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The interactive contribution of neck muscle proprioception and vestibular stimulation to subjective "straight ahead" orientation in man

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Abstract Seventeen normal subjects were asked to direct a laser point to the position they felt to lie exactly straight ahead of their body. Subjects were seated in complete darkness in an approximately spherical cabin in an upright position with the orientation of the trunk and head aligned. For both the horizontal and vertical plane, "straight ahead" judgements were closely scattered around the objective straight ahead body position. Posterior neck muscle vibration as well as caloric vestibular stimulation with ice water led to (1) an apparent motion and horizontal displacement of a stationary visual target to the side opposite to stimulation and (2) a horizontal deviation of subjective "straight ahead" perception toward the side of stimulation. Only those subjects who experienced an illusion of target motion also showed a deviation of their subjective body orientation. No systematic effect of a displacement of subjective body orientation in the vertical plane was detected. When vestibular stimulation and neck muscle vibration were combined their effects were additive, i.e. the horizontal deviation of subjective body orientation observed when either type of stimulation was applied in isolation, was linearly combined either by summation or by cancellation. The present results clearly support the assumption that afferent visual, vestibular and proprioceptive input converge to the neural generation of an egocentric, body-centred coordinate system that allows us to determine our body position with respect to visual space.

Key words Neck muscle vibration · Caloric vestibular stimulation · Subjective "straight ahead" perception Proprioceptive-vestibular interaction · Human

Introduction

For accurate motor behaviour, e.g. grasping or fixating a target, the correct perception of the target's spatial location relative to the body is essential. In recent years, strong evidence has been found that for this purpose our brain uses abstract, neural representations of space interposed between sensory input and motor output (for review see Andersen et al. 1993). These representations seem to be organized in non-retinal, egocentric coordinates. The perception of "straight ahead" body orientation appears to be closely connected with the neural generation of the reference frames that underlie the subject's mental representation of space (Ventre et al. 1984; Biguer et al. 1988; Karnath et al. 1991, 1993).

To locate the direction of gaze in space and to relate this information to the orientation of the body, i.e. to obtain body-centred coordinates of a visual target, the input from the retina has to be combined with eye-position signals as well as head-position information. Therefore, it can be expected that the perception of "straight ahead" is influenced by different external information sources.

One source is visual information. With optokinetic stimulation, for example, by rotating the visual environment in an optokinetic drum, normal subjects displace the subjective "straight ahead" toward the drum motion without being aware of it (Brecher et al. 1972). With the drum stationary, the subjective "straight ahead" judgements were close to the objective straight ahead body orientation.

A second source is vestibular information. Passive rotatory acceleration of the body about its vertical axis has been found to displace the apparent "straight ahead" in a direction opposite to that of body acceleration (Fischer and Kornmüller 1931; Morant 1959). Together with the subjective displacement of the "straight ahead" position goes the impression that a stationary light appears to move in the direction of the acceleration ("oculogyral illusion", Graybiel and Hupp 1946). Similar effects of vestibular influence on visual "straight

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ahead" have been described for caloric stimulation of one labyrinth (Hamann et al. 1992). With caloric stimulation the deviation was always toward the relatively colder ear, corresponding to the direction of the slow phase of the nystagmus.

A third source is proprioceptive information. Lackner and Levine (1979) and Biguer et al. (1988) have reported on the influence of proprioceptive signals from neck muscles in computing egocentric coordinates of visual space. Biguer et al. (1988) investigated normal subjects sitting with head and body oriented straight ahead toward a central stationary visual target. The target was presented with no visual background in a dark room. During vibration of the left posterior neck muscles subjects reported an apparent motion and displacement of the stationary visual target toward the right. When requested to point to the target, subjects showed a consistent error in pointing, and this error was in the same direction as the illusory displacement. Moreover, when subjects were asked to move the target until they perceived it as lying in their subjective midline, the target was usually located left of the physical midline.

Taylor and McCloskey (1991) replicated the observations of Biguer et al. (1988). In addition, they showed that vibration of left posterior neck muscles can alter the perceived position of the head in normal subjects. This kinaesthetic illusion was in the same direction as the visual illusion of target movement, but of smaller magnitude.

The findings reported so far indicate that visual, vestibular and neck proprioceptive input contribute to the neural generation of the reference frames that underlie the subject's mental representation of space in egocentric coordinates. Accordingly, one should expect interactive effects of the different input channels. Evidence for visual-vestibular interaction on the spatial orientation in man has been reviewed by Dichgans and Brandt (1978). The aim of the present study was to investigate another possible interaction, namely that of neck muscle proprioception and vestibular input on the subjective "straight ahead" orientation in human subjects.

Materials and methods

Subjects

Seventeen normal subjects (seven female, ten male), aged from 25 to 69 years (median 31 years) were examined. All subjects gave informed consent to participate in this study. None of the subjects had a history of vestibular or oculomotor abnormalities.

Apparatus and procedure

Subjects were seated in an opaque, light-bulb-shaped cabin with the head in the centre of the upper spherical part of the bulb (diameter 190 cm) in complete darkness with the exception of a dim laser spot. Subjects sat upright in a chair that provided adjustable support for their backs. In addition, the experimenter stabilized the head by grasping it. A spot of red light (0.5 deg of visual angle), produced by a laser, was reflected onto the inner surface of the cabin by a mirror galvanometer system situated directly above the subject's head. The subject could move the laser point by pressing one of four small directional buttons (up/down/left/right) mounted crosswise on a small box (8.5 × 5 × 4.5 cm). Each button was 1.5 cm from the centre of the box. The position of the buttons on the box corresponded with the direction in which the laser point would be steered. When a button was pressed, the laser point moved smoothly in the indicated direction with a velocity of 1 deg/s. The subject held the box in the right hand and pressed the buttons with the right thumb.

For neck muscle vibration on the left and right side, an experimental vibrator was used. Its frequency was fixed at 100 Hz with an amplitude of 0.4 mm. The tip of the vibrator, a flat disk 2.3 cm in diameter, was placed on the subject's posterior neck. Its position was individually adjusted to achieve an illusion of horizontal displacement of the stationary laser point. The testing procedure started as soon as the subject had a clear illusion of target movement. The stationary spot was then extinguished and vibration continued. The spot immediately reappeared at one of four eccentric positions described below and was then required to be adjusted to straight ahead. If no illusion could be induced, the tip of the vibrator was placed below the left/right occiput just lateral to the spine.

Vestibular stimulation was applied by cold water irrigation of the left external auditory canal with 30 ml of ice water for 1 min. During stimulation the subject sat upright in the chair with the head tilted ~60° backward. In all subjects a brisk nystagmus was induced with the slow phase to the left side. After stimulation eye movements were observed using Frenzel glasses. Testing procedures IV to VI (see below) were started 2 min after irrigation, at the time when most of the caloric nystagmus had decayed.

Each test condition started with the laser spot being pseudorandomly presented in one of four eccentric positions (+10°/+10°, −10°/−10°, +10°/−10°, −10°/+10°). (Directions were defined in the conventional way: up and right as positive, down and left as negative). The subject then had to direct the laser point to the position which was felt to lie exactly "straight ahead". Subjects verbally indicated when the position was reached. No time limit was used. The objective position of the body's spatial orientation was defined by laser position 0°/0°, which was aligned with the centre of the chair in the horizontal plane and the individual eye level of the subject in the vertical plane.

The influence of neck muscle vibration and vestibular stimulation on the subject's judgements of "straight ahead" was investigated in six different test conditions. The whole investigation took about 15 min. The following order of test conditions was used:

I. No additional stimulation ("baseline" condition)
II. Vibration of the left posterior neck muscles
III. Vibration of the right posterior neck muscles
IV. Caloric stimulation of the left external auditory canal
V. Caloric stimulation of the left external auditory canal plus vibration of the left posterior neck muscles
VI. Caloric stimulation of the left external auditory canal plus vibration of the right posterior neck muscles

Results

The subjective "straight ahead" positions were very closely scattered around the objective straight ahead body orientation (laser position 0°/0°). In test condition I, the 17 subjects steered the laser to an averaged position of 0.75° (SD 2.46°) in the horizontal plane and −0.48° (SD 3.54°) in the vertical plane. For analysis of conditions II to VI the angular deviation of each subject's judgement from that in "baseline" condition I was calculated.

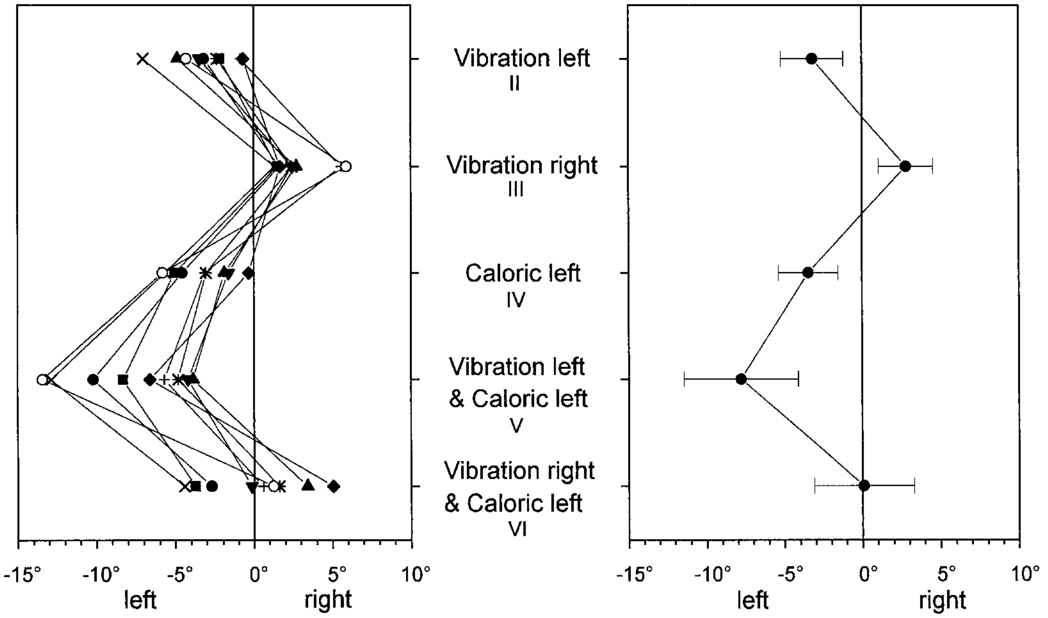

Fig. 1 Subjective "straight ahead" judgements (*horizontal plane*) in test conditions II to VI performed by the nine subjects who reported an illusion of motion with both left-sided and right-sided vibration. Presented are the angular deviation of each subject's judgement from that in "baseline" condition I (*left*) and the respective mean values (*right*)

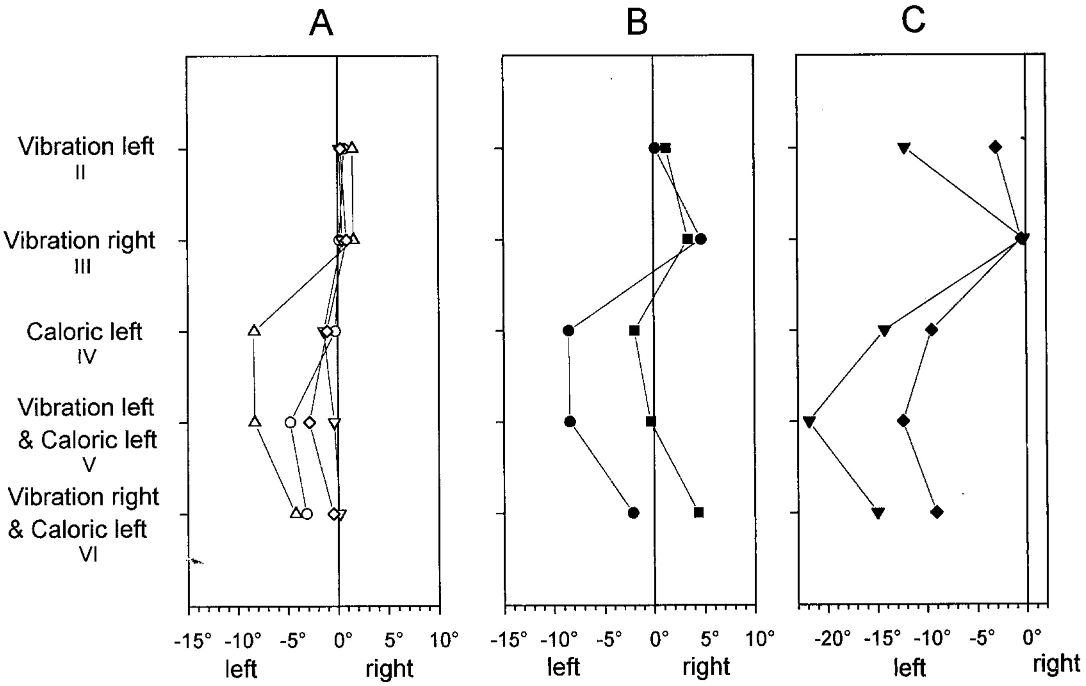

Fig. 2 Subjective "straight ahead" judgements (*horizontal plane*) in test conditions II to VI of the four subjects who reported no illusion of motion with neck muscle vibration (**A**) and of those subjects who had an illusion of motion only with right-sided vibration (**B**) or with left-sided vibration (**C**). Presented is the angular deviation of each subject's judgement from that in "baseline" condition I

During vibration of the left (conditions II and V) and right (conditions III and VI) posterior neck muscles 9 of the 17 subjects experienced a visual movement and egocentric displacement of the stationary, centrally presented laser point. The principal direction of apparent motion was to the right with vibration on the left side, and to the left with vibration on the right, although some vertical motion was sometimes reported in addition. Four subjects had no illusion either with vibration of the left or of the right neck muscles. Another four subjects only had an illusion of motion to one side: two subjects reported a rightward movement only when vibrated on the left side, and the other two subjects experienced a movement to the left only when vibrated on the right.

In contrast, all 17 subjects experienced an illusion of movement and displacement of the stationary laser point after caloric stimulation of the left external auditory canal. Although in all subjects the principal direction of motion was to the right, again some minor vertical motion was sometimes reported in addition.

Figure 1 shows the individual and the mean angular

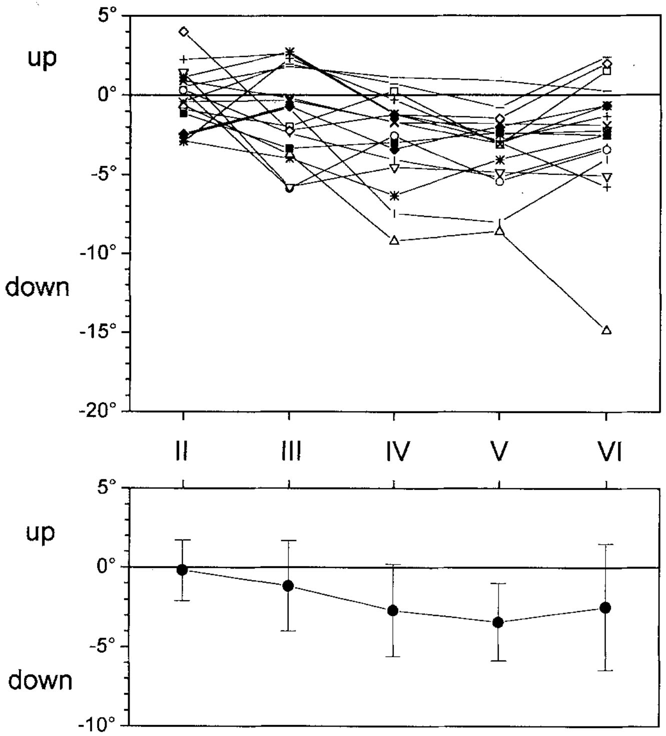

Fig. 3 Subjective "straight ahead" judgements (*vertical plane*) in test conditions II to VI performed by all 17 subjects. Presented are the angular deviation of each subject's judgement from that in "baseline" condition I (*top*) and the respective mean values (*bottom*)

deviation in the horizontal plane of the nine subjects who reported a clear illusion of laser point movement during both vibration of the left and of the right posterior neck muscles. All of these subjects showed a horizontal displacement of their subjective body orientation to the left with left-sided vibration (condition II) and to the right with vibration on the right side (condition III). A corresponding effect was seen after vestibular stimulation (condition IV). Again, the subjects displaced their subjective "straight ahead" orientation to their objective left.

In condition V, when neck muscle vibration and vestibular stimulation were simultaneously applied on the left, the leftward displacement of subjective body orientation (Fig. 1) was larger than the effect of either of the two types of stimulation when applied in isolation (conditions II and IV). The opposite effect was achieved when left-sided vestibular stimulation was combined with right-sided neck muscle vibration (condition VI). This combination seemed to neutralize the effects that both types of stimulation had when exclusively applied (conditions III and IV).

Figure 2a presents the horizontal angular deviation of the four subjects who experienced no illusion of laser point movement during vibration of either the left or the right posterior neck muscles. Figure 2b shows the deviation of the two subjects who had an illusion of movement only when vibrated on the right side, Fig. 2c exhibits the data of the two subjects who experienced an apparent motion only when vibrated on the left.

The subjects' illusion of movement of the stationary laser point was found to be highly correlated with their displacement of subjective body orientation when their neck muscles were vibrated (Fig. 2). With neck muscle vibration on the left (condition II), only the two subjects who reported an apparent movement of the stationary laser point to the right also showed a deviation of their subjective "straight ahead" position to the left. Accordingly, only the two subjects who experienced an illusion of leftward target movement also showed a deviation of their subjective "straight ahead" to the right when the posterior neck muscles were vibrated on the right (condition III).

With vestibular stimulation (condition IV), in five of

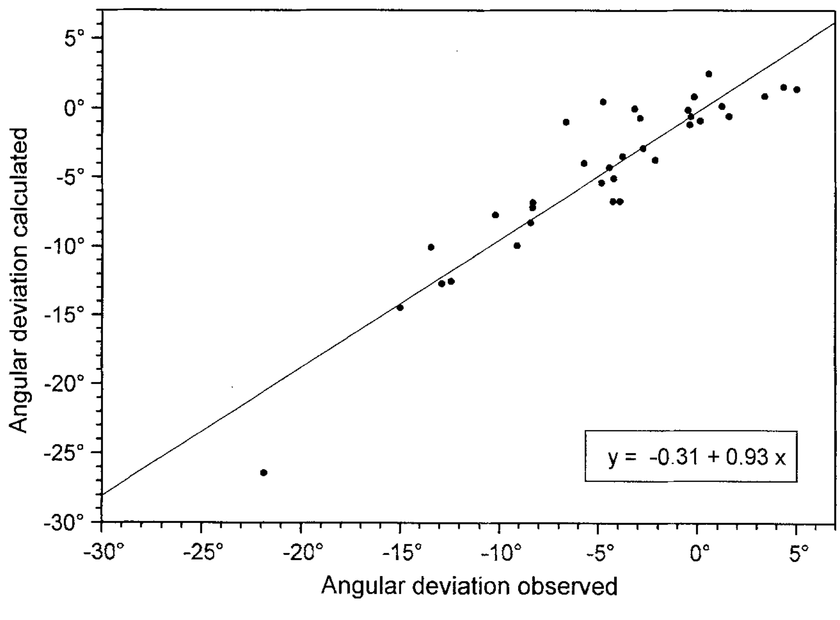

Fig. 4 Observed versus calculated disparities between subjective and objective "straight ahead" orientation (*horizontal plane*) for all 17 subjects when proprioceptive and vestibular stimulation were combined. The observed angular deviations in conditions V and VI were correlated with the sum of the respective judgements when either type of stimulation was applied alone (conditions II, III and IV)

these eight subjects a clear horizontal displacement of subjective body orientation was observed. Three subjects showed only a very mild displacement under this test condition; this was, however, in the expected direction.

In addition to the principal direction of motion, the subjects sometimes also reported a vertical motion component of the stationary laser point with vibration and/or vestibular stimulation. Figure 3 shows this angular deviation for all 17 subjects in the vertical plane. In contrast to the clear horizontal displacements of subjective "straight ahead" with proprioceptive and vestibular stimulation, in the vertical plane only a mild predominance of downward displacements was detected during caloric stimulation (conditions IV and V).

From the data illustrated in Figs. 1 and 2 it appeared that the combined effect of neck muscle vibration and vestibular stimulation on the horizontal deviation of subjective body orientation is additive. To test the hypothesis of a linear relationship between the two types of stimulation, the observed angular deviations of the "straight ahead" orientation in conditions V and VI of all 17 subjects were correlated with the sum of the respective judgements when tested alone (conditions II, III and IV). The Pearson product-moment coefficient was 0.85; the data are illustrated in Fig. 4.

Discussion

The perception of body orientation in space depends on multisensory evaluation of visual, vestibular and proprioceptive sensory input. When vision is excluded, the vestibular system, which registers position and motion of the head in space, and proprioceptive information from the neck region act together to relate trunk to space. This concept of vestibular-proprioceptive interaction was originally introduced by von Holst and Mittelstaedt (1950) and was further elaborated by Roberts (1973). Since then several lines of evidence from experimental work in animals have supported this idea (Pompeiano 1988; Wilson 1988), even though there is still an ongoing debate on how the neck (i.e. muscle spindles and cervical joint receptors) contributes to the maintenance of body orientation and balance. Cervical dorsal root fibres have strong projections to the vestibular nuclei (Brodal and Pompeiano 1957), and electrophysiologic evidence suggests that convergence of vestibular and cervical input occurs at these sites. Most vestibular neurons will respond to both vestibular and cervical dorsal root stimulation (Fredrickson et al. 1966). Stimulation of cervical muscle afferents has been shown to facilitate activity of vestibular neurons (Mori and Mikami 1973). Furthermore, neck receptors seem to play a significant role in eye-head coordination (Roll et al. 1991).

Injecting local anaesthetic around cervical dorsal roots (De Jong et al. 1977) produces severe ataxia in humans, a strong sensation of imbalance and of being pulled toward the side of the injection, a positive Romberg test with deviations and past-pointing toward the injected side, and hypotonia of the ipsilateral arm and leg. Moreover, sensations of tilting and falling as well as altered perception of verticality can be induced by electrical stimulation of the neck (Wapner et al. 1951). Finally, more recent psychophysical work, using trunk rotation relative to the stationary head, has shown that normal human subjects may derive their perception of trunk motion in space from a combination of vestibular and neck cues (Mergner et al. 1983, 1991).

In summary, there is at present strong experimental evidence that neck afferent activity plays an important role in maintenance of posture, in oculomotor control, and in the perception of body orientation in space.

One effective way to induce neck activity is to vibrate the neck muscles. Vibration of muscles or muscle tendons causes proprioceptive "misinformation" producing an illusory sensation of movement (Goodwin et al. 1972) and, for example in the case of antigravity muscles, a consequent shift in body posture (Eklund 1972).

In normal subjects, vibration applied to the neck muscles causes a displacement of subjective midline and a consistent error in pointing (Biguer et al. 1988) as well as antegrade body sway (Pyykkö et al. 1989). The secondary endings of the muscle spindles have been suggested as the receptors triggered by vibration (Eklund 1973), although afferent information from primary endings (Matthews 1966) and Golgi tendon organs (Prochazka and Wand 1980) may significantly contribute to vibration-induced body sway and perceptional effects.

The present study investigated the interactive contribution of proprioceptive input from the neck region with visual and vestibular information to subjective body orientation in humans. To evaluate this interaction on the perception of "straight ahead", we used neck proprioceptive stimulation by vibrating the posterior neck muscles and vestibular stimulation by ice water. The main observations of our study were:

1. In the dark, normal human subjects can estimate their subjective "straight ahead" very accurately with a deviation of only about ±3.5° from objective straight ahead.
2. With neck muscle vibration there was a strong positive relation between the apparent motion of a stationary target and the displacement of subjective body orientation. The principal direction of apparent target movement was to the right with vibration of the left side and to the left with vibration on the right. Only those subjects who experienced an illusion of target motion also showed a deviation of their subjective body orientation.
3. While not all subjects experienced a deviation of "straight ahead" with neck vibration, all subjects reported an apparent movement of the stationary visual target away from the stimulated ear during ice water stimulation and displaced their subjective straight ahead orientation to the side of irrigation.

4. In the vertical plane, mild downward displacements of subjective "straight ahead" were detected with caloric stimulation.
5. The vestibular and proprioceptive input to subjective body orientation combined linearly either by adding the effects or by neutralizing them.

Our data clearly support the notion of a profound impact on subjective body orientation in humans by proprioceptive input from the neck region, even though the effect is quite variable for different subjects and less effective than is vestibular stimulation.

The astonishing accuracy with which normal human subjects can estimate their straight ahead body orientation under normal conditions argues for a stable, body-centred reference frame for the evaluation of body orientation in space and further shows that under normal conditions the sensory systems tested act together in a very precise manner, supplying us with a close to optimal estimate of body orientation. A similar preciseness of subjective "straight ahead" has also been described by Hamann et al. (1992).

Caloric stimulation was just as effective as vibration of the neck muscles in inducing shifts of "straight ahead". However, while caloric stimulation induced horizontal shifts in all subjects tested, neck muscle vibration was less consistent, in that some subjects showed no effect or only a displacement to one side. This may be because it is difficult to position the vibrator for most effective stimulation.

Interestingly, the effect of caloric stimulation on the perception of subjective body orientation could be measured even after most of the vestibular nystagmus had decayed (observed with Frenzel glasses), indicating that the central neural processing that leads to a "tonic" deviation of straight ahead perception probably has a longer time constant than the induced caloric nystagmus. However, the present study did not systematically investigate the time course and correlation of nystagmus amplitude and subjective body orientation. Further investigation is needed to clarify this issue.

The observed downward displacement of subjective "straight ahead" during caloric stimulation is not surprising, since the lateral semicircular canals are the main source of the caloric-induced nystagmus and – because of their anatomical orientation (Blanks et al. 1975) – produce mainly horizontal nystagmus with moderate torsional and slight vertical components (Boehmer et al. 1992). During ice water stimulation, the vertical component of nystagmus has its slow phase downward. Thus, like the effects in the horizontal plane, where subjective "straight ahead" deviated in the direction of the slow phase of the nystagmus, in the vertical plane the deviation was expected to be downward.

In agreement with our results, a linear interaction during combined vestibular, neck and visuo-oculomotor stimulation has also been found by Mergner and coworkers (1992) for the perception of visual object motion in space. In their experiments the vestibular perception was achieved, however, by sinusoidal rotations of the subjects about a vertical axis in the horizontal plane.

In summary, our data clearly indicate that the visual, vestibular and proprioceptive input converge and interact in a rather precise manner in their contribution to the neural generation of an egocentric, body-centred coordinate system that allows us to determine our body position in space.

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