VISUAL OBJECT LOCALIZATION THROUGH VESTIBULAR AND NECK INPUTS. 1: LOCALIZATION WITH RESPECT TO SPACE AND RELATIVE TO THE HEAD AND TRUNK MID-SAGITTAL PLANES

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Abstract — Object localization in space signals in the absence of an external reference (visual, auditory, haptic) involves a signal of the head in space (vestibular). The present study asks whether signals of body position relative to the support surface (proprioceptive) are involved as well, by investigating the role of vestibular–neck interaction (dissociating head and trunk position). Normal human subjects saw a light spot (object) and continuously nulled displacement steps of the spot. They did so before and after vestibular and/or neck rotational stimulation in the horizontal plane, reproducing a predesignated object localization in space (i), relative to the head mid-sagittal (ii), and relative to the trunk mid-sagittal (iii). The predominant frequency contained in the stimuli was varied (0.05, 0.1, and 0.4 Hz). (I) Object localization in space upon whole-body rotation (vestibular stimulus) at high frequency was veridical, whereas that at low frequency fell short. Almost identical results were obtained for trunk rotation about the stationary head (neck stimulus). In contrast, when combining the stimuli in the form of head rotation on the stationary trunk, the results were veridical, independent of stimulus frequency. Additional findings obtained with a large variety of vestibular–neck stimulus combinations suggest a linear summation of vestibular and neck signals. (II) Object localization with respect to the head was approximately veridical, being independent of vestibular and neck stimulation. However, this only applied if subjects were not biased by a head-in-space motion illusion of neck origin. (III) Object localization with respect to the trunk was veridical in all conditions tested. The findings support a recently developed concept, according to which humans evaluate the kinematic state of a visual object in space by (a) relating it to that of the body support by means of an essentially ideal proprioceptive coordinate transformation, and (b) relating, in turn, the kinematic state of the support to a vestibularly derived notion of space, using a proprioceptive coordinate transformation that “knows” the vestibular transfer characteristics. One important aspect is that object localization in space always is veridical during head and trunk rotation relative to a stationary support (for example, the ground) despite non-ideal vestibular transfer characteristics. Additional findings in patients with chronic loss of vestibular function confirm this concept. © 1997 Elsevier Science Inc.

Keywords — vestibular–neck interaction; visual object localization; self-motion perception; space coordinate system; trunk coordinate system; head coordinate system; human; vestibular loss patients.

Introduction

Object localization in space in the absence of an external (visual, auditory, haptic) reference is known to involve a signal of head position in space derived from vestibular cues (1–4). In addition, neck proprioceptive afferents appear to play a role. This is suggested by a recent study (5) which showed that perceived object motion in space at low frequency is erroneous during
whole-body rotation (vestibular stimulation), whereas that during head rotation on the stationary trunk (combined vestibular–neck stimulation) is veridical. This finding, and a number of related findings on human self-motion perception, recently led us to develop a concept of how axial proprioception is involved in tasks that require a vestibularly derived notion of space (6).

The present study addresses the question of whether this concept also holds for visual object localization in space.

Psychophysical studies on vestibular–neck interaction for human self-motion perception showed that perceived trunk motion in space can be described as resulting from a linear summation of a vestibular signal of head motion in space with a neck signal of trunk excursion relative to the head [(7,8); summation applies if vestibular and proprioceptive inputs arise in co-planar planes, whereas a more complex coordinate transformation is required in the general 3-dimensional case, (6)]. Originally, this kind of vestibular–neck interaction was proposed for postural control (9,10), in order to account for the fact that trunk stabilization by means of vestibular-spinal and cervicospinal reflexes is performed as if the responsible sensor organs were located in the trunk. Experimental evidence for this reflex interaction was obtained in the decerebrate cat (11,12). Furthermore, neurons showing analogous vestibular–neck interaction have been found in the vestibular nuclei of the decerebrate cat (13) and in the vestibular nuclei and the cerebral cortex of the intact cat (14,15). However, evidence that the interaction plays a relevant role for human postural control is still scarce, a fact that is mainly related to the difficulty of coping with the vestibular and proprioceptive feedback loops in the postural control system [see (6)].

This difficulty does not exist with the psychophysical approach. By means of this approach, the concept of vestibular–neck interaction has been extended considerably. In the present form (6), it contains not only a “downward channeling” of the vestibular signal, but also an “upward channeling.” By “downward channeling” we mean that the vestibular signal is channeled downward through several coordinate transformations (by means of neck, trunk, and leg proprioceptors) to finally arrive at an internal notion of the kinematic state of the body support surface. Thus, the concept applies not only to the trunk and the seat of the rotation chair that is in fixed haptic contact with the trunk (as in the study on vestibular–neck interaction), but also to the legs and their (foot) support, as shown recently in a study on vestibular–leg proprioceptive interaction (16). An important aspect of this mechanism is that stationarity of the support during body motion is veridically perceived, despite non-ideal vestibular transfer characteristics [deficient at low frequency/velocity; (8)]. The reason is that the proprioceptive signals used for the downward coordinate transformation are given the same “error” as the vestibular signal by feeding them through an internal model of the vestibular system. As a consequence, during body rotation on stationary support, the proprioceptive signals cancel the vestibular signal, with “zero” as a result indicating “no motion.”

This part of the concept may be appreciated intuitively; when we stand passively with firm foot contact on a platform that starts to move, we primarily perceive motion of the platform, and consider motion of our bodies only a consequence of platform motion, in accordance with the physics of the situation. On the other hand, if the body support is stationary, our notion of its stationarity is not affected by head and trunk rotations.

The “upward” part of the concept is based on the observation that the perception of trunk-in-space and head-in-space rotation can be described by further adding (superimposing) proprioceptive signals of trunk-to-foot and head-to-trunk motion to the internal notion of the body support motion in space (“stack of coordinate systems”; (8,16)]. These proprioceptive signals, unlike those mentioned before, are almost ideal. A consequence is that, when the body support is stationary (for example, when we are standing on firm ground) the perception of head and trunk rotation in space is veridical.

The concept was further extended to also include the perception of visual object motion in space in the absence of a visual reference. As mentioned before, perceived motion of a visual
Object Localization in Space and to Own Body

Object is erroneous during whole body rotation (vestibular stimulation), but becomes veridical during head rotation on the stationary trunk (vestibular-neck stimulus combination), with the underlying vestibular-neck interaction being analogous to the one described above (5). Furthermore, a grossly erroneous object motion perception during low-velocity body rotation (below vestibular threshold) is considerably improved when leg proprioceptive input is added by placing the feet on a stationary support [rotating the body relative to the stationary feet (5)].

So far, the experimental evidence for the concept stems from experiments in which continuous sinusoidal rotations in the horizontal plane were used. Given that the concept equally applies to transient rotations and that the relevant information can be stored in short-term memory, it also should be applicable to object localization in space. Evidence that vestibular information following whole-body rotation can successfully be retrieved from memory has been shown in studies that used a “memory-contingent saccade” paradigm [(1-4); for analogous results with neck stimulation, see (17)].

These considerations led us to investigate visual object localization in space following vestibular and/or neck proprioceptive stimulation in normal human subjects. Furthermore, we evaluated subjects' object localization with respect to the head and to the trunk, since this represents an essential egocentric part of the localization mechanism (“object in space” = “body in space” + “object relative to body”). However, object localization with respect to the head was found to be contaminated by an erroneous percept of head-inspace rotation. This applied if subjects focused their attention on the head. We therefore also evaluated object localization relative to the head in a task in which subjects used the head as a reference, but did not attend to it (in a “straight ahead task”).

Furthermore, we asked what the consequences of vestibular loss would be for the object localization in space in the absence of visual and auditory cues. Based on previous work in patients with chronic loss of vestibular function (18), we postulated that it becomes essentially egocentric, but considered the possibility that it is contaminated by an erroneous neck proprioceptive signal.

Methods

Subjects

Fourteen normal adult subjects (Ns; mean age, 36 ± 8.2 years) and 3 patients (Ps) with chronic bilateral vestibular loss (32 ± 3.1 years) gave their informed written consent to participate in the study. The 14 Ns belonged to three subject groups. The first group performed a series of pilot experiments and consisted of the 4 authors and 3 naive Ns (in one experiment, 5 naive Ns, that is, two additional Ns from the second group). The second group performed the main experiments and consisted of 7 naive Ns. The third group performed control experiments and consisted of 3 Ns (two naive). The three Ps, whose vestibular loss was due to meningitis and/or ototoxic antibiotic treatment in early childhood, had already participated in a previous study dealing with a similar topic (18). Vestibular loss in Ps was confirmed by conventional caloric testing and almost complete absence of vestibular ocular reflex (VOR) during rotatory testing.

Apparatus

Subjects were seated on a turning chair for horizontal rotations, which was equipped with a head rotation device [see reference (8)]. Turning chair and head gear were driven by two independent position-controlled servomotors under the control of a laboratory computer which compensated for differences in the plant dynamics. The head holder carried a bite board, which was molded from each subject's dental impression. Subjects' heads were positioned, with a 15° nose-down inclination, such that the intersection of their inter-aural and naso-occipital lines was centered in the vertical rotation axis.

Test Stimuli

Rotation of the head in space (HS), which resulted from the sum of chair rotation in space (trunk in space, TS) and head gear rotation relative to the chair (head relative to trunk, HT),
was used to generate the vestibular stimulus (VEST; \( HS = TS + HT \)); pure vestibular stimulation was obtained by whole-body rotation (\( HS = TS, HT = 0^\circ \); Figure 1A). HT yielded the neck proprioceptive stimulus (NECK); for isolated neck stimulation, head gear and turning chair were rotated counter to each other so that the head remained stationary in space (\( HT = -TS, HS = 0^\circ \); Figure 1B). Rotation of only the head gear (\( HS = HT, TS = 0^\circ \)) was used for head rotation on the stationary trunk (stimulus combination \( VEST + NECK \); Figure 1C). Other stimulus combinations used will be explained below.

The rotational stimuli had a "raised cosine" velocity trajectory (stimulus velocity, \( v \), represented by a sinusoid at the frequency \( f \) in the form of a cosine, function plus offset value, \( v(t) = -A \cdot f \cdot \cos(2\pi ft) + A \cdot f \), for \( 0 < t < 1/f \), with \( t \) denoting time and \( A \) the amplitude of the angular displacement). Three different frequencies were used \( (f = 0.05, 0.1, \) and \( 0.4 \) Hz, corresponding to stimulus durations of \( 20, 10, \) and \( 2.5 \) s, respectively). The amplitude was held constant \( (A = 16^\circ, \) either to the right or left side with respect to the primary position), if not specified otherwise. The corresponding peak angular velocity values amounted to approximately \( 2.0^\circ/s, 4.0^\circ/s, \) and \( 14^\circ/s \). The use of these stimuli containing a predominant frequency allowed us to compare the present results to previous data obtained with sinusoidal rotations \( (5, 8) \). The rotations were applied in complete darkness, and auditory cues were minimized by plugging the subjects’ ears. Subjects were instructed to relax their neck muscles and not to resist or to help actively any imposed head rotation.

**Probe Stimuli**

Before and after the test stimuli, subjects were presented with a visual object which consisted of a red light spot \( (=20 \text{ cd/m}^2) \) emitted by a bright LED. The spot (diameter: \( 0.5^\circ \) of visual angle) was projected onto a cylindrical screen which surrounded the turning chair (radius: \( 1 \) m). It was projected via a mirror galvanometer, which was positioned above the head gear. Rotation of the mirror led to horizontal movement of the object on the screen at about the eye level of the subjects. The axes of chair, head rotation device and galvanometer were colinear.

The mirror galvanometer received two inputs. One input was generated by a computer and stepped the object \( 10^\circ \) either to the right or left side. At the time of the step, the object was extinguished for \( 100 \) ms. The second input into the galvanometer stemmed from a joystick which was handled by the subjects, who carried it in their hands. Upon object steps, they nulled the step displacement as fast as possible, trying to restore the instructed object location (see below).

**Experimental Procedure**

At the beginning of each run, the room was illuminated and subjects were asked to center the object in the mid-sagittal plane with respect to their bodies. In all subjects, this adjustment corresponded within \( \pm 1.5^\circ \) to the zero values of the chair and head rotation devices. It was stored as "objective" baseline value. Then the room illumination was extinguished and the first trial was started. With the head and trunk in the primary position, a first probe stimulus sequence was presented. This yielded the "subjective" baseline value for a given instruction (see below). Subsequently, the test stimuli were applied in complete darkness, followed by a second probe sequence which yielded the response to the test stimulus (see Figure 2). Thereafter, in complete darkness the same rotations as in the test stimuli were applied in opposite direction to bring subjects back to their primary position.

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![Figure 1. Test stimuli. Vestibular stimulation (VEST), resulting from head rotation in space (HS), was produced by trunk rotation in space (TS) without head-to-trunk excursion (HT). Neck proprioceptive stimulation (NECK) resulted from HT in the form of trunk rotation under the stationary head. Head rotation on the stationary trunk yielded the stimulus combination VEST + NECK.](image-url)
Object Localization in Space and to Own Body

Prior to the next trial, the room was illuminated and a pause was given, during which subjects reoriented, released their heads from the bite board, and performed moderate head shaking. A typical run consisted of 18 trials (3 frequencies × 2 directions × 3 different test stimuli) in a random order and lasted 30 to 40 min.

Instructions

In the main experiments subjects performed four tasks according to the following instructions:

1. “Attend to the position of the object relative to your trunk. Always center the object by means of the joystick with respect to the middle of your trunk.” (Trunk mid-sagittal task, or “trunk task.”)
2. “Attend to the position of the object relative to your head. Always center the object with respect to the middle of your head.” (Head mid-sagittal task, or “head task.”)
3. “First center the object with respect to the middle of your body. Remember the object’s location in space and restore this location following the trunk and/or head rotation.” (“Space task.”)
4. “Always position the object in the straight forward direction. It is up to your own preference how you solve this task.” (Subjective “straight ahead task”). (Note: The German term “Geradeaus” for straight ahead does not contain the addition “ahead.”)

Schematic Overview

An overview of the experimental paradigm can be derived from the scheme in Figure 8. With respect to the space task, the paradigm is similar to that used in a previous study on object motion perception (5). In short: Object-in-space position (OS) is determined by the step input

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Figure 2. Example of an original recording. Position traces as indicated. Full curves in uppermost trace indicate when the object was visible, dotted curves when it was extinguished (arrow; beginning of trial). Bold marks on this trace indicate the parts of the curve that were selected for analysis.
and the joystick \((J)\) input to the galvanometer. Object-to-head \((OH)\) is given by the sum of \(OS\) and \(-HS\). Given that subjects fixate the object with their eyes, as instructed, they register \(OH\) with the help of their visuo-oculomotor system (box VISOM; represented by an efference copy of eye position plus residual retinal displacement). A percept of \(HS\) and of \(HT\) is provided by the vestibular and neck proprioceptive systems, respectively (boxes VEST and NECK). The three inputs yield a percept of \(OS\) \((\psi OS)\). Deviations of \(\psi OS\) from zero \("0\"\), induced by either the object steps or the test stimuli (trunk and head rotations), are nulled with the help of the joystick. The validity of this nulling procedure has been demonstrated in the previous study [see (5)].

The paradigm can also be used for centering the object with respect to the head mid-sagittal \((head task)\) and the trunk mid-sagittal \((trunk task)\). In the head task, the most simple and straightforward way for subjects to solve the task would be to shift the object and the eyes such that they are centered with respect to the head \((OH = 0°)\). An analogous approach can be considered for the trunk task; subjects might null the sum of \(OH\) and \(HT\) \((object relative to trunk, \(OT = OH + HT\); with \(OH = -HT, OT = 0°)\).

Data Acquisition and Analysis

Position readings of the two galvanometer inputs (joystick, step signal), of the galvanometer output (object position), and of chair and head gear potentiometers as well as the LED intensity \((object on-off)\) were fed into a laboratory computer \((acquisition rate, 100 Hz)\) and stored on hard disk for off-line analysis. Using an interactive computer program, the data were displayed on a monitor as position traces. On the object position trace \((galvanometer output)\) the last 20 data points that preceded the next object step were marked (see Figure 2) and, if accepted as step response, were stored as displacement values in relation to the "objective" baseline value \((see above)\). The mean of these values before the test stimulus was taken as subjective baseline value. Values after the stimulus were related to the subjective baseline value, taking the mean difference as stimulus response.

In the main experiment, mean values \((±SD)\) of subjective baseline \((offset)\) and of stimulus response were obtained for each frequency, instruction, test stimulus, and direction \((n = 3 \times 4 \times 3 \times 2 = 64)\) across subjects. The statistical analysis included precision of baseline values and stimulus responses in terms of standard deviations across the 2nd through 5th step response in the probe sequences. Statistical significance was assessed by analysis of variance.

Pilot Experiments and Design of the Main Experiments

In the pilot experiments, the "head task" yielded grossly erroneous responses. A possible cue for this unexpected finding came from retrospective reports of the subjects for the NECK stimulus at 0.05 and 0.1 Hz in the "head task"; they perceived (erroneously) a head rotation in space with these stimuli \([obviously corresponding to the neck-induced head-turning illusion observed in a previous study; (8)]\). We therefore suspected that subjects, when attending to the head as instructed, were caught by a perceptual mode in which a head-in-space turning sensation considerably influenced their responses. This led us to search for a condition in which subjects would not attend to the head, but nevertheless choose the head as a reference for the centering of the object. This condition was found when we observed that subjects who, in a series of different tasks first were presented with the "straight ahead task," tended to use the head as a reference \((otherwise, they tended to carry over the reference of the previous task)\). We therefore included the "straight ahead task" in the study, in addition to the "head task."

A number of observations in the pilot experiments helped us design the main experiments. The parameters and procedures adopted for the main experiments are given in Table 1 \([compare also Figure 3]\).

Conventions

In the literature, localization of a visual object usually is termed egocentric if it is performed with respect to the trunk, the head, or the eyes.
In the present study, head and trunk were often dissociated. We therefore specify which body part we are referring to by using the terms head-centric or trunk-centric, and use body-centric when this distinction would be irrelevant (for example, when the head remains in primary position with respect to the trunk). Localization of a visual object with respect to external stimuli (visual, auditory, haptic) is usually termed allocentric or exocentric. In our study, subjects used for object localization in space an internal concept of external (physical) space which they derived from vestibular cues. To denote this particular condition we use the term spacecentric.

**Results**

In the main experiments, precision of baseline and response values was high (SD across the 2nd through 5th step response in the probe sequences: 0.82°, on average). Across trials, stimulus response precision was worse than baseline precision (0.93° and 0.70°, respectively; \( P < 0.001 \)), but this effect was mainly due to the negative aftereffect of the response (see Figure 3B). Baseline precision was independent of task, and response precision was independent of task, stimulus condition, direction, and frequency. Ns' baseline values showed an offset (bias) which averaged 3.9° across all subjects (positive value indicating bias toward the right side). Mean bias of individual Ns varied between 0.5° and 7.9° and was rather stable across trials; it may represent an idiosyncratic error in the visuo-oculomotor path. Response amplitudes for rightward and leftward stimuli were similar across instructions and test stimuli and therefore were pooled together. In the following, we give baseline and response values across subjects in terms of mean values (±SD), after having ascertained that there was practically no difference with respect to the corresponding median values.

**"Space Task"**

Ns' task was first to position the object with respect to the body mid-sagital (baseline value) and then to reproduce this location in space after the test stimuli (response). The results are shown in Figure 4A as a function of stimulus frequency. Note that the response of an ideal measuring device would exactly coincide with the baseline value (0°; "ideal response"), independent of the test stimulus.

**Whole-body displacement (VEST).** At 0.4 Hz, Ns reset the object almost back to its initial location, with a small error in the direction of the body excursion (2.3°). The error became progressively larger when stimulus frequency was lowered to 0.1 Hz and 0.05 Hz (9.1° at 0.05 Hz). Given that Ns' object-to-body localization is

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**Table 1. Parameters and Procedures Adopted for the Main Experiments**

<table>
<thead>
<tr>
<th>Parameters and procedures</th>
<th>Reasons for the choices</th>
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<tr>
<td><strong>Probe stimuli (object steps)</strong></td>
<td>Probe stimulus showed positive after-effect (Fig. 3A).</td>
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<tr>
<td>Right-left balancing of step direction (equal numbers; stimuli of same amplitude: 10°).</td>
<td>First response often inaccurate.</td>
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<tr>
<td>6 stimuli; first (and sixth) stimulus response omitted.</td>
<td>ISI of 1.5 s: Often inaccurate responses (low precision).</td>
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<tr>
<td>Interstimulus interval (ISI): 2.5 s.</td>
<td>ISI of 6 s: Often anticipated responses.</td>
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<tr>
<td><strong>Test stimuli</strong></td>
<td>Test stimuli were followed by negative after-effects (Fig. 3B).</td>
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<tr>
<td>VEST: Vestibular stimulus</td>
<td>Reference chosen in &quot;straight ahead task&quot; often depended on that in previous task.</td>
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<tr>
<td>NECK: Neck stimulus</td>
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<td>VEST+NECK: Combination during head rotation on stationary trunk</td>
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<tr>
<td>Each stimulus was followed by extensive break (see above).</td>
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<tr>
<td><strong>Order of task presentation</strong></td>
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<td>&quot;Straight ahead task&quot; first; order of remaining tasks randomized.</td>
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Figure 3. Aftereffects induced (A) by probe stimuli and (B) by test stimuli. (A) Nulling error of probe stimuli as a function of step amplitude (5°, 10°, and 20° to right and left side; positive and negative values, respectively). Head and trunk were in primary position. Note that 8 of the 9 Ns showed a positive aftereffect. Dashed curves give mean values (±SD). (B) Upper panels give the 2nd through 5th responses of the probe stimuli before the test stimuli, after the test stimuli, and after resetting Ns to their primary position (direction normalized; procedures as in main experiments). Mean values across 7 Ns, the 4 instructions, and the 3 test stimuli are plotted separately for the 3 stimulus frequencies used. Lower panels give the aftereffects that remained after resetting Ns to primary position (difference to baseline before the test stimulus), separately for the 3 frequencies and the 3 test stimuli (mean ± SD). Signs of errors are referred to head excursion relative to the trunk (NECK and VEST+NECK) and head excursion in space (VEST). Statistically, errors were independent of task, frequency, and test stimulus.

ideal, it is possible to extract from their responses a measure of perceived body-in-space displacement (by taking the ratio of “actual response” to “ideal response”). This yields, in terms of vestibular gain, 0.86, 0.57, and 0.44 at 0.4 Hz, 0.1 Hz, and 0.05 Hz, respectively. Thus, Ns underestimated body displacement slightly at high frequency and more pronouncedly at low frequency.
**Trunk displacement under the stationary head (NECK).** The responses resembled those with VEST. The response at 0.4 Hz was close to ideal (1.9°; that is, Ns placed the object close to their stationary heads), whereas those at 0.1 and 0.05 Hz were progressively shifted towards the trunk (9.7° at 0.05 Hz). Considering the responses in terms of neck gain (ratio of "actual response" to "ideal response"), the values amount to 0.92, 0.52, and 0.39 at 0.4 Hz, 0.1 Hz, and 0.05 Hz, respectively.

**Head displacement on the stationary trunk (VEST+NECK).** Ns' responses essentially coincided with the baseline value at 0.4, 0.1, and 0.05 Hz, which is ideal.

**"Trunk Task"**

The responses for object centering on the trunk mid-sagittal plane are given in Figure 4B. With VEST, an ideal response would be 16°, and Ns' responses are almost ideal across the three stimulus frequencies tested, apart from a slight overestimation. Also with NECK (trunk: 16°) and VEST+NECK (trunk: 0°), the responses are close to ideal, in that the object is closely aligned with respect to the trunk with either stimulus. Noticeably, response variability in terms of SD within and across subjects was lowest in the "trunk task" as compared to the "space, head, and straight ahead tasks."

**"Head Task"**

The responses for object centering on the head mid-sagittal are given in Figure 4C. With VEST (head displacement: 16°), Ns centered the object almost perfectly on the head at 0.05 Hz (16.2°), but overestimated its displacement slightly at 0.1 Hz and 0.4 Hz. With NECK (head: 0°) at 0.4 Hz, the response was essentially ideal (0.1°). However, it became progressively erroneous with decreasing frequency, being shifted in the direction of the relative head-to-trunk excursion (−5.8° at 0.05 Hz). Noticeably, Ns reported that, at low frequency, they felt their heads displaced in space in the head-to-trunk direction [neck-induced head-in-space turning illusion; see (8)]. With VEST+NECK (head: 16°), Ns' responses overshot the head by about 4° at all three stimulus frequencies.

**"Straight Ahead Task"**

As expected from the pilot experiments, Ns chose the head as a reference for this task; in Figure 4D, their responses fall close to the head lines with all three stimuli used. There were only minor deviations from an ideal response with VEST (slight overshoot) and with NECK (slight shift toward the trunk by 1.5° at 0.1 Hz and by 2.6° at 0.4 Hz), unlike with VEST+NECK (essentially ideal). The difference with the "head task" was most prominent for VEST+NECK (P = 0.001). Noticeably, after the run, none of the Ns reported a head turning sensation with NECK, unlike in the "head task."

**Control Experiments**

The above findings in the "space task" (erroneous responses to VEST and NECK, but veridical responses to VEST+NECK) support the hypothesis of a linear summation of vestibular and neck signals (see Introduction). To further corroborate this hypothesis, we tested, in addition, a large variety of different vestibular–neck stimulus combinations, using two combination sets. In one set the vestibular stimulus was kept constant (16°) and the neck stimulus was varied (−4, 0, 4, 8, 12, 16, 20°; Vest = const., NECK = var. set), and in the second set, vice versa, the neck stimulus was kept constant (16°) and the vestibular stimulus was varied (−4, 0, 4, 8, 12, 16, 20°; NECK = const., VEST = var. set). These stimuli were applied at 0.1 Hz.

A further reason for the control experiments was to test our assumption that the erroneous results obtained in the "head task" stemmed from the fact that our Ns used a spacecentric rather than an egocentric perceptual mode, identified by a head-in-space turning illusion with NECK. Therefore, the instruction in the "head task" was modified such as to focus attention on the object rather than on the head ("Attend to the object. Center it so that it is oriented in the di-
Discussion

Object Localization with Respect to the Body

There is a considerable amount of work in the literature on human egocentric visual localization, reviewed by Howard (19), which shows that the localization may be influenced considerably by the visual stimulus itself (for example, the spatial symmetry of a large visual stimulus relative to the observer) and by eccentric eye position in the orbit. In previous studies, in which visual object localization in space was used to derive a measure of perceived self-motion [for example, (1-4)], it was tacitly assumed that object localization with respect to the body is essentially ideal. Since in these previous studies, like in the present one, a small light spot served as visual object and the stimuli started from primary eye-in-head and head-on-trunk position, possible errors are likely to be small. With respect to our study, identified error sources were (a) the positive aftereffect of object steps (which we accounted for by balancing across rightward and leftward object steps), (b) the negative aftereffect that follows head and trunk displacement (leading to an error of about 0.5°, which still is contained in our data), and (c) the fact that object localization with respect to the subjective body mid-sagittal may deviate considerably from that to the "objective" one (this was taken into account by relating the stimulus response to the baseline).
Figure 6. (A–D). Responses of vestibular loss patients for object localization in space (A), with respect to trunk (B) and to head (C), and subjective visual straight ahead (D). Symbols give responses of individual patients. Otherwise, data is presented as in Figure 4.
Our concern with the assumption of an ideal egocentric object localization stemmed from a different finding. Object localization with respect to the head in the “head task” turned out to be grossly erroneous, especially with NECK, in that it was shifted off the head in the direction of the head excursion relative to the trunk at low frequency. With respect to the “space task,” however, we adhere to the assumption that it involves an essentially ideal egocentric object localization, and we offer an explanation for the finding in the “head task.”

We suspect that Ns, when attending to the head in the “head task,” were caught by a head-in-space turning illusion with NECK, which is pronounced at low stimulus frequency [see (8)]. This brought them into a spacecentric perceptual mode, in the sense that they perceived head-in-space displacement and nulled the object localization with respect to the head by creating a subjective object displacement in space of same magnitude (in terms of physical stimuli: \( \theta_{OH} = 0^\circ \), if \( \theta_{OS} = \theta_{HS} \)). This notion is further supported by the fact that the responses to both VEST and NECK were frequency dependent, while that to VEST+NECK was not, as it was found in the previous study on human self-motion perception in space [(8); note, however, that the clear overestimation observed with VEST+NECK remains unexplained].

Evidence for our assumption, that the object-to-head signal used for object localization in space is essentially ideal, is derived from the following three observations:

(a) When Ns used the head as a reference for the “straight ahead task,” the responses clearly coincided better with head position. Conceivably, Ns may have used a headcentric rather than a
spacecentric perceptual mode, in the sense that they simply nulled perceived object-to-eye and eye-in-orbit positions.

(b) The same applies to the “modified head task” in which we draw Ns’ attention to the object rather than to the head, and in which the responses coincided quite well with head position.

(c) Finally, the object localization with respect to the trunk was essentially ideal. This task, conceivably, involves a signal of the object-to-head position, which simply would have to be complemented by a trunk-to-head signal (again in terms of physical stimuli: object relative to trunk $OT = 0^\circ$, if $OH = TH$). Noticeably, the responses for this task were the most robust ones of all in the present study. We like to interpret this finding in a more general sense, by assuming that the trunk in our conditions stands for the haptically perceived body support (seat of rotation chair) and that it is the object localization with respect to the body support that is the most reliable one.

Object and Body Localization in Space

Given that the object localization relative to head and trunk used in the task of object localization in space is essentially veridical, we can use the latter data as measures of body localization in space and test whether our concept (see Introduction) applies to it.

As already mentioned in the Results, object localization in space following head and/or trunk rotations can be described by a linear summation of vestibular and neck effects, which resemble each other with respect to their dynamics. This is similar to the findings in our previous studies on human object and self-motion perception (5, 8), and we therefore interpret the data in an analogous way. Our interpretation is shown in Figure 8 in terms of a simple dynamic model, which is embedded in the schematic diagram of the experimental paradigm [for details of the model like the velocity thresholds, which explain most of the response dynamics observed in the present study, see (8)].

In the model, the boxes VISOM (visuo-oculomotor system) and NECK (neck proprioceptive system) are assumed to have essentially ideal transfer characteristics, while that of VEST (horizontal canal system) contains a high-pass filter and a velocity threshold, by which response gain is attenuated at low rotational frequency/velocity. The following processing steps are assumed to yield a perception of object-in-space displacement ($\Psi OS$):

1. The vestibularly derived percept of head-in-space displacement ($hs$) is used to internally reconstruct a trunk-in-space signal ($ts$) by summing $hs$ with a version of the neck proprioceptive head-to-trunk signal ($ht$). The latter ($-ht'$) is obtained by reversing $ht$ in sign ($-1$) and endowing it with the vestibular transfer characteristics (vest). Note that this represents the “down-channeling” of the vestibular signal by proprioceptive coordinate transformation, which was mentioned in the Introduction. Here it yields a veridical notion of the trunk’s kinematic state during head rotation on the stationary trunk.

2. Adding to the $ts$ signal the original $ht$ signal, which is essentially ideal, yields a notion of head-in-space displacement $hs'$, which is superior to the vestibular $hs$ signal, in that it is veridical with head rotation on the stationary trunk even at low frequency/velocity. This represents the “up-channeling” of the vestibular signal in the concept.

3. Finally, addition of an ideal object-to-head signal ($oh$) yields the signal for $\Psi OS$.

Computer simulations of the model yield results that closely correspond to those obtained experimentally (not shown). We therefore conclude that our concept on the role of axial proprioception for object and self-motion perception equally applies to human object localization in space, at least with respect to the neck proprioceptive input tested here.

There remains a discrepancy with a recent study (3), which reported that the vestibular responses show a gain attenuation at low stimulus velocity, while the neck responses do not. The authors themselves considered the possibility that the difference is somehow related to the fact that, for neck stimulation, their subjects’ heads were fixed by means of a clamp to the wall. We feel that this anchoring of subjects’
heads likely explains the discrepancy, leading their subjects to use the wall as a reference with neck stimulation, while in our experiments (head rotation device mounted on rotation chair), subjects could not resort to an external reference and were forced to base their perception of trunk rotation on the vestibularly derived notion of space during both vestibular and neck stimulation. Other methodological differences between the studies (the authors used a “memory-contingent saccade” paradigm) are probably of minor importance.

**Vestibular Loss Patients**

In a previous study (18) we observed that vestibular loss has a substantial influence on how Ps use their neck proprioceptive afferents. Trunk rotation under the stationary head in Ps does not elicit a trunk-in-space turning sensation (instead, Ps perceptually interpret the neck excursion as head-in-space movement). This finding was predicted from our concept of vestibular–proprioceptive interaction. The reader may appreciate this by referring to Figure 8: if the $hs$ signal is missing, the $-ht'$ neck signal becomes obsolete and is eliminated; otherwise, an erroneous $ts$ signal would arise during head rotation on the stationary trunk. The present results are in line with the previous findings; in the “space task,” Ps placed the object close to their trunk mid-sagittal planes with NECK (and similarly with VEST and VEST + NECK in Figure 6A; also in Figure 7A). Thus it appears that Ps, when deprived of visual or auditory references, resort to their trunks (actually, haptically perceived trunk support, which appears stationary to them) as a reference in tasks that require a notion of space [compare (18)].

A further, still unexplained finding in the previous study (18) was that Ps considerably overestimate the head-on-trunk excursion at mid to low frequencies (for the Ps, perceptually equivalent to a head-in-space excursion). This can be taken to explain Ps’ erroneous object localization relative to the head in the “head task,” assuming that they were caught by a “spacecentric” perceptual mode, as explained above for Ns. However, unlike in Ns, the error was only reduced or even unaffected when we tried to draw their attention away from the head towards the object in the “straight ahead task” and the “modified head task,” respectively. Possibly, they had difficulties resisting the neck-induced head-in-space turning illusion, which is much more pronounced in Ps than in Ns. In support of this interpretation, we note the finding that Ps actually used an ideal object-to-head signal in the “trunk task”; their object localization relative to the trunk, which necessarily involves an object-to-head signal (see above), was “correct.” Thus, it appears that Ps use an ideal object-to-head signal for object localization when they attend to an external reference (body support, seat of the rotation chair in our experiments), but are prone to errors when attention is drawn away from the reference.
Object Localization in Space and to Own Body

This notion is supported by our previous study on patients (18); their overestimation of head-to-trunk and trunk-in-space rotation disappeared when they were provided with an external space reference (stationary visual cue or hand contact with ground-based support). Furthermore, the hypothesis may explain why vestibular loss patients in the above mentioned “memory-contingent saccade” study (3) performed normally with neck stimulation. Given that these patients used the clamp on the wall as reference (see above), we would expect their neck response to be normal.

Taken together, we feel that the Ps’ data are compatible with our concept of how humans use proprioception for spatial orientation. With respect to object localization in space in the absence of a visual or auditory reference, Ps use the body support as a reference, like Ns, but unlike Ns are unaware of the kinematic state of the support.

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REFERENCES


