

# Human stance control beyond steady state response and inverted pendulum simplification

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**Abstract** Systems theory analyses have suggested that human upright stance can be modelled in terms of continuous multi-sensory feedback control. So far, these analyses have considered mainly steady-state responses to periodic stimuli and relied on a simplifying model of the body's mechanics in the form of an inverted pendulum. Therefore, they may have ignored relevant aspects of the postural behaviour. To prove a more general validity of a stance control model that we previously derived from such analyses, we now presented subjects with static–dynamic stimulus combinations and assessed response transients, anterior–posterior (a–p) response asymmetries, and possible deviations from the ‘inverted pendulum’ simplification (by measuring hip and knee bending). We presented normal subjects (Ns) and vestibular loss patients (Ps) with a–p support surface tilt on a motion platform under the instruction to maintain, with eyes closed, the body upright in space. In addition, subjects were to indicate perceived platform tilt with the help of pointers. We combined a fixed-amplitude sinusoidal tilt (0.1 Hz) with static tilts that were varied in amplitude and direction. We recorded upper body (shoulder) and lower body (hip) excursions in space and centre of pressure (COP) shift, and calculated the centre of mass

(COM) angular excursion. We found that: (1) Immediately prior to stimulus onset (which was highly predictable), subjects showed a small anticipatory forward lean. (2) The subsequent transient response consisted of two parts. First, the body was moved along with the platform tilt and then, in the second part, the body excursion was braked by starting tilt compensation. Upon increasing tilt amplitude, the braking point showed a pronounced saturation with for-aft asymmetry. (3) During the following prolonged tilt, the tonic body excursions saturated with increasing *static* tilt amplitude. This saturation also showed a for-aft asymmetry (backwards saturation more pronounced). In contrast, the dynamic body excursions did not depend on the static tilt stimulus. (4) Tilt compensation occurred mainly in the ankle joints, but also involved small synergistic bendings in hips and knees in fixed register to the ankle rotation. (5) After the end of the stimulus, the body returned towards primary position, followed by a pronounced and slowly decaying tonic overshoot which was mainly related to tilt amplitude and initial tonic body excursion. (6) The responses of Ps qualitatively resembled those of Ns, apart from larger body excursions, less pronounced saturations, and less for-aft asymmetries. (7) Perceived platform tilt of Ns and Ps was correlated with their postural tilt compensations, but unlike the postural responses the perceptual responses overestimated actual static and dynamic tilt by a factor of 3–4. Our findings suggest two, so far undescribed and highly nonlinear mechanisms in human stance control. (a) The braking during the transient response appears to reflect a ‘sensory reweighting switch’ by which subjects change from a control that is referenced to the support to one that is referenced to space. (b) The saturation of the tonic body excursion also reflects a sensory reweighting mechanism; by this, subjects keep their balancing within a certain excursion limit. The two mechanisms were originally

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not predicted by our stance control model, but do not invalidate it, because they can simply be added to it. Also the observed for-aft asymmetries can be accounted for (by making thresholds in the two mechanisms asymmetric). In its extended form, the model mimics the previous and the new findings. We also conclude that the ‘inverted pendulum’ simplification is a legitimate simplification. We demonstrate the utility of the model by implementing it into a humanoid robot that then mimics closely the human experimental data. Finally, we present a hypothetical concept on sensory reweighting mechanisms in human stance control, which is meant to serve as a framework for future research.

**Keywords** Posture control · Multi-sensory interaction · Model · Loss of vestibular functions · Sensory reweighting switch · Tonic excursion limiter · Human subjects · Hardware-in-the-loop simulation

## Introduction

Human upright stance is inherently unstable because gravity continuously endangers body equilibrium. Its control involves afferent information from several sensory systems (vestibular, haptic, visual, joint angle and torque; e.g. Horak and Macpherson 1996). In recent years, considerable progress has been made in the understanding of this control by introducing modern analytical methods such as systems theory analyses into the behavioural experiments and their interpretation. This allowed the development of dynamic models which showed that human stance control can be explained by continuous sensory feedback (Peterka 2002; also Ishida et al. 1997; Johansson and Magnusson 1991; Mergner et al. 2003; Maurer et al. 2006a; van der Kooij et al. 1999, 2001). In some of the models, the sensor signals are contributing to feedback without inter-sensory processing (independent sensory channel models; Peterka 2002; also Ishida et al. 1997; Johansson and Magnusson 1991). Other models, in contrast, assume interactions between two or more sensory signals. The model of van der Kooij et al. (1999, 2001) fuses several sensory signals and involves an efference copy-like signal, thereby optimising sensory information with respect to noise. In a model of our laboratory (Mergner et al. 2003, 2005; Maurer et al. 2006a), we used sensory interactions involving thresholds (no efference copy). The model is particular in that the interactions generate estimates of the external disturbances acting on the body, which are then used as feedback signals instead of the sensory signals proper. This mechanism automatically reweights sensory signals upon changes in the experimental situations (with noise optimisation) and generates a nonlinear amplitude response behaviour similar to the one we observed experimentally.

However, a number of experimental findings are challenging these models and perhaps the modelling approach in general. A major challenge comes from findings that suggest that human stance behaviour is shaped by many different sensory reweightings that are so far not covered by the models.<sup>1</sup> To list a few examples: Peterka and Loughlin (2004) observed a gain increase of subjects’ stance control loop when they changed the subject’s body support surface from a body-sway-referenced to a stable and level state. Mahboobin et al. (2005) found an attenuation of visual postural responses when there was a preceding visual stimulus and when this consisted of a moving instead of a stationary scene (also Guerraz and Day 2005). Mergner et al. (2005) observed that visual responses to a virtual reality stimulus are weaker than those to a real world stimulus and attributed this to cognitive mechanisms. Blumle et al. (2006) presented subjects with support surface tilt in the frontal plane while they were viewing a visual scene motion in the sagittal plane and observed a degradation of the lateral tilt compensation when perception of the visual scene motion became conscious (surpassed conscious detection threshold). These examples may suffice to suggest that human stance behaviour is shaped by a variety of different sensory reweighting mechanisms that are not well understood to date. We therefore asked: *Do these sensory reweightings and their large variety invalidate the modelling approach? Or can we find basic features that are common to some of them, conceptualise these, and implement them into our model?*

These questions arose when we observed two so far unknown sensory reweighting mechanisms in an experiment by which we wanted to extend our previous findings (Mergner et al. 2003; Maurer et al. 2006a). In the new experiments, we combined static tilts with previously used dynamic tilts (again no visual orientation cues). Static tilts were investigated because, behaviourally, one may meet static inclinations of the support surface such as the slope of a hill. Since support tilts are generally under-compensated, one might expect that a steep slope might lead to relatively large lasting body excursions, which functionally would be disadvantageous (risk of falling, fatigue, adaptation, etc.). We, therefore, wanted to know how subjects deal with such static inclinations and how these affect the responses to superimposed dynamic tilts. In the new experiments, in addition to the steady state responses, we also assessed the

<sup>1</sup> The term sensory reweighting means here that the nervous system adjusts the relative or absolute contribution of sensory inputs to stance control depending on environmental conditions, subjects’ perception thereof, expectations, intentions, etc. Here, we distinguish reweighting mechanisms that occur automatically in the wake of the sensory processing in the core control (e.g. Carver et al. 2006; Cenciari and Peterka, 2006; Maurer et al. 2006a) from mechanisms that are not covered by this, in that they require additional assumptions such as an involvement of cognition.

transient responses upon stimulus onset, the changes of the response during the course of the stimulation, and the after-effects following stimulus end.

The following two new findings were obtained: (a) upon tilt onset, subjects first inclined their bodies along with the platform and started an in-space compensatory response only with considerable delay; this suggested to us that they first used mainly a support-referenced control and then ‘switched’ to a space-referenced control. (b) Subjects showed a pronounced saturation of their tonic body excursions when static tilt exceeded certain limits, suggesting that they were then ‘turning on’ a mechanism by which they kept their balancing within certain tonic excursion limits. These two responses were not predicted by our model, which we had based solely on steady state responses.<sup>2</sup> We therefore asked whether the new findings would invalidate our model or, alternatively, whether it can be maintained with appropriate modifications or extensions.

Furthermore, the experiments yielded two other challenging findings that were not covered by our model. They were related to the ‘inverted pendulum simplification’ and its single and symmetric degree of freedom (body rotating ‘en block’ symmetrically about ankle joints in sagittal plane). One finding was that the subjects’ responses showed a pronounced asymmetry of the tonic tilt responses. This asymmetry is likely related to the fact that the human body shows pronounced anisotropies, such as that the forefoot is larger than the heel, or that one can bend in the hips almost exclusively forward, and so forth. It is possibly related to the for-aft asymmetry of the centre of pressure (COP), the area covered during spontaneous body sway (e.g. Popovic et al. 2000). We asked whether and how it could be accounted for in the model.

The other additional finding concerned a hip contribution to the tilt responses, which is not mimicked by our model either, again due to its ‘inverted pendulum simplification’. The simplification proceeded from the observation that the body was, indeed, rotated essentially ‘en block’ with respect to the feet about the ankle joint in our previous studies where the external disturbances were small (Mergner et al. 2003; Maurer et al. 2006a) (A further argument was that the responses in these studies were similar to those obtained in a study of Peterka 2002, that used a backboard). Using now larger tilt stimuli, the hip contribution became larger. It is known since the work of Horak and Nashner (1986; see also Kuo et al. 1998) that a–p postural responses tend to occur mainly in the ankle joints as long as external

disturbances are small and the foot support is large and firm enough to allow subjects to exert appropriate compensatory ground reaction forces, while otherwise they add, or even perform predominantly stabilising hip thrusts (‘hip strategy’). We, therefore, asked in the present study whether the larger hip contribution to the tilt responses would make the ‘inverted pendulum simplification’ obsolete.

In addition to normal subjects, we also investigated patients with chronic loss of vestibular functions, hoping that this profound sensory deficit would allow us further insight into the stance control mechanism. Vestibular input is known to play an important role in posture control, as witnessed by the fact that these patients show abnormal postural responses to support surface tilt (e.g. Maurer et al. 2000, 2006a; Creath et al. 2002). In a previous study, we could mimic the postural responses of vestibular loss patients with our model after modifying it correspondingly (Maurer et al. 2006a). We now asked whether the patients, despite their sensory deficit, perform sensory reweightings comparable to, or distinct from those of normal and whether and how their reweightings can be covered by the model.

In order to reduce cognitive influences on stance control, we gave our subjects in the present study, in addition to the balancing task, a psychophysical task (they were to indicate with the help of pointers the perceived orientation of the platform in space). The psychophysics data also served to compare the sensory processing underlying conscious perception with that used for stance control. This allowed us to extend our findings of a previous study from this laboratory (Maurer et al. 2006b), which showed that subjects overestimate the support surface tilt in their perceptual response, unlike in their postural response.

To summarise the main aims of the study, we asked whether the new postural findings invalidate our systems analysis and modelling approach or whether they can be covered by it through appropriate modifications or extensions. Furthermore, we sought for common principles and a functional interpretation of the sensory reweighting mechanisms. To further challenge the modelling approach with its idealised and simplified representations of mechanics, sensors, and actuators, we added simulations using a biped robot where these items were hardware and only the sensory processing and controller parts of the model were implemented as software, and where the tests and analyses were the same as for the human subjects.

## Methods

### Subjects

Seven normal subjects (two women, five men; mean age 34.7 years; range 22–56 years) and five patients with

<sup>2</sup> A steady-state stimulus response is originally an electronic engineering term. It means the response of a system when this reaches, after an initial transient response, in the course of a lasting stimulus or upon stimulus repetitions, an equilibrium state. Thus, the steady state response per se does not necessarily describe the full behaviour of the system, especially if this is highly nonlinear as is often the case with biological systems.

chronic bilateral loss of vestibular functions (men: 39.1 years; 38–40 years) participated in the study. Vestibular loss was diagnosed by clinical examinations (e.g. balancing problems when standing, eyes closed, on foam rubber), electronystagmography (absence of caloric and rotation-evoked nystagmus) and case histories (meningitis and ototoxic medication in childhood). Apart from additional hearing problems, patients were healthy. The study has been approved by the local ethics committee and performed in accordance with the Declaration of Helsinki (revised by Edinburgh 2000). All subjects gave their informed consent prior to their inclusion in the study.

## Stimuli

Subjects stood upright, feet side by side, on a force-transducing platform (40 × 60 cm; Kistler® platform type 9286, Winterthur, Switzerland) that was mounted on a custom built and computer-controlled motion platform (diameter, 73 cm). The motion platform was rotated in the a–p plane (pitch) about an axis through the ankle joints. Two platform tilt stimuli were combined:

1. ‘Static tilt’ (mean platform position). Different values were applied (one position per trial):  $-4$ ,  $-3$ ,  $-2$ ,  $-1$ ,  $-0.5$ ,  $-0.001$ , and  $0.001^\circ$  (no noticeable tilts),  $0.5$ ,  $1$ ,  $2$ ,  $3$ , and  $4^\circ$  ( $0^\circ$ , baseline = level; positive sign: forward = toes down; negative sign: backward = toes up;  $-4$  and  $4^\circ$  omitted in patients).
2. ‘Dynamic tilts’. They consisted of sinusoidal rotations of  $\pm 2^\circ$  ( $\pm 1^\circ$  in patients) at  $f = 0.1$  Hz and were superimposed on one of the afore-described forward and backward static tilts.

Each trial lasted 100 s and consisted of the following 5 *time periods* (example in Fig. 1):

- a. *Baseline period* (4 s); the platform was level.
- b. *Onset period* (5 s); the platform was tilted forwards or backwards in random order, starting with a half sine-wave trajectory (0.1 Hz) such that the end point represented the starting point of the first dynamic stimulus (see c, below). As example, we show in the lower inset of Fig. 1, the beginning of the stimuli that contained the six forward static tilts (normals). Not shown are those containing the six static backward tilts; they were mirror symmetric. The tilt started in 10 out of 12 trials (patients, 8 out of 10 trials) with a 4 s delay after trial onset, in 2 trials with a 9 s delay. Initial tilt direction was randomly varied. A forward static tilt could begin with a forward ( $n = 3/6$ ) or a backward initial tilt ( $n = 3/6$ ) as shown in the inset. Pilot experiments had suggested that a bias on the tonic COM excursion appeared to be low when using

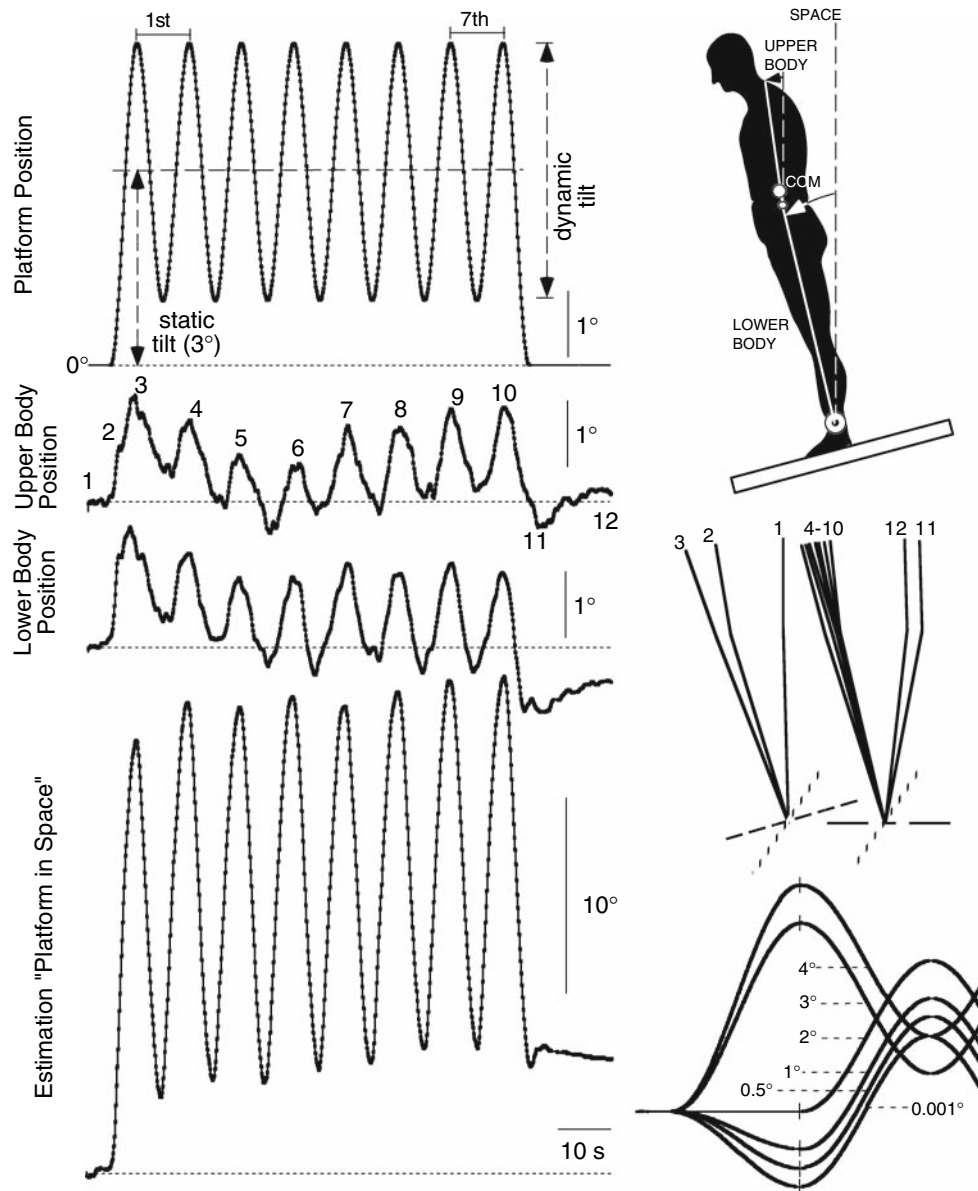
this variation. This set of stimuli together with one of stimuli in the opposite direction was used in all experiments.

- c. *Static–dynamic stimulus period* (70 s; 7 cycles, 0.1 Hz; starting points marked in lower inset of Fig. 1 by vertical bars: note that in this forward stimulus set, the steady state sinusoid starts with a negative swing with the  $3$  and  $4^\circ$  stimuli and a positive swing with the  $0.001$ – $2^\circ$  stimuli).
- d. *Offset period* (5 s); during this period, the platform was returned to primary position, again with a half sine-wave trajectory (0.1 Hz).
- e. *Post-stimulus period* (16 s) with the platform level.

Trial onset was verbally indicated to the subjects. This made stimulus onset predictable to the subjects, since it followed in 10/12 trials after 4 s (patients, 8/10 trials). The sequence of trials was randomly varied across the different static tilts, with the constraint that a session never started with the largest static tilt ( $3/4^\circ$ , patients/normals). We chose  $f = 0.1$  Hz for the dynamic tilt because previous work showed that vestibular loss patients are better able to maintain balance during slow as compared to fast platform tilts (Maurer et al. 2000, 2006a). Furthermore, the latter work suggested the limiting of the tilt amplitudes for the patients. Still, patients occasionally made a step to prevent falling during the trials (which were then repeated at later occasions), unlike the normal subjects.

## Instructions, psychophysical task, and procedures

Subjects were to stand comfortably on the platform, eyes closed, and to always keep their bodies upright in space. Their ears were plugged to minimise auditory orientation cues. In addition, they were instructed to continuously indicate their perception of platform-in-space position with the help of two pointers (concurrent indication task). One pointer was to be aligned with the space horizontal (i.e. parallel to the floor of the laboratory; ‘space pointer’), the other parallel with the platform (‘platform pointer’). The pointers were attached to a belt that subjects were wearing around their waists, one at each side. They consisted of light-weight aluminium tubes (diameter, 12 mm; length, 52 cm). Each hand was holding a pointer, with the forearms oriented parallel to the pointers and the elbow joints held near to the pointer rotation axes at the belt. Prior to the experiments, the subjects trained the indications. Each experimental trial was followed by a ‘visual recalibration’ (subjects moved the pointers under visual control; compare Mergner et al. 1991; Maurer et al. 2006b). During evaluation, the difference between the position readings of the two pointers was taken as their estimate of ‘platform-in-space’



**Fig. 1** Example of postural and perceptual responses in a normal subject during a 3° forward static platform tilt with superimposed dynamic tilts of ±2° (average of four trials). From top to bottom: traces show anterior–posterior (a–p) position of motion platform, upper body (shoulder), lower body (hip), and pointer indication of perceived platform tilt over time (note different scales of perceptual vs. postural traces). First and seventh sinusoidal cycle marked by horizontal bars. *Upper right inset*, definitions of angular position of upper body (black

arrow), lower body (white arrow) and COM in space (white circle). *Mid right inset*, stick figures of upper and lower body positions at the time during the trial indicated by numbers at top of the upper body position trace (angles are magnified by a factor of ten). *Lower right inset*, overview over the stimuli used in normals (first 20 s, beginning of the six static forward platform tilts used; backward tilts not shown; values in ° give static tilts). Note that on-direction in the family of stimuli was changing

position after a correction factor for operator performance was estimated in a visual tracking task (correction factor, 1.1; compare Mergner et al. 1991; Maurer et al. 2006b).

For each static platform tilt, four trials were performed per normal subject and two trials per patient. Between trials, brakes of 1–3 min were inserted during which subjects opened their eyes, reoriented themselves in space, and relaxed their posture.

### Recording

We recorded the centre of pressure (COP) a–p shift with the help of a force-transducing platform (Kistler®, type 9286; Winterthur, Switzerland). Furthermore, we measured 3-D translational and angular positions of hip, shoulder, and head using an optoelectronic device with three active markers per segment, fixed on a rigid triangle for each segment

(Optotrak<sup>®</sup> 3020; Waterloo, Canada; spatial resolution, 0.1 mm). Optotrak, Kistler, and pointer (potentiometer) output signals as well as the stimulus signals were sampled by an analogue–digital converter at 100 Hz and transferred on-line to a computer (IBM compatible Pentium<sup>®</sup>). The data were recorded with custom-made software programmed in LabView<sup>®</sup> (National Instruments, Austin, TX, USA).

#### Data analysis

Analysis was performed off-line with custom-made software programmed in MATLAB<sup>®</sup> (The MathWorks Inc., Natick, MA, USA). Four response curves were recorded and averaged across equal trial types for each normal subject. As already mentioned, in patients we obtained only two trials. The reason is that the patients were available only for two successive days, whereas normal subjects were available more often. The corresponding difference and a larger scatter in the data of the patients, conceivably, hampered the comparison of both the postural and the psychophysical responses (both were collected in same trials) between the two subject groups, so that we confined ourselves to make only a qualitative comparison. Also comparisons across patients' responses could be hampered; we therefore indicate statistical significance only where it was legitimate and meaningful. Angular excursions of the lower body in space and with respect to the ankle was calculated from the a–p angular and linear hip and ankle displacements, and those of the upper body in space and with respect to the hip from the shoulder and hip displacements. COM angular displacement was calculated from these signals according to anthropometric data of Winter (1990; note similarity to hip data, since the COM is located only some cm above the hip). The position data from the first 3.5 s of each trial (motion platform level) served as baseline.

#### Dynamic response (sinusoidal tilt)

The discrete Fourier transforms of the measured time series were calculated using Matlab function  $[(Y, f) = \text{dft}(X, Fs, Fpts)]$  ( $X$  = input time series;  $Fs$  = sampling frequency of time series, 100 points/s;  $Fpts$  = representing frequencies, beginning with the fundamental;  $Y$  = Fourier coefficients, complex numbers;  $f$  = frequency, Hz). In order to prevent distortions caused by the fluctuations of the DC-component (static response), the drift of the latter was eliminated before *dft* analysis of the dynamic (sinusoidal) responses. From Fourier coefficients of stimulus and response time series we calculated gain and phase values for each of the seven stimulus cycles, and coherence values across the seven cycles (compare Peterka 2002). *Gain* is defined as

amplitude ratio of response fundamental to stimulus fundamental (unity, body excursion equals platform tilt; zero, body stationary). *Phase* gives the temporal relationship between the fundamental waves ( $^{\circ}$ ; positive, lead; negative, lag). *Coherence* of 1 and 0 indicate perfect and no linear stimulus–response correlation, respectively, with noise and nonlinearities in the signals lowering the value from unity. In addition, we characterised the deviation of a response from the ideal sinusoid (in  $^{\circ}$ ), calling this 'variability'. This *variability* was calculated as one standard deviation (SD) of the residual position trajectory that remained after subtracting the Fourier fundamental from the original response (compare Creath et al. 2002). We did not use a normalisation to total power, since this would yield a measure in relation to the sinusoidal tilt and not to both, the dynamic and the static tilt (static signal not reasonably reflected in total power). And, we wanted to have it as an absolute measure (in  $^{\circ}$ ). The reason is that we assumed that this variability measure reflects mainly the noise of the control system and we wanted to compare it across different static tilt positions, for instance.

A *dft* analysis was also calculated for the *half cycles* of the sinusoid dynamic responses in order to evaluate for-*aft* asymmetries. After determining the phase in order to know the starting point of the response cycle, the response was split into two half cycles of equal length (we proceeded from the assumptions that the response to the stimulus sinusoid is a sinusoid of equal length as the stimulus with the same temporal proportion, i.e. with equal length of the two halves). For the *dft* analysis, each half cycle was duplicated and the duplicate was placed after its original. After sign reversal, the duplicate was appended by giving its starting point the same position value as the end point of the original half cycle.

#### Tonic response (static tilt)

Mean position across the dynamic response was calculated separately for each stimulus cycle.

#### Measures of hip and knee bending coordination

We obtained a measure of upper versus lower body coordination for each of the different postural responses (see below) by calculating correlation coefficients and slopes of linear regression for upper versus lower body angular excursion in space and for the inter-segmental excursion, i.e. for upper body (torso) on hip versus lower body (hip) on foot (platform). Furthermore, we obtained a measure of subjects' 'knee bending' behaviour during the trials. To this end, we correlated the recorded hip rotation with calculated hip rotation values, which we derived from the hip vertical and horizontal translation recordings. Unity correlation and

slope would indicate a rigid upper-on-lower leg coupling (no knee bending), while zero correlation and slope would theoretically indicate independent angular excursions of the two leg segments.

### Statistics and simulations

Unless stated otherwise, values in text and figures give mean values across subjects ('grand averages') and their SDs. Significance of findings (*P*-values) was tested with analysis of variance (ANOVA). *P*-values < 0.05 were taken as significant. Linear regressions were calculated using individual rather than mean values. Statistics was performed using the commercial software StatView® (SAS Institute Inc., Cary, NC, USA). Model simulations of a *dynamic computer model* were performed with MATLAB®/Simulink® (The MathWorks Inc., Natick, USA).

## Results

### Postural responses

Figure 1 shows an example of a normal subject's postural responses to the  $\pm 2^\circ$  dynamic tilt stimulus superimposed on a  $3^\circ$  static forward tilt. The body is entrained by the dynamic tilt, reaching about 25% of the platform excursion, with slight differences between upper and lower body angular excursions. The static response component of the lower body shows some decay over time towards baseline and, after stimulus end, it shows a clear overshoot (negative after-effect). These effects are not observed here in the upper body responses because they are superimposed by a slow forward, upper body lean. In the following, we characterise the postural responses mostly in terms of COM excursions in space, if not specified otherwise. After this, we describe our findings on the coordination of lower and upper body segments and finally give the psychophysical results.

For describing the postural data, we distinguished six different postural responses:

(1) *Anticipatory forward lean* (baseline period); (2) '*Initial response*' (stimulus onset period); (3) *Dynamic response* (static–dynamic stimulus period); (4) *Tonic response* (static–dynamic stimulus period); (5) '*Off response*' (offset period), and (6) '*After-effect*' (post-stimulus period).

### Anticipatory forward lean

During trial onset, subjects stood upright with closed eyes on the level platform (baseline period). After the verbal announcement of trial onset, they waited for the platform tilt. As mentioned before, the tilt occurred in most of the tri-

als (10/12) at 4 s after trial onset (9 s in 2/12 trials in normals; compare lower inset in Fig. 1; 8/10 and 2/10 trials in patients, respectively). In the averaged data, normal subjects and patients showed a small, anticipatory forward body lean. It slightly preceded the usual begin of the stimulus onset (after 4 s) and also was observed with this timing in those trials where stimulus onset actually occurred after 9 s. The anticipatory forward lean was independent of tilt direction and magnitude. Typical examples are given in Fig. 2 (oblique open arrows in panels a–d). The COM excursion averaged  $0.10 \pm 0.22^\circ$  (mean  $\pm$  SD) in normals and  $0.10 \pm 0.25^\circ$  in patients.

### Initial responses (first part of 'transient response')

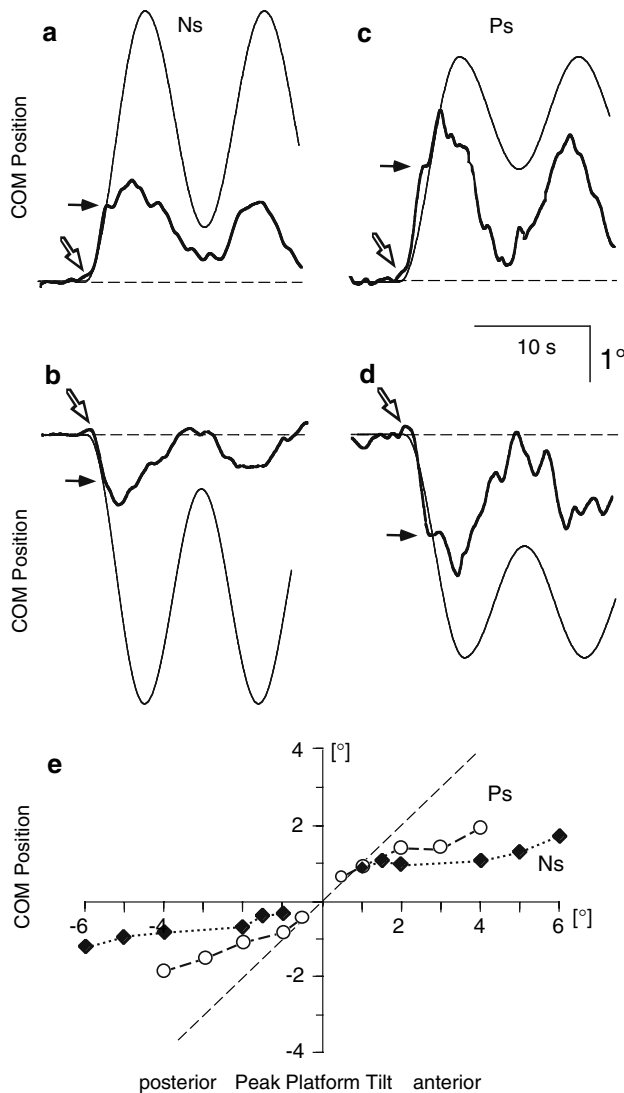
**Normal subjects** In the initial part of the tilt response, subject's COM rotated with the platform ('initial response'; examples in Fig. 2a, b). Thus, tilt compensation did not start immediately after tilt onset, although subjects expected the tilt occurrence. But they did not know tilt direction. In particular, the initial response started approximately 200 ms after tilt onset (value evaluated from COM and platform velocity traces, not shown). For the subsequent 1.40 s, COM position/velocity followed rather closely the platform position/velocity or tended to be even faster, until the body started to pass the platform. Then the body was 'braked' and tilt compensation started (marked by horizontal full arrows in Fig. 2a, b). The braking occurred when COM position reached approximately  $1^\circ$  during the forward tilts (range  $0.87$ – $1.75^\circ$  across all tilt amplitudes; Fig. 2e). The value was somewhat less with backward tilts ( $-0.27$  to  $-1.20^\circ$ ). The braking (zero velocity) occurred 2.3 s after tilt onset (mean value; range 1.80–2.95 s).

**Patients** They showed a qualitatively similar initial response with braking (Fig. 2c, d). However, COM motion was faster and its excursion larger than in normals, so that COM position/velocity was clearly exceeding platform position/velocity when the braking occurred (2.4 s after tilt onset, mean value; range 1.85–3.15 s). Similarly, like in normals, COM position at the 'braking' point depended on initial tilt amplitude (peak platform tilt) and showed a saturation, which was clearly less pronounced, however (Fig. 2e; range of saturations,  $0.58$ – $1.95^\circ$  for forward tilts and  $-0.38$  to  $-1.89^\circ$  for backward tilts).

After the braking, the tilt compensation response evolved into the first dynamic response (see below).

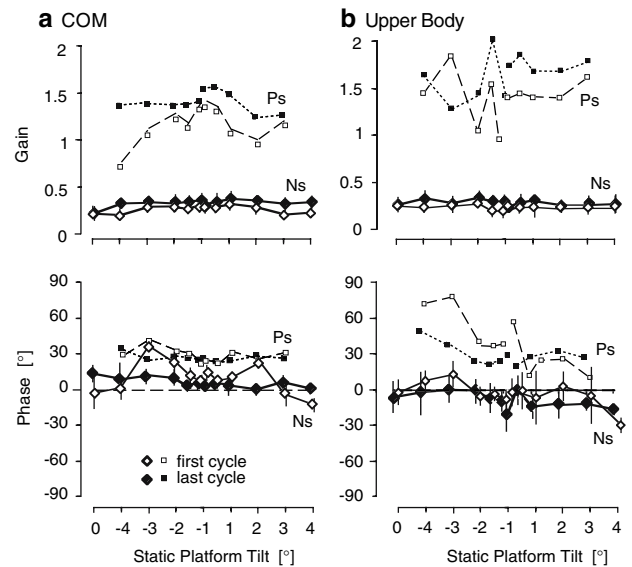
### Dynamic responses

**Normal subjects** The COM excursion that occurred in the time between the first and the second maximum or minimum



**Fig. 2** a–e Transient response with ‘braking’. a–d Position traces of COM (thick lines) and platform (thin lines) in space during the initial part of stimulus trials (averages across all normal subjects, Ns, a, b, and patients, Ps, c, d; static/dynamic platform tilt, 3/2° and 3/1°, respectively). Note small anticipatory forward lean (open arrows) and ‘braking’ of COM excursion (‘braking point’; solid arrows). e Position of COM ‘braking point’ as a function of initial tilt amplitude (peak platform tilt). Note that braking is earlier in normals (Ns; full symbols with dotted connection) than in patients (Ps; open symbols, dashed connections). Values are means across subjects. Oblique dashed line, line of identity

of platform tilt was defined as the first ‘dynamic response’ (and so forth, until the seventh, i.e. last response; see Fig. 1). Its time course resembled that of the dynamic tilt stimulus, albeit with clearly smaller amplitude. Gain and phase of the dynamic responses to the 0.1 Hz stimulus are plotted in Fig. 3a as a function of the static tilt amplitude, separately for the first and the last response. The gain curve is essentially independent of static platform tilt, be it forward or backward, and this was similar with the first and the last response. On average, gain amounted to  $0.36 \pm 0.19$



**Fig. 3** Dynamic responses (steady state). Gain (upper panels) and phase values (lower panels) of COM responses (a) and upper body responses (b) to the dynamic (sinusoidal) stimulus, plotted as a function of the superimposed static platform tilt. Data of normals (Ns, thick lines) and patients (Ps, thin lines), separately for the first (open symbols) and seventh (last) sinusoidal cycle (closed symbols). Mean values  $\pm 1$  SE across subjects. Variability in patients were several times larger than in normals and their SE bars are therefore omitted for clarity

(mean  $\pm$  SD). It increased slightly in the course of the dynamic stimulation (along with a slight decrease of the static COM excursion; see below), amounting to  $0.41 \pm 0.20$  with the seventh cycle. A separate analysis of the stimulus half-cycles revealed no statistical difference between the gain values for the forward and backward responses. The phase tended to show a slight lead, mainly with the 2 and  $-2^\circ$  static tilts in the first cycle. Coherence was high ( $\geq 0.95 \pm 0.04$ ) and variability was low ( $0.12 \pm 0.07^\circ$ ). The corresponding values for the COP: gain,  $0.77 \pm 0.37$  cm/°; phase,  $5.8 \pm 7.4^\circ$ ; coherence,  $0.96 \pm 0.02$ ; variability,  $0.32 \pm 0.16$  cm.

There were only minor differences between lower body and upper body responses, on average. Gain and phase curves of the upper body excursions with respect to the vertical are shown in Fig. 3b. Gain amounted to  $0.29 \pm 0.20$  (first cycle) and  $0.34 \pm 0.19$  (last cycle) and the phase showed a lag relative to the COM by about  $10^\circ$ . The corresponding values of the lower body were almost identical to those of the COM (panel a).

**Patients** Figure 3a also shows patients’ responses to the dynamic stimulus ( $\pm 1^\circ$ ) in terms of gain and phase plotted as a function of static tilt, superimposed on the curves of normals. The main finding is an abnormally high gain (first cycle,  $1.19 \pm 0.38$ ), which amounted to 3.3-fold of that in normals (2.6 when the difference in stimulus amplitude was

taken into account, based on previous data; Maurer et al. 2006a).<sup>3</sup> The effect of static tilt on the gain lacked statistical significance ( $P > 0.3$ ). Patients showed a larger phase lead than normals (average across all static tilts and cycles,  $29.4 \pm 18.7^\circ$ ). From the second to seventh cycle, gain increased to a value of  $1.38 \pm 0.37$  and phase remained essentially unchanged. Overall, the responses showed a high coherence ( $\geq 0.95 \pm 0.03$ ) and a low variability ( $0.12 \pm 0.06$ ; similar to normals). The separate analyses of the stimulus half-cycles showed no considerable difference between forward and backward responses.

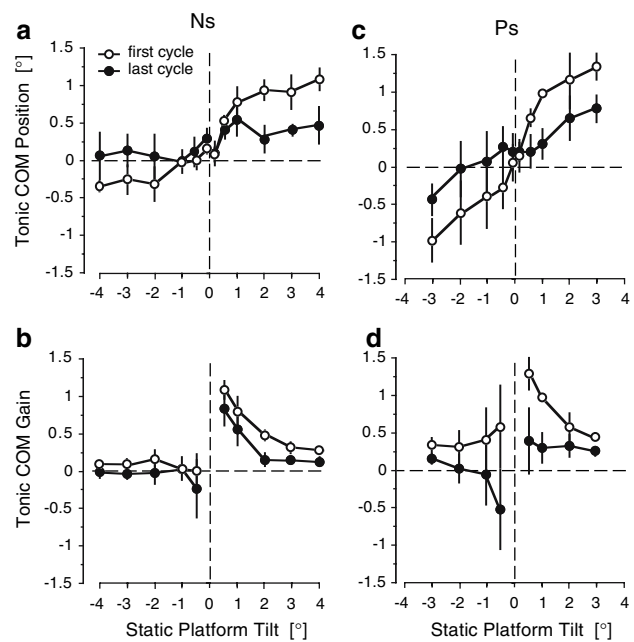
In patients, upper body excursions were larger than those of COM and lower body (Fig. 3b, gain averages as a function of tilt,  $1.48 \pm 0.69$  for first cycle and  $1.58 \pm 0.65$  for last cycle). However, inter-subject variability was high. The phase showed a lead that was slightly larger than in normals. Average values for COP: gain  $2.66 \pm 0.66 \text{ cm}/^\circ$ ; phase  $28.5 \pm 14.9^\circ$ ; coherence  $0.98 \pm 0.03$ ; variability  $0.67 \pm 0.41 \text{ cm}$ .

### Tonic response

**Normal subjects** The tonic response (mean COM position per cycle of dynamic response; see “Methods”) showed a pronounced saturation when the static forward tilt reached approximately  $1^\circ$ , on average, and when the backward tilt reached  $-0.5^\circ$  (Fig. 4a). The saturation became more pronounced with each stimulus cycle and was most pronounced with the last cycle (Fig. 4a; note that the relatively small backward response upon the first cycle is essentially cancelled with the last cycle). Figure 4b gives the data in terms of gain ( $G = 0$  meaning upright with respect to space,  $G = 1$  upright with respect to platform; values for  $0^\circ$  tilts omitted). Note that subjects tend to move somewhat with the platform during small forward static tilts, but strongly compensate the large forward tilts and even more so all backward static tilts (a behaviour which we call ‘forward tendency’ in the following).

In the separate analysis of upper and lower body, the responses were very similar to those of the COM, apart from one exception. Upon static backward tilt, subjects did not show a tonic backward lean of the upper body; they shifted it forward by a slight hip bending, instead (not shown). Retrospectively, they reported that they would prefer to fall forwards rather than backwards, because they could open the eyes and see possible obstacles and make better use of their arms to soften the fall, etc. Variability of the tonic response did not depend on static platform tilt.

<sup>3</sup> As judged from comparable data of patients in this previous study (Maurer et al. 2006a), an increase in stimulus amplitude from  $\pm 1$  to  $\pm 2^\circ$  leads to a reduction of gain by 18%, while phase is not considerably affected.



**Fig. 4** Tonic COM responses (steady state) are shown as a function of underlying static platform tilt for normals (*Ns*, **a**, **b**) and patients (*Ps*, **c**, **d**) in terms of mean position values across first (*open symbols*) and seventh (last) sinusoidal stimulus cycle (*closed symbols*). **a**, **c** COM angular position in space. **b**, **d** Gain values (tonic COM position/static platform position). Mean values  $\pm 1$  SE across subjects

**Patients** They showed clearly larger tonic COM excursions and a less pronounced saturation than normals (Fig. 4c). Like in normals, the excursions decreased from the first to the last cycle and then tended to be in forward direction with both forward and backward static tilts (‘forward tendency’; see gain curves in Fig. 4d). Patients’ upper body responses resembled the COM responses apart from an avoidance of tonic backward leans of the upper body, which was even more pronounced than in normals.

Figure 7 presents an overview of the combined tonic and dynamic responses in normals and patients by showing average COM position in space during the static–dynamic stimulus period. The saturation range during the first cycle of the tonic response (Fig. 7a, c) became slightly smaller in the course of time, which was associated with a slight increase of the dynamic responses (Fig. 7b, d). The dynamic responses were not affected by the amount or direction of the static tilt.

### Offset response and after-effect

The response to the return-to-level motion of the platform (‘offset response’) showed essentially the same gain as that of the preceding dynamic response (both in normals and patients, not shown). Thus, the offset response was not a

mirror image of the onset response, where gain was higher during the *first* part, i.e. unity or above. The offset response, together with the decay of the preceding tonic response, caused the COM to overshoot the baseline considerably upon stimulus end, before it slowly drifted backward towards baseline (similar to the lower body and unlike the upper body with its superimposed forward lean tendency; see Fig. 1). At the time 0 and 5 s after stimulus end, COM overshoot showed a statistically significant correlation with the amplitude of the static tilt both in normals ( $R: -0.77$  and  $-0.72$ , respectively;  $P < 0.0001$ ,  $N = 84$ ) and in patients ( $R: -0.85$  and  $-0.65$ ;  $P < 0.0001$ ,  $N = 50$ ). Furthermore, in normals it correlated with the first tonic response and with the decline from first to last tonic response ('adaptation'), both at times of 0 s after stimulus end ( $R = -0.67$  and  $0.52$ ,  $P < 0.0001$ ) and at 5 s ( $-0.63$  and  $0.42$ ,  $P < 0.0001$ ). Note that 'adaptation' brought COM position prior to stimulus end back close to its starting position, this essentially being independent of the amplitude of the static tilt. As a result, overshoot did not correlate with the last tonic response (at 0 s:  $R = -0.03$ ,  $P = 0.75$ ; at 5 s:  $R = -0.07$ ,  $P = 0.53$ ). In patients, correlations were clearly worse and statistically not significant.

#### Inter-segmental coordination

Differences between the upper body and lower body position curves clearly suggested that subjects' responses deviated from those of an 'inverted pendulum' (example in Fig. 1; see also the 'stick man' insets which give peak excursion values). In order to quantify this behaviour and to characterise the inter-segmental coordination, we calculated correlation coefficients and slopes of regression lines between upper versus lower body angular positions in space and between upper body(torso)-on-hip versus lower body(hip)-on-platform position values. This was done separately for the different stimulus periods defined above. Upper and lower body movements were in an almost fixed synergistic register with each other during the steady state (dynamic–static stimulus period), but dissociations between them were observed during the response transients (e.g. stimulus onset period). Static tilt amplitude had little influence on this behaviour. We therefore pooled the data across static tilts.

The results of *normals* are given in Fig. 5a. *Baseline period* (abscissa, 'base'): correlation for forward and backward sway is equally poor (during relatively small spontaneous upper and lower body sways). *Onset period, first part* (first 2 s; 'on1'): The correlation during the initial response increases almost to unity and the slope reaches approximately 0.6 with forward static tilt (0.2 with backward tilt), which means that the lower body excursion exceeds the upper body excursion. *Onset period, second*

*part* (last 2 s; 'on2'): lower body is slowed down, upper body less so, which leads to a slope of 1.66 ( $-1.09$  with backward static tilt). *Static–dynamic period*: correlation remains essentially constant at a high level (0.91, on average), as does the slope (0.65; lower body excursions  $>$  upper body). *Offset and post-stimulus periods*: correlations remain high and slopes increase towards unity (upper and lower body excursion become similar).

The torso-on-hip (hip angle) and hip-on-platform (ankle angle) correlations (not shown) confirmed the dissociation between upper and lower body in the onset period and the strong synergistic linkage in the static–dynamic stimulus period with respect to coefficient and slope. Torso-on-hip excursions amounted to approximately 24% of the hip-on-platform excursion.

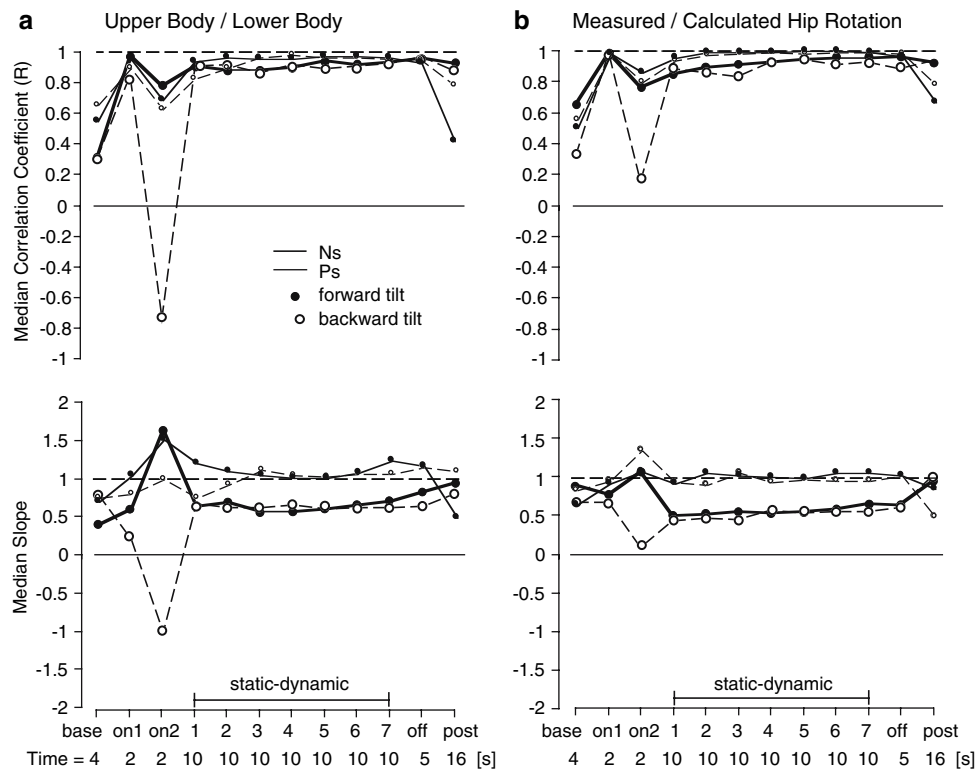
The data of the *patients* indicated that they stiffened their bodies during both the transient and the steady state responses more than normals. In the stimulus onset period, the correlation between upper and lower body excursions in space showed less dissociation than that in normals, and over the static–dynamic period, it showed a higher correlation (0.97) and a slope of approximately unity (1.05; Fig. 5a). These findings were associated with low slope values in the torso-on-hip versus hip-on-platform correlations.

Furthermore, we assessed to what extent subjects showed a 'knee bending' behaviour during the trials (Fig. 5b). We correlated recorded hip rotations with calculated hip rotations derived from the hip vertical and horizontal translation recordings (see "Methods"). During the steady state response (static–dynamic stimulus period), the correlation coefficient in normals was close to unity (Fig. 5b). The slope was approximately 0.6, meaning that upper leg excursion was less than lower leg excursion. The correlation was clearly less than unity during baseline and stimulus onset. In patients, the correlation was again higher than in normals during both stimulus onset and the static–dynamic stimulus period.

In summary, normals' responses involved some flexion at the hips and the knees. The segment movements occurred in a synergistic and coordinated way such that the upper body segments showed less excursion in space (were brought closer to the vertical) than the lower segments. This applies mainly to the steady state responses, while exceptions were noted with the transient response after the braking. Patients tend to stiffen their bodies more than normals.

#### Perception

For the indication of perceived support tilt, normal subjects adopted a simple strategy by keeping the 'space pointer' essentially in fixed alignment with their subjectively upright bodies and aligning the 'platform pointer' with



**Fig. 5** Inter-segmental coupling. Correlation coefficient ( $R$ ; upper panel) and slope values (lower panel) of linear regressions across the time series of **a** lower body positions ( $x$ -values) and upper body positions ( $y$ -values), and **b** hip rotation calculated from the markers' horizontal and vertical translations (lower body-in-space linear excursions;  $x$ -values) and measured hip rotation ( $y$ -values). Note that a rigid-body rotation would yield  $R = 1$  and slope = 1, which would mean absence of hip bending in **a** and absence of knee bending in **b**. Thick lines, normals, Ns; thin lines, patients, Ps. Open symbols, backward tilt; closed symbols, forward tilt. Median values across the 12 static platform tilts used. Abscissas give trial periods (base, baseline; on1 and on2, onset; 1–7, static–dynamic stimulus; off, offset; post, post-stimulus). The negative peak in dashed thick curves (panel **a**) corresponds to forward body excursion during backward tilt of normal subjects (while otherwise body excursion was in the direction of the tilt)

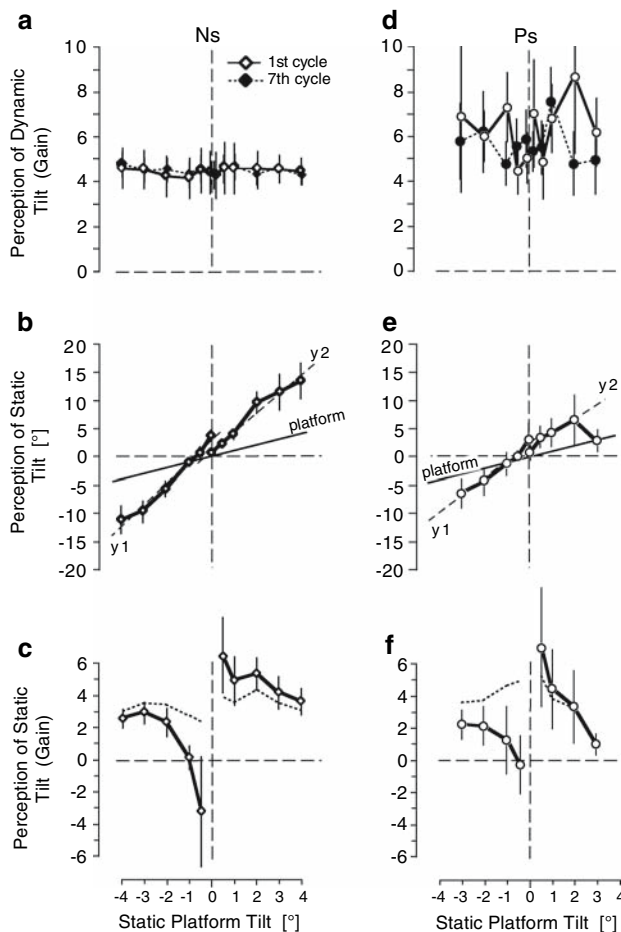
perceived platform orientation. Patients had more difficulties to do so and stopped the indications in some trials (these data were omitted). Both, normals and patients grossly overestimated the platform tilts (example in Fig. 1), in keeping with previous findings that were based on transient tilt stimuli (Maurer et al. 2006b). As detailed in “Methods”, the corrected difference of the pointer readings will be presented. In the following, we distinguish again between dynamic and tonic responses.

### Normals

Normals overestimated the dynamic tilt by a factor of approximately 4 throughout the static–dynamic stimulus period, independent of amount and direction of the superimposed static tilt (see ‘dynamic gain’ for first and last cycle responses in Fig. 6a). But inter-individual variation of gain was large, indicating strong idiosyncrasies (range 2.52–9.07). The phase was essentially ideal and similar across subjects (mean values across all static tilts: first cycle  $-2.6^\circ$ ; last cycle  $1.5^\circ$ ). Coherence values were

always high ( $>0.96$ ). The ‘variability’ measure (see “Methods”) was already low at the beginning ( $0.81 \pm 0.34^\circ$ , first cycle; mean value across all static tilts) and continuously improved ( $0.23 \pm 0.11^\circ$ , last cycle). Essentially the same results were obtained in the separate analysis of the forward versus backward half cycles. Furthermore, there were no considerable correlations of these perceptual responses with the corresponding dynamic or static postural responses in terms of head, shoulder, hip, and COM excursions in space as well as COP shifts (always  $-0.3 \leq R \leq 0.3$ ; not significant). In contrast, when we related subjects' perceptual responses to their compensatory postural response in terms of COM rotation with respect to the platform, correlation was high ( $R = -0.95$  to  $-1$ ).

Perceived static platform tilt was similarly overestimated (Fig. 6b; regression line  $y_2$ , forward tilt,  $y = 3.39x + 1.04$ ,  $R = 0.70$ ;  $y_1$ , backward tilt,  $y = 3.82x + 2.89$ ,  $R = 0.83$ ). (Note that each of the two stimulus families with forward and backward static tilts included a zero stimulus, each with a different dynamic on-direction, which led us to



**Fig. 6** Perception of platform-in-space position (calculated from pointer indications; **a–c**, Ns; **d–f**, Ps). **a, d** Gain of dynamic response to sinusoidal stimulus. **b, e** Tonic response to static tilt. Gain values thereof (**c, f**; *solid curves*, actual gain; *dotted curves*, corrected for ‘forward tendency’). *Dashed oblique lines* in **b, e** represent regression lines, separately for backward (‘y1’) and forward (‘y2’) static platform tilts (in Ps, values at 3° forward tilt not included). Mean values  $\pm$  1 SE across subjects

assume two separate response families). There was a forward bias (towards positive y-values), especially with the backward tilts. This ‘forward tendency’ is reflected in the corresponding gain curves (Fig. 6c). When we corrected for it (by accounting for the y-axis intercept in Fig. 6b), the gain curves for forward and backward tilts became similar (dotted curves). After end of the stimulus, subjects tended to maintain a forward indication, which was essentially independent of static tilt magnitude ( $P > 0.05$ ). It amounted to  $5.28 \pm 4.07^\circ$ , on average, and was neither correlated with the just described forward tendency on a single trial level nor with the postural responses.

### Patients

Patients, having considerable difficulties with balancing in most of the trials, showed rather gross variations in their

indications. Retrospectively, they reported major difficulties to operate both pointers at the same time, when they felt their bodies deviate from upright and tried to indicate this with the ‘space pointer’, while trying to align the ‘platform pointer’ with the platform (compare “Methods”). Yet, sufficient data was obtained to state that patients overestimated the dynamic platform tilts (Fig. 6d) and the static tilts (Fig. 6e, f) similar to normals.

### Discussion

Engineering systems analysis approaches to human stance control allowed several research groups to formalise this control in the form of multi-sensory continuous feedback models (see “Introduction”). We asked to what extent do given sensory reweighting phenomena challenge the validity of the modelling approach. Reweightings may occur in the large variety of postural situations and may represent nonlinear mechanisms. Do we need different kinds of models or is it sufficient to modify and/or extend the existing models?

Some sensory reweightings occur already, in the stance control model of our previous study (Maurer et al. 2006a). They arise ‘automatically’ from inter-sensory interactions and central thresholds and allow the control to cope with different stimulus magnitudes and situations. However, our model did not predict the two new findings of sensory reweighting (to be described below) that we observed in the present study when we extended our repertoire of external stimuli (by superimposing static on dynamic tilts) and included response transients into the analysis (nor would the models of others predict these phenomena, to our knowledge). In the following sections, we first describe our model in an abbreviated form and explain its failure in predicting the two phenomena (“Original model and the novel reweighting phenomena”). Then, we show that simple extensions of the model suffice to cover the new findings (“Model extensions”) and we consider functional aspects (“Functional aspects”). Finally, we discuss briefly the patients’ postural and perceptual responses (“Patients”), the observed hip responses in relation to the ‘inverted pendulum’ simplification (“Inverted pendulum simplification”), and the psychophysical findings (“Psychophysics”).

### Original model and the novel reweighting phenomena

Our model of human stance control in the sagittal plane is shown in simplified form in Fig. 8a (for details, cf. Maurer et al. 2006a). It shows four major components: the ‘Controller’, the plant (‘Physics/ Biomechanics’), the ‘Sensors’, and the inter-sensory interaction part (‘Sensor Fusions and Disturbance Estimations’). For simplicity, the actuator part

is not shown. It is assumed to have essentially perfect performance with the small excursions and torques considered here. In the ‘Controller’, an error  $e$  is derived from the difference between ‘Desired position of body in space’, the voluntary set point signal, and the estimated position as signalled by continuous feedback. The error is transformed by a PID controller (factors for proportional, integrative, derivative signals) into a command signal for the ankle torque (delay times not shown). The box ‘Physics/ Biomechanics’ contains the ‘inverted pendulum’ that comprises two rigid segments, the body B and the foot F, interconnected by the ankle joint (mechanics model and passive joint properties not shown). Two external disturbances are depicted: Gravity  $g$  exerts a ‘gravitational torque’  $T_g$  in the joint and a platform tilt leads to a foot–space rotation  $FS$ . In the box ‘Sensors’, the vestibular system (VEST) yields body–space angle and angular velocity signals, the ankle proprioceptive sensor (PROP) body–foot angle and angular velocity signals, and a ‘COP’ sensor calculates from foot pressure receptors an indirect measure of the ankle torque (for details, see Maurer et al. 2006a). *As mentioned in “Introduction”, the model is particular in that the sensor signals are not fed back directly (in terms of postural reflexes), but are processed by way of inter-sensory interactions with thresholds. Furthermore, it is particular in that the interactions yield estimates of the external disturbances, and in that these estimates are fed back for disturbance compensation (as we explain in the next paragraph).*

The sensory processing occurs in the box ‘Sensor Fusions and Disturbance Estimations’. As mentioned, the two external disturbances that are relevant in the present study are the ankle torque due to gravity  $T_g$  and support tilt leading to the foot–space angle  $FS$ . The corresponding disturbance estimates are generated in the two boxes  $\hat{g}$  and  $\hat{FS}$ . A third estimate, called ‘Estimate of External Force’, is included, but in normal subjects it is not active in the context of the present experiments, since no external push or pull stimulus was applied (it is active in patients, though, where it is used in a somewhat different way; see below). The estimates are fed into a proprioceptive ‘Body–Foot Loop’ for negative feedback. The estimate  $\hat{g}$  is derived from a vestibular body–space angular position signal (it is passed through a position threshold and transformed from head into trunk coordinates and into a measure of the COM’s gravitational torque). Its function is to compensate for the COM’s gravitational ankle torque during body lean (note that it tends to maintain the lean against gravity, but does not try to restore upright body orientation in space). The estimate  $\hat{FS}$  is derived from a vestibular-proprioceptive interaction (body–space signal combined with body–foot signal yielding foot–space signal). Since previous evidence indicated that it is shaped by a velocity threshold, we derived it from vestibular and proprioceptive velocity

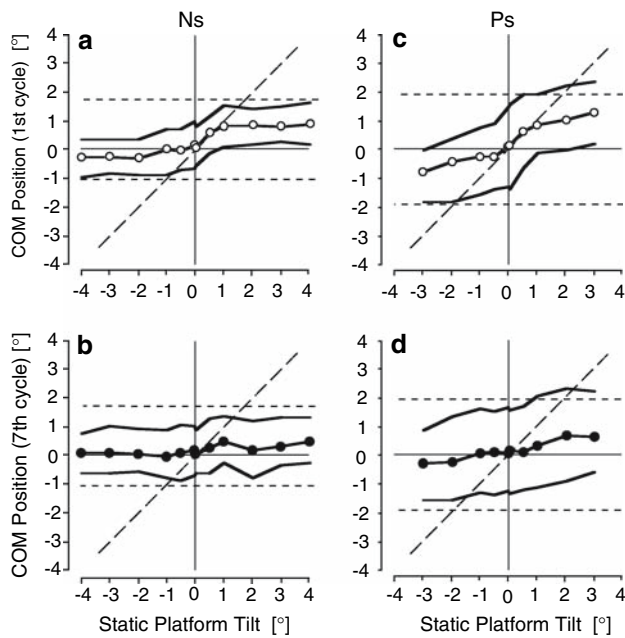
signals, before integrating it (in the mathematical sense) to yield  $\hat{FS}$  (processing not shown).  $\hat{FS}$  compensates for the body–space lean that results from foot–space angular displacement.

In the just described form, the model yielded software simulations that mimicked well the steady state responses of humans to the dynamic tilt (and pull) stimuli used in our previous study (Maurer et al. 2006a). Furthermore, the model was successfully ‘embodied’ into a biped humanoid robot, ‘PostuRob’ (Mergner et al. 2006; Tahboub and Mergner 2007). In the robot, the highly simplified representations of the sensors, actuators, and ‘inverted pendulum’ mechanics of the software model were replaced by hardware, while the controller and the sensory processing remained as software and were run on a real time PC (see “Appendix”). Thus, the robot allowed us to perform ‘hardware-in-the-loop’ simulations using the same laboratory, motion platform, stimuli, data acquisition and analyses, etc. as for the subjects. They yielded similar results as the steady state responses of our subjects and of the software model, despite the robot’s non-idealized mechanics, sensors and actuators (the latter showing ‘realistic’ noise, offsets, drifts, etc.). Both types of simulation will be considered in the next paragraphs.

However, when we simulated the stimuli of the present study with the model and the robot, and included the transient response in the analysis, we obtained two major differences between predicted and experimentally observed responses: (1) *Transient response*: The model predicted an essentially immediate *compensation of the platform tilt* after stimulus onset (by the  $\hat{FS}$  signal; its velocity threshold, being small, produced only very little delay). Thus, it failed to account for the experimental finding that the body initially would move with the tilting support and that tilt compensation would start only after considerable delay (braking of body excursion). Accordingly, it also did not describe the saturation of the braking point as a function of tilt amplitude (position) and its clear for-aft asymmetry. (2) *Effect of static tilt*: The model predicted that tonic COM excursion upon static tilt would be counteracted by a shift back towards primary position, due to the integrative component of the PID controller. This would occur with a strength essentially proportional to the COM excursion amplitude (the position threshold of  $\hat{g}$ , being small, had only a minor effect). Thus, the model failed to mimic the finding that the tonic COM excursion increased with increasing (but rather small) tilt amplitudes, until it saturated (see Figs. 4 and 7).

#### Model extensions

Our interpretation of the first finding (1, see previous paragraph) is that subjects initially adhered to a body-on-support



**Fig. 7** **a–d** Superimposed tonic and dynamic COM excursion limits plotted over static tilt amplitude (*interconnected circles* and *envelopes*, respectively). Dynamic limits were calculated separately for forward and backward stimulus half cycles. **a, b** Normals, *Ns*. **c, d** Patients, *Ps*. **a, c** First sinusoidal stimulus cycle. **b, d** Seventh (last) cycle. *Dashed horizontal lines* show, for comparison, maximal COM ‘braking positions’ of the initial responses (compare Fig. 2e). *Dashed oblique lines*, static platform positions

stabilisation, not using the  $\wedge FS$  signal yet to stabilise body-in-space. Thus, during tilt onset, they used the local proprioceptive loop to stabilise their bodies with respect to the tilted platform and the  $\wedge g$  feedback to prevent the COM from being further accelerated by gravity during the body lean. The D in the PDI controller helped them to deal with the COM’s *eigen*-inertia. Noticeably, only after the onset of the tilt did they know its direction and amplitude (while its timing was predictable in 10 of 12 trials). This might be the reason why the body-in-space stabilisation by the  $\wedge FS$  feedback would start only after some internal mechanism ‘switched’ it on. This occurred when COM angular position in space reached approximately  $\geq 1.0^\circ$  and  $\leq -0.8^\circ$ . No more braking was observed during the following stimulus periods (we therefore assumed that the switch remained closed for these periods).

In the model (Fig. 8a), we placed the switch prior to the  $\wedge FS$  processing. For its control we used a foot–space position signal  $fs$ , which was obtained from the difference of vestibular body–space,  $bs$ , and proprioceptive body–foot position signals,  $bf$  ( $fs = bs - bf$ ) and then passed it through a position threshold ( $-0.86$  to  $1.09^\circ$ ). To account for the finding that, once closed, the switch remained on during the whole stimulation period, the absolute value of this signal drives a memory (i.e. it is fed into an integrator, which is

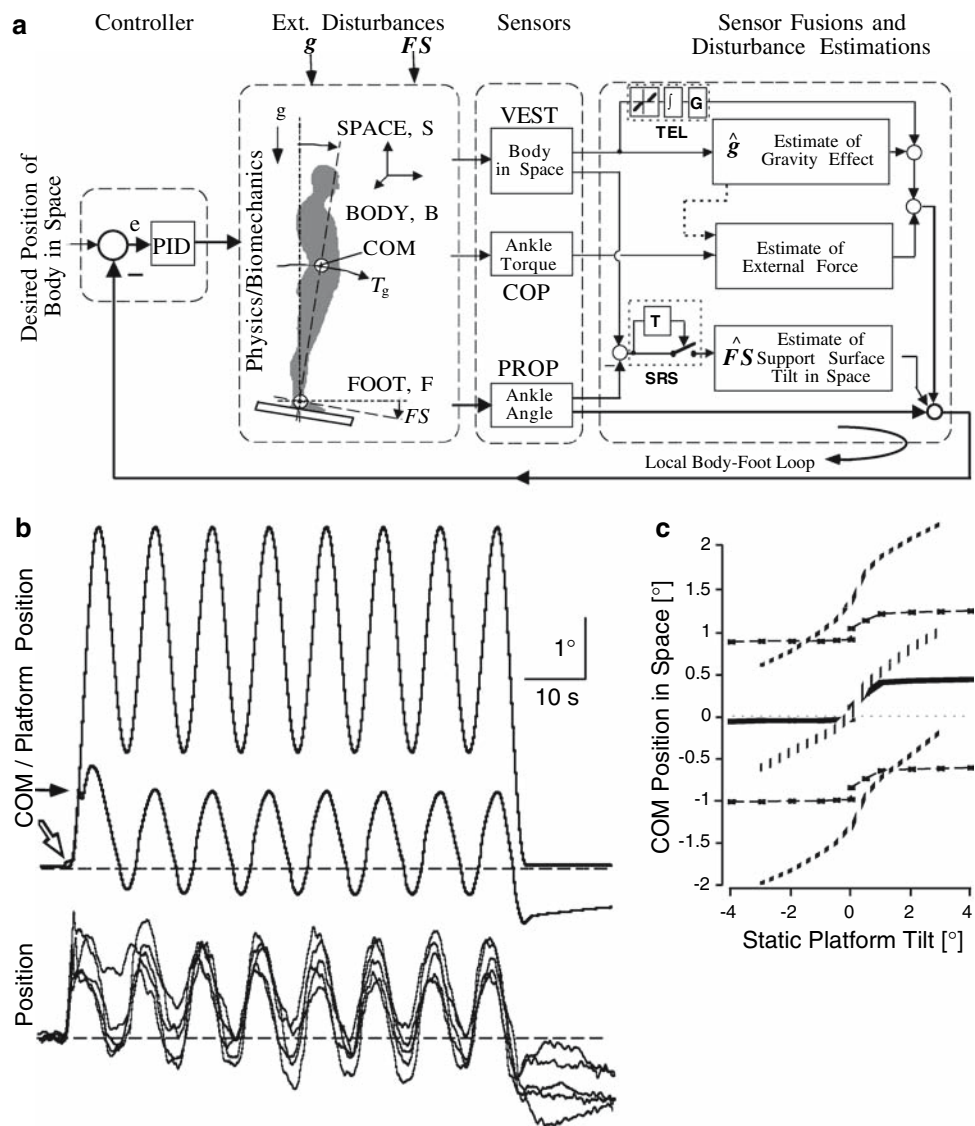
leaky, however, to allow a very slow decaying over time), the output of which actuates the switch. The switch gates a  $fs$  velocity signal ( $f's$ ) which, therefore, reaches the  $\wedge FS$  processing stage only after the switch has been closed (a distinction between velocity and position signals is not made in the wiring of the model in Fig. 8a, for simplicity). In other words, the switch represents a simple ‘circuit connector’. We assume that the switch can also be activated from cognitive sources (e.g. when direction of the tilt is predictable). We called the mechanism ‘sensory reweighting switch’ (box ‘SRS’ in Fig. 8a).

Our interpretation of the second finding (2) is that subjects allowed for lasting tonic body excursions as long as these were small. However, when the excursion exceeded  $1.7^\circ$  (with forward static tilt) and  $-1.0^\circ$  (with backward tilt), a compensatory feedback mechanism became active that counteracted and slowly reduced any excess of these limits. Also this finding could be accounted for by an addition to the model, which we called ‘tonic excursion limiter’ (‘TEL’ in Fig. 8a). Parallel to the  $\wedge g$  mechanism, a vestibular body–space position signal is fed back, after it passed through a threshold ( $-0.92$  to  $1.26^\circ$ ), a leaky integrator ( $T = 55$  s), and a gain factor ( $G = 0.6$ ). In exchange, the I component of the PID controller was strongly reduced as compared to the original model.

In this extended form, the software model and the robot predicted the old *and* the new findings. Simulation results are given in Fig. 8b (top, software model; filled arrow indicates braking point; curves below, robot). Figure 8c gives the software simulation of the tonic response as a function of the static platform tilt, together with the maxima and minima of the dynamic responses (thinner dashed lines). Note that the tonic response shows a pronounced and asymmetric saturation which is caused by the asymmetric thresholds used in TEL, whereas the dynamic response is not affected to a considerable degree. These model results reflect the qualitative characteristics of the experimental data fairly well. Note furthermore that the for-aft asymmetry resulted from the asymmetry of the thresholds used in TEL.

The way in which we implemented the two mechanisms allowed us to maintain the structure of the original model essentially unchanged. Interestingly, the two mechanisms appear to be related to each other in several ways. First, the asymmetric thresholds of both resemble each other. Second, the input signals they process resemble each other as long as the  $\wedge FS$  compensation is switched off (in that case, the vestibular  $bs$  signal, used for TEL, is similar to the  $fs$  signal, used for SRS, as long as the body–foot angle does not change considerably, i.e.  $bs \approx fs + bf$  for  $bf \approx 0^\circ$ ). Whether these similarities point to an alternative way of implementing, and perhaps merging the two mechanisms, is still open. We could conceive, however, that there may still exist other ways of implementing

**Fig. 8 a–c** Model and simulations. **a** Model containing the new additions, a tonic excursion limiter (TEL) and a sensory reweighting switch with threshold,  $T(SRS)$ .  $g$ ,  $\hat{g}$ , gravity and the postural system’s estimate of its effect on ankle torque (not identical with perceptual estimate).  $FS$ ,  $\hat{FS}$ , foot-in-space rotation stimulus and its internal estimate. **b** Simulation results. Shown are five time series of COM position from the software simulation (traces below platform traces; they are equal and thus aligned on top of each other) and the hardware-in-the-loop (HIL) simulation (‘PostuRob’; lower traces). **c** Superimposed tonic and dynamic COM excursion limits over static tilt from the software simulations for normals (solid and dashed curves) and patients (dotted curves). Compare Fig. 7



them, but currently we refrained from searching for such alternatives as long as the corresponding experimental data are still limited.

In summary, the model and robot simulations mimicked the subjects’ initial responses, steady state (dynamic and tonic) responses and the aftereffects. Furthermore, they could even be made to mimic the anticipatory response which consisted of a small forward body lean (by adding an appropriately timed ‘voluntary’ signal to the ‘Desired Position of Body in Space’ set point signal; see model in Fig. 8a and open arrow in Fig. 8b). We have also observed a similar anticipatory in other experiments (e.g. Achilles tendon vibration; to be published), and we consider it a preparatory action that brings the COM’s gravitational force vector slightly forward, from a resting position at about the heel pad towards the forefoot, i.e. towards a more optimal position in the working range for balancing.

### Functional aspects

As mentioned in “Introduction”, several different sensory reweighting phenomena can be observed in human postural behaviour. It appears essentially impossible to subsume all of them under a single common function. The two new ones reported here make no exception. Yet, a common denominator appears to be that they all appear to represent optimisations that are either added to a core of the stance control system or are producing changes in or around it. For example, with regard to our ‘sensory reweighting switch’ we assume that it allows subjects to use predominantly ankle proprioception for stance control when the support surface is firm and level for some time. Using mainly proprioceptive rather than vestibular input conceivably has the advantage of avoiding contributions from the relatively large low-frequency noise in the vestibular signal (see

Mergner 2007). However, from a certain magnitude of support tilt on and with the necessity to stabilise the body *in space*, contribution from vestibular cues is required more and more; its low-frequency noise then causes some uncertainty in balancing when vision is excluded.

With respect to this reweighting we dare *some generalization*. We like to speculate that the majority of sensory reweighting phenomena deal directly or indirectly with substitutions for the noisy vestibular signal. In our view, the vestibular-derived absolute space reference is substituted by an external reference in the environment (visual, haptic, support surface), given that this reference is experienced or known as being better suited, i.e. space-stationary, firm, level, more accurate, etc. Expressed as a general rule: sensory reweightings direct us to use the currently most reliable reference for a given postural task. They do so in two alternative ways. One group of mechanisms is part of the core control system (model in Fig. 8a without the extensions) and provides low-level, automatic, and essentially graded sensory reweightings. An example is the processing stage  $\wedge FS$  (which already produces a shift of the sensory weight from proprioception to vestibular input; see details in Maurer et al. 2006a). The other type of mechanism, represented here by the ‘sensory reweighting switch’, would involve higher-level inputs including cognition. Generally, building the control on internal representations of the external disturbances (or, phrased differently, on the internal reconstructions of the relevant external events) provides the basis for interfacing the two levels.

A similar two-step (two-level) interaction with sensory reweighting has been described by us for human self-motion perception during visual–vestibular interaction (see Mergner 2002). One still has to wait, however, for evidence whether same or similar principles apply to the contribution of vision to stance control (see “Introduction”), or likewise of a haptic reference (e.g. through finger tip touch; Jeka and Lackner 1994). Also, the rules are still open by which cognition exerts its influence on stance control (e.g. knowing that the support surface is made of solid concrete, expectations, predictions, etc.).

The functional significance of the *tonic excursion limiter* appears to be a different one. It appears to be related mainly to the finite dimensions of the foot as the base of support, i.e. to a constraint in the biomechanical rather than the sensory signal domain. Limiting the tonic body excursions, during standing on the slope of a hill for instance, probably also prevents fatigue, adaptation to an extreme end of the balancing working range, and damage to soft and hard tissues due to lasting extreme forces that would be required to prevent falling. The tonic excursion provides the basis about which the dynamic balancing occurs (here the responses to the 0.1 Hz dynamic tilts we used) and, therefore, it should remain far within the absolute stability

limits. Conceivably, COM velocity also represents a factor that is to be controlled (Pai and Patton 1997). In our experiments, however, it was COM position which did not exceed certain limits, while COM velocity appeared not to be a critical factor. We cannot exclude, however, that our subjects were not challenged in this respect or that they shaped their postural behaviour *a priori* to avoid large COM velocities.

We like to point out that the tonic excursion limiter, TEL, differs from the sensory reweighting switch, SRS, in that it transmits only to the extent that its thresholds have been crossed (compare Fig. 8a). Also, the rules of these thresholds are much less sophisticated than those in SRS. It may be a matter of taste, therefore, whether TEL should be considered an outside addition to the ‘core system’ or a part of it.

Interestingly, the saturation range of  $2.95^\circ$  ( $-1.2$  to  $+1.75^\circ$ ) of the tonic response is similar to the ‘high preference zone’ which Popovic et al. (2000) described for quiet stance [a zone of 4.0 cm in diameter of spontaneous COP shifts which, if transformed into COM excursion (factor,  $1.7 \text{ cm}^\circ$ ), yields  $4 \text{ cm}/1.7 \text{ cm}^\circ = 2.35^\circ$ ]. Furthermore, this range is well within the maximum range of  $5.9 \pm 1.1^\circ$  for stable balancing given by Robinovitch et al. (2002). The for-aft asymmetry of this range and the fact that the asymmetry also affects the aftereffects following stimulus end led us to simulate experiments by Kluzik et al. (2005). These authors found pronounced forward body tilt aftereffects following long lasting static backwards platform tilts and clearly weaker backward aftereffects following forward platform tilts. Our simulations mimicked these results quite well. Finally, simulations with very low tilt frequencies yielded a resonance behaviour of the control system at about 0.005–0.01 Hz (compare Peterka 2000) with the body being moved essentially with the tilting platform, despite the excursion limiter (note that the contribution from the  $\wedge FS$  was missing, because it fell below the aforementioned velocity threshold). Possibly these simulation results can explain findings in the literature of a body–platform instead of a body–space stabilization at low platform tilt frequencies (Walsh 1973; Gurfinkel et al. 1995; Creath et al. 2002).

## Patients

Qualitatively, patients exhibited similar behaviour as normal subjects. Especially, our new findings suggest that (1) they also switched control from a body–support to a body–space stabilization during tilt onset, and this despite of the loss of their vestibular ‘space’ sensor, and (2) they also limited their tonic body excursions upon lasting static tilts. In our previous study (Maurer et al. 2006a) we had modelled the patients’ stance control by assuming, in addition to the vestibular sensor loss, a secondary loss of the  $\wedge g$  and  $\wedge FS$

estimates with their substitution by graviceptive reaction force cues (via ‘COP’ signal in Fig. 8a; calculated from foot pressure receptors and low-pass filtered) (note that in normals, the box ‘Estimate of External Force’ receives input, dashed arrow, from the  $\hat{g}$  box, by which gravitational and inertial components become removed from the COP signal, unlike in patients where it represents an ‘Estimate of Gravitational and External Force’; not shown). Furthermore, we increased the local loop gain (factor 1.5). This model predicted the patients’ steady state tilt (and pull) responses in the previous study, but not the novel findings. We tested whether the new findings could be covered by the model when we added to it two extensions analogous to those used in the model of normals.

During platform tilt onset (1), patients initially moved their bodies with the platform, producing even some overshoot, and then braked the excursion. We assumed (in line with model simulations) that this ‘exaggerated’ initial response resulted from the proprioceptive feedback loop with an enhanced gain, while feedback from the graviceptive reaction force cues (the substitution for  $\hat{g}$  and  $\hat{FS}$ ) was missing, so that the overall loop gain was critically low. Then, for the braking, they apparently ‘switched on’ the reaction force cues, similarly as normals did with the  $\hat{FS}$  feedback. Therefore, we implemented a corresponding switch to simulate the braking, using a fast (original, i.e. unfiltered) version of the reaction force signal for the switch control and the aforementioned low-pass filter version of it for the feedback signal. A third version of the reaction force signal was used to generate, again in analogy to normals, a mechanism that would limit patients’ tonic body excursion upon lasting static tilts (2). The original signal was passed through a threshold, a leaky integrator, and a gain factor, and was implemented as an additional feedback.

In this extended form, software simulations mimicked well the patients’ old and new data. In Fig. 8c, their simulated tonic and dynamic COM excursion limits are superimposed on those of normals. Patients’ tonic excursion range is qualitatively similar to that of normals, but quantitatively it is larger, shows more for-aft symmetry, and shows clearly less saturation (compare Fig. 4c).

Similar simulation results were obtained in PostuRob after disabling its artificial vestibular sensor and the related  $\hat{g}$  and  $\hat{FS}$  estimates and implementing the two extensions described above. However, a detailed description of these simulations would be beyond the scope of the present paper and, therefore, will be presented elsewhere.

#### ‘Inverted pendulum’ simplification

We assessed to what extent the use of platform tilts that were larger in the present than in the previous study

affected subjects’ *inter-segmental movements* (Fig. 5). We found larger hip and knee contributions, but due to the above described tonic excursion limitation, the increase was moderate. As in the previous study, subjects’ tended to flex their bodies slightly towards the space vertical; with the overall postural undercompensation during the tilt (body being slightly taken with the platform), they superimposed small torso–thigh and thigh–shank erecting movements on the response about the ankle joint axes in a functionally synergistic way. Torso–thigh (hip), thigh–shank (knee), and shank–foot (ankle) responses were in fixed register with each other and their amplitudes showed a bottom-up hierarchy (ankle response largest). Therefore, we conceived that all three joints are controlled by one and the same control mode and set point signal (‘Desired position of body in space’ = 0°, upright). This assumption is supported by the preliminary results of simulations of a model with three segments and two degrees of freedom (not shown; for the model’s structure of sensory processing, see Fig. 1A in Mergner and Becker 2003). Thus, we had no evidence that subjects would change from the ‘ankle strategy’ to a ‘hip strategy’, which would mean that they would generate considerable hip thrusts to produce compensatory momentums for body stabilisation (see “Introduction”). We, therefore, continued to use the ‘inverted pendulum’ simplification when implementing the novel findings into our model.

There were two exceptions where normal subjects showed different response patterns; however, both of them were limited to transient responses. After the braking during the initial *backward* platform tilts, they generated a transient *forward* upper body excursion independent of lower body. And after the braking during the initial forward tilt, forward excursion of upper body transiently exceeded that of the lower body. Both findings still remain to be investigated in more detail and to be modelled. Patients did not show these to a considerable degree, but otherwise showed a similar inter-segmental coordination pattern, with less inter-segmental bending, though. This is possibly related to a greater subjective postural instability experienced by patients standing on the tilting platform without vision. Also normal subjects can be induced by instruction to reduced inter-segmental bending (observed in additional experiments with the instruction “Remain as straight as possible during the balancing!”, not reported here).

#### Psychophysics

Both, subjects’ and patients’ indications of perceived support surface tilt grossly overestimated the tilt. This perceptual overestimation is in contrast to the slight undercompensation of their postural tilt response (reflected by slight body lean into the direction of the platform tilt). Yet,

the perceptual response was highly correlated with the *compensatory* postural response, i.e. with subjects' counter COM movement on the tilting platform.

The findings confirm previous observations we made with transient tilt stimuli and a different indication procedure (Maurer et al. 2006b). Here we show that the overestimation is also observed with another stimulus waveform and a different indication method and that it is found not only in normal subjects, but also in vestibular loss patients. The earlier study indicated that the over-estimation stems essentially from ankle angle proprioception. We speculate that subjects built their psychophysical estimation on the notion of successfully keeping their own bodies upright in space (taking it as a 'representative of space') and referencing the tilted platform to it. The proprioceptive signal, which they used for this, appears to be clearly distinct from that they used for postural control. And it is distinct from that observed previously for vestibular-proprioceptive self-motion perception arising with passive motion stimuli in the horizontal plane (open loop situations; see Mergner 2002). Interestingly, in the previous psychophysical studies, subjects transferred the space reference (vestibular, with eyes closed) from the head via the body to the body support surface, to which they then referenced the body using an essentially veridical proprioceptive signal. It remains to be elucidated why the proprioceptive signal that subjects used in the present psychophysical responses is so erroneous. This response was also distinct from the postural response in other respects. For instance, its beginning was smooth and continuous and it did not show a braking with subsequent change of the response.

## Conclusions

There appears to be a discrepancy between the diversity and complexity of human postural behaviour on one hand and the simplistic engineering systems approaches by which researchers try to model this behaviour on the other hand. We suggest that the two can be reconciled. It is true that the brain appears to switch from one 'state' or mechanism of stance control to another when the environmental or behavioural situation changes, selecting from a 'bundle' of different learned and optimised control modes. These switches are most evident in transient responses and present themselves as sensory reweightings. For two of such sensory reweightings we show here that they can be viewed (modelled) as add-ons to a core control system that was formerly identified through steady state responses. They appear to involve high-level mechanisms such as cognition, whereas the core system is a lower-level mechanism that performs automatic sensory reweightings. In the model of the core system, sensory processing yields estimates of

external disturbances in relation to a vertical body orientation in space (here the instructed set point signal). These disturbance estimates are used for continuous compensation by feedback, rather than using the sensory signals proper as in the classical postural reflex concept. The disturbance estimates also provide a basis for interfacing the high-level sensory reweightings with the core system.

One of the sensory reweighting mechanisms identified here ('SRS') appears to belong to a group of mechanisms by which subjects try to replace noisy vestibular input by less noisy sensory inputs from references in the environment, given these are stationary (body support surface, visual scene, etc.). The other mechanism ('TEL') helps to cope with biomechanical constraints, such as the limited dimensions of the foot, and related behavioural preferences, e.g. for risking to fall forward rather than backward. Neither of the two reweightings, nor other seemingly complex findings in our results, invalidates our attempt to describe the principles of human stance control with the help of a relatively simple dynamic model, including the inverted pendulum simplification. This notion was corroborated by the additional finding that the model also worked well when embodied into the robot and then tested in the same way as the human subjects.

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## Appendix

For the hardware-in-the-loop (HIL) simulations, we implemented the model with the present additions into a biped humanoid robot ("PostuRob"). Details of the robot are described elsewhere (Mergner et al. 2006; Tahboub and Mergner 2007; <http://www.uniklinik-freiburg.de/neurologie/live/forschung/sensorfusion/posturob.html>). In the following, we briefly describe its essence. The robot's hardware structure consists of aluminium frames representing the 'body' and two feet. The body consists of two rigid legs fixed to a pelvic girdle and a spine; its main mass is represented by lead weights on the pelvis ( $m = 62$  kg). The body is connected with the feet via 'ankle joints'. It can thus pivot in the sagittal plane with respect to the feet which are freely standing on a support (same motion platform as used in the human experiments). Each leg carries a front and back pneumatic 'muscle' with 'tendon' (spring; spring constant across all four actuator sites slightly below the value that would be required to compensate for the COM's gravitational ankle torque). Three sensor systems, realized as mechatronic devices, mimic the following biological sensors (compare Fig. 8a): vestibular system (yielding signals of body angular position and velocity in space), ankle angle proprioceptive system (body-foot angular position and

velocity), and ankle torque proprioception (derived from two sources, force sensors in the muscle fixations and a COP signal calculated from plantar pressure sensors). Being interested mainly in sensor fusion aspects of stance control, we tried to obtain an essentially ideal actuator (muscle) performance. To this end, we electronically controlled the muscle–tendon system by feedback from the force sensors (bearing in mind that human spinal mechanisms may function accordingly). Sensor signals were input to, and signals for the actuator control were output from an ‘embedded PC’ (real time), which was under the control of a host PC. The control model (boxes ‘Sensor Fusions and Disturbance Estimates’ and ‘Controller’ in Fig. 8a) was downloaded on the embedded PC in a special Simulink version. The system’s dead time amounted to approximately 20 ms and the delays by the actuators to 20 ms, by the proprioceptive loop 40 ms, and by the estimators 70 ms (80 ms total reaction time of proprioceptive loop, 110 ms of estimators).

As mentioned before, the robot simulations were performed using the same methods as described above for the human subjects (same laboratory, motion platform, stimuli, etc.; same analyses). In the simulations, the stance control system proved its robustness against inaccurate sensor signals, drifts, offsets, noise, etc. and its inherent simplifications concerning mechanics and dynamics (compare Tahboub and Mergner 2007).

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