



VESTIBULAR–NECK INTERACTION AND TRANSFORMATION OF SENSORY COORDINATES

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□ Abstract—The article considers findings and concepts on vestibular–proprioceptive interaction for self-motion perception and postural control under the form of simple describing models. It points out that vestibular–neck interaction is only a small fraction of an extended mechanism of coordinate transformations. This links together the different parts of our bodies, so that sensory information arising in one part of the body can be used for perceptual or motor tasks in other parts. Particular emphasis is put on the problems that arise from imperfect signal transduction in the vestibular semicircular canal systems at low stimulus frequencies/velocities. Also, a “down-and-up-channeling” principle is suggested, by which the body support is linked via coordinate transformations to the internal notion of physical space provided by the vestibular system. Furthermore, the following question is addressed: how does the brain use visual input to overcome the vestibular deficiencies, at the risk of visual self-motion illusions? Finally, a conceptual model of postural control is presented in which a proprioceptive feedback loop that links the body to its support surface is merged with a loop for postural stabilization in space.

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□ Keywords—vestibular–neck interaction; proprioception; visual–vestibular interaction; postural control; coordinate transformation; human.

Introduction

If we want to use the sensory information provided by the sensory systems located in our heads (vestibular, visual, auditory) for postural or perceptual control of upright stance, our brain has to take into account that the head is movable with respect to the trunk and, hence, also relative to the support surface we are standing on. Consider, for example, the semicircular canals of the vestibular system and one of their targets during postural control, the leg muscles. Having a fixed orientation in the head, each canal will indicate head velocity in specific planes defined by head anatomy. It is therefore convenient, and concurs with intuition, to treat these signals as being “coded in *head coordinates*,” although the cause of these signals is an acceleration with respect to a fixed inertial coordinate system. On the other hand, the leg muscles used to compensate body sway, act about axes defined by the position of the corresponding foot on its support. Therefore, their innervation can be viewed in terms of the intended rotation (or torque) about these axes and, hence, as being “coded in *foot coordinates*.”

The way a given canal signal acts upon a given muscle in the act of stabilization obviously depends on canal orientation with respect to the foot and, hence, on head-on-trunk-to-foot

position.¹ A human investigator who wants to understand the mechanisms of postural control, may interpret this dependence as the result of a coordinate transformation. This interpretation invites further abstraction: In dealing with postural reflexes one may postulate (i) signals that directly indicate position, velocity or acceleration with respect to an inertial frame of reference (which can only be arrived at by appropriate coordinate transformations of primary sensory signals), (ii) a computation of corrective signals (for example, torques) therefrom, and finally (iii) a transformation of these desired torques into innervations coded in coordinates of the participating muscle.

Whether functional entities corresponding to these constructs exist in the real central nervous system (CNS) is, as yet, an open question. We cannot exclude that the three separate steps of the human mind outlined above are lumped into a dedicated network of neurons providing multiple (polysynaptic) connections of every canal with every muscle, as would be the case with a technical learning network trained to reproduce human postural behavior. However, we feel that the CNS is much more structured than technical networks, and that its hierarchical architecture could well accommodate abstract levels of processing between the primary sensory and motor levels, which undoubtedly would contribute to its flexibility. On the motor side, a certain type of abstraction can be recognized in the tight intraspinal coupling of synergistic muscle groups. Therefore, we conceive of the coordinate transformation as being performed in a global way, before a compound motor plan is formulated to concert muscle actions. Moreover, we know from psychophysical studies that on the perceptual level, humans can indeed transform their primary sensory signals into such abstract notions as 'head velocity in space' or 'trunk velocity in space', to name only two. Accordingly, in the present article, we proceed from the notion that coordinate transformations may con-

stitute an important organizational principle of the CNS, for both perception and motor control.

The need for a coordinate transformation of vestibular signals was anticipated by von Holst and Mittelstaedt (1) in their classical paper on the "Reafferenzprinzip", in which they state that, due to a subtractive interaction of vestibular and neck afferents, control of trunk posture by the vestibular system proceeds as if the vestibular organs were actually located in the trunk ("... der Organismus sich so verhält, als ob der "Lagesinn" normalerweise im Leib säße . . ."; p 475).² Studies in decerebrate cat support the notion of the trunk posture being controlled by a subtractive interaction of vestibular and neck afferents (2,3). Also, recordings of vestibular nuclear neurons during lateral head and/or trunk tilt in the decerebrate cat (4) and during horizontal rotations in the intact cat (5) revealed subtractive (and additive) interactions between vestibular and neck inputs. Moreover, subtractive and additive interactions of vestibular and neck afferents have also been observed in the cerebral cortex of the intact cat (6,7).

In the intact cat, certain head and body postures during natural behavior are reminiscent of what one might expect from a subtractive vestibular-neck interaction (8), whereas experimental stimulation of these inputs do not readily reveal the expected interactions. In humans, reflexes reminiscent of the cervico-spinal ones in the decerebrate cat are seen only in the first month after birth (9,10) or following extended brain lesions (11,12). In the healthy adult, by contrast, for a long time only sparse evidence for a vestibular-neck interaction in postural control was obtained (13).

More recent studies on human posture control directly support the notion of the above outlined coordinate transformation. With natural body sway during tilt of a platform, compensatory postural reactions are essentially independent of the head-on-trunk position. In contrast, the body sway resulting from galvanic vestibular stimulation changes direction in direct relation to the horizontal head-on-trunk and trunk-

¹We here proceed from the assumption that the main source of inertial stabilization of posture is the vestibular system, although somatic graviceptors may also play a role (see Mittelstaedt, this volume).

²This idea goes back to Mittelstaedt's PhD thesis of 1949 (see Mittelstaedt, this volume).

on-foot excursion (14–16). Galvanic stimulation with the head in the primary position leads to a body sway towards the ear where the anode is fixed, whereas the same stimulus with the head horizontally rotated 30° to the right side, for instance, evokes a body sway that also is shifted 30° towards the right. Apparently, the galvanic vestibular stimulus, which is fixed in head coordinates, is transformed into space coordinates by means of neck afferents—much as a physical, and hence head position dependent acceleration would be. Whereas with the physical (tilt) stimulus, this transformation compensates for head-on-trunk rotation and keeps the postural reaction constant, it makes the reaction directly dependent on the neck input with galvanic stimulation.

In everyday life we perform most of our postural reactions more or less automatically, reserving our limited capacity of attention for other tasks we are performing while standing or walking. However, we can focus our attention on, and consciously perceive, our bodies' motion and the evoked postural reactions. Therefore, it appears possible to learn about the central processing of the involved sensory cues by studying self-motion perception, using classical tools of vestibular psychophysics and developing new ones. The psychophysical approach may be advantageous in several respects. Experiments can be designed to involve primarily passive stimulations, to be open loop (no feedback by postural reaction), to be independent of the body's biomechanical properties and constraints, and to consider simultaneously or successively several individual aspects of a complex stimulus condition. Also, the psychophysical approach may reveal global aspects of the central processing that are similar to those that possibly underlie the formulation of compound motor reactions.

In the following, we will sketch a picture of how we see the role of coordinate transformation of vestibular signals for motion perception and postural control. First, we will consider the notion that coordinate transformation basically serves the purpose of reconstructing, in our brains, the physics of our bodies and the outside world. Second, we shall reconsider findings on vestibular–proprioceptive interaction for human ego–motion perception from this and other lab-

oratories. In doing so, we will interpret a previously suggested model of this interaction from the point of view of coordinate transformations between a hierarchy of superimposed coordinate systems, and we will also discuss problems arising from imperfect signal transduction by receptors. Moreover, in view of their importance for ego–motion perception, we will touch on certain aspects of the interaction of visual cues with vestibular and proprioceptive ones. Finally, we will try to link these considerations to the control of body posture and present a hypothesis on how to merge a proprioceptive feedback loop stabilizing the body relative to a pivoting support with a vestibular one controlling body posture in space. In the appendix, we give a brief outline of the mathematics describing the 3D-coordinate transformations of vestibular input by proprioceptive input, which we think may be applicable to both perception and postural control.

Transformation of Vestibular Signals

Figure 1A illustrates the need for a transformation of the vestibular signals involved in the control, or the perception, of trunk posture. A subject who intends to maintain an upright posture is tilted forward while his head is in a retroflexed position. His otolith signals will indicate head-in-space excursion (angle HS) which, in the simple situation of Figure 1A (axes of trunk and head rotation collinear), equals the sum of the trunk-in-space excursion (angle TS) and of the head-on-trunk excursion (angle HT ; $HS = TS + HT$). This relation can be interpreted as the special case of a coordinate transformation that describes how the physical TS signal acts upon the vestibular system (Figure 1B). Under more general conditions (TS -axis and HT -axis not collinear), the transformation corresponds to a matrix operation (compare Appendix).

Let us briefly state some conventions used throughout this article: Rotations about positive angles are counterclockwise (TS is negative in the example of Figure 1A), and coordinate systems are right-handed. Uppercase pairs of letters represent actual physical quantities, lowercase pairs of letters stand for an internal representa-

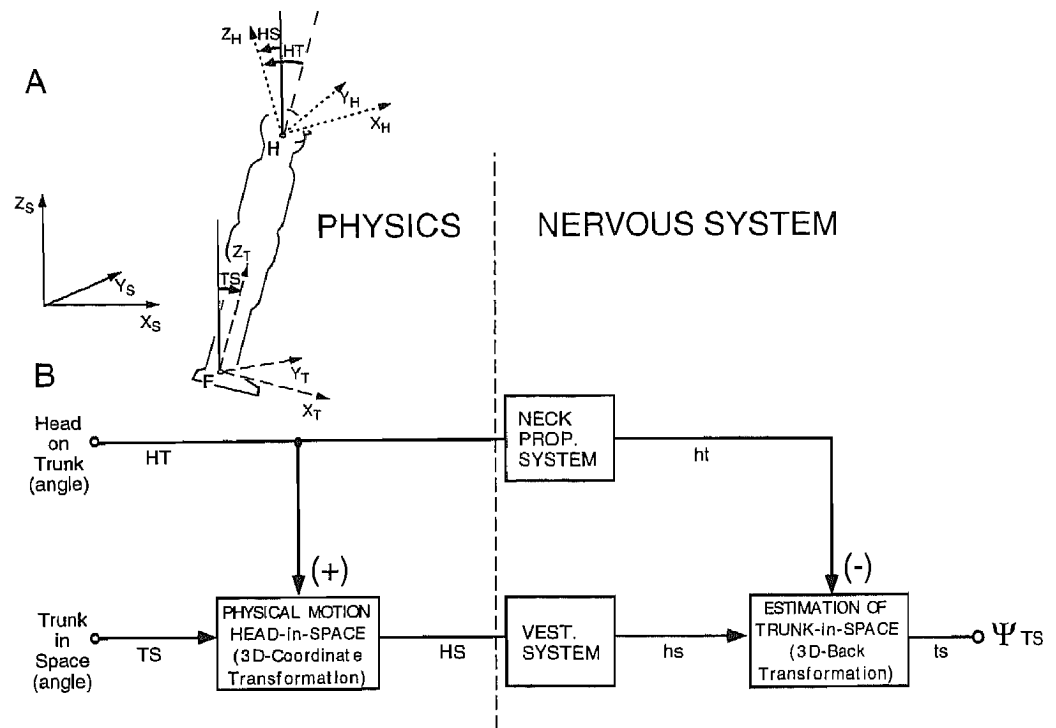


Figure 1. Schematic illustration of the need for 3D-coordinate transformation of vestibular signals used for postural control. (A) Conventions used. Head coordinates (X_H, Y_H, Z_H), trunk coordinates (X_T, Y_T, Z_T), and space coordinates (X_S, Y_S, Z_S), of a subject whose trunk is tilted forward while his head is in retroflexed position (right-handed coordinate systems). For F, "foot point", and H, "head point", see Appendix. (B) Simplified model showing how the nervous system reconstructs physical trunk-in-space (TS) motion for self-motion perception (Ψ_{TS}). The vestibular stimulus of head-in-space (HS) motion results from a coordinate transformation of TS by head-on-trunk motion (HT) corresponding to the kinematic relation between head and trunk. A back transformation of the internal representation of HS (vestibular signal hs) by the neck proprioceptive signal ht yields an estimate of TS (ts). If TS and HT are colinear, these transformations correspond to simple summations (signs in parentheses).

tion of those quantities, and the ψ -prefix stands for perception, or more precisely, the value reported by the subject.

HS , the transform of TS , causes an otolith response (hs) reflecting the magnitude of HS . In order to learn about the underlying trunk-in-space excursion, this physiological signal must be submitted to an inverse transformation using the proprioceptive signal ht as an indicator of head-on-trunk excursion. In our simple example, the inverse transformation simply consists of subtracting ht from hs ($ts = hs - ht$). Again, in the general 3D case, the mathematical description involves matrices (compare Figure 1B and Appendix). Although information on trunk position could in certain cases (fixed support of

known inclination) also be derived by proprioceptively monitoring the foot-to-leg angle, back transformation is the only means when the support surface is changing its inclination (for example balance platform).

Back transformation of vestibular signals would be a perfect means to reconstruct the behavior of body parts other than the head if the head-based sensory mechanisms were flawless. However, these transducers do not function like ideal physical measuring instruments. In particular, the well known high pass characteristics of the semicircular canals strongly affect the measurement of low frequency rotations about earth vertical axes (rotations about horizontal axes are registered by both the canals and the

otoliths, with the latter detecting the low frequency rotations that are missed by the canals). There is evidence for a partial correction of this canal deficiency by central mechanisms; primary vestibular canal afferents of squirrel monkey have a time constant of about 5 s (17), whereas secondary vestibular neurons of alert macaques exhibit time constants of up to 20 s, which reduces again to about 5 s under general anesthesia (18). Moreover, whereas the primary human time constant is estimated at 8 s [Igarashi, cited in (17)], perceptual studies suggest values of more than 20 s [see (19)]. However, a full compensation is not possible as this would require the neural implementation of mathematical integration; such a function would be unstable because of both low frequency sensory noise and inherent fluctuations. It is conceivable, though, that the imperfections of other transducers (otolith afferents, neck proprioception) are, indeed, by and large corrected by central mechanisms since, unlike for the canals, the required transfer function would not be plagued by a denominator of zero.

The low frequency deficiency of the canals poses a problem in the scheme of Figure 1B. Consider a head erect, upright standing subject whose head is slowly rotated in the horizontal plane about the stationary trunk. Given the incomplete central compensation for the high pass characteristics of the canals, the internal representation of this rotation (hs) will be too small at low frequency. In contrast, that of head-on-trunk rotation (ht) provided by neck proprioception is, according to our assumptions, essentially ideal. As a result, the back-transformation $hs - ht$ would yield a non-zero signal. Hence, the subject would experience an illusory trunk rotation and possibly a perceptual conflict with his notion of standing on a firm ground. Experimental evidence supporting the reality of this problem, and our hypothetical solution to it, will be considered below (Vestibular-Neck Interaction and Appendix).

Vestibular-Neck Interaction

We have studied vestibular-neck interaction in young healthy volunteers. Pure neck stimula-

tion was created by having the subjects sit on a Bárány chair equipped with a head rotation device that, if the chair rotated by, say, 12° to the right, counter-rotated the head by 12° to the left. By this manipulation, only the subject's trunk will rotate with respect to space, whereas his head remains stationary. Thus, only the neck proprioceptive system is stimulated ($HT = 12^\circ$ to the left), but not the vestibular system. On demand, subjects would report and quantitatively estimate each of the three aspects of this stimulus condition, namely HT , HS , TS (19,20).

Perception of Head-on-Trunk Rotation (ψ_{HT})

Using sinusoidal rotations in the dark at frequencies of 0.025 to 0.4 Hz, we found that the perception of neck rotation was almost ideal in terms of gain G and phase ($G \approx 1$; phase difference between ψ_{HT} and $HT \approx 0^\circ$). Gain is defined here as the ratio of estimated or indicated head-on-trunk angular displacement to actual displacement ($G = \psi_{HT}/HT$). Detection threshold in terms of angular velocity showed values of about $0.3^\circ/\text{s}$. Gain, phase and velocity threshold were essentially independent of stimulus frequency. In the present context we therefore will always proceed from the assumption that the compound neck proprioceptive system (which may include a central corrective mechanism; compare the Introduction) can be characterized by a transfer function of unity over the frequency range tested.

Perception of Head-in-Space Rotation (ψ_{HS})

In contrast to ψ_{HT} , the perception of head-in-space rotation during pure neck stimulation is subjected to an illusion when vision is excluded; subjects feel their heads rotated in space, with the direction being determined by the head-on-trunk excursion. The illusion is small at high frequencies (>0.1 Hz), but reaches a considerable "gain" at low frequencies (gain here denotes perceived head-in-space displace-

ment referred to the actual head excursion relative to the trunk).

Perception of Trunk-in-Space Rotation (ψ_{TS})

The perception of trunk-in-space rotation during neck stimulation presents a mirror image of ψ_{HS} : its gain is large at high frequencies and clearly decreases at low frequencies.

Remarkably, for both ψ_{HS} and ψ_{TS} , gain not only varied with frequency, but depended also on stimulus magnitude, being less (ψ_{HS}) or larger (ψ_{TS}) when stimuli of $24^\circ/s$ instead of $12^\circ/s$ peak velocity were used. Conceivably, this non-linear behavior is due to a detection threshold of trunk-in-space velocity during pure neck stimulation, which we have estimated to be of the order of $1.2^\circ/s$ (19).

During pure vestibular stimulation (head and trunk rotated as a whole), our subjects perceived no head-on-trunk rotation, in accordance with physical reality. Furthermore, they exhibited very similar ψ_{HS} and ψ_{TS} . Remarkably, gain, phase, and threshold of these vestibular perceptions resemble quite closely those of neck ψ_{TS} .

A variety of different vestibular-neck stimulus combinations was used. If the head is rotated about the stationary trunk (stimulating both the vestibular and the neck proprioceptive systems; $HS = HT$), ψ_{TS} is zero at all frequencies, that is, subjects veridically perceive the trunk as stationary. This observation led us to hypothesize that ψ_{TS} can be explained by a (linear) subtraction of the underlying vestibular and neck signals (which, for the case of head-only rotation, would indeed yield $\psi_{TS} = \psi(HS - HT) = 0$). This hypothesis was confirmed by the responses to other stimulus combinations; if these combinations involve trunk rotation, ψ_{TS} reflects the deficiencies and illusory components of its vestibular and neck constituents, respectively (which cancel only for $HS = HT$).

During head rotations about the stationary trunk, the perception of head-in-space motion (ψ_{HS}) is also veridical. It exhibits a gain close to unity and almost zero phase, in sharp contrast to the behavior during pure vestibular stimulation described above.

Figure 2 shows a signal flow diagram describing the relationships between vestibular and neck proprioceptive stimuli and the resulting perceptions ψ_{HT} , ψ_{HS} , and ψ_{TS} . For the sake of simplicity and symmetry, we here consider

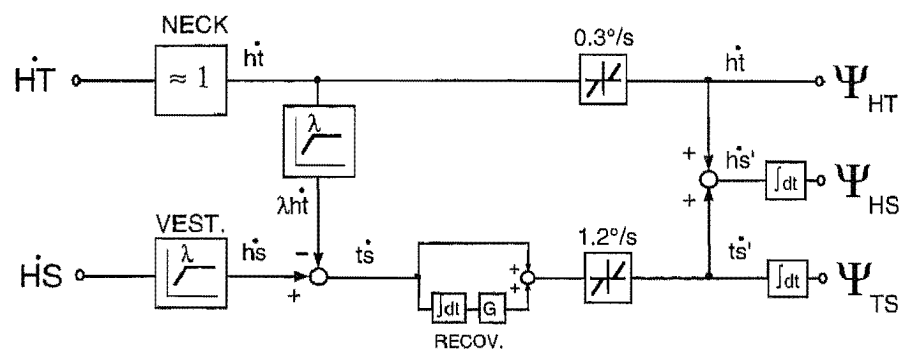


Figure 2. Dynamic model of vestibular-neck interaction for the perception of horizontal head-to-trunk, head-in-space, and trunk-in-space angular displacement (Ψ_{HT} , Ψ_{HS} , and Ψ_{TS} , respectively). In this and the following three figures, symbols with dot represent physical velocities (for example, $H'S$, $H'T$) or internal representations thereof ($h's$, $h't$, $t's$). Dashes discriminate different internal representations of same physical parameter (for example, $t's$ and $t's'$ both represent trunk velocity in space, but differ in their lower time constant). Interaction takes place at the level of the internal velocity representations, which then are integrated ($\int dt$) to yield perceived angular displacements on the output side. The velocity thresholds of $0.3^\circ/s$ and $1.2^\circ/s$ are those obtained during pure vestibular and pure neck stimulation (19). λ , transfer function of the vestibular system. RECOV., partial recovery of low frequency content, increasing time constant of $t's'$ by comparison to $t's$. For further details see text. [Simplified from (19).]

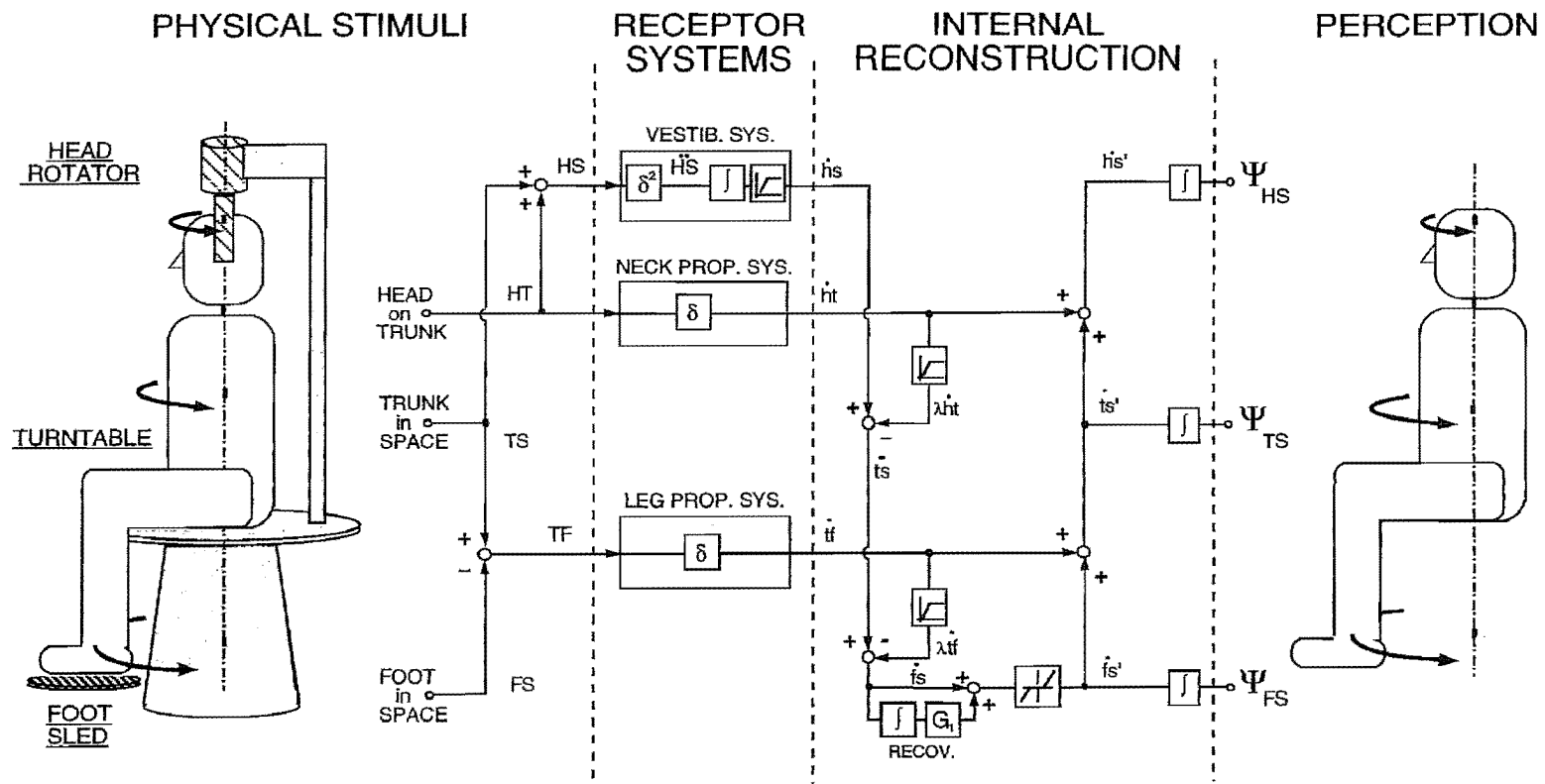


Figure 3. Model of the perception of foot, trunk, and head rotation in space (Ψ_{FS} , Ψ_{TS} , and Ψ_{HS} , respectively). Extension of model in Figure 2. The vestibular canal system reacts to angular acceleration (second derivative, δ^2 , of HS) and produces a velocity signal with high pass characteristics, by way of a "leaky" integration (J and high pass). The vestibular signal is "down-channeled" to yield a representation of foot-in-space ($f's$; Ψ_{FS}), and then "up-channeled" to yield Ψ_{TS} and Ψ_{HS} . Note that the proprioceptive signals intervening in down-channeling are given the high pass characteristics (λ) of the vestibular channel. [Slightly modified from (21).]

head-in-space velocity ($H'S$) and head-to-trunk velocity ($H'T$) as the specific physical stimuli acting upon the system, although in reality the primary stimulus for the vestibular channel is head acceleration ($H''S$) and may be head-to-trunk displacement (HT) for the neck proprioceptive channel. However, assuming linearity at the input side, the scheme in Figure 2 can easily be transformed to reflect these facts, without affecting the resulting internal velocity representations $h's$ and $h'i$ (see Figure 3).

The scheme proceeds from the basic idea that our brain creates an internal representation of trunk behavior, to begin with, because the trunk represents the natural platform for the head. The primordial role of the trunk is underlined by the observation that naive subjects generally relate to their trunks when asked to describe their orientation and movement in space in the absence of vision. Also, as a rule, patients with bilateral vestibular loss refer to their trunks in every psychophysical tasks requiring a space reference in the absence of vision. Trunk representation is obtained by summing the vestibular signal with a *modified* version of the proprioceptive neck signal ($\lambda h'i$). The modification bestows on the neck signal the transfer characteristics (λ) of the vestibular signal; in other words, the compound neck signal with unity transfer function mentioned above is passed through an internal model of the vestibular channel. As a consequence, ψTS becomes zero during head rotation on the stationary trunk ($HS = HT$), irrespective of stimulus frequency, which is "correct". With all other stimulus combinations ($HS \neq HT$), however, ψTS deviates from reality at low frequencies by $(1 - \lambda)(HS - HT)$.

As mentioned above, the internal "computations" of $t's = h's - \lambda h'i$ (or $ts = hs - \lambda ht$, if we argue in the position domain; compare Figure 1). This can be viewed as a back transformation from a head-based into a trunk-based system, which, in the more general case of rotations about different axes, must be described by matrix operations. In view of the illusions that can arise from the unavoidable imperfections of the vestibular channel (compare above), there may be a strategy in the freely behaving subject to zero $t's$ because this is the only state where his internal image of trunk-in-space behavior and

the actual TS are congruent. In behavioral terms, this would mean: When we move in an environment that does not provide us with a reliable stationary external reference and we therefore lose orientation, stopping trunk motion and, possibly, firmly anchoring our trunks (for example, by ground contact) may help us to reorient. Proceeding from such a stabilized platform, head position and movement could then be determined using only the neck proprioceptive system with its close-to-unity transfer function. The head, in turn, then would represent a reliable platform for visual orientation in space.

Stack of Superimposed Coordinate Systems

The model in Figure 2, which provides an internal representation of the trunk as a basis for the head, may be extended both further upward and further downward. By downward extension we can take into account rotations other than that of the neck, for example rotations between shoulder girdle and pelvic girdle, between the latter and the legs, and between the legs and the feet, which contribute to the head-in-space and head-to-foot excursion in an upright standing subject. To the extent that reliable proprioceptive information on these rotations is available, the brain can use the vestibular information to infer the kinematic state of the feet and, hence, of the body support surface.

Evidence for such a "downward channeling" of the vestibular signal has been obtained in a psychophysical study similar to the one described above, in which vestibular stimulation was obtained by rotating head and trunk en bloc and proprioceptive stimulation by rotating subjects' feet relative to their seated trunks (21). The results obtained were, indeed, analogous to the ones obtained with neck stimulation. Furthermore, it could be shown that leg and neck proprioceptive effects sum up linearly as long as the rotation axes are colinear.

Consequently, the model shown in Figure 2 was extended to include leg proprioception (Figure 3). In the extended model the common base for the perception of trunk and head motion in space is an internal representation of foot

(support) motion in space ($f's$), which is obtained from the vestibular signal $h's$ by subtraction of neck and leg proprioceptive signals which have been given the transfer characteristics of the vestibular signal ($\lambda h't, \lambda t'f$). Representations of trunk and head motion in space are then obtained by adding the original $t'f$ and $h't$ signals with approximately unity transfer characteristics.

We speculate that similar principles could govern the organization of postural reflexes, with the interaction of vestibular and proprioceptive inputs for legs and arms taking place at different levels of the spinal cord. This, possibly, could explain the seemingly puzzling finding that electromyographic responses evoked by galvanic vestibular stimulation have shorter latencies in the soleus muscles, when subjects maintain their balance by the feet muscles, than in the triceps brachii muscles, when they maintain their balance by holding with their arms (22). Moreover, there is direct electrophysiological evidence for a "downward and upward" channeling of vestibular information in the spinal cord; there are ascending spinal pathways that carry, in addition to muscle afferent input from limbs and neck, also vestibular information (23).

An experimenter who finds that the perception of head-in-space motion during head-on-trunk or trunk-on-foot rotation has a similar "gain" and threshold as the perception of relative motion between body parts (based on proprioception) may conclude that the head-in-space perception is primarily determined by proprioception. According to our model, he is correct if subjects are standing on firm ground. In other words, as long as subjects feel their support is stationary, they may use only proprioceptive cues for their head and trunk motion perception. Only when there is an indication of support instability do they incorporate the motion of the support inferred from down-channeling the vestibular information into their perception. Possibly, it is because of this mechanism that we so 'smoothly' can use vehicles, which at times provide a stable platform in inertial terms (during constant velocity), but may accelerate or decelerate at other times. A patient with complete vestibular loss with eyes closed, in contrast, could only make assumptions about the stability

of his or her body support, but would not have a perceptually derived confirmation of this assumption.

The principle of coordinate transformation may as well be extended upward, so as to include the perception of object motion in space. Consider a subject who is rotated on a Bárány chair while viewing a light spot that is being kept in fixed alignment with his head. The object is perceived as moving in space. The gain and phase characteristics of this perception as well as its threshold are very similar to those of the self-motion perception in this condition, that is, they reflect the characteristics of the vestibular signal (24). When the object is rotated relative to the head during the chair rotation, the resultant object motion perception can be described as the sum of the vestibular signal and a visuo-oculomotor signal; the latter is a compound of (i) an efference copy of the eye movement by which the object is being tracked, and (ii) a residual retinal slip signal.

Interestingly, the just mentioned experiments on object motion perception (24) also support the above notion of a "down channeling". Pure neck stimulation evoked an object motion illusion that could be related to the illusory perception of head-in-space rotation resulting from the same stimulation. This result could have been anticipated on the assumption that the various internal perceptions form a *consistent* picture of the outside world (an assumption which is not always borne out!). Indeed, if neck stimulation induces a non-zero ψHS and if, on the other hand, the object does not move with respect to the head, consistency requires that the object be perceived as moving along with the head.

Leg proprioceptive stimulation in these experiments (24) proved to be effective, as well. When vestibular and neck stimulation were below threshold for self-motion in space, trunk-on-leg rotation (feet touching firm ground while legs sway back and forth as chair oscillates) restored an almost veridical object motion perception. Thus, under the experimental conditions tested, it appears that the perception of object motion can be incorporated into the model shown in Figure 3. This is achieved by adding a further coordinate transformation that transforms the object(eye)-versus-head rotation (that

is, visuo-oculomotor signal) into an object-in-space signal by means of the head-in-space signal $h's'$. The last transformation can be viewed as a back-transformation of the visuo-oculomotor signal by means of vestibular signals to recover object motion in space after its distortion by a forward transformation resulting from the movements of various platforms (trunk, head) on top of each other.

Also, "artificial" neck proprioceptive stimulation by muscle vibration affects perceived location of a visual target (25–27). Furthermore, the role of proprioception for perceived motion of a visual object in haptic contact with the body has repeatedly been investigated in a meanwhile classical paradigm called the "oculobrachial illusion"; in this paradigm, a light-emitting diode (LED) attached to the stationary finger in the otherwise dark room is seen as moving if the illusion of an arm movement is elicited during vibratory excitation of muscle spindles of an arm muscle (for literature and model, see 28).

Visual–Vestibular and Visual–Proprioceptive Interaction

The "down- and up-channeling" principle outlined in Figure 3 suggests that, perceptually, the body support is linked by coordinate transformations to the internal notion of physical space provided by the vestibular system. If the support is experienced as stationary with respect to space, it is taken as a reference for trunk and head motion (two-way coordinate transformations, according to the down- and up-channeling in Figure 3). This principle has been formulated, in the first place, for situations in which vision of the surroundings is excluded. We now turn to situations where subjects are surrounded by, and are viewing, an optokinetic drum or, in a more general sense, a visual scene which may be either stationary or moving both in space and relative to the head of the subject. We shall see that matters become complicated when we include in the coordinate transformations an external object which perceptually is interpreted as a spatial reference for some reasons (for example, cognition, experience).

Let us consider for a moment the drum as just another movable part of the subject's body, and the visuo-oculomotor system as an equivalent of a proprioceptive system signaling the *relative* motion of this artificial body part. To start with, let both foot support and drum be stationary. When we then extend our principle to the visual scene (Figure 4) by adding an essentially ideal visuo-oculomotor signal $v'h$ to the internal representation of head in space ($h's'$), an internal representation of scene motion in space is created. In this situation, there is high congruency between signals related to the foot support and those related to the visual scene (for example $t's' \approx t'v$ in Figure 4). A subject estimating Ψr_s , for instance, would deliver a veridical judgment, and the experimenter would be unable to infer from this judgment whether the subject derived it from the visual or the vestibular-proprioceptive reference.

The situation is clearly different when the foot support is moving. The internal representation of head in space ($h's'$) then is affected by the non-ideal vestibular transfer characteristics ($h's' = h's + (1-\lambda)hf$; $hf = h't + \dots + 1 \cdot f$; λ , vestibular transfer function) and the scene would appear to move by $(\lambda - 1)F'S$. Moreover, even if the scene were perceptually stabilized by some unknown mechanism (for example, by cognition, suggesting that a particular scene, as it always has been, is stationary), there would be a problem with taking it, in turn, as a reference for head or trunk rotation in space, since visual-contingent and vestibular-contingent signals would be no longer congruent (for example, $t's' \neq t'v$; Figure 4), at least at those stimulus frequencies where $\lambda \ll 1$.

We see no simple solution to this problem and think that subjects in such situations have to resort to a perceptual measure of visual-vestibular conflict (see below), cognition, experience, and so on in order to decide for one or the other reference. This notion is supported by previous studies from this laboratory on human self-motion perception during various visual-vestibular stimulus combinations [sinusoidal rotations (29)], in which subjects tended to base their perception on either the vestibular-contingent or the visual-contingent reference, depending on internal or external biasing factors (for example, instruction).

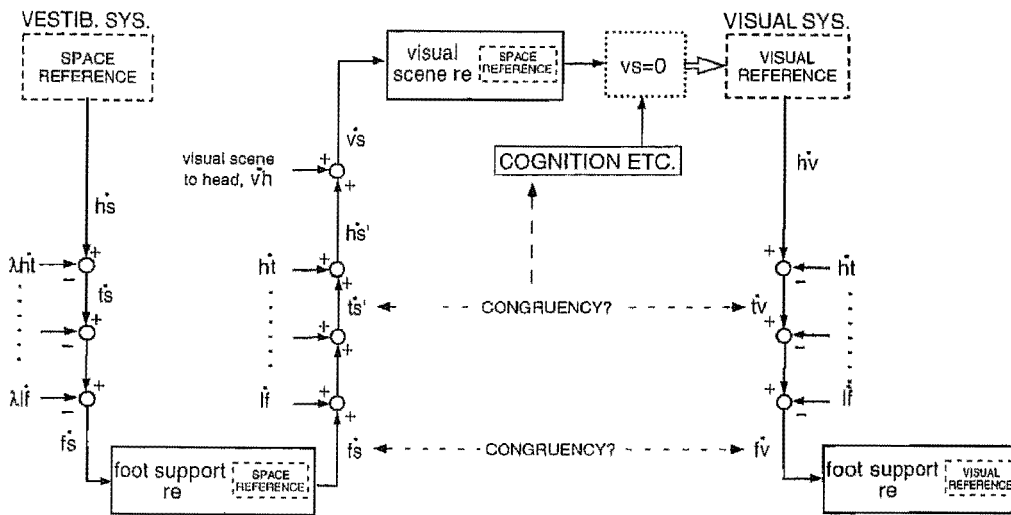


Figure 4. Extended version of the "down-and-up-channeling" principle (Figure 3), which includes the visual scene (by adding a signal of visual scene relative to head, v/h). The scene has the potential to become a spatial reference ($vs = 0$; cognition and so on). Head, trunk, and foot motion can also be referred to this visual reference, a fact that allows to evaluate congruency between visual-contingent and vestibular-contingent self-motion perceptions. Symbols as in Figure 3. $\lambda h't$, \dots , $\lambda h'f$, \dots , $\lambda t'f$ denote representations of $H'T$, \dots , $L'F$, shaped by a model of the vestibular channel, and $h's'$ and $t's'$ are representations of $H'S$ and $H'T$ obtained by internal calculation.

In these experiments, perceptual rivalry between the vestibular-contingent and visual-contingent reference for self-motion perception was sharpened by having subjects, who were sitting on a stationary turning chair, fixate at a small visual object, behind which the optokinetic background was moving. When subjects attended to this object, it appeared to move in space (Dunker's induced motion). The occurrence of this illusion facilitated circular vection (CV), that is, a state in which perceived self-rotation is solely determined by the visual channel (scene acting as seemingly stationary spatial reference). We attribute this rapid switching to CV to a mechanism that tries to minimize conflicts between object and self-motion perception.

However, we feel that rivalry between purely vestibular-contingent and visual-contingent references is not the only possible mode of visual-vestibular interaction for human self-motion perception. Visual-vestibular interaction proved to be quite different when we changed the visual stimulation and the instruction (30). Specifically, subjects were presented with only an optokinetic stimulus and were instructed to stare through the

pattern (in order to discourage them from considering it a visual object instead of a background). The subject's body and the optokinetic pattern were sinusoidally rotated, independently of each other, in order to create various visuo-vestibular stimulus combinations (see Figure 5A). As shown in the figure, if pattern rotation was in phase with chair rotation (c,d), perceived body displacement was more and more underestimated when stimulus frequency was decreased, and eventually became reversed in direction (d). In contrast, perceived displacement was essentially independent of frequency when the pattern was stationary (b) or was rotated counter to the chair (a).

Interestingly, the results could be described by a model (Figure 5B) which, without the conflict box, is analogous to that in Figure 2, in that from the vestibular signal $h's$, a version of the head-to-visual scene signal $h'v$ is subtracted, which has received the frequency characteristics of the vestibular signal. This yields an internal representation of visual scene motion in space ($v's$). Adding to $v's$ the original signal $h'v$ results in an improved signal of head rotation ($h's'$) that is superior to the vestibular $h's$ signal

in conditions where the scene is stationary. Note that an implementation of this visual improvement of the vestibular $h's'$ signal in Figure 4 would be helpful in conditions in which body and support are moved en bloc (for example, during riding in a vehicle; with $hf = 0$ in $h's' = h's + (1 - \lambda)hf$; $h's' = h's$), but could not remedy the problems outlined above for the general case (body and support moving independently of each other, $h's' = h's + (1 - \lambda)hf$; behaviorally, this would correspond to a condition in which we move within a moving vehicle and try to estimate whether the visual scene is stationary). Thus, although the scheme in Figures 4 and 5 provides solutions for special cases (foot support/visual scene stationary), there is no general solution by linear interaction for the problem of estimating self-motion in those cases where the support and/or the scene are moving. This calls for a non-linear interaction.

In the experiments just mentioned, we noted that during counter-phase stimulus combinations, the visual effect on Ψ_{HS} was considerably less when subjects looked through the pattern as

before, but nevertheless attended to it, whereas during chair rotation with the pattern stationary, the same instruction left the visual effect essentially unchanged (unpublished observations). This led us to add a further mechanism to the model in Figure 5B (thin lines); it represents a visual-vestibular conflict mechanism [compare (31,32)] in which an "expected visual signal" is derived from the visual signal $h'v$ under the assumption that $h'v$ is caused by self-motion. This expected visual signal is obtained by endowing $h'v$ with the frequency characteristics of the vestibular channel ($\lambda h'v$; in the model it is actually the same as the one used to construct $v's$). Subtraction of this signal from the vestibular signal yields a conflict signal that, when high (as during pure visual stimulation), suppresses the visual contributions to λHS in the model. Interestingly, with a pure visual stimulus under the form of velocity step, the model predicts an illusory Ψ_{HS} with delayed onset (and gradual build up), similar to that of CV occurring with optokinetic stimulation at constant speed [see (33)].

We have mentioned these aspects of visual-

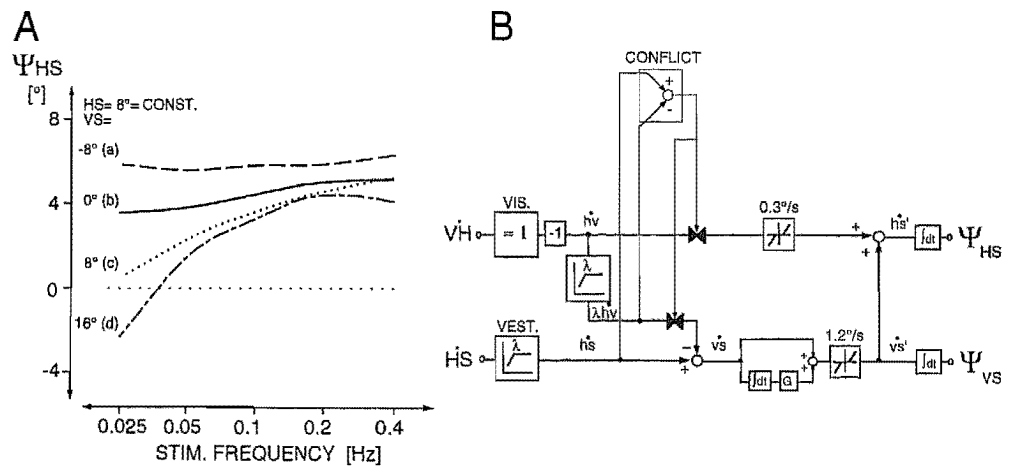


Figure 5. Self-motion perception in a special condition of visual-vestibular interaction not covered by the scheme in Figure 4. (A) Experimental findings. Sinusoidal whole-body rotation on a turning chair (HS: peak displacement, $\pm 8^\circ$) was used, combined with four different optokinetic stimuli: a, rotation of visual scene with respect to space, VS, in counter-phase with, and at same amplitude as HS; b, scene stationary in space; c, scene in phase and of same amplitude as HS; d, scene in phase with, and with double amplitude of HS. The fairly low gain at high frequency (0.5 to 0.7) may be due to an adaptational phenomenon linked to frequent repetitions of the stimuli [see (19)]. Gain of perceived self-motion (Ψ_{HS}) exhibited little dependence on optokinetic stimulus at high frequency, but was increasingly modified by optokinetic stimulation when stimulus frequency decreased, with response phase even being reversed in combination d. (B) Model used to describe the results. Note analogy to model in Figure 2. $V'H$, velocity of visual scene motion relative to head. A measure of visual-vestibular conflict is added, which transiently (vestibular time constant) suppresses the visual contribution to Ψ_{VS} and Ψ_{HS} by means of a "choke control" (double black triangles). [From (30), slightly modified.]

vestibular interaction here to point out the fact that the coordinate transformations from vestibular to visual space suggested in Figure 4 may often be obscured by other mechanisms, which try to either suppress (conflict) or enhance CV (Dunker's induced motion) on the one hand, and to make use of the visual input to overcome the deficiency of the vestibular (canal) system for low stimulus frequencies/velocities, on the other hand.

Little is known, so far, of coordinate transformations in terms of visual-proprioceptive interaction for self-motion perception (right part of Figure 4, downward channeling from visual reference). In previous pilot experiments, we have investigated the effect of trunk rotation under the stationary head (neck stimulation) over a frequency range of 0.025 to 0.8 Hz in a perceptual state of a stable CV (29). Gains of visually and neck induced Ψ TS were similar, being essentially independent of stimulus frequency. Thus, it came as no surprise when we found that Ψ TS during combined stimulations can be described by a simple summation of neck and visually induced effects.

Postural Control

If vestibular input is to be used for postural control of upright stance, this necessarily involves coordinate transformations. As mentioned in the Introduction, there is some direct experimental evidence for the occurrence of such transformations. In the following, we shall discuss a conceptual model of postural control that, at least qualitatively, takes this evidence into account, and that incorporates a very similar notion of coordinate transformation as the one considered in the context of ego-motion perception. The model has been developed as a hypothetical answer to the question of how a proprioceptive feedback loop for body stabilization *relative* to the support surface could cooperate with one for body stabilization *in space*. The model (Figure 6) resembles in its basic aspects those shown in Figures 1 through 5. It considers a person standing on a platform, with the platform being pivotable in space and the body being tilted en bloc relative to the platform

(about point F; see inset). Only displacements in vertical rotation planes are considered.

In the *proprioceptive feedback loop* (solid lines), it is the angle between body and foot (BF) which is being sensed and controlled. For the sake of simplicity, we let $BF = 0^\circ$ if the longitudinal body axis is perpendicular to the foot support. As long as this support is in a horizontal and stable position, $bf = 0$ constitutes the desired state of the proprioceptive loop (bf , internal representation of BF). Any deviation from this state (caused, for example, by an externally applied torque during a push against the body) evokes a compensatory muscle torque acting on the ankles to reduce this deviation.

A way to activate solely the proprioceptive loop would be to stimulate selectively muscle proprioceptors by vibration (tonic vibration reflex; box VIBR. STIM. in figure 6). For a somewhat more natural example, consider a subject who stands on an unstable platform, holding his body in place by seizing a ground-based post, and tries to keep the platform in its initial horizontal position. There is evidence that in such a situation, where body equilibrium is safe, the vestibular loop considered below no longer contributes to the "postural" reactions of the legs (34). Note that we assume that the direct loop has properties of an automatic load compensation [similar to equilibrium point models (35, 36)], receiving a single input (set point signal) from a supervisor (here the vestibular loop) that considers more global aspects of the behavioral situation.

The *vestibular loop* (dashed) basically infers whether the support is actually stable and horizontal, or not. To this end, it creates an internal representation, fs , of the orientation of the foot, and hence of the support, with respect to space (FS). Signal fs then is used to change the set point of the proprioceptive loop to a value of $-fs$; the proprioceptive loop responds to this change by a corresponding adjustment of BF which, assuming perfect control, results in $BF = -FS$ and therefore keeps the body upright in space ($BS = BF + FS = 0$).

How does the vestibular system create the foot representation fs ? On the physical side of the model, the position of the foot relative to space (FS) is kinematically transformed by the

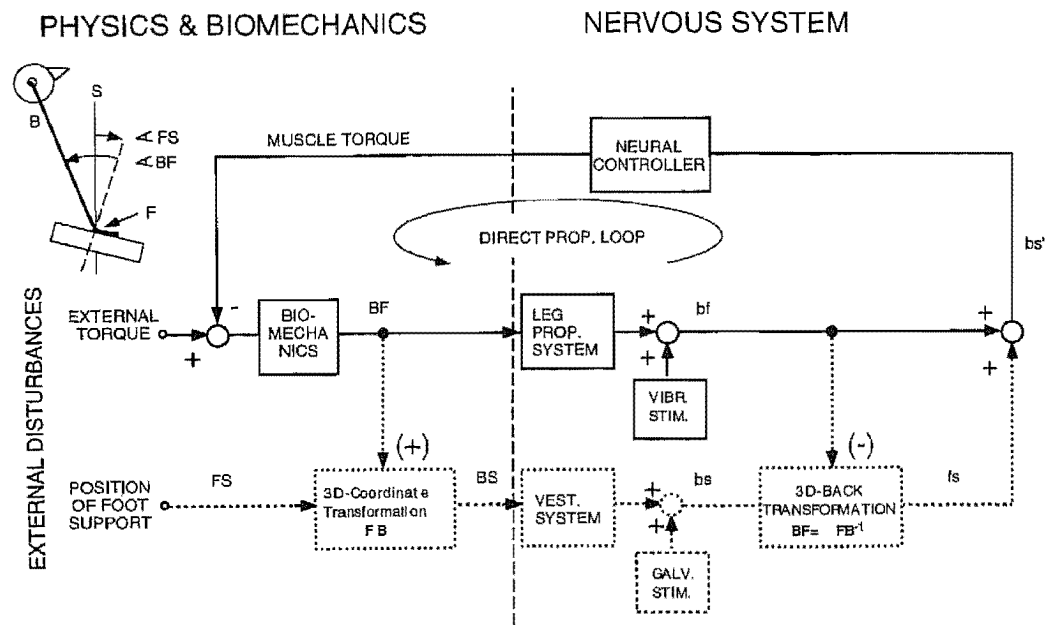


Figure 6. Conceptual model of vestibular-proprioceptive interaction for postural stabilization of upright stance. Note that, as in Figure 1, interaction here is shown in terms of angular displacement, not velocity, for the sake of simplicity. BF, body-on-foot angle; BS, body-in-space angle. For details, see text.

body-to-foot orientation (BF) to yield BS , which acts on the vestibular system. On the side of the central nervous system, the resulting vestibular representation of body-in-space behavior (bs) then is submitted to a neural back transformation ($BF = FB^{-1}$) in which the leg proprioceptive signal bf intervenes. The result is fs , the "vestibular image" of FS , which, in the case of co-planar rotations, simply corresponds to $bs - bf$. Note that after injection of fs into the proprioceptive loop, a "vestibulo-proprioceptive image" of body orientation in space (bs') arises, which will be different from the vestibular image bs if the BF transformation introduces errors or if the intervening bf signal is distorted to endow it with the characteristics of the vestibular channel (note, however, that in the vertical planes low frequency input is provided by the otolith systems).

By way of this mechanism, it should be no problem to balance the body on a rigid tilted platform with the help of the direct proprioceptive loop, since the vestibular-proprioceptive loop always adds what is needed for a compensation of the tilted support.

Finally, it is clear from Figure 6 that the sig-

nal path from galvanic vestibular stimulation (box GALV. STIM.) traverses only the central back transformation (in contrast to external physical stimuli, which act through both a forth and back transformation) and is therefore well suited to study the characteristics of this neural stage. Corresponding experimental results have been mentioned in the Introduction.

Conclusion

We have tried to point out that the classical concept of vestibular-neck interaction actually is only a small fraction of an extended mechanism that links together the different parts of our bodies and that allows sensory information arising in one body part to be used for perceptual or motor tasks in other body parts. The mechanism also provides linkages between the body and the outside world, for instance, with a visually or haptically perceived object or reference. It would be a simplistic view, however, to conceive of perceptions and motor reactions as

being governed under all circumstances by the straightforward linear chain of transformations sketched in Figures 3 and 4. The following points, some of which have already been touched on, are meant to qualify this view:

1. As already discussed for the transformation in the sensory domain, the brain has to deal with the problem of imperfect signal transmission by the receptors systems. Transformation from the sensory to the motor domain presents a challenging problem, into which a number of recent studies have given some insight [see 37,38]. From this work it appears that "reconstructed" sensory signals of the kind described in the previous sections and neuronal activity representing frames of references can be found in several brain structures (38). However, in many cortical areas, the information appears to be 'distributed' in neuron assemblies in a way reminiscent of the hidden layers of a technical network [planar gain fields (37)]. Finally, on the motor side we meet a high level of complexity in almost each joint. Overall, error accumulation and potentiation across several transformations appears to present a major problem.

2. 3D-coordinate transformations would seem to be, at least mathematically, demanding operations, so that any simplification is probably welcome. For example, simplifications could be derived from the limited degrees of freedom of many joints, as well as from voluntary motor strategies not to use every available degree (39).

3. It might be advantageous, in certain conditions, to use a reference other than the vestibular space reference. The visual scene as a reference is certainly better than the vestibular one in terms of signal quality (for example, spatial resolution). This requires a forth and back channeling (forth, in order to evaluate the kinematic state of the visual reference; back, because all other perceptions then have to be referred to this

object) and a mechanism for deciding which reference to use. Once the visual scene is taken as a reference, this notion could be maintained for some time, during which the chain of coordinate transformations is shorter (down-channeling in the right half of Figure 4, as opposed to down- and up-channeling in the left half of Figure 4).

4. A "consistency manager" would seem to be necessary to link different but mutually inter-related perceptions to one and the same reference (as, for example, object and self-motion perception) in order to avoid a perceptual paradox [see "object motion paradox" in (29)].

Finally, we point out that the study of coordinate transformations may also be of interest to the clinician, since one would expect that various diseases of the peripheral and central nervous system affect this mechanism. For example, in patients with chronic bilateral vestibular loss, neck stimulation does not elicit a trunk turning sensation (40). This could be predicted by noting that coordinate transformation by means of the $h\dot{\tau}$ neck signal in Figure 2 becomes obsolete when there is no signal $h\dot{\tau}$'s, vestibular patients would use a simple "head-in-space from head-on-trunk" method, rather than the more complicated method of Figure 2. A further finding was that, during head rotation, these patients considerably overestimate head-on-trunk and head-in-space excursion at mid to low frequencies (40). In the future, it may be interesting to scrutinize the effects of various diseases of the nervous system from the point of view of coordinate transformation, a matter that has hardly been considered or tested clinically. So far, only little and still preliminary work has been performed in this direction, dealing mainly with patients suffering from hemineglect (41-43).

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Appendix

Three-Dimensional Coordinate Transformation

In order to achieve conceptual simplicity, in the previous sections of the article, only rotations within one plane, or alternatively, about one axis or about several parallel axes were considered. Obviously, a fully three-dimensional description is necessary for more general situations (for example, when the axis of the head-on-trunk rotation is not parallel to the axis of the trunk-to-space rotation). It is the aim of this appendix to develop the mathematics which can be used to describe such transformations and which are needed for computer simulations of the ideas developed above.

Let us consider a simple "two-joint-model," similar to the one sketched in Figure 1, in which the trunk as a whole, from feet to neck, is considered as a rigid rod. The head is allowed to rotate about any axis through a point *H*, which roughly corresponds to the head joints (crossing point of interaural and naso-occipital lines). The trunk in turn can rotate with respect to a space-fixed coordinate system about any axis through a "foot point" *F*. In addition, translations of the foot point *F* are possible. Depending on the situation under study, it would be straightforward to generalize this model by introducing additional rotational degrees of freedom, for example, through the hip-joints or through the knees, as is discussed for example in reference (1).

Mathematically, the position of the head with respect to the trunk is described by 3 rotational degrees of freedom, for example, by 3 angles. Analogously, the position of the trunk with respect to fixed space is described by 3 rotational and 3 translational degrees of freedom. Consequently, a complete description of the static posture of the model body is given by 9 numbers. The dynamic description accordingly requires 9 time-dependent functions. The mathematical expressions for velocities and accelerations of any point in the model body will involve the first and second time-derivatives of these 9 functions.

In the following, translations are described by specifying the coordinates of the point *F* in a

Cartesian, space-fixed coordinate system. The description of rotations is slightly more complicated. The most intuitive way is to indicate (i) the axis about which the rotation is performed and (ii) the angle. However, this description becomes unwieldy when one is interested in more complex rotational motions in three-dimensional space, with rotation axes whose orientation and position are varying with time.

Therefore, other parameterizations rely on the fact that rotations form a mathematical group and can be represented by 3×3 -matrices. To explain this in more detail, we introduce the following three coordinate systems:

- (S): The immobile, space-fixed system. The z-axis is vertical, the x- and y-axes are horizontal.
- (T): The mobile, trunk-fixed system. The z-axis is along the trunk, the y-axis is parallel to the line between the shoulders, and the x-axis is perpendicular.
- (H): The mobile, head-fixed system. The z-axis is along the vertical head axis, the y-axis is parallel to the interaural line, and the x-axis is perpendicular.

On upright standing, the axes of all three coordinate systems are not rotated with respect to one another. The following relations hold for *any quantity of vector character* in these coordinate systems:

$$\mathbf{x}_T = \mathbf{TS} \cdot \mathbf{x}_S$$

$$\mathbf{x}_H = \mathbf{HT} \cdot \mathbf{x}_T$$

$$\mathbf{x}_H = \mathbf{HT} \cdot \mathbf{TS} \cdot \mathbf{x}_S.$$

Here, \mathbf{x}_H , \mathbf{x}_T , \mathbf{x}_S stand for one and the *same* physical quantity of vector character, for example, the gravitational force or an angular velocity, as measured in the three different coordinate systems. In the following, vector quantities are typeset as bold face lower case letters, for example, \mathbf{x} , and matrices as pairs of bold face capitals, for example, \mathbf{TS} . \mathbf{TS} is an orthogonal 3×3 -matrix, which maps (S)-coordinates into (T)-coordinates, and analogously, \mathbf{HT} is an orthogonal 3×3 -matrix that maps (T)- into (H)-coord-

dinates. The third of these equations follows by inserting the first into the second. The orthogonal (or synonymously, rotation) matrices \mathbf{HT} and \mathbf{TS} are characterized by the following properties:

$$\begin{aligned}\mathbf{HT}^t \cdot \mathbf{HT} &= \mathbf{1} = \mathbf{TS}^t \cdot \mathbf{TS} \\ \det \mathbf{HT} &= \mathbf{1} = \det \mathbf{TS}.\end{aligned}$$

Thus, the inverse matrix \mathbf{HT}^{-1} is identical with the transpose \mathbf{HT}^t , and we shall occasionally denote it by \mathbf{TH} . The above properties imply that only 3 out of 9 matrix elements are independent. Hence, \mathbf{TS} and \mathbf{HT} contain the 6 rotational degrees of freedom of the model body (2,3).

There are several conventions for parameterizing rotation matrices by three numbers. For example, the three Euler angles [see, for example, (2) or (4)] specify the magnitudes of three successive rotations about three predefined axes. However, for numerical purposes (that is, computer simulations), it is more convenient to employ the full 3×3 matrices, so that we do not need any explicit parameterization of the rotation matrices.

Special consideration has to be taken to describe position vectors (mathematically: affine vectors), since the three different coordinate systems have their origins in different places. Let \mathbf{f} be the position vector of the foot point F — which is the origin of the trunk-system in Figure 1 — as measured in (S)-coordinates. \mathbf{f} contains the three translational degrees of freedom of the model. Furthermore, let \mathbf{h} be the position vector of the point H — which is the origin of the head-system in Figure 1 — as measured in (T)-coordinates. By definition, \mathbf{h} is a constant. Then, for any position vector the following relations hold:

$$\begin{aligned}\mathbf{r}_T &= \mathbf{TS}(\mathbf{r}_S - \mathbf{f}) \\ \mathbf{r}_H &= \mathbf{HT}(\mathbf{r}_T - \mathbf{h}) \\ \mathbf{r}_H &= \mathbf{HT}(\mathbf{TS}(\mathbf{r}_S - \mathbf{f}) - \mathbf{h}).\end{aligned}\quad [1]$$

In the special case of rotations in a single plane (colinear axes), we denote the angle of rotation with the same letters as the corresponding matrix; for example, \mathbf{TS} would be the angle corresponding to rotation \mathbf{TS} . The combination of two successive rotations in the same plane, for example, $\mathbf{HS} = \mathbf{HT} \cdot \mathbf{TS}$ is equivalent to the addi-

tion of the angles $\mathbf{HS} = \mathbf{HT} + \mathbf{TS}$ and, likewise, $\mathbf{TS} = \mathbf{HS} - \mathbf{HT}$ is equivalent to $\mathbf{TS} = \mathbf{HT}^{-1} \cdot \mathbf{HS} = \mathbf{TH} \cdot \mathbf{HS}$. These correspondences served as a recipe for generalizing the uni-planar models of the previous sections to full 3D models.

Dynamical Input

How can dynamic processes be described? First we consider translational stimuli. If the initial position of the foot point F is \mathbf{f}_0 and F is moved with a velocity $\mathbf{v}(t)$, the following simple relation holds:

$$\mathbf{f}(t) = \mathbf{f}_0 + \int_0^t \mathbf{v}(t') dt'$$

or in differential form:

$$\frac{d}{dt} \mathbf{f}(t) = \mathbf{v}(t). \quad [2]$$

The situation is more complicated for rotations. Let the trunk rotate with respect to fixed space with an angular velocity vector $\omega_{TS}(t)$, with the foot point F as the fix point of the rotation. Remember that any rotational motion is uniquely described by such an (possibly time-dependent) angular velocity vector, whose direction specifies the instantaneous axis of the rotational motion and whose length measures the instantaneous rotation velocity. Then between the (S)-to-(T) transformation matrix $\mathbf{TS}(t)$ and $\omega_{TS}(t)$ the following equation holds, in analogy to equation [2]:

$$\frac{d}{dt} \mathbf{TS}(t) = \mathbf{TS}(t) \cdot \begin{pmatrix} 0 & \omega_{TS,3}(t) & -\omega_{TS,2}(t) \\ -\omega_{TS,3}(t) & 0 & \omega_{TS,1}(t) \\ \omega_{TS,2}(t) & -\omega_{TS,1}(t) & 0 \end{pmatrix}. \quad [3]$$

The mathematically interested reader might note that each row in the resulting matrix on the right-hand side is equivalent to the vector product of ω_{TS} with the corresponding row of \mathbf{TS} . The rows of $d/dt \mathbf{TS}$ can also be viewed as the instantaneous velocities relative to fixed space of the tips of the unit vectors \mathbf{e}_x , \mathbf{e}_y , \mathbf{e}_z of the (rotating) trunk system. A similar matrix equation governs the time evolution of the matrix \mathbf{HT} , which describes the position of the head with respect to the trunk. The corresponding angular velocity is called ω_{HT} .

In our computer simulation of the control of trunk posture (Figure 1), the time evolution equations for **TS** and **HT** are solved numerically (box 3D-Coordinate Transformation). The input data is given by $\mathbf{v}(t)$ and the trunk-to-space and head-to-trunk rotation velocities by $\omega_{TS}(t)$ and $\omega_{HT}(t)$. The computer simulation was implemented in SIMULINK/MATLAB (The Math Works, Inc). The time evolution of **TS** (and analogously **HT**) is obtained by

$$\mathbf{TS}(t + \Delta t) = \mathbf{TS}(t) \cdot \mathbf{R}(\omega_{TS}, \Delta t). \quad [4]$$

R is the orthogonal matrix that corresponds to the exact solution of equation [3] for a constant angular velocity ω_{TS} . The time step Δt is finite, but small compared to the time scale in which $\omega_{TS}(t)$ varies. This integration method conserves the orthogonality of **TS**.

Note that, whereas the time-evolution of the translational variable $\mathbf{f}(t)$ is given by 3 separate, uncoupled equations for its 3 components, equation [3] tightly mixes up all 9 components of **TS**(t). Care must be taken to discriminate between the different coordinate systems. For example, the matrix **TS** is a linear operator which acts on vectors in (S)-coordinates. Hence ω_{TS} in equation [3] is the trunk-to-space angular velocity measured in (S)-coordinates.

Given the translational velocity \mathbf{v} , the two angular velocities ω_{TS} (trunk in space) and ω_{HT} (head versus trunk), and the initial state of the model at time t_0 (that is, the initial translations and angular displacements \mathbf{f}_0 , **TS**₀, and **HT**₀), then for any time $t > t_0$, the state of the model body can be completely described using the matrices **TS**(t) and **HT**(t), and the vector $\mathbf{f}(t)$, which all are functions of time. From these, all physiologically interesting quantities (for example, the sensory input acting on the semicircular canals and the otolith organs) can be calculated (see below). Furthermore, **HT**(t) itself is the sensory input for the proprioceptive system of the neck muscles.

Angular Velocity of the Head with Respect to Space

In this paragraph we are looking for an expression that describes the sensory input for the

vestibular canals. Because of their physical property of sensing inertial forces, the canals measure the angular velocity of the head with respect to space, which is composed of the angular head-on-trunk and trunk-to-space velocities, symbolically $\omega_{HS} = \omega_{HT} + \omega_{TS}$. However, in the simulation program, as in nature, ω_{HT} is represented in (T)-coordinates and ω_{TS} in (S)-coordinates, whereas the result, ω_{HS} , is afterwards required in (H)-coordinates. Therefore, the calculation that is performed within the box 3D-Coordinate Transformation of Figure 1 has the form

$$\omega_{HS} = \mathbf{HT}(\omega_{HT} + \mathbf{TS}\omega_{TS}). \quad [5]$$

Hence, ω_{HS} represents the projection of the instantaneous head angular velocity in space upon the coordinate axes of the head-fixed system. Since this head coordinate system has fixed relations to the canal system, ω_{HS} determines the stimuli acting on the semicircular canals.

Total Translational Acceleration of the Otolith Organs

The sensory input for the otolith organs is their translatory (linear) acceleration. It results from three sources:

- 1) linear acceleration of the foot point F,
- 2) centripetal acceleration due to rotation of trunk and head,
- 3) gravitational acceleration.

Mathematically it can be described by the following set of equations:

$$\mathbf{r}_S = \mathbf{ST}(\mathbf{TH} \cdot \mathbf{r}_H + \mathbf{h}) + \mathbf{f},$$

$$\mathbf{a}_S = \frac{d^2}{dt^2} \mathbf{r}_S - \mathbf{g},$$

$$\mathbf{a}_H = \mathbf{HT} \cdot \mathbf{TS} \cdot \mathbf{a}_S. \quad [6]$$

In the first equation, in order to calculate the acceleration of the otolith organs due to the dynamic behavior of the model body, we relate the otolith position to the *inertial frame of reference* (S). Note that the first equation is the re-

verse of the third equation in [1]. The anatomical parameter r_H specifies the location of the otolith organs and is given in (H)-coordinates. The position vector \mathbf{h} of the point H (heads joints) is in (T)-coordinates, and \mathbf{f} is the position vector of the foot point F. As result we obtain \mathbf{r}_s , the otolith position in (S)-coordinates.

In the second equation, the acceleration \mathbf{a}_s of the otoliths is obtained by twice differentiating \mathbf{r}_s with respect to time and subtracting the space-fixed vector of gravitation \mathbf{g} . Finally, in order to determine the projection of this acceleration upon the head coordinate system (which determines the direction of the acceleration-related forces with respect to utriculus and sacculus) the back transformation from (S) to (H) in the third equation of [6] is required.

Back Transformation

As already noticed, the posture of the model body is completely characterized by the two matrices **TS** and **HT**, and the foot point vector \mathbf{f} . In this section, we discuss how an internal representation of **TS** and its time derivative (essentially ω_{TS}) can be reconstructed by the brain from the available afferent information in order to obtain an internal representation of body posture and movement in space [compare (4)].

For this we consider the angular velocity of the head ω_{HS} as signaled by the canal system (ω_{HS}^*) and the head-to-trunk orientation **HT** sensed by the neck proprioceptive system (**HT***; asterisk denoting brain signals such as afferent activity and internal representations of physical quantities). Then, the angular velocity of the trunk relative to fixed space, measured in trunk coordinates, can be obtained by inversion of the equation [5]:

$$\omega_{TS}^{(T)*} = (TH^* \omega_{HS}^*) - \omega_{HT}^*. \quad [7]$$

For colinear rotations this means that the head-on-trunk angular velocity is subtracted from the total (head-in-space) angular velocity to yield the trunk-in-space angular velocity. Note that at this stage of the reconstruction, $\omega_{TS}^{(T)*}$ is represented in (T)-coordinates. The trunk-to-space orientation **TS*** can then be estimated by an in-

tegration similar to the one in equation [4], using the information from $\omega_{TS}^{(T)*}$. In Figure 1, these operations are implemented in the box 3D-Back-Transformation.

Similarly, an internal representation of the position of the feet (\mathbf{f}^*) can be obtained by two integrations (that is, by inversion of equations [6], calculating \mathbf{f}^* from \mathbf{a}_H^* under consideration of ω_{HS}^* , **HT***, and **TS*** and the knowledge about the initial orientation (and magnitude) of the gravitational field. Thereby, in the mathematical sense, the orientation and position of the body can be fully reconstructed.

In the previous sections we have pointed out that the canal signal ω_{HS}^* is plagued by high pass transfer characteristics (see Figure 2), which appear to be more or less isotropic in all directions. In contrast the low frequency characteristics of ω_{HT}^* are practically ideal. As a result, if the reconstruction of ω_{TS}^* is performed directly as suggested by equation [7], ω_{TS}^* has the same undesirable high-pass characteristics.

However, the consideration made in section Vestibular-Neck Interaction can be applied: Let us denote by λ the canal transfer function (that is, $\omega_{HS}^* = \lambda \omega_{HS}$). Bestowing the same transfer characteristics on ω_{HT}^* , thus replacing ω_{HT}^* in equation [7] with the modified proprioceptive signal $\lambda \omega_{HT}^*$, a modified version of ω_{TS}^* is obtained. This improved signal is, for example, zero (veridical), with head rotation on the stationary trunk. As mentioned in the same section, an improved $\omega_{HS}^{*'}$ can be obtained by a further coordinate transformation, using

$$\omega_{HS}^{*' } = \mathbf{HT}^* (\omega_{TS}^{*' } + \omega_{HT}^*).$$

We simulated the coaxial conditions like "head rotation on the stationary trunk" or "trunk forward tilt with the head in retroflexed position", as mentioned in the sections Transformation of Vestibular Signals as well as Vestibular-Neck Interaction. The three-dimensional simulation model was implemented using, for simplicity, the experimentally observed vestibular transfer characteristics for all three canal planes. Our experimental findings were well described by the model, as was the case with our earlier 2D models (19,21). For the vertical planes, we implemented an independent channel for otolith signals, using at present ideal transfer character-

istics, apart from a detection threshold (also, no attempt was made to merge canal and otolith signals, since little is known to date about canal-otolith interaction for self-motion perception and postural control). For both the canal and the otolith channels, we applied various head and trunk rotations about non-colinear axes, like the condition of a body-in-space sway in

lateral direction with a concurrent horizontal head-on-trunk rotation mentioned in the Introduction. The appropriate functioning of the model was verified by comparing its reconstruction of trunk and head orientations with the "actual" orientations. These simulations confirmed that the models presented in the previous sections are not restricted to uniplanar situations.

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