Abstract The three pairs of semicircular canals within the labyrinth are not perfectly aligned with the pulling directions of the six extraocular muscles. Therefore, for a given head movement, the vestibulo-ocular reflex (VOR) depends upon central neural mechanisms that couple the canals to the muscles with the appropriate functional gains in order to generate a response that rotates the eye the correct amount and around the correct axis. A consequence of these neural connections is a cross-axis adaptive capability, which can be stimulated experimentally when head rotation is around one axis and visual motion about another. From this visual-vestibular conflict the brain infers that the slow-phase eye movement is rotating around the wrong axis. We explored the capability of human cross-axis adaptation, using a short-term training paradigm, to determine if torsional eye movements could be elicited by yaw (horizontal) head rotation (where torsion is normally inappropriate). We applied yaw sinusoidal head rotation (+10°, 0.33 Hz) and measured eye movement responses in the dark, and before and after adaptation. The adaptation paradigm lasted 45–60 min, and consisted of the identical head motion, coupled with a moving visual scene that required one of several types of eye movements: (1) torsion alone (-Roll); (2) horizontal/torsional, head right/CW torsion (Yaw-Roll); (3) horizontal/torsional, head right/CCW torsion (Yaw+Roll); (4) horizontal, vertical, torsional combined (Yaw+Pitch-Roll); and (5) horizontal and vertical together (Yaw+Pitch). The largest and most significant changes in torsional amplitude occurred in the Yaw-Roll and Yaw+Roll conditions. We conclude that short-term, cross-axis adaptation of torsion is possible but constrained by the complexity of the adaptation task: smaller torsional components are produced if more than one cross-coupling component is required. In contrast, vertical cross-axis components can be easily trained to occur with yaw head movements.

Keywords VOR · Torsion · Cross-coupling · Adaptation

Introduction
A perfect angular vestibulo-ocular reflex (VOR) must ensure that in response to motion of the head (actually the ocular orbits), the eyes rotate not only by the correct amplitude but also around the correct axis to ensure that the object of interest remains stable upon the fovea. In other words, the amplitude and the angle of the angular velocity vector of eye rotation must be matched to the requirements dictated by the motion (both rotation and translation) of the orbits relative to the location of the target of interest. This requirement implies the existence of an adaptive neural mechanism that monitors not only the magnitude of the VOR response but also the alignment of the axis of eye rotation with that of the stimulus, and recalibrates both of them as necessary.

The adaptive mechanism that maintains correct eye alignment during vestibular stimulation has been investigated previously by imposing an artificial error signal (visual-vestibular mismatch) orthogonal to the direction of head rotation, such as vertical image motion with horizontal head rotation or vice versa (e.g., Schultheis and Robinson 1981; Baker et al. 1986; Harrison et al. 1986;...
Peng et al. 1994; Fukushima et al. 2000). Berthoz et al. (1981) showed that subjects who wore left-right reversing prisms for several days were able to change the gains of horizontal and torsional VOR. Here, we further investigated this mechanism in normal humans using a roll (torsional) visual stimulus coupled to rotation of the head around the yaw axis. We were particularly interested in the adaptive capabilities for induction of this cross-coupled torsional oculomotor response for four reasons. First, in contrast to the yaw (horizontal) and pitch (vertical) VORs, the gain of the oculomotor response to a pure roll stimulus (around the naso-occipital axis) is less than 1.0 (Tweed et al. 1994). This leads to an anisotropy, with an axis shift, whenever a roll stimulus is combined with a pitch or yaw stimulus. The retinal slip that necessarily accompanies this “off-axis” VOR is apparen-tly of relatively little consequence to visual performance, as this seeming imperfection seems well tolerated in natural behavior. The reasons for a smaller gain of ocular counterroll to static head tilt with near viewing have been discussed (Misslisch et al. 2001). Second, the gain for visual following (pursuit- or OKN-like tracking of a scene) around the roll axis is much lower than is that of smooth pursuit of targets moving horizontally or vertically (Cheung and Howard 1991; Van Rijn et al. 1994). VOR adaptation has been tied, at least partly, to pursuit capabilities (Lisberger et al. 1984; Shelhamer et al. 1994). Third, the detection of torsional retinal slip requires the analysis of a large segment of the visual field, whereas prolonged horizontal or vertical slip of images on the fovea (and pursuit tracking alone) suffice to induce an adaptive change in the yaw or pitch VOR. Finally, comparison of cross-axis adaptation of torsion alone compared to both torsion and vertical motion, and to vertical motion alone, is of interest because normally the same pairs of semicircular canals provide torsional and vertical compensatory eye movements, albeit with different patterns of excitation and inhibition. Some preliminary aspects of part of this work were reported in Takagi et al. (2001).

**Materials and methods**

We studied four subjects, ages 21–54 years, after informed consent had been obtained. Procedures were approved by the Institutional Review Board of The Johns Hopkins University School of Medicine. Eye movements were recorded from one eye (left in three cases, right in one case) with the dual magnetic search coil technique (Robinson 1963; Collewijn et al. 1975) at a sampling rate of 500 Hz. For the specification of the eye movements (and visual stimulus movements, see below) we used a right-hand coordinate system, with the x-axis pointing from the occiput toward the nose, the y-axis pointing from the right ear toward the left ear, and the z-axis pointing up. Thus, positive angular velocities correspond to left (z-axis), down (y-axis), and clockwise (x-axis) rotations of the eye (from the subject’s point of view). In the cubic field coil frame of 1.02 m width three orthogonal magnetic fields of frequency 55.5, 83.3 and 42.6 kHz are generated. For in vitro calibration, offsets are zeroed with the scleral search coils shielded from the fields in a metal pipe. Gains are determined by aligning the sensitivity vectors of the dual scleral search coil in the direction of the fields. Three signals (one for each field direction) are recorded for each of the two eye coils. The calibration factors determined as above yield the cosine of the angle of each sensitivity vector and the field directions, and thus the x-, y-, and z-components of the vector. After orthogonalization of the two sensitivity vectors, the orientation of the scleral search coil can be expressed as a rotation vector \( r = (r_x, r_y, r_z) \). The direction of \( r \) gives the axis about which the coil has to be rotated to reach the current position, when the axis of the coil was aligned with the x-axis at zero. The length of \( r \) is given by \( \tan(\phi/2) \), where \( \phi \) is the rotation angle of the rotation into the current orientation.

At the beginning of each recording, the subjects fixated a target straight ahead, and the coil position obtained was “subtracted” from all following positions according to Haslwanter (1995). Eye velocity was then calculated according to \( \omega = (\text{d}(\text{d}r/\text{d}t) + (r \times (\text{d}(\text{d}r/\text{d}t))/ (1+r^2)) \) (Haslwanter 1995), and expressed in a head-referenced frame. Recordings of at least 10 cycles of sinusoidal chair movement (corresponding to 30 s) were made before and after the training period. A target straight ahead was briefly flashed during these recordings to help ensure a constant state of mental effort to fix upon a stable reference point in space.

**Stimuli**

For vestibular stimulation, subjects were rotated sinusoidally about an earth-vertical axis, at \( \pm10^\circ \) and 0.33 Hz, with the head held upright with a bitebar. Visual stimuli were presented binocularly with a head-mounted “virtual reality” display (ProView 60, Kaiser Electro-optics, Inc.) with a visual field of 48°x36° (HxV). The images consisted of a square grid, with lines 0.45° in width and separated by 8.6°. The center of the image was marked by a dot (diameter 1.6”). The images were constructed so as to require a viewing distance of optical infinity. For the specification of the movements of the visual stimulus we used the same right-hand coordinate system as above for eye movements.

We combined head rotation with cross-axis visual stimulus motion in various patterns. For labeling purposes, we describe these in terms of the visual motion that occurs while the head is moving to the left. There were five different visual-vestibular stimulus arrangements:

1. Pure counterclockwise rotation of the image (-Roll condition), which called for a torsional response to the yaw VOR and also a cancellation of the horizontal component of the yaw VOR.
2. Rightward and counterclockwise rotation of the image (Yaw-Roll condition), which called for a torsional response but no change in the horizontal component of the yaw VOR.
3. Rightward and clockwise rotation of the image (Yaw-Roll condition), which also called for a torsional response (but in the opposite direction from the Yaw-Roll condition) and no change in the horizontal component of the yaw VOR (see Fig. 1 for the visual feedback presented).
4. Rightward and upward movement and counterclockwise rotation of the image (Yaw-Pitch-Roll condition), which called for an upward and torsional eye movement but no change in the horizontal component in response to the yaw VOR.

![Fig. 1 Visual image motion feedback presented to the subject at three different head positions in the Yaw+Roll stimulus condition](image)