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Neck proprioception compensates for age-related deterioration of vestibular self-motion perception

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Abstract Vestibular functions are known to show some deterioration with age. Vestibular deterioration is often thought to be compensated for by an increase in neck proprioceptive gain. We studied this presumed compensatory mechanism by measuring psychophysical responses to vestibular (horizontal canal), neck and combined stimuli in 50 healthy human subjects as a function of age (range 15–76 years). After passive horizontal rotations of head and/or trunk (torso) in complete darkness (dominant frequencies 0.05, 0.1, and 0.4 Hz), subjects readjusted a visual target to its remembered prerotational location in space. (1) *Vestibular-only stimulus* (whole-body rotation); subjects' responses were shifted towards postrotatory body position, this only slightly at 0.4 Hz and pronounced at 0.1 and 0.05 Hz. These errors reflect the known physiological drop of vestibular gain at low rotational frequency. They exhibited a slight but significant increase with age. (2) *Neck-only stimulus* (trunk rotated, head stationary); the responses showed errors similar to those upon vestibular stimulation (with offset towards postrotatory trunk position) and this again slightly more with increasing age. (3) *Vestibular-neck stimulus combination* during head rotation on stationary trunk; the errors were close to zero, independent of stimulus frequency and the subjects' age. (4) *Opposite stimulus combination* (trunk rotated in the same direction as the head, but with double amplitude); the errors were clearly enhanced, essentially reflecting the sum of those with vestibular-only and neck-only stimulation. Taken together, we find a parallel increase in neck- and vestibular-related errors with age, in seeming contrast to previous studies. We explain our and the previous findings by a vestibular-neck interaction model in which two different neck signals are involved. One neck signal is used, in combination with the vestibular signal, for estimating trunk-in-space rotation.

It is internally shaped to always match the vestibular signal, so that these two signals cancel each other out when summed during head rotation on stationary trunk. Because of this matching, perceived trunk stationariness during head rotation on the stationary trunk is independent of vestibular deterioration (related to stimulus frequency, age, ototoxic medication, etc.). The other neck proprioceptive signal, coding head-on-trunk rotation, is superimposed on the estimate of trunk-in-space rotation, thereby yielding a notion of head-in-space. This neck signal remains essentially unchanged with vestibular deterioration. Generally, we hold that the transformation of the vestibular signal from the head down to the trunk proceeds further to include the hip and the legs as well as the haptically perceived body support surface; by this, subjects yield a notion of support kinematics in space. As a consequence, spatial orientation is impaired by chronic vestibular deterioration only to the extent that the body support is moving in space, while it is unimpaired (determined by proprioception alone) during body motion with respect to a stationary support.

Keywords Vestibular-proprioceptive interaction · Vestibular deterioration · Compensation · Age · Object localisation · Model · Human subjects

Introduction

Anatomical studies indicate that the number of vestibular hair cells (Rosenhall 1973), ganglion cells (Richter 1980), and nerve fibres (Bergström 1973) progressively decline with increasing age. Reports on corresponding changes in vestibular function, however, are less clear. For instance, some studies reported only a slight decrease in the gain of the vestibulo-ocular reflex (VOR) with age (Paige 1994; Peterka et al. 1990). As a synopsis of these earlier findings, there appears to be some deterioration of vestibular functions with age, which appears to be less pronounced than the corresponding morphological changes. A still open question is to what extent and in which

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way deterioration of vestibular input, related to age or other causes such as ototoxic medication, is chronically compensated for.

Deterioration of vestibular input is often thought to lead to a compensatory increase in the gain of neck afferent input. This notion goes back to the observation that bilateral loss of vestibular input and of the VOR is followed by an increase in the cervico-ocular reflex (COR), which normally is very weak, in both monkeys (Dichgans et al. 1973) and humans (Kasai and Zee 1978). The notion was adopted also to explain other enhanced neck responses observed following vestibular deterioration. This applies, for instance, to the movement illusion of a stationary visual target evoked by neck muscle vibration. This illusion, which cannot be explained fully in terms of a COR effect and therefore appears to arise at perceptual levels (Biguer et al. 1988), was found to be enhanced in patients with vestibular deficits (Strupp et al. 1998). Furthermore, the illusion was found to be more pronounced in healthy elderly subjects as compared to younger subjects, a finding which was considered to reflect an upregulation of the neck signal related to the vestibular deterioration with age (Strupp et al. 1999).

The above concept of an upregulation of neck gain upon vestibular deterioration is problematic, however. Given that neck proprioception is involved in the sensorimotor control of the head-on-trunk stabilisation, for instance, an above-normal increase in neck gain might be detrimental for this stabilisation. Even if one assumes that the increase is restricted to a version of the neck signal that is selectively used for orienting (oculomotor and perceptual) functions, the compensatory function of this neck signal would be restricted to behavioural situations where the head is rotated with respect to the stationary trunk. As regards the neck proprioceptive gaze stabilisation in vestibular loss subjects, one can assume that most naturally occurring head-on-trunk rotations are performed actively, while most head-in-space rotations occur passively upon motion of the trunk or the body support. In fact, the neck-related compensatory eye movement upon active head rotation has a shorter delay and appears to be more pronounced than the one with passive neck stimulation (this difference is usually acknowledged by using the terms 'active COR' versus 'passive COR'; for literature, see Maurer et al. 1998).

Concerning the perceptual effects of neck stimulation, we have compared self-motion perception in vestibular loss patients (Schweigart et al. 1993) with that in normal subjects obtained in an earlier study (Mergner et al. 1991) during various combinations of horizontal head-on-trunk and trunk-in-space rotations (natural neck and vestibular stimuli, respectively). We have shown that the self-motion perception of the patients during neck stimulation is abnormal. But this abnormality reflects a loss of one out of two neck signals involved, occurring in association with the loss of the vestibular signal, rather than representing an upregulation of the neck gain in general (see Schweigart et al. 1993, and 'Discussion').

With this in mind we reconsidered the aforementioned age-related increase in the neck-evoked perceptual shift of visual target location in space by Strupp et al. (1999). The methods we used differed from this previous study mainly in three respects. First, we used natural neck proprioceptive stimulation instead of muscle vibration; the natural stimulation has the advantage that it can be quantified precisely (defined in terms of amplitude, dominant frequency, etc.). Second, we used a task in which subjects indicated the localisation of a visual target in space before and after vestibular and neck stimulation, a procedure which allows precise psychophysical measures to be obtained (Maurer et al. 1997; Mergner et al. 2001). Third, we complemented the neck stimuli by vestibular stimuli as well as by combinations of the two stimuli. By this we aimed to include into our considerations the functional significance of the neck signal and its interaction with the vestibular signal.

Materials and methods

We studied 50 healthy subjects (Ss; 28 males and 22 females). Their age ranged from 15 to 76 years (mean \pm SD, 36.4 \pm 19.7 years). All Ss gave their informed consent. Subjects were in a good state of health at the time of investigation and, according to a questionnaire which all Ss answered, they had no history of vertigo or other neurological diseases. Integrity of vestibular function was ascertained by using caloric irrigation and rotational testing, measuring VOR with sinusoidal stimulation at 0.05–0.4 Hz with conventional electronystagmography or the use of Frenzel's glasses. In test trials we ascertained that Ss understood and followed the instructions; if this could not be ascertained, they were excluded from the experiments. The study was approved by the local Ethics Committee of the Freiburg University Clinics (108/97 and 256/01).

Apparatus, stimuli and procedures

The methods described in the following were originally developed in earlier studies of Maurer et al. (1997) and Mergner et al. (2001). In short, Ss were seated on a Bárány turning chair, with their heads fixed to a head holder by means of a dental bite-board in primary head-to-trunk position (head aligned with sagittal torso axis). The head holder was mounted on the chair. Both devices could be rotated about the same axis in the horizontal plane. They were driven by independent servomotors under computer control, which served also to match their dynamics. The chair was surrounded by a cylindrical screen (radius 1 m) onto which a red light spot ('target'; luminance \approx 20 cd/cm², diameter 0.5° of visual angle) was projected at eye level by means of a mirror galvanometer mounted above the Ss' heads, coaxial with the other rotation devices. The galvanometer received two independent input signals for horizontal rotation: (1) a computer-generated signal was used to present Ss with random target positions and then to repeatedly step the target by 10° to the right or left side (see Fig. 1), and (2) a potentiometer signal from a hand-held joystick by which Ss moved the target for their repeated responses.

At the beginning of each session and while the room was still illuminated, Ss were asked to align the target with their subjective mid-sagittal ('straight ahead'). They were instructed to remember the target position on the screen (in space) and always to reproduce this position whenever the target became visible again during the following experimental trials in the otherwise dark laboratory.

The trials consisted of four parts (see example in Fig. 1):

1. Indication of straight-ahead target position in darkness. After the room lights were extinguished, Ss were presented with the target at a random position in space. They were to bring the target by means of the joystick to the mid-sagittal position, as they had done before in the illuminated room. After 2.5 s, the target was extinguished for 200 ms. During this time the computer-generated signal stepped it by 10° randomly to the right or left side, forcing Ss to repeat the response. This process was repeated subsequently for a total of three responses in this 'indication sequence'.
2. Dark period and rotation stimulus. The target was extinguished and Ss remained in complete darkness for a variable period of time, during which their heads and/or trunks were rotated to either the right or left side (see below). They were to remember the prerotational target position in space.
3. Updating of the remembered prerotational target position. The target was presented again at a random position in space. Subjects were to reproduce its prerotational position in space. They did so 6 times in this 'indication sequence' [cf. (1) above].
4. Waiting period. In the dark, the chair and/or the head holder were rotated back to their primary positions with a velocity below the vestibular threshold. Thereafter, the screen was illuminated and Ss released their heads from the bite board to perform moderate head shaking and to perceptually reorient in space.

Rotational stimuli

During the dark period (2), one of the following combinations of vestibular and neck stimuli was applied:

- Vestibular-only (Vest). Starting from the primary position, the chair was rotated to the left or right (whole-body rotation).
- Neck-only (Neck). The chair was rotated as before, but simultaneously the chair-mounted head holder was rotated by the same amount as, but in the opposite direction to, the chair. This manoeuvre kept the head stationary in space while the trunk was rotating. We define the direction of the Neck stimulus by the relative excursion of the head with respect to the trunk.
- Vestibular-neck combination during head rotation on the stationary trunk (Vest + Neck). The previous two stimuli were combined by rotating the head holder on the stationary chair.
- Opposite vestibular-neck combination (Vest-Neck). The chair was rotated with double amplitude and simultaneously the head holder with the standard amplitude, but in the opposite direction. In doing so, the total head-in-space rotation (Vest) had the standard amplitude and was combined with the head-on-trunk rotation (Neck) of the same magnitude, but in the opposite direction.

Parameters of rotational stimuli

The stimuli consisted of smoothed ramp-like angular displacements starting from the primary position. The final displacement of the vestibular and neck stimuli was always 16° (standard amplitude; either to the right or left). The velocity profile was approximately bell shaped ['raised cosine' function, $v(t) = -A \cdot f \cdot \cos(2\pi f t) + A \cdot f$; with t = time, A = angular displacement = 16° , f = frequency]. The dominant frequencies used were $f=0.05$, 0.1 , and 0.4 Hz (stimulus durations, 20, 10, and 2.5 s, and peak angular velocities, 1.6, 3.2, and 12.8°/s, respectively). The rotation devices did not generate noticeable noise or vibration. Auditory orientation cues from the apparatus in the room were minimised by plugging Ss' ears. Subjects were instructed to relax their neck muscles during the stimuli and not to resist or actively follow the head-on-trunk excursion. Their horizontal head torque exerted against the head holder was recorded with a torsional strain gauge system.

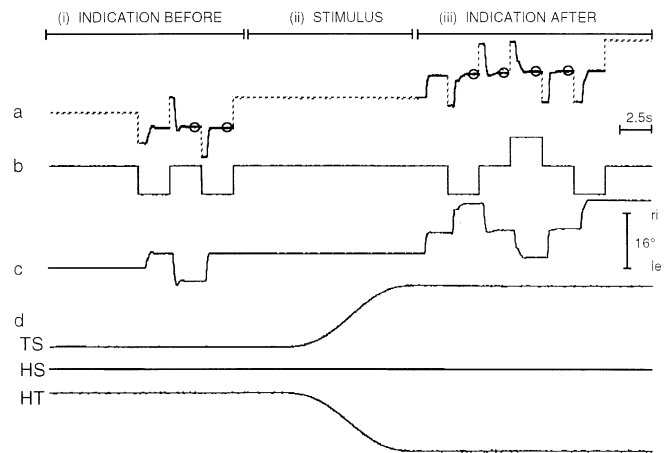


Fig. 1 Experimental paradigm used (example showing indication of remembered visual target location after neck stimulation with 0.1 Hz dominant frequency). The traces give: (a) target position (dashed/solid lines, target extinguished/visible; circles indicate samples used for analysis); (b) step input (inducing a sequence of target displacements, thereby forcing the subject to repeat the indications); (c) joystick signal (by which subject performs the indication); and (d) position signals of trunk (chair) in space (TS), head in space (HS) and head on trunk (HT). The plot shows the first three trial periods: (i) 'Indication of straight-ahead target position in darkness', (ii) 'dark period and rotation stimulus', and (iii) 'updating of the remembered prerotational target position' (not shown is fourth period, 'waiting period') (ri right, le left). For further methodological details, see 'Materials and methods'. Note that the postrotational indication is offset to the right with respect to the prerotational one, corresponding to an error of 14.4° in the direction of trunk displacement

Experimental session

Each session consisted of 24 trials: 4 stimuli (Vest/Neck) \times 3 frequencies \times 2 directions. The order of these trials was randomised. Longer breaks were given after each 4th–6th trial. A session usually lasted for 45 min. Experiments were repeated 4 times on different days.

Data acquisition and analysis

The potentiometer readings of the remote control of the target (joystick) and of the head torque versus the head holder were fed into a laboratory computer together with the on-off signals of target and background illumination and the position readings of the Bárány chair, the head rotation device, and the galvanometer (sampling rate 50 Hz; for measures of stimulus dynamics, noise, etc., see Mergner et al. 2001). Data were displayed online on a computer screen and stored simultaneously on hard disk for offline analysis. Analysis was performed using an interactive computer program, which automatically marked and averaged the last 20 data points that preceded each step displacement of the target (Fig. 1, circles in trace a); if correctly marked, they were accepted and stored. From these data we evaluated:

1. Prerotational indications of subjective straight ahead in the dark. We took the mean value across the 2nd and 3rd indication during the trial period (1) of each trial (always containing target steps to either side). The 1st indication was dismissed because it showed rather large variations and to balance the number of indications in each direction. The position readings were referenced to subjects' indications in the illuminated laboratory prior to the experiment.

2. *Postrotational indications.* For the trial period (3) we took again the mean value (\pm SD) across the 2nd–5th response in this indication sequence. The target steps for these four indications in the pseudorandom indication sequence always contained two target steps to each side; the 1st indication was again dismissed, because it showed rather large variations, and the 6th was dismissed to balance the number of indications in each direction.

The postrotational responses were referenced to the mean prerotational indication. Thus, Ss' responses are given in terms of reproduction errors of a match-to-sample task. An 'ideal' postrotational reproduction of prerotational target position would correspond to 0° . Since the visuo-oculomotor signals used for the reproduction are close to ideal, the errors predominantly reflect deficiencies arising in the vestibular and neck derived updating of trunk and head position after the rotational stimuli (see Mergner et al. 2001).

In the analysis, we calculated the mean of each subject's responses across the four trial repeats (\pm SD, $n=4$; as a measure of intrasubject, intertrial variability). Furthermore, we calculated from these values an average across all subjects (\pm SD, $n=50$; as a measure of intersubject variability). Statistics was performed by using ANOVA (StatView, Abacus Concepts; details are given in the 'Results').

Results

Prerotational indication of subjective straight ahead in the dark averaged $0.04^\circ \pm 2.55^\circ$ (mean \pm SD) across all 50 subjects and all trials (median value, -0.08° ; lower/upper 95% confidence interval of the median, $-0.35^\circ/0.27^\circ$; positive sign, deviation towards right). This value corresponds closely to the subjects' indication with the room light being on prior to each experiment (taken to be 0°). Intrasubject variability across trials (SD) amounted to $2.04^\circ \pm 1.30^\circ$, on average. The difference between the 2nd and 3rd response in the indication sequence across all subjects and trials averaged 1.06° .

Postrotational indications of prerotational target position varied as a function of frequency and combination of the rotational stimuli. An overview across all subjects is given in Fig. 2a–d. In this figure the indication errors are given as a function of stimulus frequency (abscissas) and stimulus combination (panels a–d). Since the data for rightward and leftward stimuli were statistically not different, they were pooled and plotted in relation to postrotatory trunk and head positions (dashed and dotted horizontal lines in Fig. 1a–d, respectively; thin full lines indicate prerotational target position corresponding to an error of 0°).

Vestibular-only stimulation (Vest, Fig. 2a)

After the 16° whole-body rotation at 0.4 Hz, Ss reproduced prerotational target position almost correctly (mean response is offset by 1.40° towards body excursion, i.e., Ss slightly underestimated the excursion; when viewed as vestibular gain in terms of reproduced versus actual displacement, $14.6^\circ/16^\circ$, $G=0.91$). The reproduction error became considerably larger at 0.1 Hz (8.13° ; vestibular

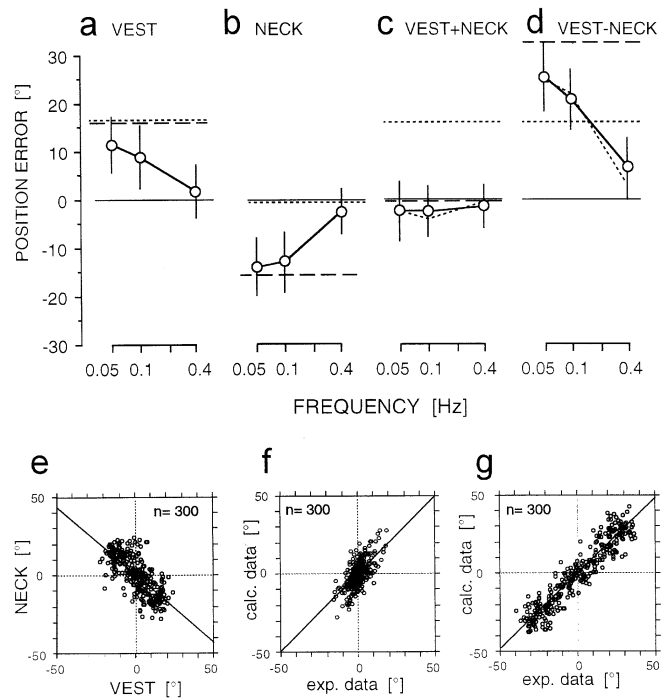


Fig. 2a–g Overview of subjects' localisation errors following the rotational stimuli. **a–d** Mean errors (interconnected circles; \pm SD) as a function of stimulus frequency, separately for the four different vestibular and/or neck stimulus combinations used. The data of right and left stimulus directions are pooled. *Dotted curves* in **c** and **d** give predicted results of the stimulus combinations Vest + Neck and Vest-Neck (linear summation of results in **a** and **b** for monomodal Vest and Neck stimuli, respectively). *Dashed and dotted horizontal lines* give postrotational trunk and head position respectively. **e–g** Correlation plots of individual data (across all stimulus frequencies) for Neck vs Vest (**e**) as well as for predicted vs measured data with the stimulus combinations Vest + Neck (**f**) and Vest-Neck (**g**)

gain, $G=0.49$) and even more so at 0.05 Hz (11.07° ; $G=0.31$). Upon questioning, some of the Ss reported in the 0.05-Hz trials that they experienced no body rotation (the reproduction errors of these Ss were close to 16°).

Neck-only stimulation (Neck, Fig. 2b)

Upon trunk rotation under the stationary head the reproduction responses were offset in the direction of the trunk displacement. The responses resembled those in Vest in that the reproduction error was small at 0.4 Hz and increased at 0.1 and 0.05 Hz (-2.88° , -13.60° , and -13.70° , respectively; negative sign indicating that direction was counter to head-on-trunk excursion; see 'Materials and methods'). According to their retrospective reports, at 0.4 Hz Ss perceived the trunk as being displaced and the head as stationary in space. Perceived trunk displacement became small at 0.1 Hz and was even absent in some Ss at 0.05 Hz; at these frequencies the head was perceived as rotated in space in the direction of the head-on-trunk excursion (in line with our previous

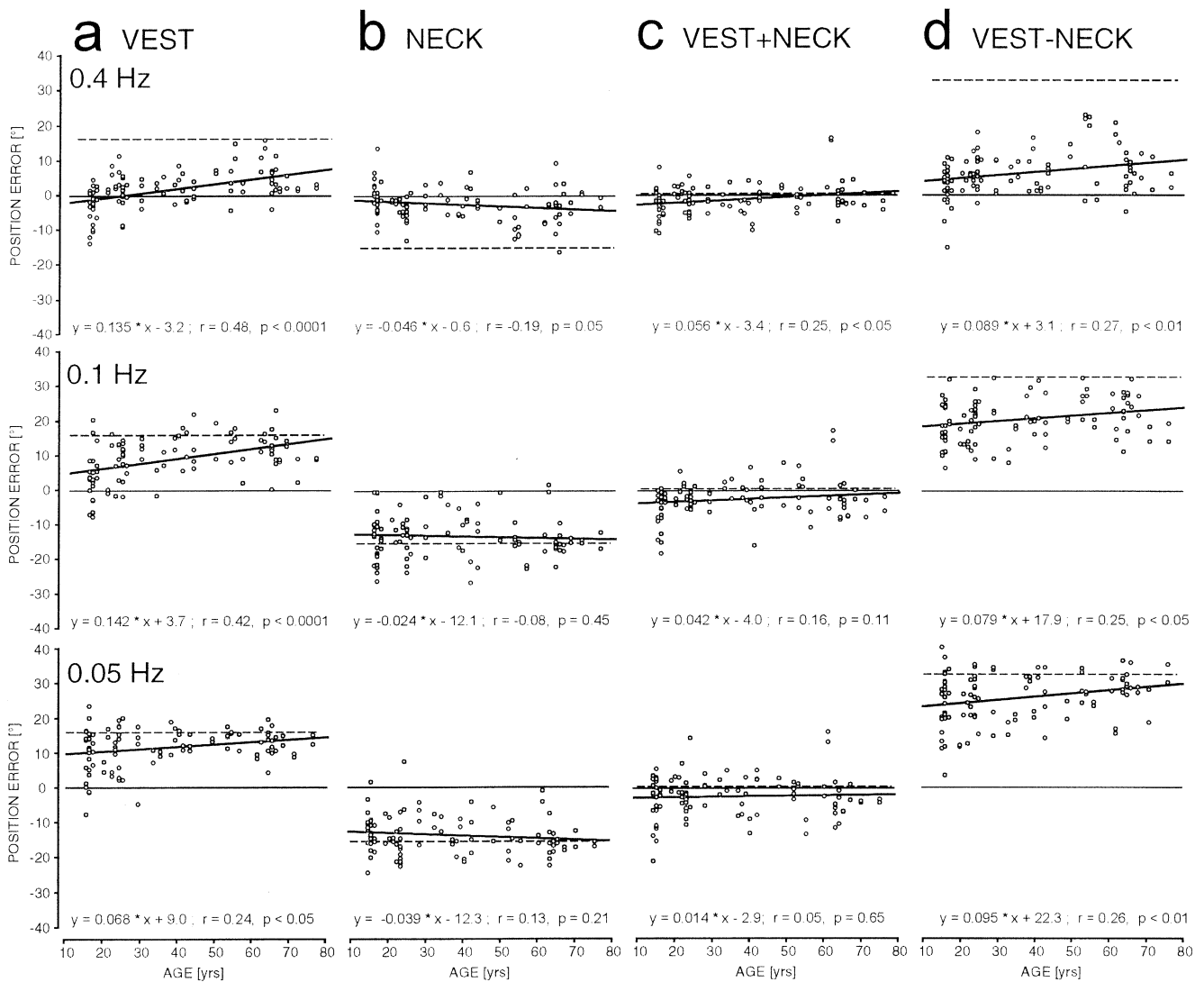


Fig. 3a–d Age dependency of vestibular and neck evoked reproduction errors. Subjects' individual responses are plotted as a function of age, separately for the four stimulus combinations (*columns a–d*) and for the three stimulus frequencies used (*rows*).

Otherwise, presentation is analogous to that in Fig. 2a–d (as a guide, only postrotational trunk position is given by *dashed lines*). Results of regression analyses are given below each panel

findings of a neck-induced head-in-space motion illusion with these stimuli; see Mergner et al. 1991). Subjects' errors upon Neck were closely related to those to Vest (panel e in Fig. 2; $y = -0.87x + 0.32$, $r = -0.73$, $P < 0.0001$).

closely corresponded to the measured one. Furthermore, we correlated calculated and experimental data on the level of the individual data (Fig. 2f). The correlation was highly significant ($y = 0.99x + 0.39$, $r = 0.65$, $P < 0.0001$).

Vestibular-neck combination during head rotation on the stationary trunk (Vest + Neck, Fig. 2c)

Opposite vestibular-neck combination (Vest-Neck, Fig. 2d)

Subjects' responses were almost veridical in that they deviated only slightly from the prerotational target position (0°) at all frequencies (-2.40° , -2.51° , -1.35° at 0.4, 0.1, 0.05 Hz, respectively). These results suggested that errors obtained with Vest and Neck cancel each other out by a mechanism that internally sums the two inputs. To test this notion we summed the corresponding mean error curves; the calculated error curve (dashed in Fig. 2c)

Subjects' responses were clearly offset towards the trunk, and this offset increased as frequency decreased (6.77° , 20.76° , 25.96° at 0.4, 0.1, 0.05 Hz, respectively). These results were compatible with the aforementioned summation hypothesis of Vest and Neck responses. Summation of the corresponding mean error curves (after sign reversal of the Neck responses to account for the 'opposite combination') indeed yielded a calculated error

curve that closely corresponded to the measured one (dashed lines in Fig. 2d). On the level of the individual data, there was a statistically significant correlation between calculated and measured errors (Fig. 2g; $y=0.97x+0.23$, $r=0.94$, $P<0.0001$).

Note from a global view on Fig. 2a–d that Ss' errors covary with trunk excursion and not with head excursion (which is especially obvious in panel c with Vest + Neck; for further consideration, cf. 'Discussion').

The effect of age

In Fig. 3 we display the reproduction errors of the individual Ss as a function of age, separately for the four stimuli (columns) and the three stimulus frequencies used (rows; as a guide we again give the trunk displacement, horizontal dashed lines). The age effects are given by the regression lines (corresponding equation, coefficient, and probability are indicated at the bottom of each panel). Further statistical analysis of the data was restricted to Vest and Neck (after sign reversal of the Neck data). It was performed with an ANOVA with the two 'within' factors Frequency (0.4, 0.1, 0.05 Hz) and Stimulus combination (Vest, Neck) and the 'between' factor Age (restricted to a bin width of decades, i.e., 10–19, 20–29, ..., 60–70 years). As can be expected from Fig. 2, there was a significant effect of frequency ($F=126.8$, $P<0.0001$). Age also had a significant effect ($F=4.9$, $P<0.005$) in that the error increased with age. Finally, there was no significant difference between the effects observed with Vest and those with Neck ($F=3.2$, $P=0.08$; this P value reflects the tendency of the errors with Neck to be slightly larger than those with Vest). There were no statistically significant interactions between the factors. Thus, the age effect was independent of stimulus frequency and of the two stimulus modalities.

As shown in Fig. 2, the frequency dependent errors almost completely vanished with Vest + Neck and increased with Vest-Neck. A similar effect might be expected for the age effect. Indeed, the age effect was essentially absent with Vest + Neck (see regression analyses in Fig. 3c) and clearly present with Vest-Neck (Fig. 3d).

Response variability

As to the variability of Ss' responses, we distinguished between three measures (cf. our previous study, Mergner et al. 2001):

1. *Indication precision.* Taking the SD values across Ss' responses within the indication sequence (period *iii* of Fig. 1; SD across 2nd–5th indications), we obtained a measure of how precisely Ss were repeating the spatial target location in space, which they remembered during their response. It averaged 1.3° across all trials and Ss. There was no statistical difference across

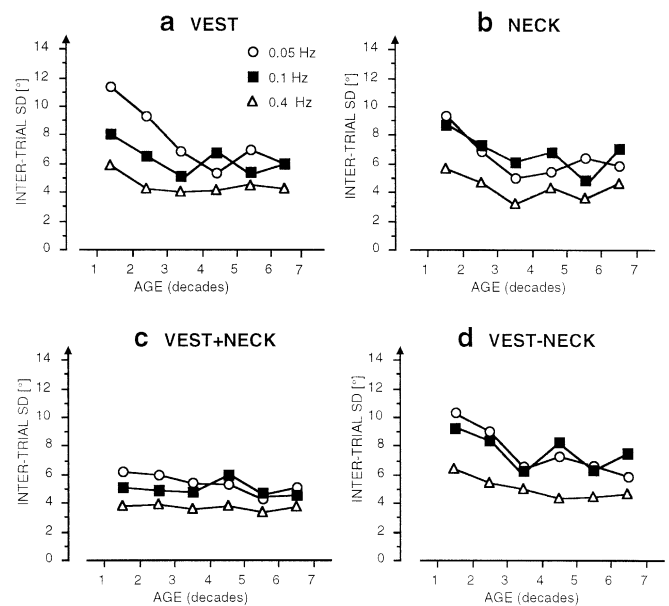


Fig. 4a–d Mean intraindividual response variability (intertrial SD values across the four trial repeats) as a function of age. The data are plotted separately for the different stimulus combinations (panels a–d) and frequencies (symbols). Note that this variability measure is always smallest at 0.4 Hz and smaller with Vest + Neck (c) than with the other three stimulus combinations (a, b, d). Note furthermore that the variability in these other combinations is larger in the youngest subjects than in the older ones

stimulus combinations and frequencies. It was also similar across age, with a trend for a minimum in the age group 30–39 years.

2. *Intertrial variability.* This variability measure (intra-subject mean of the SD values across the four trial repeats and two stimulus directions) has been shown to reflect mainly the 'noise' in the memory trace of target location (Mergner et al. 2001). Averaged across all subjects and stimulus frequencies, it was largest with Vest-Neck (7.2°), intermediate with Vest (6.7°) and Neck (6.3°), and smallest with Vest + Neck (4.7°). These values are somewhat larger (by $\approx 1.5^\circ$) than those obtained in our previous study; the comparison is somewhat hampered, however, by considerable methodological differences with the previous study (well practised subjects, rotational frequencies 0.1 and 0.8 Hz, centric as well as eccentric target locations). The values are plotted in Fig. 4a–d across subject's age, separately for the three stimulus frequencies and stimulus combinations. Generally, variability was lowest at the highest frequency (as in our previous study) and considerably larger at 0.1 Hz and even more so at 0.05 Hz (overall means 4.6° , 6.8° , and 7.2° , respectively). A surprising finding shown in Fig. 4a, b, d was that this variability measure was largest in the youngest subjects with all stimulus combinations apart from Vest + Neck (where it was similar across age).
3. *Intersubject variability.* This measure is given by the SD bars in Fig. 2. There was a tendency also for this

value to be smaller with Vest + Neck than in the other three stimulus combinations and to be smaller at 0.4 Hz than at 0.1 Hz and 0.05 Hz.

Discussion

Generally, deterioration of vestibular afferents with age appears to be pronounced, while degradation of vestibular functions with age appears to be moderate (see 'Introduction'). One likely reason is the well known principle of nature to start life with an abundance of cerebral and peripheral nerve cells to cope with their age-related reduction, so that a symptomatology does not occur until the number reaches a critical value. In addition, symptomatology can be circumvented to a certain degree by a number of other mechanisms, such as changes in behavioural strategies as well as neural compensatory mechanisms on a network basis. Such a compensatory mechanism is given by a change in neck proprioception in relation to vestibular deterioration. The present work confirms this phenomenon and tries to qualify the underlying mechanisms in its functional context.

Before considering the present findings, we address briefly some methodological problems related to the evaluation of the vestibular and neck derived self-motion perception. The perception was assessed with the help of a spatial localisation procedure which involved visuo-oculomotor function. This function was essentially the same across the variables considered here (stimulus frequency and combinations, age) and therefore should not bias the differential effects observed. Furthermore, we have shown in a previous study (Mergner et al. 2001) that a purely visuo-oculomotor reproduction of a remembered visual target location in space is performed almost perfectly, on average, at least in situations where subjects fixate the target with their eyes. The approach requires a number of methodological precautions which we have established in our previous work (Maurer et al. 1997; Mergner et al. 2001) and applied here. They comprise, among others, the use of a 'remote control' for indication in an intrasensory match-to-sample procedure (thereby avoiding sensorimotor 'distortions' as they are found with hand or eye pointing procedures). Finally, one may consider the eye movements occurring during the rotational stimuli in complete darkness a problem. However, we have shown previously for an eye pointing task (saccades to remembered target location in space) with the same combinations of rotational stimuli that the responses are independent of whether subjects fixate a head-fixed target or produce in complete darkness VOR and/or COR during the rotations (Mergner et al. 1998a). This finding is compatible with the notion that current eye position is taken into account in an almost ideal way (see Mergner et al. 2001). Taken together, we proceed in the following from the assumption that the errors we obtained in the study (reproduction of remembered target location following head and/or trunk rotations) essentially reflect

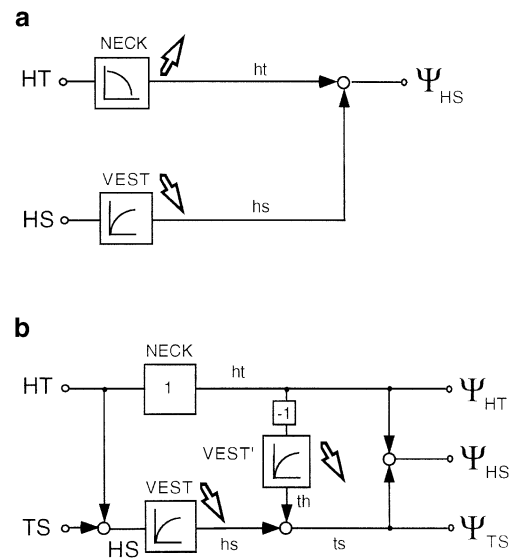


Fig. 5a, b Two models of vestibular-neck interaction (simplified). **a** Most parsimonious model, which describes the perception of head-in-space (Ψ_{HS}) by summation of a vestibular and a neck signal with reciprocal transfer characteristics (symbolised in box Vest by high-pass filter and in box Neck by low-pass filter, respectively). **b** Model representing a vestibular-neck interaction concept established by Mergner et al. (1991, 2001) (*HT*, *HS*, *TS* head-to-trunk, head-in-space, and trunk-in-space position, respectively; internal representations denoted by *corresponding lowercase letters*, perception derived thereof given by Ψ). Hollow downward/upward arrows symbolise decrease/increase of gain. Further details in text

the vestibular and neck contributions to our Ss' self-motion perception.

We found that our Ss' vestibular responses showed a small, but statistically significant, deterioration with age. Similarly, the reproduction errors upon neck stimulation tended to increase with age. This finding would be in line with a previous study by Strupp et al. (1999), who observed that the illusory motion of a stationary visual target upon neck muscle vibration increases with age. These authors took their finding to indicate an increase in neck proprioceptive gain related to an age-dependent vestibular deterioration. We hold that our findings, which included in addition the effects of vestibular and combined vestibular and neck stimulation, are able to explain these observations and to shed some light on the compensation of vestibular deterioration.

To explain our view, we consider in Fig. 5a, b two concepts of vestibular-neck interaction with each other, one (a) representing the most simple one we can think of and the other one (b) representing a concept we have established over the last few years (see Mergner et al. 2001). Both schemes focus on the fact that visual target localisation in space requires, in addition to a visuo-oculomotor notion of target-to-head position (omitted here, but considered in Mergner et al. 2000, 2001; Schweigart et al. 1999), also a vestibular-neck-derived notion of head-in-space position (Ψ_{HS}). The two schemes are functionally equivalent to a large degree (i.e. if details

such as detection thresholds are not considered; see Mergner et al. 2001), in that the neck input brings about a low-pass signal for Ψ_{HS} , which sums with the high-pass vestibular signal such that Ψ_{HS} is veridical (broad band-pass) during head rotation on the stationary trunk. The two models differ from each other in that in panel a the vestibular input is directly summed with one neck signal (showing frequency characteristics reciprocal to the vestibular ones), while there are two neck signals in panel b.

One of the neck signals in Fig. 5b (*ht*) shows approximately ideal frequency characteristics and codes head-to-trunk rotation (in line with previous findings of the corresponding head-to-trunk self-motion perception, Ψ_{HT} ; Mergner et al. 1991). The other represents an internal estimate of trunk-to-head (signal *th*, sign reversed version of *ht*), which internally has received the transfer characteristics of the vestibular signal (box Vest'). It yields in combination with the vestibular signal (*hs*) an internal notion of trunk-in-space (Ψ_{TS}). Note that Ψ_{TS} is always veridical when the head is rotated on the stationary trunk (*hs* and *th* signals cancel each other, so that $t_s=0^\circ$). Also Ψ_{HS} is then veridical, in that the veridical head-to-trunk signal (*ht*) is combined with the *ts* signal. On the other hand, Ψ_{HS} during neck-only stimulation yields a combined effect of *ht* and *th*, i.e. an illusion of head-in-space rotation at low frequencies, as described earlier (Mergner et al. 1991). Both models, a and b, produce this illusion. Note, however, that the model in panel b, although slightly more complicated, shows more explanatory power in that it describes more experimental findings (i.e. those for Ψ_{HS} as well as for Ψ_{TS} and Ψ_{HT} ; see Mergner et al. 1991). Note furthermore that equivalence of the model also applies to any vestibular deterioration (indicated in Fig. 5a, b by oblique downward arrows) and presumed associated compensatory changes of the neck signal. According to the version in panel b the compensation consists of a degradation of the neck signal *th* parallel to that of the vestibular signal *hs*, thereby predicting a degradation of the neck evoked Ψ_{TS} , parallel to the vestibular evoked one, while Ψ_{HT} and Ψ_{HS} during head rotation on the stationary trunk would not be affected (in this situation the two estimates are identical). These predictions were confirmed in a previous study on vestibular loss patients (Schweigart et al. 1993).

It is true that the model in panel a can also be extended to yield in addition to Ψ_{HS} also Ψ_{TS} and Ψ_{HT} . However, such an alternative topology could largely be excluded in a previous study with simulations of the models that included measured detection thresholds of the perception as well as biological noise (Mergner et al. 2001; see also below, response variability with Vest and Neck). Furthermore, we would like to point out that the vestibular-proprioceptive interaction considered here is only part of a more complex orientation mechanism (see Mergner et al. 1993, 1997). According to this concept, normal Ss use intersegmental proprioceptive inputs to perform a coordinate transformation of the vestibular

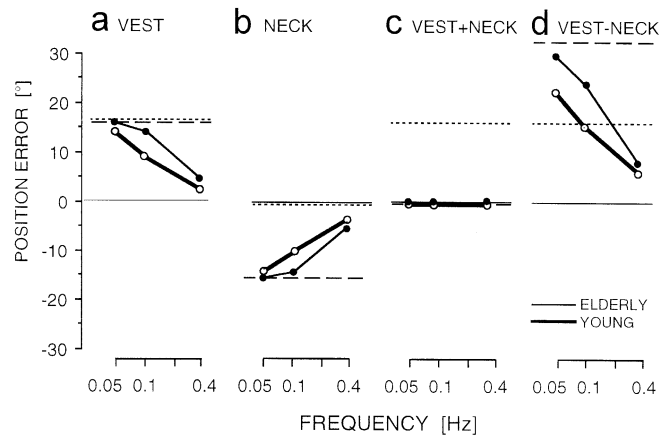


Fig. 6 Simulations performed with the vestibular-neck interaction model shown in Fig. 5b. Presentation is analogous to that in Fig. 2. By modifying gain and detection threshold (see text), we mimicked the effect of age in elderly subjects as compared to young subjects. Note that reproduction is veridical with Vest + Neck, independent of age

signal via the trunk and the legs to the perceived body support surface. On the thus derived internal estimate of support kinematics in space, they superimpose an estimate of body (head, trunk, etc.) motion with respect to the support, thereby yielding a notion of body-in-space motion. In this concept, vestibular loss patients do not perceive the support motion in space, but only the self-motion with respect to the support (in line with the observation that they show an essentially normal behaviour whenever moving on firm ground).

We used an extended version of the model shown in Fig. 5b (one that includes the sensory transfer characteristics and the visuo-oculomotor aspects of the task; see Mergner et al. 2001) to demonstrate that it is able to describe the data shown in Fig. 2 for the different stimulus combinations. Furthermore, we explored to what extent the model can describe the effects of a moderate vestibular deterioration such as that with age. To this end we varied in the model the detection thresholds T for *ts* and *ht* and the gain G for *ts* (young: $T_{ts}=0.6^\circ/s$, $T_{ht}=0.1^\circ/s$, and $G_{ts}=0.95$; elderly: $T_{ts}=1.2^\circ/s$, $T_{ht}=0.3^\circ/s$, and $G_{ts}=0.75$, respectively; T and G are not shown in Fig. 5b for the sake of brevity). These values were derived from observations in our previous work with only a few subjects, though (focusing on the youngest versus the oldest Ss in the study of Mergner et al. 1991, 2001). The results of the simulations are shown in Fig. 6a–d. They parallel, qualitatively at least, our experimental findings.

Noticeably, self-motion perception with head rotation on the stationary trunk is determined according to our model primarily by neck proprioception (the *ht* signal, since $t_s=0^\circ$). In this situation our Ss' reproduction errors did not show any considerable increase with age. This finding suggests that proprioception per se is not affected to a major degree by age. It is true that there are studies in the literature reporting some deterioration and threshold elevation of proprioception with age (e.g. Skinner et al.

1984; Pai et al. 1997), but the effects appear to be very subtle and considerably smaller than that of the vestibular signal.

Precision of indication (intratrial variability) in our Ss was similar to that found in our previous study (Mergner et al. 2001) and was essentially independent of age. Also intertrial variability, which appears to reflect a measure of the 'noise' of the memory trace for target location (see Mergner et al. 2001) was similar to that found before with respect to both the overall amount and the dependency on the stimulus combinations (variability of the self-motion perception shows a similar magnitude to that of vestibular and neck evoked eye movements, although both are only loosely related to each other; see Mergner et al. 1998b; also Peterka and Benolken 1992). An unexpected finding was that variability was larger in the youngest Ss versus the older Ss (>30 years; see Fig. 4). This may possibly be related to the higher detection thresholds in the older Ss. Variability of the vestibular signal is considerably higher than that of the proprioceptive signal and necessitates a relatively high detection threshold (approximately 3 times higher) to achieve perceptual stability of body and target position at rest (see Mergner et al. 2001). In our data the variability was high with Vest, Neck, and Vest-Neck as compared to Vest + Neck (cf. Fig. 4a–d). Noticeably, this minimisation of noise (variability) with head rotation on the stationary trunk is predicted by the model in Fig. 5b, while that in Fig. 5a would yield similar or even larger noise when comparing whole body rotation (input HS) with head rotation on the stationary trunk (inputs HS + HT).

In *conclusion*, we hold that the mechanism by which humans combine vestibular and proprioceptive inputs compensates not only for the vestibular deterioration which normally occurs at low rotational frequencies, but also for that associated with disease (e.g. vestibular loss due to basal meningitis) and with age. The reason is that humans reference their self-motion perception by means of reliable proprioceptive input primarily to the body support surface and use the vestibular input to take into account the support kinematics in space. This internal estimate of support kinematics is established with the help of proprioceptive signals which are centrally shaped so as to match the current vestibular transfer characteristics. As a consequence, the self-motion perception is affected by vestibular deterioration only to the extent that the support moves in space, while it is normal with firm ground.

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