Exp Brain Res (2002) 143:350–358
DOI 10.1007/s00221-001-0996-2

RESEARCH ARTICLE

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The perception of body orientation after neck-proprioceptive stimulation

Effects of time and of visual cueing

Received: 7 May 2001 / Accepted: 27 November 2001 / Published online: 30 January 2002

Abstract Different sensory systems (e.g. proprioception and vision) have a combined influence on the perception of body orientation, but the timescale over which they can be integrated remains unknown. Here we examined how visual information and neck proprioception interact in perception of the "subjective straight ahead" (SSA), as a function of time since initial stimulation. In complete darkness, healthy subjects directed a laser spot to the point felt subjectively to be exactly straight ahead of the trunk. As previously observed, left neck muscle vibration led to a disparity between subjective perception and objective position of the body midline, with SSA misplaced to the left. We found that this displacement was sustained throughout 28 min of continuous proprioceptive stimulation, provided there was no visual input. Moreover, prolonged vibration of neck muscles leads to a continuing disparity between subjective and objective body orientation even after offset of the vibration; the longer the preceding vibration, the more persistent the illusory deviation of body orientation. To examine the role of vision, one group of subjects fixated a central visual target at the start of each block of continuous neck vibration, with SSA then measured at successive intervals in darkness. The illusory deviation of SSA was eliminated whenever visual input was provided, but returned as a linear function of time when visual information was eliminated. These results reveal: the persistent effects of neck proprioception on the SSA, both during and after vibration; the influence of vision; and integration between incoming proprioceptive information and working memory traces of visual information.

Keywords Straight-ahead perception · Visual memory · Neck muscle vibration · Human

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Introduction

Our perception of how our body is oriented in space and how external objects are located with respect to us, depends on integration of information from several different senses (Jeannerod and Biguer 1987; Andersen et al. 1993; Karnath 1994a, 1997; Andersen 1997; Driver and Spence 1998). Even our visual experience depends not only upon stimulation by light on the retina, but also upon proprioceptive information indicating the position of the eyes in the orbit (Jeannerod and Biguer 1989; Gauthier et al. 1990; Bridgeman and Stark 1991), and of the head on the trunk (Taylor and McCloskey 1991). The influence of neck-muscle proprioception on the elaboration of egocentric coordinates for visual space was studied by Biguer et al. (1988). They investigated normal subjects sitting with head and body oriented directly towards a central, stationary spot of light. During vibration of left posterior neck muscles, which induces the false afferent signal that these muscles have lengthened (thus mimicking the proprioceptive signal for a trunk rotation relative to the head), subjects reported apparent motion and displacement of the stationary visual target towards the right. When requested to point to the target, subjects exhibited a consistent error in pointing towards the same direction as the illusory displacement. The magnitudes of both the displacement and the motion illusions were dependent on vibration amplitude. Moreover, when the target was moved until the subjects perceived it as lying on their subjective straight ahead (SSA), this was usually placed to the left of the objective physical midline. These results indicate that artificial afferent head-on-trunk signals, induced by vibration of left posterior neck muscles, result in a displacement of the perceived orientation of the body in space. These basic findings have since been confirmed (Roll et al. 1991; Taylor and McCloskey 1991; Karnath et al. 1994).

Some subsequent work highlights the interactions of neck-proprioceptive input with other sensory sources contributing to the perception of body orientation in space. Roll et al. (1991) have compared the influence of eye-muscle and neck-muscle proprioception on subjective body orientation, by vibrating these sets of muscles either alone or in combination. They found an additive combination of the two proprioceptive channels and postulated that proprioceptive cues from eye and neck muscles might be further integrated with retinal signals about the position of visual objects. Karnath et al. (1994) have investigated perception of the SSA during vestibular and/or neck-proprioceptive stimulation, again in healthy subjects. They also found evidence for an additive combination of different input channels. When caloric vestibular stimulation was combined with neck muscle vibration, horizontal deviation of the SSA was a linear sum of the two sources of stimulation, so that the effects of combining stimulation could enhance or neutralise the influence, compared with either type of stimulation alone. Mergner et al. (1992, 1997) have similarly observed a linear integration of vestibular and neck-proprioceptive inputs in the perception of object motion or self-motion.

The above experiments were all conducted in darkness, to exclude the contribution of vision to perceiving the SSA. But the extensive literature on “visual dominance” (Held and Hein 1958; Rock and Harris 1967; Lackner and Graybiel 1979; Lund 1980) suggests that visual information may be weighted more heavily than inputs from other senses, for a range of spatial judgements. Experiments using vibration stimuli to induce apparent self- or object-motion, or to elicit swaying reactions, have also revealed dominance of vision over proprioceptive signals. That is, the effects of proprioceptive vibratory stimulation observed in darkness were found to disappear or become less effective in a structured visual context (Eklund 1973; Lackner and Levine 1979; Velay et al. 1994).

Here we examine how visual information about the straight-ahead orientation may be combined with neck proprioception. We also study the timescale over which each of these modalities can exert an influence. The first experiment investigates the influence of different intervals of neck muscle vibration on the stability of perceived body orientation, to assess whether the influence of neck proprioception is sustained throughout lengthy periods of prolonged muscle vibration or whether it habituates instead. We also examined whether the decalibrating effect of neck proprioception on the SSA continues for some time after termination of the vibration stimulus. In the second experiment, we investigated how visual influences may combine with proprioception, and in particular how the effect of vision may decline over time following the onset of total darkness. These studies allowed us to examine not only the integration of on-line afferent inputs from different senses, but also integration involving memory traces for information presented to a particular modality.

Materials and methods

Subjects

Previous research showed that neck muscle vibration does not induce kinaesthetic illusions in all subjects, perhaps due to differences in individual sensitivity for transcutaneous vibratory stimulation of neck muscle spindles (see Lackner and Levine 1979; Biguer et al. 1988). We therefore first screened subjects, by presenting a stationary red laser spot while vibrating the left posterior neck muscles in the manner described, and testing for illusory displacement of the spot. Eighteen subjects (67% of those initially recruited) experienced a clear, illusory visual movement and displacement of the stationary, centrally presented laser spot to the right side (cf. Biguer et al. 1988). No subjects had a history of vestibular or oculomotor abnormalities. The subjects gave their informed consent to participate in the study, which was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Six of these healthy subjects (all men, ranging in age from 26 to 65 years, median 29.5 years) took part in experiment 1. The other 12 subjects participated in experiment 2, where they were randomly divided into two further groups of 6, the “control group” (2 women, 4 men, ranging in age from 23 to 36 years, median 27.5 years) and the “visual-memory group” (3 women, 3 men, ranging in age from 24 to 66 years, median 25 years).

Apparatus

Subjects sat in an opaque, light-bulb-shaped cabin with their head in the centre of the upper spherical part of the bulb (diameter 190 cm). The whole investigation was conducted in complete darkness except for the illumination of a target LED in some conditions. Subjects sat upright in a chair that provided adjustable support for their backs. A four-point, pilot-style seat belt prevented trunk movement. A chin rest restrained head motion. In addition, head position was measured on-line by an electromagnetic front coil that was fixed on the subject’s head. Its position was measured by three orthogonal magnetic fields, generated by three pairs of Helmholtz coils, mounted in a cube-like configuration on the outer surface of the upper spherical part of the bulb. Subjects were verbally instructed to re-adjust head position if it ever exceeded a tolerance of ±1° during the experiments.

A spot of red laser light (0.27°) was reflected at the subject’s eye level (set for each individual) onto the inner surface of the cabin, by a mirror galvanometer system situated directly above the subject’s head. The objective position of the body’s spatial orientation was defined as 0°, aligned with the midsagittal plane of the subject’s body (and the centre of the chair). The subjects could move the laser point in the horizontal plane by pressing one of two directional buttons (left/right) mounted on a small box (each button 1.5 cm from the box centre). When the button was pressed, the laser point moved smoothly in the indicated direction with a velocity of 3.7°/s. The subjects held the box in their right hand and pressed either button with their right thumb. For neck muscle vibration, an experimental vibrator was used (Ling Dynamic Systems, V201), with a frequency of 80 Hz and amplitude of 0.4 mm.

Measurement of SSA

The laser spot randomly appeared for each judgement at one of 5 positions (–10°, –5°, 0°, +5° or +10°) in the horizontal plane.

(Directions are defined in the conventional way, with right of the body's midsagittal plane as positive, left as negative.) The task was to direct the laser point, by means of button presses, to the position felt to lie exactly straight ahead of the body's midsagittal plane. Subjects indicated verbally when they had reached this position to their satisfaction. The trials were arranged in blocks of ten, with each judgement being separated by 15 s. The laser spot was presented twice at each of the five positions in a pseudorandom order. The SSA score was determined by averaging over trials.

Measuring the "no-vibration baseline",
the "hand-vibration control", and the "neck-vibration baseline"

Procedure

Each satisfactorily screened subject was first given one practice session at measuring SSA, for 5 min. Ten minutes later, the SSA was measured formally, but without any experimental stimulation whatsoever ("no-vibration baseline"), using the method described here (i.e. ten trials, with two at each of the five possible start locations for the laser spot, in pseudorandom order). To control for the possibility that any effects on SSA, when subsequently vibrating the left posterior neck muscles, might somehow be caused by nonspecific factors (e.g. those associated with *any* form of proprioceptive stimulation on the body's left side, such as arousal influences), the vibrator's tip was then positioned in the middle of the subject's left palm for the "hand-vibration control" measurements. After 3 min of continuous vibration of the left hand, SSA was measured for ten trials during continuous vibration of that hand.

On terminating this "hand-vibration control" procedure, vibration was then applied to the left posterior neck muscles. The vibrator was fixed on a stable tripod, and the tip of the vibrator (a flat disc of 2.3 cm diameter), was placed on the subject's left posterior neck. Its exact position was individually adjusted to produce a clear illusion of horizontal displacement for a stationary laser point. Three minutes after this neck vibration started, SSA was again sampled for ten trials. This measurement served as the "neck-vibration baseline": for comparison with the effects of shorter or more prolonged periods of neck vibration; to determine any effects of time since vibration offset; and finally (in experiment 2) for comparison with visual influences and their own decay against time.

Results

The results obtained for the no-vibration baseline, the hand-vibration control and the neck-vibration baseline measurements are shown in Fig. 1 for all subjects investigated in experiments 1 and 2. Without vibration, the subjective body orientation was scattered closely around the objective SSA body orientation (laser position 0°). For those six subjects who took part in experiment 1, the intersubject mean position was +1.4° (SD 4.6°) in the horizontal plane. With vibration of the subject's left hand, no reliable alteration in the subjective perception of body orientation was observed; the mean deviation was +2.4° (SD 4.6°). Finally, with vibration of the left posterior neck muscles, a clear deviation of the SSA towards the left was detected (as previously reported by Biguer et al. 1988; Karnath et al. 1994). The intersubject mean position with this type of stimulation lay –6.2° (SD 3.9°) left of the objective body midline. A repeated-measures ANOVA for SSA orientation with "condition" (No-vibration baseline, Hand-vibration control, Neck-vibration baseline) as the within-subject factor revealed a significant main effect ($F_{2,\,10}$=61.1, P<0.001). Post hoc paired t-tests showed that the neck-vibration condition differed reliably from the other two conditions [t(5)=6.92 for neck vs no vibration, and t(5)=9.66 for neck vs hand vibration; both P<0.001], while there was no statistical difference between the no-vibration and the hand-vibration conditions [t(5)=2.36, P=0.06].

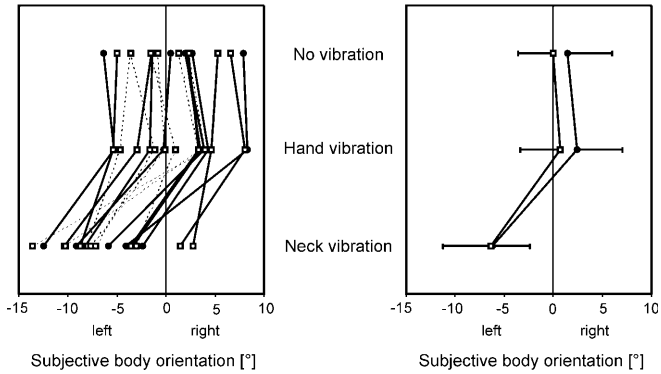

Fig. 1 Subjective body orientation measured without any vibration, with vibration of the left hand, or with vibration of the left posterior neck muscles. The six subjects who participated in experiment 1 are represented by *filled symbols*; the 12 subjects investigated in experiment 2, by *open symbols*. *Left:* The mean judgements of each single subject are presented. Each *line* represents a single subject. The 12 subjects of experiment 2 (*open symbols*) are further differentiated into those subjects from the control group (*solid line*), and those subjects from the visual-memory group (*dashed line*), but note that all subjects had undergone identical conditions at this point in the experiment. *Right:* the intersubject mean subjective body orientations for the three different vibration conditions for all six subjects in experiment 1 (*filled symbols)* and separately for all 12 subjects in experiment 2 (*open symbols)*

In the 12 subjects who took part in experiment 2, SSA judgements without vibration were also scattered closely around the objective straight ahead body orientation (laser position 0°). The intersubject mean position was +0.01° (SD 3.6°) in the horizontal plane (Fig. 1). With vibration of the subject's left hand, no reliable alteration in the subjective perception of body orientation was observed. The mean deviation was +0.7° (SD 4.1°). Finally, with vibration of the left posterior neck muscles, a clear deviation of SSA towards the left was detected in these subjects (Fig. 1). The intersubject mean SSA with this type of stimulation lay –6.4° (SD 4.9°) to the left of the objective body midline. A repeated-measures ANOVA for SSA orientation with condition (No-vibration baseline, Hand-vibration control, Neck-vibration baseline) as the within-subject factor revealed a significant main effect ($F_{2,22}$=28.45, P<0.001). Post hoc paired t-tests showed that the Neck-vibration condition differed reliably from the other two [t(11)=5.4 for neck versus no vibration, and t(11)=5.5 for neck versus hand vibration; both P<0.001], while there was no statistical difference between the no-vibration and the hand-vibration conditions [t(11)=1.7, P=0.12].

Experiment 1

The first study investigated the influence of different neck-vibration durations on the stability of the perceived SSA. It tested whether the influence of neck proprioception is sustained until the end of an extensive period of prolonged muscle vibration, or instead habituates; and also whether its decalibrating effect continues for some time after termination of the vibration.

Procedure

Directly after the no-vibration baseline, hand-vibration control, and neck-vibration baseline measurements, vibration started again on the left posterior neck muscles and continued for either 1 min, 5 min, 15 min or 30 min. The different vibration intervals were applied in a pseudorandomized order. Each of the six subjects participated in all conditions during two sessions. During the 5-, 15- and 30-min vibration interval, SSA orientation was measured 3 min before vibration ended, using the procedure described above under “Measurement of SSA”. During the 1-min vibration interval, a different procedure was necessary, as otherwise the brief interval of vibration did not allow sufficient time for SSA measurement. Here the spot was randomly presented at one of the five horizontal positions 30 s after vibration started. The subjects then had to adjust the laser point continuously to the most satisfactory SSA position, and the laser position was recorded every 10 s.

Immediately before the vibration terminated, the laser spot was presented at the mean SSA position measured in the previous block. Subsequent to the offset of vibration (i.e. immediately following 1 min, 5 min, 15 min or 30 min of vibration), the SSA was continuously reported by subjects for the next 3 min. As before, they were instructed to set the spot exactly at the currently perceived midsagittal plane of the body. They were explicitly told to re-adjust the position whenever they had the impression that the position of the laser spot no longer corresponded with the perceived orientation of the body. Laser position was registered every 10 s throughout these 3-min periods that followed the termination of neck vibration.

For data analysis, the angular deviation of each subject’s judgement from his individual no-vibration baseline was calculated. In order to analyse the effect of different durations of preceding neck vibration on SSA judgements after termination of the vibration, the time until the deviated SSA position corresponded again with that measured in the no-vibration baseline was determined. The criterion for such correspondence was three successive SSA judgements lying within ±1 SD of the no-vibration baseline. The time to achieve this return to the no-vibration baseline was calculated by linear interpolation between the last SSA judgement outside and the first judgement within this area.

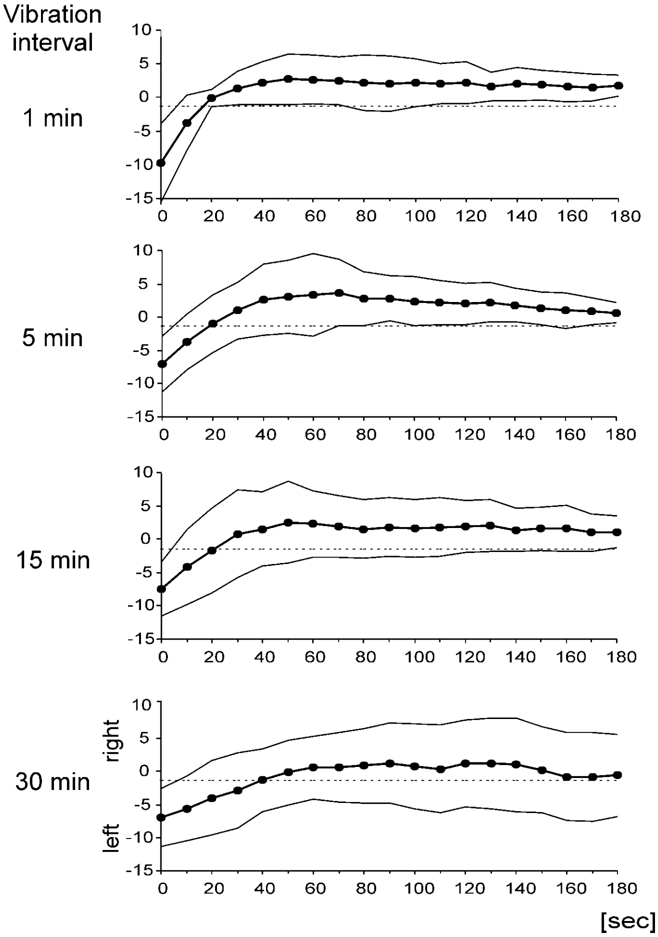

Fig. 2 Mean deviation and standard deviation of subjective “straight ahead” (SSA) from the SSA position measured without vibration (the latter set as 0° here). The deviations subsequent to the 1-, 5-, 15- and 30-min neck-vibration intervals are shown. The *broken line* indicates SSA position minus one standard deviation as measured without vibration. Values are averaged over the six subjects in two different sessions. *Negative values* indicate a leftward bias of SSA, *positive values* a rightward bias

Results

To analyse whether the duration of neck vibration has some impact on the extent of SSA deviation, an analysis of variance was carried out. It examined the influence of the factors Session (2) and Duration of vibration interval (1 min, 5 min, 15 min vs 30 min) on the SSA deviation at the end of the vibration intervals, in a within-subject, repeated-measures design. No terms approached significance. This shows that the duration of the vibration stimulus had no influence on the extent of SSA deviation.

When neck stimulation terminated, the subjects continuously adjusted SSA position for the subsequent 3 min. (If the SSA position measured previously without vibration, i.e. the no-vibration baseline data shown in Fig. 1, was not reached during this 3-min period of continuous adjustment, registration of SSA continued further, but this was necessary for only 3 of the 48 cases of SSA registration.) Figure 2 gives an overview of the mean SSA position in the post-stimulation period following the 1-, 5-, 15- and 30-min vibration intervals. When stimulation terminated, the leftward bias of SSA decreased continuously. A period of slight overshoot of SSA position to the right followed in all conditions. Figure 2 shows that the longer the neck-vibration interval had lasted, the longer the illusory deviation of body orientation persisted after neck vibration terminated. The mean time until SSA position corresponded again with that measured previously without vibration increased from 14.4 s (SD 5.7) after the 1-min neck vibration to 114.2 s (SD 127.5) after 30 min of continuous neck vibration.

To take into account differences between subjects in the absolute extent of SSA deviation, the time until SSA corresponded again with the no-vibration baseline was related to the extent of SSA deviation under experimental neck vibration for each subject. Figure 3 illustrates this quotient (degrees per second), which corresponds to the *velocity* of decrease in SSA deviation after neck vibration terminated. This confirms that the longer the neck vibration was applied, the slower the return to a normal SSA when the vibration was terminated. An analysis of variance examined the factors Session (2) and Duration of vibration intervals (4), on the scores for “velocity of SSA decrease” in a within-subject, repeated-measures design. A highly significant effect of the duration of vibration intervals was found ($F_{3,47}$=12.37, P<0.001). Post hoc comparisons using an adjusted alpha-level revealed signifi-

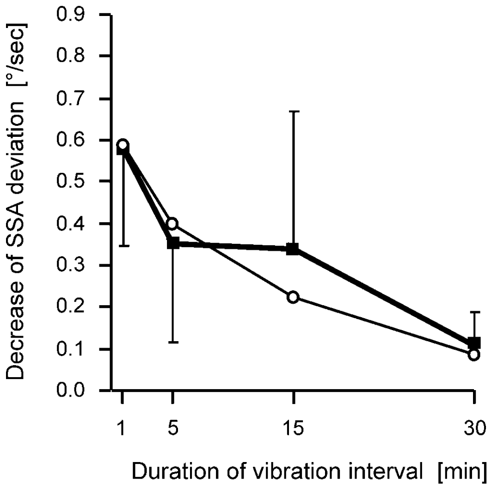

Fig. 3 Decrease in SSA deviation determined after the 1-, 5-, 15- and 30-min intervals of neck muscle vibration. The velocity of this decrease (degrees per second) is illustrated, showing the means (*filled squares*) and standard deviations as well as the median (*open circles*) of the six subjects in two different sessions

cant differences in the velocity of SSA decrease between the 1-min and the 30-min vibration intervals [$t(11)=6.08$, $P<0.001$], and also between the 5-min and the 30-min vibration intervals [$t(11)=3.40$, $P=0.006$].

Experiment 2

While experiment 1 only compared SSA judgements at the *end* of various periods of neck vibration, experiment 2 was designed to examine whether the influence of neck proprioception may be sustained *throughout* a lengthy period (28 min) of prolonged muscle vibration. More importantly, experiment 2 also explored whether *visual* information about the straight-ahead orientation is combined with neck proprioception, and how this influence of visual information might decline over time following the onset of total darkness. The latter point allowed us to examine not only the integration of on-line afferent inputs from different senses, but also integration involving memory traces for information presented to a particular modality.

Procedure

Directly after measuring SSA in the no-vibration baseline, the hand-vibration control, and the neck-vibration baseline, neck vibration was applied continuously for another 22.5 min on the left posterior neck muscles. Thus, together with the period needed to measure the neck-vibration baseline, an interval of 28 min of continuous neck muscle vibration was applied. Two groups of subjects underwent test conditions that differed in a crucial systematic way.

Control group

SSA judgements were sampled in three blocks of ten trials, each lasting 2.5 min, with each such block being preceded by 5 min, where the only stimulation was the continuous neck muscle vibration.

Visual-memory group

The only difference in experimental procedure for this group was that, during the 5 min between each block of SSA judgements, subjects not only underwent continuous neck muscle vibration, but were also presented continuously with a central visual target (a green LED), thus providing visual information about the objective straight ahead. They were instructed to fixate and attend this visual target throughout the 5-min period between SSA judgements. Horizontal eye-position was measured by an eye monitor (ASL 210) using the infrared reflection technique (Young and Sheena 1975). The permitted tolerance of eye deviation was ±1° in the horizontal plane, and subjects were verbally instructed to refixate the LED whenever eye position exceeded this.

This central LED was extinguished whenever SSA judgements were made, with the red laser spot being switched on instead, so that the conditions during measurements of the SSA were identical in all respects to the other group, differing only in whether a central target had been visible during the preceding period. Comparing the successive measurements within each block of ten trials of straight ahead judgement (each judgement being separated by 15 s) allows the determination of any effects of the time elapsed since visual stimulation. After the last SSA measurement in a block, the laser spot was switched off and the green central LED re-illuminated. As with the control group, there were three 2.5-min blocks of straight ahead judgements, each preceded by 5-min periods. Neck-muscle stimulation was continuous throughout.

Results

For analysis of the subsequent measurements (i.e. every successive trial in the three blocks that were each preceded by 5 min of further neck stimulation), the SSA position as measured after the very first 3 min of neck vibration (i.e. the neck-vibration baseline; data shown in Fig. 1), was used to calculate the angular deviation of each subject's subsequent judgement from his or her own neck-vibration baseline. Figure 4 shows this relative angular deviation, for each successive trial of SSA measurement, obtained in blocks of 10 after the three subsequent periods of vibration.

In the control group, who were not presented with any visual information in the 5 min that preceded each block, no relevant change of SSA deviation was observed (see Fig. 4) from the neck-vibration baseline as established in Fig. 1. This shows that the effect of neck-proprioceptive stimulation on the SSA was *fully maintained* throughout the additional 22.5 min of neck-muscle stimulation (and thus for a total of 28 min, when the duration of the initial baseline measurement during neck vibration is included). In dramatic contrast, the mean displacement of SSA diminished by more than 5° for the visual-memory group on the first trial in a block (i.e. shortly after their visual stimulation ended). That is, the SSA was placed within 1° of the objective midline on this first trial (see Fig. 4). Statistical comparison of SSA judgements obtained at the first trial of each block was carried out with a repeated-measures ANOVA for this variable, with Subject group (control group, visual-memory group) as the between-group factor and Block (1st block, 2nd block, 3rd block) as a within-group factor. The analysis revealed a significant main effect for factor subject groups

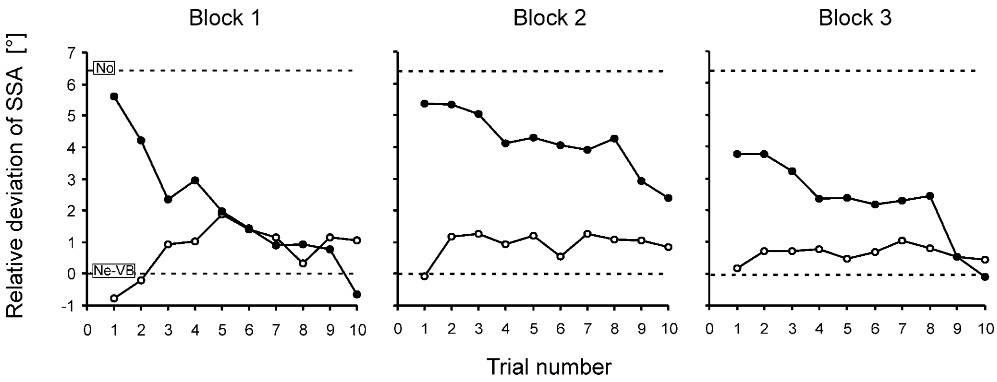

Fig. 4 Angular deviation of subjective straight ahead (*SSA*) position in experiment 2, relative to the judgements obtained after the first 3 min of neck vibration that was taken as the "neck-vibration baseline" (*Ne-VB*; the individual data contributing to this baseline are shown for the neck-vibration condition in Fig. 1). Positive values indicate that SSA deviation diminishes (i.e. shifts rightwards toward the objective midline) with respect to the neck baseline, any negative values indicate a further increase. The "no-vibration baseline" (*No*) was measured before neck vibration started. The three separate graphs illustrate means for each trial in the first, second and third block of SSA measurement, averaged across the subjects in the control group (*open circles*) or visual-memory group (*filled circles*). Ten trials were conducted in each block, with an inter-trial interval of 15 s. Neck-muscle vibration was continuous throughout

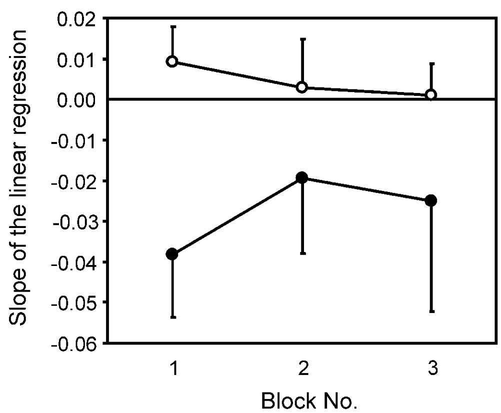

Fig. 5 Mean slopes of the linear regressions averaged across the subjects for each group in experiment 2, obtained in the three blocks of SSA measurement. *Open circles*, control group; *filled circles*, visual-memory group. Negative values indicate that the leftward deviation of SSA induced by neck vibration was diminished during the period of fixating the central visual target, and then increased again systematically for successive trials (see Fig. 4) when this central LED was extinguished

($F_{1,10}$=24.06, P<0.01), indicating that the two groups differed significantly at the first trials of the three blocks.

During the subsequent trials of measurement in a block (and thus with increasing time since the experimental visual stimulation), the deviation in the SSA due to neck vibration re-established itself in an apparently linear manner for the visual-memory group (Fig. 4), even though the neck vibration itself was continuous throughout. By the tenth measurement trial in a block, the SSA had reached approximately the initial deviation determined by the neck-vibration baseline, to a similar extent as in the control group. Note that this general pattern was observed in each of the three successive blocks of SSA measurement (see Fig. 4) and was apparent for every subject in the visual-memory group. Statistical comparison of SSA judgements obtained at the tenth trial of each block was carried out with a repeated-measures ANOVA for this variable with Subject group (control group, visual-memory group) as a between-subject factor and Block (1st block, 2nd block, 3rd block) as a within-subject factor. The analysis revealed no significant effects, indicating that there were no significant differences between the two groups at the tenth trials of the three blocks.

The observed trends were evaluated by linear regression. In the visual-memory group, the r^2-values for the regression were 0.89 in the first block of SSA measurement, 0.85 in the second, and 0.82 in the third block, indicating a substantial linear trend. The slopes of the regression lines were averaged across subjects for each block, and the resulting mean slopes are presented in Fig. 5, with standard errors shown. No consistent departure from a zero slope was found in the control group. By contrast, the slopes for the visual-memory group were consistently negative. This corresponds to the deviation of SSA induced by neck vibration initially being diminished, shortly after the period of attending the central visual target, and then re-emerging with the passage of time during which no central visual target was presented for the visual-memory group (see Fig. 4).

Discussion

Appropriate elaboration of body orientation normally depends upon symmetrical inputs from various afferent systems. If this afferent balance is disturbed, e.g. by lateralized lesions or by asymmetric stimulation, the perception of straight-ahead body orientation can be deviated to one side. Such deviations associated with asymmetric neural deficits have been found in patients with acute unilateral peripheral vestibular disorder (Hörnsten 1979), with hemianopia (Ferber and Karnath 1999), with optic ataxia (Perenin 1997) and with hemispatial neglect

(Heilman et al. 1983; Karnath 1994b; Ferber and Karnath 1999). Similar deviations have also been observed to follow asymmetric stimulations in normal subjects, for vestibular (Fischer and Kornmüller 1931), optokinetic (Brecher et al. 1972) and neck-proprioceptive manipulations (Jeannerod and Biguer 1987). Several recent studies have examined the combined influences of inputs from different receptors and different input modalities (Roll et al. 1991; Mergner et al. 1992, 1997; Karnath et al. 1994) and have shown that they may be integrated in an additive manner.

The present study confirmed and extended the effect of neck-proprioceptive input on the perception of body orientation in healthy subjects. Like previous studies, we found that asymmetric neck-proprioceptive stimulation leads to a disparity between subjective perception of body orientation and objective midlines. When asked to indicate the SSA during left neck muscle vibration, subjects adjusted the laser spot to the left of their midsagittal plane, by more than 6° on average. In contrast, nonspecific sensory stimulation on the left side of the body (in the present experiment, vibration of the left hand) did not significantly alter the position of the SSA. A novel aspect of both the present experiments lies in their demonstration that the influence of neck proprioception was fully maintained throughout 28 min of continuous neck muscle vibration (see Fig. 4). This clearly implies that the neck-muscle contribution to perception of the straight ahead orientation does not habituate over such long periods of continuous stimulation.

A previous study showed that short neck muscle vibration can induce a long-lasting postural sway while standing, with a mean shift of about 1.3 cm in the anterior-posterior direction for about 9–10 min (range 1–19 min) after vibration terminated (Wierzbicka et al. 1998). In general accord with these findings, the present experiment 1 demonstrated that vibration of neck muscles can lead to a prolonged disparity between subjective and objective body orientation, which continues for some time even after offset of the vibration. However, unlike the effect on the standing body posture (Wierzbicka et al. 1998), the effect of neck muscle vibration on SSA perception seems to last for a shorter period. The present data showed that the longer the vibration interval lasted, the longer the illusory deviation of SSA body orientation persisted after vibration was terminated. This may indicate that the sensory input from the neck proprioceptive system contributes to a relatively stable and enduring neural representation of body orientation in space, rather than contributing only to a peripheral reflex loop and/or inducing nystagmic eye movements at the time of vibration (Popov et al. 1999).

The study by Popov et al. (1999) has shown that vibration of the dorsal neck muscles in healthy subjects can elicit a discrete nystagmus, with slow-phase eye deviations towards the side of stimulus application reaching cumulative amplitudes between 0.5° and 1°. Since our subjects directed the laser spot to a mean SSA position of about –6° on the left side during left neck vibration, such small nystagmic eye-movements cannot provide a sufficient explanation for the observed results. Moreover, the present observation that prolonged neck vibration led to SSA deviation for some time *after* the vibration ended seems unlikely to be explained by any slight nystagmus also.

Our present findings concerning the prolonged effects of neck vibration on SSA judgements raise the possibility that such stimulation might be useful in the rehabilitation of asymmetric spatial deficits, as in unilateral spatial neglect. Spatial neglect is a laterized disorder that involves a characteristic failure to explore the side of space contralateral to brain injury, typically to the right hemisphere (Heilman et al. 1993). It has already been shown that asymmetric stimulation such as vestibular stimulation (Rubens 1985), optokinetic stimulation (Pizzamiglio et al. 1990) and proprioceptive stimulation by neck vibration (Karnath et al. 1993) can transiently ameliorate such deficits. Here we show that, in the normal system, the deviation in SSA induced by prolonged asymmetric neck vibration does not habituate under stimulation and has effects which endure after the vibration terminates. This raises the interesting possibility that neck-vibration interventions in neglect patients might analogously show such enduring effects, which could be used for the purpose of rehabilitation if they could be shown to extend over even longer periods than those used here.

In fact, substantial recovery of spatial neglect that outlasts the duration of the stimulation has recently been demonstrated following neck muscle vibration (Ferber et al. 1998; Schindler I, Kerkhoff G, Karnath H-O, Keller I, Goldenberg G, unpublished work). The latter study evaluated the long-term efficacy of combined vibration plus exploration training versus that of visual exploration training alone. The authors observed a specific and lasting reduction of neglect symptoms with neck muscle vibration which was superior to visual exploration training alone at follow-up testing 2 months after discharge. Although the effects observed in the present normal study may be too short to fully account for this patient result, nevertheless they point to one possible mechanism that might lead to long-term modifications.

A further novel aspect of the present findings concerns the modulating effect of visual stimulation, in the form of a central fixation point, upon the influence of neck-muscle proprioception, and the decay of this influence against time once the stimulus was removed. Subjective straight-ahead measurements taken shortly after termination of this fixation point showed much less influence of the continuous neck vibration. This influence then gradually increased, in an approximately linear manner, with the passage of time in complete darkness. The same extent of deviation for the SSA as found in subjects with no fixation point was reached within a couple of minutes (see Fig. 4). Evidently, the central visual stimulation could overcome the influence of the neck stimulation, perhaps reflecting “visual dominance”. Moreover, this influence of the visual stimulation continued for some time even after the fixation light was extinguished, in the form of a memory trace that gradually faded with time, as apparent in the slope of the functions for the visual-memory group in Fig. 4. These findings are in accordance with earlier studies showing that vision can dominate other modalities in determining subjective body orientation (Eklund 1973; Lackner and Graybiel 1979; Lackner and Levine 1979; Fiorentini et al. 1982; Velay et al. 1994).

A unique feature of the present study was that it examined the role of *remembered* visual information, not merely current stimulation, in order to determine the timescale over which crossmodal integration and visual dominance may take place with regard to the elaboration of egocentric space. We found that the influence of visual stimulation on the perception of body orientation, overriding neck proprioception, continued for some time even after the fixation after the light was extinguished. Further work could test whether this visual memory takes the form of a perceptual trace for the location of a central visual landmark, and/or of a proprioceptive (or even motoric) trace for the associated central eye position. We favour the former interpretation somewhat, since all subjects rapidly saccaded to the (pseudorandom) location where the laser beam appeared at the start of each trial in the SSA task (i.e. they did not hold central fixation once the LED was extinguished). Whatever the exact form of the visual memory trace, the present results unambiguously show that some form of visual memory is integrated with proprioceptive inputs in determining the SSA, and that this integration is sensitive to the delay over which the visual memory must be held. These findings from human performance may relate to recent data on single units in the monkey parietal lobe (Andersen et al. 1993; Snyder et al. 1998). For instance, neurons in area LIP have been observed whose visual responses are modulated by neck-proprioceptive inputs, and which continue to show visual responses even during delay periods where the visual stimulus is extinguished. Such “delay” activity may be the neural instantiation of the gradually fading memory trace that we found here to influence judgements of the SSA.

Acknowledgments This work was supported by grants to H.-O.K. from the Deutsche Forschungsgemeinschaft and the Bundesministerium für Bildung, Wissenschaft, Forschung und Technologie; and by a Medical Research Council (UK) Programme grant to J.D.

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