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Effect of gaze on postural responses to neck proprioceptive and vestibular stimulation in humans

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1. We studied the effect of gaze orientation on postural responses evoked by vibration of neck dorsal muscles or by galvanic stimulation of the vestibular system during quiet standing in healthy humans. Various gaze orientations were obtained by different combinations of horizontal head-on-feet (−90, −45, 0, 45, 90 deg) and eye-in-orbit (−30, 0, 30 deg) positions. The instantaneous centre of foot pressure was recorded with a force platform.
2. With a symmetrical position of the vibrator relative to the spine, neck muscle vibration elicited a body sway in the direction of the head naso–occipital axis when the eyes were aligned with it. The same result was obtained both during head rotations and when the head and trunk were rotated together.
3. For lateral eye deviations, the direction of the body sway was aligned with gaze orientation. The effect of gaze was present both with eyes open and eyes closed. After long-lasting (1 min) lateral fixation of the target the effect of gaze decreased significantly.
4. Postural responses to galvanic vestibular stimulation tended to occur orthogonal to the head naso–occipital axis (towards the anodal ear) but in eight of the 11 subjects the responses were also biased by the direction of gaze.
5. The prominent effect of gaze in reorienting automatic postural reactions indicates that both neck proprioceptive and vestibular stimuli are processed in the context of visual control of posture. The results point out the importance of a viewer-centred frame of reference for processing multisensory information.

One of the most important problems the brain has to solve for governing the interaction between the personal and extrapersonal space is the formation of the appropriate reference frame for sensory–motor transformations (Berthoz, 1991; Andersen *et al.* 1997; Lacquaniti, 1997; Mergner *et al.* 1997). For equilibrium control, visual, vestibular and proprioceptive signals are the major sources of information. However, the co-ordinate systems in which these signals are collected are different. Visual motion stimuli are primarily processed in the eye-centred frame of reference, the vestibular signals are directly linked to head orientation in space, neck proprioception indicates only head motion relative to the trunk, and limb proprioception is collected in arm or leg-referenced co-ordinates. Thus, multisensory interaction for equilibrium control may not result from a simple convergence of raw sensory inputs of different modalities but may imply appropriate co-ordinate transformations.

Muscle proprioception brings information about the position of one body segment relative to another. It is possible to study the role of proprioception for posture control by applying vibrations (which activate predominantly Ia afferents of muscle spindles; Bianconi & van der Meulen, 1963; Burke *et al.* 1976; Roll & Vedel, 1982) to specific muscles (Eklund, 1972; Lackner & Levine, 1979; Roll *et al.* 1989, 1998; Quoniam *et al.* 1990; Gurfinkel *et al.* 1995; Hlavacka *et al.* 1995; Ivanenko *et al.* 1999). When applied to a standing human subject with the head, trunk and eyes in a primary position (straight ahead), neck muscle vibration causes forward body lean (Gregoric *et al.* 1978). Rotation of the head to the shoulder redirects the sway so that it becomes more lateral: stimulation of either the left or the right side of the neck, with the head turned to the left, induces a left lateral component of body sway, and with the head turned to the right induces right lateral sway (Smetanin *et al.* 1993). The direction of this response and its dependence on head orientation, the increase in the response on unstable supports (Ivanenko *et al.* 1999), the asymmetry in the response shown in unilateral labyrinthine-defective patients (Popov *et al.* 1996) and the absence of the response in bilateral labyrinthine-defective patients (Lekhel *et al.* 1997) led to the hypothesis that the sway is an involuntary response due to a central interpretation of neck afferent and vestibular signals of head motion. According to this hypothesis, neck vibration would mimic muscle lengthening: in the absence of a change in vestibular input the head may be interpreted as stable in space and the trunk as tilted backwards with respect to the support surface, therefore postural reactions may occur in the forward direction (see Lekhel *et al.* 1997).

For vestibular signals, the head orientation relative to the trunk must be taken into account in order to control human posture. Indeed, a high degree of convergence between vestibular (otolith and canal) and neck inputs has been found in the lateral and inferior vestibular nuclei (see Wilson, 1991). However, vestibular–neck interaction is only one step of the co-ordinate transformations that link the head to the support surface. It has been shown that an externally applied galvanic current to the mastoids can depolarize the vestibular nerve and increase firing frequency of vestibular afferents on the side of the cathode and decrease it on the side of the anode (Goldberg *et al.* 1982). The application of galvanic stimuli to the human mastoids results in body sway towards the anodal side (Baldenweck, 1927). This artificial vestibular stimulation has revealed some general properties of the postural control system. For instance, Nashner & Wolfson (1974) demonstrated that the head-on-trunk position modulates considerably the direction of postural reactions. Later studies emphasized that the direction of body sway in response to labyrinth stimulation depends on the head orientation relative to the feet, not relative to the trunk (Lund & Broberg, 1983).

For visual stimuli, an ability to transform information from the retinotopic reference frame into a stable body- and space-related co-ordinate system during eye, head and body movements is required in order to interpret correctly self-motion and to achieve perceptual stability of the extrapersonal space (Crowell *et al.* 1998). In response to linear or angular movement of the visual surroundings, human subjects sway in the same direction as that of the visual stimuli, whatever the position of the eyes in space. Thus, the direction of visually induced body sway is reoriented according to eye-on-feet orientation (Wolsley *et al.* 1996). Furthermore, extraocular proprioception plays an important part in the organization of whole-body posture and in inter-relating the body with the extrapersonal space: vibration of eye muscles can elicit prominent body sway in a direction that depends on the stimulated muscle (Roll *et al.* 1989).

In the context of a multisensory control of balance, we tested whether gaze orientation might modulate automatic postural responses to stimuli that are not directly related to the visual modality. For this purpose we applied vibratory stimuli to neck muscles as well as galvanic stimulation to the vestibular system of subjects standing in upright posture in various combinations of eye-in-orbit and head-on-feet positions. We found a systematic effect of gaze on the direction of postural responses and argue that a viewer-centred frame of reference is used to process multisensory information for the descending control of posture.

METHODS

Experimental set-up

Thirteen normal subjects (6 males, 7 females, aged 20–39 years) participated in the study. None of the subjects had any history of neurological disease or vestibular impairment. Informed consent was obtained after the experimental procedure had been explained, according to the protocol of the Ethics Committee of the Santa Lucia Institute. Subjects stood on a force platform (Kistler 9281B; Kistler Instruments Ltd, UK) which we used to measure the displacement of the centre of pressure (CP) in the sagittal and frontal directions. In the standard protocol, the room lights were switched off and the subjects wore goggles with dark lenses, allowing them to fixate a red light spot, but preventing them from viewing the room background. Because it is known that during neck vibration subjects are conscious about their body sway (Lekhel *et al.* 1997) and may interfere voluntarily with the automatic response, they were given the instruction to stand relaxed without resisting the applied perturbation. Orientation of the head, shoulders and waist was monitored by a three-dimensional Optotrak (Northern Digital, Waterloo, Ontario, Canada) system. Eight infrared-emitting markers were placed on the subject's head, shoulders and pelvis as shown in Fig. 1*A*.

Parameters of vibration

Stimulation of neck muscle proprioceptors (~0·8 mm, 50 Hz sinusoid) was carried out by means of an electromechanical vibrator (DC motor, Graupner Speed 300, Kirchheim, Germany, equipped with eccentric rotating masses), 6·2 cm long and 3·0 cm in diameter. The vibrator was fixed to the back of the neck (trapezius and splenius tendons, at the level between the 5th and 7th vertebrae) by means of an elastic shoulder girdle. Care was taken to place the vibrator in a symmetrical position with respect to the spine in all tested orientations of the head (Fig. 1*B*). In fact, if vibration is applied asymmetrically it may induce lateral displacements even when the head and eyes are in the primary (straight ahead) direction (Smetanin *et al.* 1993). In two subjects we tested different frequencies (in the range 40–100 Hz) and amplitudes (0·5 and 0·8 mm) of neck muscle vibration in order to verify whether the direction of the postural response could depend on the stimulus parameters. In four subjects we compared the effect of vibration obtained with two identical vibrators connected in parallel and placed separately on each side of the cervical spine with that induced by a single vibrator placed symmetrically relative to the neck mid-line. The comparison was performed for one head orientation (45 deg to the right) and three gaze positions (−30, 0, 30 deg).

Neck muscle vibration protocol

Seven subjects participated in the experiments with neck muscle vibration. The centres of the heels were placed on marks 12 cm apart and the feet were splayed out at approximately 30 deg. Before each trial the participant was asked to orient his/her head towards one of the following directions: straight ahead, 45 deg left, 45 deg right, 90 deg left, 90 deg right. Then he/she was instructed to keep his/her head still and to fixate a red light spot (diameter 0·25 deg of visual angle, at a distance of 2·3 m) placed at the sightline height either straight ahead, or 30 deg to the right or 30 deg to the left relative to the required head position. Thus, 15 different combinations of horizontal head-on-trunk (H) and eye-in-orbit (E) positions (5 H × 3 E) were recorded for each subject. Because 90 deg head rotations are at the end of the physiological range, subjects were allowed to accompany head motion with a small rotation of the shoulders relative to the feet (on average, this was measured to be to 12 ± 6 deg).

Two separate sessions were performed. In the first session, we recorded the spontaneous body sway during 20 s periods of quiet standing in each of the 15 positions. In the second session, we recorded the direction of the postural response evoked by neck muscle vibration. In this case the duration of each trial was always 30 s: after 5 s of quiet standing, muscle vibration was applied for a 15 s period.

In another experiment we asked the same subjects to rotate their trunks (T) by 45 deg to the left or to the right without changing head position relative to the shoulders. In this case different head-on-feet orientations were obtained by torso rotations and the vibrator was maintained in the same position as that before the rotation of the trunk.

In addition to the standard protocol involving fixation of the red spot in an otherwise darkened room, we also tested the effect of gaze on body sway both in full light and with eyes closed, with the head turned 45 deg to the right. Eye-in-orbit position was −30, 0 and 30 deg relative to the head in light. In the eyes-closed condition, we instructed the subjects to turn their heads and then to gaze towards the position of an imagined target located −30, 0 and 30 deg relative to the head. Horizontal eye movements were recorded by means of the electro-oculographic (EOG) technique (custom designed). Calibration was performed before and after each trial.

Data analysis

The signals were digitized at 50 Hz. A sway response vector was computed for each subject by connecting the mean CP position over the last 10 s interval of vibration with the pre-stimulus position (5 s interval before stimulation). Thus, the transient period following the stimulus onset, which usually lasted for a few seconds, was excluded. Statistical analysis (within-subjects ANOVA) was performed on the direction of sway response vector. $P < 0{\cdot}05$ was considered significant.

The two-dimensional distribution of the spontaneous CP oscillations during 20 s of quiet standing was quantified by means of orthogonal linear regression. Briefly, the $X-Y$ covariance matrix of the CP displacement across the subjects' pooled data in each experimental condition was factored by means of Singular Value Decomposition and scaled to 95 % tolerance ellipses (see McIntyre *et al.* 1997).

Galvanic stimulation of the vestibular system

In 11 subjects we studied the effect of gaze on the direction of body sway induced by galvanic stimulation of the vestibular system. Five of the subjects were drawn from the sample that participated in the experiments with neck muscle vibration. Electrodes with an area of 10 cm^2 were attached to the skin over the left and right mastoid bones and a square-wave current pulse (1 mA, 4 s duration) was delivered by means of a custom-designed constant current stimulator triggered by the computer. These parameters of stimulation were chosen as they gave rise to measurable and reproducible body sway but little or no cutaneous sensation. The cathode was applied to the right side. In this experiment, the subject's feet were placed close to each other to increase the effect of galvanic stimulation, which has been shown to depend on stance width (Day *et al.* 1997). The subjects were instructed to take different head-on-feet orientations (0 deg, 45 deg to the right and 45 deg to the left) and then different eye-in-orbit (−30, 0, 30 deg) positions by fixating the same red spot as in the protocol with neck muscle vibration. Trials were randomized.

Ten galvanic stimuli were delivered for each condition and the response CP displacements in the sagittal and frontal plane were averaged (similar to Lund & Broberg, 1983). The slope of the orthogonal linear regression of the mean $X-Y$ CP displacement (estimated as the first eigenvector of the $X-Y$ covariance matrix) from the start to the end of the stimulus characterized the direction of body sway response.

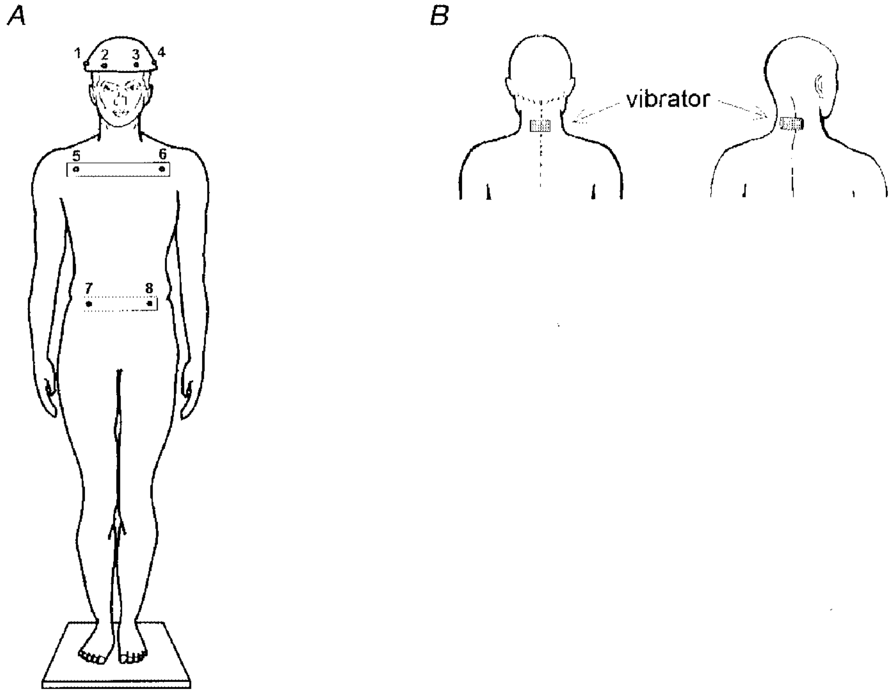

Figure 1. Experimental set-up

A, location of markers placed on the body to measure head, shoulder and pelvis orientation in the horizontal plane. *B*, location of a vibrator in different head-on-trunk orientations (0 and 45 deg).

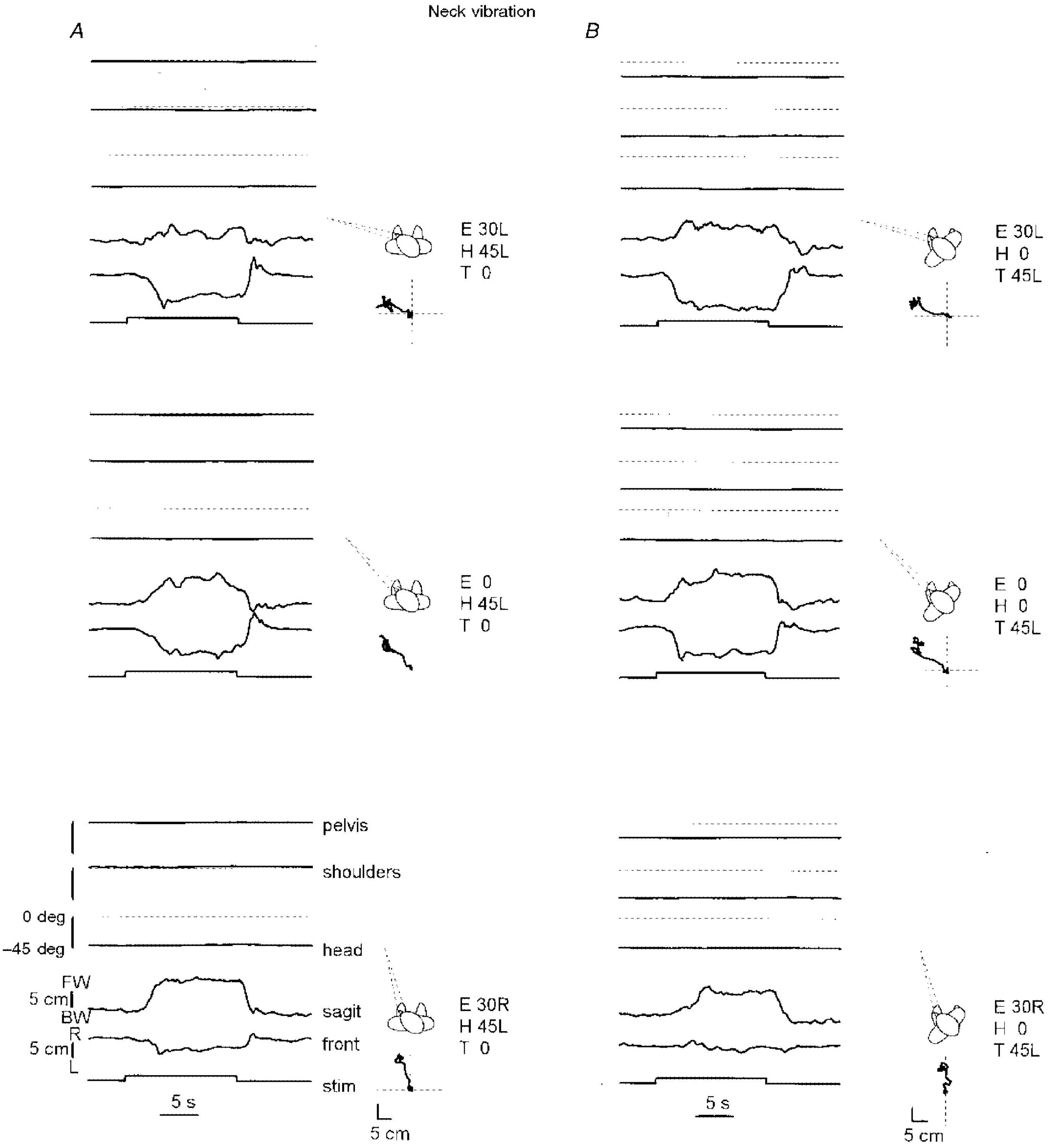

Figure 2. Samples of sagittal and frontal components of the sway response induced by vibration of the dorsal neck muscles with different eye-in-orbit (E), head-on-trunk (H) and trunk-on-feet (T) positions

In *A*, the head was turned 45 deg to the left; in *B*, the head and shoulders were turned together 45 deg to the left. In *A* and *B*, each test condition is indicated by a schematic drawing (top right in each panel). The bottom right diagrams in each panel represent X–Y plots of the CP displacement from the beginning of recording until the end of stimulation. Labels and calibrations in the bottom left panel in *A* also apply to all other panels. Abbreviations in this and other figures: sagit, sagittal; front, frontal; stim, stimulus; FW, forward; BW, backward; R, right; L, left; xR, x deg right; xL, x deg left; 0, 0 deg.

RESULTS

Body sway during neck muscle vibration

All subjects displayed a prominent body sway following neck muscle vibration. The mean amplitude of the CP displacement, regardless of the experimental condition, for a 50 Hz, 0·8 mm vibratory stimulus was 6·2 ± 1·9 mm (mean ± S.D.). Changing the frequency (40–100 Hz) and the amplitude (0·5 mm, 0·8 mm) of vibration did not appreciably modify the direction of body sway response in the two subjects tested.

Figure 2*A* shows traces from one representative subject with the head rotated 45 deg leftward and with different eye directions. Before each trial the subject turned his/her head 45 deg to the left and then he/she was asked to fixate the target. Sway response developed during several seconds after the beginning of vibration; afterwards the body oscillated around a new position of the CP. With a symmetrical (relative to the spine) position of the vibrator, the sway response was approximately in the direction of the head (45 deg to the left) when the subject fixated straight ahead (middle panel). When the eyes were deviated 30 deg to the left or to the right, the body sway was systematically biased in the direction of gaze. A similar sway was displayed when the trunk was rotated 45 deg to the left (Fig. 2*B*). The actual shoulder rotation was 42 ± 5 deg and the pelvis rotation 31 ± 7 deg (pooled across subjects and conditions). During neck vibration, head yaw orientation did not change significantly (mean absolute change, 2 ± 2 deg). Intraindividual variability of body sway direction (as examined in three subjects studied on three different days with head 45 deg to the right and 45 deg to the left with three eye-in-orbit positions) was 9 ± 4 deg.

Figure 3 illustrates the pooled results from all subjects. In every combination of eye and head deviation but the median, the mean postural reaction tended to be directed

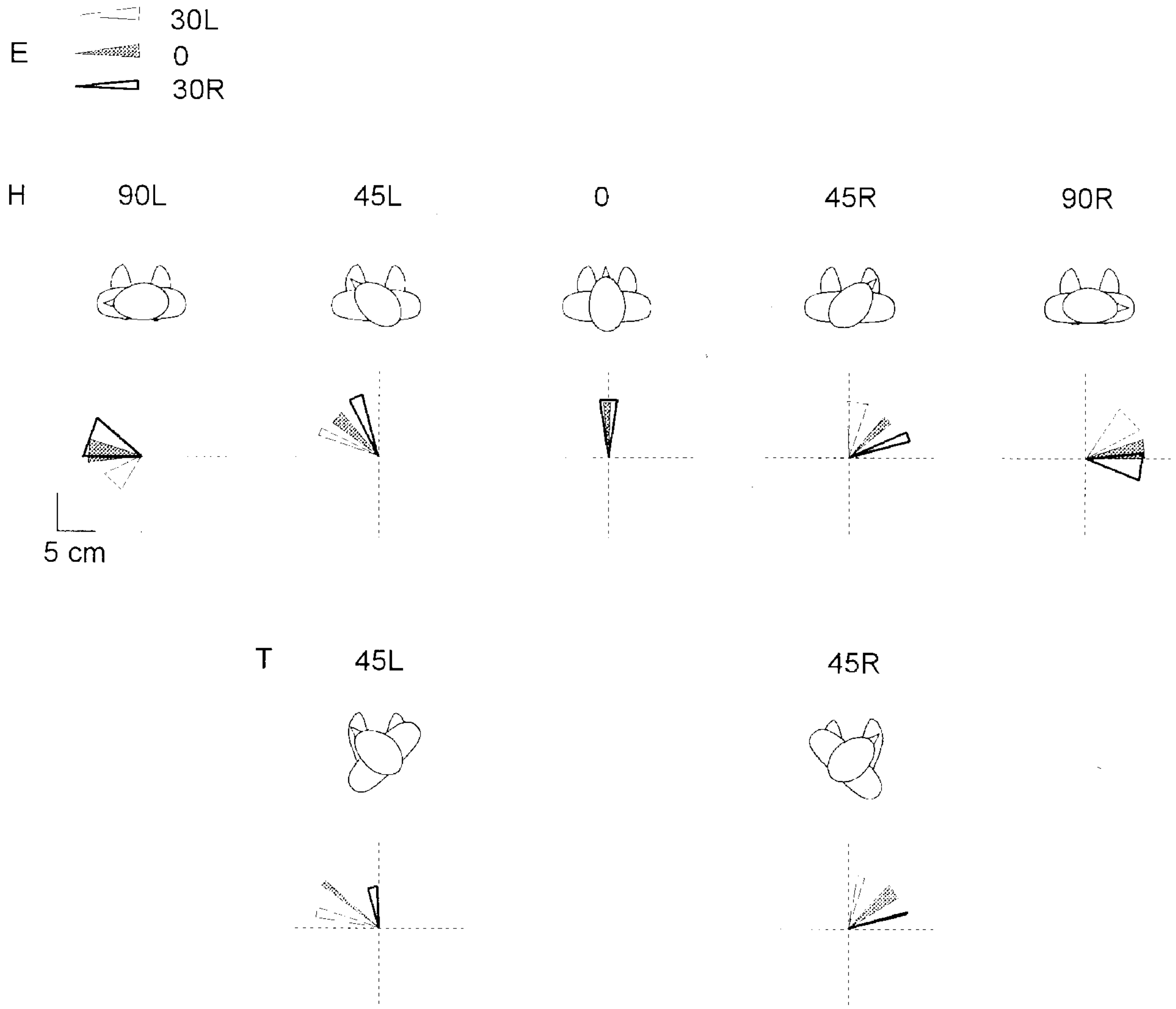

Figure 3. Vector representation of averaged postural responses to neck muscle vibration recorded with various head-on-feet and eye-in-orbit positions

Each head and shoulder orientation is indicated by a schematic drawing. Sectors represent ± S.D. values around the mean direction of sway response. Sector amplitude represents the mean amplitude of sway deviation.

towards the visual target, not towards the direction of the head or the trunk. The effects observed after 45 deg torso rotations (Fig. 3, bottom) were the same as those observed with the head rotated 45 deg to the left and 45 deg to the right. The effect of gaze was highly significant ($F_{2,12} = 14{\cdot}5$, $P < 0{\cdot}002$, ANOVA). The interaction between head and gaze orientation was significant because of the peculiarity of the mid-position ($F_{8,48} = 4{\cdot}4$, $P < 0{\cdot}001$). Trunk and head 45 deg deviations did not differ from one another ($F_{1,6} = 4{\cdot}1$, $P > 0{\cdot}22$). For all lateral head positions ($\mathrm{H} \neq 0$), the difference between gaze direction and the direction of body sway was 3 ± 18 deg.

Perceptual effects

With a symmetrical position of the vibrator relative to the spine, most subjects did not perceive an illusory lateral target displacement while fixating the small light spot in darkness during or after neck muscle vibration. Only one subject occasionally reported an illusory target motion during neck muscle vibration, although its direction was not consistent and typically he perceived an upward target displacement. On the other hand, subjects reported a direction of sway that qualitatively corresponded with the direction of the actual body sway. Thus, the vibration-induced postural response was not a correction for a distorted perception; instead, the perception was an accurate reflection of reality.

With bilateral neck vibration, none of the four tested subjects reported illusions of target motion and the effect of gaze on the body sway response was not significantly different from that observed using a single vibrator placed symmetrically relative to the cervical spine ($F_{1,3} = 0{\cdot}003$, $P > 0{\cdot}96$, 2-factor within-subjects ANOVA).

The influence of history of head position

The lack of gaze influence in the neutral head position ($\mathrm{H} = 0$) could be related either to an exceptional role of this middle head orientation (the most 'natural' body configuration) and/or to some pre-conditioning event related to how head-on-feet orientation was achieved. Indeed, all lateral head orientations studied were obtained by turning the head or the trunk away from the neutral position just before (10–20 s) the beginning of stimulation. To test these hypotheses, we asked the subjects to move their heads slowly from centre to right (about 50 deg), then to the left and then to the centre again (Fig. 4*A*). Then, he/she had to fixate the target (30 deg to the right or to the left). Ten seconds later, the stimulus induced body sway towards the direction of gaze with a prominent lateral component (Fig. 4*A*, left panel). Then the subject kept the head and trunk aligned with the feet while fixating the same target for 1 min before another stimulus was delivered. During this second stimulus, the CP was displaced along the antero-posterior direction with no lateral component (Fig. 4*A*, right panel). When all the participants were subjected to the same pre-history in the neutral head position they displayed a significant bias towards gaze deviation. The difference between gaze and body sway direction was -6 ± 7 deg for rightward and 5 ± 8 deg for leftward eye deviations with prior head motion, whereas it was -25 ± 9 deg for rightward and 23 ± 11 deg for leftward eye deviations without prior head motion.

This effect of history could also be seen when the head was rotated away from the neutral position, indicating that the previous finding was not specific to the neutral head orientation. The left panel of Fig. 4*B* shows that the vibration-induced body sway tended to be in the direction of gaze several seconds after the head had been turned 45 deg to the left but it was rotated towards head orientation after 1 min of lateral target fixation.

This dependence of sway response on the time elapsed from the change in head orientation was observed in six of the seven subjects and was not simply related to the history of head position with respect to the trunk since it was also observed when the trunk and head were rotated together. In one subject, however, a prominent effect of gaze was present even after 1 min of lateral target fixation following a change of head orientation, as well as when the head was in the neutral position.

Body sway during neck muscle vibration in full light and with eyes closed

In full light, the effect of gaze on the body sway response was not significantly different ($F_{1,6} = 4{\cdot}6$, $P > 0{\cdot}07$, 2-factor within-subjects ANOVA) from that observed in darkness, as tested with the head turned 45 deg to the right and the eyes turned −30, 0 and 30 deg relative to the head. Again, the direction of body sway tended to align with gaze direction.

With eyes closed, all subjects displayed a prominent influence of gaze direction on the vibration-induced body sway response. Figure 5 shows a sample case. The subject gazed at an imaginary target. For lateral fixations this resulted in gaze orientations greater than 30 deg (40 and 45 deg for left and right eye deviation, respectively, at the stimulus onset) that slowly decayed with time. The sway response was prominently biased in the direction of gaze orientation.

Spontaneous body oscillations in normal posture

We wondered whether a bias towards gaze direction could be observed also in the spontaneous body oscillations during static normal posture. Figure 6 shows that, unlike those induced by neck vibration, the spontaneous sways of the CP during quiet standing did not display any prominent and consistent dependence upon the direction of eye deviations. The amplitude of these oscillations was much smaller than the amplitude of stimulus-induced CP displacements. The 95% tolerance ellipses did not show any systematic bias towards the direction of either head or gaze.

For all head and gaze orientations studied, the mean ratio between the two ellipse axes was $1{\cdot}72 \pm 0{\cdot}38$. The mean orientation of the ellipse long axis (relative to the trunk antero-posterior axis) was 1 ± 13 deg, indicating that oscillations in the sagittal plane were larger than those in the frontal plane. The average ellipse area in the head neutral position (H = 0) was 1·0 cm^2 whereas in lateral head positions (H $\neq$ 0) it was 1·6 cm^2, indicating slightly reduced stability in lateral head orientations ($F_{4,8} = 5\cdot2$, $P > 0\cdot024$, Fig. 6). There was no effect of gaze on the ellipse area ($F_{2,8} = 0\cdot58$, $P > 0\cdot58$).

Galvanic stimulation of the vestibular system

We tested whether the effect of gaze was confined to the response to somatosensory neck inputs or whether it could also be revealed in postural reactions to vestibular stimuli.

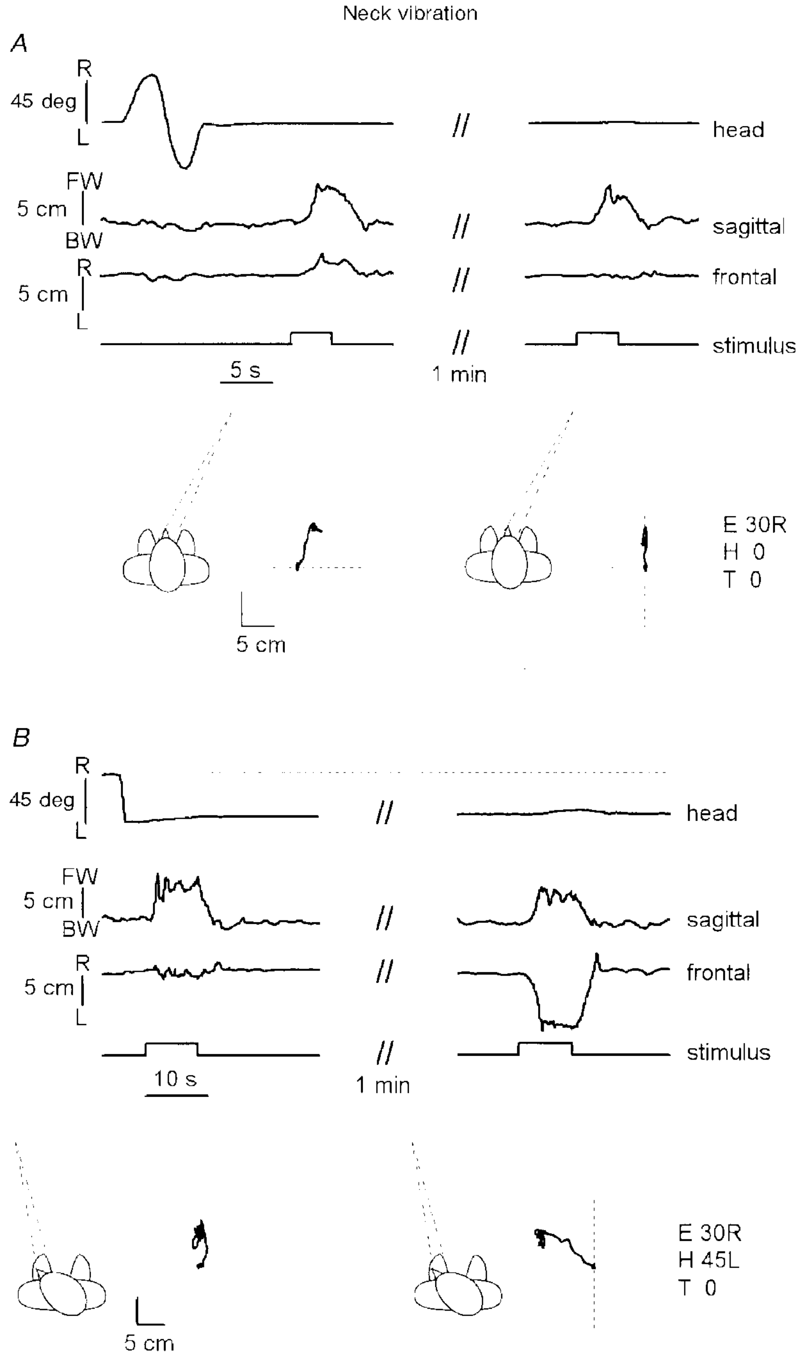

Figure 4. Effect of history of head position and target fixation

A, sway response to 4 s neck vibration in the neutral head position while the subject fixated a target located 30 deg to the right with the head and feet aligned with each other. Several seconds after head right–left rotation, the subject tended to sway in the direction of gaze. After 1 min of continuous target fixation the body swayed in the direction of the head. *B*, sway response to 8 s neck vibration just after the head was turned 45 deg to the left and gaze 30 deg to the right and after 1 min of target fixation. In *A* and *B*, the bottom right diagrams in each panel represent *X*–*Y* plots of the CP displacement from the beginning to the end of the stimulus.

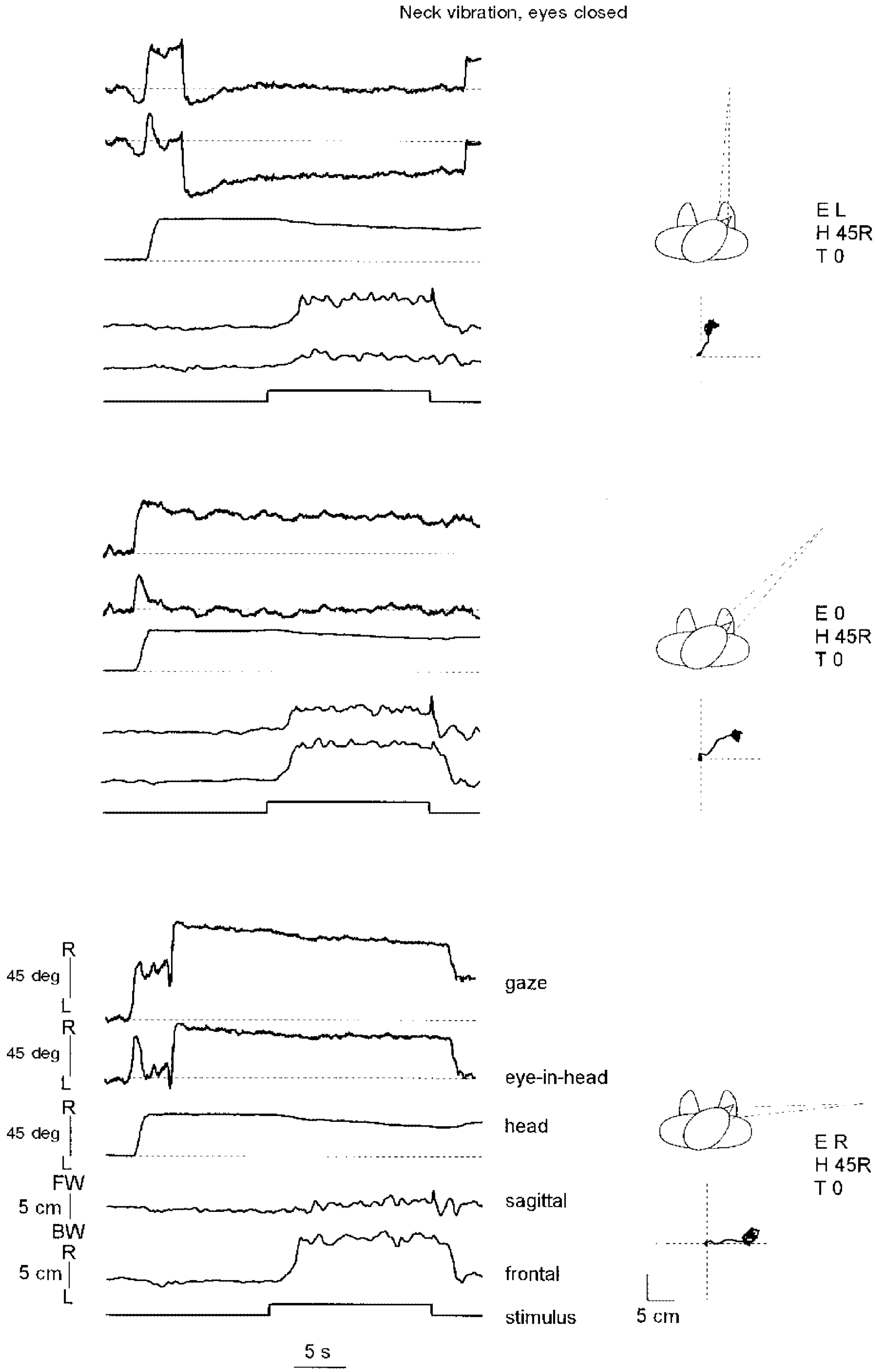

Figure 5. For legend see facing page.

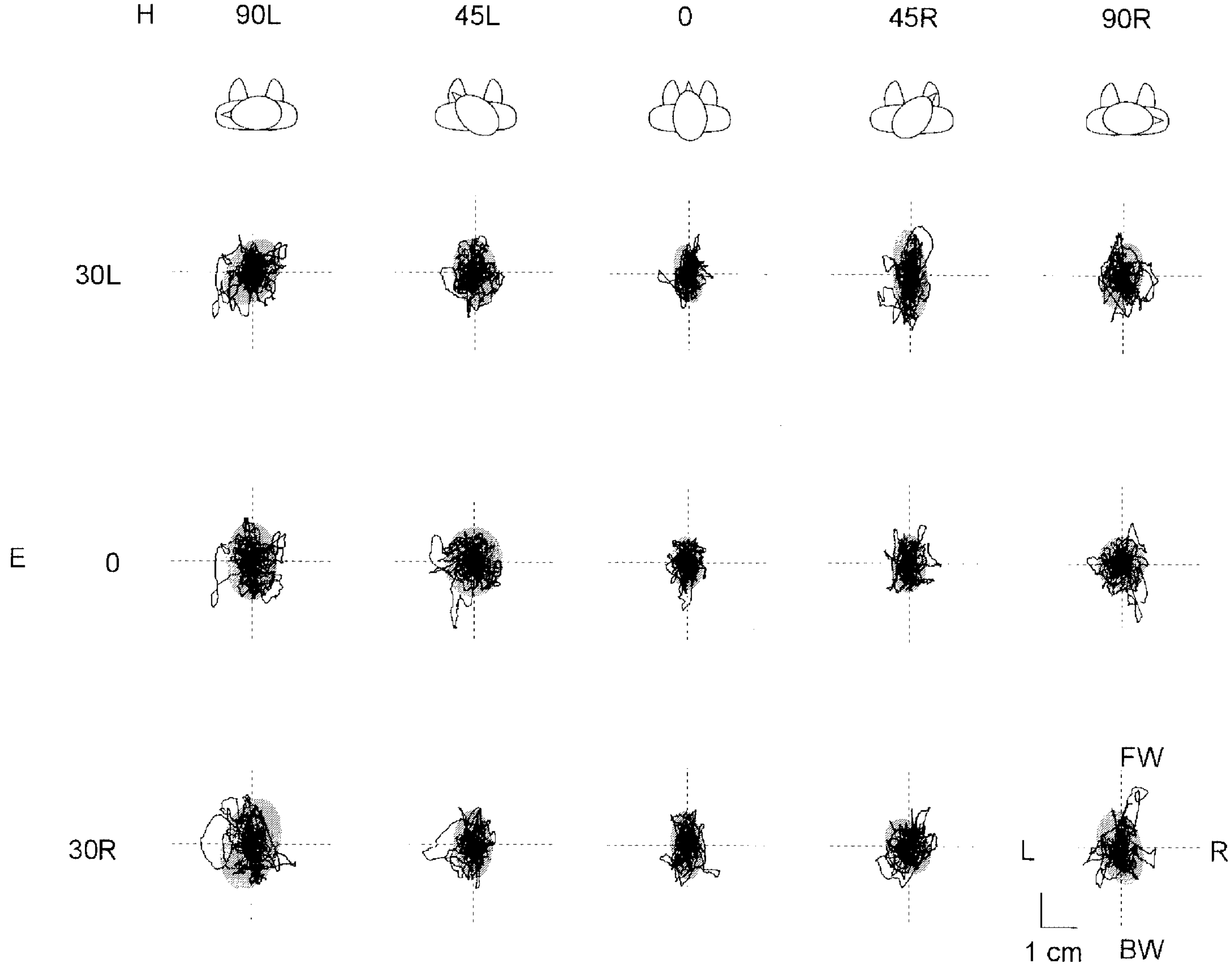

Figure 6. Two-dimensional spontaneous oscillations of the CP around the mean position during 20 s in all 15 combinations of head-on-feet and eye-in-orbit orientations

Each trace represents the pooled CP displacement data for all subjects. The shaded areas superimposed on the CP traces represent the 95% tolerance ellipses of CP displacements.

For this purpose the direction of the body sway induced by galvanic stimulation of the vestibular system was studied in 11 subjects with different eye-in-orbit and head-on-feet orientations. On average, the body tilted towards the anode, that is to the left relative to the head (−85 ± 17 deg for all head-on-feet orientations, pooling all gaze responses together). However, the body sway response could be biased towards the direction of gaze. In the three conditions shown in Fig. 7 (head 45 deg to the right, eyes 30 deg left, 0 deg and 30 deg right) the body sway traces were rotated towards the sightline and tended to be orthogonal to it (Fig. 7). The inter-trial variability in the CP displacement responses is shown by the s.d. bands (dashed lines in Fig. 7).

Table 1 shows the mean difference in the direction of body sway between two conditions: when fixating targets 30 deg to the left and 30 deg to the right of the head (data from all head orientations, −45, 0, 45 deg, were pooled together). For five of the 11 subjects, sway responses for left and right eye positions differed by almost 60 deg, that is the nominal angle between the two eye positions. In three other subjects

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Figure 5. Effect of gaze direction on the body sway response to a 15 s neck vibration with eyes closed

The subject was asked to move his/her head, with eyes closed, 45 deg to the right, and the eyes towards an imagined target located −30, 0 and 30 deg relative to the head. The gaze signal was obtained by summing together eye-in-head (EOG) and head-in-space signals. The bottom right diagrams in each panel represent X–Y plots of the CP displacement during the 20 s period (covering the stimulus and a 5 s period before stimulation). Labels and calibrations given in the bottom panel also apply to the top and middle panels.

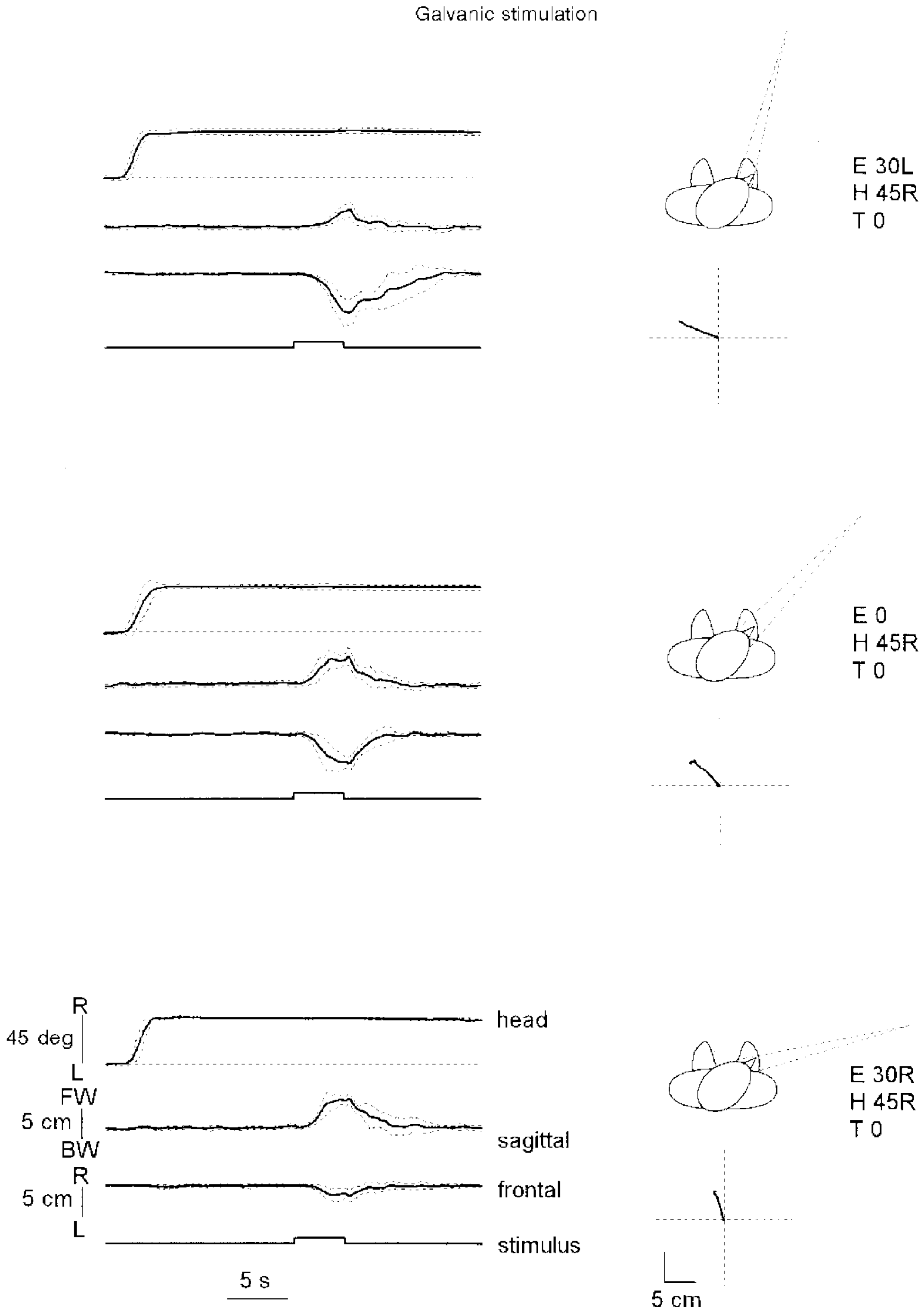

Figure 7. Sway response induced by a 4 s galvanic stimulation while fixating on a target located 30 deg to the right

Results shown are the mean of 10 trials for each gaze direction from one subject. Dashed lines represent ± 1 S.D. Just before target fixation, the subject was asked to turn his/her head 45 deg to the right from the normal middle position. The bottom right diagrams in each panel represent X–Y plots of the CP displacement during the 8 s period (covering the stimulus and a 4 s period before stimulation). Labels and calibrations given in the bottom panel also apply to the top and middle panels.

the difference was statistically significant but lower than 30 deg. For the remaining three subjects there was no statistically significant effect of gaze. The mean gaze-induced difference in body sway response was 32 ± 23 deg.

DISCUSSION

Viewer-centred frame of reference

Our results confirmed the previous findings that: (i) in neutral head, trunk and eye orientation, neck muscle vibration evokes forward body sway while galvanic vestibular stimulation elicits lateral body sway towards the anodal side, and (ii) head rotation reorients postural responses according to the head-on-feet position. However, the direction of postural reactions to stimulation of both neck proprioceptive and vestibular afferents was systematically biased by the direction of gaze. This effect was observed in all head-on-feet orientations after the head had been actively moved to those positions (Figs 2–5 and 7). When the head and trunk were turned together, the effect of gaze was unchanged with respect to simple head rotation (Figs 2 and 3). Therefore, the results suggest that during and after head rotations, neck proprioceptive and vestibular signals for posture control are processed in a viewer-centred reference frame.

Target fixation in darkness was not crucial. Similar directional gaze-dependent body sways in response to neck muscle vibration were observed with eyes closed (Fig. 5) or even with eyes open when the subject was asked to turn his/her head and to look laterally either to the left or to the right.

The mechanisms explaining the postural reaction to the two types of stimuli used in this study are the following. (a) Neck vibration is believed to be interpreted as a backward body tilt with respect to the vertical (see Lekhel *et al.* 1997). Proprioception signals muscle lengthening, hence, head-on-trunk flexion. However, because the vestibular input is constant, the head might be interpreted as stationary and the trunk tilted backwards with respect to the support surface, therefore the postural reaction occurs in the forward direction. It is considered unlikely that body sway results from a simple cervico-spinal response (Magnus, 1924) since: (i) the subjects showed the same body sway direction when head and trunk were turned together (Figs 2*B* and 3), and (ii) it was shown that the direction of body sway is coherent with illusory or hypnotically suggested head orientations rather than with the actual head orientations (Gurfinkel *et al.* 1989, 1992; Smetanin *et al.* 1993). (b) Galvanic stimulation of the vestibular system is normally interpreted as a lateral tilt of the body relative to gravity as sensed by the labyrinthine organs (Popov *et al.* 1986; Fitzpatrick *et al.* 1994; Hlavacka *et al.* 1995; Day *et al.* 1997). The subjects react to the perturbation by tilting the body laterally towards the opposite side.

Table 1. The effect of gaze on the direction of body sway during galvanic stimulation of the vestibular system in different subjects

Subject	$\Delta\alpha$ (deg)
1	59
2	56
3	56
4	54
5	46
6	27
7	20
8	17
9	8
10	7
11	−1
Mean	32
S.D.	23

Data from all head orientations (−45, 0, 45 deg) were pooled together. $\Delta\alpha$, the difference in the direction of body sway between two conditions: when fixating targets 30 deg to the left and 30 deg to the right.

Previous studies on the interactions between posture and vision have usually focused on the role of retinal factors in the dynamic control of whole-body posture. Few have dealt with the relationship between postural control and gaze control and the associated proprioceptive feedback from extraocular muscles (Roll *et al.* 1989; Wolsley *et al.* 1996). It has been shown that the signals from eye-in-orbit and head-on-trunk position as provided by proprioception and efference copies of the motor commands can reorient visually evoked postural responses (Wolsley *et al.* 1996). This finding makes logical sense if one takes into account that eye-on-feet position is finally important for the visual control of balance. Interestingly, vibration of eye muscles *per se*, without any additional vestibular or somatosensory stimulation, can elicit a prominent change in whole-body orientation relative to the vertical. Thus vibration, applied to the medial and lateral rectus of a subject's eye, has been found to induce lateral body sway, while vibration applied to the superior or inferior rectus evoked forward or backward whole-body displacement (Roll *et al.* 1989). Thus, extraocular proprioception may, like other proprioceptive inputs from the neck or postural muscles, play an important part in the organization of whole-body posture and in inter-relating body space with extrapersonal space.

The effect of gaze observed in the present study is striking because neither neck vibration nor galvanic vestibular stimulation belong to the visual modality and should theoretically elicit reactions coherent to head-on-trunk or head-on-feet orientation. One can hypothesize that postural reactions are aimed at stabilizing the visual input. Reactions to neck vibratory stimuli occurred in the direction of gaze, reducing retinal slip. Responses to galvanic stimulation were also linked to gaze direction in such a way that retinal slip was maintained invariant of gaze orientation. Yet, the retinal input does not seem to play a major role in determining sway responses; indeed, the effect of gaze was also observed with eyes closed (Fig. 5). Alternatively, the results may arise from eye proprioception or the efferent control of gaze, and changes in gaze orientation may directly affect, via the descending pathways, the excitability of networks controlling the tonic activity of postural muscles. The observed dominance of gaze can be related to the problem of multisensory integration which implies a fusion of different inputs and the formation of a common reference frame for the internal representation of body posture and external perturbations (Mittelstaedt, 1983; Droulez & Darlot, 1989; Gurfinkel *et al.* 1989; Lacquaniti, 1997; Ivanenko & Grasso, 1997; Grasso *et al.* 1998).

On the other hand, the results showed that gaze orientation *per se* has no systematic effect on the direction of spontaneous body oscillations during normal standing (Fig. 5). This result seems to be consistent with a previous finding that the stability of standing posture is not significantly influenced by static head turns or tilts (Paludetti *et al.* 1989). Spontaneous deviations of the CP from the reference point characterize the steady state of standing posture and result from a mixture of mechanical and neural factors (Gurfinkel *et al.* 1965; Collins & de Luca, 1993).

Lability of gaze effect

The gaze-dependent bias of automatic sway responses to neck muscle vibration was labile. It was influenced by the time elapsed from a change of head in space orientation (Fig. 4). Physical properties of muscle spindles (lying in neck or trunk muscles) such as their thixotropy (Proske *et al.* 1993) may be responsible for a progressive change in the sensitivity to mechanical stimuli and may thus account for the effect of history. However, (a) unlike the direction of sway response, the amplitude did not change after long-lasting eye deviation, (b) the effect was observed also when trunk and head were rotated together, and (c) the effect of gaze could not be modulated by changing either the frequency or the amplitude of the vibration. More likely, these observations suggest that the effect of history may be due to some central mechanisms (for instance, a leakage in the firing rate of gaze-related brainstem neurones when eyes are maintained at a fixed eccentricity; see Berthoz, 1988). Cognitive factors such as attention, internal representation or the extent of visual dependence can determine or modulate the influence of gaze on body sway responses. Central processing might also account for the amount of inter-individual variability especially for the response to galvanic stimulation (Table 1). Whatever the physiological meaning of lability may be, it must be stressed that the effect of gaze observed in our standard conditions is systematic and reproducible and should thus reflect some inherent properties of multisensory interactions for the control of posture.

Illusory visual and postural effects

It is known that vibration of neck muscles can induce a visual illusion of displacement of a small visual target viewed in the dark (Biguer *et al.* 1988; Roll *et al.* 1989; Smetanin *et al.* 1993) or of head rotation (Karnath *et al.* 1994). Pointing movements towards the target are similarly affected, confirming that the representation of directions in visual space is modified by neck vibration. In our case, subjects did not perceive an illusory lateral target displacement while fixating the small light spot in darkness during or after neck muscle vibration. The absence of illusory lateral target displacement could be due to the symmetrical position of the vibrator relative to the spine. On the other hand, subjects tended to be aware of the actual direction of sway. Their reports confirmed previous findings that proprioceptive information along the whole body dominates the perceptual effect of body sway (Lackner & Levine, 1979; Fitzpatrick *et al.* 1994).

Nevertheless, it is worth stressing that the illusions of a whole-body inclination evoked by vibration of various muscles, as opposed to the illusions of a local joint rotation in a sitting posture, might be evoked in standing position when the actual body movement is prevented (Lackner & Levine, 1979; Smetanin *et al.* 1993). In this condition, the direction of the illusory whole-body tilt is typically opposite to that of the actual body sway, as has been shown for both muscle proprioceptive (Lackner & Levine, 1979) and labyrinth (Fitzpatrick *et al.* 1994) stimulation. It is therefore possible that the reaction to head-related sensory perturbation represents a whole-body postural adjustment due to an altered internal representation of body orientation.

Neurophysiological substrates

The gaze signals have a powerful control of the vestibulo-ocular, vestibulospinal and reticulospinal systems (see Berthoz, 1988, for a review). Many neurones of those systems show a tonic or phasic eye-position-related activity and also receive cortical inputs. The visual receptive fields of neurones in different cortical regions are modulated by the position of the eye in the orbit, for instance, in V1, V3a, PO, MT, MST, 7a, LIP, PMv and dorsolateral prefrontal cortex (see Andersen *et al.* 1997; Lacquaniti, 1997; for reviews). On the other hand, the direction of gaze, i.e. the position of the eyes in space, is coded on the basis of proprioceptive signals originating from all the body segments involved in a given configuration. Indeed, multimodal signal processing, including neck somatosensory, visual and vestibular signals, is a characteristic of vestibular responses recorded in single cells of the brainstem vestibular nuclear complex, in vestibular structures of the cerebellum, the thalamus and cerebral cortex. Furthermore, neuronal activity of some of these neurones in the dark could also be modified by rotation of the hip region, although no systematic quantitative studies on the importance of this somatosensory input were performed (Grüsser *et al.* 1992).

The fact that many neuronal centres are involved in the complex mixture of automatic and programmed motor organization led to the idea that posture can no longer be considered simply as the summation of static reflexes (Massion, 1992; Lacquaniti, 1992; Horak & Macpherson, 1996). It has been shown recently that galvanic vestibular stimulation activates numerous cortical regions in humans (Lobel *et al.* 1998). An intriguing issue in posture control might be the participation of cortical areas which are known to perform global co-ordinate transformations linking the body to the extrapersonal space (Andersen *et al.* 1997; Rolls *et al.* 1997); however, the role of the cerebral cortex in postural mechanisms is still uncertain.

As a general conclusion, the findings highlight the importance of a viewer-centred reference frame for interpreting neck proprioceptive and vestibular (as well as visual) signals. Despite the artificial nature of neck proprioceptive and vestibular stimuli used in the present experiments these results may reveal the nature of multisensory interaction and provide further information about the internal representation for body posture. Finally, the time history of the gaze effect points to the inherently dynamic nature of reference frames for the control of human posture.

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