ELSEVIER

Brain Research Reviews 28 (1998) 118–135

BRAIN RESEARCH REVIEWS

Short review

Interaction of vestibular, somatosensory and visual signals for postural control and motion perception under terrestrial and microgravity conditions—a conceptual model

Thomas Mergner [a,*], Thomas Rosemeier [b]

[a] *Neurology, University Clinics, Neurozentrum, Breisacher Str. 64, D-79106 Freiburg, Germany*
[b] *Department of Astrophysics, University of Tübingen, Auf der Morgenstelle 10, D-72076 Tübingen, Germany*

Abstract

This article considers the intersensory interaction mechanisms and biomechanical aspects of human spatially oriented behavior and asks to what extent these are interrelated on earth by gravity and how they might be affected under microgravity. The interactions between vestibular, somatosensory and visual inputs for postural control are obscured by several complications (biomechanics, multi-body dynamics, multimodal feedback control, cognition etc.). However, they can be revealed in psychophysical studies on human self-motion perception. Based on such studies, we present a conceptual model, which we think is valid also for postural control. It accounts for the multi-segmental structure of the body, allowing local control of inter-segmental joints, but uses one global reference system for all segments, which is derived from the intersensory interactions. We hold that, at a sensory level, the system is tied together by linkages between vestibular, visual and somatosensory information which develop through experience of inertial and gravitational reaction forces. On earth these linkages are established even in the absence of active behavior by gravity, allowing the incorporation of one's body and its support into a notion (Gestalt) of ourselves in the environment. Under microgravity, in contrast, the linkages have to be actively established for postural and perceptual stability in the environment (e.g., by grasping a handle on the wall). From this work we recommend that future research under altered gravity conditions should be guided by models that include biomechanics, considerations of intersensory interaction and dynamic control mechanisms. Such an integrative conceptual framework will be helpful for reaching a general understanding of spatially oriented behavior.

Keywords: Vestibular–visual–somatosensory interaction; Postural control; Coordinate transformation; Biomechanics; Microgravity; Human

---

Contents

---

[*] Corresponding author. Neurologische Klinik, Neurozentrum, Universitätsklinikum, Breisacher Str. 64, D- 79106 Freiburg, Germany. Fax: +49-761-270-5390; E-mail: mergner@sun1.ruf.uni-freiburg.de

PII: S0165-0173(98)00032-0

---

1. Introduction

On earth, its gravitational force field not only allows us to detect the directions of up and down, but also dramatically shapes our motor behavior and our afferent and reafferent sensory inputs. Therefore, the condition of microgravity experienced during orbital space flight (free fall) is unique in many respects, the most relevant of which are summarized below from the viewpoint of biomechanics and sensory–motor physiology. It will be shown that the two aspects are closely interrelated and entail a number of secondary problems, such as the loss of the most basic point of reference for our behavior on earth (‘ground’) and a disturbance of certain inter-sensory interactions.

1.1. Biomechanics and related somatosensory functions

Under terrestrial conditions, the main task of postural control is to counteract the effects of gravity (see Ref. [51]). This antigravity activity constitutes most of the output of the motor system while standing. It is achieved by activating one’s muscles to produce joint torques that compensate for the destabilizing effects of the gravitational forces on the body segments. The joints’ orientation with respect to the gravitational vector, i.e., our momentary posture, determines how much torque is required. Consequently, passive postural changes require compensation by a change in the motor forces opposing gravity to restore a given point of equilibrium and any active change in motor output (e.g., leaning forward) requires a postural change that produces a new point of equilibrium. Under microgravity, in contrast, any posture is in equilibrium without any muscle forces, a fact which demands a profound change in control strategy.

On earth ground reaction forces result from, and are predetermined by the gravitational forces. They are modified when we try to move the body’s center of mass (COM); a movement of the COM is obtained by changing the center of pressures, COP, with respect to the COM’s projection on the support [64]. In microgravity, in contrast, the area of support (and reaction forces) is no longer predetermined, but always has to be actively established anew (e.g., by grasping a handle by hand). Therefore, control strategies such as the one just described are no longer valid.

Furthermore, joint morphology is adapted to our actions working against the gravitational forces, as are the working ranges of the sensory systems involved. Under microgravity the forces acting on the joints and the conditions of the proprioceptive sensors are changed. The same holds for sensors in the body tissue, which react to gravitation-induced strain, as well as for the haptic sensors in the foot, which detect changes in the ground reaction forces during standing.

When standing, our body consists of a superposition of several platforms (body segments) which are mobile with respect to each other. On earth, the support reaction forces determine the functional hierarchy of segmental movements. A torsional movement at the level of the legs, for instance, will rotate the upper body relative to the stationary feet. In contrast, during a gymnastic maneuver like standing on one’s head, the same movement would rotate only the feet and the body would remain stationary. In microgravity, the geocentric hierarchy of body segments no longer applies and the result of intersegmental movements is determined only by the mass (inertia) of the segments, unless one of the segments is actively anchored to a support.

There is evidence that forces which normally are either constantly present (gravity) or occur predictably during motion (e.g., centrifugal pseudoforces during movements with rotation component) are compensated for by internally generated signals which anticipate the external ones (compare Lackner, this volume). It can be assumed that, under microgravity, the internal signals that are normally related to gravity are initially released inappropriately, which disturbs perception and posture, but they are gradually adapted over time.

Roll et al. [53] studied proprioception under microgravity using muscle vibration. They observed that sensitivity of muscle proprioception is maintained, but found the tonic vibration reflex in flexor muscle enhanced and the postural response and tilt illusion, normally occurring with ankle flexor vibration, suppressed, unless the axial foot support force was restored artificially. In contrast, the responses to ankle extensor vibration were normal. Thus, it appears that, despite the altered gravity condition, some postural response patterns are maintained. This would be in accordance with results obtained with active movements under microgravity; axial synergies during upper trunk movements are similar to those on earth, despite the fact that astronauts show abnormal postures during the first days in space [28]. These and related findings are not well understood to date.

1.2. Gravitational component of the vestibular signal

The vestibular organ represents an inertial measuring device which allows us to sense, in the absence of external sensory cues (vision etc.), self-motion with respect to the six degrees of freedom in space (three rotational and three translational; see Ref. [63]). However, this information is not automatically available. It has to be synthesized from the signals of two subsystems, the semicircular canal system (which senses angular acceleration) and the otolith system (which senses linear acceleration). Synthesis is required because the signals provided by the two subsystems are not ideal, due to physical properties of the sensors.

The canal system (comprised of three orthogonal canals) reacts to angular head acceleration, but encodes angular head velocity due to an integration (in the mathematical sense) by the mechanical properties of the cupula–endolymph system. Whilst working well in the mid- to high frequency range of rotational stimuli, the integration becomes imperfect at low frequencies (< 0.1 Hz), mainly due to viscous forces in the small canals of the labyrinth. Therefore, we underestimate, or even fail to detect earth-horizontal body rotations in space at low frequency. The otolith system, on the other hand, is a biological linear accelerometer (or, more accurately, a differential-density accelerometer [50]), so information on both head tilt relative to the gravitational vector and head translation in space are superimposed in a compound signal of the afferent otolith input to the CNS (see GIF[gravitoinertial force]-resolution problem, [31]). Yet, on a behavioral level, we are able to distinguish body tilt from body translation rather well, and the perception of rotation is veridical, at least if in earth-vertical planes. This fact generally is explained by a central otolith-canal interaction, which (i) improves the canal signals for earth-vertical rotations using gravitational information contained in the otolith signal, and (ii) uses the canal signals to separate tilt and translation components from the compound otolith signal. Given this, one could expect that the absence of the gravitational component in the otolith signal under microgravity leads to disturbances in the otolith-canal interaction. Several models of this interaction have been proposed (see Ref. [15]), but specific predictions as to the effect of microgravity have not been made to our knowledge. In a recently developed model on otolith-canal interaction (Mergner and Glasauer, in preparation) angular velocity signals derived from both canals and otoliths are fused, which allows to improve the estimate of angular velocity and, at the same time, the direction of gravity can be predicted. Thereby, the gravito-inertial force resolution problem can be solved. Magnitude of gravity in the model is assessed by a different mechanism, which scales the gravity (and, by the same token, the translation) estimate by way of a fast ‘adaptation’. As simulations show, the model mimics well the data of different paradigms involving passive body rotation and/or translation. Interestingly, when g is changed to a very low level in the model, the system ‘adapts’ to this state (absence of g no longer estimated as ‘falling’), with the result that the basic functions are reestablished, but the estimates of rotation and translation tend to show fluctuations over time when ‘biological noise’ is added to the input signals.

Astronauts have reported a number of misperceptions and illusions occurring after entry into microgravity, like illusory self-motion (or surround motion) and self-orientation, various forms of subjective inversion of the own body and/or the spacecraft. However, the reports show a large inter-subject variability, and there appear to be variations over time as well, superimposed on adaptational changes [17,23]. More consistent are reports on impaired position constancy, errors of perceived self-motion and nausea occurring during head or body movements, which contribute to the so-called space *motion* sickness (SMS). Also, falling is not experienced by the astronauts, despite the fact that the so-called microgravity condition actually is a free-fall condition in low-altitude (200–300 km) orbital flights (the spacecraft falls at about $9.8\ \mathrm{m/s^2}$ towards earth, but because of its translation it falls on a quasi stable flight path above earth). The perceptual phenomena are still not completely understood and, therefore, cannot be predicted very well, at present.

Given that central canal–otolith interaction is affected under microgravity, functions that require an interaction of the vestibular signals with other modalities might also be affected. It has repeatedly been suggested that there exist, at the level of central sensory processing, linkages between otolith graviception and somatosensory graviception, since gravitoinertial forces always act on both the vestibular apparatus and the body as a whole. As pointed out by Stoffregen and Ricio [59] the two graviceptions are always congruent on earth. An exception would be the selective reduction of somatosensory graviception in under-water experiments, known to severely impair divers’ judgments of body orientation. However, under microgravity *both* constituents of the gravitational linkage are missing, whereas those related to rotational and translational body movements are preserved. At present, there exists no conceptual framework on how the linkages work, what functions they serve, and what the consequence of the abolition of the gravitational component under microgravity (or its attenuation on Mars with its weaker gravity) would be.

Finally, it is to mention that there are gravity-dependent somatosensory inputs in addition to those directly evoked by ground reaction forces. Gravity-induced torques in the intersegmental joints probably are also detected and used for postural control in certain conditions. Furthermore, Mittelstaedt [44,45] found, in a number of elegant experiments, evidence for somatic graviceptors in the human trunk. The functional role of these pseudo-vestibular graviceptions is still not clear, to date. They will not be included in the following considerations, but the reader should be aware of these additional sources of information.

1.3. General aspects

In view of the impacts of gravity on biomechanics and sensory–motor function described above, it comes to no surprise that the latter are impaired under microgravity. The condition is currently of major scientific interest mainly for two reasons. Firstly the sensory–motor impairment represents a serious safety hazard to astronauts and endangers the success of manned space missions. Consequently, a considerable part of the present research aims to meliorate the astronauts' discomfort, sensory–motor performance and general health problems. Secondly the condition is a unique opportunity to gain insight into a number of important brain functions. The performance of astronauts is impaired in some respects, but in others it is surprisingly good for this extreme environment. We may tend to take it for granted that astronauts adapt to microgravity, because on earth our sensory–motor functions must be very flexible. It is a challenge for science to elucidate the mechanisms that are responsible for this built-in flexibility and robustness and to reveal their limitations. Immediately upon entry into microgravity, astronauts may primarily resort to cognition to overcome unexpected perceptual and motor problems. During the following hours, days and weeks, adaptational mechanisms start to help. They are of utmost importance, also for many aspects of our life on earth (e.g., when coping with new terrestrial environments, diseases, aging etc.), but may create serious problems after return to earth following long-term space flight.

In the following sections, we concentrate on *intersensory interaction* for spatially oriented behavior and ask the question, to what extent the interaction mechanisms might be shaped by gravity and therefore would likely be affected under microgravity. As a guideline we present a global concept of the interaction. The presentation will comprise three parts. First we give an overview of relevant aspects of intersensory interaction with an emphasis on a number of unsolved problems related to postural control. Then we present the concept, which we derived from psychophysical work, and show that fusion of vestibular and somatosensory inputs may solve some of these problems. Finally we extend the concept to also include visual input. In the Conclusion we consider impacts of our view on future research under altered gravity conditions.

Our descriptions consider information processing in the CNS as occurring on a rather abstract level. For example, our brains' notion of a visual object's location in space may be based on neuronal interactions of several sensory signals, e.g., a retinal (visual) signal, an oculomotor efference-copy signal and a signal of head position in space. An abstract description of the processing would be to formulate coordinate transformations of the internal image of the object from a retinotopic via a craniotopic into a spatiotopic reference frame. Furthermore, we proceed from the notion that humans can transform their primary sensory signals into such abstract notions as 'head velocity in space' or 'trunk position in space' etc. (these notions can be assessed in psychophysical experiments) and that analogous levels of abstraction can be assumed for sensory-to-motor transformation and the motor side (compare Ref. [37]).

2. Overview

The term intersensory or multisensory interaction is used for different sensory mechanisms. One usage stresses mainly the redundancy aspect. For instance, the saliency of a visual stimulus is increased if it coincides spatially and temporally with an auditory stimulus, thus decreasing the detection threshold (compare Ref. [58]). Following the nomenclature of robotics, one could call this interaction a signal fusion. However, if the temporal and/or spatial characteristics of these stimuli differ enough, they are perceived as two distinct items (no fusion). Similarly, sometimes visually and vestibularly derived notions of space are congruent (and are fused), while in another conditions they are in conflict with each other and only one is chosen as a reference. This is different from other types of interaction, for instance when two or more sensory signals of different modalities are used to obtain information which would otherwise be unavailable. An example would be the above mentioned evaluation of the location of a visual object in space based on retinal (object-on-eye), oculomotor efference copy (eye-in-orbit) and head-in-space signals. The linkage of these signals gives rise to a signal of new quality (supramodal). In this last example the term sensor fusion would always be appropriate.

In the following we first point out what is known at present about intersensory interaction in postural control. We then consider intersensory interaction in gaze stabilization for comparison, before returning to current concepts in postural control and highlighting the most relevant problems.

2.1. The need for a conceptual framework of intersensory interaction in postural control

Many authors use the vague term 'multisensory integration' when referring to the well known fact that postural control depends on the interaction between several sensory inputs (visual, vestibular and somatosensory). This is because postural control is impaired if one of these cues is absent or modified due to a disease or some experimental interference. For example, impairment has been shown in patients with severe somatosensory deficits due to polyneuropathy when compared to normal controls and postural stability is worse when eyes are closed than when they are open (see overview [20]). Furthermore, it has been shown that the presence of visual input reduces spontaneous sway in the low frequency range more than in the high frequency range (see Ref. [4]), a finding which is in line with the limited dynamic bandwidth of visual input known for optokinetic eye stabilization (see Refs. [56,57]) and self-motion perception [40]. However, so far no clear picture of how the sensory inputs interact has emerged from these studies [29]. What might be the reasons?

Fig. 1 depicts the 'multisensory integration' view by previous authors [26] for postural control in terms of a feedback model. In this model a specific concept of intersensory interaction is missing; the sensory signals are simply summed, before having an impact on the muscle actuators that lead to joint torques which null body excursions. This simple view is not tenable, as we will show. Before doing so, however, we like to point out that the figure nicely illustrates a number of problems which we face when trying to investigate the sensory interactions. They are obscured by (i) the fact that we are dealing with a multimodal negative feedback system so the response to one input (e.g., visually induced body sway) will normally lead to involvement of the other inputs (the sway activates vestibular and somatosensory loops), (ii) the complexity of the output of the loop, which involves a concert of many muscles in an action and the immensely complicated mechanics, including those of intersegmental coupling (multibody dynamics are so complex that they cannot be intuitively appreciated or easily calculated, but should be simulated), and (iii) cognitive factors, because stimulus conditions may give rise to ambiguous interpretations (it is nowadays generally accepted that it is not the sensory signal itself that evokes a postural response, but its perceptual interpretation). The possibility that cognition shapes postural responses has led previous researchers to evaluate mainly the very early part of responses (e.g., in the EMG), which is hardly a solution to the problem.

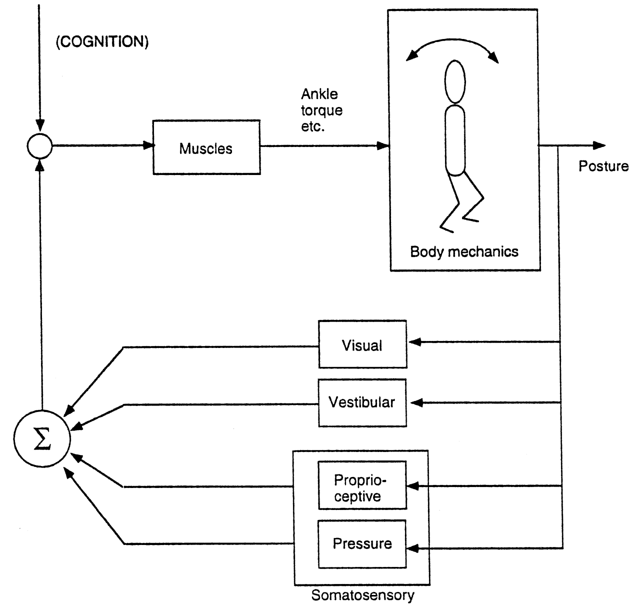


Fig. 1. A simple multimodal feedback model of human postural control (modified from Ref. [26]).

With respect to the sensory interaction, the simple summation hypothesis in the scheme is blind to a number of problems.

(1) For instance, the model does not take into account the fact that the sensory organs may reside in different parts of the body (e.g., the vestibular and visual organs in the head and the somatosensory system for the haptic contact with the ground in the feet). There is clearly the need for coordinate transformations across mobile body segments.

(2) The sensory information coded by each of the signals is unique (vestibular: head motion in inertial space, visuo-oculomotor: relative motion between head and visual scene, somatosensory input from foot: pressure or shear induced by relative motion between sole and support). However, there may exist intersensory congruency in certain behavioral conditions. This applies to spontaneous body sway of an upright standing subject in stationary visual surroundings on stable ground. Then, the signals carry congruent information, given that the brain 'knows' about the stationarity of the visual scene and the body support. In the mid-frequency range, where the inputs have essentially ideal transfer functions, they become even functionally equivalent with respect to encoding the sway. Yet, we behave in an environment where the body support and large objects in our visual field are often moving, which would create vital danger for the individual if the sensory inputs were not interpreted in the correct way. Thus, other solutions than the simple summation in the model are required.

(3) The sensory inputs are known to differ considerably in their dynamics. We will show that the summation of signals having clearly different dynamics may successfully broaden the bandwidth of a system in some cases, but may create problems in other cases.

2.2. Looking at gaze stabilization

A comparison with the stabilization of gaze may appear helpful, since this also involves the three sensory systems under consideration (i.e., vestibular, visual and somatosensory) and has been studied more in detail. Furthermore, the mechanism is rather simple, being mainly based on brainstem reflexes. Because of these reasons one could think that it might serve as a blueprint for a concept of postural stabilization, at least with respect to its intersensory interaction mechanisms. We will show below (Section 2.3) that this is not the case.

The well-defined aim of gaze stabilization is accurate vision, i.e., to keep the eye on a visual scene to give sufficient time for visual processing. This task is primarily performed by the optokinetic reflex (OKR; see Refs. [56,57]). Despite the limited dynamics of the visual input, it successfully keeps the eyes on moving stimuli in our surroundings, since these movements usually are not very fast. Fast movements occur normally during self-motion (e.g., head movements). They are compensated for by the vestibulo-ocular reflex (VOR) which stabilizes the eyes in space. During head or body rotations proprioceptive afferents are also activated and lead to proprioceptive reflexes on the eyes, like the cervico-ocular reflex (COR; see Ref. [39]). However, the COR is prominent only shortly after birth, but then becomes weak and plays no functionally relevant role in intact adult mammals and humans. A possible reason is that eye-in-space stabilization by the VOR is functionally more useful than a proprioceptive eye-on-body stabilization (because the former includes passive whole-body movements, unlike the latter).

The most functionally relevant aspects of VOR-OKR interaction may be appreciated from the model shown in Fig. 2, which is kept simple by hiding the transfer functions of VOR and of OKR (including dead time and non-linear gain characteristics of the latter) in the respective boxes. It consists of a negative feedback loop formed by the OKR, which shows a high gain (> 10, when measured open loop). The VOR is added to this loop in the form of a feed forward path with unity gain and a directional sign opposite to the head-in-space movement that evokes it. Simple summation is used in this model. However, the vestibular input is not adding to the feedback loop (only to the extent that VOR gain deviates from unity, such that the sum of the eye-in-head = EH response and the head-in-space = HS movement is not zero). It does not interfere with the visual mechanism in the low to mid-frequency range (< 0.8 Hz) where OKR dynamics are good. A functionally relevant interaction of VOR and OKR occurs only at high frequencies (> 0.4 Hz) due to the OKR's limited band width, which improves vision of stationary but not of moving objects. This simple model describes the basic features of gaze stabilization. More complex models in the past were dealing with particular aspects, like the fact that both VOR and OKR share common neuronal circuits in the brainstem (those used for a prolongation of the vestibular time constant; see Refs. [48,52]). Our simple view is intended to ease the comparison with postural stabilization (see below).

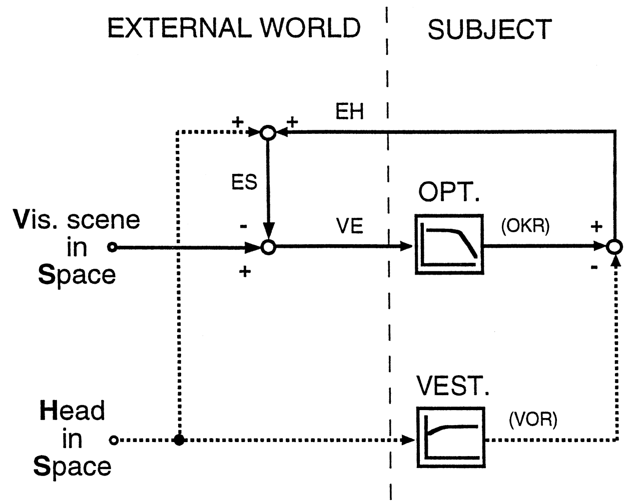


Fig. 2. Model of visual–vestibular interaction for gaze stabilization. The optokinetic system (box OPT.) represents a negative feedback loop (via the optokinetic reflex pathway, OKR; solid lines) which tends to keep the eyes on the visual scene, while the vestibular system (VEST.) compensates for movements of the head (mobile platform for the eyes) in the form of a negative feed forward (via the vestibulo-ocular reflex pathway, VOR; dotted lines). VE, visual scene motion relative to the eye; EH, eye-in-head movement; ES, eye-in-space. Slightly modified from Ref. [56].

2.3. Global aspects of postural stabilization

A conspicuous difference between postural stabilization and gaze stabilization is that each of the three main sensory inputs (vestibular, visual, somatosensory) receives feedback during postural reactions. Another difference is that somatosensory input is of particular importance for postural control; the contextual and task-dependent interpretation of this input is required to define: (i) Body geometry (i.e., whether the body is bent or erect, whether the head with its visual and vestibular sensors is turned, etc.), (ii) which body area receives ground reaction forces (e.g., which body part momentarily carries the weight, which part is best suited to control equilibrium), (iii) the quality of the body's contact with the support (slippery?, feet standing on a narrow support? etc.), and (iv) the kinematics and kinetic state of the support and the body. These aspects and their complexity underline the fact that postural control cannot be built on simple reflexes like VOR and OKR in gaze stabilization.

These aspects have been considered and summarized in the past in the form of global concepts. In one concept, for instance, the brain is thought to synthesize afferent information and internal knowledge in the form of a 'postural body schema' [10,16] as a basis for postural reactions. Similarly, Roberts [51] demanded a kind of 'Gestalt' concept for sensory information processing. Concepts of this kind are still awaiting implementation in the form of dynamic models. Researchers with an engineering background started to do so, for instance in the form of an 'optimal estimator' model [7]. Such models have to include, in addition to afferent information, also internal models of the sensors, the body and the force fields.

One particular aspect that has not received enough attention in the past concerns the location of sensor and effector organs within the body. With gaze stabilization the relevant sensor systems (vestibular, visual) and effectors (external eye muscles) all are located in the same body part (head). In contrast, with postural control, somatosensory input arises remotely from the sensors in the head, and the effectors (skeletal muscles) are also distributed across different body parts (extremities and trunk). This poses the need for intersensory and sensory–motor coordinate transformations across mobile body segments. Transformation from one coordinate system to another always is six-dimensional (3 rotational, 3 translational). This applies for a multisegmental body even if the degree of freedom of a given intersegmental joint is restricted. In the special condition of coplanar rotation, vector transformation simplifies to a vector summation of angles or angular velocities. In most of our experimental work described below we used such coplanar rotations, and we refer therefore to the transformations as vector summations, but are aware of the fact that the transformations actually are six-dimensional.

Bearing in mind that intersensory interaction for postural control is hidden behind other complex mechanisms (multi-body dynamics, multimodal feedback etc.), we started several years ago to perform psychophysical experiments on the interaction between vestibular, somatosensory and visual inputs for human ego-motion perception. Having a subject firmly placed on a turning chair, estimating perceived self-motion avoids the problems arising from biomechanics and feedback control. Furthermore, cognition can be well controlled by appropriate checking that the subject complies with the instructions given. In such a condition it is also rather easy to evaluate the transfer characteristics of the responses, which we compared to the known transfer characteristics of the sensor systems. Also, we measured different aspects of the various stimulus combinations applied (e.g., perceived rotation of head in space as compared to head relative to the trunk). Collecting multiple outputs (responses) for a given set of inputs thus helped us when we tried, in a system analysis approach, to model the signal processing in the ‘black box’, i.e., in the CNS. We feel that our psychophysical findings allow us to formulate a more comprehensive concept of intersensory interaction than hitherto was possible by posturographic or electrophysiological means.

Our psychophysical findings may serve as a blueprint for developing a model of postural control if one accepts that perception and postural control deal with similar problems and are closely interrelated (apart from the fact that a model of posture would have to include, in addition, biomechanical aspects etc. and ‘internal knowledge’ of these aspects). Perception, as it reveals itself in psychophysical experiments, indicates the brain’s interpretation of the physical events which affect our bodies in the external world. Conceivably, this requires knowledge of the multi-segmental structure of the body, locus of where, at the body, the reaction forces are having impact etc. It comes as no surprise, therefore, that the findings obtained in the psychophysical studies closely resemble the mechanisms which govern postural control (rather than those for the gaze stabilization). However, we would like to forestall possible misunderstandings: We are not meaning that perception anticipates and determines the postural reaction, but that the two arise in parallel, are congruent to a certain extent, and possibly influence each other.

One could object that animal experiments in the past have shown that postural control depends, at least to a considerable extent, on reflex-like mechanisms. We hold, however, that this evidence stems mainly from decerebrate animals. It is now generally believed that the reflexes (vestibulo-spinal, cervico-spinal etc.) are present at birth and come under the control of higher CNS centers during ontogenesis, but may be released from inhibition by decerebration. Possibly, they may show up in the intact adult in situations which require very fast reactions (rescue reactions). Normally, however, they play no relevant role in postural control (compare below, Section 3.7, early and weak EMG responses to galvanic stimulation). A reason why one may intuitively tend to think in terms of reflexes, is that maintenance of posture in most everyday conditions is more or less automatic. However, motor activities which we perform many times each day (e.g., climbing stairs) are often performed automatically, but by no means represent reflexes. A further objection could be that postural reactions have to be fast and complex mechanisms, as those involved in self-motion perception, would come too late to prevent imbalance; this point will be considered at a later stage (Section 3.7).

3. A concept on vestibular–somatosensory sensor fusion

3.1. Previous work

Interaction between vestibular and somatosensory inputs for postural control was postulated in the past for two reasons. One reason, already mentioned before, is that gravito-inertial forces always effect both the vestibular organs and the body’s somatosensory system, so that it is likely that the brain links the two pieces of information together. However, this notion has not yet been worked out in detail. The other reason is that the vestibular signal arising in the head has to be transformed to yield a measure of trunk motion in space, if it is to be used for postural control, since most of the body’s mass is located in the trunk. The latter reason goes back to observations and inferences by von Holst and Mittelstaedt [44,62] who suggested that, due to a subtractive interaction of vestibular and neck afferents, control of trunk posture by the vestibular system proceeds as if the vestibular organ was located in the trunk. Postural adjustments of spontaneously behaving cats and horses were found to be reminiscent of this kind of vestibular–neck interaction [49]. Interactions between vestibulo-spinal and cervico-spinal reflexes in the decerebrate cat are indeed compatible with the summation hypothesis [24,27], as are those found with neuron recordings in the vestibular nuclei and the vestibular cortex [1,8,34].

Related postural studies in intact adult humans are still scarce at present. Semiquantitative evidence for the notion of vestibular–neck interaction comes from a few studies which evaluated vestibularly evoked postural reactions for different static head postures. Consider a blindfolded subject who is spontaneously swaying in a given direction. If he changes his head position, there will be changes of the vestibular receptor units that are activated by the body sway, along with changes in neck input. His postural responses remain the same, however. This would be expected if the changes in vestibular input are accounted for by those in the neck proprioceptive input. In the experiments mentioned [18,25,46,61], noticeably, galvanic vestibular stimulation was used to evoke the sway, so that the vestibular input during the head turn remained constant and only the neck input changed. As a result, sway direction changed along with the head turn, compatible with the notion that vestibular input is indeed transformed by neck afferents. Surprisingly, however, analogous results were obtained when, instead of turning the head, the body was turned on the stationary feet [18,25,61]. Is this still compatible with the notion that vestibular input is used to stabilize the center of body mass in the trunk? A solution of this problem was provided by our psychophysical studies on vestibular–proprioceptive interaction, which showed that the vestibular signal is first channeled down to the body support and then up again (see below, Sections 3.3 and 3.4).

3.2. Psychophysical work

The psychophysical studies on vestibular–proprioceptive interaction for human self-motion perception suggest that proprioception is involved in two ways. First, proprioception along the entire body axis is used to evaluate motion of the body support in space by transforming a vestibular signal to the feet (‘head-in-space’ + ‘foot-to-head’ yielding ‘foot-in-space’). This coordinate transformation will be called ‘down-channeling’. Second, a different set of proprioceptive signals is used to determine body motion relative to the support (head-on-foot; up-channeling). The two mechanisms together yield a notion of body motion in space.

Before presenting details of the experimental evidence, the reader may intuitively appreciate the concept by considering a blindfolded subject who is standing on a platform that is set into motion. Asked about his perception, the spontaneous answer will be that the platform was set into motion. Movement of the own body is considered a consequence of platform motion. Thus, the physics of the situation has been correctly interpreted. By this we mean that the subject successfully reconstructed the situation from sensory inputs and other sources of information. We hold that vestibular input plays an important role in this reconstruction, since judgments of self-motion in such conditions are clearly impaired in patients with loss of vestibular function (see Ref. [55]).

The psychophysical evidence for the down- and up-channeling concept was obtained in experiments with passive horizontal rotations of the head, trunk or feet in space and relative to each other, using special rotation devices for these body segments [36,41]. They were performed with the subject in a sitting position, but we hold that the essence of the findings applies equally well to a standing subject. Sinusoidal stimuli were applied at different frequencies and peak displacements, with subjects making judgments of head, trunk, or foot motion in space or relative to each other in the form of concurrent indications (by means of pointers) or verbal estimates. From the indications we obtained gain and phase plots over frequency. In additional experiments, detection thresholds were obtained. A parsimonious description of the findings was obtained in the form of a dynamic model which reflects our view of how the sensory signals are processed in the CNS to yield the various types of self-motion perception encountered.

3.3. Down-channeling

A schematic summary of the ‘up- and down-channeling’ concept is shown in Fig. 3 in terms of the model (A) and the most relevant psychophysical findings (B; schematic gain vs. frequency plots). Only the vestibular–neck interaction is considered here, with head-in-space rotation (HS) as vestibular input and head-on-trunk rotation (HT; generated by trunk rotation under the head) as proprioceptive input (see A). For the down-channeling concept the estimates of trunk-in-space (ΨTS) are relevant.

HS during whole body rotation yielded veridical values for ΨTS (Fig. 3Bh) at high frequencies, whereas estimates fell short at low frequency. This finding reflects the known high pass transfer characteristics of the canal system (which apparently can only be partially corrected for centrally, yielding a prolongation of the peripheral to the behavioral time constant from 5 s to 20 s) and a rather high detection threshold for stimulus velocity, which is of central origin (see Ref. [41]). Both frequency characteristics and threshold together are denoted in the following as λ (for labyrinthine transfer function; in the box ‘VEST’ in Fig. 3A). The HT-evoked ΨTS (Fig. 3Bg; sign of response was opposite to that of HT) was similar to the vestibular one, as was its detection threshold. These findings for HT were surprising, since proprioception proper, i.e., HT-evoked ΨHT (Ba), was veridical from low to high frequencies (denoted by a transfer function of unity in the ‘Prop’ box) and the threshold was considerably lower. We therefore assume that the neck signal used for ΨTS has been given centrally the vestibular transfer characteristics (λ). With

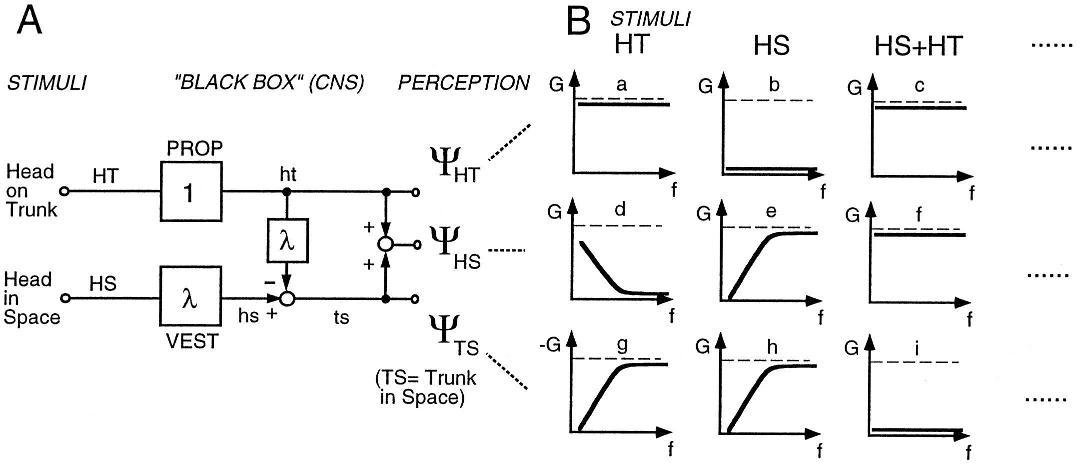


Fig. 3. *A* Model of vestibular–neck interaction for the perception of horizontal head-on-trunk, head-in-space and trunk-in-space angular displacement (ΨHT, ΨHS and ΨTS, respectively). Corresponding input signals, upper case letters; internal representations thereof, lower case letters. The vestibular system (VEST) is considered to show a deficient transfer function (λ) and the proprioceptive system (PROP) an ideal transfer function (unity). Simplified from Ref. [41]. *B,a–i* Schematic presentation of psychophysical findings for the three perceptual judgments (rows) obtained with different stimuli (columns). Gain (G) vs. stimulus frequency (f) plots (dashed lines, unity gain). Details in text.

both the vestibular and the neck signal having now the same transfer function, their sum during combined stimulation (same magnitude, opposite signs during head rotation on the stationary trunk) should yield zero (i.e., subjective stationarity of the trunk). This was indeed the case when the HS + HT combination (head rotation on stationary trunk) was tested (Bi). For other combinations (not shown) ΨTS was erroneous, yet still reflecting summation of its two non-ideal constituents.

These findings for ΨTS were implemented in the model by giving a version of the internal neck signal (ht) the vestibular transfer characteristics (λ) and summing it, after sign reversal, with the internal vestibular signal (hs; note that we present internal signals in lower case letters and signals in physics in capitals). This step of interaction corresponds to a solution of two of the above mentioned problems of sensor fusion: (i) A matching of dynamics of the two input signals, and (ii) a coordinate transformation of the vestibular signal from the head to its support (here the trunk). Under formal aspects, the transformation $ts = hs - \lambda ht = \lambda(HS - HT)$ yields an internal representation of trunk-in-space, which is veridical if HS = HT, i.e., if the head rotates on the stationary trunk. Continuing in an analogous way further downwards, one arrives at a signal for foot-in-space, which again is veridical if the feet and their support are stationary [36]. Thus, in the physiologically prevalent condition of firm ground, this is perceived as stationary, in spite of the inadequacy of the vestibular signal. However, when the support is moving, the 'vestibular deficit' (λ) is reflected in the perception of the movement.

3.4. Up-channeling

For the up-channeling concept the estimates of head-in-space (ΨHS) are considered. We start with head rotation on a stationary trunk (HS + HT) as a stimulus. ΨHS with this stimulus was found to be veridical across all frequencies (Fig. 3Bf). This was in contrast to HS-evoked ΨHS which showed the 'vestibular deficit' (Be; similar response as HS-evoked ΨTS). We therefore assume that the HS + HT-evoked ΨHS primarily reflects the ideal neck signal observed before for HT-evoked ΨHT (see above and Fig. 3Ba). A superposition of this ideal neck signal on the HS + HT-evoked ΨTS (zero) would, indeed, yield an ideal ΨHS. Given this simple solution, one would predict that a HT-evoked ΨHS should reflect the sum of two neck signals, an ideal one (that for ΨHT) and the one used for ΨTS, which carries the 'vestibular deficit' and is opposite in sign. Consequently, the sum of the two during HT (trunk rotation under stationary head) should result in a veridical ΨHS at high frequency (zero, meaning head subjectively stationary) and an illusion of a head-in-space rotation at low frequency ('vestibular deficit' showing up without vestibular stimulus). This was indeed observed (Bd). Taken together, the results could not be explained in terms of a simple two-signal summation (vestibular and neck), but required a third one. Expressed in mathematical terms: $\Psi HS = \lambda HS + (1 - \lambda)HT$, so that $\Psi HS = HS$, if $HT = HS$ (head rotation on stationary trunk). Or, from the view of down- and up-channeling: $\Psi HS = (\lambda HS - \lambda HT) + HT$, with $\Psi TS = (\lambda HS - \lambda HT)$.

Analogous findings were obtained for vestibular–leg proprioceptive stimulus combinations [36]. Thus, the up-channeling mechanism transforms our internal image of the kinematic state of body support to the different body segments by means of an essentially ideal proprioceptive signal. For simplicity the view may be reversed by stating that we evaluate motion of our body relative to the support, and by taking into account the support motion in space, we learn the body's motion in space. We would like to stress again that, in the most prevalent condition of a stationary support, self-motion perception in the absence of external cues (visual, auditory or tactile) is primarily referred to body support and determined by an ideal proprioceptive signal alone, and therefore it is veridical. We would also like to point out that, in the concept as a whole, it is the 'vestibular deficit' which unravels the existence of two different proprioceptive signals for the down- and up-channeling, because for stimuli in the mid- to high frequency/velocity range (λ becoming unity) the mechanism would not be visible in the experimental data.

At first sight, the 'vestibular deficit' might be considered a special problem of the canal input in the horizontal plane, since for vertical rotations the canal system is functionally complemented by the otolith system. However, recent results suggest that the threshold for perceiving pure otolith stimuli (translational motions) is of a comparable order of magnitude [19] (comparable in the sense that the body sway of a standing subjects evokes both head translations and rotations). Furthermore, the vestibular threshold for postural control also appears to be comparable [47].

3.5. Extension of the concept beyond self-motion perception

Visual object motion perception receives input not only from retinal cues, but also from extra-retinal cues such as an oculomotor efference-copy (e.g., when object motion perception results from tracking the object with a smooth pursuit movement without considerable retinal slip). Similarly, a head-fixed object is seen as moving in space during whole-body rotation; in this condition the input stems from vestibular cues. Thus, object-in-space motion perception in the absence of an external reference may be related to a vestibularly derived notion of space as a reference by the transformations object-on-retina (eye), eye-in-orbit (head), and head-in-space (compare above, Section 2). If the signals involved had ideal transfer functions and transformations were exact then perception would be veridical, and an additional proprioceptive contribution would not be required.

However, we have shown that (a) the vestibular signal involved is not ideal, (b) proprioception is involved, and (c) the above described down- and up-channeling principle also applies to visual object motion perception [38]. The same is true for memory-contingent object localization in space following vestibular and neck stimulation in a pointing task [30] and a saccade task [32]. Summarizing the findings for object motion perception: if we view a stationary visual object in the dark while a proprioceptive stimulus is applied (rotation of body or feet under stationary head), the object is seen as moving in space. This object motion illusion, which can also be obtained with proprioceptive stimulation by means of muscle vibration [5,54,60], is weak at high rotational frequencies, but stronger with decreasing frequency. This is just the opposite to the frequency behavior of the vestibular evoked object motion perception; motion of a head-fixed object during whole-body rotation is increasingly underestimated with decreasing frequency. In contrast, perceived object motion is veridical if vestibular and proprioceptive inputs are combined during head rotation on the stationary trunk or feet, independently of stimulus frequency. The model shown above (Fig. 3A) can be extended by a retinal and an oculomotor signal to describe these phenomena [38].

3.6. Implementation of the down- and up-channeling in a concept of postural control

In the following we consider, for simplicity, an organism consisting of two linked segments, i.e., a base and a superimposed mobile segment which contains the vestibular organ as a position sensor (we call the latter segment 'body'). A proprioceptive sensor measures the joint angle. As a first step, let body posture be controlled by the proprioceptive sensor (Fig. 4A). Two different conditions are considered:

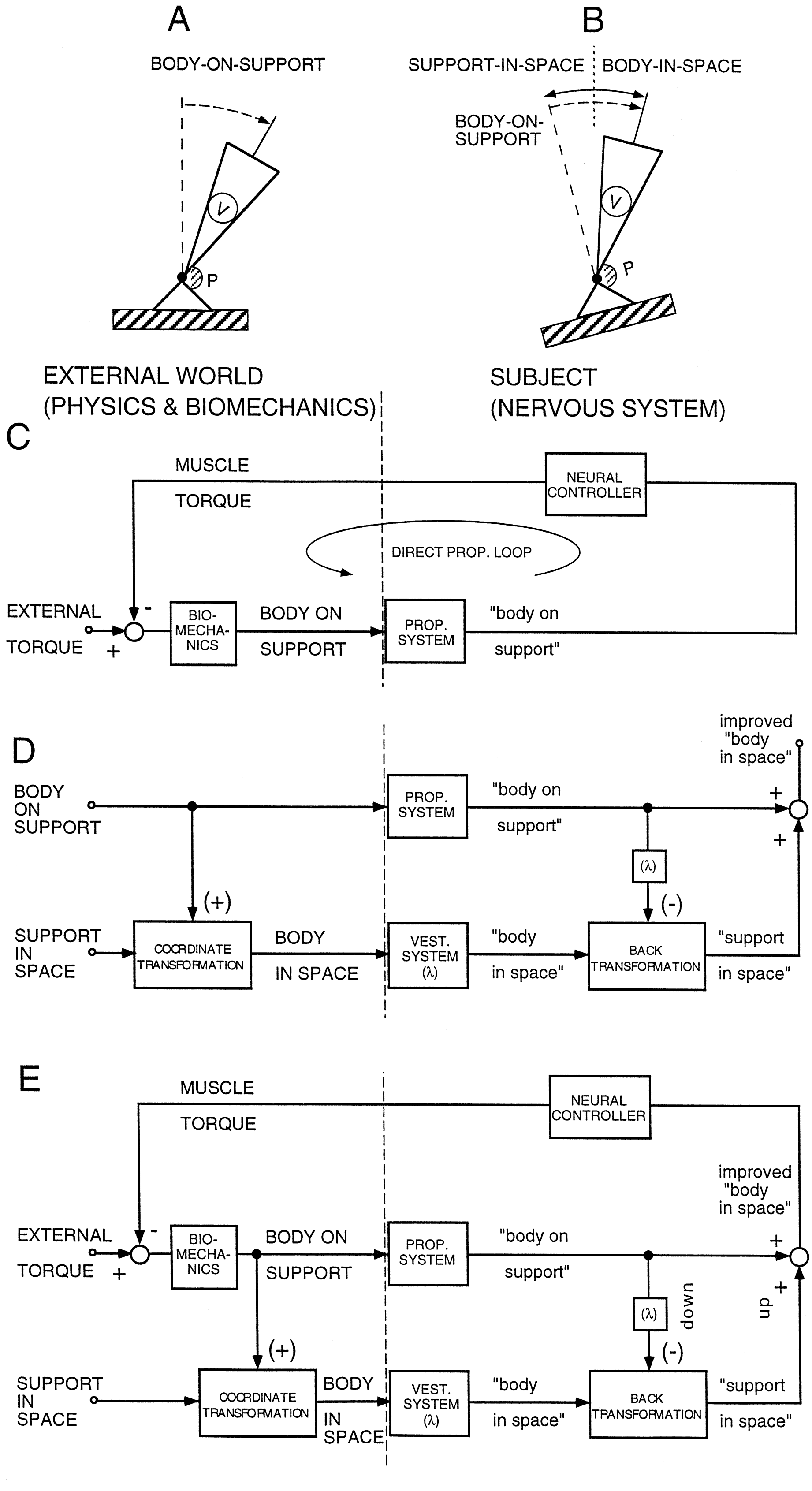
(1) Some external force (e.g., a pull or push) or internal cause (e.g., transient muscle weakness on one side) is leading to an excursion of the body, with the support remaining stationary. The excursion is sensed by proprioception (Fig. 4, panels A and C). The internal signal of this excursion (indicated by lower case letters in C) is transformed by a neural controller into a muscle torque that counteracts the excursion ('direct proprioceptive loop'). A control by means of the vestibular sensor would not be required.

(2) A support-in-space tilt is applied, superimposed on the body-on-support excursion (Fig. 4B). In the model, the resulting body-in-space tilt reflects a transformation of body position into space coordinates (left half of Fig. 4D). Body-in-space tilt is measured by the vestibular sensor. Why is the vestibular signal not added to the proprioceptive signal for postural control, as depicted in Fig. 1? This approach would be applicable in condition 1, but would lead to a compromise between a body-in-space and a body-on-support stabilization in condition 2. If, however, an internal reconstruction of support-in-space tilt is performed by means of a proprioceptive back transformation (right half of Fig. 4D) and this signal is then added to the proprioceptive body-on-support signal, body-in-space stabilization could be performed equally well in the two conditions.

Why not use the vestibular body-in-space signal alone for the control? We see several advantages to the control by vestibular–somatosensory fusion (compare Fig. 4E, combination of models in C and D):

(i) Given the vestibular signal carries a deficit (λ; see above), this would be eliminated by the back transformation, at least when applying body excursion on stationary support (condition 1). Thus, a patient with vestibular loss would be able to maintain equilibrium as long as the support is stationary.

(ii) The mechanism may easily be applied to a multisegment body, where each intersegmental joint is controlled according to its contribution to the overall excur-



sion, but can also be adjusted individually by a central set point for the postural control or by a command signal (see below).

(iii) The configuration of the transformation chain and the locus of reaction can be adjusted to the particular situation by including a haptic contact bridge between down and up-channeling, which is defined by the body's area of support. For instance, in the microgravity condition, as well as on earth, the chain could be anchored to the wall by grasping a handle.

(iv) The vestibular signal as a provider of a reference can be substituted under appropriate conditions by a visual signal or it can be replaced by some reference signal that is merged from several sensory inputs and is shaped by cognition (e.g., a Gestalt-like notion of the body's state in a given situation). Note that the concept allows for local control, but uses the same (here vestibular) global reference system as a common linkage across the different joints.

(v) The above issues (i–iv) make the system very robust with respect to local disturbances and highly flexible with respect to variations of behavioral conditions. Consider, for instance, a waiter who serves a glass full of liquor; his goal is to stabilize the glass with respect to inertial forces ('in space'). This would be achieved by linking the glass via the hand, the arm etc. to the body support and, given this is not stationary, via the up-channeling to the vestibular (inertial) reference (balancing the COM and orienting the head in space then would become secondary tasks).

Note that we assume that the direct loop has properties of an automatic load compensation, similarly to equilibrium point models [6,12], receiving an input in the form of a set point signal from a supervisor (here the vestibular loop) that considers more global aspects of the behavioral situation. Note furthermore that in situations, where body equilibrium is safe, the vestibular loop would no longer have to contribute to the postural reaction (compare [13]).

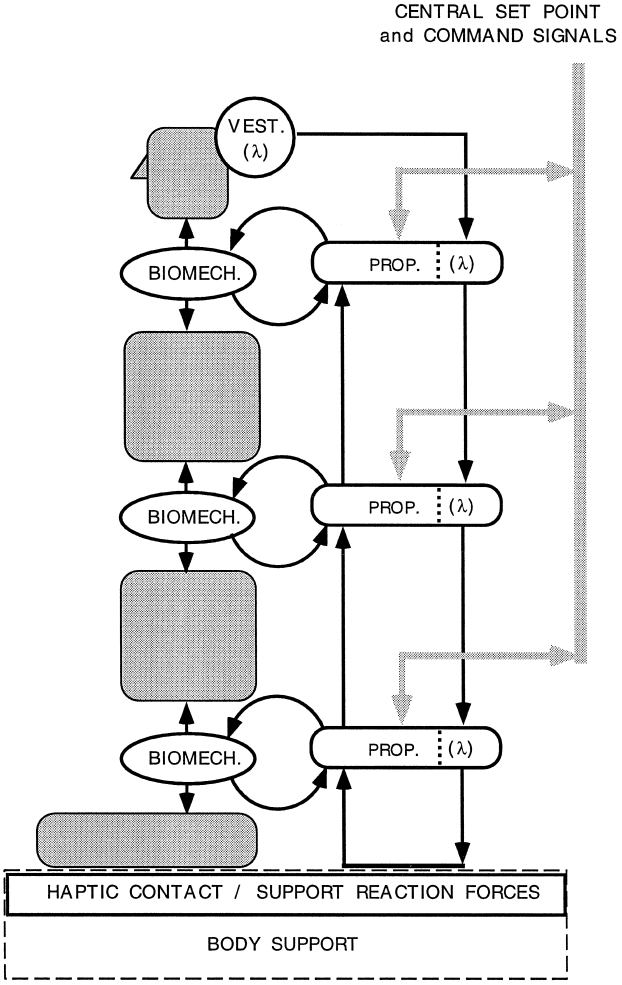


Fig. 5. Extension of the postural control model (Fig. 4E) in schematic form to a four-segment body. The location on the body where the transition between down- and up-channeling occurs is defined by haptic contact with the body support and the reaction forces. The up-going signal defines the set point for each local proprioceptive loop. Furthermore, descending and ascending channels (gray arrows) are added for an additional central set point or command signal and for afferent signals to higher levels of the CNS.

How to implement the multisegmental structure of the human body in the model? A simplified scheme of this for a four-segment body is given in Fig. 5 (compare [36]). The proprioceptive system at each intersegmental level is used to control the local joint (box 'biomechanics') by means of a direct loop, but is used, in addition, for the coordinate transformations of the vestibular signal (down-transformation carrying λ). The body locus where the transition between down- and up-channeling occurs is defined by the haptic contact with the body support and the reaction forces. The up-going transformation defines the set point for each joint. Furthermore, the local loops can be under the control of other set point or command signals, e.g., from central origin for a voluntary movement, and inform higher centers about the local condition. The fact that the vestibular set point signal is fed in via the up-going transformation would be advantageous in view of the geocentric hierarchy of body segments produced by gravity (see Section 1.1); a postural reaction in the lowest joint

---

Fig. 4. *A,B* Schematic drawing of a body which rotates on a base relative to a support which is either stationary (A) or is tilted in space (B). V, 'vestibular' sensor; P, 'proprioceptive' sensor. *C* Simple 'postural' control model which tends to bring the body of panel A in an upright position with the help of 'proprioceptive' input. *D* Internal reconstruction ('Nervous System'; right half of panel) of support motion in space (Physics and Biomechanics, left half, and B) with the help of the 'vestibular' and 'proprioceptive' sensors (internal reversal of 'external' coordinate transformation, using a proprioceptive signal that carries the 'vestibular deficit', λ). Adding a proprioceptive signal with ideal transfer function yields an improved 'body in space' signal (free of λ, if support is stationary). *E* Fusion of the models in *C* and *D* into a postural control model which is advantageous to the pure proprioceptive (C) or a pure vestibular control model (see text).

automatically affects all segments above. Based on this concept and realistic sensor models, we developed a dynamic control system which successfully maintains balance of a biomechanical computer model of a multisegmental human body, with the responses resembling human data on movable platform. Interestingly, the model reveals nicely what we would call 'supramodal control'; it is not the 'vestibular' or the 'proprioceptive' signal which determines the response (one or the other can remain below threshold), but the internal signal of platform motion in space derived from these two signals by sensor fusion.

From a biomechanical and control point of view it is advantageous to have a combination of both, a global reference system, which represents a basis for a control strategy to handle a multi-body system, and local control units, by which the computational complexity of the system as a whole is reduced and flexibility is given. Similar views have a long tradition in posture research, going back to the concept of Bernstein [3], who postulated the necessity of breaking up the complex control task into several units that show a hierarchical order. It is also reminiscent of the notion of Nashner et al. [42,43] who distinguish between postural synergies (achieving a particular goal by a given spatio-temporal pattern of muscle activity) and postural strategies (high level decisions about the way how to achieve a given goal; e.g., by 'ankle strategy' or by 'hip strategy').

Finally, we may consider what the main differences between the posture model in Fig. 4E and the gaze model in Fig. 2 are? This question may be raised even if vision is not included in the posture model, yet, and proprioception is absent in the gaze model, because the direct proprioceptive loop in the posture model is similar to the OKR loop in the gaze model. Note that the vestibular signal is fed back in the posture model, but not in the gaze model. Furthermore, proprioception is used, in addition, for the coordinate transformation of the vestibular signal (nothing comparable would be required for the OKR). In general, the multisegmental structure of the human body and the locus of impact of the support reaction forces in the posture model (Fig. 5) have no counterpart in the gaze model. Interestingly, however, the situation is different for the gaze mechanisms which are used to redirect the eyes towards remembered target locations in space following a body movement. Then, a notion of the body movement has to be retrieved from short term memory; the information stems from a previous self-motion perception which is based on the proprioceptive down- and up-channeling of the vestibular input as described above (see Ref. [32]).

3.7. *Evidence for a physiological 'hardware implementation' of the concept*

The down- and up-channeling concept explains some puzzling findings in earlier postural studies. For example, when measuring the electromyographic (EMG) responses evoked by galvanic vestibular stimulation, one finds that the soleus muscle shows shorter latencies in a body balancing task by the feet as compared to the triceps brachii muscle in one in which the arms are used [9]. Such a time difference would indeed result, if the sequence of down- and up-transformation of the vestibular signal proceeded as a series of temporally distinct steps propagated along the spinal representations of the body segments. Noticeably, this applies only to the late, functionally relevant galvanic response in the EMG, whereas the early and rather weak EMG response, which does not elicit considerable postural reactions and may represent the relict of a reflex from ontogenesis, shows a shorter latency in the arm than the leg, as one would expect from the respective distances from the labyrinths.

Another intriguing finding is that proprioceptive activation by vibration on the back of the body leads to leaning forward if vibration is applied at the level of the neck, whereas it leads to a lean backward if applied to leg muscles. This can be explained by assuming that neck muscle vibration above the COM activates only the down-channeling for postural control, while leg muscle vibration affects both the down- and up-channeling, with the latter predominating (for details, see Ref. [35]).

These considerations raise the question whether the down- and up-channeling only represent a conceptual construct or whether there exist neuroanatomical and neurophysiological substrates for it. In other words: Is there evidence for an ascending pathway in the spinal cord that carries vestibular and proprioceptive information, in addition to the well-known down-going vestibulo-spinal projections? This evidence exists. It has been shown in the cat that spinal neurons, which project to the lateral reticular nucleus in the brainstem, carry both vestibular and proprioceptive signals [11]. We therefore hold that there is a 'hardware implementation' of the concept or, at least, a spinal hardware counterpart to what is processed at higher central levels.

A hardware implementation of the concept would give the system a fast reactivity. However, one may still object that the many and complex computations of the coordinate transformations, for instance, would require considerable processing time. As a solution of this problem we conceive of the possibility that these computations result from information being fed through a particular path in a complex network. Given that this path is largely predetermined beforehand by setting the appropriate 'switches' (weights at the nodes), one could conceive of a processing that is fast enough to be approximately 'on-line'. There is, indeed, evidence that postural reactions are shaped to a considerable degree by recognition processes prior to the onset of reaction. For instance, in experiments on the initiation of hopping responses to overbalancing, Roberts [50] observed responses for which he found no vestibular error signal that would indicate the nature of the stimulus condition. It is to say, however, that Roberts still goes further than we would do at the present stage. He calls the response he found an ‘anticipatory pre-emptive action’. By ‘pre-emptive’ he means that the response is initiated so early and in such a way that postural reflex mechanisms even need not to come into play (or do not reach threshold).

4. Including visual input into the concept

As already mentioned above, visual cues are known to make a major contribution to postural control and motion perception. The interaction of this input with vestibular and somatosensory inputs is not fully understood at present due to its high complexity. Nevertheless, we try in the following to create a conceptual framework for this interaction, where we build upon the down- and up-channeling principle. After having displayed this view we consider how the interaction may be affected in microgravity.

Consider a subject standing upright in a stationary room who is viewing a picture on the wall (Fig. 6A). In analogy to the vestibular mechanism described above, we assume that down- and up-channeling also exist for the visual input. With respect to *down-channeling*, we assume that the subject infers the kinematic state of his body support from the visual object (taken as a reference), from proprioceptive information along the body axis and from haptic ground contact. This notion may be appreciated intuitively; if relying on visual input as a reference for self-motion, i.e., if fully locked in a visually induced self-motion perception while sitting on a rotation chair, one perceives the chair as moving and self-motion only a consequence of chair motion. However, we do not assume such a fixed coupling as between vestibular input and the somatosensory input evoked by support reaction forces.

As for the *up-channeling*, we assume that it takes place in our internal image of the outside world. This is represented here by our ‘knowledge’ of a fixed geometric relationship between ground and wall of the room. This ‘knowledge’ links the visual and somatosensory inputs together into one coherent ‘Gestalt’ of the condition, even when the subject is leaning: As long as the foot point and visual fixation point remain constant, a coupling exists between the two sensory signals, since a change in body lean angle (proprioceptive signal of head-on-ground) systematically covaries with that of the visuo-oculomotor angle (between visual axis and head). Possibly, we are referring to this knowledge-based intersensory coupling when we consider ourselves ‘spatially oriented’; it allows the brain to extract from visual and proprioceptive inputs congruent information on body lean, stationarity of the picture on the wall etc.

This concept is still hypothetical, mainly because we know very little at present about the ‘cognitive aspects’ of these perceptual mechanisms. A bit more is known about visual-proprioceptive interaction. 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 stable vection (visually induced self-motion perception; see Ref. [33]). Gains of visual-only and of neck-only trunk turning perception were similar and the result of interaction could be described by a simple summation of the two inputs across the stimulus frequencies tested.

How would the vestibular signal join in into this scenario? We consider two situations. One has just been mentioned, i.e., a body lean of the subject in the stationary room. The result of the vestibular down- and up-channeling then is congruent with the visual–somatosensory derived notion of body lean. The vestibular contribution would yield two beneficial effects. One effect is that information redundancy improves perception quality (saliency). Another effect would be that the vestibular information can be taken to substitute the ‘knowledge’ of the fixed spatial relationship between ground and wall, since one may derive from it that both the support and the visual object are stationary. Thus, we are normally able to verify our internal image of the stationarity of the outside world with the help of vestibular input, while a vestibular-loss patient would only have his ‘knowledge’.

The other situation, which we consider, is motion of the room as a whole (e.g., of a closed funicular cabin). In this situation the vestibular input arises, together with corresponding ground reaction forces, independently of the visual–somatosensory derived Gestalt. The room is then perceived as moving with respect to an unseen (vestibularly derived, i.e., inertial) global reference. Postural control in the latter situation is to be based, conceivably, on the inertial reference, while in the former situation it can rely on both, the vestibular–somatosensory and the visual–somatosensory information.

Fig. 6B shows how we think the two systems are inter-related. It shows on the left side the previously described vestibular–somatosensory channeling and on the right side the visual–somatosensory one. In the situation of the moving room (‘visual scene in space’, ‘$\neq 0$’) the visual part is simply coupled to the vestibular one by coordinate transformation. Another view would be that in this situation the visual room is experienced as moving within an unseen global reference frame (the vestibular or inertial one). Still another way to describe the relationship would be to say that vestibular (inertial) cues are required to specify the meaning of a visual stimulus, since this defines only the relative motion between a visual object and one’s body, but not its motion in space. Noticeably, an uncoupling between the vestibular and visual parts (not shown) can occur in certain experimental conditions, e.g., if subjects get locked in a solely visually determined perceptual state (see Ref. [33]).

In the situation of a body lean in a stationary room, the vestibular notion of visual scene motion in space is veridi-

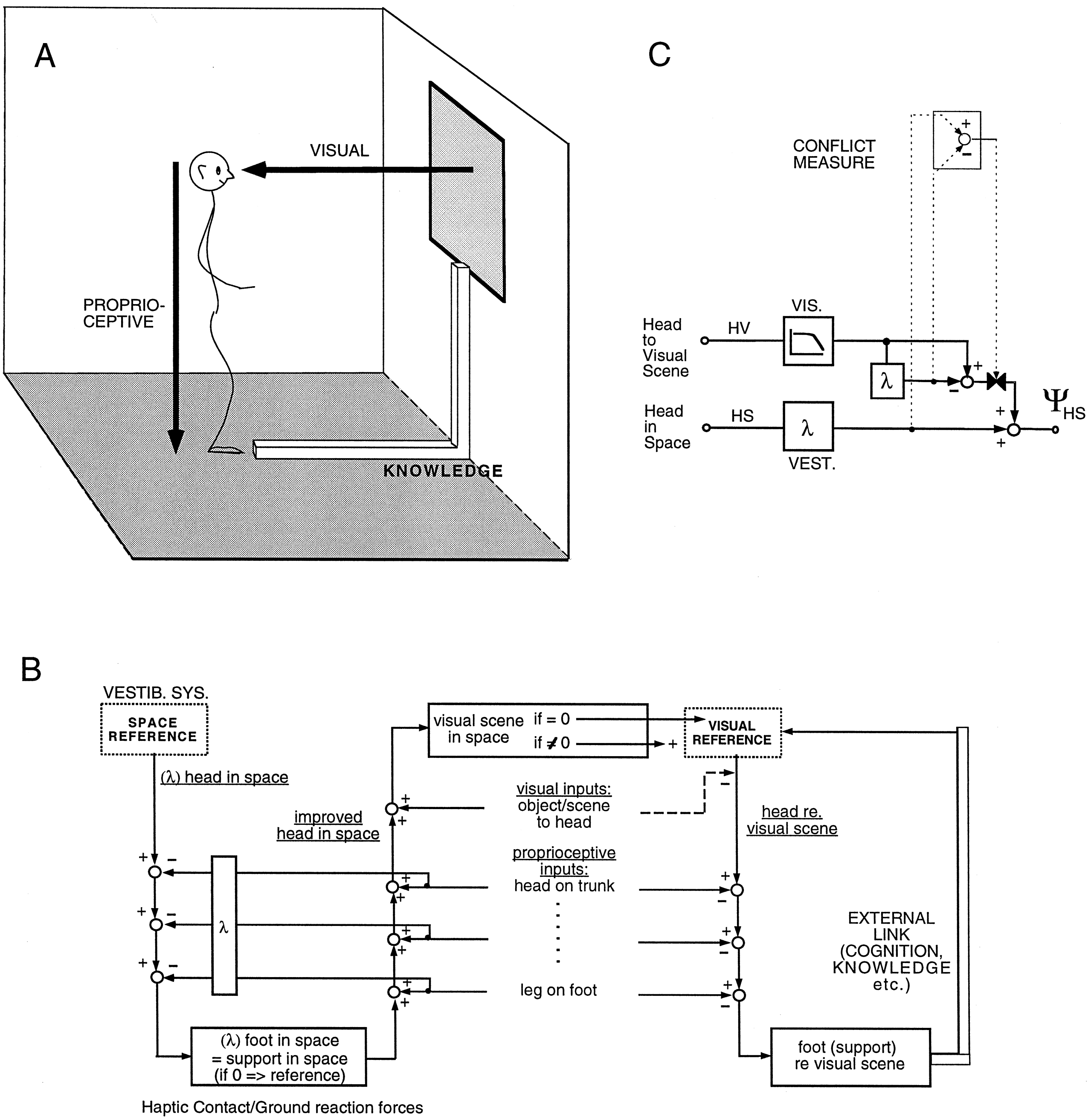


Fig. 6. *A–C*. Combination of the vestibular–somatosensory channeling mechanism with a visual–somatosensory one. *A* Schematic illustration of a closed loop formed by a visual–proprioceptive channeling which links the body support to a visual reference both via proprioception and via the outside world in the form of a cognitive channeling (knowledge on fixed spatial relationship between ground and wall). *B* Combination of the vestibular–somatosensory and visual–somatosensory mechanisms in the form of chains of coordinate transformations (left and right half of panel, respectively). Congruency between the results of the two mechanisms (e.g., between perception of head-in-space and head-re.-visual scene motion) is given if foot support and visual scene are stationary (box 'visual scene in space = 0'). Otherwise ('≠ 0') the visual reference becomes linked to the vestibular reference. *C* Simplified model of visual–vestibular interaction. It is based on a fusion mechanisms of the two inputs (full lines) and on a mechanism which measures visual–vestibular conflict (dotted) and suppresses the visual contribution to ΨHS, depending on measured conflict (suppression mechanism symbolized by throttle). Note that the visual input is assumed to have a limited bandwidth similar to that of the OKR in Fig. 2.

cal (scene subjectively stationary, because vestibular and proprioceptive signals in the down-channeling path cancel each other and the proprioceptive ones in the up-channeling, to which the visual signal adds, have essentially ideal transfer characteristics; part ' = 0' in box 'visual scene in space'). In the visual–somatosensory channeling the scene and the support are also veridically perceived as stationary (sum of visual and proprioceptive signals yielding zero). Veridicality of perception in both parts applies not only to the visual scene, but also to all body segments (perceived trunk and head motion in space etc.) and to the support. These congruencies unequivocally define this situation and are considered to yield a special perceptual state, in that vestibular and visual reference frames merge into one. Consequently, subjects can rely solely on the visual reference and check from time to time on the background for congruency, which would greatly reduce the required amount of signal processing.

The linkage between the two channeling mechanisms is critical and will be considered in more detail in the following. Note that in the moving room situation the up-channeled signals on the vestibular side of the scheme (Fig. 6B) carry the 'vestibular deficit' (λ). With a head-fixed scene or in the dark, a very slow whole-body movement is indeed underestimated or not even detected at all (see above). On the other hand it is well known, that such a slow movement in an illuminated environment with space-stationary scene is correctly perceived, and that slow movements of the scene, in turn, may evoke an illusion of self-motion (vection). As it may be appreciated intuitively from everyday experience, and has repeatedly been shown experimentally, we use visual information to compensate for the 'vestibular deficit', but do so only to the extent that we are not fooled by self-motion illusions (although they are easily produced in laboratory conditions, they occur only rarely in 'real life'). This requires, conceivably, a visual–vestibular interaction mechanism which dynamically weights the visual cues in conditions in which the visual scene is stationary, but shifts the weight towards the vestibular cues if the scene is not a suitable reference because it is moving.

Such a mechanism was originally suggested by Zacharias and Young [67]. We identified a similar, functionally equivalent mechanism [22,37,40] which is described in the following in a simplified form (Fig. 6C). It consists of two parts. One part is a sensor fusion of vestibular and visual signals in a way analogous to the one described above for vestibular–proprioceptive interaction. In the model perceived head motion in space, $\Psi\mathrm{HS} = \lambda\mathrm{HS} + (1 - \lambda)\ \mathrm{HV}$ (HV, motion of head relative to visual scene). Self-motion is veridical if HS = HV (self-motion in a stationary visual environment). With a moving scene, in contrast, the visual contribution to the self-motion perception has to be suppressed, leaving from the visual signal only what is needed to compensate for the 'vestibular deficit'. This is obtained in the model by measuring visual–vestibular conflict arising with head motion in terms of $\lambda\mathrm{HS} - \lambda\mathrm{HV}$ (conflict is zero with head movement in a stationary visual environment and $\neq 0$ if scene is moving) and using the result of this measure to suppress the visual contribution. Simulations obtained with this model showed a close correspondence to experimental data [37,40].

It remains to be stated that several aspects of the visual information used for self-motion perception and postural control are not considered in our concept. For instance, it has been shown that local changes in a visual image, which arise with perspective changes of objects during self-motion ('optic flow'), can be directly used for self-motion perception and postural control [2,14,21]. Mechanisms of 'figure and ground' (perceptual interpretation of a visual stimulus as a 'moving object' vs. 'background') and attentional mechanisms (focusing of ones attentions onto different items of a complex scenario) also play a role [33]. However, we hold that the above concept would be suited to serve as a framework to which such mechanisms can be added.

How would the change to free fall affect the visual–vestibular interaction in our concept? Conceivably, with the body in a free-floating state the intersensory linkages that are formed between otolith signal and body support would be lost. Also, spatial orientation during movement would be less reliable due to changes in canal–otolith interaction (see Section 1.2) and somatosensory input (Section 1.1). These effects should equally apply to posture and movement control (see Section 1.1). We would assume that, as a consequence, the visual information becomes functionally more relevant. This, possibly, explains previous observations of an enhanced weighting of visual self-motion cues during and following a longer period under microgravity (see Refs. [65,66]). With respect to inertial forces, it is true that they are still effective under microgravity, so that vestibular, haptic-proprioceptive and visual linkages of the kind described by the concept would be created if astronauts use an abutment (e.g., handle on the wall) when moving. However, there would not be a continuous automatic linkage as on earth, and the vestibular and proprioceptive reafferent signals would be somewhat different (Sections 1.1 and 1.2).

5. Conclusion

This article is not meant to suggest particular experiments under microgravity. Rather it is meant as a plea to embed our knowledge, which has been accumulated in the past on human spatial behavior on earth and under microgravity, into a broad conceptual framework and to use this as a guideline for future research in space and under altered gravity conditions (e.g., on Mars). This framework would be incomplete if it did not include biomechanics and multi-body dynamics, since these shape to a considerable degree our postural behavior and the related perception (we assume that the down- and up-channeling mechanisms described here develop through experience of inertial and gravitational reaction forces). Also, the feedback (and possibly feed forward) loops used for postural control still have to be worked out. The complexity of the human organism and of its interaction with the environment may discourage researchers from taking such a global approach. We hold, however, that current developments in computer science and robotics provide us with a number of tools which allow an integrative approach to be taken, alternating in an iterative way between dynamic modeling and experiment and thereby overcoming the immense complexity of the system. This approach aims to establish formal descriptions of the problems and their solutions and allows revisable predictions to be made for future research. It is certainly distinct from the one which tries to solve the question of how the mechanisms are implemented in the brain on a neural or molecular level (a question which, conceivably, is much more difficult to solve).

Acknowledgements

Supported by DFG, Me 715. We like to thank T.D.M. Roberts for his valuable comments.

References

[1] D. Anastasopoulos, T. Mergner, Canal-neck interaction in vestibular nuclear neurons of the cat, Exp. Brain Res. 46 (1982) 269–280.

[2] G.J. Andersen, Classification of visual processes for the control of posture and locomotion, in: T. Mergner, F. Hlavacka (Eds.), Multisensory Control of Posture, Plenum, New York, 1995, pp. 131–138.

[3] N. Bernstein, Co-ordination and Regulation of Movements, Pergamon, New York, 1967.

[4] A. Berthoz, M. Lacour, J.F. Soechting, P.P. Vidal, The role of vision in the control of posture during linear motion, In: R. Granit, O. Pompeiano (Eds.), Reflex control of Posture and Movement, Progr. Brain Res. 50 (1979) 197–209.

[5] B. Biguer, I.M. Donaldson, A. Hein, M. Jeannerod, Neck muscle vibration modifies the representation of visual motion and direction in man, Brain 111 (1988) 1405–1424.

[6] E. Bizzi, N. Hogan, F.A. Mussa-Ivaldi, S. Giszter, Does the nervous system use equilibrium point control to guide single and multiple joint movements?, Behav. Brain Sci. 15 (1992) 603–613.

[7] J. Borah, L.R. Young, R.E. Curry, Optimal estimator model for human spatial orientation, Ann. New York Acad. Sci. 545 (1988) 51–73.

[8] R. Boyle, O. Pompeiano, Convergence and interaction of neck and macular vestibular inputs on vestibular neurons, J. Neurophysiol. 45 (1981) 852–868.

[9] T.C. Britton, B.L. Day, P. Brown, J.C. Rothwell, P.D. Thompson, C.D. Marsden, Postural electromyographic responses in the arm and leg following galvanic vestibular stimulation in man, Exp. Brain Res. 94 (1993) 143–151.

[10] G. Clement, V.S. Gurfinkel, F. Lestienne, M.I. Lipshits, K.E. Popov, Adaptation of postural control to weightlessness, Exp. Brain Res. 57 (1984) 61–72.

[11] J.D. Coulter, T. Mergner, O. Pompeiano, Effects of static tilt on cervical spinoreticular tract neurons, J. Neurophysiol. 39 (1976) 45–62.

[12] A.G. Feldman, Once more for the equilibrium point hypothesis (lambda model), J. Mot. Behav. 18 (1986) 17–54.

[13] R. Fitzpatrick, D. Burke, S. Gandevia, Task-dependent reflex responses and movement illusions evoked by galvanic vestibular stimulation in standing humans, J. Physiology 478 (1994) 363–372.

[14] J.J. Gibson, The Ecological Approach to Visual Perception, Houghton Mifflin, Boston, 1979.

[15] S. Glasauer, D.M. Merfeld, Modelling three dimensional vestibular responses during complex motion stimulation, in: M. Fetter, D. Tweed, H. Misslisch (Eds.), Three-Dimensional Kinematic Principles of Eye-, Head-, and Limb Movements in Health and Disease, Harwood, Amsterdam, 1997, pp. 387–398.

[16] V.S. Gurfinkel, Y.S. Levik, K.E. Popov, B.N. Smetanin, Body scheme in the control of postural activity, in: V.S. Gurfinkel, M.E. Ioffé, J. Roll (Eds.), Stance and Motion: Facts and Concepts, Plenum, New York, 1988, pp. 185–193.

[17] D.L. Harm, D.E. Parker, Perceived self-orientation and self-motion in microgravity, after landing and during preflight adaptation training, J. Vestib. Res. 3 (1993) 297–305.

[18] F. Hlavacka, M. Krizkova, O. Bodor, T. Mergner, Adjustment of equilibrium point in human stance following galvanic vestibular stimulation: Influence of trunk and head position, in: G. Gantchev, V. Gurfinkel, D. Stuart, M. Wiesendanger (Eds.), Motor Control VII, Motor Control Press, Tuscon, AZ, 1996, pp. 289–293.

[19] F. Hlavacka, T. Mergner, B. Bolha, Human self-motion perception during translatory vestibular and proprioceptive stimulation, Neurosci. Lett. 210 (1996) 83–86.

[20] F.B. Horak, J.M. Macpherson, Postural Orientation and Equilibrium, in: L.B. Rowell, J.T. Shepherd (Eds.), Handbook of Physiology, Section 12: Exercise: Regulation and Integration of Multiple Systems, Oxford Univ. Press, New York, 1966, pp. 255–292.

[21] J.J. Koenderink, Optic flow, Vision Res. 26 (1986) 161–180.

[22] O. Kolev, T. Mergner, H. Kimmig, W. Becker, Detection thresholds for object motion and self-motion during vestibular and visuo-oculomotor stimulation, Brain Res. Bull. 40 (1996) 451–458.

[23] J.R. Lackner, P. DiZio, Multisensory, cognitive, and motor influences on human spatial orientation in weightlessness, J. Vestib. Res. 3 (1993) 361–372.

[24] K.W. Lindsay, T.D. Roberts, J.R. Rosenberg, Asymmetric tonic labyrinth reflexes and their interaction with neck reflexes in the decerebrate cat, J. Physiol. (Lond.) 261 (1976) 583–601.

[25] S. Lund, C. Broberg, Effects of different head positions on postural sway in man induced by a reproducible vestibular error signal, Acta Physiol. Scand. 117 (1983) 307–309.

[26] M. Magnusson, R. Johansson, Characteristic parameters of anterior–posterior body sway in normal subjects, in: B. Amblard, A. Berthoz, F. Clarac (Eds.), Posture and Gait: Development, Adaptation and Modulation, Elsevier, Amsterdam, 1988, pp. 177–186.

[27] D. Manzoni, O. Pompeiano, U.C. Srivastava, G. Stampacchia, Responses of forelimb extensors to sinusoidal stimulation of macular labyrinth and neck receptors, Arch. Ital. Biol. 121 (1983) 205–214.

[28] J. Massion, V. Gurfinkel, M. Lipshits, A. Obadia, K. Popov, Axial synergies under microgravity conditions, J. Vestib. Res. 3 (1993) 275–287.

[29] J. Massion, M.H. Woollacott, Posture and equilibrium, in: A. Bronstein, T. Brandt, M.H. Woollacott (Eds.), Clinical Disorders of Balance, Posture and Gait, Arnold, London, 1996, pp. 1–18.

[30] C. Maurer, H. Kimmig, A. Trefzer, T. Mergner, Visual object localization through vestibular and neck inputs: I. Localization with respect to space and relative to the head and trunk mid-saggital planes, J. Vestib. Res. 7 (1997) 119–135.

[31] D.M. Merfeld, Modeling the vestibulo-ocular reflex of the squirrel monkey during eccentric rotation and roll tilt, Exp. Brain Res. 106 (1995) 123–134.

[32] T. Mergner, G. Nasios, D. Anastasopoulos, Vestibular memory-contingent saccades involve somatosensory input from the body support, NeuroReport 9 (1998) 1469–1473.

[33] T. Mergner, W. Becker, Perception of horizontal self-rotation: Multisensory and cognitive aspects, in: R. Warren, A.H. Wertheim (Eds.), Perception and Control of Self-Motion, Lawrence Erlbaum, Hillsdale London, 1990, pp. 219–263.

[34] T. Mergner, W. Becker, L. Deecke, Canal-neck interaction in vestibular neurons of the cat's cerebral cortex, Exp. Brain Res. 61 (1985) 94–108.

[35] T. Mergner, B. Bolha, W. Becker, A modified version of the center-of-mass balancing hypothesis, psycoloquy.97.8.04 ('electronic journal') 1997.

[36] T. Mergner, F. Hlavacka, G. Schweigart, Interaction of vestibular and proprioceptive inputs, J. Vest. Res. 3 (1993) 41–57.

[37] T. Mergner, W. Huber, W. Becker, Vestibular–neck interaction and transformations of sensory coordinates, J. Vestib. Res. 7 (1997) 347–367.

[38] T. Mergner, G. Rottler, H. Kimmig, W. Becker, Role of vestibular and neck inputs for the perception of object motion in space, Exp. Brain Res. 89 (1992) 655–668.

[39] T. Mergner, G. Schweigart, F. Botti, A. Lehmann, Eye movements evoked by proprioceptive stimulations along the body axis in humans, Exp. Brain Res. 120 (1998) 450–460.

[40] T. Mergner, G. Schweigart, O. Kolev, F. Hlavacka, W. Becker, Visual–vestibular interaction for human ego-motion perception, in: T. Mergner, F. Hlavacka (Eds.), Multisensory Control of Posture, Plenum, New York, 1995, pp. 157–168.

[41] T. Mergner, C. Siebold, G. Schweigart, W. Becker, Human perception of horizontal head and trunk rotation in space during vestibular and neck stimulation, Exp. Brain Res. 85 (1991) 389–404.

[42] L. Nashner, G. McCollum, The organization of human postural movements: A formal basis and experimental synthesis, Behav. Brain Sci. 8 (1985) 135–172.

[43] L. Nashner, M. Woollacott, The organization of rapid postural adjustments of standing humans: An experimental–conceptual model, in: R.E. Talbott, D.R. Humphrey (Eds.), Posture and Movement, Raven Press, New York, 1979.

[44] H. Mittelstaedt, Interaction of eye-, head-, and trunk-bound information in spatial perception and control, J. Vestib. Res. 7 (1997) 1–20.

[45] H. Mittelstaedt, Somatic Graviception, Biological Psychology 42 (1996) 53–74.

[46] L.M. Nashner, P. Wolfson, Influence of head position and proprioceptive cues on short latency postural reflexes evoked by galvanic stimulation of the human labyrinth, Brain Res. 67 (1974) 86–88.

[47] R.J. Peterka, M.S. Benolken, Role of somatosensory and vestibular cues in attenuating visually induced human postural sway, Exp. Brain Res. 105 (1995) 101–110.

[48] T. Raphan, V. Matsuo, B. Cohen, Velocity storage in the vestibulo-ocular reflex arc (VOR), Exp. Brain Res. 53 (1979) 229–248.

[49] T.D.M. Roberts, Neurophysiology of Postural Mechanism, Butterworths, London, 1978.

[50] T.D.M. Roberts, Otoliths and uprightness, in: R. Granit, O. Pompeiano (Eds.), Reflex Control of Posture and Gait, Progr. Brain Res. 50 (1979) 493–499.

[51] T.D.M. Roberts, Understanding Balance: The Mechanics of Posture and Locomotion, Chapman & Hall, London, 1995.

[52] D.A. Robinson, Vestibular and optokinetic symbiosis: an example of explaining by modelling, in: R. Baker, A. Berthoz (Eds.), Control of gaze by brainstem neurons. Elsevier, Amsterdam, 1977, pp. 49–58.

[53] J.P. Roll, K. Popov, V. Gurfinkel, M. Lipshits, C. Andre-Deshays, J.C. Gilhodes, C. Quoniam, Sensorimotor and perceptual function of muscle proprioception in microgravity, J. Vestib. Res. 3 (1993) 259–273.

[54] R. Roll, J.L. Velay, J.P. Roll, Eye and neck proprioceptive messages contribute to the spatial coding of retinal input in visually oriented activities, Exp. Brain Res. 85 (1991) 423–431.

[55] G. Schweigart, S. Heimbrand, T. Mergner, W. Becker, Role of neck input for the perception of horizontal head and trunk rotation in patients with loss of vestibular function, Exp. Brain Res. 95 (1993) 533–546.

[56] G. Schweigart, T. Mergner, W. Becker, Eye stabilization by vestibulo-ocular reflex (VOR) and optokinetic reflex (OKR) in macaque monkey: Which helps which?, Acta Otolaryngol. 115 (1995) 19–25.

[57] G. Schweigart, T. Mergner, I. Evdokimidis, S. Morand, W. Becker, Gaze stabilization by optokinetic reflex (OKR) and vestibulo-ocular reflex (VOR) during active head rotation in man, Vision Res. 37 (1997) 1643–1652.

[58] B.E. Stein, M.A. Meredith, The Merging of the Senses, MIT Press, Cambridge/MA, 1993.

[59] T.A. Stoffregen, G.E. Riccio, An ecological theory of orientation and the vestibular system, Psychol. Rew. 1 (1988) 3–14.

[60] J.L. Taylor, D.I. McCloskey, Illusions of head and visual target displacement induced by vibration of neck muscles, Brain 114 (1991) 755–759.

[61] T. Tokita, Y. Ito, K. Takagi, Modulation by head and trunk positions of the vestibulo-spinal reflexes evoked by galvanic stimulation of the labyrinth. Observations by labyrinthine evoked EMG, Acta Otololaryngol. (Stockh.) 107 (1989) 327–332.

[62] E. von Holst, H. Mittelstaedt, Das Reafferenzprinzip (Wechselwirkungen zwischen Zetralnervensystem und Peripherie), Naturwissenschaften 37 (1950) 464–476.

[63] V.J. Wilson, G. Mellvil Jones, Mammalian Vestibular Physiology, Plenum, New York, 1979.

[64] D.A. Winter, A.B.C. (Anatomy, Biomechanics and Control) of Balance During Standing and Walking, Waterloo Biomechanics, Waterloo, 1996.

[65] L.R. Young, J.C. Mendoza, N. Groleau, P.W. Wojcik, Tactile influences on astronaut visual spatial orientation: human neurovestibular studies on SLS-2, J. Appl. Physiol. 81 (1996) 44–49.

[66] L.R. Young, M. Shelhamer, Microgravity enhances the relative contribution of visually-induced motion sensation, Avat. Space Environ. Med. 61 (1990) 525–530.

[67] G.L. Zacharias, L.R. Young, Influence of combined visual and vestibular cues on human perception and control of horizontal rotation, Exp. Brain Res. 41 (1981) 159–171.