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Egocentric orientation is influenced by trained voluntary cyclorotary eye movements

A CYCLOROTARY eye movement is a motor response of the eye made around the visual axis. Counter-rolling of the eye, for example, occurs during lateral head tilt[1-5]; conjugate rotary nystagmus can be induced by a large rotating field[6-9]; and disjunctive cyclotorsions can occur during ordinary convergence[10,11]. Because none of these torsional eye movements can be produced as an isolated voluntary response, eye torsion has always been classified as an involuntary response, a reflex. Using a visual-feedback procedure, however, we have trained humans to make conjugate voluntary cyclotorsional eye movements up to 30 degrees in magnitude[12]. We have also demonstrated that these large torsional movements are not visually induced and can be made in the absence of any visual stimulus. Accompanying the training and performance of these eye movements were a number of striking illusions related to one's own sense of body orientation. Because these newly trained eye movements are unprecedented, it is of interest to characterise accompanying illusions in detail, comparing them with other illusions of self rotation induced through vestibular[13] and visual[14,15] inputs. In this paper we compare the effects of trained cyclorotary eye movements with head and whole body tilts, showing a quantitatively similar change in egocentric orientation for each type of tilt. As such, our findings suggest the possibility of shared mechanisms affecting the stability of one's internal frame of reference, both for eye and body movements.

The exact method of training and testing of voluntary torsion using visual biofeedback has been detailed elsewhere[12]. A subject was seated in a dark room with head movements fixed by a full mouth bite plate. A vertical $11 \times 0.25°$ flash was presented monocularly to generate a vertical afterimage. This afterimage was then imaged in space next to a line of light of equal colour, brightness and size (real line stimulus). The subject was instructed to keep this afterimage line matched parallel to the real line only by cyclorotating the eyes. With practice, the subject gradually acquired the ability to rotate the eye(s) to match greater and greater inclinations of the real line. These cyclofixations were trained at the rate of about $0.8° h^{-1} d^{-1}$ for 35 d (Fig. 1*a*). Using similar methods for 5–10 h of additional training, subjects were trained to make torsional slow pursuit (Fig. 1*b*) and torsional saccades (Fig. 1*c*). Individual frame analysis of 35-mm slides or 16-mm motion pictures filmed simultaneously were used to objectify the cyclorotary eye movements. Measurements from photographs used radial iris markings or limbal–scleral blood vessel junctions in relation to a visible and stable reference marker. Accuracy of measurements was ±10 min.

During initial training, but not during final experimentation, subjects often felt that their heads and bodies were 'rolling laterally' and sometimes experienced associated visual illusions. Accompanying these changes in egocentric orientation were intermittent sensations of stomach nausea, headache and general body fatigue. The most dramatic of these illusions occurred as a distinct 'hallucinatory barrage' at least twice to each subject during initial training. Associated with eyelid tremor, the nearly vertical and parallel lines would appear to move independently, becoming almost horizontal and also appearing curved or wiggly. Accompanying these peculiar visual illusions were very powerful sensations of body flotation and/or rapid downward falling in the direction of the voluntary cyclotorsion. Although self-induced, these sensations show similarities to those experienced by pilots in conditions in which conflicting visual and orientational information can occur[16]. It should be noted that these gross and episodic disorientations occurred only during initial training.

In this report, we restrict our quantitative observations to a more constant and milder sensory illusion of body tilt, persisting even after a long period of training. To examine this shift in egocentric orientation and to make comparisons with other situations involving vestibular and neck proprioceptive input, we have devised a control and three test situations. Two subjects felt a rod pivoted about its centre so as to rotate in the frontal plane and adjusted it to the apparent vertical in the dark under each of the following conditions (Fig. 2, top): (1) the real line stimulus was viewed in otherwise dark surroundings at one of several angles of tilt (S); (2) voluntary eye torsion was used to match an otherwise vertical afterimage to specific tilts of the real line (E); (3) a head tilt was used to match the orientation of the real line to that of the afterimage (H); and (4) head and body were both tilted by means of a rotating chair in complete darkness (B).

All tilts and rotations were presented in 3° increments over a range of ±9.0°. In condition H, the reflexive counter-torsion of the eye was less than 1° (average 0.6°) for even the largest 9° tilts; consequently, actual tilts of the head are slightly underestimated. Before each trial, the experimenter randomly displaced the rotatable rod to ensure that subjects could not memorise hand or rod positions.

The results are graphed in Fig. 2 (bottom). Condition S, as a control, demonstrated that the presence of the inclined real stimulus line had essentially no influence on the subjects' sense of vertical, changing it by only 3% of the real line's tilt. Such a line has also been shown to induce essentially no torsional movements of the eyes[12]. Therefore, it can be concluded that the presence of the inclined real line in conditions E and H is of little consequence.

Voluntary torsion (condition E), however, caused marked shifts in the position of apparent vertical as did the two other conditions (H and B). All adjustments were overestimated in the opposite direction to eye, head or body tilts and by an amount which was virtually identical in all three conditions (Fig. 2). It should also be noted that the results for conditions H and B confirm previous reports[17,18]. Because the results are so

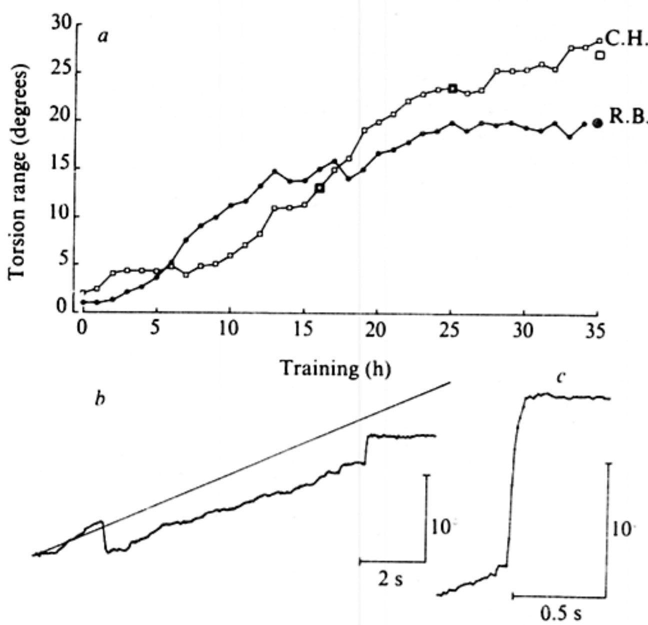
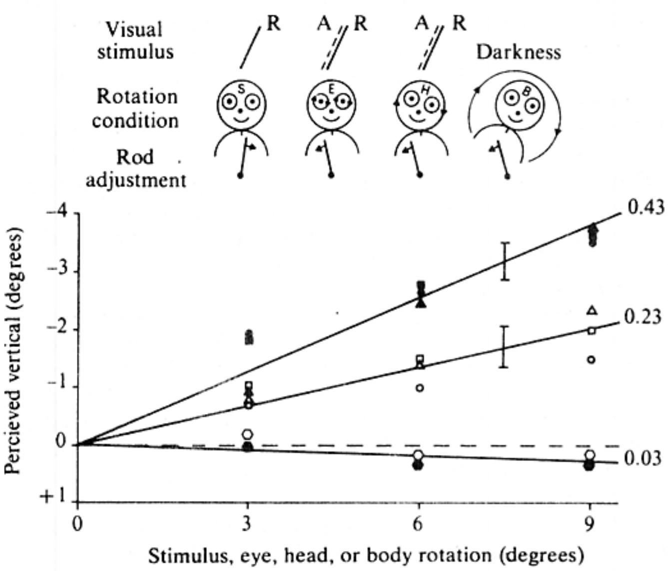


Fig. 1 *a*, Training of voluntary torsion. Maximum torsional range measured psychophysically (small symbols) or photographically (large symbols) plotted against hours of training. *b*, Voluntary cycloversional slow pursuit. Solid line represents a tracing moving at the correct velocity of $1.6° s^{-1}$. Photographed at 24 frames s^{-1}. *c*, Time course of a voluntary torsional saccade. Photographed at 64 frames s^{-1}.

Fig. 2 A laterally rotatable rod was adjusted to perceived vertical in the dark by subjects in different conditions of rotation over a range of ±9° (top). The visual stimulus for each condition is shown: R, real line; A, afterimage line. Both R and A are set to vertical when eyes are at rest and straight ahead. Rotation conditions are defined as follows: S, real line stimulus rotation only (control); E, voluntary eye torsion defined by an afterimage match to tilts of the real line; H, head tilt defined by an afterimage line match to tilts of the real line; B, body and head tilt in complete darkness. Graph shows the change in perceived vertical as a function of rotation. Rod settings for conditions E, H and B were in the opposite direction to any direction of physical rotation (abscissa) by a factor of about one-third (average slopes of 0.23 and 0.43 for subjects C.H. and R.B.). Control condition (S) showed essentially no effect (average slope = 0.03). $n = 40$ for each data point. Error bars on regression lines indicate average s.e. mean for the combined data of C.H. (bottom line) and R.B. (top line), based on 468 df. R.B.: ●, S; ▲, E; ■, H; ●, B; C.H.: ○, S; △, E; □, H; ○, B.



similar in the three conditions, we averaged the data and plotted a single regression line for each subject, arriving at a slope of 0.23 for subject C.H. and 0.43 for subject R.B. If 1.0 is defined as a gain factor whereby a perfect vertical rod adjustment could be made, a gain factor for the subjects' sense of vertical or egocentric orientation can be determined by adding 1.0 to each slope. Thus, C.H. and R.B. overestimated their turning by an average factor of 1.23 and 1.43, respectively.

These experiments suggest that for each subject, there is a constant overcompensation signal determining egocentric orientation, regardless of whether the eye is voluntarily rotated (voluntary cyclofixation), the otoliths and neck proprioceptors are stimulated (head tilt condition), or the otoliths are stimulated without significant neck proprioception stimulation (whole body tilt). In this case of voluntary torsion, as well as for other examples of the perceptual effects of eye torsion[17,19], the compensatory signal could arise either as an outflow, originating from a torsional command centre, or as an inflow, originating from eye muscle receptors. The results do not indicate the source of the compensatory signal.

What is surprising is that the motor act of voluntary torsion, which is independent of vestibular or visual stimulation, can, by itself, induce quantitatively identical sensations to actual head and body rotations. This similarity suggests that there might be a common pathway for each effect. Electrophysiological recordings from the vestibular nerve, for example, show that moving visual scenes produce signals that are similar to a motion stimulus to the semicircular canals[20–23], a result which could be the physiological basis for the recent finding that egocentric orientation can be altered by rotating visual fields[14]. Perhaps a similar sharing of circuitry exists with respect to the newly trained response of voluntary eye torsion.

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