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Multisensory control of human upright stance

Received: 18 July 2005 / Accepted: 27 September 2005 / Published online: 24 November 2005
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Abstract The interaction of different orientation senses contributing to posture control is not well understood. We therefore performed experiments in which we measured the postural responses of normal subjects and vestibular loss patients during perturbation of their stance. Subjects stood on a motion platform with their eyes closed and auditory cues masked. The perturbing stimuli consisted of either platform tilts or external torque produced by force-controlled pull of the subjects' body on a stationary platform. Furthermore, we presented trials in which these two stimuli were applied when the platform was body-sway referenced (i.e., coupled 1:1 to body position, by which ankle joint proprioceptive feedback is essentially removed). We analyzed subjects' postural responses, i.e., the excursions of their center of mass (COM) and center of pressure (COP), using a systems analysis approach. We found gain and phase of the responses to vary as a function of stimulus frequency and in relation to the absence versus presence of vestibular and proprioceptive cues. In addition, gain depended on stimulus amplitude, reflecting a non-linearity in the control. The experimental results were compared to simulation results obtained from an 'inverted pendulum' model of posture control. In the model, sensor fusion mechanisms yield internal estimates of the external stimuli, i.e., of the external torque (pull), the platform tilt and gravity. These estimates are derived from three sensor systems: ankle proprioceptors, vestibular sensors and plantar pressure sensors (somatosensory graviceptors). They are fed as global set point signals into a local control loop of the ankle joints,

which is based on proprioceptive negative feedback. This local loop stabilizes the body-on-foot support, while the set point signals upgrade the loop into a body-in-space control. Amplitude non-linearity was implemented in the model in the form of central threshold mechanisms. In model simulations that combined sensor fusion and thresholds, an automatic context-specific sensory re-weighting across stimulus conditions occurred. Model parameters were identified using an optimization procedure. Results suggested that in the sway-referenced condition normal subjects altered their postural strategy by strongly weighting feedback from plantar somatosensory force sensors. Taking this strategy change into account, the model's simulation results well paralleled all experimental results across all conditions tested.

Keywords Postural control · Dynamic model · Multisensory integration · Sensor fusion · Set point principle · Vestibular system

Introduction

Human upright stance is maintained by a posture control mechanism the goal of which is to maintain the orientation of the body upright and thereby the center of mass (COM) above the base of the foot support. The maintenance of body uprightness during external stimuli is controlled mainly by a sensory negative feedback mechanism (e.g., Johansson and Magnusson 1991), which involves cues from visual, vestibular and ankle angle proprioceptive receptors (overview: Horak and Macpherson 1996). Recent work that investigated the postural responses of normal subjects and vestibular loss subjects to body support motion and visual scene motion has shown that the system can, in fact, be described by a simple, multisensory feedback model (Peterka 2002). Furthermore, postural responses to external force stimuli in the form of pull were described by us by means of a multisensory feedback model

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(Mergner et al. 2003). A more complex model of human upright stance, which derives an optimal control signal from multisensory feedback, has been implemented by van der Kooij et al. (1999, 2001).

These models differ from each other in the way they deal with changes of the external stimulus condition, which may require appropriate changes in the 'weights' of the sensory signals. The models of Peterka (2002) and van der Kooij et al. (2001) represent extremes in this respect. The former makes no assumptions on how the weighting is performed and how the sensory signals may interact (in the following, we refer to it as the 'independent channel' model; see also Peterka and Loughlin 2004). The latter, in contrast, uses complex intersensory interactions in an 'optimal estimator' procedure to perform a sensory weighting ('optimal estimator' model). Our model (Mergner et al. 2003) is basically similar to the independent channel model, but in addition assumes simple intersensory interactions ('intersensory interaction' model; see also Mergner 2004).

Our study investigates two aspects that highlight the differences between the 'intersensory interaction' model and the 'independent channel' model. The first aim is to determine the extent to which force-related sensory information contributes to postural control and how this information can be integrated with position and motion-related sensory information. The second aim is to determine if relatively simple sensory interaction mechanisms can be identified that account for the ability of the postural control system to automatically cope with a variety of stimulus and environmental conditions.

More specifically, the first aim is to determine if postural control can be viewed primarily as a kinematic control system or, if kinetic, force-related control also plays a role. For example, in the original model of Peterka (2002) the control signals are motion and position related, although a later version included force-related feedback (Peterka 2003). In the kinematic view of posture control, any perturbation, such as a platform tilt or an externally applied force, which tends to produce a given body excursion, should evoke the same compensatory response, i.e., the same counteraction that tries to prevent the excursion. On the other hand, different reactions may be expected if the posture control mechanism is able to distinguish between these two stimuli. There is considerable literature on the role of force feedback for posture and gait (overviews: Dietz 1993; Duysens et al. 2000), but these studies have not yet tried to compare model simulations to human postural control data across different experimental conditions in an attempt to determine the contribution of kinetic feedback to postural responses.

In our approach, we focus mainly on pressure receptors in the plantar soles, which are known to transmit force information to the postural control system. Evidence comes from clinical work showing that sensory loss in the feet, for instance in the wake of a distal neuropathy, can severely affect postural stability (Horak et al. 1990; Inglis et al. 1994; Thoumie and Do

1996). Further evidence comes from studies in which plantar sensors were either inactivated or stimulated (Magnusson et al. 1990; Wu and Chiang 1997; Kavounoudias et al. 2001; Maurer et al. 2000, 2001). Maurer et al. (2001) referred to these cues as a 'somatosensory graviception', meaning that their functional role would be to inform the brain about the gravitational ground reaction forces and their spatial distribution when a body leans on a stable support, for instance. The cue, possibly in combination with a 'visceral graviception' (Mittelstaedt 1996) and force receptors in tendons and joints, would complement the classical 'vestibular graviception' and explain why patients with bilateral vestibular loss are able to balance on a slowly tilting support surface even when deprived of visual orientation cues (Maurer et al. 2001).

Our model, which includes both kinetic and kinematic sensory signals, was able to predict the responses to kinetic stimuli (Mergner et al. 2003). But it remained to be determined if it also predicts the responses to other stimuli, such as platform tilts. In the present study, we therefore directly compare the postural responses to platform tilt and pull on the body in the absence of visual and auditory orientation cues. Furthermore, we extend this comparison by applying the two stimuli, in addition, with a body-sway-referenced platform (BSRP; performed by making the body support follow the body sway in such a way that the proprioceptive feedback loop of the ankle joint angle is opened). Since we consider here only small body-sway excursions and since these occur mainly in the ankle joints, this procedure provides an experimental situation with clearly reduced kinematic sensory feedback. Finally, we compare the responses of subjects with normal vestibular function to those of patients with chronic bilateral loss of vestibular function. By this, we wanted to learn more about how somatosensory graviception can be used to substitute for vestibular graviception.

The second aim of this study is to understand the way in which the orientation cues interact with each other and thereby achieve appropriate sensory feedback even across widely varying stimulus conditions. Our previous work suggested that these interactions can be described by the combination of simple summations and thresholds, with the thresholds emerging in the postural responses in the form of amplitude or velocity nonlinearities (decreasing response gain with increasing stimulus amplitude or velocity).

The intersensory interaction in our model (Mergner et al. 2003) has two major aspects, which have to be considered when it comes to comparing the model to other possible solutions. One aspect is that it creates internal estimates of the external stimuli, and it is these estimates which then provide the feedback, rather than directly the sensory signals. Consider, for example, a platform tilt stimulus, i.e., a change in foot (support) angle in space (angle FS; see Fig. 1). It leads to a body-in-space excursion (BS) which also depends on the concurrent body-on-foot (support) excursion

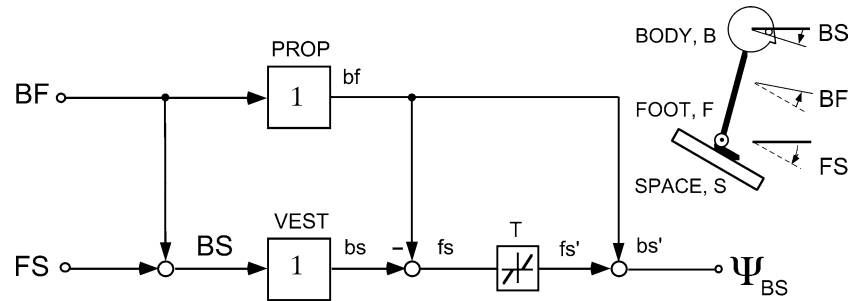


Fig. 1 Schematic presentation of a sensory ‘re-weighting’ in relation to changes in external stimulus condition, which is performed by combining intersensory interaction (in the form of simple summation) with a detection threshold. The model derives an estimate of body-in-space angle BS (Ψ_{BS}) during various combinations of body-on-foot angle, BF, and foot (support)-in-space angle, FS ($BS = BF + FS$; compare *inset*). Let the aim of the model be to achieve the most accurate estimate in the most common stimulus condition (which is the situation of a stationary body support, $FS = 0^\circ$). A vestibular sensor (VEST) is used to

register BS (internal representation, bs ; it is taken to be contaminated by large noise) and an ankle joint proprioceptive sensor (PROP) is used to register BF (bf ; low noise). The FS stimulus is internally reconstructed from the bs and bf signals ($fs = bs - bf$) and then fed through a detection threshold which is given a value slightly higher than the vestibular noise. Ψ_{BS} is most accurate (shows lowest noise) in the situation of stationary support ($\Psi_{BS} = bs' = bf + fs'$; for $fs' = 0^\circ$, $\Psi_{BS} = bf$). The more the support motion occurs, the more Ψ_{BS} becomes determined by the noisy vestibular signal

(BF; $BS = FS + BF$). An internal representation of BF (bf), derived from ankle joint proprioceptive input, is fused in the model with a vestibular representation of BS (bs), yielding an internal estimate of the foot (support)-in-space motion (fs ; $fs = bs - bf$). The fs signal is then used to cope with the FS stimulus. The concept for this kind of intersensory interaction was derived from psychophysical work which showed that human self-motion perception deals with multisensory stimulus estimates rather than with direct sensory signals (overview: Mergner et al. 1997; Mergner and Rosemeier 1998). A sensorimotor control by means of internal estimates based on ‘reconstruction’ of external stimuli has also been advocated for pursuit eye movements by Yasui and Young (1975) and for re-orienting body turns by Diekmann et al. (2004). We conceive that the use of such internal stimulus estimates in sensorimotor control is advantageous as compared to the ‘‘raw’’ sensory signals when it comes to use memory for prediction of a stimulus, to draw profit from cognition, to plan movements, etc.

The second aspect which emerged from the psychophysical work is that the intersensory interaction can give rise to an automatic change in sensor weighting as a function of stimulus condition.¹ A schematic explanation is given in the form of the simple perceptual model in Fig. 1. It explains why an estimate of body-sway angle in space (Ψ_{BS}) can be accurate even if the corresponding vestibular bs signal is inaccurate (it is very noisy, unlike the proprioceptive bf signal; see Mergner et al. 2001). The essential point is that an internal estimate of FS, the

signal fs , is derived in the way described above and then fed through a detection threshold which has a value that is slightly larger than the vestibular noise. The result is that the Ψ_{BS} estimate is determined by the accurate proprioceptive bf signal alone whenever the support is stationary ($fs' = 0^\circ$; $\Psi_{BS} = fs' + bf = bf$). Stationary support (firm ground) applies to most situations of our everyday life. During motion of the support, on the other hand, fs passes the threshold and adds, together with the vestibular constituent and its noise, to the Ψ_{BS} estimate. Thus, the contribution of BS (and bs) to the output increases with increasing FS, i.e., a sensory re-weighting occurs.

In the psychophysical work on which we based our postural model, we could directly measure the thresholds experimentally and then implement them into perception models (where they were thought to reside centrally and serve perceptual stabilization by suppression of low-frequency noise; Mergner et al. 1991, 1993, 2001). We conceive that the intersensory interaction mechanisms in the postural control mechanism are also combined with thresholds and therefore produce sensory re-weighting effects. But these thresholds cannot be measured directly and their effects remain to be determined.

In the work of Peterka (2002), the postural responses showed a non-linear behavior, in that an increase in stimulus amplitude led to a decrease in response gain, a finding which was related to a re-weighting of the sensory signals. Such a response behavior can be produced by thresholds; they affect small sensory stimulus signals relatively more than large ones, with a corresponding effect on sensory feedback and thus loop gain, so that body excursion is relatively better counteracted with large as compared to small stimuli. We therefore implemented central thresholds into our model that described the postural responses to pull stimuli (Mergner et al. 2003) and were able to successfully mimic this

¹We use in the following the term *sensory re-weighting* and define it as a modification of the strength of a sensory signal on its central route, i.e., from the output of the sensory system to the input of the actuator system, by some interfering mechanism(s). By this definition, we try to distinguish it from effects that result from frequency characteristics or non-linearities of the sensor systems, which are known at least in part.

behavior. However, there remained several problems. For instance, the thresholds used in the postural model were much lower than those we used before in our psychophysical model. How effective would these lower thresholds be in a sensory re-weighting across different stimulus conditions? Can we obtain valid estimates of the thresholds even though we cannot measure them directly? To answer these questions, we applied in the current study an optimization procedure that adjusted the parameters of our model such that the simulated data would optimally predict the experimental data. Details of this optimization procedure and the model are given in [Appendix](#). Parts of the responses to pull stimuli were described in our previous study (Mergner et al. 2003).

Methods

Subjects

Experiments were performed in 10 subjects. Six of these were adults (age 34–53 years; two females and four males) who had no known history of vertigo and balance problems and showed normal performance in routine clinical electronystagmographic testing of vestibular function ('normal subjects'). The other four subjects (age 33–42 years; all males) were recruited for showing severe loss of vestibular function ('VL patients'). This loss was assumed on the basis of routine clinical examinations and included balance problems when standing on foam rubber with eyes closed and absence of caloric nystagmus and of rotation-evoked vestibulo-ocular reflex (VOR) in electronystagmographic tests, as well as on the basis of the patients' case histories (meningitis and ototoxic medication in childhood). Apart from hearing problems and slight dizziness during rapid head movements, patients showed no neurological symptoms and subjectively experienced no difficulties in equilibrium control during everyday life. In compliance with the Helsinki declaration (1964), all subjects gave their informed consent to the study which was approved by the local Ethics Committee of the Freiburg University Clinics.

Experimental setup and procedures

All experiments were conducted with subjects standing upright on a custom-built motion platform with heels slightly apart (5 cm between the inside edges of the feet) and the elbows held close to the torso. The two hands were held at shoulder level, each holding a rope that was loosely hanging from the ceiling. Moving the hands down would put tension on the ropes and thereby allow the subjects to stabilize themselves in case they felt body equilibrium severely endangered. In the hands-up position subjects would not obtain a somatosensory spatial orientation cue from this safety setup. During the

stimulus trials, subjects kept their eyes closed and performed mental arithmetic. Earplugs minimized auditory spatial orientation cues. Subjects were instructed to always maintain an upright body posture in space during the stimulus trials.

The motion platform was driven by position-controlled servomotors and could either be held stationary in space or could be rotated, under the control of a laboratory computer, in the sagittal plane with the rotation axis through the subjects' ankle joints. An external force (pull) could be applied to the subjects in the sagittal direction. The pull was generated using reciprocal action of two force-controlled cable winches (servomotors; force measured with strain gauges), under computer control, through cables attached to the front and back of a body harness worn by the subjects. The harness, consisting of an upholstered stiff plastic covering the front and back of the torso from shoulders to waist, did not hamper hip bending.

The setup allowed us to apply two different stimuli in the anterior–posterior (a–p) plane:

1. *Tilt of the body support surface*. Platform rotations were performed with sinusoidal stimulus waveforms at four frequencies (0.05, 0.1, 0.2 and 0.4 Hz) and three peak angular displacements ($\pm 1^\circ$, $\pm 2^\circ$ and $\pm 4^\circ$) at each frequency.
2. *Pull on the torso*. An external force stimulus was generated by the cable winches via the body harness. The force amplitudes were selected to produce five different torque amplitudes (± 1 , ± 2 , ± 4 , ± 8 and ± 16 N m) about the subjects' ankle joints at five different frequencies (0.05, 0.1, 0.2, 0.4 and 0.8 Hz). The two stimuli were applied in two different platform conditions. In one condition, the input to the platform was independent of body position, being exclusively driven by the tilt signals called for by (1) and (2) above (sinusoids and zero, respectively). In the other condition (BSRP condition; see [Introduction](#)), there was an additional input signal derived from the subject's hip angular position. This input provided a 1:1 coupling of the platform to the subjects' COM angular position with an essentially negligible time delay (< 40 ms) and position error ($< 5\%$).

Combining the two stimuli with the two platform conditions, we obtained four different experimental conditions (see examples in Fig. 2A–D):

- (a) *Tilt of the platform alone* (TILT; Fig. 2A).
- (b) *Tilt of the platform combined with BSRP* (TILT + BSRP; Fig. 2B). Note that in this condition the platform position follows the sum of the sinusoidal tilt stimulus and the angular excursion of the COM relative to earth vertical. As a result, the ankle angle becomes 'clamped' to the value of the tilt stimulus.
- (c) *Pull on the torso alone* (PULL; Fig. 2C). The stimulus is applied to the subject during stance on a stable support surface.

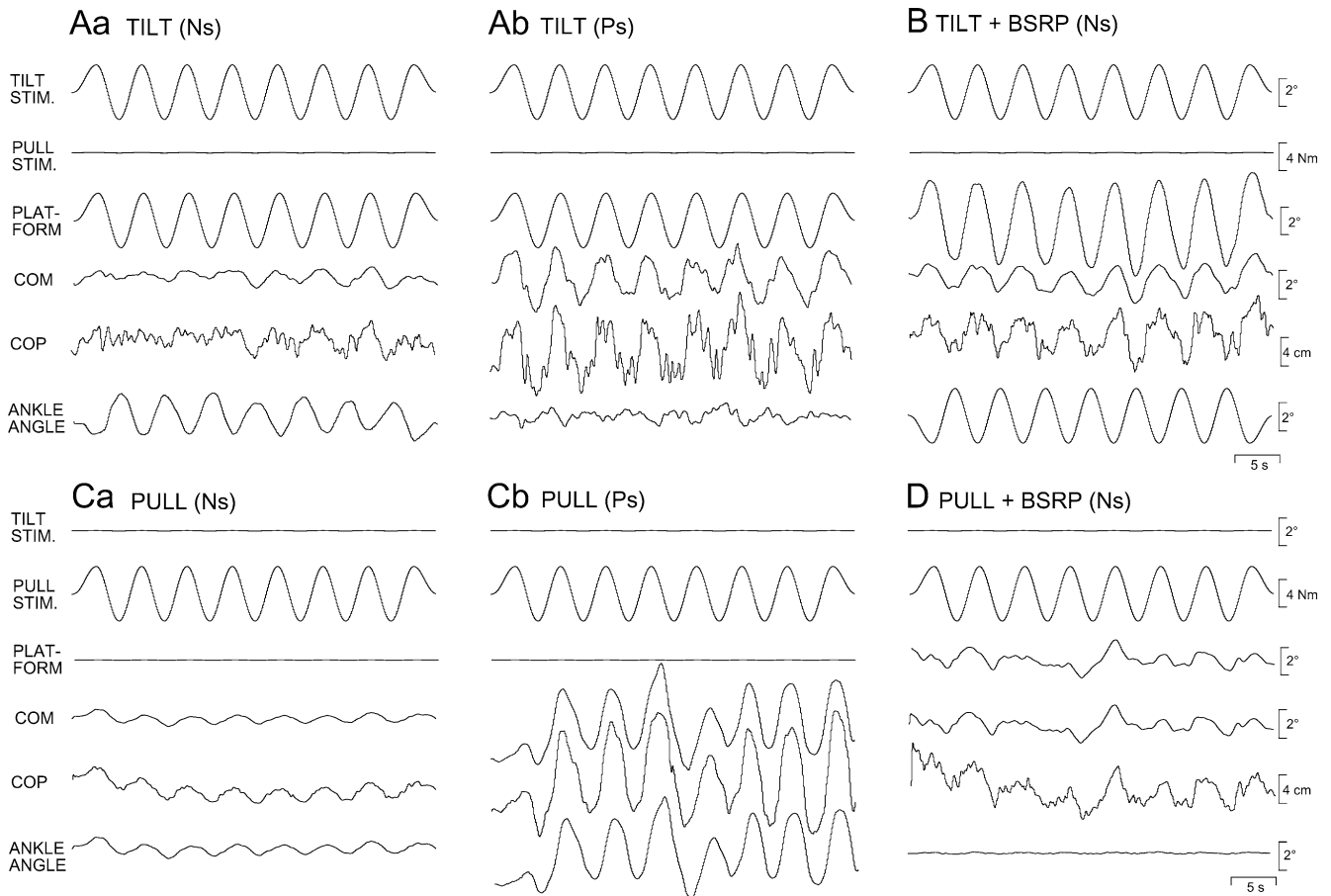


Fig. 2 Examples of postural responses of a normal subject (**Aa, B, Ca, D**) and a vestibular loss patient (**Ab, Cb**) to the TILT stimulus (**Aa, Ab**), TILT + BSRP stimulus (**B**), PULL stimulus (**Ca, Cb**)

and PULL + BSRP stimulus (**D**). *COM*, center of mass; *COP*, center of pressure; *BSRP*, body-sway-referenced platform

(d) *Pull on the torso combined with BSRP* (PULL + BSRP; Fig. 2D). In this condition, the PULL is applied while the platform follows the angular excursion of the COM and the ankle angle therefore remains essentially constant. The four experimental conditions were performed in separate 30–60 min recording sessions with each stimulus frequency and amplitude being presented in a separate trial. Trial durations ranged from 28 to 120 s and included 4–32 cycles of the stimuli, depending on stimulus frequency. Trials were presented in randomized order, except that those without BSRP were always performed prior to those with BSRP, to allow subjects to become accustomed to testing before presenting the rather unfamiliar BSRP conditions. Appropriate rest periods were provided between trials, and sessions were separated by periods of > 6 h.

In addition, after each trial subjects were asked to give a verbal estimate of whether they experienced a platform tilt, a pull on the body or some other form of external stimulus. These reports were used to determine whether subjects could distinguish between platform tilt

(kinematic stimulus) and body pull (kinetic stimulus) at a perceptual level.

Response parameters, data acquisition and data analysis

Mounted on the motion platform was a force-transducing platform (Kistler®, platform type 9286, Winterthur, Switzerland) by which we registered the shifts of subjects' center of pressure, COP, in the a–p direction (in the coordinates of the 'COP platform'). We transformed this measure into space coordinates by taking into account the momentary tilt position of the platform in space in the experiments in which the motion platform was rotated (conditions a, b and d).

We also measured the angular excursion of the motion platform in space as well as subjects' hip-to-ankle and shoulder-to-hip angular excursions in the sagittal plane (in degree). These parameters were obtained by means of an optoelectronic motion-measuring device with active markers (Optotrak 3020®, Waterloo, Canada; rigid triangles, carrying three markers, were fixed to the platform as well as to subjects' shoulder and hip girdles).

The COP and angular excursion data were calculated online by means of PCs, which produced corresponding analog output signals. These signals were fed together with the signals for the tilt and pull stimuli and for platform position into another PC via analog–digital converter and were recorded with a 100 Hz sampling rate (see examples in Fig. 2). The data were recorded with software programmed in LabView® (National Instruments, Austin, TX, USA) and analyzed offline with custom-made software programmed in MATLAB® (The MathWorks Inc., Natick, MA, USA). COM angular displacement was calculated from the shoulder-to-hip, hip-to-ankle and ankle (platform)-in-space angular displacements according to anthropometric data of Winter (1990). Intra-subject averages were obtained for at least six cycles of each stimulus presentation, before calculating averages across subjects. The SD values of the intra-subject mean values were taken as a measure of intra-subject variability and the SD values of the inter-subject mean values as a measure of the inter-subject variability (both measures were obtained in Fourier space, i.e., before separating gain and phase values; see below).

A spectral analysis was performed on the tilt and pull stimuli versus the response waveforms of COP and COM using a discrete Fourier transform (applied to the raw data, with averaging in Fourier space using transforms of single cycles, i.e., a window corresponding to cycle length). Fourier coefficients at the frequency corresponding to the stimulus frequency were used to calculate gain (peak response amplitude divided by peak stimulus amplitude) and phase (relative timing of the response compared to the stimulus). Gain is given in centimeter/degree units for the a–p COP shift and without units for the COM excursion in the tilt experiments (a and b). The corresponding units in the pull experiments (c and d) are centimeter/Newton meter and degree/Newton meter, respectively. A COM gain value of zero would indicate that the stimuli had no effect on the subjects' COM angle (due to 'ideal compensation'), while COM gain values >0 indicate imperfect compensatory responses. COP gain values are indicative of the corrective ankle torque generated in response to tilt and pull stimuli. Phase values indicate the temporal characteristics of the COM and COP in relation to the stimuli. Estimates of the degree of linear correlation between the stimulus and COP and COM responses as a function of the frequency were calculated in the form of 'coherence functions' from the smoothed power spectra according to Bendat and Piersol (2000). Coherence values can vary between 0 (no linear correlation) and 1 (perfect correlation without noise) and tend to lie in between these two extremes, with a value of ≥ 0.5 indicating a substantial correlation. Further analyses were performed using a spreadsheet program (Microsoft Excel®) and a statistics program (StatView®, SAS Inc., Cary, NC, USA).

Gain and phase change patterns as a function of stimulus frequency were used to characterize the

dynamic behavior of the postural control system. In Discussion, we present a model of postural control that predicts these patterns for the four experimental conditions. Model simulations, implemented in Simulink/MATLAB®, were used to predict sway evoked by the four experimental conditions (a–d) and these predictions were used in an optimization procedure to identify parameters of the model. Details of the parameter identification procedure are described in Appendix.

Results

TILT stimulus condition

Normal subjects

Normal subjects had no difficulty maintaining balance on the tilting platform with eyes closed. A typical example of a normal subject's tilt-evoked COM angular excursions and the associated COP shifts is given in Fig. 2Aa (in degrees and centimeter, respectively; stimulus: $\pm 2^\circ$ tilt at 0.2 Hz). Note that the subject's body-on-foot support (ankle angle) excursions are counter to support-in-space (platform) excursions, but are slightly smaller, so that there remained small body-in-space (COM) excursions in the direction of the stimulus. Thus, the subject slightly under-compensated for the platform tilt.

Expressed in terms of gain and phase, the averaged results of the COM responses of all normal subjects are given in Fig. 3a. The data are plotted as a function of stimulus frequency, separately for the $\pm 1^\circ$, $\pm 2^\circ$ and $\pm 4^\circ$ tilt stimuli. Note that COM gain showed a significant decrease with increasing stimulus frequency ($P < 0.05$; see Discussion and simulated data for explanation of the slight 'dip' in gain at 0.2 Hz and the associated phase lag). Furthermore, COM gain decreased with increasing stimulus amplitude. Thus, the COM excursion was relatively largest with the $\pm 1^\circ$ tilt at 0.05 Hz ($G = 0.58$) and smallest with the $\pm 4^\circ$ tilt at 0.4 Hz ($G = 0.19$). COM phase was essentially independent of stimulus amplitude, but varied with frequency, being close to 0° at 0.4 and 0.2 Hz and developing a lead at 0.1 and 0.05 Hz. COM coherence (lowest panel of Fig. 3a) was clearly above 0.5 with all stimulus frequencies and amplitudes, indicating that the linear stimulus/response relationship was stronger than stimulus-unrelated activity such as spontaneous COM sway.

Variability of COM gain decreased with increasing stimulus amplitude, essentially independent of frequency, and variability of COM phase increased with increasing frequency, essentially independent of stimulus amplitude. This applied to the SD values representing the cycle-by-cycle variability (intra-subject variability; vertical bars on mean COM gain and phase values in Fig. 3a) and to the SD values across subjects' mean responses (inter-subject variability; not shown). Generally, there was a close correspondence between these two

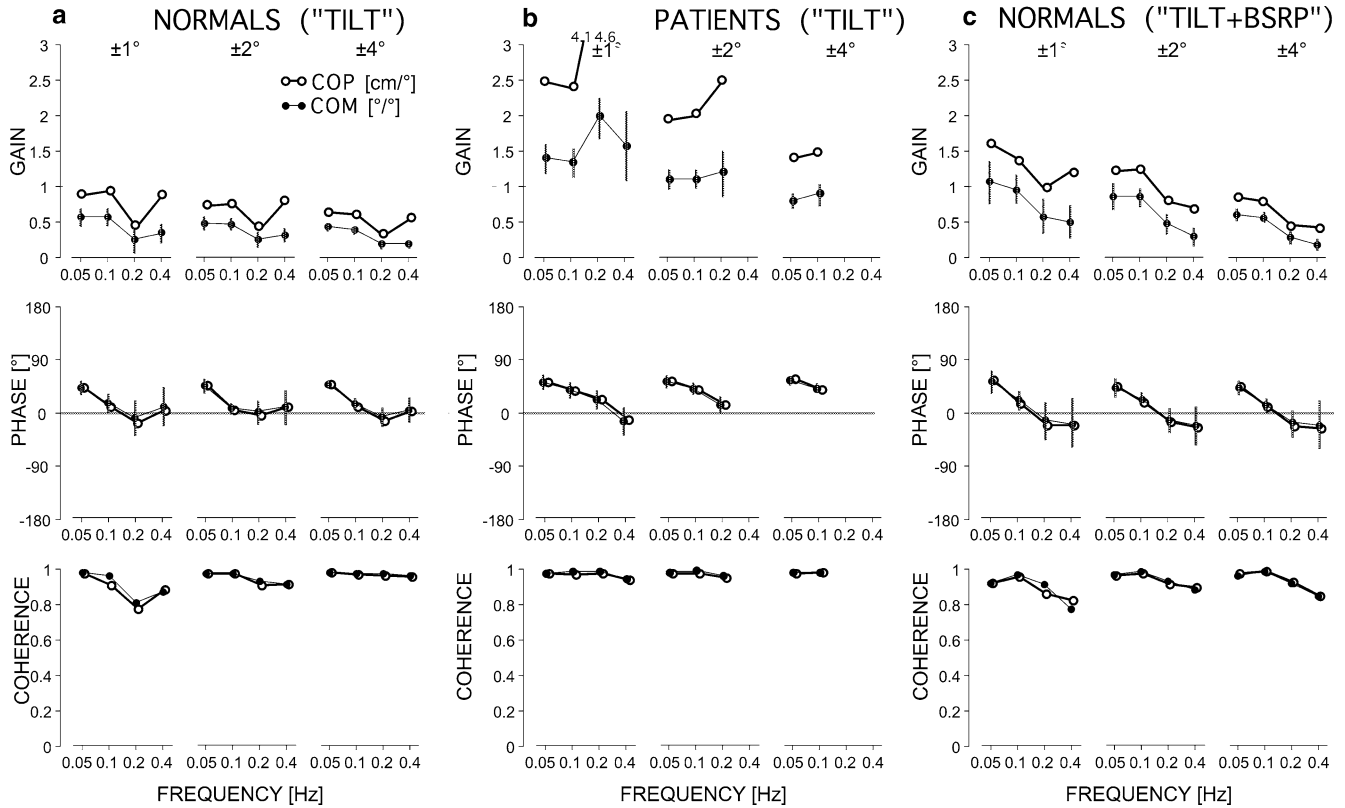


Fig. 3 Responses to the TILT stimulus (**a, b**) and the TILT + BSRP stimulus (**c**) of the normal subjects (**a, c**) and the vestibular loss patients (**b**). The response curves give mean values for the gain of COM angular excursion and COP shift, the corresponding phases and the stimulus–response coherence (vertical bars on COM gain and phase values, SD values of within-

subjects trial repeats). These values are plotted over stimulus frequency, separately for the three stimulus amplitudes used. Missing data in panel b represent ‘falls’ of the patients. Note that gain of COM and COP changes not only as a function of stimulus frequency, but also of stimulus amplitude, while the corresponding phase values change only with frequency

variability measures in both normal subjects and the VL patients, so that we give in the remainder of the paper only the intra-subject variability. Interestingly, a re-evaluation of these gain and phase variations in absolute values (degrees and seconds) revealed that the two effects can be explained across all frequencies and amplitudes by essentially the same ‘spontaneous’ amplitude variation, on the order of $\pm 0.1^\circ$, and the same temporal variation, on the order of ± 150 ms.

When comparing the COM gain and phase data with the corresponding angular hip and upper body excursion data, from which the COM values were calculated, we noted that the COM data closely resembled the hip data (as can be expected, since the COM is located only a few centimeters above the hip girdle; see Winter 1990). However, excursions of the upper body were consistently smaller than those of the COM (factor of 0.7, on average) indicating some additional compensatory righting of the upper body on the hip. We refrained here from a further consideration of this phenomenon, leaving it for a future detailed analysis in the context of multi-segment postural control.

Mean COP closely co-varied with mean COM in that their phase and coherence curves almost coincided and in that the gain curves showed similar characteristics

related to stimulus frequency and amplitude (COP gain in centimeter/degree, however). This applied to the responses at 0.05 and 0.1 Hz, where the COP shift is known to reflect mainly the torque required to support the slowly varying excursion of the COM’s gravitational vector on the foot support base. Small differences were observed at 0.2 and 0.4 Hz and were explained by the known fact that with increasing stimulus frequency the COP becomes more and more associated with the acceleration of the COM rather than COM displacement.

VL patients

The patients had difficulties maintaining balance with eyes closed on the tilting platform. They were unable to stand during the largest stimulus ($\pm 4^\circ$) at 0.2 and 0.4 Hz and during the $\pm 2^\circ$ stimulus at 0.4 Hz (i.e., the three stimuli with the highest peak angular tilt velocities, here $5^\circ/\text{s}$, $10^\circ/\text{s}$ and $5^\circ/\text{s}$, respectively). Although showing considerable body excursions, they were able to maintain stance during stimuli with the lower peak velocities ($< 5^\circ/\text{s}$). A typical example of a patient’s response to $\pm 2^\circ$ tilt at 0.2 Hz is given in Fig. 2Ab. Note

that the patient hardly compensated for the tilt; there were only very small ankle angle excursions counter to the platform excursions, so that the COM moved essentially with the platform. Superimposed on these ankle and COM responses were faster oscillations, which were even more prominent in the COP trace, reflecting the strong activity produced by these subjects while trying to stabilize their bodies.

The gain and phase plots for the VL subjects are shown in Fig. 3b. Overall, COM and COP gain values were 2–5 times larger than those of normal subjects, but showed a similar tendency to decrease with increasing stimulus amplitude. Furthermore, the gain curves showed a tendency to increase with stimulus frequency, unlike in normal subjects (missing values are due to ‘falls’ that occurred with peak velocities $\geq 5^\circ/\text{s}$). The phase curves were similar to those of normals. The *coherence* values were close to unity. Intra-subject variability of COM gain (vertical SD bars in Fig. 3b) was generally larger in the patients as compared to normal subjects by a factor of 2–3 and showed an increase with peak stimulus velocity. In contrast, SD values of COM phase were similar to those in normal subjects.

The findings resemble those obtained in a previous study in which the same subjects, instead of closing their eyes, viewed a homogeneous visual scene without spatial orientation cues (Maurer et al. 2000). The present and the previous data can be taken to indicate that the patients try to stabilize their bodies with respect to the body support surface rather than in space during the tilt stimulus.

Retrospective reports

Normal subjects always correctly identified the stimulus as tilt of the platform. At the lower tilt velocities VL patients experienced a combination of tilt and an involuntary body lean. With the high-velocity stimuli, they usually were unaware of the tilt and experienced only the involuntary body lean.

TILT + BSRP stimulus condition

Normal subjects

An example of the angular excursions of the COM relative to earth-vertical (and the associated COP displacement) of a normal subject is given in Fig. 2B. The COM and COP excursions are clearly larger compared to the TILT stimulus condition (Fig. 2Aa).

The gain, phase and coherence plots for COM and COP obtained in the TILT + BSRP condition (Fig. 3c) were qualitatively similar to those obtained in the TILT condition (Fig. 3a) in that the gain decreased with both stimulus amplitude and frequency, while the phase changed with frequency but was essentially independent of stimulus amplitude. The main differ-

ence was an increase in COM and COP gains by a factor of approximately 2 for the $\pm 1^\circ$ and $\pm 2^\circ$ stimuli at 0.05 and 0.1 Hz, while the increase at 0.2 and 0.4 Hz and at all frequencies with the $\pm 4^\circ$ stimulus was clearly less. COM and COP phase values were similar to the TILT condition at 0.05 and 0.1 Hz, but differed slightly at 0.2 and 0.4 Hz in that they showed a small lag. Coherence, although slightly lower than in the TILT condition, was still above 0.8, on average. Intra-subject variability changed with stimulus frequency and amplitude in a similar way as in the TILT condition, but the gain SD values were about twice as large as in the TILT condition and also the phase SD values were slightly larger.

VL patients

Patients were unable to maintain equilibrium in the TILT + BSRP condition.

Retrospective reports

Normal subjects reported a considerable increase in effort to maintain upright stance as compared to the TILT condition. They experienced their reactions to the platform tilt as insufficient and felt forced to exert “push against” the platform tilt. In general, they were not aware of the fact that their ankle joint angles remained the same during their efforts. Patients were not able to give a reason for their failure to stabilize on the platform.

PULL stimulus condition

Normal subjects

Figure 2Ca shows an example of the pull response of a normal subject to the $\pm 4 \text{ N m}$ stimulus on stationary support surface at 0.2 Hz. Unlike with the TILT condition, the subject’s ankle angle excursions are now in phase with the stimulus and the COM excursion.

Figure 4a gives the mean COM and COP responses across normal subjects for the five different stimulus frequencies and the five different peak ankle torques. COM gain showed a decrease with increasing stimulus magnitude, for instance from 0.2 with the $\pm 1 \text{ N m}$ –0.1 Hz stimulus to 0.02 with the $\pm 16 \text{ N m}$ –0.1 Hz stimulus. Thus, the small stimuli were counteracted relatively less than the large ones. COM gain also changed with stimulus frequency showing a peak at 0.1–0.2 Hz and decreasing values at lower and higher frequencies. At the higher frequencies, it tended to show a hyperbolic decrease with increasing stimulus amplitude towards a minimum value of about $G=0.02$. COP gain showed similar characteristics. Thus, the gain characteristics of the pull responses were qualitatively similar to those obtained with the tilt stimulus.

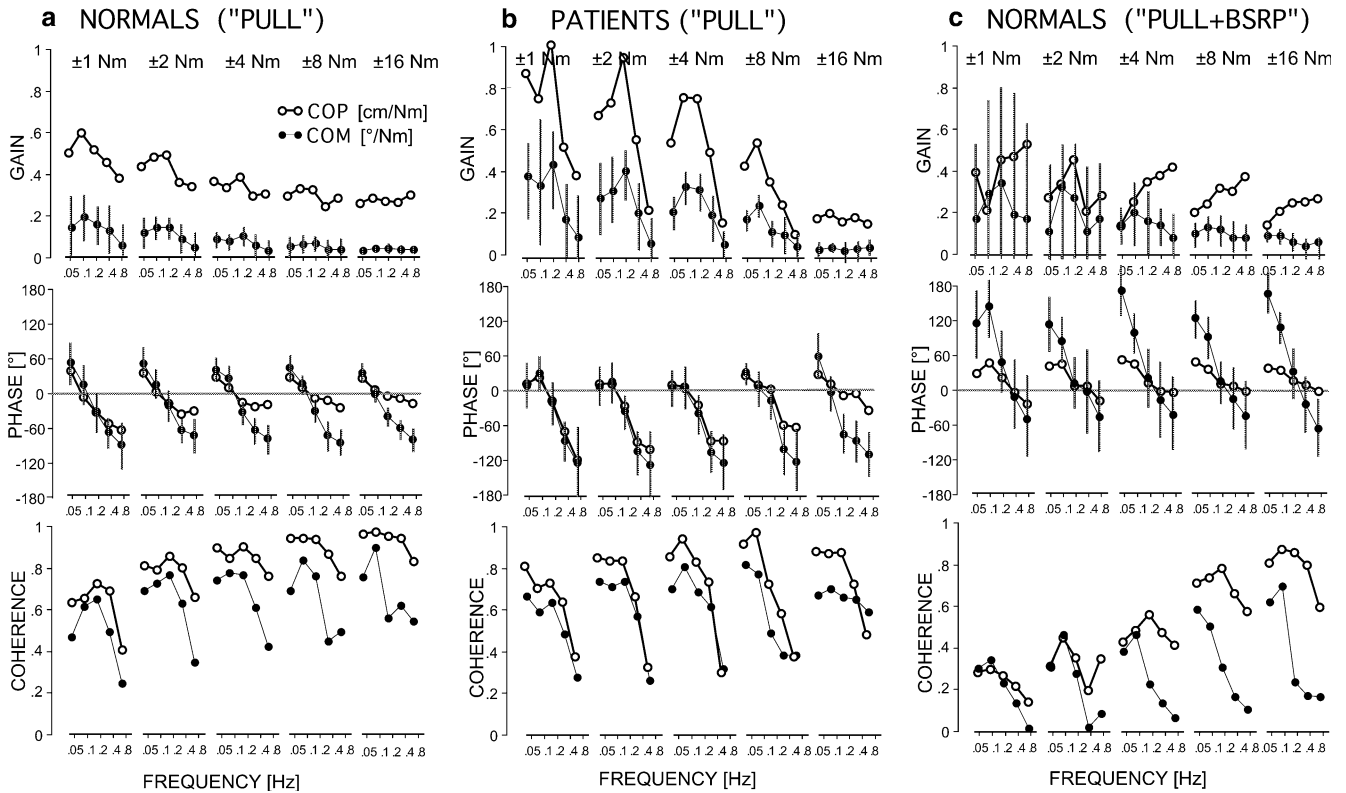


Fig. 4 Responses to the PULL stimulus (**a**, **b**) and the PULL + BSRP stimulus (**c**) of the normal subjects (**a**, **c**) and the vestibular loss patients (**b**). Presentation is analogous to that in Fig. 3. As in the previous figure, gain of COM and COP changes as a function of both stimulus frequency and amplitude and phase does so with frequency. In addition, COP phase depends here on stimulus amplitude, unlike COM phase. Note the small dissociation

of phase between COP and COM with the PULL stimulus (**a**, **b**) and pronounced dissociation of gain and phase curves between COM and COP with the PULL + BSRP stimulus (**c**). Note furthermore that the responses of the patients are similar to those of normal subjects, apart from larger gain values in the mid- to low-frequency range with the 1–8 N m stimuli

The COM phase showed an increasing lag at frequencies of 0.2 Hz and above, unlike with the tilt stimulus. However, like the tilt stimulus, COM phase was essentially independent of stimulus amplitude. The COP phase, in contrast, became clearly dissociated from the COM phase, unlike with the tilt stimulus. COP showed less lag at 0.4 and 0.8 Hz than the COM phase, and the difference between COP and COM phases increased with increasing pull stimulus amplitude.

Coherence values for COP were less than those obtained with the tilt stimuli and the corresponding values for the COM were even less. There was a tendency for an increase in coherence with increasing stimulus amplitude with both COM and COP. Intra-subject variability showed features similar to the TILT condition, in that COM gain SD values decreased with increasing stimulus magnitude. In addition, phase SD values showed a tendency to increase with increasing frequency (exceptions being the values for the ± 1 and ± 2 N m stimuli at 0.05 and 0.1 Hz).

VL patients

Patients were able to maintain balance with the pull stimuli. In the example shown in Fig. 2Cb (± 4 N m,

0.2 Hz), the response of the patient resembled that of the normal subject (Fig. 2Ca), apart from considerably larger excursions of COM and COP.

In addition, mean COM and COP gain curves (Fig. 4b) resembled those of normal subjects (Fig. 4a), apart from considerably larger gain values. Gains decreased with increasing stimulus amplitude, with a tendency to reach a minimum level with the ± 16 N m stimuli (absolute COM and COP excursions $< 1^\circ$ and < 3 cm, respectively). Furthermore, the gain depended on stimulus frequency, with a peak around 0.1–0.2 Hz and with lower gains at frequencies both higher and lower than the peak. The phase curves were also similar to those of normal subjects, including the increasing dissociation between COP and COM phases at 0.4 and 0.8 Hz with increasing stimulus amplitude. The majority of coherence values were > 0.5 for both COM and COP. The changes in coherence with frequency and amplitude were similar to those in normal subjects (exception being COP coherence at high frequencies, which were smaller than those in normal subjects). Intra-subject variability in patients was consistently larger than in normal subjects for both the COM gain and phase. But similar to normal subjects, gain SD values decreased with increasing

stimulus amplitude and phase SD values increased with increasing frequency.

Retrospective reports

Both normal subjects and patients experienced a sinusoidally oscillating pulling or pushing force on stable support surface. This applied to the ± 4 , ± 8 and ± 16 N m stimuli. The ± 1 and ± 2 N m stimuli, in contrast, were not always perceived consciously. Yet, the responses were essentially the same whether subjects consciously experienced the stimuli or not.

PULL + BSRP stimulus condition

Normal subjects were able to maintain stance with their eyes closed on the sway-referenced platform during the pull stimuli. Stance in this condition was associated with a large and irregular body sway. However, the averaging process was able to reduce this variability so that a consistent pattern of responses across frequencies and amplitudes could be discerned. An example of the original responses from one subject (± 4 N m–0.2 Hz stimulus) is shown in Fig. 2D. Body sway did not follow the stimulus as clearly as in the PULL condition, in part due to the increased irregular body sway (compare COM and COP traces in Fig. 2Ca).

Mean COM and COP gain and phase curves are shown in Fig. 4c. The COM gain curves are qualitatively similar to those obtained with stationary platform, showing again the non-linearity related to stimulus magnitude and the modulation in relation to frequency. However, COM gain was higher than in the PULL condition by a factor of approximately 2. In contrast, the COP gain curves showed a qualitative change compared to the PULL condition, in that gain tended to increase, rather than decrease, with stimulus frequency above 0.2 Hz. Yet, a COP gain decrease with stimulus magnitude occurred. Finally, the overall COP gain level was not increased compared to the PULL condition.

There was a pronounced dissociation between COM phase and COP phase. But, unlike in the PULL condition, the dissociation was due to a large phase shift of the COM response towards phase lead, which reached approximately 180° at 0.05 Hz. This effect was essentially independent of stimulus magnitude, as in the PULL condition. Thus, it appeared that normal subjects produced a counter-leaning body position when compensating on BSR platform for the pull stimulus at this low frequency. This counter-leaning position allowed gravity to act on the body to counteract the external pull stimulus. The COP phase, in contrast, showed hardly any change compared to the PULL condition.

Coherence with the ± 1 and ± 2 N m stimuli was clearly below 0.5, due to the high response variability as indicated by the large intra-subject variability in the COM gain SD values (the parametric description of

COM gain dispersion in the figure holds only for the ± 4 – ± 16 N m stimuli, whereas it is inappropriate for the ± 1 and ± 2 N m stimuli, because the mean gain minus SD yields negative values). Stimulus–response coherence improved with the larger stimuli and exceeded the 0.5 value for the COP responses to the ± 8 and ± 16 N m stimuli.

VL patients

Patients were not able to maintain balance on the sway-referenced platform with eyes closed (but could do so, after opening their eyes in alarm). Without visual orientation cues, they were not able to balance on the BSRP even in the absence of any further external perturbation.

Retrospective reports

Normal subjects reported that they did not experience the pull stimuli with almost all stimuli (exceptions occurred with the ± 8 and ± 16 N m stimuli; then subjects reported an increased effort to perform the task).

Discussion

The aims of this study were to investigate the postural responses of humans to external perturbations during upright stance and to determine whether a simple posture control model with sensory feedback is able to describe these responses. In particular, we wanted to test whether the data and their modeling would support the notion of a sensor for contact forces being involved in the feedback control. Furthermore, we wanted to test the hypothesis that a combination of simple sensory interaction and threshold mechanisms could predict the response behavior across a wide variety of stimulus conditions and amplitudes. In the following, we first give a brief account of the most relevant findings and then develop the posture control model.

Main features of experimental data (normal subjects)

In the TILT condition, gain of the COM response tended to decrease with increasing frequency. In addition, gain showed an amplitude non-linearity in that it decreased with increasing amplitude. In contrast, phase showed essentially no variation with amplitude changes and relatively little change with frequency. Similar response characteristics were obtained in the PULL condition; COM gain clearly depended on stimulus frequency and amplitude, while COM phase was essentially independent of stimulus amplitude, although the dependency on frequency was slightly more pronounced and the patterns of the gain and phase curves were slightly different than in the TILT condition. The COP

responses showed similar characteristics as the COM in the TILT condition apart from slight gain increase at high frequency. Similar response characteristics were found in the PULL condition (apart from a phase dissociation between COP and COM with increasing stimulus amplitude at high frequency).

In the TILT + BSRP condition, the COM gain and phase curves qualitatively resembled those obtained with the tilt stimulus alone. However, there was a clear quantitative gain difference (increase by a factor of about 2). In addition, there was a small change in phase (more lag at 0.2 and 0.4 Hz). The COP responses showed similar features. In the PULL + BSRP condition, the COM gain curves were qualitatively similar to those obtained with the pull stimulus alone, showing a decrease with increasing stimulus amplitudes and frequencies. But gain was increased by a factor of about 2 compared to the PULL condition. Furthermore, the COM phase curves showed a clearly steeper slope than in the PULL condition, which was mainly due to a pronounced phase lead at low stimulus frequencies. The large low-frequency phase lead indicates that the COM was essentially leaning counter to the pull stimulus. The COP changes with frequency differed greatly from the COM results. Specifically, COP gain tended to increase with increasing frequency while COM gain decreased, and COP phase showed a much smaller change with frequency than COM phase.

Formal description and interpretation of the experimental data by the intersensory interaction feedback model

The challenge of the modeling effort was to find a relatively simple, physiologically plausible model that could account for the complex patterns of COM and COP gain and phase changes. Our model is shown in Fig. 5 in a slightly simplified version as compared to its original form (Mergner et al. 2003). Originally, the model was designed on the basis of sensory interaction principles derived from psychophysical studies (see Introduction). After giving an overview on its structure, we rebuild it on the basis of model fits to the experimental data, starting from a simple, purely linear feedback system and then including additional features needed to capture the non-linear aspects of the experimental data. At present, we neglect possible contributions from prediction mechanisms that were possibly invoked by the use of sinusoidal stimulation [having in mind that the measured dynamics and estimated dead time value are similar to those reported by Peterka (2002), who used a pseudo-random stimulus].

The most pertinent features of the model are described briefly with details given in Appendix. The model considers rotations of an ‘inverted pendulum’ (body, B, including head, trunk and legs) in the sagittal plane of space (S) about the ankle joint. The ankle joint links the body to the foot (F) which is

pressed by gravity onto the surface of the platform (see inset next to the PHYSICS part of the model in Fig. 5). There are two external stimulus inputs, one being an EXTERNAL TORQUE, the other being TILT of the platform that produces a change in a foot-in-space angle (input FS). The torque stimulus tends to accelerate the body, depending on body inertia (calculated in the box labeled BODY INERTIA). The effect of gravity adds in as GRAVITY TORQUE as a function of BS (calculated in the box labeled mgh). The body-to-foot angle (BF) is determined by $BF = BS - FS$. The angle BF contributes, via the box labeled BIOM (for biomechanics representing passive stiffness and damping factors), a passive torque which sums with the active MUSCLE TORQUE to produce the ANKLE TORQUE. The combined torques determine the COP excursion (conversion in the box labeled COP).

In experimental conditions that exclude visual and auditory orientation cues, we assume that sensory feedback arises mainly from three sensor systems: ankle proprioceptors (PROP), vestibular sensors (VEST) and plantar pressure sensors (somatosensory graviceptors, SOMAT). The PROP and VEST sensors yield internal representations of BF and BS, the bf and bs signals, respectively, and the SOMAT sensor yields an internal representation of ankle torque (τ_{ank}). In order to obtain internal estimates of the external stimuli: (1) the bs signal is used to calculate an internal representation of the torque due to gravity (τ_{grav} ; value is proportional to bs) and intersensory interactions are used to yield internal representations of (2) the pull stimulus (τ_{ext} , see Appendix) and (3) of platform tilt ($fs = bs - bf$). The two torque signals are then converted into signals of equivalent angular COM excursion before summing them with the fs signal and the bf signal (local loop). This sum is then fed into a neural controller [box PID, for P (proportional), I (integrative), D (differential) factors] for transformation to produce an adequate corrective torque. The various delay times in the system are represented by a single dead time element (box Δt), for simplification (see Appendix).

As a general organizing principle, we suggested a hierarchy of the sensory feedback signals (Mergner et al. 1997, 2003; Mergner and Rosemeier 1998). According to this concept, a ‘local loop’ of proprioceptive feedback stabilizes the body on the foot support, accounting for body inertia (bold continuous and dashed paths in figure from BF via bf, box PID, MUSCLE and ANKLE TORQUES to BS). The internal estimates of the external stimuli (fs , τ_{grav} and τ_{ext}) are viewed as set point signals which upgrade the local body-on-support loop into a body-in-space control which compensates for the external stimuli. For example, consider a platform tilt stimulus (input FS). Upright stance during the FS tilt is maintained when the internal fs estimate produces a set point change in the local loop that produces a BF tilt which compensates the FS tilt (BS remains $\approx 0^\circ$ if BF is made $\approx -FS$).

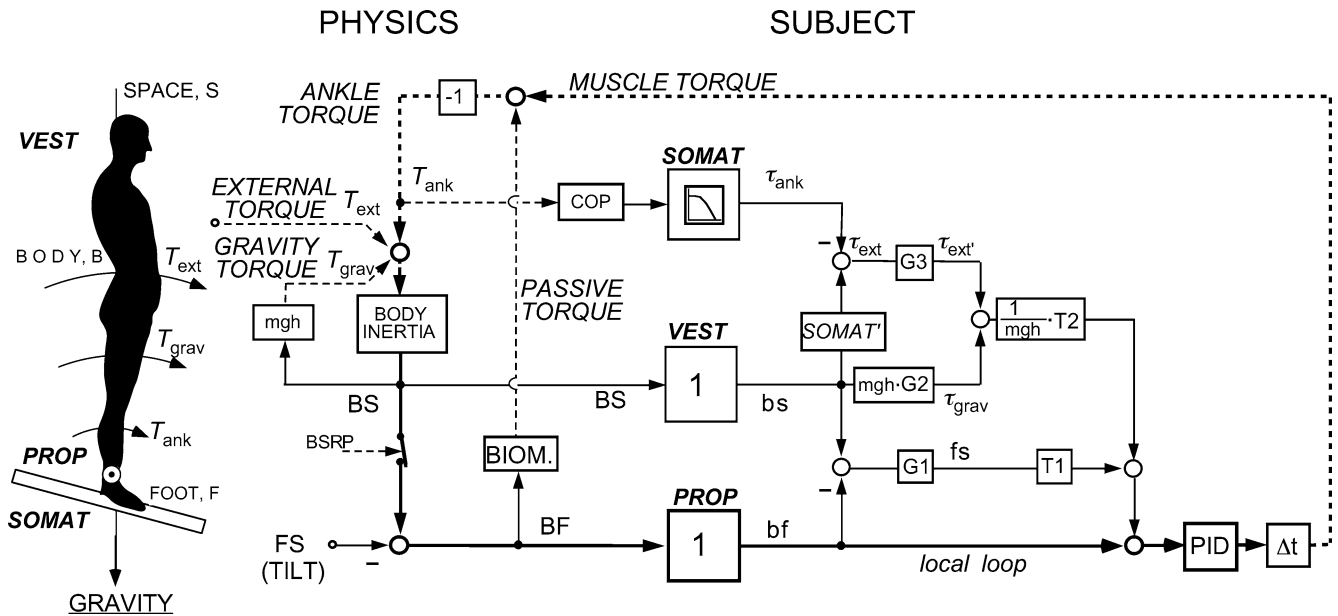


Fig. 5 Multisensory model of posture control. *Inset* defines ‘PHYSICS’ part (*left*). It consists of an ‘inverted pendulum body’ (one segment for head, trunk and legs) that pivots about the ankle joint on a potentially rotating platform (axis through the ankle joint). Two experimental stimuli are considered, an EXTERNAL TORQUE stimulus (pull on the body) and tilt of the body support surface (which yields a change in the foot-in-space angle, FS). BF, body-to-foot angle; BS, body-in-space angle; BSRP, body-sway-referenced platform (open switch mimics the BSRP condition). Box BIOM (for biomechanics) represents the transformation of BF into ankle torque. Subjects’ anthropometric parameters are contained in the boxes ‘BODY INERTIA’ and ‘mgh’. Dashed lines represent external torques and continuous lines represent angles (e.g., BS). All

delays in the system are represented as one dead time (Δt). ANKLE TORQUE leads to a shift of the COP (box COP). The ‘SUBJECT’ part of the model (on the *right*) establishes internal representations of the external stimuli. PROP, proprioceptive sensor; VEST, vestibular sensors; SOMAT, plantar pressure cue (‘somatosensory graviceptor’; symbol represents low-pass frequency characteristics); SOMAT’, internal inverse model of the body (includes a low-pass filter with characteristics corresponding to SOMAT); bf, bs and fs, internal stimulus estimates of BF, BS and FS, respectively; τ_{grav} , estimate of COM’s gravitational pull; τ_{ext} , estimate of external pull; T1, T2 and T3, detection thresholds; G1–G3, gains of internal stimulus estimates

Although first attempts to predict experimental data with the model were successful (Mergner et al. 2003, 2005), in the following we subject the model to a more stringent testing by questioning whether each of its elements is necessary to describe the experimental data. We first ask which features of our experimental data can be explained by a linear model and what the benefit is of each sensor. Then we add sensory interactions and thresholds and ask whether their addition further accounts for the experimental data. Specifically, an optimization procedure was used to identify model parameters and determine the extent to which a given model configuration accounted for the experimental data (for quantification, we used a ‘fit error’, with a value of unity indicating that the distance between experimental and simulated responses in Fourier space equals a gain of unity, on average; see Appendix).

Linear model fits

We start by considering only the TILT and PULL conditions (no BSRP) and by assuming that sensory feedback is provided exclusively by the PROP sensor. In the model, the sensor is given ideal transfer characteristics (PROP=1). The PROP sensor together with the PID

controller and the dead time forms the aforementioned local loop and, given the appropriate adjustments of the parameters, yields a successful body-on-support stabilization in the unperturbed state. We have already investigated this simplest form of a sensory feedback stance control in an earlier study and explained with it the characteristics of a variety of spontaneous sway measures (Maurer and Peterka 2005; Peterka 2000). At this stage, the model is identical to the model used in Maurer and Peterka (2005) (i.e., same values for PID parameters and time delay; see Appendix). The model in this form, but with slightly larger PID parameter values, also successfully predicted the responses to the pull stimulus on stationary support across the frequencies tested.

In contrast, the model in this form could not accurately predict the responses to platform tilt. The reason is that ankle proprioception produces a corrective torque that tends to orient the body to the tilted platform. Accordingly, the optimization procedure tried to make the PID control infinitely stiff, attempting to reduce the influence of gravity that produces a body lean greater than the platform tilt angle (mean fit error across tilt and pull stimuli >0.5). The model predictions improved considerably after adding the VEST sensor and the τ_{grav} signal with the G2 gain element in Fig. 5 (fit error=0.17).

The model configuration so far was not able to account for the experimental data in the BSRP conditions (fit error >0.2). Specifically, the model configuration could not account for the pronounced phase lead of the COM at low stimulus frequencies in the PULL + BSRP condition (which was not present in the TILT + BSRP condition). Conceiving that this phase behavior cannot be attributed to a proprioceptive body-on-support stabilization or to a vestibular body-in-space stabilization, we added the SOMAT torque sensor based on the hypothesis that the COM phase lead reflects compensation based on COP information. This addition of the SOMAT torque sensor further reduced the fitting error (0.16). However, the optimization procedure suggested a further improvement if we allowed for different parameter sets for the BSRP and non-BSRP conditions (mean fit error of 0.12 across the two platform conditions).

Up to this point, the model still represents an independent channel model or, if we now added the fs pathway, could be transformed into one (i.e., into a functionally equivalent form without intersensory interactions). Furthermore, the model simulation results still suffer from the fact that they do not account for the decrease in response gain observed with increasing stimulus amplitude in the four experimental conditions.

Addition of threshold elements

A simple way to account for the decrease in response gain with increasing stimulus amplitude is to introduce detection thresholds (an additional effect would be that the model can no longer be transformed into an equivalent independent channel model). In our psychophysical work, the thresholds of the sensory signals could either be velocity or position thresholds (note that the effects are different: e.g., for a given sine wave stimulus with constant amplitude, the velocity threshold affects low-frequency signals relatively more than high-frequency signals because peak velocity increases with frequency, a fact which does not apply to a position threshold). We therefore left this point initially open. Thresholds were implemented into the local loop path (bf), the fs signal (which we now added), the τ_{grav} signal and the τ_{ext} signal. The optimization procedure was applied two times, once for the stimuli without BSRP and once for the stimuli with BSRP. The results were similar in the two simulations, in that no considerable threshold resulted for the bf signal, a velocity threshold for the fs signal and essentially the same position threshold for the τ_{grav} and the τ_{ext} signals (which could be fused into one threshold, T2, for both signals, as shown in Fig. 5). The parameter values obtained are given in Table 1. The remaining fitting error after including the thresholds was 0.053 for the stimuli without BSRP and 0.079 for the stimuli with BSRP.

Note from Table 1 that the PID factors of the neural controller, the time delay, the passive stiffness and damping values and the fs gain and threshold values

were very similar in the two parameter sets. Using the estimated parameters, we performed simulations for the TILT and PULL stimulus conditions without and with BSRP. The results are shown in Fig. 6a–d. These results show that the model is able to give a good description of the experimental data of the normal subjects (compare Fig. 6 simulation results with Figs. 3a, c, 4a, c). Interestingly, the simulated data for normals' responses to TILT showed a slight 'dip' in the COM and COP gain curves (Fig. 6a), similar to the experimental data (Fig. 3a). The effect was actually brought about by a slight gain increase at 0.4 Hz, where the system tended to show a slight resonance.

The main differences between the two parameter sets in Table 1 are the gain values for τ_{grav} and τ_{ext} . The gain values indicate that in the conditions without BSRP, a τ_{grav} signal with a high gain (1.52) is enough to explain the data, while the τ_{ext} signal could be dismissed. In contrast, in the conditions with BSRP, the gain of the τ_{ext} signal raised to a considerable value (0.66), and the τ_{grav} signal showed a corresponding decrease in value. These gain changes would not automatically be brought about by the re-weighting effects due to intersensory interactions plus thresholds. Therefore, they likely reflect a change in control strategy produced by the subjects in conditions with BSRP. We had suggested such a strategy change in our previous study (Mergner et al. 2003).

Sensory re-weighting effects

The combination of simple sensory signal summations and detection thresholds in the model effectively produces a sensory re-weighting in relation to stimulus amplitude, frequency, and stimulus conditions. To assess this sensory re-weighting quantitatively, we used model simulations, calculating the relative contribution of each internal stimulus estimate at the summing junction prior to the neural controller. Specifically, the weights were determined by measuring the root-mean square value of each internal estimate relative to the sum of all four constituents. Since one has to assume that the human control system contains noise which helps the signals to surpass the thresholds, we fed into the model a noise signal in terms of a disturbance torque (for a similar approach used to describe spontaneous sway in young adults, see Maurer and Peterka 2005). The results of the weighting assessments are given in Fig. 7.

In the TILT stimulus condition (Fig. 7a), the weight of the fs signal increased and that of the vestibular (τ_{grav}) signal decreased with both amplitude and frequency, whereas the weights of the proprioceptive bf signal (≈ 0.4) and the somatosensory τ_{ext} signal (0.0) remained essentially constant. The pattern of re-weighting was similar in the TILT + BSRP condition (Fig. 7c; note that even the bf contribution was similar, despite the fact that proprioceptive feedback was disabled; the contribution is attributable to the ankle joint stimulus, see Fig. 2B).

Table 1 Model parameters after fitting normal subjects' experimental data in the TILT and PULL stimulus conditions and the two stimuli with BSRP (body-sway-referenced platform) conditions

NC, neural controller (PID);
Signals: fs, foot-in-space; τ_{grav} , internal estimate of the gravitational torque; τ_{ext} , internal estimate of the pull stimulus

Model parameters	Normal subjects	
	Without BSRP	With BSRP
Proportional part of NC (N m deg^{-1})	15.1	14.9
Derivative part of NC (N m s deg^{-1})	4.40	4.24
Integral part of NC ($\text{N m s}^{-1} \text{ deg}^{-1}$)	1.33	1.39
Time delay (s)	0.17	0.16
Passive stiffness (N m deg^{-1})	0.91	1.08
Passive damping (N m s deg^{-1})	0.68	0.37
Gain of fs signal (G1)	0.79	0.81
Threshold of fs signal (deg s^{-1}) (T1)	0.17	0.18
Gain of τ_{grav} signal (G2)	1.52	1.00
Gain of τ_{ext} signal (G3)	0	0.66
Threshold of τ_{grav} and τ_{ext} (deg) (T2)	0.16	0.09

In the PULL condition (Fig. 7b), the feedback was essentially determined by the bf and τ_{grav} signals alone ($fs = \tau_{\text{ext}} = 0^\circ$). The weight of the τ_{grav} signal decreased with increasing stimulus frequency at low stimulus magnitudes and increased with stimulus frequency at high stimulus magnitudes. Across stimulus magnitudes, τ_{grav} increased by about 40%, and the bf signal showed a complementary decrease. In the PULL + BSRP condition (Fig. 7d), the bf contribution was zero (no proprioceptive stimulus and no proprioceptive feedback). The fs signal showed a weight increase with frequency and the τ_{grav} signal showed a decrease with frequency. In addition, the τ_{grav} signal decreased at the higher stimulus magnitudes as the τ_{ext} signal contribution increased. Interestingly, repetition of these simulations without adding noise yielded very similar results (apart from minor differences with the $\pm 1 \text{ N m}$ PULL stimulus).

Note that the criteria of our definition of sensory re-weighting (see Introduction) are here fulfilled in so far that the weight changes shown in Fig. 7a–c are 'central' in origin and not brought about by non-ideal transfer characteristics of the sensors involved (VEST and PROP were taken to be ideal). This does not apply to the weight changes in relation to stimulus frequency changes in Fig. 7d (PULL + BSRP) because here the SOMAT sensor with its presumed low-pass filter characteristics becomes involved (see Appendix for this still preliminary assumption). These changes are, however, small as compared to those occurring with stimulus amplitude changes.

Taken together, the findings of Figs. 6 and 7 demonstrate that the model predicts the experimental data and that these predictions are the result of considerable sensory re-weightings which occur with changes in stimulus amplitude and frequency as well as across stimulus conditions. However, one could argue that a posture control that is based mainly on vestibular cues would suffice to cope with most experimental situations (Mergner 2004). What would then be the advantage of the sensory re-weightings? As pointed out in Introduction, there is evidence that the vestibular signal contains relatively large noise (Mergner et al. 2001; van der Kooij et al. 2001), so that its substitution by a proprioceptive signal, for instance, is desirable whenever possible. It

remains to be shown in the future that this is, in fact, a major aim of sensory re-weighting. Another aim could possibly be to avoid the use of the SOMAT cues (and feedback from other force sensors) because of the possibility of instability due to positive feedback (see Appendix). Furthermore, the particular form we chose to represent the weighting mechanism (summation plus threshold) provides a means by which the nervous system can directly react to stimulus changes and thereby would be resistant to instability associated with sudden changes in environmental conditions. However, it is likely that this mechanism is also modifiable as a consequence of adaptation during a prolonged stimulus presentation or in response to cognition or expectation, etc.

The presumed change in the subjects' control strategy in the stimulus conditions with BSRP appears to represent more than just a sensory re-weighting. Possibly, this relates to the fact that subjects have to perform postural stabilization in this condition solely by adjusting ankle torque, whereas normally ankle torque tends to be coupled with ankle angle. Anyway, we could not identify any model structure or sensory integration scheme that could explain the pattern of experimental results in both the BSRP and non-BSRP conditions without introducing a parameter change that represents a change in control strategy in addition to a change in sensory weighting. Therefore, our current conclusion is that compensation for some conditions requires more than sensory re-weighting.

Patients' responses

Patients' pull responses on stationary platform were similar to those of normal subjects, apart from higher response gains (larger body excursions) with stimuli at mid to low frequency. Conceivably, the larger body excursions may reflect a reduction in overall sensory input with incomplete compensation (i.e., the overall loop gain is too low). Based on responses in the PULL condition, one could postulate that patients used solely proprioceptive cues for their sensory feedback control. However, our previous work suggested that patients also

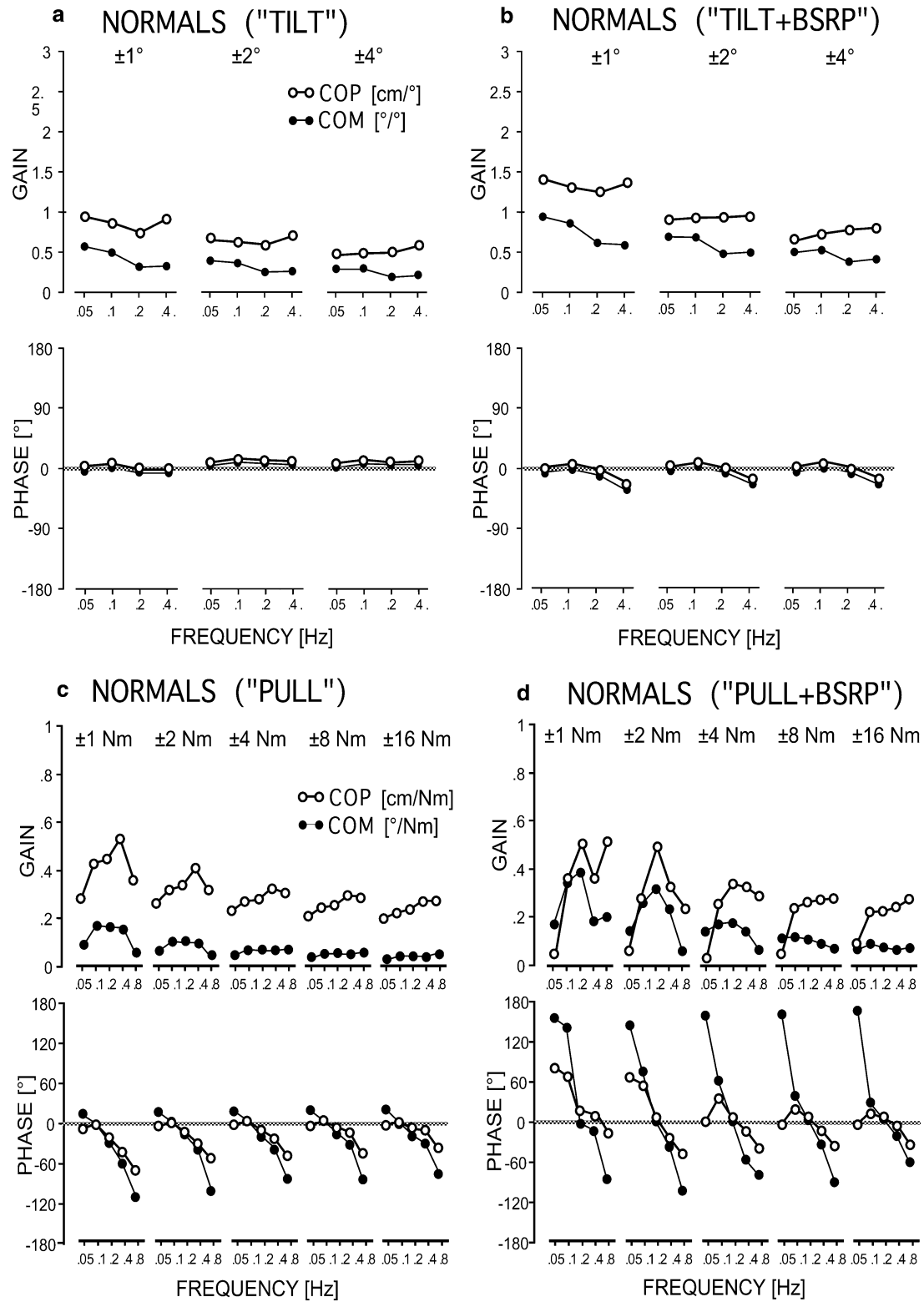


Fig. 6 Simulation results for normal subjects responding to the TILT stimulus (a), the TILT + BSRP stimulus (b), the PULL stimulus (c) and the PULL + BSRP stimulus (d) using the model

of Fig. 5. Compare results in a and b with the experimental data in Fig. 3a, c, respectively, and results in panels c and d with the experimental data in Fig. 4a, c

use, at least during platform tilt, sensory information about gravitational reaction forces, which we assumed to stem from plantar pressure receptors (Maurer et al.

2000). Somatosensory graviceptive cues would not allow patients to distinguish between the pull evoked by an external contact force versus that arising from gravity

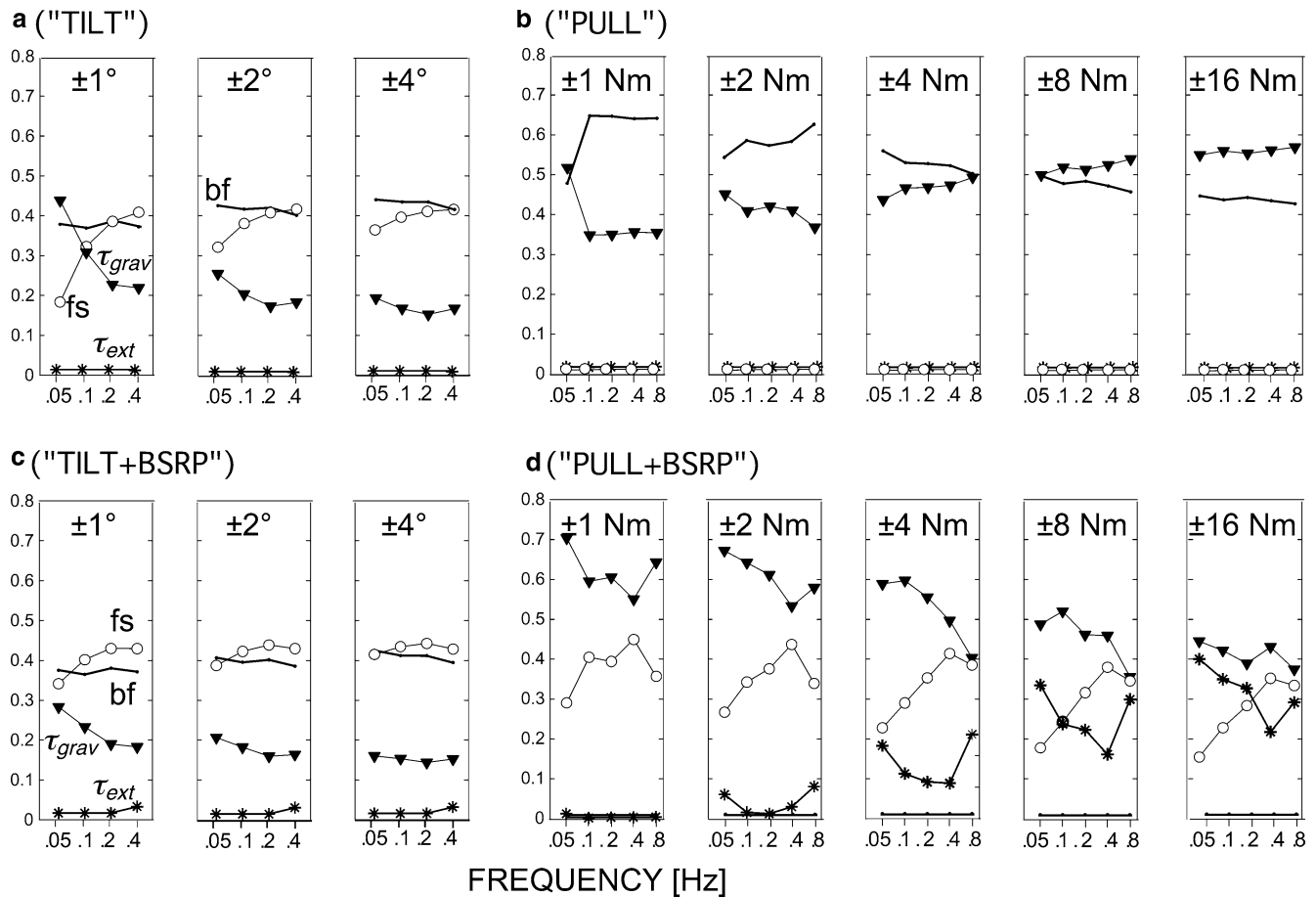


Fig. 7 Simulation results for the relative 'sensory weights' of the four internal stimulus representations (fs, bf, τ_{grav} and τ_{ext} signals) as a function of stimulus frequency and amplitude across the four

stimulus conditions (**a** TILT, **b** PULL, **c** TILT + BSRP, **d** PULL + BSRP). Sum of all weights equals unity

during body lean away from earth vertical, whereas normal subjects would be able to do so with the help of vestibular cues (see [Appendix](#)). Patients indeed failed to keep balance with the pull stimuli in the BSRP condition, while normal subjects were able to do so. In addition, patients' tilt responses supported our notion of a sensory contribution from somatosensory force receptors. The patients were able to stabilize on the tilting platform when stimuli were restricted to the low amplitude and frequency range, although with abnormally large body excursions. On BSRP, in contrast, they would always fall, even in the absence of tilt and pull stimuli.

In the modeling, we considered in a first step solely a proprioceptive feedback. However, this model failed to describe the experimental results obtained with the 4° tilt stimuli, which were clearly better than the predicted ones. When we added the SOMAT sensor (including a threshold of about 0.6°, which corresponds to a COP displacement of about 1 cm), the simulations accurately described the present experimental findings for both the tilt and pull stimuli. These results suggest that the patients may control small body excursions entirely with proprioceptive cues, but use in addition somatosensory

force cues, at least with large stimuli, to prevent the center of ground reaction force from shifting beyond the base of support given by the feet. The model correctly predicted the experimental finding that patients cannot maintain stance in the BSRP condition.

General considerations

We showed that our multisensory interaction model, which originally was motivated by 'top down' concepts and by principles derived from psychophysical studies, is able to describe our experimental findings in posture control. This is consistent with the idea that there are certain parallels between sensory perception and sensorimotor control. We are aware that many more receptor systems than the three sensors considered here are involved in postural control in the test conditions we investigated, but contend that these three are the most relevant ones and are the essential minimum to describe the present findings. In the same token, we are aware of the fact that other model topologies, for instance more complex ones, may yield simulation results similar to those obtained here. But we consider our approach only

as a first step towards an understanding of the multi-sensory nature of human postural control. In view of the system's high degree of flexibility and robustness, we conceive that many more steps will have to follow. Our approach to focus the modeling on the role of inter-sensory interactions in postural control clearly distinguishes it from related work in the literature (e.g., Nashner 1972; Johansson and Magnusson 1991; van der Kooij et al. 1999; Jeka et al. 2000; Peterka 2002).

Acknowledgments DFG Me 715/5-2,3; NIH AG17960

Appendix

This provides additional specifications of our intersensory interaction model (Fig. 5) and then gives a description of the optimization procedure used for parameter identification.

The PHYSICS portion of the model in Fig. 5 performs a transformation from joint torque into body-in-space rotation, BS. Prior to this, the body-to-foot (support) rotation, BF, is transformed by the box BIOM (for biomechanics) into PASSIVE TORQUE. This passive torque is assumed to arise from the stiffness and damping properties of the muscles and tendons and is proportional to BF and BF velocity (PASSIVE TORQUE = $K_{pas} \times BF + B_{pas} \times dBF/dt$, where K_{pas} is a stiffness factor and B_{pas} a damping factor; direction of passive torque becomes opposite to the direction of the BF signal, see Fig. 5). There is no time delay associated with this passive torque component. The values given in Table 1 for the stiffness and damping correspond roughly to those of Peterka (2002) who estimated them to be in the range of 10% of the P and D parts of the neural controller, respectively (see below). This range is similar to that estimated by van der Kooij et al. (2005).

The PASSIVE TORQUE is combined with the active MUSCLE TORQUE to yield the ANKLE TORQUE. The box labeled '-1' on the latter signal represents the negative effect of the sensory feedback loop via the MUSCLE TORQUE and of the PASSIVE TORQUE. The ANKLE TORQUE acts together with the EXTERNAL TORQUE and the GRAVITY TORQUE on the BODY INERTIA box where this summed torque is transformed into the angular displacement BS by inertia effects described by the equation: $T/J = d^2BS/dt$ (T , torque; J , body moment of inertia about the ankle joint, calculated from our subjects mean values for body mass and COM height above the joint, $mh^2 = 72.0 \text{ kg m}^2$). The GRAVITY TORQUE is calculated from BS by the equation: $mgh \sin(BS)$ (m , COM mass, 74.9 kg; h , COM height, 0.98 m above ankle axis; g , acceleration due to gravity, 9.81 m/s^2).

Two perturbing stimuli were applied to the system: (a) a contact force (pull) that produced the EXTERNAL TORQUE stimulus and (b) an angular displacement of the foot support in space (input FS). The effect of FS on BF is given by $BF = BS - FS$. With the platform level

and held stationary in space (foot-in-space angle, $FS = 0^\circ$ and the BSRP switch in the closed position), the body-to-foot angle (BF) is coupled 1:1 to the body-in-space angle (BS). However, if FS is made to exactly match BS, this 1:1 coupling is eliminated and the body-to-foot angle becomes either "frozen" ($BF = 0^\circ$; this is represented in the figure by making $FS = 0^\circ$ and opening the switch BSRP) or exclusively determined by the tilt stimulus ($BF = -FS$; this is represented in the figure by applying the FS stimulus and opening the switch BSRP). The latter two model configurations correspond to the PULL + BSRP and to the TILT + BSRP conditions, respectively.

The afferent interface between the PHYSICS part and the SUBJECT part of the model is represented by three sensors. We assume that BF is sensed by ankle proprioception (PROP), BS by the vestibular system (VEST) and COP shifts by plantar somatosensory receptors (SOMAT).

PROP is taken to stem mainly from spindle receptors in the ankle joint muscles and to inform the brain about the angle BF (yielding its internal representation, bf) with broadband frequency characteristics (the 1 in box PROP represents ideal transfer characteristics). Evidence for a role of PROP in posture control comes from the observation that direct stimulation of muscle spindles by muscle vibration during stance produces body sway, which linearly combines with vestibular evoked sway (e.g., Hlavacka et al. 1996).

The VEST sensor is considered to contain two parts, one representing the canal system, the other the otolith system. We assumed that, by way of a canal-otolith interaction (not shown; see Merfeld 1995; Mergner and Glasauer 1999; Zupan et al. 2002), the semicircular canal transfer characteristics are improved in the vertical rotational planes such that an essentially veridical internal representation of body-in-space angular position results (output signal bs of box VEST which is given ideal transfer characteristics, 1).

SOMAT is taken to register reaction forces. It is represented by plantar somatosensory pressure receptors deep in the foot arch, which provide a low-pass-filtered estimate of COP shift at the foot soles (note the low-pass filter symbol in box SOMAT; further details below and in experimental studies of Maurer et al. 2000, 2001). The assumption of a low-pass filter is derived from the experimental work and requires further evaluation (for the simulation we used a first-order filter with a cutoff frequency of 0.8 Hz).

The SUBJECT part of the model is thought to contain two functional subdivisions. The first would be the proprioceptive bf signal which we consider to form, together with a transformation by a neural controller and the system's efference, a 'local feedback loop' that stabilizes the ankle joint and takes into account body inertia (e.g., during voluntary movements; see Mergner 2004). The second subdivision represents the three internal estimates of the external stimuli.

An estimate of the support surface tilt (FS)

The estimate of FS is in the form of $fs = bs - bf$. The bs and bf signals used for this fusion are thought to stem originally from vestibular and proprioceptive velocity signals, respectively, which we omitted here for simplification. Thus, also fs would actually carry velocity information and the presumed threshold of it therefore represents a velocity threshold (in the simplified version of Fig. 5, we run the fs signal before the velocity threshold through a differentiation and after it through an integration; box T1, applied after an additionally scaling by a gain factor, G1). In the parameter identification procedure (see below) we originally applied thresholds for both a fs velocity and position part of the parameter space. The procedure demonstrated that the velocity threshold alone could account for the experimental data.

An estimate of the external torque stimulus (τ_{ext})

The estimate of τ_{ext} is based on the physics of inverted pendulum motion. Specifically, the dynamics of inverted pendulum motion are given by:

$$\begin{aligned} J \frac{d^2 BS}{dt^2} &= mgh \sin(BS) + T_{ank} + T_{ext} \\ &= T_{grav} + T_{ank} + T_{ext}, \end{aligned}$$

where T_{grav} is the gravitational torque caused by body lean, T_{ank} the ankle torque, T_{ext} the externally applied torque, J ($=72.0 \text{ kg m}^2$) the moment of inertia of the body (not including the feet) about the ankle joint axis. The internal estimate of external torque, τ_{ext} , is derived using internal estimates of the physical variables BS and T_{ank} :

$$\begin{aligned} \tau_{ext} &= \left(J \frac{d^2 bs}{dt^2} - mgh \sin(bs) \right) - \tau_{ank} \\ &\approx \left(J \frac{d^2 bs}{dt^2} - mgh \times bs \right) - \tau_{ank}, \end{aligned}$$

where τ_{ank} is the internal estimate of T_{ank} provided by the SOMAT output and bs the internal estimate of BS provided by the VEST output.

The input to the SOMAT box is COP displacement (in meters) calculated in the COP box by multiplying ANKLE TORQUE by $-1/mg$ ($=-0.00136$, with the minus sign representing the fact that a negative ankle torque, using the sign convention shown in the inset of Fig. 5, produces a positive COP value; see Winter et al. 1998, for the equations relating torque to COP).

The internal estimate τ_{ank} is subtracted from the output of the SOMAT' box to obtain τ_{ext} . The SOMAT' box performs the operation $J \times d^2 bs / dt^2 - mgh \times bs$, with $mgh = 721 \text{ kg m}^2 / \text{s}^2$.

The SOMAT' box represents an internal inverse dynamics model of the body. Model simulations showed that the subtraction of τ_{ank} from the torque estimate provided by the inverse model in SOMAT' gave an accurate estimate of EXTERNAL TORQUE. However,

relatively small errors in τ_{ext} , such as those produced by errors in the internal model parameters J , m or h or by errors in sensing τ_{ank} , resulted in unstable postural control. The sensitivity to errors in the τ_{ext} estimate was greatly reduced if higher frequencies were eliminated from the calculation of τ_{ext} by including a low-pass filter in both the SOMAT and the SOMAT' boxes (first-order filter with 0.8 Hz cutoff frequency). The low-pass filter in the SOMAT box could be interpreted as reflecting earlier experimental findings that the SOMAT sensor output is mainly used with low-frequency stimuli (Maurer et al. 2000, 2001). The matching low-pass filter in the SOMAT' box would then be interpreted as providing a match of the inverse internal model dynamics to those of the SOMAT sensor.

The τ_{ext} estimate was additionally scaled by a gain factor (G3). The value of G3 was adjusted by the optimization procedure to explain the experimental results.

An estimate of the gravitational torque (τ_{grav})

The τ_{grav} estimate is obtained from the vestibular derived estimate of body lean, bs , by the scaling factor mgh (with the implicit assumption that $\sin(bs) \approx bs$ for small angles). This τ_{grav} estimate was additionally scaled by a gain factor (G2). The value of G2 was also adjusted by the optimization procedure to explain the experimental results.

In the model of the normal subjects, τ_{ext} and τ_{grav} are combined and then transformed into an equivalent of the COM angle with respect to the earth vertical such that a body tilt by this equivalent COM angle would produce a torque that matched the combination of τ_{ext} and τ_{grav} . This equivalent angle is then passed through the angular position threshold (T2).

In the model of the vestibular loss patients, VEST and the fs signal were set to zero, and G3 and T2 were adjusted to fit the experimental data. Thus, chronic vestibular loss is thought to lead, in addition to the loss of vestibular signals (bs , τ_{grav}), also to the loss of internal estimates of external torque and foot-in-space that are derived using bs . Noticeably, the minus sign that τ_{ext} receives in the model reflects the fact that, for example, a negative ankle torque would be interpreted by a vestibular loss patient as a positive body lean, which would produce an even greater negative ankle torque required to reduce the body lean. This represents a positive force feedback loop in the model that can lead to instability. Instability can be avoided if it is assumed that patients have found a way to eliminate the body acceleration component of τ_{ank} ($J \times d^2 bs / dt^2$) such that only the COM-related component remains ($mgh \times bs$). In normals subjects the elimination of the acceleration component occurs via the box SOMAT'.

As mentioned in Discussion, the various delay times in the system are represented by a single dead time element (box Δt). This even included the local loop, since the study of Peterka (2002) identified a similarly long time delay in a condition where postural control is likely

to be dominated by proprioception, i.e., in vestibular loss subjects standing eyes closed on a tilting surface. Admittedly, future studies are still needed to clarify if a single time delay provides an adequate representation.

In a feedback system, the COP is not independent from the COM. The relationship between COP, representing ANKLE TORQUE (van der Kooij et al. 2005), and the torque-evoked COM displacement, representing body movement, is mainly determined by the biomechanical properties of the body. Applying external forces to the human body further influences the relationship between COP and COM, however, in a predictable way (van der Kooij et al. 2005). Therefore, a separate model fit to experimental COP data would not be justified.

The optimization procedure, by which we estimated model parameters from the experimental data, was initially applied to data from the 37 test trails that were obtained in the TILT and PULL conditions (4 TILT frequencies times 3 amplitudes plus 5 PULL frequencies times 5 amplitudes). The procedure varied the model parameters shown in Table 1, using the Matlab Optimization toolbox function 'fminsearch' (which is based on the so-called simplex search method of Nelder–Mead; see Lagarias et al. 1998) in order to minimize the deviation between the simulated responses and the corresponding experimental data (in polar coordinates; as mentioned before, an error of unity would indicate that the value of the distance between experimental and simulated responses equals a gain of unity). With each iteration of the search, simulated responses to the 37 stimulus conditions were obtained from the model using Matlab Simulink, the simulated data were analyzed in the same manner as the experimental data, and a scalar error function was evaluated that compared the difference between simulated and experimental results. Then, the search procedure changed the parameters and the error function was re-evaluated. This sequence was repeated until parameters were identified which minimized the error function. In a second application of the optimization procedure, parameters were identified for the TILT + BSRP and PULL + BSRP conditions.

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