Combined Influence of Vergence and Eye Position on Three-Dimensional Vestibulo-Ocular Reflex in the Monkey

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Received 27 September 2001; accepted in final form 15 July 2002

Misslisch, H., and B.J.M. Hess. Combined influence of vergence and eye position on three-dimensional vestibulo-ocular reflex in the monkey. J Neurophysiol 88: 2368–2376, 2002; 10.1152/jn.00796.2001. This study examined two kinematical features of the rotational vestibulo-ocular reflex (VOR) of the monkey in near vision. First, is there an effect of eye position on the axes of eye rotation during yaw, pitch and roll head rotations when the eyes are converged to fixate near targets? Second, do the three-dimensional positions of the left and right eye during yaw and roll head rotations obey the binocular extension of Listing’s law (L2), showing eye position planes that rotate temporally by a quarter as far as the angle of horizontal vergence? Animals fixed at near visual targets requiring 17 or 8.5° vergence and placed at straight ahead, 20° up, down, left, or right during yaw, pitch, and roll head rotations at 1 Hz. The 17° vergence experiments were performed both with and without a structured visual background, the 8.5° vergence experiments with a visual background only. A 40° horizontal change in eye position never influenced the axis of eye rotation produced by the VOR during pitch head rotation. Eye position did not affect the VOR eye rotation axes, which stayed aligned with the yaw and roll head rotation axes, when torsional gain was high. If torsional gain was low, eccentric eye positions produced yaw and roll VOR eye rotation axes that tilted somewhat in the directions predicted by Listing’s law, i.e., with or opposite to gaze during yaw or roll. These findings were seen in both visual conditions and in both vergence experiments. During yaw and roll head rotations with a 40° vertical change in gaze, torsional eye position followed on average the prediction of L2: the left eye showed counterclockwise (ex-) torsion in down gaze and clockwise (in-) torsion in up gaze and vice versa for the right eye. In other words, the left and right eye’s position plane rotated temporally by about a quarter of the horizontal vergence angle. Our results indicate that torsional gain is the central mechanism by which the brain adjusts the retinal image stabilizing function of the VOR both in far and near vision and the three dimensional eye positions during yaw and roll head rotations in near vision follow on average the predictions of L2, a kinematic pattern that is maintained by the saccadic/quick phase system.

INTRODUCTION

When animals move their head, without compensatory eye movements the image of the visual surround would shift across the retina and greatly degrade vision. To avoid retinal slip, the rotational vestibulo-ocular reflex (VOR) spins the eyes around the same axis as the head but in the opposite direction. This theoretically optimal VOR behavior would stabilize the image on the entire retina. In the absence of vergence, i.e., for distant target viewing, the optimal VOR strategy exists in the monkey (Misslisch and Hess 2000) but not in humans with the latter showing a compromise between optimal VOR and Listing’s law behavior (Misslisch and Tweed 2001; Misslisch et al. 1994, 1996; Solomon et al. 1997; Thurtell et al. 1999; Tweed et al. 1994a). What happens with the optimal VOR strategy observed in monkeys during far viewing when using near targets, i.e., when the vergence system, which converges or diverges the eyes to allow fixation of targets at different depths, plays a part? The first goal of this study was to determine the effect of eccentric eye position on the yaw, pitch, and roll VOR when the eyes were converged to fixate eccentric targets placed on a 0.1- and 0.2-m distant isovergence screen (requiring 17 and 8.5° vergence). In addition, we examined whether the near VOR depended on peripheral visual input by testing subjects with and without presentation of a structured visual background.

Listing’s law is a kinematic constraint on eye movements, which has been shown to be valid for saccades, fixations (e.g., Ferman et al. 1987b; Minken et al. 1993; Tweed and Vilis 1990), and smooth pursuit (Haslwanter et al. 1991; Tweed et al. 1992) when subjects were refixating between or tracking far targets (with the head upright and stationary). When describing eye positions as rotations (around fixed axes) away from a special reference position called primary position, Listing’s law implies that the eye rotation axes are confined to a roughly fronto-parallel head-fixed plane, called Listing’s plane, which is orthogonal to the gaze direction in primary position (Tweed and Vilis 1990; von Helmholtz 1867). Listing’s law is modified by the degree of horizontal vergence. When fixating near targets, the position planes of each eye (best called primary planes) (see Tweed 1997) rotate temporally by a certain angle. Dividing the experimentally determined angle of the primary planes by the vergence angle yielded a ratio of 0.21 in monkeys (Misslisch et al. 2001) and ratios ranging between 0.17 and 0.25 in humans (Bruno and van den Berg 1997; Kapoula et al. 1999; Mikhail et al. 1995; Minken and van Gisbergen 1994; Mok et al. 1992; Somani et al. 1998; Steffen et al. 2000; Tweed 1997; van Rijn and van den Berg 1993). Theoretical considerations suggested that the optimal ratio is 0.25: this value rotates the eyes such that images of the visual plane—the plane containing both lines of sight—in the two retinas are perfectly aligned (Tweed 1997; van Rijn and van den Berg 1993). This
kinematic pattern has been termed the binocular extension of Listing’s law or L2 (Tweed 1997). Do eye positions during head rotations lie on temporally rotated primary planes when the eyes are converged? As a second aim of this study, we examined the influence of L2 on three-dimensional (3D) eye positions during yaw and roll head rotations.

We found that VOR eye rotation axes were not affected by eccentric eye position when torsional gain was high—independent of the degree of vergence or the visual condition. During yaw and roll head rotations with different near target elevations, the 3D positions of the left and right eye lay on average in temporally rotated planes, i.e., they followed the kinematic pattern predicted by L2. While the former finding excludes an influence of Listing’s law or L2 on VOR velocity, the latter finding indicates an adherence of 3D eye position to L2, maintained by the quick phase system.

METHODS

Animal preparation

We implanted a head-holding device as well as dual search coils on both eyes (Hess 1990) in two female rhesus monkeys (Macaca mulatta; abbreviated SU and JU, who participated in our previous study on the influence of eye position on the VOR in far viewing) (see Misslisch and Hess 2000). Surgical procedures were performed under sterile conditions with the animals in deep anesthesia. Animals were treated with antibiotics and analgesics postsurgically. All procedures were in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and approved by the Veterinary Office of the Canton of Zurich.

Measurement and representation of 3D eye position and eye velocity

We applied the magnetic field search coil technique (Robinson 1963) to measure the 3D angular position of the two eyes (Skalar, eye position meter 3000). Coil voltages, head position, and head velocity signals, as well as a photodiode signal indicating full-field illumination, were sampled at 833 Hz (Cambridge Electronic Design, Model 1401 plus) and stored on hard disk for off-line analysis.

The measured eye position was calibrated as described in detail elsewhere (Hess et al. 1992). 3D eye positions were expressed as rotation vectors, and the eye’s orientation while looking at a straight-ahead target was chosen as reference position (Haustein 1989; Hess et al. 1992). Using these eye position recordings, we computed the eye angular velocity vector, Ω, as described in Hepp (1990). We expressed the angular eye position and eye velocity vectors in a head-fixed, right-handed coordinate system with the x, y, and z axes pointing along the nasoocipital, interaural and longitudinal head axis. By definition, positive directions of the coordinate axes represented clockwise, downward and leftward components (as seen from the subject’s point of view) of eye position and eye velocity.

Experimental set-up and protocols

Animals were seated in a primate chair with the head restrained in an upright position so that the anterior side of the lateral semicircular canals was elevated by roughly 15°. The primate chair was fixed within the inner frame of a vestibular rotator, equipped with three motor-driven axes (Acutronic, Jona, Switzerland). The rotator was surrounded by a lightproof sphere of 0.8-m radius. Onset and profiles of sinusoidal chair rotation were computer-controlled.

Animals were used to fixating distant targets during vestibular stimulation for water reward (Misslisch and Hess 2000). In the present experiments, we trained animals to fixate near targets placed either eccentrically at 20° up, down, left, and right or at straight ahead. Two sets of experiments were done, with targets located on an isovergence surface at a distance of 0.1 m (required horizontal vergence of 17°) or 0.2 m (horizontal vergence of 8.5°). The quality of fixation and convergence was controlled with behavioral windows.

We tested the VOR in eccentric eye positions using sinusoidal yaw, pitch, and roll chair rotation at 1 Hz (amplitude ±5°; peak velocity: 31.4°/s). Near targets were visible throughout the 4-s test period. All experiments were performed either with (optokinetic random dot pattern visible: 8.5 and 17° vergence experiments) or without a structured visual background (with only the near target visible: 17° vergence experiments). Because the elevation of the arc containing the near target LEDs had to be fixed manually, experiments were carried out in blocks of 10 repeated trials (e.g., 10 yaw head rotations while looking at the LED located 20° up). Vestibular stimulation started when a monkey kept fixation on a close target for 500 ms. Animals were then asked to fixate the earth-stationary near target, keeping the gaze lines converged, during the 4 s of the subsequent head rotation. A trial was aborted when the monkey interrupted target fixation. Animals were rewarded with water for successful trials. For each visual condition (within-without structured background), the total number of trials was 110 (10 trials each for gaze 20° up, 20° down, and center during yaw; 10 trials each for gaze 20° left, 20° right, and center during pitch; and 10 trials each for all 5 gaze directions during roll).

Data analysis

Quick phases of vestibular nystagmus were removed from 3D eye position and eye velocity data by means of a semi-automatic computer program that used thresholds for the second derivative of 3D eye velocity (jerk). Each trial was inspected visually and incorrectly placed markers were identified and corrected interactively. By setting markers, data were limited so that the first (last) sample corresponded to the onset (offset) of vestibular stimulation.

We determined 3D VOR velocity as a function of head velocity and eye position by performing the same multivariable function fitting (Press et al. 1988) as used in our previous studies (Misslisch and Hess 2000; Misslisch et al. 1994, 1996) in which the details of this method are given. Briefly, we fitted a 3 × 13 generalized gain matrix, which yielded the minimal least-squared error to fitted 3D eye velocity. The columns of this matrix represent the influence of ocular drift, torsional, vertical, and horizontal head velocity, and the product of the three components of head velocity with each of the components of eye position on 3D eye velocity. Using this matrix, we then determined, for each animal and each visual condition, the orientation of 3D VOR eye velocity for each combination of vestibular stimulation and eccentric eye position. This method accurately described the experimental data as can be seen in the examples of VOR responses derived from the best-fit generalized gain matrices (black curves in Figs. 1 and 2). To quantify the effect of eye position, we computed how far the eye position, we computed how far the eye rotation axis tilted for a 20° change in vertical (yaw, roll) or horizontal (pitch, roll) gaze direction, away from straight ahead (swing angle). For example, when the orientation of the eye rotation axis during yaw head rotation was 1° up when gaze was center and 3° up when gaze was 20° up, then the swing angle amounted to 3 − 1 = 2° (up). In this case (yaw, gaze 20° up), the prediction of Listing’s law is that the axis of eye rotation swings 10° up (in the direction of gaze). In the case of roll rotation with gaze 20° up, the prediction of Listing’s law is that the eye rotation axis swings 20° down opposite to the direction of gaze (see Misslisch and Hess 2000) (parallel projection model with torsional gain = 0.5). Thus we defined that positive or negative swing angles during yaw or roll were in the direction in accordance with Listing’s law.
RESULTS

Orientation of binocular eye rotation axis during yaw, pitch, and roll VOR when viewing near eccentric targets

Figure 1 shows an example of VOR eye velocities during sinusoidal yaw head rotation at 1 Hz (4 cycles) with the monkey fixating near targets in different positions, i.e., 20° up, center, and 20° down (top to bottom). Data obtained from the left and right eye are plotted in the left and right column, respectively. In each panel, gray thick curves are horizontal (main component) and torsional eye velocity, black curves are derived from the best-fit generalized gain matrix and the dotted curve is horizontal head velocity.

The close match between data and best-fit curves demonstrate that the fitted matrices accurately describe the data (see Methods). More importantly, if vertical eye position influenced the orientation of the VOR eye rotation axis as predicted by Listing’s law or L2, we should see a considerable change in the torsional velocity component as gaze changes from 20° down to 20° up (Misslisch et al. 1994). As revealed by inspecting Fig. 1, this is not the case: torsional eye velocity is only slightly modulated (in both eyes) when gaze is 20° up, less so when gaze is center and insignificantly when gaze is 20° down, suggesting that the axis of slow phase eye velocity is hardly effected by a very large vertical change in eye position.

This result is much more readily seen when plotting the horizontal versus the torsional component of eye velocity (Fig. 2). As in Fig. 1, left and right eye velocities are shown in the left and right column, and data obtained for fixating near targets at 20° up, center or 20° down are drawn in the top, middle, and bottom panels. The gray thick curves are the tips of the eye angular velocity vectors and the superimposed black thin curves represent the best-fit to the data. By definition, the angular eye velocity vector points along the eye rotation axis, with its length being proportional to the speed of eye rotation and the direction of rotation is determined by the right-hand rule: when the thumb of the right hand points along the rotation axis then the fingers curl round in the direction of the eye’s movement. For instance, eye velocity vectors pointing upward along the ordinate (z axis of our coordinate system) represent leftward eye motion and vectors pointing rightward represent
clockwise (cw) eye motion. Examining the orientation of the eye velocity vectors and their best-fit curves for the various gaze directions reveals that the VOR eye rotation axis of both eyes is tilted a little back when the eyes are looking 20° up (top); when gaze is center, this tilt becomes less; and when gaze is 20° down, there is almost no tilt. That is, the axes are approximately aligned with the ordinate, which means that the eye oscillates almost exclusively horizontally around a head-vertical axis. Overall, the effect of a 40° change in vertical eye position on the binocular eye rotation axes during yaw stimulation is negligible compared with the predictions of Listing’s law (half-angle rule): 7° tilt of eye rotation axis, in the direction of gaze) and L2 (see Mok et al. 1992).

This result was seen in all trials and in all other types of vestibular stimulation (Fig. 3). In other words, the effect of eye position on the VOR rotation axis is insignificant not only during yaw (Fig. 3A) but also during pitch (Fig. 3B) and roll (Fig. 3, C and D) head rotations. The three panels in each subplot of Fig. 3 show examples of the curves derived from the best-fit generalized gain matrices computed for the left (black) and right (gray) eye data. Figure 3A plots the same best-fit velocity vectors for the left and right eye as in the left and right column of Fig. 2. As mentioned in the preceding text, here the rotation axes of the left and right eye are closely aligned and basically unchanged by a large change in vertical eye position. Figure 3B shows the best-fit vertical (ordinate) and torsional (abscissa) eye velocity components obtained during pitch head rotation. The rotation axes of the two eyes are very little affected by a 40° change in horizontal eye position (Fig. 3B), i.e., the eye motion produced by the pitch VOR in near viewing does not depend on gaze azimuth. Plotting horizontal (Fig. 3C) or vertical (Fig. 3D) versus torsional eye velocity shows that also during head roll the orientation of the left and right eye’s rotation axes are invariant for large changes in vertical (Fig. 3C) or horizontal (Fig. 3D) eye position.

The orientation of the VOR’s eye rotation axis (“swing angle,” see METHODS) depended on torsional gain and on the type of vestibular stimulation. Figure 4 summarizes the swing angles averaged over both monkeys as a function of torsional gain. Data were obtained during yaw with vertical (Fig. 4A), pitch with horizontal (Fig. 4B), and roll with vertical (Fig. 4C) or horizontal (Fig. 4D) gaze changes indicated by → or ← pointing arrows). Positive angles denote a tilt of the eye rotation axis in the direction of gaze, e.g., upward tilt when gaze was 20° up in yaw, and negative angles represent a tilt opposite to the direction of gaze. Because for all types of vestibular stimulation the swing angles were highly symmetrical for up versus down and left versus right gaze, we computed an average swing angle ± SD from all 20 trials obtained for any condition (e.g., 10 trials each during yaw with gaze 20° up and 20° down). The data shown in Fig. 4 were collected while monkeys were fixating a near target requiring a horizontal vergence angle of 17°, either with (○ and □) or without ( ● and ■) a full-field visual background.

Two main results are seen in Fig. 4. First, the amount of the averaged swing angles was typically smaller than a few degrees, i.e., close to zero, when torsional gain was large (monkey JU, ○ and ●), but somewhat larger when torsional gain was low (monkey SU, □ and ■). The dependence of the swing angles on torsional gain was similar as for the VOR in far vision (→ and ← in Fig. 4) (obtained from Eq. A1 in Misslisch and Hess 2000). An exception to that rule is the pitch VOR, where swing angles were invariably very small and independent of torsional gain. Second, the small swing angles

FIG. 3. Slow phase eye rotation axes during yaw, pitch, and roll head rotations in near viewing do not depend on eye position. A: example of best-fit left (black) and right (gray) eye rotation axes during yaw head rotation with gaze 20° down, center, and 20° up. Same data as in Figs. 1–2. B–D: eye rotation axes during pitch (40° horizontal gaze change) and roll (40° vertical or horizontal gaze change). All data collected without visual background.
were invariantly positive during yaw or pitch and negative during roll stimulation. This pattern is qualitatively consistent with a VOR whose function is a compromise between optimal (full-field) retinal image stabilization and Listing’s law (far-viewing condition: Misslisch and Hess 2000; Misslisch and Tweed 2001; Misslisch et al. 1994). However, quantitatively the swing angles are far from the predictions of Listing’s law or L2 (see preceding text).

The same pattern was observed when horizontal vergence was smaller (8.5°), i.e., when the near target was 20 cm away from the eyes (Fig. 5); the amount of swing angles was close to zero when torsional gain was large (\( \square \)) and the amount of swing angles was somewhat larger when torsional gain was low (\( \bigcirc \)); and virtually no tilt of the eye rotation axis during pitch, independent of torsional gain.

**Interaction of vergence (binocular extension of Listing’s law) and yaw or roll VOR**

The monkeys that participated in this study kept horizontal vergence fairly stable throughout the 4 s of near target fixation. Figure 6 shows two examples of this general observation, plotting horizontal vergence during the 10 trials each of yaw (left) and roll stimulation (right) while looking 20° up, center

![Swing angles in the 8.5° horizontal vergence condition show the same dependence on torsional gain during yaw and roll but not during pitch head rotations. Note curves of swing angles predicted from a half-angle rule (\(- - -\)) and a full angle rule (\(\cdot\cdot\cdot\)) as a function of torsional gain. Data were obtained with a visible full-field background. Same format and symbols as in Fig. 4.](image-url)
or 20° down (top to bottom). In these examples, the near target was 10 cm in front of the monkey’s eyes (17° vergence) and the structured background was not visible. As can be seen in the graphs, horizontal vergence was somewhat smaller than the expected ideal value of 17°. For all three experiments—17° vergence condition with and without visual background, 8.5° vergence condition with visual background—the average gain of horizontal vergence in subject JU or SU was 0.92 ± 0.03, 0.87 ± 0.04, and 0.85 ± 0.03 or 1.03 ± 0.06, 1.01 ± 0.07, and 0.76 ± 0.08.

As mentioned in the introduction, if 3D eye position during head rotations with near target viewing adhered to the binocular extension of Listing’s law, L2, then the slow phase torsional position of the left and right eye should systematically depend on their vertical position. For instance, when gaze is 20° down, one should see counterclockwise (negative) torsion in the left eye and clockwise (positive) torsion in the right eye, and vice versa when vertical eye position is 20° up. We performed two experiments in which we had the subjects change vertical eye position over a 40° range: yaw and roll head rotation with gaze 20° up, center, or 20° down. In the pitch experiment, we varied gaze not in elevation, but in azimuth (20° left, center or 20° right), to determine the effect of eye position on the axis of eye rotation (3D eye velocity) so that we did not evaluate the adherence of 3D eye position to L2 during pitch head rotations.

Figure 7, A and B, illustrates that during yaw (top) or roll (bottom) head rotation with gaze 20° up, center, and 20° down (gray data) 3D eye position, on average, follows L2. More specifically, when the monkey was looking 20° down, mean torsional slow phase eye position (see best-fitted black line in Fig. 7A), was negative (counterclockwise) in the left eye (left) and positive (clockwise) in the right eye (right). The opposite pattern was seen when the animal was looking 20° up. In this example, quantifying the temporal tilt of the best-fit eye position planes yielded 3.6 and 3.9° for the left and right eye during yaw, 4.6 and 3.5° for the left and right eye during roll. 3D eye position was kept around the temporally tilted planes by the VOR quick phases. This is illustrated in Fig. 7B, which plots torsional versus vertical position of quick phase endpoints of the same data during yaw (top) or roll (bottom) head rotation with gaze 20° up, center, and 20° down (gray dots). When the monkey was looking 20° down, mean torsional quick phase end position (see best-fitted black line in Fig. 7B), was negative (counterclockwise) in the left eye (left) and positive (clockwise) in the right eye (right).
wise) in the right eye (right). The opposite pattern was seen when the animal was looking 20° up. The temporal tilt of the best-fit straight lines through quick phase endpoints yielded (mean ± SD) 3.4 ± 2° and 4.4 ± 1.9° for the left and right eye during yaw, 4.9 ± 5.4° and 3.7 ± 5.5° for the left and right eye during roll (goodness-of-fit for straight line fit with 1 df: \(\chi^2 = 0.988/0.623\) for the left/right eye during yaw and \(\chi^2 = 0.948/0.791\) for left/right eye during roll). A similar pattern was found when plotting torsional versus vertical position of quick phase onsets. These results suggest that it is the quick phases of VOR that keep 3D eye position around tilted planes. Computing the quotients between these angles of temporal plane rotation and the amount of vergence (see Fig. 6), i.e., calculating the L2 factors, yielded values close to 0.25.

Figure 8 summarizes the L2 factors for all yaw and roll conditions where the targets were placed over a 40° vertical range. In both monkeys and in all conditions—17 or 8.5° vergence, visible or nonvisible background—the L2 factors were near 0.25, the value expected if 3D eye position during yaw and roll head rotation in near vision perfectly adhered to the binocular extension of Listing’s law (Tweed 1997).

**Discussion**

When monkeys viewed near eccentric targets, their yaw and roll VOR rotated the eyes approximately around the same axis as the head with the axes being more or less collinear if torsional VOR gain was large or weak. The axis of eye rotation produced by the pitch VOR did not depend on (horizontal) eye position nor on torsional gain, invariably spinning the eyes around an axis that was almost collinear with the head’s rotation axis. These findings indicate that Listing’s law or L2 did not play a role in determining the orientation of VOR eye velocity. 3D eye positions during yaw and roll head rotations lay on average in temporally rotated planes, meaning that mean ocular torsion in each eye depended in its own way on vertical eye position. Because slow phase eye velocity was not influenced by L2, this result suggests that it is the quick phase system that maintains adherence of 3D eye position to L2.

**Influence of eye position on VOR eye velocity in near vision**

In three conditions—yaw and roll while looking up or down and roll while looking left or right—we found that the axis of eye rotation was almost not influenced by the 40° change in eye position (Figs. 1–5). Deviations from this collinearity of eye and head rotation axes were very small when torsional gain was high (more than 0.8) and somewhat larger when torsional gain was lower (Figs. 4 and 5). In the fourth condition—pitch while looking left and right—the eye and head rotation axes were well aligned, independent of torsional gain. The visibility of a structured background did not affect these results, although the torsional gain was consistently larger in the conditions with visual background (Fig. 4).

A prominent effect of eye position on the axis of eye rotation, i.e., on eye velocity, is expected if the VOR in near vision were to follow Listing’s law (e.g., Tweed and Vilis 1990; von Helmholtz 1867) or L2 (Mok et al. 1992). In the first case, the eye velocity vector should tilt by half the gaze change (10° if gaze changes 20°) and similarly in the second case. Our data indicate that both kinematic constraints do not play much of a role in determining the orientation of slow phase eye velocity in near vision.

There is increasing evidence for the notion that the torsional gain is involved in the control of the VOR’s eye rotation axis. A previous study on the monkey 3-D VOR in far vision (Misslisch and Hess 2000) showed that normal monkeys have torsional gains close to one and—despite large changes in eye position—VOR eye rotation axes aligned with the head’s rotation axis. This optimal VOR behavior stabilizes the entire retinal image. However, it is not hard-wired. For instance, prominent swings of the VOR eye rotation axis in eccentric eye positions can be induced by weakening the torsional gain due to plugging of the monkey’s vertical semicircular canals (Misslisch and Hess 2000).

Moreover, the intricate behavior of the human VOR—with the eye rotation axis tilting about a quarter to a third as far as, and in the direction of, the gaze line during yaw (Misslisch et al. 1994, 1996; Misslisch and Tweed 2001; Palla et al. 1999; Solomon et al. 1997) or pitch (Misslisch and Tweed 2001; Misslisch et al. 1994, 1996) and about as far as the gaze line but in the opposite direction during roll (Misslisch and Tweed 2001; Misslisch et al. 1994, 1996)—can be modeled by a single factor: a weak VOR in the torsional dimension (Misslisch and Tweed 2001). That the torsional VOR is weak is a well-known fact (Berthoz et al. 1981; Collewijn et al. 1985; Ferman et al. 1987a; Misslisch and Tweed 2000; Robinson 1982; Seidman and Leigh 1989; Tweed et al. 1994b). Because the human VOR favors stabilization of foveal and perifoveal retinal areas, it can also limit the range of ocular torsion, i.e., reduce the deviations from Listing’s law. Thus human and nonhuman primates seem to share the same common mecha-
nism underlying the VOR’s performance in the stabilization of the retinal image: adjustment of the torsional gain.

Why does the monkey VOR deviate sometimes from the optimal VOR behavior? Maybe our subjects sometimes paid more or less attention to the task of stabilizing gaze. That cognitive factors influence the human VOR performance to a great extent is a well-known fact (e.g., Barr et al. 1976; Møller et al. 1990a,b). Another possible answer may lie in the observation that if there was a significant tilt of the eye rotation axis, then this tilt was always in the directions consistent with Listing’s law—in the direction of the gaze line during yaw and pitch and opposite to the direction of the gaze line during roll (positive/negative swing angles in Figs. 4—5). In other words, the brain may balance several factors such as minimizing ocular torsion (Listing’s law), image stability over certain parts of the retina and energy expenditure. The situation becomes even more complicated in near vision. Here, the distance and eccentricity of the target and the distance of the eyes relative to the head’s rotation axis greatly influence the kinematics of the VOR. Disentangling the relative contribution of these factors is beyond the scope of this study, however.

**Influence of vergence on VOR eye position**

This study showed that slow phase eye positions in response to yaw and roll head rotations with vertically placed near targets oscillated around temporally rotated planes (Fig. 7). Thus down gaze in the left or right eye was accompanied, on average, with counterclockwise or clockwise (ex-) torsion. Likewise, up gaze in the left or right eye went along with clockwise or counterclockwise (in-) torsion, respectively. The amount of temporal eye position plane rotation equaled roughly the one predicted by the binocular extension of Listing’s law, L2, namely a quarter times the horizontal vergence angle (Tweed 1997). But how can we explain that while slow phase eye velocity clearly violates the prediction of L2, 3D eye position during yaw and roll head rotation does on average adhere to L2? The obvious answer to this question is that quick phases rather than slow phases maintain L2 in near vision.

What is the advantage of the L2 behavior observed during yaw and roll head rotations during viewing of near targets placed at 20° up, center and 20° down? In 1997, Tweed proposed the visual-motor theory of binocular control in his attempt to explain the L2 pattern of eye positions found during fixations of near targets (humans: Bruno and van den Berg 1997; Kapoula et al. 1999; Mikhail et al. 1995; Minken and van Gisbergen 1994; Mok et al. 1992; Somani et al. 1998; Steffen et al. 2000; Tweed 1997; van Rijn and van den Berg 1993; monkeys: Misslisch et al. 2001). On one hand, L2 keeps the images of the visual plane aligned; on the other hand, L2 cyclorotates the eyes about their lines of sight to keep them near their zero-vergence primary positions. Our data indicate that during the yaw or roll experiments the quick phases help the stereoptic system in aligning the visual planes of the left and right eye.

When tested with distant targets, we found earlier that the monkey VOR does not obey Listing’s law at all but optimizes a purely visual variable, i.e., stabilization of the entire retinal image (Misslisch and Hess 2000). As the present study shows, the monkey 3D eye positions during yaw and roll head rotations in near vision do show the L2 pattern, due to the action of the quick phase system, suggesting that slow and quick phases balance visual and motor variables in up and down gazes. In any case, it seems that (binocular) vision is the dominating factor in determining the eye’s motion during head rotations both in far and near vision. For instance, Misslisch et al. (2001) found that ocular counterroll is normal in far but reduced in near vision because ocular torsion would disrupt stereopsis in the latter case. Thus it seems that the phylogenetically young stereoptic system takes precedence over the phylogenetically older VOR system both in the static (counterroll) and dynamic (rotational) VOR.

We thank E. Buffone, B. Disler, and A. Züger for excellent animal care and technical assistance.

This work was supported by the Swiss National Science Foundation Grant 31–47 287.96 and by the Betty and David Koetser Foundation for Brain Research.

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