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## Torsional and horizontal vestibular ocular reflex adaptation: three-dimensional eye movement analysis

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**Abstract** This study used visual-vestibular conflict to effect short-term torsional and horizontal adaptation of the vestibulo-ocular reflex (VOR). Seven normal subjects underwent sinusoidal whole-body rotation about the earth-vertical axis for 40 min ( $\pm 37^\circ/s$ , 0.3 Hz) while viewing a stationary radial pattern fixed to the chair ( $\times 0$  viewing). During adaptation and testing in darkness, the head was pitched either up or down  $35^\circ$  to excite both the horizontal and torsional VOR. The eyes were kept close to zero orbital elevation. Eye movements were recorded with a dual search coil in a three-field magnetic system. VOR gain was determined by averaging peak eye velocity from ten cycles of chair oscillation in complete darkness. The gain of the angular horizontal VOR (response to rotation about the head rostral-caudal axis) was significantly reduced after training in both head orientations. Angular torsional VOR gain (head rotation about the naso-occipital axis) was reduced in both head orientations, but this reached statistical significance only in the head down position. These results suggest that torsional and horizontal VOR gain adaptation, even when elicited together, may be subject to different influences depending upon head orientation. Differences between head up and down could be due to the relatively greater contribution of the horizontal semicircular canals with nose-down pitch. Alternatively, different VOR-adaptation processes could depend on the usual association of the head down posture to near viewing, in which case the torsional VOR is relatively suppressed.

**Keywords** Vestibulo-ocular reflex · Adaptation · Eye movements · Torsion

### Introduction

During earth-vertical axis rotation with the head pitched up or down, there is both yaw and roll rotation, exciting both the aHVOR and aTVOR, respectively. Torsional eye velocity, defined here as rotation of the eye about an axis parallel to the head's naso-occipital ( $x$ ) axis, is therefore induced in pitch head positions. The horizontal component of slow phase eye velocity is reduced by the cosine of angle between the head  $x$ -axis and plane of head rotation, and the torsional component increases according to the sine of the same angle (Fetter et al. 1994).

The gain of the aTVOR in humans and monkeys is less than that of the aHVOR (Berthoz et al. 1981; Tweed et al. 1994; Seidman and Leigh 1989; Seidman et al. 1995). Due to this gain anisotropy, when the axis of head rotation lies between its yaw (rostrocaudal  $z$ ) axis and roll (naso-occipital  $x$ ) axis, the slow-phase angular velocity vector tilts toward the stronger ( $z$ , aHVOR) axis (Yue et al. 1994; Fetter et al. 1994).

Yaw head rotation alone can generate torsional components of slow phase eye velocity under a variety of conditions. A torsional component of eye velocity is present when the eye is not in Listing's primary position, causing a tilt in the angular velocity axis in the direction of vertical eccentricity in the orbit (due to the partial Listing's law behavior of the angular VOR, Misslisch et al. 1994). Cross-axis adaptation paradigms can also introduce a torsional eye velocity component when coupled to horizontal eye velocity during yaw rotation (Takagi et al. 2001; Angelaki and Hess 1998).

Slippage of images on the retina is an effective error signal that can be used to drive adaptation of the gain of the horizontal and vertical VOR (Gonshor and Melvill Jones 1976). Torsional retinal slip, or rotation of the visual surround about the optic axis, is unique in that it does not result in the fovea being taken away from the

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fixation target and there is no pursuit system present that can generate a torsional eye velocity to decrease any slip. Torsional optokinetic responses *are* present, however, and torsional VOR responses to head roll can be decreased by presenting a full-field visual stimulus moving with the head (Leigh et al. 1989; Straumann et al. 1992). Imagining a target that is moving with the head during rotation in darkness can be used to cancel the VOR in the horizontal direction (Barr et al. 1976). This was found to have a minimal effect with cancellation of the roll VOR (Leigh et al. 1989).

Adaptation of the roll VOR, when stimulated in isolation, has been demonstrated in monkey (Bello et al. 1991; Angelaki and Hess 1998) and in human (Berthoz et al. 1981) independently from the angular vertical VOR (aVVOR), even though the aVVOR and aTVOR involve the same semicircular canals and extraocular muscles. Here, we stimulated the roll and yaw VOR simultaneously and sought to determine if each would be adapted by training to the same extent, or if each component were modified according to its own "adaptability." In the former instance, the same percentage change would occur in each direction, and the orientation of the axis of eye velocity before and after adaptation would be the same. In the latter case, if the aHVOR and aTVOR were modified disproportionately, then the eye angular velocity vector after training would be expected to tilt toward the less modified component. The total VOR response would then be the vector sum of each component (yaw and roll) modified by a different percent change.

Here we addressed the following questions: Do horizontal and torsional VOR adaptation occur in humans when elicited together, and does adaptation occur to the same degree within each component? Is there a difference between training with the head up and down in the degree of adaptation found? Preliminary results from these studies were presented previously (Solomon et al. 1996).

## Materials and methods

Before and after a 40-min training period, three-dimensional eye movements were recorded with a dual scleral search coil (manufactured by Skalar, Delft, Netherlands) mounted on one eye, using a magnetic field system (Rommel type system modified by A.G. Lasker, Baltimore). The three fields produced by a chair-fixed coil frame (side length: 1.02 m) oscillated at different frequencies (55.5, 83.3, and 42.6 kHz) with intensities of 0.088 gauss. The subject's head was positioned upright with the bite bar oriented horizontally (facing straight ahead) or pitched up 35° or down 35° with respect to the magnetic fields by a bite bar. An inclinometer was used to reposition the head such that the eyes remained in the center homogeneous portion of the magnetic fields.

During training, subjects viewed a stationary radial pattern fixed to the chair ( $\times 0$  viewing) while the chair oscillated sinusoidally about an earth-vertical axis at 0.3 Hz, with a maximal excursion of  $\pm 20^\circ$ , which corresponds to a peak velocity of 37°/s. The pattern was a tangent screen, 35° wide and 30° high, with the center located 1.07 m from the subject's eyes. VOR gain was determined by averaging peak slow-phase eye velocity from ten cycles of chair oscillation in darkness with the head oriented horizontally and in the adapted position. An electronic window, which gave an audio signal to the subject if the eyes deviated more than 10° from 0°

elevation in the orbit, was used to minimize any effect of vertical eccentric eye position. This was necessary since VOR responses follow a partial Listing's law (Misslisch et al. 1994), so a vertical eye position away from primary position would introduce a confounding torsional eye velocity. The orientation of Listing's plane was determined for each subject with the head upright during each experiment by recording eye position during fixation, plotting eye position as rotation vectors and finding the best fit plane containing these vectors using a least squares method. Primary position is defined as the vector normal to this plane.

The in vitro calibration procedure for the dual search coils is explained in detail elsewhere (Straumann et al. 1995). Eye position and angular velocity were calculated from rotation vectors using the method described previously (Straumann et al. 2000). Each experimental trial was begun with the subject's gaze directed straight ahead, irrespective of head position. This initial fixation served as the reference position from which the rotation vectors, and eventually eye positions in degrees, were calculated. All head positions described in this paper are in pitch (sagittal plane).

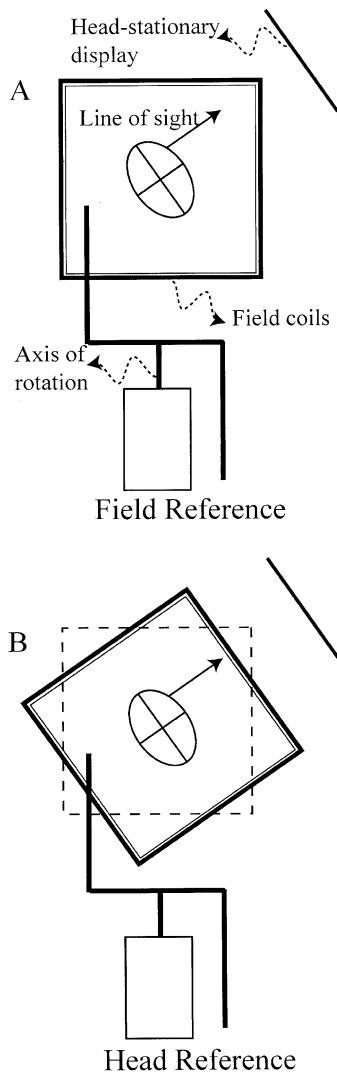
The VOR in darkness was tested with subjects either imagining an earth-fixed target before and after training, or imagining a chair-fixed target (suppression) but only after training. At the onset of these recordings, an LED was illuminated in the straight-ahead position on the wall (at 120 cm from the eyes) or mounted on the chair (at 107 cm), respectively, and extinguished prior to the onset of rotation to establish the reference position.

Seven normal volunteer subjects were studied, and informed consent was obtained from each according to a protocol approved by the local institutional review board for human subject protection. Three subjects completed both head up and head down adaptation experiments on different days, while two subjects were tested with head up only and two with head down only. Statistical analysis was performed using a one-tailed *t*-test for comparing pre- and post-training responses, with the alternative hypothesis being that adapted responses were smaller than control. Two-tailed *t*-tests were used to compare mean vertical eye positions during testing in darkness.

### Reference frames and conventions

All coordinate systems herein are defined according to the right-hand rule. For the head, the positive *x* direction points outward from the nose, *y* outward from the left ear and *z* upward from the top of the head. Thus, positive values of eye velocity indicate movement downward, leftward and torsional with the upper poles of the eyes toward the right shoulder. The head horizontal position (zero pitch) was defined by orienting the bite bar in the earth-horizontal plane. When the head is in the horizontal position and the eyes are looking straight ahead, eye, head and coil coordinates are equivalent. All of these systems rotate with respect to the space fixed reference when the chair is turned.

When the head is pitched in the coil field, the four different sets of coordinate axes must each be considered: space-fixed, field-coil-based, head-fixed, and eye-fixed. Eye movements were measured by the search coil relative to the field coils. The orthogonal arrangement of the field coils determines their coordinate frame. Eye angular velocity in this paper is shown in a head-referenced coordinate system. Although recorded in field-coil coordinates, eye rotations shown were transformed into head-fixed coordinates by rotating the rotation matrix by the angle of head pitch (Fig. 1). Horizontal eye velocity therefore represents eye rotation about the head-fixed *z*-axis, which is not parallel to either the axis of vestibular stimulation or the *z* magnetic field. The data were not rotated into Listing's plane; therefore "primary position" and the "reference position" are not necessarily the same (Van Opstal 1993). The angular vestibular stimulus delivered by the chair was oriented parallel to the earth-vertical axis, while the angular acceleration was transduced in a head-fixed system by the semicircular canals. In our analysis, we attributed the horizontal component of eye angular velocity (eye rotation about the head *z*-axis) to stimulation of the aHVOR, in proportion to the projection



**Fig. 1** **A** Actual configuration of the head (ellipse), field coils and tangent screen during training in the head up position while rotating in the rotary chair about the vertical axis. The solid arrow represents the line of sight, with the eyes near zero deg elevation in the orbit. The axes drawn on the side view of the head correspond to the horizontal and torsional VOR axes (major and minor ellipse axes, respectively). **B** Data are presented as if the field coils were actually configured as shown, with the head yaw axis and the coil vertical axis parallel (dotted line indicating actual field coil orientation). Thus horizontal eye movements shown are made about the z-axis of the head, not about the space vertical axis

**Table 1** Average data for all subjects with the head in both positions. Velocities are in degrees per second with standard deviations in parentheses. Gains are with respect to the projection of the vestibular stimulus onto the head yaw (horizontal) and roll (torsion) axes. Asterisk indicates a significant ( $p < 0.05$ , one-tailed  $t$ -

		Preadaptation		Postadaptation	
		Velocity (°/s)	Gain	Velocity (°/s)	Gain
Head up	Horizontal	51.3 (6.1)	0.85	31.2 (11.7)*	0.51 (61%)
	Torsion	16.4 (2.1)	0.39	13.9 (2.7)	0.33 (85%)
Head down	Horizontal	48.8 (7.1)	0.81	34.8 (9.9)*	0.57 (71%)
	Torsion	20.2 (5.8)	0.48	14.1 (4.5)*	0.33 (70%)

of the vestibular stimulus vector onto the head z-axis. Likewise, eye rotation about the head x-axis was considered the result of aTVOR stimulation when there was a component of the vestibular stimulus along the head x-axis. Tilts in eye angular velocity axes were determined from the ratio of the average peak horizontal velocity to the average peak torsional velocity.

Expected gains for each component of the aVOR were determined by the projection of the stimulus angular velocity vector (oriented parallel to gravity) onto the head's roll or x-axis (torsional VOR) and yaw or z-axis (horizontal VOR). The maximum peak-to-peak stimulus velocity was  $74^\circ/\text{s}$ ; therefore when the head was pitched  $35^\circ$  in the sagittal plane, the ideal horizontal eye velocity would be  $74 \cdot \cos(35) = 60.6^\circ/\text{s}$ , and the torsional velocity that would fully compensate for head rotation would be  $74 \cdot \sin(35) = 42.4^\circ/\text{s}$ .

## Results

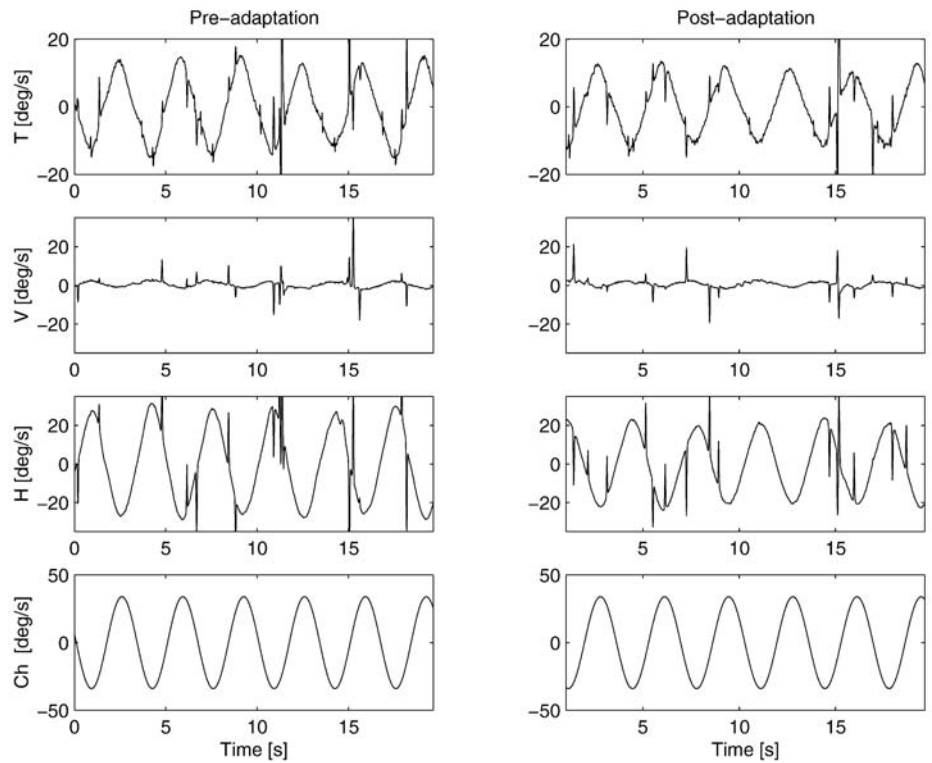
Following training, all subjects showed a decrease in aHVOR gain measured in the dark while imagining an earth-fixed target. Adaptation with head up and with the head down was not equivalent, however. The gain of the aTVOR was significantly adapted only with training in the head-down orientation. A sample of eye and chair velocity before and immediately following head down training, demonstrating a decrease in both horizontal and torsional eye velocity, is shown in Fig. 2.

For all subjects, aHVOR gains in the head up position prior to adaptation ranged from 0.75 to 0.95, and 0.67 to 0.91 with head down. After training, horizontal gains decreased significantly in both positions, ranging from 0.34 to 0.78 with the head up ( $p = 0.005$ ) and 0.33 to 0.70 with the head down ( $p = 0.015$ ). Table 1 contains the eye velocities and standard deviations from which these gains were calculated. Preadaptation, aTVOR gains ranged from 0.31 to 0.44 in the head up position, and there was no significant difference in torsional gains after training (range 0.24–0.41,  $p = 0.061$ ). With the head down, aTVOR gain reduction after adaptation did reach statistical significance, from a range of 0.31 to 0.64 before training, to 0.23 to 0.51 following training ( $p = 0.049$ ). Data from each individual are graphed in Fig. 3.

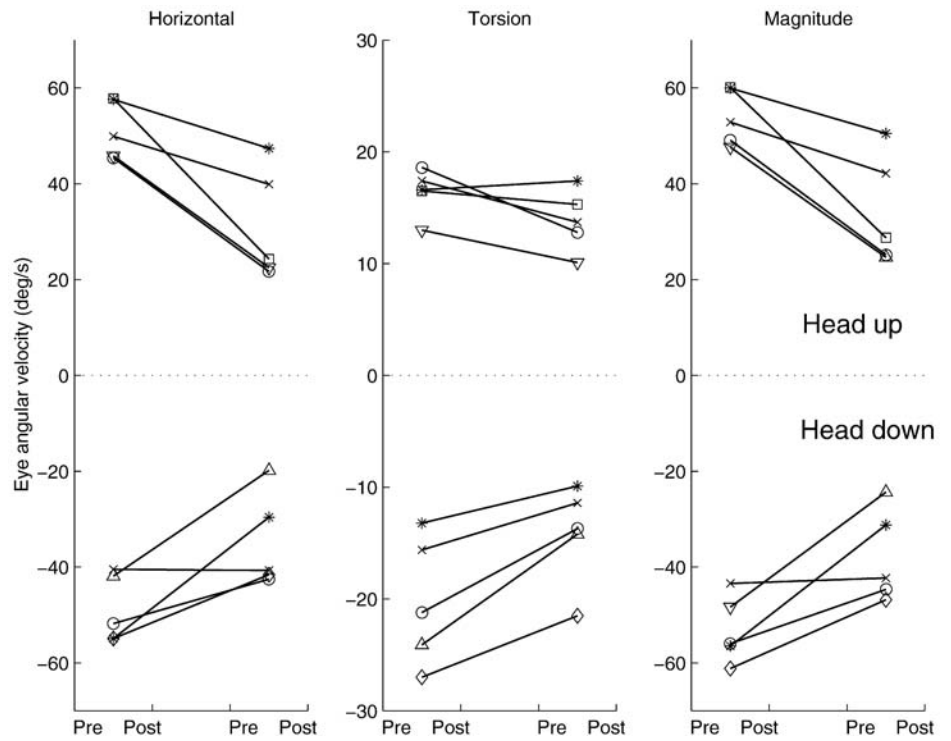
Because subjects were not naïve to vestibular testing, suppression of the VOR with an imaginary head-fixed target was included to ensure that subjects were not unconsciously reducing their post-training gains through this means. Gains during suppression were always

test) difference from preadaptation values. Since not all subjects completed experiments with the head up and down, no intraindividual statistical comparisons were made comparing head up and head down responses. Postadaptation gains are followed by the percentage of the pre-training value in parentheses

**Fig. 2** Data from vertical axis sinusoidal rotation in a subject with the head pitched downward, before and after 40 min of adaptation in the same head position. *T*, *V*, and *H* represent torsion, vertical and horizontal eye angular velocity in °/s, with positive values indicating movement of the upper pole of the eye toward the right shoulder for *T*, and the front of the eye moving downward (positive *V*), and leftward (positive *H*). *Ch* represents chair velocity, with positive values corresponding to leftward velocity. Note the decrease in *T* and *H* velocities after ×0 viewing



**Fig. 3** Each subject is represented by a different symbol, with pre- and postadaptation responses connected by a line. On each graph, positive eye velocities represent peak-to-peak responses with the head pitched upward, with negative values for head down trials. The horizontal component is shown on the left, and torsional responses in the middle graph. The graph on the right represents total eye speed, or the magnitude of the VOR response vector regardless of orientation



significantly lower than both pre- and postadaptation gains. This does not exclude the possibility that subjects were using an intermediate degree of suppression during postadaptation testing, even though they were instructed to imagine an earth-fixed target.

In the head down position, horizontal and torsional components were both decreased by approximately the same amount after training (29% and 30% reductions, respectively). In the head up position, the horizontal

component was reduced 39% after training, while the torsional response only decreased by 15% (not significant).

There was no significant difference in mean vertical eye position across subjects during testing before and after adaptation, in either position. With the head pitched up, mean vertical eye position (standard deviation) before training was  $1.62^\circ$  ( $5.25^\circ$ ) vs.  $-1.28^\circ$  ( $5.30^\circ$ ) after training ( $p=0.92$ ). With the head down, pre-training was  $0.52^\circ$  ( $3.12^\circ$ ) vs. post-training  $0.96^\circ$  ( $6.22^\circ$ ) ( $p=0.89$ ). The differences in mean vertical eye position within subjects was also calculated between pre- and post-training. There was no significant difference between the changes in mean vertical eye position before and after training in the two head orientations. The mean difference with head up was  $0.35^\circ$  ( $7.58^\circ$ ) and  $0.44^\circ$  ( $3.12^\circ$ ) with the head down ( $p=0.98$ ). Thus we are confident that no systematic effect of vertical eye position could account for the differences shown above.

## Discussion

This study was intended to determine if the aHVOR and aTVOR adapted to the same degree when elicited concurrently during rotation around the earth-vertical axis. Unexpectedly, we found that short-term aVOR adaptation occurred differently according to pitch head position: in the head down position, the aTVOR and aHVOR adapted to the same degree; in the head up position, the aHVOR adapted the same as with head down, but the amount of aTVOR gain decrease did not reach statistical significance in our sample. It may be that the various generators of torsional eye velocity (aTVOR, gain anisotropy, partial Listing's law strategy) contribute differently in head up vs. head down positions, and are adaptable to different degrees. It should also be noted again that not all subjects were tested in both head orientations. We will discuss various mechanisms that might explain our findings.

Which semicircular canals are activated depends upon head pitch

One simple explanation is based on the fact that when the head is pitched downward, the VOR response is dominated by input from the horizontal semicircular canals (SCC), but with the head pitched upwards, the vertical canals also make a considerable contribution (e.g., Tusa et al. 1996). Torsional eye velocity was generated in monkeys with all four vertical SCC plugged (Yakushin et al. 1995, 2001). It may be that torsional eye velocity generated from activation of the horizontal SCC can be adapted more effectively—at least for these relatively brief periods of training—than torsional eye velocity generated from combined horizontal and vertical canal activation.

Listing's plane is not strictly head fixed

During vestibular stimulation, non-compensatory torsional slow-phase eye velocity is generated when the eye is not in Listing's primary position (PP), which is defined by the orientation of Listing's plane (LP). However, LP counter pitches when subjects are pitched forward, but not when pitched backward with respect to gravity (Bockisch and Haslwanter 2001). Since LP only rotates at most  $3.4^\circ$ , and the partial Listing's law followed by the VOR is approximately a 1/4 angle rule, the most the angular eye velocity vector should tilt is about  $0.9^\circ$ . In fact, angular velocity vectors (projected onto the  $x-z$  plane) tilted from  $17.9^\circ$  before to  $25.2^\circ$  after adaptation. (Since the torsional velocity did not adapt, the axis tilted toward the torsional, or  $x$ , -axis.) By comparison, in the head down position the mean axes were  $22.6^\circ$  and  $23.0^\circ$  before and after training, respectively. This indicates that both the horizontal and torsional components adapted to the same extent in the head down position. Thus any systematic orientation of LP could not explain the up-down asymmetry in adaptation found.

Differences in aVOR gain between rotation with head up vs. with head down

One must also consider that there might be differences in the baseline aTVOR gain between up and down head positions. If this were the case, the amount of retinal slip driving adaptation would be different and might lead to different adaptive responses. This, however, cannot be an explanation since there were no preadaptation differences in aTVOR gain as a function of head orientation. The gain of the aTVOR does decrease with convergence (Averbuch-Heller et al. 1997), and vision is not required for this to occur (Bergamin and Straumann 2001). Binocular eye position was not recorded, so we cannot rule out the possibility that subjects' eyes may have been more converged during testing in darkness after adaptation in the head down orientation, accounting for the apparently greater amount of adaptation seen. Nevertheless, we conclude that neither changes in Listing's law behavior nor different baseline aTVOR gains in different head positions account for the different adaptive responses.

Functional significance of angular torsional VOR plasticity

Might there be some functional reason for the difference in aTVOR adaptation with head orientation? In response to roll motion of the head, a compensatory eye movement response that stabilizes images on the peripheral retina is helpful in the perception of depth and orientation of objects. In foveate species, however, the aTVOR does not contribute to maintaining high acuity/high resolution vision. Accordingly, in contrast to the horizontal or vertical aVOR there might be less of a premium on an

adaptive mechanism to maintain the fidelity of the aTVOR reflex. Even though gain adaptation of the aTVOR is well documented (Berthoz et al. 1981; Angelaki and Hess 1998), the fact that there is a gain anisotropy indicates that adaptation takes place in a selective or incomplete fashion.

Thus, there is some torsional slip associated with almost every head rotation. Some degree of torsional slip during head motion is certainly well tolerated as images still remain close to the fovea. If torsional retinal slip is a 'way of life,' why have a mechanism that adaptively suppresses it? We suppose that an adaptive mechanism for eliminating inappropriate torsion would be called upon when one single pattern of retinal slip was repetitively associated with a single pattern of head motion. Such a circumstance would signal the presence of a lesion and would demand an adaptive readjustment. Adaptation to more complicated patterns of retinal slip associated with head motion would be more difficult and likely take longer. This does seem to be the case, for example, when adaptively cross-coupling torsion to the horizontal VOR using a roll optokinetic stimulus during yaw axis head rotation (Trillenberget al. 2003).

Furthermore, there are instances in which aTVOR response will interfere with stable, single vision; when the eyes are converged as when viewing a near target, ocular counterroll due to either otolith or canal stimulation induces vertical eye misalignment and diplopia, since the axes of eye rotation are head fixed and not parallel to the lines of sight (Bergamin and Straumann 2001; Misslisch et al. 2001). Thus, the nervous system must be adept at not allowing the aTVOR to influence ocular alignment, particularly when working at near, or when viewing the body or a carried object during locomotion. Following this logic, if near work is usually associated with the head pitched relatively down, one might predict that the aTVOR adaptive mechanism is more important with the head in this attitude. Given the relatively small number of subjects reported here, further experiments would be needed to confirm these findings, to distinguish the possible roles of gravitational or neck afferent cues and to control for any possible effect of convergence.

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