Modulation of Saccade Curvature by Ocular Counterroll

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PURPOSE. On close inspection, it can be seen that most saccadic trajectories are not straight but curve slightly; in other words, they are not single-axis ocular rotations. The authors asked whether saccade curvatures are systematically influenced by static ocular counterroll (OCR).

METHODS. OCR was elicited by static whole-body roll position. Eight healthy human subjects performed horizontal and vertical saccades (10° amplitude; 0° and 10° eccentricity; head-fixed coordinate system) in upright and ear-down whole-body roll positions (45° right, 45° left). Three-dimensional eye movements were recorded with modified dual-search coils at 1000 Hz.

RESULTS. Saccade curvature was systematically modulated by OCR depending on saccade direction. In the horizontal-vertical plane, primarily vertical saccades were modulated with downward saccades curving toward the upper ear and upward saccades curving toward the lower ear. Modulation of saccade curvature in the torsional direction correlated significantly with OCR only in abducting saccades.

CONCLUSIONS. No universal mechanism, such as visual-motor coordinate transformation or kinematic characteristics of the saccadic burst generator, alone could explain the complex modulation pattern of saccade curvature. OCR-induced changes of the ocular motor plant, including transient force imbalances between agonist eye muscles (vertical rectus and oblique muscles) and shifting eye muscle pulleys, are suitable to explain the found direction-dependent modulation pattern.

(Invest Ophthalmol Vis Sci. 2009;50:1158–1167) DOI: 10.1167/iovs.08-2453

I t is commonly assumed that a saccade between two visual targets consists of a single-axis rotation of the ocular globe about a head-fixed axis. Mathematically, a single-axis rotation implies that the positional trajectory between movement onset and offset is straight when expressed as quaternion or rotation vectors.1–3 Listing’s law states that, with the head not moving, these rotation vectors lie in a plane, called Listing’s plane.4 Tweed and Villis5 have shown that visually guided saccades, at least to a first approximation, are single-axis rotations and obey Listing’s law.

If the orientation of the ocular rotation axis changes during a saccade, its trajectory becomes curved. Saccades with curvatures in the horizontal-vertical plane can be elicited by displacing the visual target shortly after its appearance in a so-called double-step paradigm.6 Clearly, such curved saccades cannot result from a single-axis rotation. However, single-axis rotations are not a necessary condition for saccades to obey Listing’s law. In fact, Minken et al.7 showed that even strongly curved double-step saccades lie in Listing’s plane though their rotation axes change during displacement.

On close examination, even normal saccades are slightly curved.8 Systematic analysis of saccadic transients in the horizontal-vertical plane demonstrated curved trajectories predominantly during oblique saccades.9 Three-dimensional (3D) measurements of saccades also revealed transient curvatures in the torsional direction, called blips.10 Blips evoked by horizontal saccades systematically depend on direction and gaze elevation; blips evoked by vertical saccades are idiosyncratic but consistent on repetition.11 In contrast to deviations in the horizontal-vertical plane, torsional transients by definition violate Listing’s law.

In the present study, we asked whether saccade curvature depends on torsional eye position. A torsional offset that is added to eye positions before, during, and after saccades can be introduced by tilting the subject’s head in the roll plane.12 Given that this ocular counterroll (OCR), which leads to a shift of Listing’s plane along the naso-occipital axis,12,13 modifies the configuration of the extracocular muscles and their pulleys,14 we expected increasing saccadic curvatures if they were the result of altered ocular motor plant characteristics. Alternatively, central mechanisms of signal transformation from retinal input to ocular motor output could also lead to predictable saccadic curvatures, depending on OCR.15

The study of saccade curvature requires high-resolution and artifact-free measurements of ocular trajectories in three dimensions. The dual-search coil technique is considered the gold standard because of its high temporal and spatial resolution.16,17 Nonetheless, time and again, the validity of the torsional signal with standard search coils in humans has been questioned.18 Therefore, we opted to base our analysis on measurements with search coils with a modified exiting wire19 to ensure maximal torsional accuracy and validated the main findings with 3D video-oculography.

METHODS

Subjects

Eight healthy subjects (29 – 45 years; three women, five men) volunteered for the experiment. Informed consent was obtained from all subjects after the experimental procedure was explained. The protocol was approved by a local ethics committee and was conducted in accordance with the ethical standards laid down in the Declaration of Helsinki for research involving human subjects.

Setup

Subjects were seated on a turntable with three servo-controlled, motor-driven axes (Acutronic, Jona, Switzerland). Pillows and safety belts minimized movements of the body. The head was restrained with an individually molded thermoplastic mask (Sinmed, Reeuwijk, Netherlands).
Data Analysis

Ocular traces were analyzed with MatLab software (version 7.0.1; MathWorks, Natick, MA). Three-dimensional eye positions were lowpass filtered with a Savitzky-Golay filter23 (quadratic polynomial; 11 ms window size) and were expressed as rotation vectors1,22 in a head-fixed coordinate system that rotated with the subject. A rotation vector, \( \mathbf{r} \), described the instantaneous orientation of the eye as a single rotation from the reference position looking straight ahead. The rotation vector \( \mathbf{r} \) was oriented parallel to the axis of this rotation, and its length was defined by \( \tan^{-1}(r) \cdot 360/\pi \). From rotation vectors, angular velocity vectors \( \omega_{x,y,z} \) were derived.23 Angular velocity vectors point along the instantaneous rotation axis, and their lengths were proportional to the rotational speed.

Saccades were sorted according to gaze direction. Each saccade, including 1 second of presaccadic and 3 seconds postsaccadic fixation, was processed by a computer program and was interactively selected. Selection criteria included start and end positions in proximity to the visual targets, maintained before and after saccadic fixation, and absence of blinks. On average, 79% \( \pm \) 6% SD of 720 saccades per subject were accepted for further analysis. Horizontal, vertical, and torsional traces were aligned to the median eye position during the 250-ms fixation period preceding the saccade. Individual traces were shifted along the time axis such that they aligned at the instant saccades passed a level of 3°.

Video Setup for Complementary Eye Movement Recordings

Three-dimensional eye movements were binocularly recorded at 200 Hz with 3D video-oculography25 (Eye Tracker Version 1C/2003; Chronos Vision, Berlin, Germany) mounted on the thermoplastic mask. For every experimental condition, the system was calibrated at 0° \( \pm \) 10° horizontal and vertical positions.28 To optimize pupil tracking and torsion analysis, pupils were constricted with pilocarpine 0.5% eye drops. Raw video data were processed with the iris tracker software (version 2.1.6.1; Chronos Vision). Pupil tracking to obtain horizontal and vertical eye positions was performed using an algorithm based on...
RESULTS

To analyze the 3D kinematic properties of saccades, horizontal, vertical, and torsional components of rotation vectors were plotted against each other in different planes, corresponding to different views of the trajectories. Figure 1 depicts horizontal and torsional curvatures during 10° downward saccades in upright, 45° left-ear-down, and 45° right-ear-down whole-body roll positions for a typical subject. In the vertical-horizontal plane (Figs. 1A-C), the view from the subject’s perspective, downward saccades of the viewing left eye were curved to the right in an upright position (Fig. 1B). The horizontal curvature became larger in left-ear-down position (Fig. 1A) and even reversed in right-ear-down position (Fig. 1C). Curvature increased slightly with 10° adduction (right gaze) and decreased with 10° abduction (Fig. 1B), compared between overlays of left and right gaze. In the vertical-torsional plane (Figs. 1D-F), there was little curvature compared with the trajectories in the vertical-horizontal plane (Figs. 1A-C). In this example, intorsional curvature increased slightly in left-ear-down position (Fig. 1D). Upward saccades of the same left eye (data not shown) deviated to the right as well with the subject in upright position. Contrary to downward saccades, rightward curvature of upward saccades increased in the right-ear-down position and decreased in the left-ear-down position.

Figure 2 shows horizontal saccades of the same subject as in Figure 1. Adducting rightward 10° saccades of a viewing left eye at −10°, 0°, and 10° vertical eccentricity in upright, left-ear-down, and right-ear-down positions. (A-C) Eye position in the horizontal-vertical plane (projection from the subject’s perspective). Starting positions are aligned for clarity; (D-F) Horizontal-torsional plane. Separate saccade trajectories represent different vertical eccentricities corresponding to panels (A) to (C). (A, D) 45° left-ear-down whole-body roll position (LED). (B, E) Upright position (up). (C, F) 45° right-ear-down whole-body roll position (RED).

![Figure 2](https://iovs.arvojournals.org/pdfaccess.ashx?url=/data/journals/iovs/932958/)
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was determined by the maximum of the derivative of angular velocity. This slightly increased at the contralateral ear-down position. In abducting saccades, intorsional curvature showed downward curvature that increased in right-ear-down position.

![Figure 3](https://iovs.arvojournals.org/pdfaccess.ashx?url=/data/journals/iovs/932958/)

**Figure 3.** Analysis of the curvature of a typical 10° downward saccade in a left eye. (A) Vertical-horizontal plane (projection from the subject’s perspective). Bold trace: trajectory from saccade onset to saccade offset. Thin trace: subsequent catch-up saccade. Dashed line: straight connection between onset and offset. Arrow: eye position at peak acceleration. (B) Traces of torsional (light gray), vertical (black), and horizontal (dark gray) rotation vector components (converted to degrees). Dashed vertical lines: saccade onset and offset. Solid vertical line: peak acceleration. (C) Traces of angular velocity vector components. (D) Trace of the derivative of angular velocity vector length.

Saccade offset was defined 4 ms after velocity crossed the threshold of 30°/s.27 Saccade onset was defined 4 ms before angular velocity crossed the threshold. A negative transient in the horizontal eye position represented the rightward curvature of the saccade (Fig. 3B, dark-gray trace). As a result of the horizontal transient, the velocity trace of the horizontal component appeared biphasic (Fig. 3C, dark-gray trace).

To analyze the behavior of the ocular rotation axis during saccades, we used angular velocity vectors.23 Note that angular velocity vectors are oriented horizontally during vertical displacements and vertically during horizontal displacements; directions of vectors follow the right-hand rule. For example, the angular velocity vector of a downward saccade points to the left along the (positive) \( \omega_z \)-axis.

Figure 4 shows angular velocity vectors of three typical downward saccades in a left eye. In the upright position, angular velocity vectors formed a loop with an early negative and later a positive vertical component added to the main positive horizontal component (Fig. 4B; same saccade as in Fig. 3). This loop reflects the rightward curvature of the downward saccade. The nonlinear trajectory implies that the orientation of the ocular rotation axis was not stable during the saccade but rotated clockwise (from the subject’s view) in the vertical-horizontal plane. Mean angular velocity vector (bold arrow) of the saccade, however, pointed horizontally to the left, as expected if the eye were finally to reach the vertically displaced target. The initial angular velocity vector from saccade onset to peak acceleration (empty arrow) pointed down and to the left, indicating a rightward deviation at the beginning of the saccade. In the torsional direction (Fig. 4E), angular velocity vectors were closely aligned during the entire saccade, indicating no torsional curvature in the upright position.

Roll tilt toward the left ear (Figs. 4A, D) increased the loop of angular velocity vectors in the vertical-horizontal plane, corresponding to an increase of horizontal curvature of the downward saccade. Roll tilt toward the right ear (Figs. 4C, F) decreased the loop of angular velocity vectors in the vertical-horizontal plane. In the torsional direction, however, angular velocity vectors remained almost aligned in both ear-down positions.

Saccade curvature was quantified by the angle between the initial angular velocity vector and the mean angular velocity vector in the respective plane. The sign of the angle was determined by the sign of the direction of the saccade multiplied by the sign of the direction of the deviation according to the right-hand rule. For example, a downward saccade (positive) with a rightward curvature (negative) resulted in a negative deviation angle.

Figure 5 summarizes the modulation of horizontal curvature of saccades made along the vertical meridian by different roll positions for all subjects. Except for one extreme value, mean horizontal curvature in downward saccades of viewing left eyes scattered around zero in the upright position (Fig. 5A, up). In the right-ear-down position, curvature systematically increased toward the left (upper) ear and vice versa. Upward saccades of viewing left eyes showed a similar pattern: Curvature scattered around zero in the upright position (Fig. 5C, up) but systematically increased toward the lower ear in the ear-down position. The right eye followed the same rule when viewing (Figs. 5B, D): downward saccades curved toward the upper ear, and upward saccades curved toward the lower ear in the ear-down position.

Figure 6 depicts torsional curvature of vertical saccades of all subjects using the same definition as in Figure 5. Downward saccades of viewing left eyes predominantly showed a small extorsional curvature when subjects were in the upright position (Fig. 6A). In contrast to saccade curvature in the vertical-horizontal plane (Fig. 5A), there was no consistent modulation.
pattern by roll position in the torsional direction. Viewing right eyes showed a mirrored pattern with extorsional saccade curvature in the upright position (Fig. 6B). Upward saccades exhibited a small extorsional curvature in the upright position (Figs. 6C, D). In contrast to downward saccades, upward saccades showed a small but systematic modulation by roll position (Fig. 7). Torsional curvature of upward saccades showed a small but significant modulation by roll position with intorsion of the lower eye.

For statistical analysis, right eyes were mirrored as left eyes, and all eyes were pooled (n = 16 eyes of eight subjects). To quantify the modulation of saccade curvature by roll position, linear regression was performed for each eye through curvature of every saccade in left-ear-down, upright, and right-ear-down positions. Figure 7 summarizes the results for saccades showed a small but systematic modulation by roll position with intorsion of the lower eye.

For a visual validation of our results, we compared the magnitude of saccade curvature was related to the amount of OCR. If so, subjects with higher OCR amplitudes should show greater modulation of saccade curvature as a function of whole-body roll. OCR amplitudes from the 45° left-ear-down to the 45° right-ear-down position (mean 12.0° ± 4.2° SD, both eyes pooled) were correlated against the slopes from Figures 7A-B and 8A-B as a measure of modulation of saccade curvature. Vertical saccades showed significant correlation between horizontal curvature and OCR (Pearson correlation coefficient for downward saccades, r = 0.73, P = 0.0012; for upward saccades, r = 0.51, P = 0.043). In contrast, the correlation between vertical curvatures of horizontal saccades and OCR was not significant. Torsional curvatures of horizontal and vertical saccades did not significantly correlate with OCR, except for abducting saccades (r = 0.62, P = 0.01).

For a visual validation of our results, we compared the dual-search coil recordings with 3D video-oculography. Figures 9A-F show 3D video-oculographic data collected from the same subject and during the same paradigm as in Figure 1. Downward saccades showed the same modulation pattern of horizontal curvature, with a small offset between both recording methods (Fig. 9G). Torsional curvature of downward sa-
direction (qualitative summary, Fig. 10). OCR predominantly influenced horizontal curvatures of vertical saccades. Downward saccades curved to the upper ear, whereas upward saccades curved to the lower ear in roll positions. Vertical curvature of horizontal saccades was also slightly modulated by ear-down positions (Figs. 8A, B), but the direct correlation with OCR did not reach significance. Modulation of saccade curvature by OCR was also found in the torsional direction, but this effect was significant only in abducting horizontal saccades.

To explain the complex modulation patterns of saccade curvatures by OCR, we considered different mechanisms along the path of signal transformation from retinal input to ocular motor output. Saccade curvatures could arise as a result of a

DISCUSSION

The purpose of this study was to explore the influence of OCR on the kinematics of saccades. We found a specific modulation pattern of saccade curvature by OCR, depending on saccade
Mechanism 1: Mismatch between Retinal and Ocular Motor Coordinates

A mismatch between the sensed oculocentric target directions and head-fixed ocular motor commands during OCR could explain the horizontal curvatures of vertical saccades in ear-down positions. As in Schworm et al., 45° head-roll induced approximately 6° OCR in our subjects. Hence, head-fixed targets appear rotated clockwise by 6° in the right-ear-down position. Therefore, the target for a downward saccade appears down and shifted to the left, and the target for an upward saccade appears up and shifted to the right. The initial motor command would aim toward the perceived, not the actual, target location if OCR were not considered by the visual-motor transformation mechanism. To prevent a directional mismatch between the end point of the saccade and the target, an adaptation-driven mechanism ensures that during the latter part of the saccade, the initial directional error is corrected and the saccade trajectory curves toward the actual target. This mechanism would hold not only for vertical but also for horizontal saccades. The horizontal curvature of vertical saccades is compatible with this hypothesis, but the pattern of vertical curvature during horizontal saccades is not.

Although OCR reduces the roll-tilt of the visual input in ear-down positions, perceptual studies demonstrated that subjects tend to overestimate the angle of the perceived earth vertical in body roll positions less than 60°. This observation, called the e-effect, was also found if subjects had to indicate earth vertical (not body vertical) directly with saccadic eye movements. Contrary to the coordinate transformation hypothesis described, such a perceptual hypothesis would explain results only for vertical curvature of horizontal saccades but not for horizontal curvature of vertical saccades.

Mechanism 2: Kinematic Imperfections of the Saccadic Burst Generator

There has been a long debate about whether the explicit implementation of Listing’s law for saccades occurs at the level of premotor neurons, the ocular plant, or both. Tweed and Vilis described a model of neural controller that takes into account the noncommutativity of rotations to encode a 3D eye position signal in Listing’s plane. The existence of a saccadic burst generator that takes into account current eye position has been questioned by several authors, though a commutative controller invariably produces torsional deviations during and after saccades. The amplitudes of those so-called blips, however, is considerably smaller than predicted in the computer model. This observation led to the idea that Listing’s law is implemented at the level of eye muscle pulleys. These structures, consisting of connective tissue and smooth muscles, change extracocular muscle pulling directions as a function of eye position. Such a mechanical implementation of Listing’s law is suitable to simplify the neural control of saccades. Recent experiments in monkeys confirmed that horizontal eye
movements still obey Listing’s law when they are elicited by microelectric stimulation of the abducens nerve. The preservation of Listing’s law during such nonphysiological activation of the lateral rectus muscle further supports the notion that this law is implemented at the level of the ocular motor plant.

Indeed, our data show no universal modulation pattern as predicted by a kinematic mechanism but do show a pattern that is different depending on saccade direction. In addition, there is a striking disparity between the modulation of saccade curvature in the horizontal-vertical plane compared with the torsional direction. For example, clear horizontal modulation of vertical saccades is scarcely reflected in ocular torsion (Fig. 7A). This dissociation further argues against an explicit 3D saccadic burst generator and in favor of a mechanical implementation of Listing’s law.

**Mechanism 3: Characteristics of the Ocular Motor Plant**

The dynamics and kinematics of saccades are determined by force changes in agonist eye muscles. Although agonist activity during horizontal eye movements is restricted to one muscle, agonist activity during vertical eye movements involves two muscles. Unless their secondary actions in the torsional and horizontal directions cancel, the eyes will deviate from a straight vertical trajectory. For example, both the superior oblique and the inferior rectus muscle contract during downward saccades. Secondary actions of these muscles in the torsional (superior oblique, intorsion; inferior rectus, extorsion) and horizontal (superior oblique, abduction; inferior rectus, adduction) directions must cancel each other for a saccade to be perfectly downward.

OCR leads to an imbalance between the two coagonist eye muscles for downward saccades. During intorsion, the superior oblique muscle contracts and stretches the inferior rectus muscle. Considering the length-tension curve of eye muscles, the shorter (precontracted) superior oblique muscle will develop less traction than the longer (stretched) inferior rectus muscle. Hence, OCR reciprocally changes the dynamic characteristics of the two coagonist eye muscles. This transient force imbalance between the two vertically pulling coagonist muscle.
horizontal and vertical saccade curvature

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FIGURE 10. Modulation of saccade curvature by whole-body roll position in a left eye (qualitative summary plot). Horizontal and vertical saccade curvature as seen from the subject’s perspective. Shaded gray: significant correlation between modulation of saccade curvature and OCR amplitude. ab, abduction; ad, adduction; LED, left-ear-down position; RED, right-ear-down position.

Dynamic interactions of agonist eye muscles in vertical saccades and shifting eye muscle pulleys are both suitable to explain such a direction-dependent modulation pattern by OCR. Additional insights can be expected from studies of saccade curvature in patients with individual eye muscle palsies.42

Acknowledgments

The authors thank Oliver Bergamin, Sarah Marti, Antonella Palla, Alexander Tarnutzer, and Albert Züger for assistance and the reviewers for their helpful comments.

References