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RESEARCH ARTICLE

Potential roles of force cues in human stance control

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Abstract Human stance is inherently unstable. A small deviation from upright body orientation is enough to yield a gravitational component in the ankle joint torque, which tends to accelerate the body further away from upright ('gravitational torque'; magnitude is related to body-space lean angle). Therefore, to maintain a given body lean position, a corresponding compensatory torque must be generated. It is well known that subjects use kinematic sensory information on body-space lean from the vestibular system for this purpose. Less is known about kinetic cues from force/torque receptors. Previous work indicated that they are involved in compensating external contact forces such as a pull or push having impact on the body. In this study, we hypothesized that they play, in addition, a role when the vestibular estimate of the gravitational torque becomes erroneous. Reasons may be sudden changes in body mass, for instance by a load, or an impairment of the vestibular system. To test this hypothesis, we mimicked load effects on the gravitational torque in normal subjects and in patients with chronic bilateral vestibular loss (VL) with eyes closed. We added/subtracted extra torque to the gravitational torque by applying an external contact force (via cable winches and a body harness). The extra torque was referenced to body-space lean, using different proportionality factors. We investigated how it affected body-space lean responses that we evoked using sinusoidal tilts of the support surface (motion platform) with different amplitudes and frequencies (normals $\pm1°$, $\pm2°$, and $\pm4°$ at 0.05, 0.1, 0.2, and 0.4 Hz; patients $\pm1°$ and $\pm2°$ at 0.05 and 0.1 Hz). We found that added/subtracted extra torque scales the lean response in a systematic way, leading to increase/decrease in lean excursion. Expressing the responses in terms of gain and phase curves, we compared the experimental findings to predictions obtained from a recently published sensory feedback model. For the trials in which the extra torque tended to endanger stance control, predictions in normals were better when the model included force cues than without these cues. This supports our notion that force cues provide an automatic 'gravitational load compensation' upon changes in body mass in normals. The findings in the patients support our notion that the presumed force cue mechanism provides furthermore vestibular loss compensation. Patients showed a body-space stabilization that cannot be explained by ankle angle proprioception, but must involve graviception, most likely by force cues. Our findings suggest that force cues contribute considerably to the redundancy and robustness of the human stance control system.

Keywords Human · Stance control · Multi-sensory interaction · Force/torque cues · Load compensation · Vestibular loss · Robustness · Redundancy

Introduction

Maintenance of human upright body posture is closely linked to controlling the effects that gravity exerts on the body. This refers mainly to the fact that deviations from an upright body orientation result in gravity exerting a torque about the ankle joint, which then accelerates the body further away from upright and, unopposed, may lead to fall ('gravitational torque'). Therefore, in order to maintain a

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given body-space lean angle, a compensatory ankle torque must be generated ('gravity compensation'). It is widely accepted that this torque is controlled by sensory feedback of kinematic information on body-space angle and angular velocity derived from the vestibular system. And, if the visual surroundings and the body support surface are stationary, also visual cues and ankle angle proprioception contribute to the stabilizing feedback (e.g. Johansson and Magnusson 1991; Fitzpatrick et al. 1996; van der Kooij et al. 1999; Alexandrov et al. 2001; Peterka 2002; Kiemel et al. 2002; Maurer et al. 2006; van der Kooij and de Vlugt 2007). Less is known about the role that kinetic cues (force, torque, pressure) play for gravity compensation in human stance control, although these cues have been extensively studied by electrophysiological methods in man and several animal species (for review, see Duysens et al. 2000).

The present study is aimed to better understand what force/torque cues contribute to gravity compensation. Evidence for such a contribution comes from recent studies of stance stabilization in patients with somatosensory deficits of the feet as well as in healthy subjects in whom such deficits were induced experimentally (literature, see Maurer et al. 2001). These studies suggest that force cues from pressure receptors in the feet register the shifts of the center of pressure (COP) during body lean ('somatosensory graviception', see Maurer et al. 2001; also Kavounoudias et al. 2001; Mergner et al. 2003; Stal et al. 2003; Meyer et al. 2004; Maurer et al. 2006).

A role of force cues is also suggested by the ability of patients with chronic bilateral vestibular loss (VL) to maintain equilibrium when presented with sinusoidal tilts of the body support surface (motion platform) with eyes closed, at least within a restricted range of tilt amplitudes and velocity/frequency values (Maurer et al. 2000, 2006; also Creath et al. 2002, Schweigart and Mergner 2008). In such a situation, patients dispose of only two kinds of sensory cues: (1) the just mentioned COP cues (proportional to body-space lean with static or slow body excursions), and (2) ankle proprioceptive cues (sensing body-support angle, given the foot sole is in full contact with the support). Since the patients often do better than a body-support stabilization on the tilted support, showing a body-space stabilization, they likely involve COP cues. This led us to conclude that force cues add redundancy to the human stance control system so that it can cope with internal disturbances such as vestibular loss ('spare tire' for gravity compensation).

We confirmed this notion by model simulations (Maurer et al. 2006; Schweigart and Mergner 2008; Mergner et al. 2009). This argument may need a justification. Our previous work on human stance control has convinced us that a purely narrative account of the underlying mechanisms is almost impossible. We feel that the interpretation of experimental results and the validation of pertinent hypotheses are only feasible by translating these hypotheses into models that allow for a simulation of the proposed information processing, and this all the more as the addition of further cues increases its complexity. A quantitative match of model and experimental results then can confirm that the proposed mechanism is compatible with reality and can be used to make further predictions. Accordingly, in several of the following considerations we refer to modelling and its results.

In normal subjects, the evidence for a force contribution of the kind conjectured above is less impressive, so far. When we eliminated ankle proprioception in blindfolded normal subjects by tilting their support in concert with their ankle joint angle (using a body sway referenced platform, BSRP) and disturbed them by sinusoidal pull stimuli, we obtained responses that could not be explained by pure kinematic feedback, but could be modelled by including force cues (Mergner et al. 2003; Maurer et al. 2006). However, these results do not prove that force cues are used in every day situations since their use could have been a special control 'strategy' prompted by the artificial elimination of ankle proprioception on the BSRP. Also the observation of Peterka (2003), that model fits to low-frequency experimental data can be improved by adding a force feedback to an otherwise purely kinematic model does not provide an unambiguous proof for the intervention of kinetic cues. Indeed, later work showed that similar effects can result if kinematic feedback is conditioned by a non-linear low pass element (see 'tonic excursion limiter' of Schweigart and Mergner 2008).

Understanding the role of force cues in normals may not be so straight forward as that of the gravitational torque compensation in vestibular loss patients. As described elsewhere (Mergner et al. 2003; Maurer et al. 2006) the force cue signal contains several components and is to be decomposed if one wants to use a constituent of it for stance control (see "Discussion"). One of the constituents in addition to the gravitational one is the torque that is generated by external forces such as a push or pull having impact on the body ('external torques'). In our model, we used the force cues to estimate and compensate the external torque. As concerns the gravitational torque, the model derives it from a vestibular body-space signal, which is easier to achieve (see below). This vestibular estimate of the gravitational torque requires, however, continuous knowledge of body mass and its distribution and, conceivably, a veridical vestibular signal. If these requirements are not fulfilled, the model automatically compensates for this, drawing more and more on the force cues for gravity compensation. It does so by way of an interaction between force cues and vestibular cues (details in "Discussion").

A situation where the vestibular estimate of the gravitational torque becomes erroneous in normals is when they lift an object with some weight, for instance. This changes total body mass and its distribution. As just mentioned, these two parameters are relevant for the estimate. Yet, as it is known and an everyday experience, stance control is then hardly affected, and this even if the load amounts to half the body weight or more (Heglund et al. 1995). Our model does accordingly, coping for the erroneous estimate of the gravitational torque by drawing on the force cues. Thus, according to our model, the force cues that yield the vestibular loss compensation in VL patients are used by normals not only for external force compensation, but also for gravitational load compensation.

In this view, external force compensation and gravitational load compensation in normals draw on the same mechanism. Thus, the model that we formerly used to predict external force compensation also predicts findings on gravitational load compensation. These predictions led us to perform the present study. Before we explain the experimental paradigm that we used to address gravitational load compensation, we clarify some relevant aspects.

One aspect concerns the fact that lifting a weight leads not only to an increase in gravitational ankle torque, but in addition to an increase in the body's weight and in its inertia. However, we aimed to experimentally access gravitational load compensation without interfering with possible weight and inertia compensation mechanisms for the following reasons. First, we think that the updating of the internal knowledge of body weight and inertia requires different sensory information. The update of body inertia requires sensing the effects of active lean movements, and that of body weight a spatial integration of pressure receptors in the feet (noticeably, the latter sense is to be distinguished from the above force cues in so far that these register COP position and shift rather than the scalar quantity of weight). Second, the updatings may occur at different times. Third, gravitational load compensation may change upon changes in body mass distribution without fixed relation to body weight and inertia (e.g. with a forward swing of the arms). Noticeably, internal estimation of body weight and its inertia is not yet covered by our model.

Another aspect is that we made so far a number of simplifications. One is that the force/torque cues are not reflecting directly the gravitational or external torque, but rather the active ankle torque that the stance control loop produces in response to the external disturbances. Furthermore, contributions to the force cues come not only from the gravitational and external torques, but also from the active torque that the control system generates to deal with body inertia, and there is in addition a passive torque from viscous-elastic elements in the ankle joint (see Maurer et al. 2006). And, finally, we related the force/torque cues so far only to receptors in the feet. Conceivably, there likely are several more sensor systems involved along the causal chain that mechanically links the force produced by the muscles to the normal ground reaction forces under the feet. An example would be the Golgi tendon organs (GTOs; see Duysens et al. 2000). However, within the framework of the inverted pendulum simplification we use for our stance control model, one can assume that the various sensors within this chain register essentially equivalent force/torque information.

The experimental paradigm we used in the previous study (Mergner et al. 2003; Maurer et al. 2006) consisted of separate presentations of sinusoidal tilt and pull stimuli (pull exerted through force-controlled cable winches on a body harness). In the present study, we coupled tilt and pull stimuli to create a situation that mimics gravitational load compensation. To this end, we evoked body-space lean responses by tilt stimuli and modified the lean-related gravitational torque by adding to/subtracting from it an equally lean-related (lean-referenced) external torque. As before, we performed the experiments in both normal subjects and vestibular loss patients and compared experimental data with model predictions.

Methods

Subjects

Experiments were performed in 11 subjects. Seven were healthy adults (age 21–55 years, 3 females and 4 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 4 subjects (age 33–40 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 that was approved by the local Ethics Committee of the Freiburg University Clinics.

Experimental setup

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 would 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 was rotated, under the control of a laboratory computer, in the sagittal plane with the rotation axis through the subjects' ankle joints. In order to evoke body-space lean responses, 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 ($\pm 1°$, $\pm 2°$ and $\pm 4°$) at each frequency.

In addition to the tilt stimuli, 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 (servo motors), 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 pull stimuli were applied approximately 10 cm above subjects' center of mass, COM, in fixed register with measured body-space lean (see below).

Data acquisition

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

In addition, we measured the angular excursion of the motion platform in space as well as subjects' hip-foot and shoulder-hip angular excursions in the sagittal plane (in deg). These parameters were obtained by means of an opto-electronic motion-measuring device with active markers (Optotrak 3020®, Waterloo, Canada). We used rigid plastic triangles on which three active markers of the recording system were fixed. The triangles were attached to the subjects' hips and shoulders by clamping them to closely fitting clothes, and to a rigid bar on the platform. With the help of 3 cameras the Optotrak system evaluates the 3D positions of the 3 markers per triangle with a time resolution of 200 Hz. A PC calculated then on-line 3D translational and angular positions (6D-position/-motion) of each triangle, reconverted the values into analog signals, from which we obtained upper body (UB) and lower body (LB) excursions in space, respectively. The UB and LB excursions were used to calculate center of mass (COM) angular excursion about the ankle angle axis (see below, "Data analysis") which is referred to as body-space (BS) angle in the following.

The COP and angular excursion data were calculated on-line by means of PCs, which produced corresponding analog output signals. These signals were fed, together with the signals of the tilt and pull stimuli and of platform position into a computer system (IBM compatible Pentium®) via analog-digital converter and were recorded with a 100 Hz sampling rate. The data were recorded with software programmed in LabView® (National Instruments, Austin, Texas).

Pull on torso

We applied the external force in fixed register with the gravitational torque (T_{grav}). This is schematically explained in Fig. 1a–c. In the example in b, the forward body-space lean upon forward platform tilt is associated with a forward angular excursion of the center of mass, COM, which leads to a forward excursion of its gravitational vector, F_{grav}, relative to the body axis. The result is a gravitational torque (not shown) that depends on the body mass (m) and height (h) of the COM above the ankle joint ($T_{grav} = m \times g \times h \times \sin[BS]$ or, with small angle approximation, $m \times g \times h$ [BS]; BS body-space angle, i.e. COM angular excursion; g gravitational acceleration). For purpose of on-line feedback of the external force, we used an electronically reconstructed estimate of BS based on shoulder and hip angular excursion derived from Optotrak. T_{grav} adds to the muscle torque at the ankle joint (Fig. 1c). Normally, it would entail a forward shift of the COP and a change in the corresponding force/torque cue signals. In the example of Fig. 1b, however, BS is transformed, as just described ($m \times g \times h \times \sin[BS]$), into an external force (F_{ext}) that is applied via the cable winches such that it neutralizes F_{grav} ($F_{sum} = F_{grav} + F_{ext}$) and, thereby, neutralizes T_{grav}. Figure 1c shows this in terms of a wiring diagram. The transfer function between BS and F_{ext} varied less than 2% in gain and less the 3 deg in phase up to a frequency of 5 Hz. For the example in b, the value in the box 'gain factor' would be -1 (T_{grav} is then neutralized by the external torque T_{ext}).

In our experiments, we used five different gain factors, -1.5, -1, -0.5, 0, and 0.5. The angle BS was obtained from the Optotrak™ registration, m and h from the

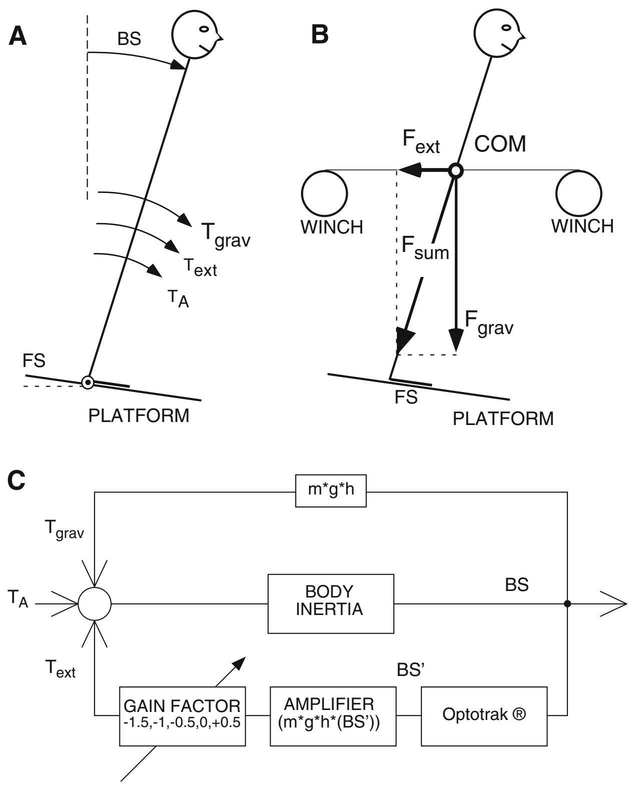

Fig. 1 Schematic representation of the experimental paradigm we used to investigate gravitational load compensation. Changes in gravitational torque were mimicked using an external force that was referenced to body-space lean. **a** Conventions used. *BS* body-space angle (here forward lean), *FS* foot-space angle evoked by, and equal to platform tilt (forward), T_{grav} gravitational torque, T_{ext} external torque evoked by external contact force, *TA* ankle torque (passive and active). **b** The effect of the external contact force, F_{ext}. The COM's (center of mass's) gravitational pull F_{grav} upon forward platform tilt and body-space lean is opposed by the F_{ext} (generated by cable WINCHes) such that F_{grav} swings back and becomes aligned with the ankle joint ($F_{sum} = F_{grav} + F_{ext}$). This nulls the gravitational torque T_{grav} and shifts the COP (center of pressure) under the ankle (T_{grav} and COP not shown), mimicking a situation where the body mass has been nulled. **c** Wiring diagram of the setup. BS, generated by ankle torque *TA* and its action on body inertia, is physically transformed ($m \times g \times h$) into T_{grav} (*m* body mass, *h* its height above joint, *g* gravitational acceleration). It feeds back onto *TA* with positive sign. To change the effect of T_{grav} experimentally, T_{ext} is summed to it via a second feedback loop. This is generated using a measured BS signal, BS′ (via Optotrak), an amplifier that mimics the transformation into a gravitational torque, and an adjustment of the gain factor. The gain factor in the example of panel **b** is −1

subjects. Individual fine adjustments of the amplifier (box AMPLIFIER) were obtained for static tilts prior to the trials and furthermore during the experiments whenever trials with the factor −1 were used. This is illustrated in Fig. 2 that shows examples for the factors 0 and −1 of a normal subject. Panel a shows the COM angle and platform angle (0.1 Hz, ±1° tilt) together with the external pull force and the COP as a function of time in the situation where the pull force is zero (factor 0). Panel b gives the corresponding traces for the gain factor −1. The external pull force is derived from the COM excursion (angle BS) and reversed in sign. As a result the COP no longer shows a modulation in relation to BS. Note that also the subject's force sensors would no longer register this modulation. There remain small variations in the COP trace which reflect all the other active ankle torques that are continuously produced in the stabilizing control. Conceivably, since the subject carries a foot with mass and dimension, the alignment of F_{sum} with his body is certainly not as perfect as with the inverted pendulum model shown in Fig. 1. Yet, nulling the COP is a good approximation for nulling the gravitational ankle torque (van der Kooij et al. 2005).

Experimental procedures

In the group of normal subjects, we used all four tilt frequencies ($f = 0.05$, 0.1, 0.2, 0.4 Hz), each with all three angular excursions (±1°, ±2°, and ±4°). Together with the five different factors for the external torque, there resulted $4 \times 3 \times 5 = 60$ different trials.

Pilot experiments suggested, in line with previous experiments from this laboratory (Maurer et al. 2006), that VL patients have balance problems with the ±4° tilt stimulus at 0.4 Hz and the ±2 and ±4° tilt stimuli at 0.4 Hz with eyes closed. Furthermore, they had difficulties maintaining balance on the tilting platform when the superimposed pull had the factors −1.5 and 0.5. We therefore restricted their experiment to two frequencies ($f = 0.05$, 0.1 Hz) and two amplitudes each (±1 and ±2°). Furthermore, we limited the number of external force factors to three (−1, −0.5, 0; number of trials, $2 \times 2 \times 3 = 12$). With these limitations, patients were able to maintain balance, but still showed abnormally large body excursions.

All trials were repeated 3 times in random order. Subjects were given a short break between trials (10–15 s). Total measuring time for normal subjects (about 3 h) was split into 3–4 recording sessions. VL patients performed one session (40 min). Trial durations were 80 s for the 0.05 Hz stimuli (4 cycles), and 40 s for the 0.1, 0.2, and 0.4 Hz stimuli (4, 8, and 16 cycles, respectively).

Data analysis

The data were analyzed off-line with custom-made software programmed in MATLAB™(The MathWorks Inc., Natick, MA, USA). COM angular displacement was calculated from the upper body-lower body (shoulder-hip) angle, lower body-foot (hip-foot) angle, and foot (platform)-space angle according to anthropometric data of Winter (1990). As mentioned before, body-space angle (BS) is used synonymously for the COM angular displacement. The SD values of the inter-subject mean values were taken as a

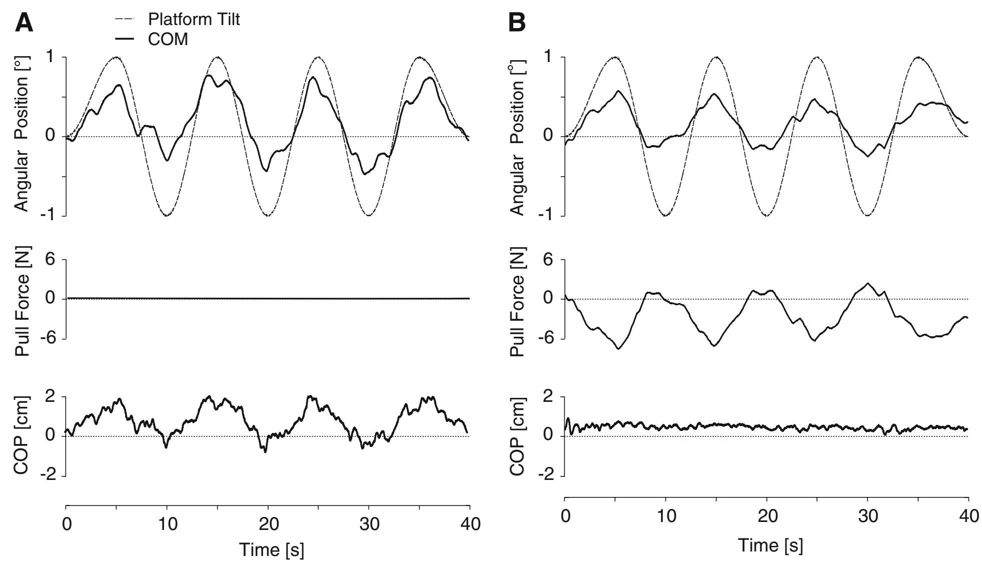

Fig. 2 Typical body-space lean responses of a normal subject upon platform tilt (0.1 Hz, ±1°). **a** External force factor of 0 (no external pull force). **b** External force factor of −1 (compare Fig. 1b). The panels show (traces from top) the angular position of COM ('body-space lean') superimposed on platform position, the applied pull force, and the COP. Note that the COP trace in b no longer carries a modulation in relation to the COM excursions, unlike in **a**

measure of the inter-subject variability (obtained in Fourier space).

A spectral analysis was performed on the tilt stimuli versus the response of COP and COM using a discrete Fourier transform. Fourier coefficients at stimulus frequency were used to calculate gain (peak response amplitude divided by peak stimulus amplitude) and phase (relative timing between response and stimulus). The gain measures have units of cm/° for the COP shift upon platform tilt, and no units for COM angular excursion upon platform tilt (both quantities are in °). In all experimental conditions, zero gain means that the tilt stimulus evoked no COM excursion in space (viewed, vice versa, in terms of a compensatory righting response with respect to the platform, the gain is unity) and gain values >0 indicate COM excursion into the tilt direction (compensatory responses too small or absent). The findings will be explained in terms of COM excursions (body-space lean responses) rather than COP shifts. Significance of findings was tested with analysis of variance (ANOVA) with ε-adjustments of the degrees of freedom for sphericity unless stated otherwise (SuperANOVA, Abacus Concepts, Berkeley, CA).

Gain and phase curves plotted as a function of stimulus frequency were used to characterize the dynamic behavior of the postural control system. The curves were compared to corresponding curves obtained by simulations of our stance control model (Maurer et al. 2006 and "Discussion"). The model simulations were implemented in Simulink/MATLAB™, as was an optimization procedure that we used to identify parameters of the model (for details, see Maurer et al. 2006). In brief, the procedure varied defined model parameters, using the Matlab Optimization toolbox function 'fminsearch' (which is based on the 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. With each iteration of the search, simulated responses to the 60 stimulus conditions (normals) were obtained, the simulated data were analyzed in the same manner as the experimental data, and a scalar error function was evaluated representing 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 yielded a minimum of the error function.

Results

Normal subjects

Normal subjects had no difficulty maintaining balance on the tilting platform with eyes closed. A typical response of a normal subject is shown in Fig. 2a. It was obtained using a 0.1 Hz, ±1° tilt and an external force factor of 0 (no external pull force). During the forward tilts, the subject allows for forward COM excursions up to more than half of the tilt amplitude. In contrast, during the backwards tilts, the subject allows only for small backward COM excursions. We have observed this kind of asymmetric tilt responses also in previous studies (Maurer et al. 2000, 2006) and investigated and modeled it in a recent study (Schweigart and Mergner 2008). Here, it will not be considered further when we express in the following the steady state responses in terms of gain and phase.

Figure 2b gives the same subject's response for the same tilt stimulus, but the external force factor now is −1 (i.e. the external torque is equal in amplitude and opposite in sign to gravitational torque of BS, which thereby becomes neutralized). The consequence is that the COP trace no longer carries a modulation evoked by the COM excursions, as was the case before without the external force in Fig. 2a. In other words, the COP shift that normally results from body-space lean is missing here. The amount of pull force applied for neutralizing the COM forward excursion of approximately 0.5° is −6 N. Noticeably, despite this considerable pull force opposite to the tilt, there remains a COM excursion in the tilt direction, the response being approximately 35% smaller than it was before without pull in Fig. 2a.

The averaged COM gain and phase data of all normal subjects is shown in Fig. 3. The data are plotted as a function of the gain factor of the external force (abscissas), separately for the three platform tilt amplitudes and the four stimulus frequencies. First, we describe briefly the effects of stimulus frequency and amplitude, because they resemble those we have observed previously (Maurer et al. 2006).

Increasing tilt frequency (rows A–D of Fig. 3) while keeping tilt amplitude constant led to a decrease in gain, and this similarly across the three amplitudes tested and across the data obtained with the 5 different external force factors ($F = 29.6$; $p < 0.0001$). The phase, being close to 0° at 0.05 and 0.1 Hz, developed a lag at 0.2 and 0.4 Hz ($F = 8.3$; $p = 0.0001$). Unlike in our previous work, the phase lag was particularly pronounced at 0.2 Hz with the ±2 and ±4° stimuli (reaching −57°) in relation to the external force factor, for unknown reasons.

Increase in tilt amplitude from ±1 to ±2 and to ±4° (columns a–c of Fig. 3) also led to a decrease in gain ($F = 18.8$; $p < 0.0001$). This effect was independent of tilt frequency and the external force factor. The response phase showed no considerable change with increasing tilt amplitude ($F = 3.6$; $p = 0.07$). In the previous work, we considered the effect to represent an amplitude non-linearity related to central detection threshold-like mechanisms.

The external force factor also affected the response gain ($F = 7.1$; $p = 0.0002$), whereas the response phase was not consistently affected ($F = 1.47$; $p = 0.23$). The gain effects will be further described in relation to the mean gain values obtained with the external force factor 0 (no external force), starting with the 0.1 Hz, ±1° stimulus (Fig. 3Ba). Decreasing the factor from 0 to −0.5, −1, and −1.5 means applying pull force counter to tilt direction. This changed the effect of the body-space lean on the gravitational torque as if body mass was counter-acted by more and more upthrust. It led to a decrease in the gain of the COM excursion, starting from a value of 0.49 and reaching 0.27 with the factor −1.5. Thus, even when the external torque amounted to −1.5 times the gravitational torque (yielding a reversal of COP shift direction) was the COM excursion still in the direction of the tilt, albeit showing some reduction in gain. These findings applied similarly across the four stimulus frequencies and the three stimulus amplitudes tested.

Applying the external force factor 0.5 means that the pull is applied in the direction of tilt and body-space lean and enhances the ankle torque as is the case if a load is added to the body. This led to a slight increase in COM gain (0.52) in Fig. 3Ba. Across all trials, however, COM gain remained essentially the same ($F = 0.023$; $p = 0.88$). The phase showed again no consistent change ($F = 0.18$; $p = 0.67$). Thus, the overall effect of the external force factor was asymmetric in that it showed a decrease with decreasing external force factor and tended to saturate with the increase in this factor (see also replot in Fig. 6a).

VL patients

The patients were able to maintain stance during all stimuli presented, but showed larger COM responses than normals for comparable tilt stimuli ($F = 202.8$; $p < 0.0001$). Their gain and phase curves (inter-subject mean and SD values) are plotted in Fig. 4 over the external force factor (abscissas). Note that VL patients were presented with fewer trials compared to normals, using only two frequencies (0.05 and 0.1 Hz), two tilt amplitudes (±2° and ±4°), and three external force factors (−1.0, −0.5, and 0). Their data resembled those of normals in so far that the two external force factors −0.5 and −1 led to decrease in COM gain as compared to the trials with the factor 0 ($F = 14.5$; $p = 0.0013$), similarly with the two frequencies and the two amplitudes. COM gain decreased with increasing stimulus amplitude ($F = 18.3$; $p = 0.0027$), which qualitatively is again similar to normals. And, although COM gain was abnormally large, also variability of COM gain and phase (vertical SD bars in Fig. 4) was similar to that of normals. The phase was slightly abnormal. Essentially independent of stimulus frequency and amplitude, it showed a slight advance by 10-20° with the external force factor 0, which became less with the factors −0.5 and −1 ($F = 15.6$; $p = 0.0011$).

Note that patients' COM gain values across all trials were almost two times larger than those of normals. This is similar to the findings in our previous study (Maurer et al. 2006) in which we investigated the same VL patients with platform tilts and pull stimuli, but not with a combination of both. Furthermore, it is important to notice that their COM gain is smaller than unity with most trials (body is inclined slightly away from the platform vertical towards the space vertical even with the factor 0 trials). This suggests that the patients involved a graviception from force cues for their stabilization, since with solely the ankle angle proprioception they could have achieved a body-platform stabilization at best at the low tilt frequencies used.

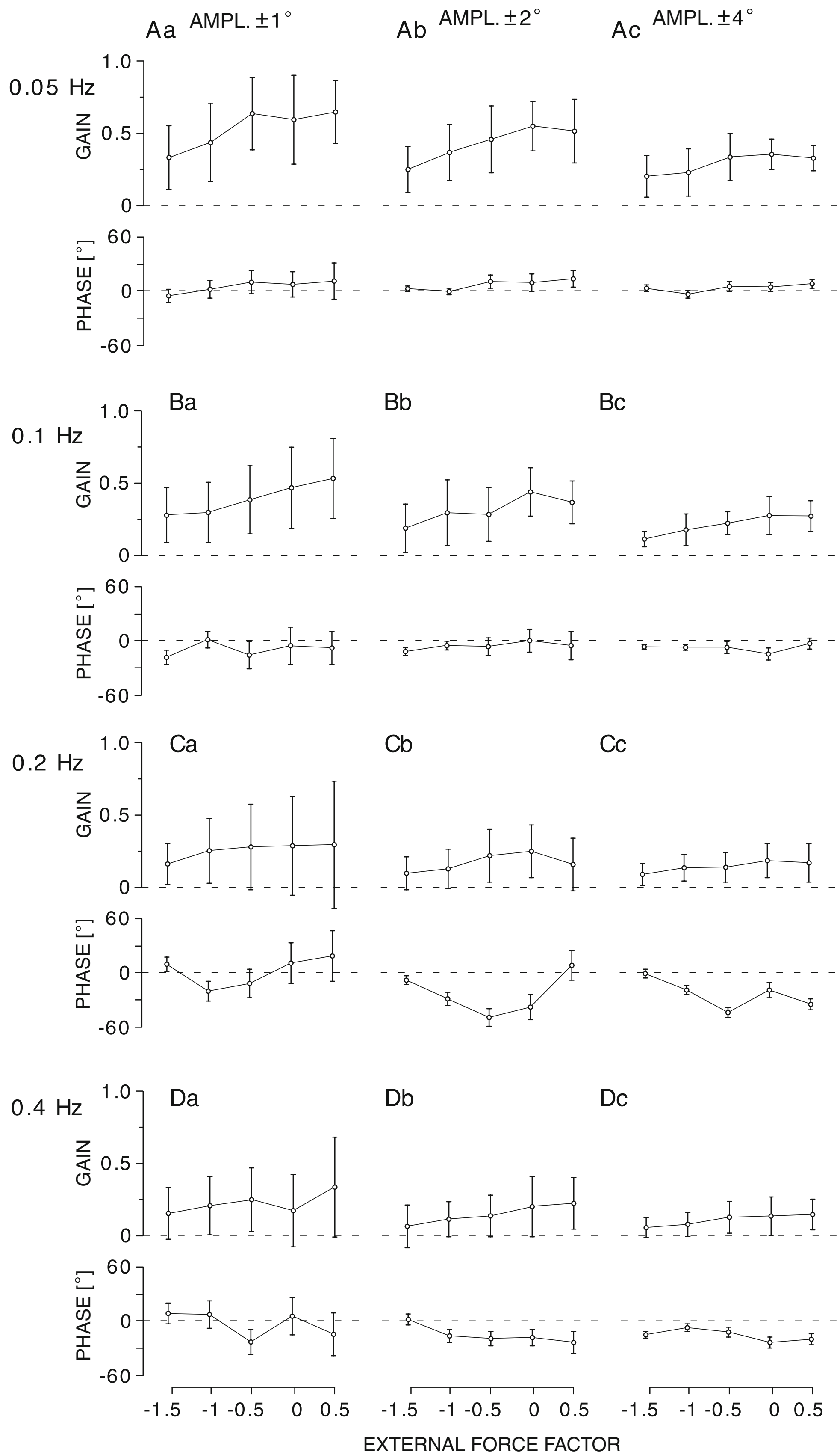

Fig. 3 Averaged COM responses of normal subjects (mean values and inter-subject SD values). Plotted are gain and phase curves as a function of the gain factor of the external force (abscissas), separately for the four platform tilt frequencies (rows a–d) and the three amplitudes (columns a–c). A gain factor of 0 means no external force, while 0.5 means that an external force is generated in the direction of the gravitational torque. This yields an external torque whose magnitude is half of the gravitational torque that occurs normally (i,e, in the factor 0 condition). Negative factor values correspond to external forces/torques counter to gravitational torque (compare Fig. 1)

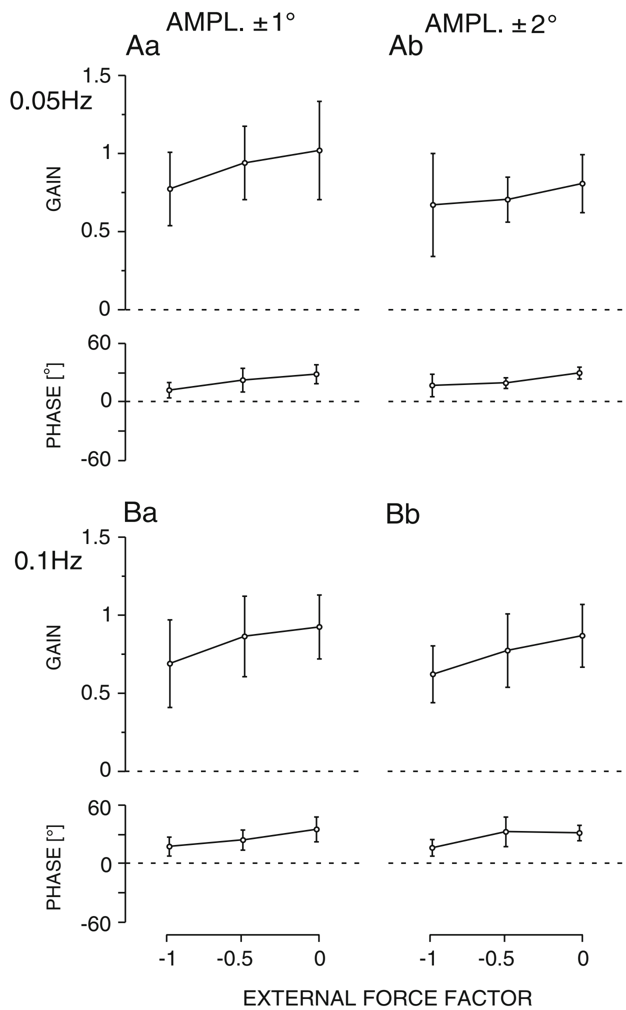

Fig. 4 Averaged COM responses of VL patients (conventions as in Fig. 3). Compared to normals, VL patients were presented with fewer trials, using only two frequencies (0.05 and 0.1 Hz, a–b), two tilt amplitudes (±2° and ±4°, a–b), and three external force factors (−1.0, −0.5, and 0; abscissas). The patients were able to maintain stance during all stimuli presented, but showed abnormally large COM excursions

Discussion

Research over recent years has provided evidence that human stance control can be modeled and mimicked by means of a sensory feedback mechanism (see "Introduction"). Several sensor systems contribute to this control, with the weight of the individual sensory contributions depending on, and changing with a number of factors, such as the external situations and the disturbances they contain, the magnitude of the disturbances (see above, 'amplitude non-linearity'), the sensory information that is picked up (e.g. by opening or closing the eyes), cognition, failures that may arise internally within the body in sensors, control, and actuators, etc. Conceivably, current stance control models cannot yet cover this wide range of flexibility and robustness of the system (we speak of flexibility in relation to external disturbances and robustness in relation to internal disturbances). Yet, we hold that our stance control model (Mergner et al. 2003; Maurer et al. 2006) provides an architectural basis for them in that it autonomously covers the compensation of the external and internal disturbances across changing situations. And, it provides a basis for the implementation of add-on mechanisms (Schweigart and Mergner 2008).

The present work proceeds from the hypothesis that a considerable contribution to the system's flexibility and robustness stems from force receptors, in that these add redundancy as well as specificity and stability to the system, as we will explain in the following. Before doing so, however, we shortly recall the experimental paradigm and the main findings of the present study and explain the main features of the model. Emphasis is put on those features that are relevant for understanding how the force cues contribute to gravitational load compensation in normals and to vestibular loss compensation in patients.

Experimental paradigm and findings

We mimicked changes in gravitational ankle torque as they occur when the body mass or its distribution is changed. We did so by generating a body lean-referenced external ankle torque and varied its proportionality factor. With a factor of −1, for instance, the force cues register 'no lean associated COP shift' although the platform tilt evokes a body-space lean (compare Fig. 1). This mimics a loss of gravitational torque as it may occur due to buoyancy when one is immersed in water. On the other hand, the factor of 0.5 mimics an increase of the gravitational torque as it occurs upon lifting a heavy load. In these situations, the vestibular-derived estimate of the gravitational torque is erroneous (recall from "Methods" that the torque is calculated from the vestibular body-space lean signal, gravity, and known values of body mass and its height above the joint). How are the force cues helping subjects to cope with this error?

We first consider the experimental findings of normals. The pull-evoked and lean-referenced external torque scaled the tilt responses of normals in a systematic way. The effects were relatively small and tended to be asymmetric for the negative versus positive external force factors (cf. Fig. 3). Increasing the negative factor (pull counter to the body-space lean) led to a decrease in COM gain, while this showed a saturation with the factor 0.5 (pull in the direction of the lean). (We restricted the positive value of the factor to 0.5, because pilot experiments had shown that normals tend to become unstable with factors >0.5). Conceivably, to explain these findings, one needs to consider the complex interplay in the control loop between physics (e.g. body inertia, gravity), the several sensors involved, the feedback character of the control, and biomechanics (passive torque by viscous-elastic elements in the joints). As already mentioned in "Introduction", we used for this a dynamic model.

Model

An overview over the model is shown in Fig. 5a. The main principle is that a proprioceptive negative feedback loop ('local loop', heavy lines and arrows) adjusts a body-foot (support) angle BF to a given primary position (set point signal is added at summing junction before controller, not shown, representing perpendicular body orientation with respect to level platform). The required ankle torque is achieved by means of a controller (PID P, proportional factor; D, derivative; I, integrative). BF can be disturbed by an external torque T_{ext} (e.g. upon a contact force such as the pull), a gravitational torque T_{grav}, and a change in foot (support)-space angle FS arising with tilt of the support surface. This is prevented by a multisensory disturbance rejection in the form that the external disturbances are internally estimated by means of inter-sensory interactions (estimates τ_{ext}, τ_{grav}, and *fs*, respectively) and in that these estimates are then fed into the negative feedback loop. Further details are given in Maurer et al. (2006) and Mergner (2007).

There are several advantages to use the principle of disturbance rejection for stance control. A major advantage is that it copes well with the variety of behavioral situations by automatically yielding adequate weights for each sensor at any moment (Maurer et al. 2006). The reason is that only four external disturbances have to be estimated and rejected (apart from T_{ext}, T_{grav}, and FS also body support surface translation, to be dealt with elsewhere). Interestingly, in our model the principle of disturbance rejection is implemented using simple inter-sensory interactions, whereas related engineering solutions use so-called observers that include a kind of efference copy signal and internal models of body dynamics and sensors (see Mergner 2007).

Details of the inter-sensory interactions are shown in Fig. 5b (full lines and arrows). We focus here on the estimates τ_{grav} for the physical quantity T_{grav} and τ_{ext} for T_{ext}. Note that τ_{grav} is derived from the vestibular signal bs (that codes body-space angle BS), taking into account body mass and its height above the joint (compare "Methods"). The estimate τ_{ext} is derived from τ_a that codes via the COP the ankle torque T_A. As mentioned before, T_A contains four components, T_{ext}, T_{grav}, an active torque component (proportional to body-space acceleration) related to the body's eigen-inertia, and a passive torque component (compare Fig. 5a and "Introduction"). One has to internally estimate the latter three components and to eliminate them from τ_a before yielding τ_{ext}. These estimations are performed in box SOMAT'. Note that one of the estimates represents a version of the vestibular T_{grav} estimate, τ_{grav}' (similar to τ_{grav}, but with negative sign and slightly different dynamics and gain; not shown).

What happens if τ_{grav} (and also τ_{grav}') is erroneous due to a too low vestibular signal or to a missing vestibular signal in vestibular loss patients or to a change in *m* or *h* when body mass or its distribution is changed? Let us assume that τ_{grav} and τ_{grav}' are too small, i.e. they are carrying a negative error. Subtraction of τ_{grav}' from τ_a then yields a too large τ_{ext} estimate, that is a positive error. This positive error tends to make up for the negative error of τ_{grav}. Noticeably, the positive error stems from the force cues. (One may call this an internal automatic sensory reweighting).

On the basis of these considerations, which we derived from our previous experiments and the model, we designed the present experiments on gravitational load compensation in normals and predicted the results. Using an automatic model fitting procedure across all 60 trials (see "Methods"), we calculated a mean square fitting error (zero/unity error refers to zero/unity gain when expressing the distance between experimental and simulated responses in polar coordinates in terms of gain and averaging across all trials). In doing so, we proceeded from the model parameters of our previous study, where one parameter set was for the condition without BSRP and another set for the condition with BSRP (Maurer et al. 2006). These parameters are given in Table 1. The fitting error for the present data obtained with the parameter set without BSRP from the previous study amounted to 0.087. This is somewhat higher than the corresponding value in the previous study (0.055; Maurer et al. 2006; 37 trials, tilt and pull stimuli were presented separately). Keeping G_3 zero and allowing the optimization procedure to adjust G_1 and G_2 (see Table 1) yielded a reduction of the fitting error to 0.61. Allowing it then to adjust G_3 in addition to G_1 and G_2 yielded almost the same error (0.062), although G_3 was given now a value of 0.66 (same as in previous parameter set with BSRP). Thus, the fitting error procedure alone did not allow us to decide whether or not normal subjects were drawing on force cues in the present experiments.

However, when inspecting the simulated gain and phase curves, there was a considerable difference between model versions with and without force contribution. To illustrate this, we compare in Fig. 6 the experimental data (panel A) with simulated data that we obtained with $G_3 = 0$ (panel B) and $G_3 = 0.8$ (D; panel C is added to also give an intermediate value of $G_3 = 0.4$). The figure shows COM gain and phase curves for the ±2° stimulus, superimposing the data of 0.05, 0.1, and 0.4 Hz trials (0.2 Hz data omitted because of the abnormal phase; see "Results"). Note that the simulated gain and phase curves

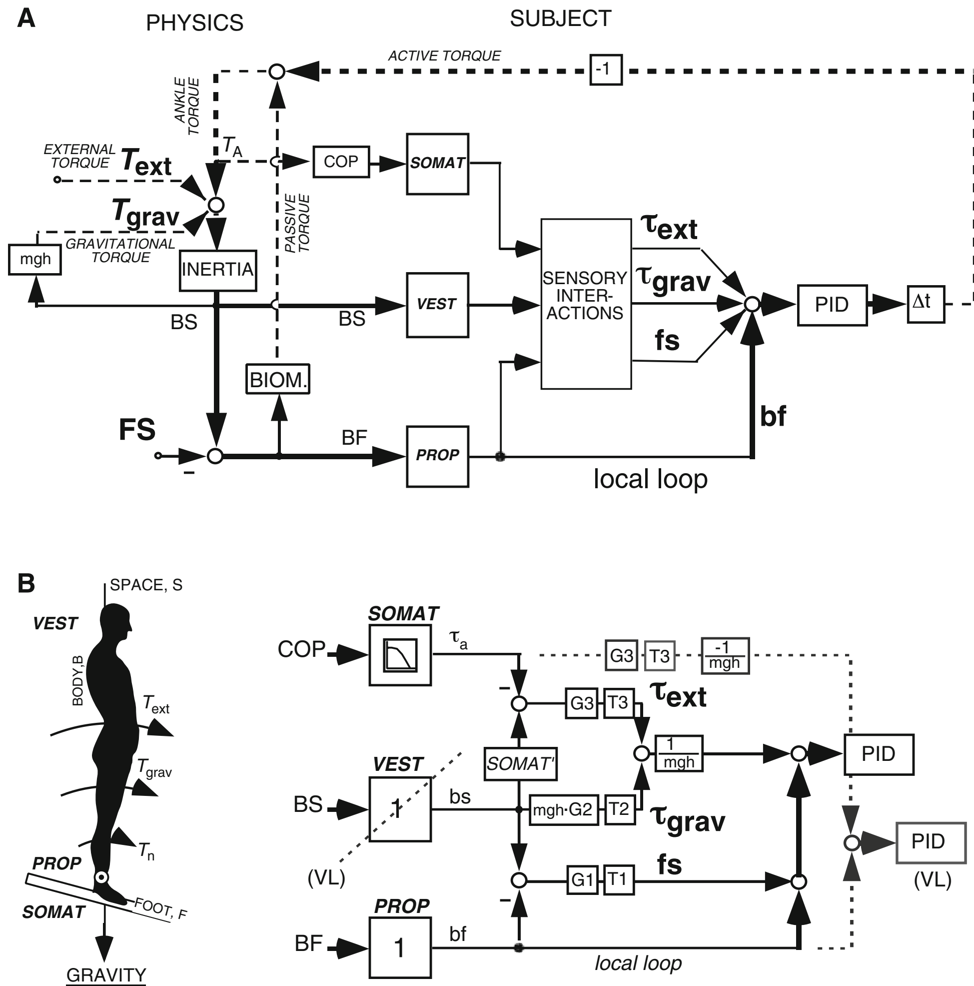

Fig. 5 Stance control model. **a** Overview. '*PHYSICS*' part (left) consists of an 'inverted pendulum body' (one *segment* for head, trunk, and legs) that pivots about the ankle joint on a motion platform (rotation axes of body and platform through joint; conventions indicated in inset). Three external stimuli (disturbances) are considered (*bold*): T_{ext}, external torque (evoked by external contact force, i.e. pulling on body). T_{grav}, gravitational torque (arising from body-space lean BS × mgh; *m* body mass, *h* its height above joint, and *g* gravitational acceleration). *FS* foot-space angle (equal to tilt of the body support surface). Further parameters are: *BF* body-foot angle (generates, via box BIOM, for biomechanics, passive torque and inputs into control system). *T*A, ankle torque. *Box* INERTIA, for body inertia, transforms sum of all torques into BS. *Box* COP, for center of pressure, transforms ankle torque into COP shift. Dashed lines and arrows represent torques (e.g. *T*A) and continuous ones angles (e.g. BS). In the '*SUBJECT*' part of the model (on the right), three sensors are assumed: *PROP* proprioceptive, *VEST* vestibular, *SOMAT* force/torque cues. *Box* SENSORY INTER-ACTIONS creates internal estimates of the external disturbances (τ_{ext}, τ_{grav}, *fs*). These are fed into a proprioceptive feedback loop ('*local loop*'; *bold full* or *dashed lines* or *arrows*). *Box* PID, controller with proportional, integrative, and derivative factors. *Δt* lumped representation of all delays in system. **b** Details of the sensory interactions (see text). τ_a, *bs*, and *bf* represent sensor signals of *TA*, *BS*, and *BF*, respectively (note low pass filter symbol in *box* SOMAT). Box *SOMAT'* derives vestibular estimates of gravitational torque and eigen-inertia torque component for extraction from τ_a. G_1–G_3, gains of internal stimulus estimates; T_1, T_2, and T_3, detection thresholds; mgh and 1/mgh, transformations from angle into torque and torque into angle, respectively. *Dotted lines* and *arrows* give reduced model for vestibular loss (VL) patients

obtained with $G_3 = 0.8$ tend to saturate with increasing external force factor (abscissa; D) and that this is qualitatively similar to the experimental data (A). In contrast, in the simulated data with $G_3 = 0$ (B), the gain curves tend to develop an essentially exponential increase and the phase curve an increasing lag when the external force factor is increased from −1.5 to 0.5 (intermediate slopes were obtained with the intermediate $G_3 = 0.4$; C). Similar results were obtained for the ±1 and ±4° stimuli. Increasing the gain of τ_{grav} while keeping that of τ_{ext} constant did not produce a slope pattern similar to the experimental data.

We take these findings as evidence for the presumed contribution from force cues. We like to mention, however, that the evidence owes mainly to the data obtained with the external force factor 0.5. Concerning only the negative factor values, the data do not allow to decide whether normals used the force cues or not.

Table 1 Model parameters adapted from Maurer et al. (2006, Tab. 1) and model gain factors (G_1–G_3) after fitting normal subjects' experimental data with and without force cues

Model parameters				
Proportional part of NC (Nm deg^{-1})	15.1			14.9
Derivative part of NC (Nm s deg^{-1})	4.4			4.24
Integral part of NC (Nm s^{-1} deg^{-1})	1.3			1.39
Threshold of *fs* signal (deg s^{-1}) ($T1$)	0.17			0.18
Threshold of τ_{grav} and τ_{ext} (deg) ($T2$)	0.16			0.09
Time delay (s)	0.17			0.16
Passive stiffness (Nm deg^{-1})	0.91			1.08
Passive damping (Nm · s deg^{-1})	0.68			0.37
Gain of *fs* signal (G_1)	0.79	0.92	0.98	0.81
Gain of τ_{grav} signal (G_2)	1.52	1.53	1.22	1.00
Gain of τ_{ext} signal (G_3)	0	0	0.66	0.66
	Maurer et al. (2006), without BSRP	Force cues $G_3 = 0$	Force cues $G_3 = 0.66$	Maurer et al. (2006), with BSRP

NC neural controller (PID), *BSRP* body sway referenced platform; Signals: *fs* foot-in-space, τ_{grav} internal estimate of the gravitational torque, τ_{ext} internal estimate of the pull stimulus, *m* COM mass 74.9 kg not including the feet, *h* COM height 0.98 m above ankle axis, *J* body moment of inertia about the ankle joint, 72.0 kg m^2; low pass filter in the SOMAT box, first order with a cut off frequency of 0.8 Hz

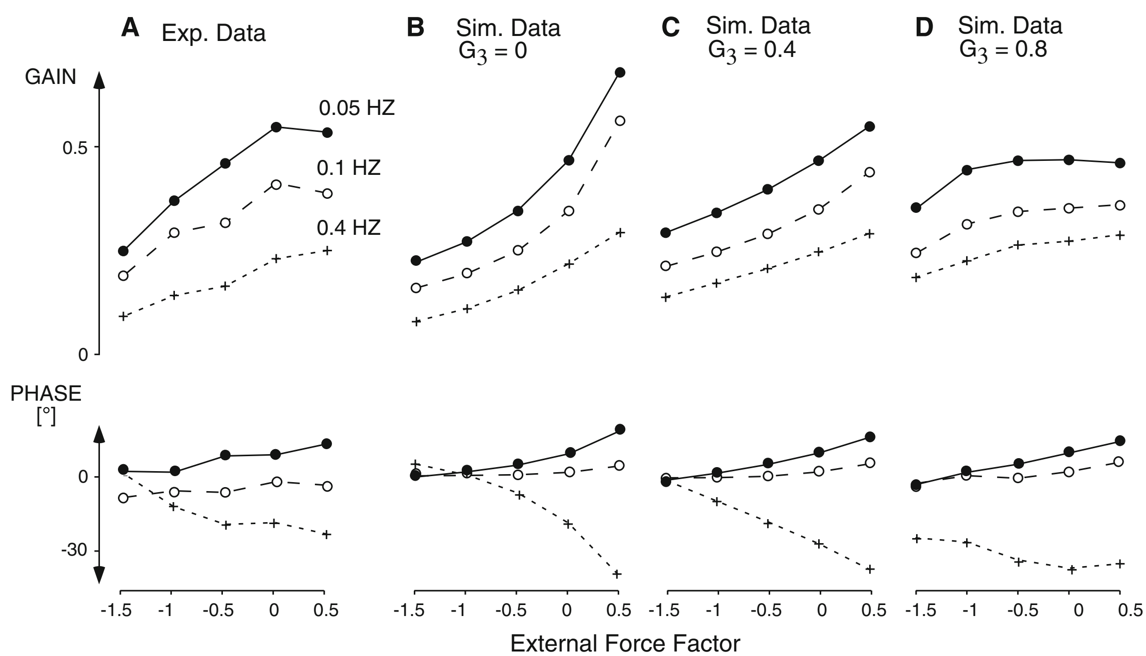

Fig. 6 Comparison of experimental and model-predicted data. **a** Replot of gain and phase curves as a function of external force factor obtained with ±2° stimulus, superimposing the data at 0.05, 0.1, and 0.4 Hz (0.2 Hz data omitted). **b–d** Predictions of corresponding curves upon giving τ_{ext} a gain of zero (**b**), 0.4 (**c**), and 0.8 (**d**)

However, we like to point out that our normal subjects reported on retrospective request that they consciously perceived the pull stimuli with the factor 0.5 trials and with the negative factors trials. This shows that they were internally reconstructing the external force stimulus, at least at the level of conscious perception.

To improve intuitive understanding of the role of the force cues, we measured in model simulations what each of the three disturbance estimates *fs*, τ_{grav}, and τ_{ext} and the proprioceptive signal *bf* contribute to the feedback in the loop. We simulated the situation $G_3 = 0.8$ at 0.05 Hz, ±2° in Fig. 6d and compared it with that of Fig. 6b ($G_3 = 0$). The analysis was performed by probing into *fs*, τ_{grav}, τ_{ext}, and *bf* as if they were outputs, using the same Fourier transform as with the experimental and simulation COM output data. The phase data were omitted for simplicity, giving instead

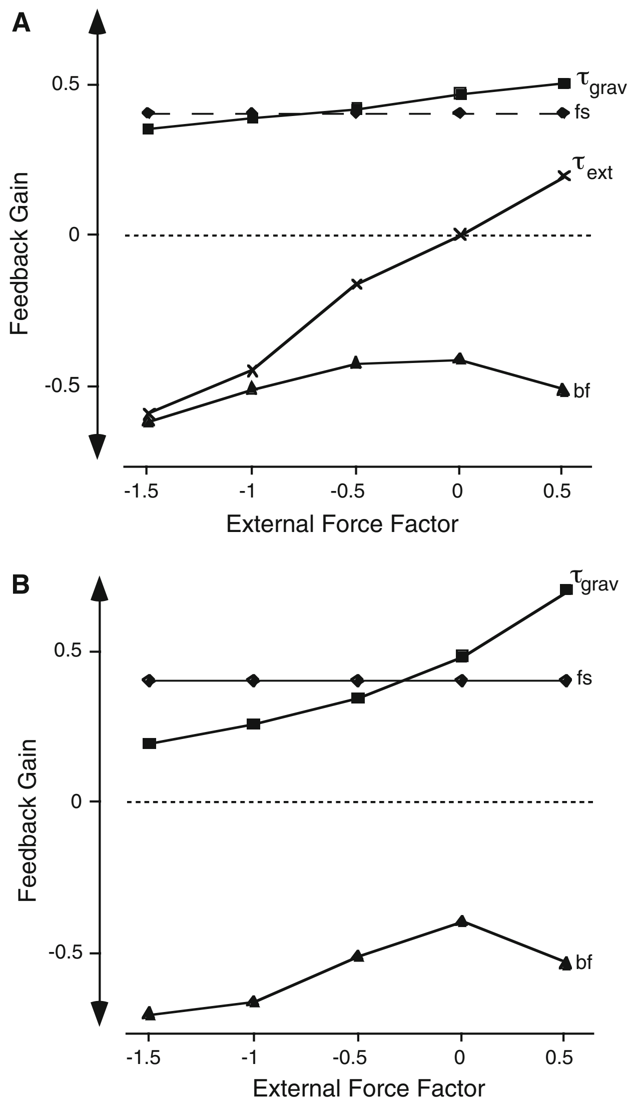

Fig. 7 Contributions of the three disturbance estimates *fs*, τ_{grav}, and τ_{ext} and the proprioceptive signal *bf* to the feedback gain. Simulations were obtained with model of Fig. 5a, b and refer to 0.05 Hz COM gain curves shown in Fig. 6d (**a** $G = 0.8$) and Fig. 6b (**b** $G = 0$). Further details in text

the gain values a positive/negative sign when the phase values ranged from +30 to −30°/−150 to 210° ('inphase'/'counter-phase' signals). Using the 0.05 Hz stimulus reduced the dynamic effects of body inertia and of the low pass filter of SOMAT in Fig. 5b. The gain values are again plotted over the external force factors used for the pull (Fig. 7a, b).

In Fig. 7, the curve of the signal *fs* in panel a ($G_3 = 0.8$) is similar to that in panel b ($G_3 = 0$) because it simply reflects the platform tilt. The proprioceptive signal *bf* is in both panels negative, which reflects the fact that the body-foot excursion is essentially counter to the foot (support)-space tilt. This signal tends to deflect in the negative feedback control the body in the direction of the platform tilt, together with the physical quantities passive ankle torque (due to viscous-elastic elements; not shown) and gravitational torque (not shown). In contrast, the estimate *fs* shows positive values and thus tends to keep the body upright, together with τ_{grav} that also shows positive values. Addition of τ_{ext} to the control as a further disturbance estimation and compensation removes to a large degree the effect of the external pull; the τ_{grav} and *bf* curves in panel a become more parallel to the abscissa compared to those in panel b. A consequence for the COM gain curves is that they show clearly less variation with the external force factors in Fig. 6d as compared to Fig. 6b.

Thus, an effect of adding the force cues and the derived estimate τ_{ext} and its compensation is that the control loop acts more specifically, meaning that they increase gain to the extent that, and at the time when an external contact force or a gravitational load effect has impact. This is advantageous over a general increase in loop gain by an increase in PID controller factors, for instance, because the loop gain then would be unnecessarily in excess in situations without such disturbances. High loop gains in biological systems may cause problems for control stability, as these systems often show relatively long delay times and high noise. In this sense, the principle of specific disturbance estimation and rejection appears advantageous for maintaining stability of the control loop.

Furthermore, the force cues add redundancy to the system and thereby improve its flexibility and robustness. It improves flexibility in the sense that τ_{ext} takes over what is missing in τ_{grav} in the wake of gravitational load compensation in normals. And, it improves robustness in the sense that τ_{ext} takes over what is missing in τ_{grav} in the wake of vestibular loss in the patients. As mentioned in "Introduction" and "Results", however, force cues cannot fully make up for loss of vestibular information, as evidenced by the restrictions of their balance control on a tilting platform. And they do not allow VL patients to stabilize on a compliant support surface (sand, foam rubber, rocker board, etc.) for reasons considered elsewhere (Mergner et al. 2009).

An important functional aspect of the disturbance estimation and rejection in our model is that it changes the relative contributions of the sensors involved in stance control with the behavioral situation ('sensory re-weighting'; Horak and Macpherson 1996). The force cue mechanisms described in this study adds to the sensory reweighting mechanisms we described before. They occur automatically by the inter-sensory interactions and the thresholds in our model (see Maurer et al. 2006) as well as by add-ons to the model in the form of switches, which may involve cognition (Schweigart and Mergner 2008). Their complexity and non-linear features, conceivably, complicate 'black box approaches' to the system enormously, making simple 'verification' or 'falsification' tests questionable. We therefore expect progress in this field mainly from comparing among dynamic models as to their power to describe and predict experimental data.

Vestibular loss

VL patients showed in previous studies a body-space stabilization when balancing on a moving support surface with eyes closed ("Introduction") and they did so in the present study even though we superimposed on the tilt a body lean-referenced pull stimulus ("Results"). But the amplitude and frequency ranges of the tilt stimuli that they were able to cope with were abnormally small, and these ranges now became somewhat more restricted with the superimposed pull. One reason for the restrictions are the abnormally large COM excursions evoked by the tilt. They appear to reflect that the gain of their control loop is abnormally low. With the architecture of our model, one would expect a decrease of loop gain following loss of one of the sensors. As we will show in the following, VL patients partially, but not fully compensate for this gain decrease.

The model part depicted in Fig. 5b also contains our hypothesis of a vestibular loss compensation by means of the force cues and τ_{ext}. The vestibular loss and the resulting modification of the model is indicated by dotted grey lines and arrows. It is assumed that loss of the vestibular sensor entails loss of the vestibular-related estimates τ_{grav} and *fs*. There remain the estimate τ_{ext} and the proprioceptive ankle angle (local) loop as inputs to the PID controller of the patients. Model simulations showed, however, that further changes were necessary to make the control stable and to mimic the patients' experimental data. This was achieved by decreasing the time constant of the low pass filter in the box SOMAT (note filter symbol), and increasing the loop gain (which we did by increasing the factors in the PID controller) and by finding a certain balance between these two modifications. Despite this, the loop gain could not be increased to normal values in the tilt situation (further details below and in Maurer et al. 2006; Schweigart and Mergner 2008; Mergner et al. 2009).

We take these simulation results and their correspondence with the experimental results as support of our hypothesis of a vestibular loss compensation by means of the force cues. We like to emphasize, however, that force cues and vestibular cues are not simply interchangeable in stance control. As mentioned above, the use of force cues is complicated by the fact that they contain several components and require decomposition if one wants to use them for stance control. VL patients appear to have considerable difficulties with this (Mergner et al. 2009). On the other hand, to derive from the vestibular signal information on gravitational torque is complicated by the fact that it requires knowledge of current body mass and its distribution. The combination of both the vestibular and force cue signals is more efficient for disturbance estimation and rejection than either one or the other alone could be (cf. above, disturbance specific responses, in context of Fig. 7). Therefore, normal subjects likely use both for their stance control. This leaves open the possibility, however, that they may avoid the use of force cues in particular situations, e.g. in situations where their contribution is dangerous, or when it is negligible (as appears to be the case with the -1.5 and -1 external force factor in Fig. 6b–d).

Conclusions

With a forward or backward body-space lean off the vertical, such that the COM is no longer exactly above the rotation axes of the ankle joints, there arises a 'gravitational pull' on the COM that leads to a gravitational ankle torque. In current concepts on sensory feedback in human stance control, this torque is estimated and accounted for on the basis of a vestibular body-space lean signal, i.e. a kinematic signal. We posit here, and provide experimental evidence for our notion, that subjects involve force cues when the vestibular estimate of the gravitational torque becomes erroneous or is lost. In normal subjects, the vestibular estimate may become erroneous following a change in body mass upon lifting a load, for instance. Then, a signal derived from the force cues makes up for the error (gravitational load compensation). Another situation where the force cues are used is following vestibular loss (VL patients). Thus, the force cues improve the flexibility and robustness of the human stance control system by providing an automatic gravitational load compensation and a vestibular loss compensation. This extends the role that they normally play, which is to yield an estimate of, and to compensate for external contact forces.

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