

# Vertical Divergence and Counterroll Eye Movements Evoked by Whole-Body Position Steps About the Roll Axis of the Head in Humans

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**Kori, A. A., A. Schmid-Priscoveanu, and D. Straumann.** Vertical divergence and counterroll eye movements evoked by whole-body position steps about the roll axis of the head in humans. *J Neurophysiol* 85: 671–678, 2001. In healthy human subjects, a head tilt about its roll axis evokes a dynamic counterroll that is mediated by both semicircular canal and otolith stimulation, and a static counterroll that is mediated by otolith stimulation only. The vertical ocular divergence associated with the static counterroll too is otolith-mediated. A previous study has shown that, in humans, there is also a vertical divergence during dynamic head roll, but this report was not conclusive on whether this response was mediated by the semicircular canals only or whether the otoliths made a significant contribution. To clarify this issue, we applied torsional whole-body position steps (amplitude 10°, peak acceleration of 90°/s<sup>2</sup>, duration 650 ms) about the earth-vertical (supine body position) and earth-horizontal (upright body position) axis to healthy human subjects who were monocularly fixating a straight-ahead target. Eye movements were recorded binocularly with dual search coils in three dimensions. The dynamic parameters were determined 120 ms after the beginning of the turntable movement, i.e., before the first fast phase of nystagmus. The static parameters were measured 4 s after the beginning of the turntable movement. The dynamic gain of the counterroll was larger in upright (average gain: 0.48 ± 0.10 SD) than in supine (0.36 ± 0.10) position. The static gain of the counterroll in the upright position (0.21 ± 0.06) was smaller than the dynamic gain. Divergent eye movements (intorting eye hypertropic) evoked during the dynamic phase were not significantly different between supine (average vergence velocity: 0.87 ± 0.51°/s) and upright (0.84 ± 0.64°/s) positions. The static vertical divergence in upright position was 0.32 ± 0.14°. The results indicate that the dynamic vertical divergence in contrast to the dynamic ocular counterroll is not enhanced by otolith input. These results can be explained through the different patterns of connectivity between semicircular canals and utricles to the eye muscles. Alternatively, we hypothesize that the small dynamic vertical divergence represents the remaining vertical error necessary to drive an adaptive control mechanism that normally maintains a vertical eye alignment.

## INTRODUCTION

Divergent vertical ocular deviation, i.e., skew deviation, combined with conjugate ocular counterroll (lower eye exerted) is an important neurological sign that may be present as a consequence of labyrinthine (Halmagyi et al. 1979; Wolfe et al. 1993), brain stem (Brandt and Dieterich 1994), or cerebellar (Mossman and Halmagyi 1997) lesions. If, in addition, the

head tilts toward the lower eye and in the same direction as the ocular counterroll, the syndrome is called *ocular tilt reaction* (Brandt and Dieterich 1987; Westheimer and Blair 1975). It has been proposed that this ocular tilt reaction may reflect an asymmetric input of ascending afferents carrying otolith (Dieterich et al. 1989; Halmagyi et al. 1979; Wolfe et al. 1993) or a combination of otolith and semicircular canal signals (Brandt and Dieterich 1993; Dieterich and Brandt 1992; Lopez et al. 1992). To date, it is unclear whether a skew deviation is just an exaggerated physiological reflex (vestibular-ocular reflex) due to asymmetric vestibular signals or to a breakdown of mechanisms that normally maintain vertical eye alignment. To understand the pathophysiology of the ocular tilt reaction better, it is important to find out whether ocular counterroll in healthy subjects is already associated with a small vertical divergence and, if so, whether these vestibularly evoked divergent vertical eye movements are due to otolith and/or semicircular canal inputs.

In human subjects, head roll evokes counterrotations of both eyes about head-fixed axis that are oriented approximately parallel to the stimulus axis. This vestibuloocular response is called *ocular counterroll* and is *conjugate* (Collewijn et al. 1985; Diamond and Markham 1983). A *dynamic* and a *static* counterroll can be distinguished. The dynamic counterroll is mediated by both otolith and semicircular canal stimulation because the gain of the torsional eye movement response is higher in upright than in supine position (Groen et al. 1999; Morrow and Sharpe 1993; Schmid-Priscoveanu et al. 2000). The static counterroll, observed after positioning the head in a roll tilt position, is mainly due to otolith stimulation, but somatosensory inputs might also play a small role (Krejcová et al. 1971).

Less is known of the vertical eye movements associated with dynamic and static counterroll. Betts et al. (1995) reported a vertical ocular divergence with the hypertropic eye on the side of the lower ear, when subjects were laying in a side position. They measured subjectively this vertical divergence with a Hess screen.<sup>1</sup> Clearly, this static vertical divergent response is otolith-mediated. Using video-oculography, Jáuregui-Renaud et al. (1998) measured the eye movements of three healthy

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<sup>1</sup>The Hess screen test measures the horizontal and vertical deviation between both eyes in the absence of fusional constraints (Hess 1916).

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subjects during oscillations around the naso-occipital axis in upright and supine positions at 0.1 and 0.4 Hz. In the dark at 0.4 Hz, two of the subjects showed a significant increase of vertical divergent movements. The torsional gain, however, increased significantly in only one of the subjects in the upright position.

Taken together, the data on vertical divergent movements do not yet allow a conclusion on a probable common mechanism for the vertical divergent and counterroll responses. The reports are conflicting and, hence, the role of the otoliths during the dynamic phase of the responses remains unclear. We attempted to clarify this issue by strictly controlling eye position during vestibular stimulation. This was achieved by letting the subjects monocularly fixate a visual target straight ahead. By covering the other eye, the vertical fusional reflex was not activated and, at the same time, the direction of the line-of-sight was restricted. This tight control of gaze during head roll stimulation was crucial, because a change of the line-of-sight tilts the eye rotation axis away from the stimulus axis (Misslisch et al. 1994). Since the pursuit system is not effective in the torsional direction, fixating a light dot straight ahead on an unstructured background or in complete darkness has only a small effect on the gain of the torsional vestibulo-ocular reflex (Leigh et al. 1989). In healthy human subjects, we applied whole-body position steps about the roll axis of the head in the upright and supine positions and measured the torsional, vertical, and horizontal movements of both eyes with dual search coils. By comparing the evoked eye movements between the two stimulation conditions, we quantified the contribution of the otoliths to the dynamic component of both the vertical vergence and counterroll responses. Specifically, we asked whether vertical vergence and counterroll were directly linked to each other, both statically and dynamically, as part of a fixed ocular movement pattern. Alternatively, the relative contribution of the otoliths and semicircular canals to the static and the dynamic components of vertical vergence and counterroll could differ. The results from all six subjects in this study supported the latter hypothesis.

## METHODS

### *Subjects*

Six healthy human subjects (3 males and 3 females, between 25 and 56 years old) participated in this study. Subjects were informed of the experimental procedures. The protocol was approved by a local committee and was in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

### *Experimental setup*

Subjects were seated on a turntable with three servo-controlled motor driven axes (prototype built by Acutronic, Jona, Switzerland). The head was restrained with an individually molded three-point-mask (Sinmed BV, Reeuwijk, The Netherlands). The subject was positioned so that the center of the interaural line was at the intersection of the three axes of the turntable. Movements of the body were minimized by evacuation pillows and safety belts. The head was surrounded by an aluminum coil frame (side length 0.4 m) through which three orthogonal magnetic fields with frequencies of 55.5, 83.3, 41.6 kHz were produced. The synchronous detection of the amplitude-modulated signals yielded instantaneous voltages induced by the three magnetic fields (Lasker 1995). With a bandwidth filtering of 0–90 Hz,

the peak-to-peak noise was  $0.2^\circ$  in the torsional and  $0.1^\circ$  in the horizontal and vertical directions.

### *Eye movement recordings*

Three-dimensional eye movements were recorded binocularly with dual scleral search coils (Skalar Instruments, Delft, The Netherlands) (Collewijn et al. 1985; Robinson 1963). For calibration, the voltage offsets of the system were zeroed by placing the search coils in the center of a metal tube to shield them from the magnetic field. Then the relative gains of the three magnetic fields were determined with the search coils mounted on a gimbal system that was placed in the center of the coil frame. Details of the calibration procedure can be found in detail elsewhere (Straumann and Zee 1995). After local anesthesia of the conjunctiva and cornea with oxybuprocaine 0.4%, the search coil annuli were placed around the cornea of both eyes. Eye and chair movements were digitized at a frequency of 1000 Hz with 16-bit resolution and stored on a computer hard disk for off-line processing.

### *Experimental protocol*

On the three-dimensional turntable, subjects were moved in the upright or supine position. Then the turntable axis that was oriented parallel to the x-axis of the coil frame (torsional axis) rotated the whole body of the subject clockwise or counterclockwise by  $10^\circ$  with a bell-shaped velocity profile and a peak acceleration of  $90^\circ/s^2$ . The duration of the step was 650 ms. Ten position steps were applied to each side in both supine and upright body positions.

During the position steps about the roll axis of the head, the right eye was covered to avoid vertical fusion that might minimize the skew deviation; the left eye was fixing a laser target (diameter  $0.1^\circ$ ) projected straight ahead onto an unstructured background to keep the gaze direction of this eye constant during the vestibular stimulation. The distance of the target was 1.52 m in upright and 1.76 m in supine position. Experiments were performed in dim light.

### *Data analysis*

The data analysis was performed with an interactive program written in MATLAB Version 11. The three-dimensional eye position was expressed in rotation vectors. A rotation vector  $r = (r_x, r_y, r_z)$  describes the instantaneous orientation of a body as a single rotation from the reference position; the vector is oriented parallel to the axis of this rotation and its length is defined by  $\tan(\rho/2)$ , where  $\rho$  is the rotation angle. The coordinate system of rotation vectors was defined by the three head-fixed orthogonal axes of the coil frame with the x-axis pointing forward, the y-axis leftward, and the z-axis upward. The signs of rotations about these cardinal axes were determined by the right-hand rule, i.e., clockwise, leftward, and downward rotations, as seen by the subject, were positive.

From the rotation vectors, three-dimensional angular velocity vectors  $\omega$  were computed, using the formula (Hepp 1990)

$$\omega = 2(dr + r \times dr)/(1 + |r|^2)$$

where  $dr$  denotes the derivative of  $r$  and  $\times$  the cross product. Angular eye-velocity vectors are oriented parallel to the instantaneous ocular rotation axis; their lengths denote the velocity of rotation. For convenience, the lengths of rotation and angular velocity vectors are given in degrees ( $^\circ$ ) and degrees per second ( $^\circ/s$ ), respectively, but the right-hand rule is maintained when describing the orientation of these vectors.

## RESULTS

In all subjects, whole-body steps about the roll axis of the head in upright and supine position evoked an ocular counter-

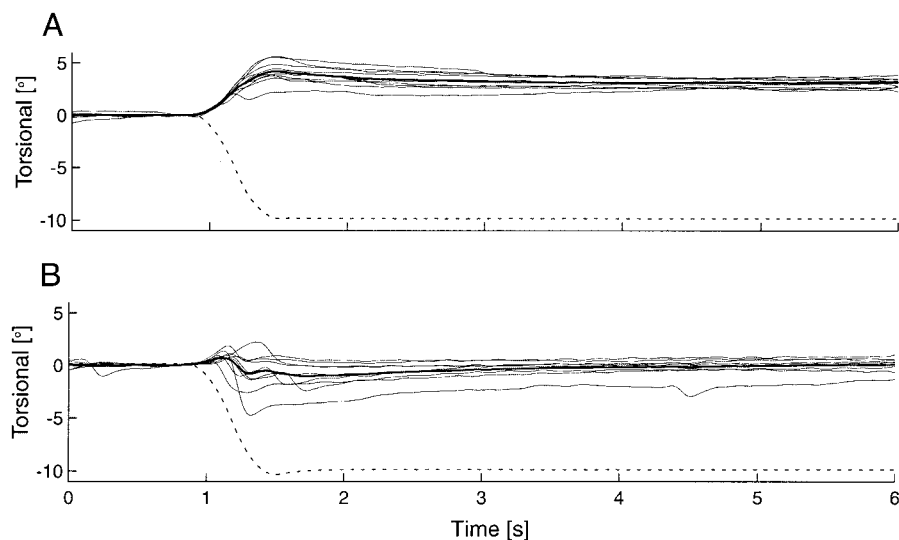


FIG. 1. Example (*subject 1*) of torsional movements of the covered right eye (viewing left eye not shown) in response to position steps of  $10^\circ$  about the roll axis of the head to the left. Thin lines: torsional eye position traces from individual trials. Thick line: median torsional eye position signal. Dashed line: turntable position in the roll plane. *A*: in the upright position, there was both a dynamic and static ocular counterroll. *B*: in the supine position, only a dynamic counterroll was evoked.

roll. A typical example is shown in Fig. 1, where the thick solid line represents the median torsional eye position of 10 trials (thin lines) at each moment in time. In upright position, both dynamic and static torsional eye responses were elicited (Fig. 1A). In supine position, quick phases of nystagmus shortly after the beginning of the turntable rotation moved the eye back or even beyond the zero torsional baseline (Fig. 1B).

The vertical and horizontal components of evoked eye movements were processed in the same way, i.e., by computing the median trace of the 10 responses. Vergence eye movements were analyzed by subtracting the median traces of the right eye from the median traces of the left eye. The analysis of static responses was based on rotation vectors, and the analysis of dynamic responses on angular velocity vectors. The eye movements evoked by turntable steps about the roll axis of the head to the right and left were symmetric. In the following, we only report on eye movements elicited by stimulation to the left.

Figure 2 summarizes the torsional, vertical, and horizontal movements of both eyes during torsional position steps in upright and supine position in a typical subject (*subject 2*). In upright position (Fig. 2, A–C), the ocular counterroll evoked by whole-body steps was conjugate (Fig. 2A). Vertical eye movements, however, were clearly disconjugate both in the dynamic and the static phase of the response (Fig. 2B). The phenomenon that the viewing eye was the one moving was probably due to the fact that the fovea usually is not exactly aligned with the optical axis (Carpenter 1988; Howard and Rogers 1995) and the fact that the torsional rotation axis of the turntable was head-centered, not eye-centered. Both these effects, however, could not have influenced the consistent vertical vergence response, because the horizontal movements of both eyes were found to be approximately conjugate (Fig. 2C). No consistent pattern of horizontal eye movements was found during the dynamic phase. During the static phase, however, both eyes shifted horizontally to the side with the higher ear (in this case the right side).

Vestibular stimuli about the naso-occipital axis in the supine position (Fig. 2, D–F) evoked only a small torsional conjugate eye movement response during the dynamic phase, and no static counterroll (Fig. 2D). Vertical eye movements showed variable amounts of divergence during the dynamic phase, but conjugacy during the static phase (Fig. 2E). The horizontal

movement components were conjugate at the beginning of the vestibular stimulation, but then the eyes diverged somewhat (Fig. 2F).

Two moments in time after the beginning of the turntable movement were defined to quantify the dynamic and static behavior of eye movements evoked by the vestibular stimulus in the roll axis of the head in supine and upright body position: 1) at 120 ms the dynamic parameters and 2) at 4 s the static parameters. For the torsional component, we computed the dynamic torsional gain by dividing the torsional eye velocity by the torsional chair velocity. For the horizontal and vertical components, it was not possible to compute a gain; hence, we took the velocity values of the eye for further data analysis. As static parameters, 4 s after the beginning of the turntable movement, we determined the three-dimensional position of both eyes. For the torsional component a static gain was computed by dividing the torsional eye position by the turntable position in the roll axis.

For all six subjects, Fig. 3 shows the dynamic and static torsional gains in upright and supine positions during the turntable step in the roll axis of the head. In both body positions, the torsional dynamic gains were significantly above zero; the average dynamic gain was 0.48 in upright position and 0.36 in supine position (Fig. 3A). This difference was significant. The static torsional gains in upright position (Fig. 3B) had an average of 0.21 and therefore were smaller than the corresponding dynamic gains, but still significantly different from zero. Obviously, there was no static counterroll in supine position. Averages and standard deviations are given in Table 1.

To compare the torsional eye movements with the vertical and horizontal ones better, Fig. 4 and Table 1 summarize the torsional, vertical, and horizontal velocities (dynamic responses) and positions (static responses) of the covered right eye of all six subjects in supine and upright body positions. The dynamic torsional velocities were significantly larger in upright than in supine position (Fig. 4A). The average velocity of the dynamic torsional component was  $3.6^\circ/\text{s}$  in upright position and  $2.6^\circ/\text{s}$  in supine position. There was also a significant difference in the static torsional eye position between upright and supine, with the torsional position in upright significantly different from zero (Fig. 4B). The average position of the static torsional component was  $2.09^\circ$  in upright position and  $-0.13^\circ$

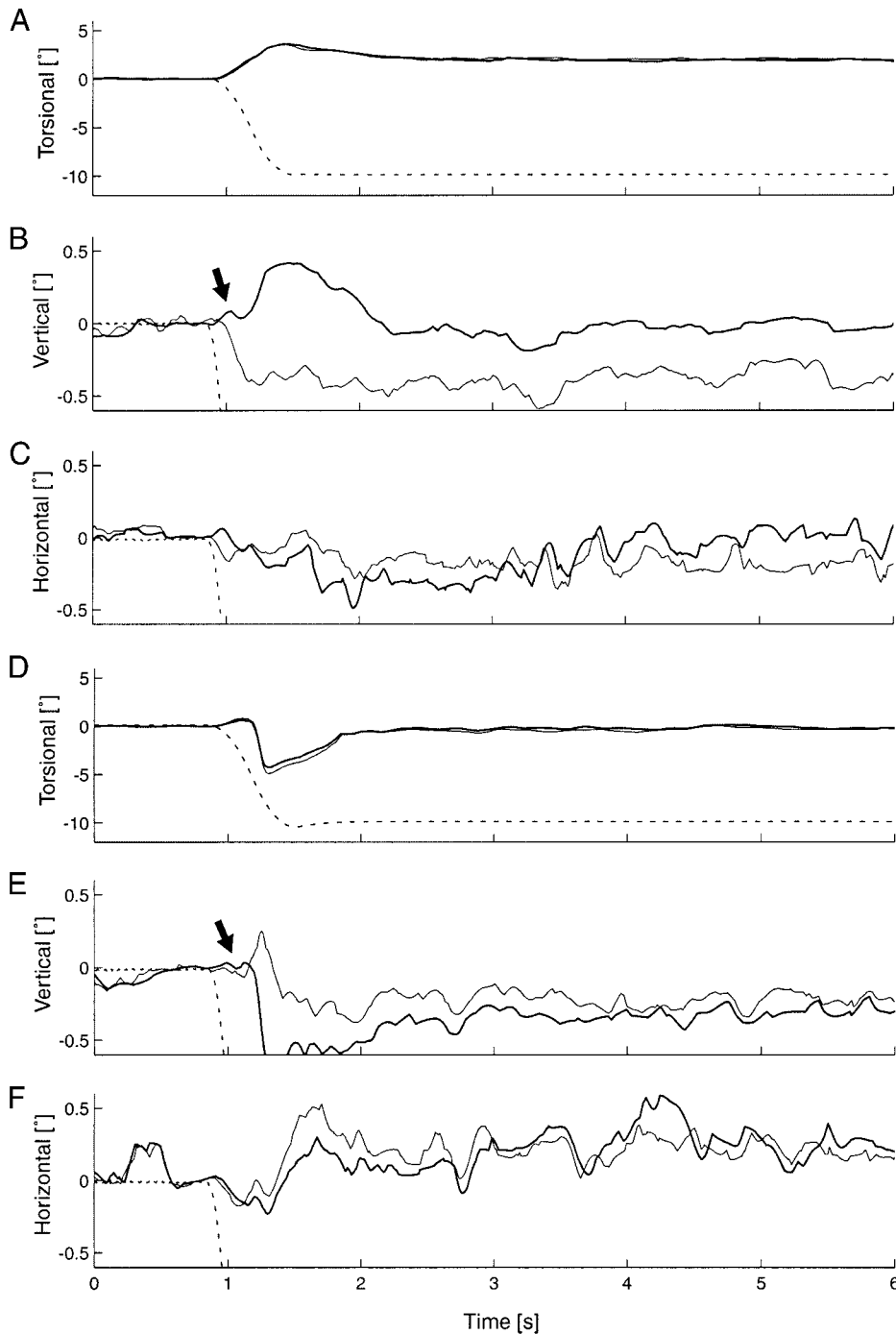


FIG. 2. Example (*subject 2*) of median eye position traces (overlays of 10 trials) evoked by turntable position steps in the roll plane. Trials in *upright* (A–C) and *supine* (D–F) body positions. Thick line: right eye position. Thin line: left eye position. Dashed line: turntable position in the roll plane. (A, D) torsional, (B, E) vertical, and (C, F) horizontal eye position components. Torsional eye movements were conjugate in both upright (A) and supine (D) body position. In supine position, there was only a dynamic, but not a static torsional eye response and a large anticompensatory saccade of about  $5^\circ$  shortly ( $\sim 200$  ms) after the beginning of the turntable movement (D). In both the upright and supine position, the vertical position traces of the two eyes diverged already shortly after the beginning of the turntable movement (dynamic phases in B and E, see arrows), but only in the upright position the vertical divergence remained (B). Note that in this particular subject a large vertical divergence movement appeared during the first quick phase in supine position (E). In upright position, both eyes shifted horizontally contralateral to the chair tilt (C), but in supine position the shift was to the ipsilateral side (F).

in supine position. The dynamic vertical velocities showed no differences between upright and supine positions (Fig. 4C). During static roll stimulation, there was a significant difference of vertical eye position between supine and upright (Fig. 4D); in upright position the covered right eye (on the side of the upper ear) was significantly lower (positive according to right-hand rule) than in the supine position. The average static vertical eye position was  $0.2^\circ$  in upright and  $0.01^\circ$  in supine position. During the dynamic phase, the median horizontal velocities were unchanged between upright and supine positions (Fig. 4E). In the static phase, however, there was a significant horizontal displacement of the covered eye to the side with the higher ear in the upright position (Fig. 4F).

A summary of the torsional, vertical, and horizontal vergence responses to the whole-body step movements about the roll axis of the head in both supine and upright positions is given in Fig. 5 and Table 2. Torsional eye movements were conjugate in the upright and supine positions during both the dynamic (Fig. 5A) and static (Fig. 5B) phases of vestibular stimulation. During the dynamic phase, the vertical divergence in upright and supine positions were significantly different from zero, but there was no difference between the two body positions (Fig. 5C). The average dynamic vertical divergence was  $0.84^\circ/\text{s}$  in upright position and  $0.87^\circ/\text{s}$  in supine position. During the static phase, the average vertical divergence was  $0.32^\circ$  in upright position and  $-0.05^\circ$  in supine position. Thus



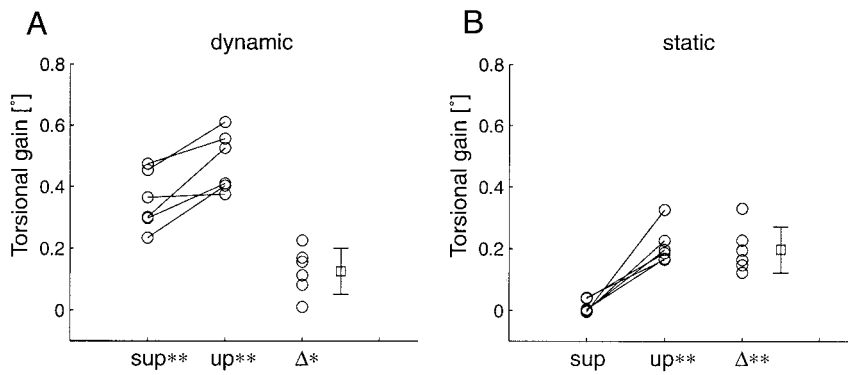


FIG. 3. Comparison of median dynamic (A) and static (B) torsional gains of the right covered eye in all subjects in supine (sup) and upright (up) positions. Both dynamic and static gains increased in upright position.  $\Delta$ : differences of median torsional gains between the two positions. Square with error bars: average of  $\Delta \pm 1$  SD. Significance levels of the paired *t*-test: \**P* < 0.05 and \*\**P* < 0.01.

the results show a significant vertical divergence during the static phase in upright position (Fig. 5D). There was no difference between the horizontal vergence elicited in upright and supine positions during both the dynamic (Fig. 5E) and static (Fig. 5F) phases.

DISCUSSION

The present study investigated the contribution of the otoliths to the counterroll and skew deviation observed in healthy human subjects during a head tilt about the roll axis. To eliminate possible contributions of the cervico-ocular reflex, whole-body step movements were applied. This stimulus evoked 1) a dynamic counterroll that was larger in upright than in supine position; 2) a dynamic vertical divergence (intorting eye hypertropic) that was not affected by body position; and 3) a static counterroll and vertical divergence (intorting eye hypertropic) in upright position.

Earlier studies using sinusoidal oscillations in the roll plane have demonstrated dynamic counterroll in healthy subjects (Averbuch-Heller et al. 1997; Collewijn et al. 1985; Diamond and Markham 1983; Peterka 1992). Recently, we showed that the gains of dynamic counterroll were significantly smaller in the supine position than in the upright position (Schmid-Priscoveanu et al. 2000), confirming the contribution of both the semicircular canals and the otoliths to the dynamic counterroll. In the present study, in which subjects were not oscillated but stimulated with impulses of velocity, the dynamic gain of ocular torsion was again significantly increased by the otoliths (~40%). One study, however, reported unchanged torsional gains in the upright and supine positions during passive roll tilt (Tweed et al. 1994). These results could be due to a different analytical method for computing gain. The authors determined the three-dimensional VOR-gain matrices by pooling the data from rotations about horizontal, vertical, and torsional axes and assuming vectorial summation of gains in

three dimensions, which is only an approximation to the actual VOR behavior.

It is well known that ocular counterroll can be also evoked by static head roll (Diamond and Markham 1983), but the gain is considerably smaller than during dynamic counterroll (Averbuch-Heller et al. 1997; Collewijn et al. 1985; Diamond and Markham 1983). In our study, the gain of the static counterroll was less than half of the dynamic counterroll in upright position (~45%).

Betts et al. (1995) described a vertical divergence during static roll tilt in healthy subjects using the Hess screen (hypertropic eye ipsilateral to the head tilt). We were able to replicate this finding of a static vertical divergence; the average static vertical divergence was 0.32° when the head was rolled 20° from the upright position.

Jáuregui-Renaud et al. (1998) reported that a vertical divergence can be also evoked by oscillatory dynamic roll tilt. Whether additional otolith input in upright position could enhance this response remained unclear, since the coordinate system of three-dimensional eye velocity was not specified and, hence, the effect of eye position could not be derived from the published data. The authors reported that two of the three subjects showed a significant increase of vertical divergence velocity in the upright position compared with the supine position. Our results, which are based on position steps and the precise control of eye position by monocular fixation, show that there is no significant increase of vertical divergence velocity by otolith input. A limitation of the dynamic data in our study, however, has to be taken into account; because of intervening quick phases, which appeared very shortly after the beginning of the turntable movement, dynamic vertical divergence was determined after 120 ms. We therefore do not know whether, in the absence of quick phases, a larger dynamic vertical divergence would have developed a few milliseconds later.

A model of the vestibular system that includes dynamic counterroll and dynamic vertical divergence must solve the

TABLE 1. Gain, velocity, and position of torsional, vertical, and horizontal eye movements

	Gain		Velocity (dyn), %s			Position (stat), °		
	Dyn T	Stat T	T	V	H	T	V	H
Upright	0.48 ± 0.1	0.21 ± 0.06	3.57 ± 0.57	0.63 ± 0.7	-0.08 ± 0.57	2.09 ± 0.6	0.05 ± 0.18	0.44 ± 0.39
Supine	0.36 ± 0.1	0.01 ± 0.02	2.61 ± 0.8	0.6 ± 0.76	-0.13 ± 0.41	-0.13 ± 0.21	-0.32 ± 0.08	0.14 ± -0.19
$\Delta$	0.13 ± 0.08	0.2 ± 0.08	0.95 ± 0.47	0.03 ± 0.6	0.04 ± 0.41	2.22 ± 0.53	0.37 ± 0.19	0.58 ± 0.48

Values given are average and standard deviations. Number of subjects was six. dyn, dynamic; stat, static; T, torsional; V, vertical; H, horizontal;  $\Delta$ , average and standard deviation of the difference between upright and supine positions.

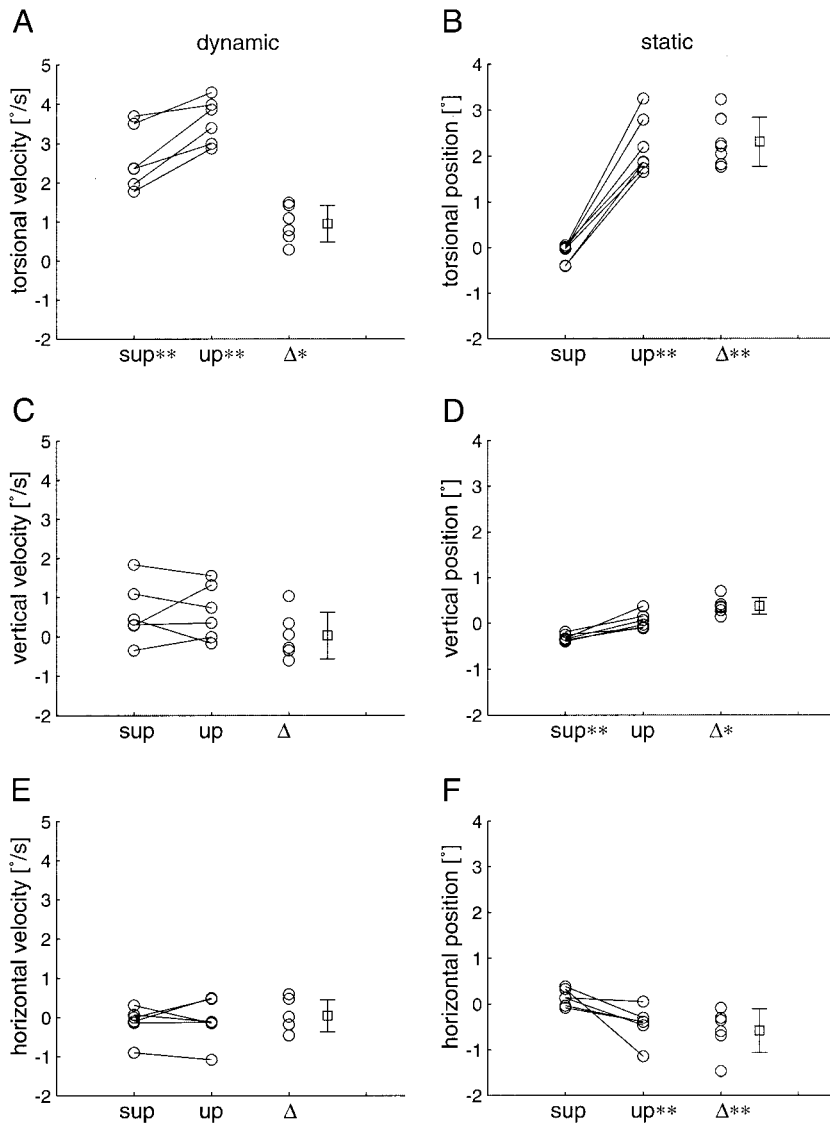


FIG. 4. Comparison of medians of torsional (A), vertical (B), and horizontal (C) velocities (dynamic) and torsional (D), vertical (E), and horizontal (F) positions (static) of the right covered eye in all subjects. Dynamic: only the torsional component of velocity increased significantly in upright position (A). Static: all three components of eye position changed significantly in upright position (B, D, F). Symbols as in Fig. 3.

following problem that is posed by the experimental results described: Dynamic counterroll has a higher gain with additional otolith contribution, but dynamic vertical divergence does not. On the other hand, both static counterroll and static vertical divergence are evoked by otolith input. This can be explained through the different contribution of the otoliths and semicircular canals during head roll. Unilateral utricular stimulation in cats (Suzuki et al. 1969) induced mainly a contraction of the oblique muscles and, to a lesser extent, a contraction of the recti muscles. The stimulation of the semicircular canals, on the other hand, led to a stronger contraction of the recti muscles than of the oblique muscles. This could explain why only during the static phase of the response in upright position, when just the otoliths are stimulated, a small vertical divergence is elicited. During the dynamic phase, however, when both otolith and semicircular canal are stimulated, due to the main contribution of the semicircular canals to vertical divergence, no significant difference can be appreciated between the upright and supine positions. Recently, Cremer et al. (2000) reported a single case of a patient with an isolated posterior semicircular canal fistula in whom ear pressure led to a con-

jugate vertical-torsional nystagmus but no skew deviation. Stimulation of the posterior semicircular canal leads to an activation of the ipsilateral superior oblique and contralateral inferior rectus, both of which are eye depressors. Thus vertical conjugate eye movements are expected. Similarly, stimulation of the anterior semicircular canal leads to an excitation of the ipsilateral superior rectus and contralateral inferior oblique, also with conjugate vertical eye movements since both muscles are elevators. However, a simultaneous stimulation of both semicircular canals (as it happens during head roll) might result in a vertical divergence; the primary action of the superior rectus is that of elevation and would prevail over the depression of the ipsilateral superior oblique since this is only its secondary action. In the other eye, a depression which is the primary action of the inferior rectus would prevail over the elevation of the inferior oblique because this is its secondary action.

An alternative explanation is also purely hypothetical: Vertical divergence might inherently be a part of the torsional vestibulo-ocular reflex in that the intorting eye is driven upward by activation of the superior rectus muscle, while the extorting eye is driven

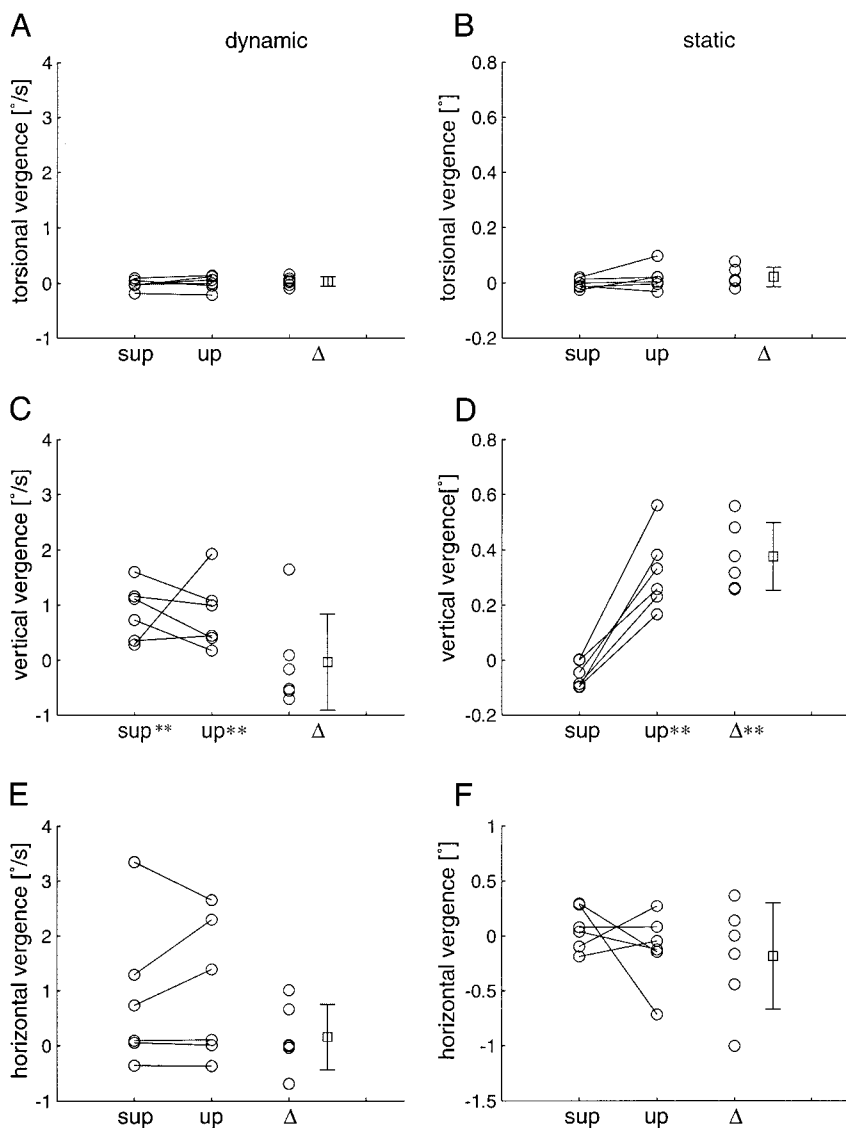


FIG. 5. Comparison of medians of torsional (A), vertical (B), and horizontal (C) vergence velocities (dynamic) and torsional (D), vertical (E), and horizontal (F) vergence positions (static). Dynamic: only vertical eye velocities were significantly divergent, both in upright and supine position (C). Static: a divergent vertical eye position was only seen when the subject was rolled in the upright position (D). Symbols as in Fig. 3.

downward by activation of the inferior rectus muscle, because, as we mentioned before, the vertical action of the recti muscles exceeds the antagonist vertical action of the oblique muscles. During binocular vision, the static vertical divergence can easily be overcome by the vertical fusional reflex. This reflex, however, is too slow to suppress the dynamic vertical divergence (latency ~160 ms). For the prevention of dynamic vertical diplopia during torsional vestibular stimulation, only an adaptive control mechanism, e.g., via the cerebellum (Leigh and Zee 1999; Raymond et al. 1996) is realistic. The remaining dynamic vertical divergence,

which is unchanged with or without otolith stimulation, might simply reflect the minimal dynamic error necessary to drive this adaptive control mechanism to maintain vertical alignment. In pathologic circumstances the vertical misalignment becomes manifest because the otolith (Dieterich et al. 1989; Halmagyi et al. 1979; Wolfe et al. 1993) and, sometimes in addition, semicircular canal (Brandt and Dieterich 1993; Dieterich and Brandt 1992; Lopez et al. 1992) signals are so asymmetric that the hypothetical adaptive control mechanism breaks down.

To confirm our hypothesis of an active suppression mecha-

TABLE 2. Vergence values of torsional, vertical, and horizontal eye movements

	Vergence					
	T		V		H	
	Dyn, %s	Stat, °	Dyn, %s	Stat, °	Dyn, %s	Stat, °
Upright	0.01 ± 0.13	0.02 ± 0.04	0.84 ± 0.64	0.32 ± 0.14	1.02 ± 0.128	-0.11 ± 0.33
Supine	-0.02 ± 0.09	-0.003 ± 0.02	0.87 ± 0.51	-0.05 ± 0.05	0.86 ± 1.35	0.07 ± 0.2
Δ	0.03 ± 0.01	0.02 ± 0.04	-0.04 ± 0.88	0.38 ± 0.12	0.16 ± 0.6	-0.18 ± 0.49

Values are given as averages and standard deviations. Number of subjects was six. For abbreviations, see Table 1.

nism of vertical divergence by the CNS, it will be necessary to record binocular three-dimensional eye movements during torsional vestibular stimulation in patients or animals with specific lesions. If for instance, the cerebellar flocculus would be the main structure that adaptively suppresses the dynamic vertical divergence during head roll, we expect that patients with floccular lesions (e.g., cerebellar atrophy) would show an increase in the velocity of the vertical divergence during the torsional position step. It is known that cerebellar disease often leads to an eye-position-dependent, vertical ocular misalignment (Versino et al. 1996). It would be of no surprise if in these patients large vertical divergence movements during vestibular stimulation could be observed. So far we only know that specific cerebellar lesions including the nodulus and uvula may cause a static vertical divergence in the context of an ocular tilt reaction (Mossman and Halmagyi 1997).

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