin{pmatrix} 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \end{pmatrix}, \quad \hat{2} = \begin{pmatrix} 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & -1 \\ 1 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 \end{pmatrix}, \quad \hat{3} = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & -1 & 0 \\ 0 & 0 & 0 & -1 \end{pmatrix}
\]

(C2)

In the coordinates \( \vartheta \) and \( \phi \), the gaze vector expressed in this Clifford basis is:

\[
\hat{g} = \cos(\vartheta)\cos(\phi)\hat{1} + \cos(\vartheta)\sin(\vartheta)\hat{2} - \sin(\vartheta)\hat{3}
\]

(C3)

A rotation of gaze from one position to another is obtained by conjugating the gaze vector \( \hat{g} \) with the rotation operator

\[
R(\hat{n}, \rho) = I \cos(\rho / 2) - \sin(\rho / 2)(n_x\hat{2} + n_y\hat{3} + n_z\hat{12}),
\]

specifying the angle \( \rho \) and the axis \( \hat{n} \) in terms of the three Clifford products \( \hat{23} = \hat{2}\hat{3}, \hat{31} = \hat{3}\hat{1}, \hat{12} = \hat{1}\hat{2} \) (for details see Snygg 1997):

\[
\hat{g}' = R\hat{g}R^{-1}
\]

(C4)

The inverse rotation operation \( R^{-1} \) is \( R^{-1} = R(\hat{n}, -\rho) \).

To compute the rotation operator for a rotation of the eye about the current gaze position \( \hat{g} \), we compute the basis vectors tangential to the coordinates \( \vartheta \) and \( \phi \) (Fig. A2):
\[
\gamma_\phi = \frac{\partial \hat{g}}{\partial \phi} = -\sin(\phi) \cos(\theta) \hat{\gamma}_1 - \sin(\phi) \sin(\theta) \hat{\gamma}_2 - \cos(\phi) \hat{\gamma}_3
\]  
(C5a)

\[
\gamma_\psi = \frac{\partial \hat{g}}{\partial \psi} = -\cos(\phi) \sin(\theta) \hat{\gamma}_1 + \cos(\phi) \cos(\theta) \hat{\gamma}_2
\]  
(C5b)

and from these two vectors the Clifford product \( \gamma_{\phi\psi} \), which represents the oriented tangent plane to the current gaze direction at position \( \theta, \phi \). Taking the metric of this coordinate change from the flat Euclidean space to the spherical non-Euclidean space into account, yielding a factor \( \cos(\phi) \) (i.e., the square root of the determinant of the metric tensor), we write:

\[
\hat{\gamma}_{\phi\psi} = \gamma_\phi \gamma_\psi \cos(\phi) = \cos(\phi) \cos(\theta) \hat{\gamma}_{23} + \cos(\phi) \sin(\theta) \hat{\gamma}_{31} - \sin(\phi) \hat{\gamma}_{12}
\]  
(C5c)

Finally, to compute the motion of gaze during circular pursuit as illustrated in Fig. A3A (see also Fig. 2A, B), we first write the rotation operator for moving gaze from straight ahead to up about the y-axis, \( P = I \cos(\phi / 2) - \sin(\phi / 2) \hat{\gamma}_{31} \), then the rotation about the x-axis, \( R = I \cos(\psi / 2) - \sin(\psi / 2) \hat{\gamma}_{23} \), and finally the counter rotation of the eye about the current gaze direction, \( R' = I \cos(\rho / 2) - \sin(\rho / 2) \hat{\gamma}_{\phi\psi} \). The compound rotation of gaze is then obtained by conjugating the gaze vector in primary position with the compound rotation operator \( (R')^{-1}RP' \) (which is a function of the angles \( \theta, \phi, \psi, \) and \( \rho \))

\[
\hat{g}' = (R')^{-1}RP^{-1} \hat{g}PR^{-1}R'
\]  
(C6)

In the same way, the rotation of \( \hat{h} \) and \( \hat{v} \) (see Fig. 2A) can be computed. With any two of these vectors, we obtain the associated eye position (rotation) vector \( E = \tan(\psi / 2) \hat{e} \) with rotation axis \( \hat{e} \) and roll angle \( \psi \) (relative to straight ahead) as illustrated in Fig. A3B.

From these analyses in the eye position domain, three important observations can be made (Fig. A3A): First, although torsion does not accumulate under the imposed counter roll condition requiring \( \rho = -\psi \), it can not completely be compensated, i.e. Listing’s law cannot be preserved: Note the continuous deviation of the moving rotation axes from the frontal plane during one pursuit cycle (3D-view and projections of trace of \( \hat{h} \) in panel A and D of Fig. A3). Second, torsional eye position modulates at twice the spatial frequency of circular pursuit (1° amplitude for circular pursuit with eccentricity =15°). Third, Donders’ law is not fulfilled except at the four cardinal eye positions. For example, if circular pursuit terminates at position C with a saccade back to the starting position A, the eye carries with it a residual torsion that was built up during
circular pursuit from B to C (Fig. A3A and B). It can be demonstrated that this is always the case no matter how the counter roll angle \( \rho \) is being defined as a (smooth) function of \( \psi \).
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**Figure 1:** How does the oculomotor system comply with Donders’ law during a closed eye movement sequence that includes a phase of smooth target tracking along a curvilinear path? Suppose that after interception of the target’s path with a saccade from A to B, an observer tracks the target from B to C along a curvilinear path. How must the eye move such that it lands in the same three-dimensional angular orientation as required by Donders’ law when the observer saccades back from C to A? $\psi$: angle subtended by line segments AB and AC; $d\psi/dt$: angular velocity of target moving fronto-parallel to the observer from B to C; $\Omega_{ver}$, $\Omega_{hor}$: vertical and horizontal angular eye velocity.

**Figure 2:** Compensation of ocular torsion during circular tracking. $A$ and $B$: For tracking a circularly moving target along the shortest path the eye would have to rotate about the forward pointing axis x. This would change the orientation of the eye, indicated by the three mutually orthogonal vectors $\hat{g}$, $\hat{h}$, and $\hat{v}$, from their orientation in primary position parallel to coordinate axes x, y, z (gaze along segment OA) to $\hat{g}$, $\hat{h}$, and $\hat{v}$ shown in position B and subsequently to $\hat{g}'$, $\hat{h}'$ and $\hat{v}'$ in position C. *Front view C:* To minimize a change of torsion, the eye best counter rotates about an axis that is at any time parallel to the gaze line such that the angles subtended by the vector $\hat{v}'$ (at position C) and $\hat{v}$ (at position B) or equivalently $\hat{h}'$ and $\hat{h}$ remain minimal. *Side view D:* This counter rotation about the gaze line can not completely compensate changes in ocular torsion except in the positions B ($\psi$ =0°), right (90°), down (180°) and left (270°). $A$: intersection of sphere with positive x-axis; $\hat{e}_x$, $\psi$: axis (parallel to x) and angle of target rotation; $\hat{g}$, $\rho$: axis and angle of counter roll; $\hat{g}$, $\hat{g}'$: vectors parallel to gaze line segments OB, OC.

**Figure 3:** Tracking of a target moving along an elliptic path in the frontal plane showing smooth slow phase segments alternating with quick phases. $A$: Torsional ($E_{tor}$), vertical ($E_{ver}$) and horizontal ($E_{hor}$) eye position traces with second order sinusoidal fits superimposed (black solid line for torsion, white solid lines for vertical and horizontal traces; responses to clockwise and counterclockwise target motion as indicated by superscripts). $B$: Enlarged view of the same responses (x 3) showing
that the vertical and horizontal slow phase segments exhibit systematically smaller slopes than the fitted sinusoids. Target ellipse with major axis vertical 20°, minor axis horizontal 10°; spatial frequency 0.1 Hz. Data from subject mi.

**Figure 4:** Relationship between amplitude, peak velocity and duration of quick phases. *A:* Vertical (gray dots) and horizontal peak velocity components (black dots) during clockwise and counterclockwise tracking as a function of quick phase amplitudes. *B:* Torsional peak velocity components versus amplitudes (clockwise in gray; counter clockwise in black). *C, D:* Duration as a function of amplitude and peak velocity as a function of duration of quick phase vectors (including all three dimensions). Data from subject mi; amplitude 15°, frequency 0.067Hz (155 quick phases across a total of 12 response cycles).

**Figure 5:** Eye-position related (EPV) versus slow phase-related (SPV) angular eye velocity during curvilinear target tracking (three cycles superimposed). *A:* Sinusoidal fits (up to 3rd harmonic order) of angular eye position (solid line for torsion (E_tor), dashed lines for vertical (E_ver) and horizontal (E_hor) eye position). Note the high precision of vertical and horizontal eye position modulation and the relative large quick phases in torsion. *B, C:* Slow phase angular eye velocity superimposed by eye position-related angular velocity (dashed lines) and slow phase-related angular velocity (based on fitting the extended generic Listing model, LSPV) (solid lines). Note the small disparities between the two fitting curves in torsion and vertical slow phase velocity. Target ellipse with major axis 20° oriented vertically; minor axis 15°; spatial frequency 0.1 Hz (data from subject mi).

**Figure 6:** Relation between gaze direction, estimated rotation axis of target motion, and ocular rotation axis (three cycles superimposed). *A.* Gaze direction expressed as normalized gaze vector (\( \hat{g} \)). *B.* Estimated rotation axis (\( \hat{n} \)) of target motion. *C.* Estimated ocular rotation axis (\( \hat{f} \)). *D.* \( \lambda \) as a function of response phase, determining the geometric relation between the three vectors \( \hat{n}, \hat{g}, \) and \( \hat{f} \) across the cycle. Note that *A* to *C* show results of solving the equation (1) for three trials of circular pursuit superimposed together with the corresponding \( \lambda \) in *D.* Target eccentricity 15°, frequency 0.067Hz (data from subject mi).
**Figure 7**: Spatial relation between normalized gaze direction, estimated rotation axis of target motion, and ocular rotation axis. *A*. Superimposed projections of three traces outlined by the gaze vector (\(\hat{g}\)) in the target plane (TP) and the ocular rotation axis (\(\hat{f}\)) in the frontal plane through the eye (FPe, see inset). *B* and *C*. Top and side views showing that the \(\hat{g}\)-traces move perfectly in TP, parallel to the FPe-plane while the \(\hat{f}\)-traces in the FPe-plane wobble in x-direction. Note stability of the estimated rotation axis \(\hat{n}\) of target motion throughout the three cycles. Circular pursuit amplitude 15°, frequency 0.067 Hz counter clockwise; three trials superimposed (subject mi).

**Figure 8**: *A*. Plots of \(\lambda\) as a function of gaze eccentricity \(\varepsilon\) (*solid black traces* centered at about 5°, 10° and 15°). Inset A: During each tracking cycle, \(\lambda\) described a small loop due to the disparity between the rotation plane of the eye and the plane of target motion. Target cycles with \(r = 5°, 10°\) and 15° (*vertical dashed lines*); number of superimposed \(\lambda\)-cycles at each eccentricity, \(N=8\); spatial frequency 0.1Hz (data from mi475). Fitted function \(\lambda(\varepsilon) = a + b / \cos(\varepsilon)\) (*thick gray line*); \(a = 0.014 (\pm 0.006); b = 0.986 (\pm 0.006)\) (median values ± mean absolute deviation). *B*. Geometric relation between gaze eccentricity \(\varepsilon\) and \(\lambda\). Unit gaze vector \(\hat{g}\); estimated axis of target rotation \(\hat{n}\); estimated direction vector of eye velocity \(\hat{f}\) (no torsional component).

**Figure 9**: Reverse computation of torsional eye position modulation (averages ±SD). *A*. Reverse-computed torsional eye position using the rotation-precession motion for clockwise (*left*) and counter clockwise (*right*) circular tracking shown in Figure 2. *B*. Torsional eye positions reverse-computed from least-squares fits of angular eye velocity after removal of quick phases (slow phase-related angular velocity) for clockwise (*left*) and counter clockwise (*right*) circular tracking. *C*. Torsional, eye positions reverse-computed from least-squares fits of eye position-related angular velocity for clockwise (*left*) and counter clockwise (*right*) circular tracking. Note that torsional eye position in *B* runs off compared to *A* and *C*. Angular velocity from circular pursuit, amplitude 15°, frequency 0.067Hz, 6 response cycle (subject mi).

**Figure 10**: Sketch of the rotation–precession motion of the eye during tracking of a target that moves around a circle in a fronto-parallel plane, clockwise from the observer’s vantage point. *A*. In gaze-up
the eye will move next to the right and down to keep tracking the target (indicated as dashed circle projected onto the eye). Due to Listing’s law, it can not use the shortest path by moving about the forward pointing axis but rather rotates about an axis that itself rotates clockwise about the forward pointing axis. B. Medio-sagittal view showing that the momentary axis of rotation (\(\Omega\)) underlying this motion is forward tilted by half the angle of gaze eccentricity (\(\epsilon\)). During rotation around the circle it traces out a cone as indicated by the dashed lines. C. Orientation of the momentary rotation axis after it has moved through an angle \(\psi\) pointing gaze halfway between up and right. Medial rectus (mr), lateral rectus (lr), inferior rectus (ir), and superior rectus muscle (sr). For simplicity not shown are superior and inferior oblique muscles. \(\Omega\): angular eye velocity; \(d\Omega/dt\): angular eye acceleration.

**Figure A1**: Angular eccentricity (\(\epsilon\)) and torsional angular deviation (\(\psi\)) of target T. \(\hat{g}\): unit gaze direction vector (parallel to segment OT); \(\hat{e}_z, \hat{e}_x\): Cartesian unit direction vectors of z-, x-coordinate axis (\(\hat{e}_y = \hat{e}_z \times \hat{e}_x\) not shown).

**Figure A2**: Angular elevation (\(\phi\)) and azimuth (\(\vartheta\)) and associated unit direction vectors \(\hat{y}_o\) (tangential to horizontal great circle through T, pointing into direction of increasing \(\vartheta\)'s), \(\hat{y}_\phi\) (tangential to vertical meridian through T, pointing into direction of increasing \(\phi\)'s), and \(\hat{y}_{\phi\vartheta} (= \hat{y}_\phi \hat{y}_\vartheta\), normalized Clifford product of \(\hat{y}_\phi\) and \(\hat{y}_\vartheta\), parallel to instantaneous gaze direction); \(\hat{e}_z, \hat{e}_x\) as in Figure A1; T: target.

**Figure A3**: Simulation of smooth circular tracking of a target at an eccentricity of 25°.

A: 3D view of circular path traced out by the target /gaze line, starting at position B (gaze up: line segment OB) and the associated figure-eight path of the orthogonal gaze complement (line segment OB’). Note that as gaze moves from straight ahead (line segment OA) up to B, its vertical orthogonal complement (segment OD’), moves along the vertical meridian from D’ to B’. Similarly, as gaze moves from B along a circle to C and further to D, the orthogonal complement moves from B’ along a figure-eight loop to C’ and further to D’. B: Eye position traces E_tor, E_ver, and E_hor associated to the described circular gaze motion, starting at B, plotted against the roll angle \(\psi\) (angle of rotation about
x-axis, zero for gaze in position B). Dashed vertical lines indicate eye positions (clockwise, down, left: positive) corresponding to labels B, C, and D in panel A. C: Projections of associated rotation axis, \( \hat{n} \), onto y-z plane (frontal view), x-y plane (top view), and x-z plane (side view). Note significant x-component of rotation axis (top and side view).
A behind view

B top view

C side view

\[ f = \hat{n} + \lambda \hat{g} \quad (\lambda < 0) \]
A

\[ \lambda(\varepsilon) = \cos(\varepsilon) \]

B

\[ \lambda:1 = 1: \cos(\varepsilon) \]
Table 1: Average Coefficients of Determination ($R^2$) for circular pursuit ($r=15^\circ$, 0.1Hz)

le (n = 40); mi (n = 52); pi (n = 34); xa (n = 28); n = number of cycles

<table>
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<th>Sinusoidal fits (up to 2$^{nd}$ harmonic)</th>
<th>Listing fits</th>
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<td>$\Omega_{\text{tor}}$</td>
<td>$\Omega_{\text{ver}}$</td>
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<tr>
<td>le</td>
<td>0.06 ± 0.20</td>
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<tr>
<td>mi</td>
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<tr>
<td>pi</td>
<td>0.18 ± 0.17</td>
<td>0.97 ± 0.01</td>
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<tr>
<td>xa</td>
<td>0.13 ± 0.07</td>
<td>0.87 ± 0.03</td>
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Table 2: Relative power of 2nd harmonic

Similar results for circular pursuit at lower frequency (0.067Hz).

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<thead>
<tr>
<th></th>
<th>$\Omega_{tor}$</th>
<th>$\Omega_{ver}$</th>
<th>$\Omega_{hor}$</th>
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<tr>
<td><strong>cw</strong></td>
<td>0.13 ± 0.12</td>
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<td>&lt;0.001</td>
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<tr>
<td><strong>ccw</strong></td>
<td>0.19 ± 0.15</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
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Circular pursuit (r=15°, 0.1 Hz, n=109)
Table 3: Fits of $\lambda_{\text{exp}} = a + b/\cos(\epsilon)$

<table>
<thead>
<tr>
<th></th>
<th>Circular pursuit (r = 5°, 10°, 15°; 0.1 Hz)</th>
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<tr>
<td></td>
<td>a</td>
<td>b</td>
<td>$R^2$</td>
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<tr>
<td>le</td>
<td>0.042 ± 0.01</td>
<td>0.96 ± 0.01</td>
<td>0.997</td>
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<tr>
<td>mi</td>
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<td>0.99 ± 0.006</td>
<td>1.00</td>
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<tr>
<td>pi</td>
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<td>1.002 ± 0.019</td>
<td>1.00</td>
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Table 4: Average Coefficients of Determination ($R^2$) for reconstructed ocular rotation

Same data as in Fig 9 (circular tracking, $r=15^\circ$, 0.1 Hz, 6 response cycles, from 3 exp. sessions)

<table>
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<tr>
<th></th>
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<td></td>
<td>$E_{tor}$</td>
<td>$E_{ver}$</td>
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<td>Slow phase-related</td>
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<td>0.994 ± 0.002</td>
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<tr>
<td>Extended Listing model</td>
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<tr>
<td>Eye position-related</td>
<td>0.988 ± 0.005</td>
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