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journal homepage: www.elsevier.com/locate/arcontrolA neurological view on reactive human stance control[☆]T. Mergner^{*}

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ABSTRACT

During biped stance or locomotion, humans show remarkable skills in reactive balancing upon external disturbances. Mainly four types of external disturbances are relevant for stance: the field force gravity, contact forces such as a push or pull against the body, as well as body support surface rotation and translational acceleration. It is known from clinics that sensory loss severely impairs the balancing. Three sensory inputs are instrumental: vestibular, joint angle, and joint torque. System identification studies currently try to understand how humans are able to flexibly cope with changes in, and superposition of the disturbances. A solution is presented in this article. The article first describes the control problem and then reviews recent evidence for a PD (proportional-derivative) controller, for multisensory feedback, and for sensory reweighting as a key to understand the flexibility. On this basis, a recent disturbance estimation and compensation (DEC) model is introduced. It builds on two concepts from previous psychophysical studies of human self-motion perception. First, inputs from several sensory transducers are fused to establish sensors that provide explicit measures of the physical variables (sensor concept). Second, a processing level, interleaved between sensors and feedback (meta level), performs online sensory estimations of the external disturbances. These estimations are then fed into a local proprioceptive feedback loop, yielding corresponding disturbance rejections. Previous work on using the DEC model to describe human reactive balancing data is briefly reviewed. Then, novel work is presented, in which voluntary control over the reactive balancing is added to the DEC model. A prediction method for anticipating self-produced and external disturbances is suggested and corresponding software and hardware (robot) simulations are presented. The results serve as guidelines for future human experiments. Since the DEC model is very simple, we concluded that its behavioral flexibility and fault tolerance goes together with computational parsimony, an equally important biological constraint.

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1. Introduction

The human ability to maintain upright stance in the presence of external disturbances such as gravity or body support surface motion has intrigued researchers over the last century. Interest arose from basic neuroscience (Roberts, 1978) and from clinicians who diagnose and treat balancing problems (Bronstein, Brandt, & Woollacott, 1996). Nowadays, interest also comes from robotics where the technical evolution of humanoid robots has just started. Engineers welcome inspiration from nature's evolution that already lasts millions of years. In turn, biologists and clinicians profit from using the engineers' abstraction and modeling tools and even build humanoids as testbeds for their concepts and

models (neurorobotics; Kawato, 2008; Mergner & Tahboub, 2009; Seth, Sporns, & Krichmar, 2005; Webb, 2001).

This article reports on neurological approaches that try to abstract and model the principles of human active balancing. These principles are only partially known, yet. With further progress, they will be re-embodied in robots for neuroscientific proof of principle and medical purposes. Medical interest is high, because balancing problems are disabling many neurological patients during walking and other activities.

Neuroscientific interest in human balancing arises from the fact that it represents a prototype of a multi-tasking and modular sensorimotor control. It is *reactive*, in that it is controlled by sensory feedback when humans are exposed to unforeseen external disturbances. Its task is body stabilization in the sense that the body is prevented from falling over. This may apply to different desired body-support (body on support) or body-space (body in space) orientations. Often, the task is to maintain a desired body-space orientation for stabilizing a given eye or hand workspace. The balancing represents then the platform onto which volitional ('proactive') self-movements are superimposed.

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The balancing is relatively simple when it is restricted to the anterior–posterior, a–p, plane and when the body sway angles are small. Then, head, arms, trunk, and legs essentially form a rigid segment, or link, that tends to sway about an axis through the ankle joints. Experimentally, fixing a subject's body to a backboard may enforce this. The situation allows treating body biomechanics as a single 'inverted pendulum' (e.g. Gage, Winter, Frank, & Adkin, 2004). This balancing is called the 'ankle strategy'.

In some situations, the balancing involves the hips to various degrees, depending on a number of factors such as disturbance magnitudes or restrictions of foot support, motor, or sensory conditions ('hip strategy'; Fujisawa et al., 2005; Horak & Nashner, 1986). Then, in addition, the knees may get involved (Alexandrov, Frolov, & Massion, 1998). Very large disturbance magnitudes may even evoke 'rescue reactions' such as steps, hopping, or holding with the hand. These reactions are then usually superimposed on the ankle joint stabilization. The latter (the ankle strategy) will be the main focus of this article.

Roboticians who build humanoids can mostly use established engineering methods for controlling their technical artifacts. In contrast, neurologists who try to identify, abstract, and model the human stance control system face largely unknown territory and must be open to so-far unconsidered control methods. They have to take into account many known and unknown biological constraints that differ from the technical ones, because of differences in material, history and requirements of biological evolution, etc. But neurologists may be guided by clinical experience, for example concerning the sensorimotor development during childhood or functional impairments due to sensory loss. A major challenge for them is to explain how humans, despite considerable biological 'complications' (e.g. relatively long neural transport delays, noisy and inaccurate sensors, etc.), are able to deal very flexibly with changing external situations and imperfect internal conditions and yet are even able to perform voluntary activities and reactive balancing at the same time.

The article mainly addresses these flexibility and multi-tasking issues, raising the following questions: (1) how do humans reconstruct from available sensory inputs the enormous variety of external disturbance scenarios? (2) How do they transform the acquired information into disturbance compensation? (3) How does the control method achieve its impressive flexibility that allows it to cope with the richness of environmental situations and behavioral demands (and is providing, in addition, high tolerance against internal failures)? (4) How does the system achieve multitasking of volitional (proactive) and reactive control?

To provide answers to these questions, the article first reviews recent modeling work of human stance control, starting with methodological aspects and the most relevant sensors before considering controller and multisensory feedback. The flexibility issue follows, this with the focus on a recent model from our laboratory, before novel concepts on the proactive-reactive multitasking are presented. The multitasking issue will be restricted to the prediction of self-produced disturbances and external disturbances. The new concepts are tested in both, software and robot simulations.

Since the article mainly addresses researchers from the technical fields, it out-sources detailed clinical and biological background information to the appendices. To neurologists, who may also show interest in the article, these details are indispensable for compatibility checks with the biological knowledge base.

2. Basic aspects of human reactive stance control

The measuring and analysis of spontaneous or stimulus evoked sway is called posturography. The sway is generally characterized in terms of kinematic and kinetic variables such as center of mass

(COM) rotation about the ankle joint and center of pressure (COP) shifts on the support surface, respectively. The previously often used electromyography (EMG) recordings do not allow a clear distinction between these physical variables, but may be helpful in measuring additional aspects such as latencies. For system identification, dynamics models are formulated on the basis of the human experimental data. Currently, competitions among different models begin to develop as to their describing and predicting power.

2.1. Methodological aspects

Balancing is often investigated in response to three external mechanical stimuli, which are body support surface tilt, surface translation, and contact force (e.g., a push or pull having impact on the body). One then speaks of *perturbed stance*, while quiet stance is called *unperturbed stance*. However, the standing body as an inverted pendulum is inherently unstable. Gravitational torque arising with its angular excursions away from the ideal gravitational vertical tends to tip it over. Therefore, gravity will here be considered the fourth external stimulus.

Clinical and experimental work indicates that humans use different sensor types for their reactive balancing (ankle angle, ankle torque, and vestibular; Appendix A, sensor concept). Specific sensory impairments in patients may lead to specific restrictions in their balancing skills. For example, unlike healthy subjects, vestibular-loss patients inevitably and immediately fall in situations where sensing body orientation in space is required for stance stability, such as during standing with eyes closed on a body sway referenced platform (BSRP; see below).

Because the sensors and the physical variables they measure play such an important role, a stance control modeling should consider the underlying physical stimuli in some detail. A description of these stimuli and their effects on the sensors are given below. Only the sensors that are instrumental for balancing are considered, for simplicity (vestibular, joint angle, joint torque). Visual and tactile orientation cues as well as foot sole shear cues remain unconsidered, because they are not instrumental.

The *four external mechanical stimuli* are given in Fig. 1 (force field gravity, \mathbf{g} , external contact force, F_{ext} , support surface tilt with foot-space angular displacement, α_{FS} , and support translation with foot-space translational acceleration, \ddot{x}_{FS}) together with their effects on the sensors in the inverted pendulum scenario. Since it is assumed that very large and fast body movements do not occur during stance, the field forces centrifugal and Coriolis forces need not to be considered. Furthermore, foot height may be neglected, since it is relatively small, and for simplicity it is assumed that all rotations occur at the ankle joint and that foot-support contact is fixed.

Total ankle torque T_A is related to angular body-space motion by

$$T_A = J \cdot \frac{d^2 \alpha_{\text{BS}}(t)}{dt^2} \quad (1)$$

where J represents the body's moment of inertia about the ankle joint (not including the feet) and α_{BS} the body-space angle (primary position is vertical, $\alpha_{\text{BS}} = 0^\circ$). In the absence of any disturbances, T_A equals the actively produced muscle torque, T_a . In the presence of disturbances, T_A comprises four components in addition to T_a :

$$T_A = (T_g + T_{\text{in}} + T_{\text{ext}} + T_p) + T_a \quad (2)$$

where T_g is the gravitational torque, T_{in} the inertial torque, T_{ext} the external torque, and T_p the passive joint torque (from stiffness and viscosity of the muscle-tendon system, joint capsule, etc.). The torques T_g , T_{in} , T_{ext} , and T_p represent disturbances that challenge the control of T_A (exerted by T_a) and therefore must be

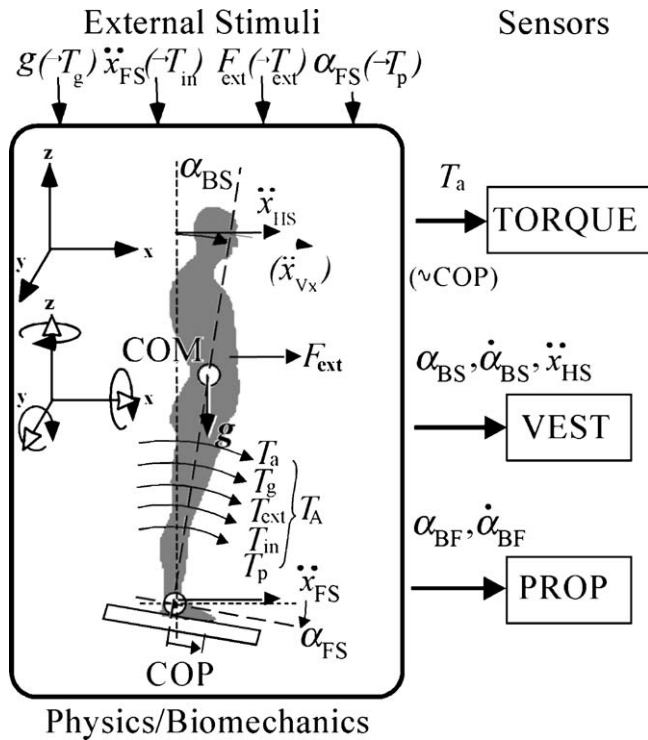


Fig. 1. Inverted pendulum scenario. It shows the four relevant external stimuli, the torques that are effective at the ankle joints, the three sensors that are instrumental for reactive balancing in humans, and the physical variables measured by the sensors.

compensated for by T_a . The disturbing torques arise from the four external stimuli in the following way:

- (1) The gravitational torque T_g is related to α_{BS} by

$$T_g = m \cdot g \cdot h \cdot \sin(\alpha_{BS}) \quad (3)$$

where m is the COM mass, h is the COM distance above ankle joint axis, and $g = 9.81 \text{ m/s}^2$ is the gravitational acceleration.

(2) The inertial torque T_{in} becomes a disturbance upon translational acceleration of the support surface (here horizontal). Its dependence on the foot-space translational acceleration \ddot{x}_{FS} and on the current body-space angle α_{BS} is given by

$$T_{in} = -\ddot{x}_{FS} \cdot m \cdot h \cdot \cos(\alpha_{BS}) \quad (4)$$

(Note that Newton's dot notation of derivatives is used for fixed or already defined kinematic variables.) An a-p inertial torque disturbance may furthermore arise from centrifugal acceleration, for example during a horizontal support rotation with the body standing eccentric and facing inward or outward (not shown).

(3) The external torque T_{ext} in Fig. 1 results from a horizontal pull force F_{ext} exerted on the body (above the COM, such that foot-support shear forces can be neglected). The torque T_{ext} is related to F_{ext} and the momentary angle α_{BS} in the form:

$$T_{ext} = F_{ext} \cdot h' \cdot \cos(\alpha_{BS}) \quad (5)$$

where h' denotes the height of force impact above the ankle.

(4) The passive ankle torque T_p makes the tilt of the foot support surface a disturbance stimulus. During the tilt with the foot-space angular excursion α_{FS} , body inertia tends to maintain body-space orientation, leading to a body-foot excursion α_{BF} . The torque T_p , which tends to take the body into the direction of the tilt, arises in the form:

$$T_p = -K_p \cdot \alpha_{BF} - K_D \cdot \frac{d\alpha_{BF}(t)}{dt} \quad (6)$$

with K_p representing a stiffness (proportional) factor and K_D a damping (first derivative) factor (passive joint impedance). Primes are added here to the proportional and derivative factors to distinguish them from those of the PD controller below. Note that foot-space orientation is defined here as $\alpha_{FS} = 0^\circ$ if support surface and foot sole are level, i.e. at a 90° angle with respect to the vertical body-space orientation, $\alpha_{FS} = 0^\circ$; with this definition, $\alpha_{BF} = 0^\circ$ if $\alpha_{BS} = 0^\circ$ and $\alpha_{FS} = 0^\circ$.

Whether the passive body properties T_p and T_{in} facilitate or hamper balancing depends on the external stimulus condition. The torque T_p tends to facilitate balancing in the above conditions 1–3 and to hamper it in condition 4. The torque T_{in} hampers balancing in 2, whereas body inertia 'helps' balancing in 1, 3, and 4.

A reflexive body-foot stabilization that is produced through a negative ankle angle proprioceptive feedback loop (see below, Fig. 3) is synergistic with T_p . Unlike the passive torque, the reflexive proprioceptive torque is associated with a considerable time delay. For certain considerations in the following, we will refer to the sum of both, the reflexive torque and the passive torque (T_p) as the 'proprioceptive' torque.

Not shown in Fig. 1, but included in the following considerations, is the BSRP disturbance condition (Ishida, Imai, & Fukuoka, 1997; Maurer, Mergner, & Peterka, 2006; Nashner, Black, & Wall, 1982; Peterka, 2002). In this condition, body-space sway (α_{BS}) is externally measured and fed via amplifiers into the control of the supporting motion platform. This yields a α_{FS} -to- α_{BS} coupling such that the ankle angle (α_{BF}) remains constant and no joint angle proprioceptive feedback results during body-space excursions. The BSRP condition may help clinicians to identify vestibular loss. Healthy subjects are able to balance, eyes closed, with BSRP during spontaneous sway and external disturbances (platform tilt and contact force stimuli), whereas vestibular-loss patients fail to do so (see Maurer et al., 2006).

Fig. 1 also gives the main physical variables that arise with the four stimuli and are measured by the following three sensor systems:

(a) *Ankle angle proprioception* (PROP). It yields measures of body-foot angle α_{BF} and angular velocity $\dot{\alpha}_{BF}$, which are essentially ideal (i.e. which show unity sensor transfer function over the here considered range of body sway amplitudes and velocities, $<8^\circ$ and $<80^\circ/\text{s}$, and frequencies, 0–3.2 Hz).

(b) *Vestibular system* (VEST). It yields broad band pass measures of vertical body-space angle α_{BS} and angular velocity $\dot{\alpha}_{BS}$. In addition, it provides a measure of translational head-space acceleration (see Section 3.4), which shows high pass characteristics (see Mergner, Schweigart, & Fennell, 2009). Therefore, one may actually distinguish between a vestibular rotation sensor and a vestibular translation sensor (omitted here for simplicity).

(c) *Ankle torque sensor* (TORQUE). The torque measure may be derived from Golgi tendon organs of ankle muscles (located at the muscle-tendon junctions) or from COP sensing pressure receptors deep in the foot soles. Its contribution to stance control shows low pass characteristics (see Maurer et al., 2006).

Clinical and experimental evidence suggesting that these sensors play an important role in stance control is given in Appendix A. There, it is explained that the sensors do not exist as single distinct devices, but result from internally fusing the signals from various sensory transducers ('sensor concept'). The evidence for the concept stems mainly from psychophysical measurements of human self-motion perception. In this concept, it is justified using unity as sensor transfer function for α_{BS} , $\dot{\alpha}_{BS}$, α_{BF} , and $\dot{\alpha}_{BF}$ in the human stance control model (which represents a simplification compared to earlier models that implemented transfer characteristics of individual transducers instead of the sensors; e.g. Nashner, 1972).

Furthermore, psychophysical studies showed that humans use the vestibular signals for perceiving not only head-space motion,

but also trunk-space motion (e.g. of motion of the COM in the torso) or foot-space motion (or even foot support-space motion, given fixed haptic foot-support contact). This is achieved through inter-link sensory coordinate transformations using, for example, neck proprioception during head-trunk movements (Appendix B).

With each of the stimuli shown in Fig. 1 and the head free to move with respect to the trunk, more than one sensor becomes involved in the compensation. This complicates the identification of the individual sensors' contributions to the corresponding stimulus compensations. However, on the basis of systems analysis approaches and comparisons between human experiments and model simulations, identification is possible. The following part of this section is mainly restricted to such comparisons. This omits many other important findings or leaves them to Appendix A, such as findings on sensory loss effects or on artificial selective stimulation of sensory transducers (e.g. vestibular receptor activation by galvanic current, or muscle spindle activation by tendon vibration). Exceptions will be systems analysis findings of vestibular-loss patients, which will be briefly mentioned.

In summary, the most relevant external stimulus types to be considered for posture control are the field force gravity, contact forces, support surface translational acceleration and support surface rotation. With the human body's biomechanics modeled as a single inverted pendulum, the stimuli mechanically affect stance through torque disturbances (gravitational, external, inertial, passive). For disturbance estimation and compensation, three sensors (vestibular, ankle angle, ankle torque) appear to be instrumental.

2.2. Sensory feedback control

Distinction between unperturbed versus perturbed stance reflects a tradition in posturography, but is here and in the following not meant to imply crucial differences in the control method.

2.2.1. Unperturbed stance

The passive ankle joint stiffness (K_P) is too weak to maintain the body upright during quiet stance (Loram & Lakie, 2002; Morasso & Sanguineti, 2002; Peterka, 2002). Instead, quiet stance is controlled actively, which is reflected in a continuously changing 'spontaneous' sway. Power density plots of the sway exhibit a clear preponderance at low frequencies (Carpenter, Frank, Winter, & Peysar, 2001). The sway is not fully explained by internal motions due to heartbeat, breathing, etc., but appears to reflect mainly fluctuations of the active torque. Possible sources are sensor noise, central processing noise, and irregularities in actuator performance. Complete sway suppression appears not to be a goal of stance control, possibly because it helps nutrition of joint cartilage, prevention of sensory adaptation, etc.

As a result of the sway, the COM excursion and the gravitational torque it evokes vary over time. This represents a sensory stimulus that in turn evokes changes in active torque (see basic feedback control scheme in Fig. 2). The active torque stands out in the COP as rapid variations (Winter, Patla, Prince, Ishac, & Gielo-Periczak, 1998). Comparing experimental findings of such COM and COP changes with corresponding simulations using a COM angle control model, Masani, Vette, and Popovic (2006) concluded that a simple feedback system with PD control is capable of describing the sway. The approach took considerable neural time delays into account (mainly from neural transport). The work confirmed earlier results obtained in a system identification study of perturbed stance by Peterka (2002; stimuli were pseudo-random support surface and visual tilts, BSRP, and more). Peterka identified a PID controller, but later changed this to a PD controller with additional force feedback for a better model fit with the experimental data (Peterka, 2003).

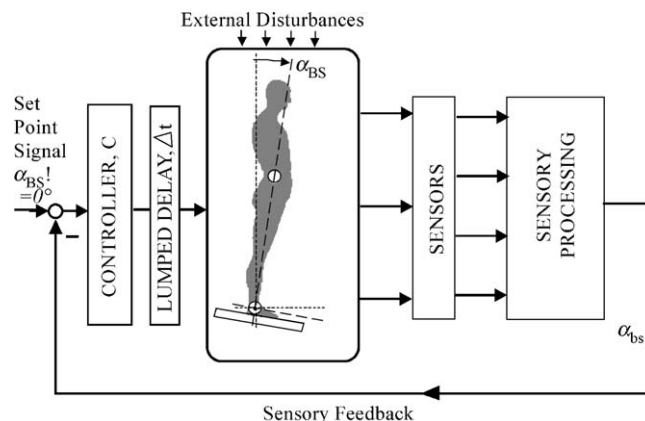


Fig. 2. Stance control scheme. Here and in the following the neural representation of the physical variables is indicated by using lower case subscripts instead of upper case (i.e., α_{bs} is neural representation of body-space angle α_{BS}).

For different delay times, the models of Masani et al. (2006) and Peterka (2002, 2009) showed that the regions of stable COM vary with different PD controller parameters (i.e. with the proportional controller gain factor K_P and the derivative factor K_D). These theoretical K_P - K_D -stability regions are large for feedback delays shorter than 100 ms and shrink with increasing delay. The identified lumped time delay is approximately 150 ms (Peterka, 2002, 2009; also Maurer et al., 2006; 200 ms in Johansson, Magnusson, & Akesson, 1988). Identified human controller factors were found to be within the stability region. The gain of K_P is low, exceeding only slightly the value that is required to resist the gravitational torque ($m \cdot g \cdot h$; see above, Section 2.1). The identified value of the K_D gain value, when considered in relation to the corresponding K_P gain value, is somewhat less than half of this. These low values help to avoid system instability due to the feedback time delay. They are, in addition, underlying the relatively slow speed and smooth trajectories of postural movements of humans and their compliance upon external disturbances (as compared to many industrial robots).

The models used by Masani et al. (2006) and Peterka (2002) use linear continuous controllers. In contrast, other studies advocated an intermittent controller. Recent arguments for intermittent control include, for example, the occurrence of regularly occurring fluctuations in neural output during quiet stance (Lakie & Loram, 2006). But this behavior may possibly be better explained by nonlinearities that reside in the sensory processing part of the feedback, rather than in the controller (Appendix C and below).

2.2.2. Perturbed stance

In a study on perturbed stance (Fitzpatrick, Burke, & Gandevia, 1996), small disturbances were used and the identified loop gain was low. A conclusion of the authors was that feedback control alone does not allow stable balancing with large disturbances. Peterka (2002) and Maurer et al. (2006) observed that disturbance compensation, which is incomplete (only partial) with small disturbances, increases with increasing stimulus magnitude (here referred to as 'amplitude nonlinearity' of the response, see Section 3). Peterka was able to fit his model to human response gain and phase functions under the assumption of a 'sensory channel reweighting'. This reweighting is assumed to cover not only stimulus amplitude effects, but also to be relevant across stimulus conditions. When starting support surface tilt, for example, it yields an increase in vestibular (body-space) feedback gain and a decrease in proprioceptive (body-foot) gain, which makes the tilt compensation more efficient than when both gains were equal, as before the tilts started. Later work provided further evidence for the notion of sensory reweighting in the human stance control

system (e.g. Peterka & Loughlin, 2004). Details of the underlying mechanisms were left open.

The continuous versus intermittent control issue was recently reconsidered by van der Kooij and de Vlugt (2007). The authors collected responses to multi-sinus support translation stimuli and compared them to simulated data from a variety of different models with and without intermittency-producing nonlinearities (e.g. amplitude or velocity thresholds). They found no evidence for a dominance of intermittent control. Yet, they could not exclude a combination of an inner continuous feedback loop with outer discontinuous ones. Such architecture is assumed in the model described below (Section 3). There, the experimentally observed amplitude nonlinearities are accounted for by thresholdings (as constituents of automatic sensory reweighting mechanisms).

The systems analysis studies of Peterka (2002, 2003), Mergner, Maurer, and Peterka (2003), and Maurer et al. (2006) confirmed previous evidence for the three sensors in Fig. 1 (Appendix A; Peterka included in addition vision). The authors successfully simulated disturbance responses obtained in vestibular able subjects using their models (which share basic similarities). Furthermore, responses of vestibular-loss patients could be simulated after conservatively modifying the models. Two results are mentioned here:

- (a) In vestibular-able subjects, using tilt and pull stimuli with BSRP leads to a pronounced increase of the body-space excursions during balancing. In addition, spontaneous sway is clearly enlarged by BSRP. These findings substantiate that ankle angle proprioception makes an important contribution to stance control. Recall that the BSRP opens the feedback loop of proprioceptive input that arises with body-space sway.
- (b) Also vestibular loss leads to a pronounced increase of body excursion in tilt and pull responses with eyes closed (tilts with peak velocities $>5^\circ/\text{s}$ often lead to fall). Yet, the fact that the vestibular-loss patients still tend to orient their bodies upright with respect to the earth vertical during tilt indicates that they involve ground reaction force cues in their balancing (Mergner, Schweigart, Fennell, & Maurer, 2009). The force cues alone are insufficient for their balancing, however (see Appendix A for force or joint torque sensors). The patients inevitably and immediately fall when they are tested in the BSRP condition.

These studies continued early and pioneering systems analysis work of Hajos and Kirchner (1984), Ishida and Imai (1980), Johansson et al. (1988), Nashner (1972), Talbott (1980), and others (overview mainly from engineering viewpoint on studies before 1990 and many basic aspects, Johansson & Magnusson, 1991). But they also differ from these in that they (i) emphasize multisensory aspects in the experimental design and modeling and (ii) fit the models to findings across different stimulus parameters and conditions in healthy subjects and patients.

In summary, reactive human stance control is well described by multisensory feedback models in which at least a continuous inner loop exists and the controller includes a derivative ('predictive') term as well as some form of rapid loop gain adjustment ('adaptivity') related to stimulus magnitude. The adjustment appears to occur, at least in part, with sensory reweightings in the feedback. Generally, the reweightings enable the system to cope 'ad hoc' with different stimulus conditions.

3. Multisensory integration

Differences between the above-mentioned models mainly concern the problem how humans succeed to adequately and immediately respond to unforeseen external disturbances of changing magnitude and type. Most studies attribute this ability

to sensory reweightings through some multisensory integration mechanism, but this mechanism is modeled differently or not at all yet. Peterka (2002) conservatively and parsimoniously used in his model several reflex-like sensory feedback loops in parallel with fixed continuous connections, calling it a 'independent sensory channel model'. The reweighting was performed by externally adjusting the weighting factor of each channel. Other authors published models that perform automatic sensory reweightings. There have mainly been two approaches.

One group of adaptive sensory integration models uses an indirect method of sensory reweighting (van der Kooij, Jacobs, Koopman, & Grootenboer, 1999; van der Kooij, Jacobs, Koopman, & van der Helm, 2001; Kuo, 2005). The reweighting results from the processing of a 'sensory integration center' in which multiple sensory signals are combined with centrally generated information with the aim to find the most accurate sensory representation for a given environmental situation under noise optimization principles using Kalman filters. For example, when body-space excursions are small and multisensory information is available, the optimization prefers proprioceptive signals to vestibular signals since the latter show higher noise (while otherwise the measures of both are equivalent in this situation). The required additional information includes internal models of the relevant physics and biomechanics, dynamics and noise aspects, and a 'efference copy' of the motor command for a given joint. Thus, the sensory integration center is uniquely constructed for, and adapted to, a single joint and its role in a given task. In the study of van der Kooij et al. (2001), the model successfully mimicked an amplitude-dependence of body sway evoked by visual surround rotations and a number of qualitative stance performance criteria from the literature.

The other approach is from the author of this article and his colleagues. It uses exclusively *inter-sensory interactions* for disturbance estimation. This involves thresholdings in the sensory interaction network for sensory reweightings. Its development was motivated mainly biologically. It assumes two instrumental building blocks, i.e. (i) stand-alone sensors and (ii) online sensory disturbance estimation, both being optimized by biological evolution over many millions of years. The biological optimization would include some compromise between computational parsimony and redundancy with fault tolerance ('graceful degradation').

The first building block is a 'sensor concept' derived from psychophysical evidence (Appendix A). It implies that signals from different sensory transducers are fused to yield sensors that provide measures of physical variables such as α_{BS} or \ddot{x}_{Vx} and already show some noise and accuracy optimization. An example is the fusion of head-space angular and translational acceleration transducer signals in the vestibular sensor that provides gravito-inertial motion and orientation information (Appendix A.1). With task specific additions, a given sensor may then be used for various behavioral functions. For example, the vestibular system is used not only for stance stabilization, but also for gaze stabilization, spatial orientation, and autonomic functions.

The concept of the other building block, the inter-sensor processing, is also derived from psychophysical studies (Appendix B). They showed that the sensor signals do not directly reach conscious human self-motion perception. Rather, an additional processing level is interleaved ('meta level'). At the meta level, sensor signals are fused with each other and with cognition to yield estimates of the external disturbances having impact on the body. An intuitive example is the self-motion perception that arises with passive body rotation on a motion platform. Humans experience the platform as moving and the motion of the own body as a consequence of the platform motion, which is physically correct. The reverse happens in the sensory processing where the motion information stems from a vestibular

head-space signal. The motion information (in space coordinates) is then transferred through proprioceptive coordinate transformations from the head via the trunk and the legs to the feet and the body support (Mergner, Huber, & Becker, 1997). Thus, perception of the platform-space motion represents here a sensory reconstruction of the external physical event.

The meta level concept was implemented into a stance control model under the assumption that it applies not only to perception, but in similar form also to reactive sensorimotor control (Mergner, T., Maurer, C., & Peterka, 2002; Mergner et al., 2003). This represents a plausibility assumption that draws on a mostly valid action-perception congruency (Mergner, 2002). At an early stage of its development, the meta level model was compared to a reflex model where vestibular and force cue signals were directly fed back in a reflex-like way, i.e. without inter-sensory interactions (simulation study using conceptually ideal models; Mergner, 2004). Interestingly, similar simulation results were obtained, but the meta level model complied better to experimental findings such as a proprioceptive contribution to stance control (Section 2.2.2).

The calculations underlying the sensory disturbance estimations at the meta level are described in the following section (also Maurer et al., 2006). Fig. 3 gives an overview on the contributions of the three sensors to the four disturbance estimations. Furthermore, it shows that the disturbance estimates, rather than the sensor signals, are used for disturbance rejection, by injecting them into a 'local proprioceptive feedback loop'. As a result, the rejection is instantaneously effective in the feedback. Another effect is that the local loop, which on its own performs ankle angle (body-foot) stabilization, is transformed into a body-space angle control (Section 3.1). In the following, the meta level model will be called disturbance estimation and compensation model (DEC model).

3.1. Estimate of foot support-space rotation $\hat{\alpha}_{FS}$

During support surface rotation about the ankle joint axes, the passive proprioceptive body-foot torque and the reflexive proprioceptive body-foot torque (generated by the local loop in Fig. 3) tend to take the body along with the support tilt, thereby disturbing stance (Section 2.1). Compensation of the tilt is assumed to occur through an estimate of the tilt, $\hat{\alpha}_{FS}$. In the feedback loop, $\hat{\alpha}_{FS}$ reduces the reflexive proprioceptive contribution to T_a and

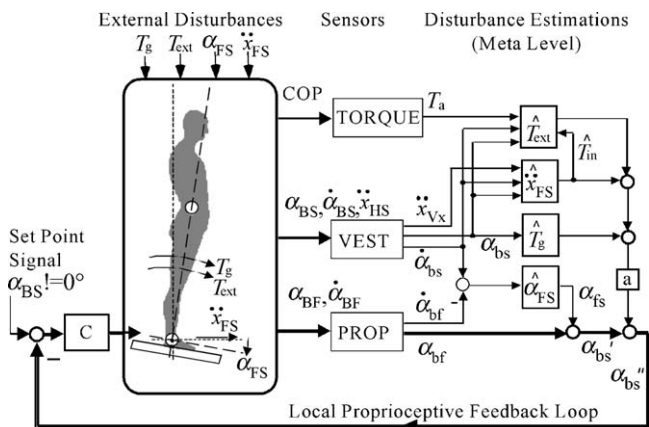


Fig. 3. Disturbance estimation and compensation model (DEC model) of human reactive stance control. It performs online sensor-based estimations of external disturbances. For disturbance compensation, it feeds the estimates (rather than the sensor signals) into the proprioceptive ankle angle feedback loop for disturbance rejection. In small box a, estimated torques are converted into body-space angle equivalents ($a \sin(T/mgh)$; T , sum of all estimated disturbance torques). Details of estimations are given in Figs. 5–8.

adds a vestibular contribution (compare wiring diagram in Fig. 6A; the effects of $\dot{\alpha}_{bf}$ and α_{bf} have opposite signs and partially cancel each other, while $\dot{\alpha}_{bs}$ is added).

The estimate $\hat{\alpha}_{FS}$ is derived from the vestibular body-space angular velocity signal $\dot{\alpha}_{bs}$ and the proprioceptive body-foot angular velocity signal $\dot{\alpha}_{bf}$, which are summed to yield an internal foot-space velocity signal $\dot{\alpha}_{fs}$ in the form of

$$\dot{\alpha}_{fs} = \dot{\alpha}_{bs} - \dot{\alpha}_{bf} \quad (7)$$

Further processing comprises a velocity threshold ($0.18^\circ/s$), a scaling factor ($G = 0.75$), and a mathematical integration. The threshold and scaling factor were identified in Maurer et al. (2006).

The estimate $\hat{\alpha}_{FS}$ then feeds a signal α_{fs} into the proprioceptive α_{bf} feedback loop, yielding a body-space signal

$$\alpha'_{bs} = \alpha_{fs} + \alpha_{bf} \quad (8)$$

Here and in the following, the prime (e.g. of α'_{bs}) discriminates different internal representations of the same physical variable. Note from the above equation that the α_{fs} signal changes the feedback control from a body-foot (local or relative) control into a body-space (or absolute) control. With perfect sensor signals, the two proprioceptive contributions to α'_{bs} would cancel each other, leaving the vestibular contribution that tries to stabilize the body in space. However, because of the threshold and of the non-ideal scaling of $\hat{\alpha}_{FS}$, the compensation clearly undershoots (under-compensation).

This vestibular contribution to the feedback comes with a disadvantage, however. The $\dot{\alpha}_{bs}$ signal contains relatively large noise with fluctuating drifts (Mergner, Nasios, Maurer, & Becker, 2001; Mergner, Schweigart, & Fennell, 2009; Mergner, Siebold, Schweigart, & Becker, 1991). The slower the tilt, the more remains the $\dot{\alpha}_{fs}$ signal subthreshold and the less becomes the feedback contaminated by this noise. With stationary support, which behaviorally is the prevailing situation, the threshold represents a kind of 'noise minimization'. Corresponding simulations were presented in Mergner, Schweigart, and Fennell (2009; Fig. 3). Additionally, the threshold affects the overall vestibular feedback gain (a reweighting effect). The faster the tilt, the larger the proportion of the $\dot{\alpha}_{fs}$ signal that exceeds the threshold becomes.

For engineers, possibly surprising is the relatively low scaling factor of $\hat{\alpha}_{FS}$ (which is similar to the estimates that follow below) and the clear under-compensation of the tilt response. Improving sensory body-space lean information during tilt (e.g. by combining visual and vestibular inputs) improves the compensation (Maurer, Mergner, Bolha, & Hlavacka, 2000; Maurer et al., 2006). This appears to be an effect of a better scaling and, possibly, of a somewhat lower threshold. The underlying mechanisms and the visual-vestibular interactions still have to be identified.

3.2. Estimate of gravitational torque \hat{T}_g

The estimate is calculated from a vestibular body-space angle signal α_{bs} that is converted into an internal gravitational torque signal:

$$T'_g = m \cdot g \cdot h \cdot \sin(\alpha_{bs}) \quad (9)$$

(compare Section 2.1), where $m \cdot g \cdot h$ is a learned quantity (box b in Fig. 5A). Before this, the α_{bs} signal has been scaled by a factor ($G = 0.8$) and passed through a threshold (0.16°). The signal T'_g is fed into the α'_{bs} feedback loop, after re-converting it into a body-space angle equivalent signal (box a, Fig. 3).

Omitting the angle-torque conversion and torque-angle back-conversion is possible here. This omission would make \hat{T}_g formally a kinematic estimate of body-lean with respect to the gravitational vertical, where knowing $m \cdot g \cdot h$ is not necessary. Presenting here,

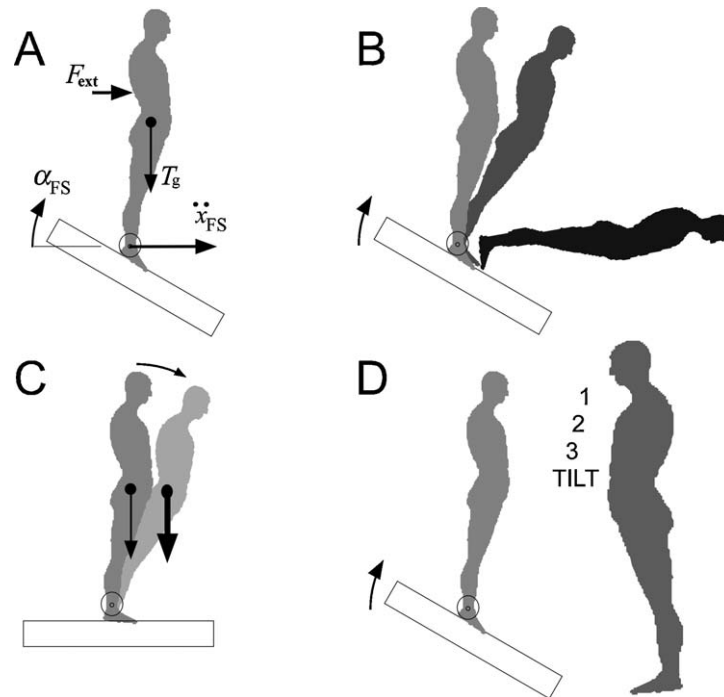


Fig. 4. Volitional effects on reactive stance control. (A) Reminder of the four external disturbances. (B) Voluntary change of control policy (switching on or off disturbance estimates or changing their scalings). Example shows switching off the α_{FS} compensation during support surface tilt, which changes body-space stabilization (light grey body) into body-support stabilization (median grey). Additional extinction of T_g leads to fall (dark grey). (C) Prediction and anticipation of self-produced disturbance. Example illustrates increase in T_g during voluntary body-space lean forward. (D) Prediction and anticipation of external disturbances. They may be triggered by cognition (e.g. expectation) or a sensory signal (here through acclimation).

instead, the torque estimate is mainly for didactic reasons (and for future applications where centrifugal and Coriolis forces are included in the estimate that then becomes a field force estimate).

To appreciate the functional role of \hat{T}_g , consider a support surface tilt. If the gravity compensation by \hat{T}_g were the only disturbance compensation that is fed into the local loop, it would make the body move with the platform tilt, preventing it from tipping over due to gravity (compare Fig. 4B). For maintaining a desired upright body-space orientation during the tilt, $\hat{\alpha}_{FS}$ is necessary in addition. (This is in contrast to the vestibulo-spinal reflex of the classical postural reflex concept, which alone maintains the desired body-space orientation. Details of the reflex concept are given in Appendix D).

3.3. Estimate of external torque \hat{T}_{ext}

The estimate \hat{T}_{ext} , which stems from the external contact force stimulus F_{ext} in Fig. 1, is derived from a sensor signal of active ankle torque, T'_a (torque sensors, see Appendix A.3). The calculation has the form

$$T'_{ext} = T'_A - T'_g - T'_{in} - T'_p - T'_a \quad (10)$$

where T'_g is taken from Section 3.2 and T'_{in} from Section 3.4 (compare Fig. 7A). The passive torque T'_p is assumed to not be internally known and will be neglected in the following because it is small (<15% of the active ankle torque T'_a ; Peterka, 2002; as mentioned before, the reflexive proprioceptive torque is part of T'_a). An internal measure of the total ankle torque T'_A is calculated from body-space acceleration using the vestibular input $\hat{\alpha}_{bs}$ in the form

$$T'_A = J \frac{d\hat{\alpha}_{bs}}{dt} \quad (11)$$

where J' is a learned measure of the body's moment of inertia (without feet). Further processing of \hat{T}_{ext} comprises again a scaling (factor 0.8), a thresholding (0.18° , if transformed in angle equivalence), and the transformation into a body-space angle equivalent (box a in Fig. 3). In addition, a first order low pass filtering of the sensor signal and the other constituents is performed (0.8 Hz; see Maurer et al., 2006).

A result of parameter fitting to the human data (Maurer et al., 2006) was that $\hat{T}_g, \hat{\alpha}_{FS}$, and the local loop (i.e. inputs from vestibular and proprioceptive sensors) were more relevant than \hat{T}_{ext} (that receives its main input from joint torque input). Exceptions were two extreme stimulus conditions, where good model fitting did require \hat{T}_{ext} (also Cnyrim, Mergner, & Maurer, 2009). This may mean that normal subjects do not need to use \hat{T}_{ext} as long as contact force disturbances are small. Omission of \hat{T}_{ext} may then be advantageous, because its calculation is complex and errors may affect the system's stability. Its role as a 'spare tire' in case of vestibular loss is unequivocal, however (Mergner, Schweigart, Fennell, et al. 2009).

3.4. Estimate of foot-space translational acceleration \hat{x}_{FS}

This estimate has not been considered in our previous studies for reasons given below. Its description in the following is novel.

Translational acceleration of the feet in the space horizontal plane \hat{x}_{FS} is calculated from two vestibular signals. One of these is the linear acceleration signal of the vestibular sensor in the head \hat{x}_V^1 in which

$$\hat{x}_{Vx} = \hat{x}_{FS} \cdot \cos(\alpha_{BS}) + \hat{\alpha}_{BS} \cdot d \quad (12)$$

¹ Vector $\hat{x}_V = (\hat{x}_{Vx} \cdot \hat{x}_{Vy})^T$.

where $\dot{\alpha}_{BS} \cdot d$ represents the tangential acceleration during eccentric rotation with d giving the distance of the vestibular sensor in the head from the ankle. Here, we consider for simplification the body (legs, trunk, and head) as vertical and the occurring body leans as small and slow, so that $\cos(\alpha_{BS}) \approx 1$ (and the head vertical vestibular signal \hat{x}_{Vy} can be neglected). Therefore, the translational estimate is derived in the form

$$\hat{x}_{FS} = \hat{x}_{Vx} - \frac{d(\dot{\alpha}_{BS})}{dt} \cdot d' \quad (13)$$

where $\dot{\alpha}_{BS}$ is the other vestibular signal and d' represents the internal knowledge of d (compare Fig. 8A). Noticeably, the vestibular linear acceleration signal shows high pass characteristics (see Fig. 10B in Mergner, Schweigart, & Fennell, 2009). This was not considered here, for simplification. Further processing of \hat{x}_{FS} again comprises scaling and thresholding (values not yet assessed experimentally). Model simulations confirmed that \hat{x}_{FS} yields a valid estimate of \hat{x}_{FS} (see also Section 4.3).

For use in the control, an internal measure of the evoked inertial torque T'_{in} is obtained from \hat{x}_{FS} and the vestibular signal α_{BS} through:

$$T'_{in} = -\hat{x} \cdot m \cdot h \cdot \cos(\alpha_{BS}) \quad (14)$$

The term $\cos(\alpha_{BS}) (\approx 1)$ is omitted in Fig. 8A in the wake of the small angle simplifications. Finally, the transformation into a body-space angle equivalent is performed (box a in Fig. 3).

A copy of T'_{in} is used in the estimation of \hat{T}_{ext} ; it removes the inertial torque disturbance in the T'_a sensor signal (see above, Section 3.3). Therefore, if \hat{x}_{FS} is omitted, and with it the copy of T'_{in} , the compensation of T_{in} is automatically delegated to the \hat{T}_{ext} compensation. Therefore, it is difficult to provide experimental evidence that \hat{x}_{FS} is an essential constituent of human stance control (a reason why we did not include it in our previous studies). Generally, one might argue that T_{in} has the same effect on ankle torque as a push or pull contact force stimulus. So, why treat it separately? For a solution of this question one may consider additional ways of using \hat{x}_{FS} in stance control, for instance in cognition and volition (below, Section 4.3).

In summary, a method for an automatic sensory reweighting is described, which allows humans to cope with situations where the four external disturbances have impact on their stance. It involves an online multisensory processing level ('meta level') that is interleaved between the sensors and their use in feedback control. At the meta level, fusion and thresholding of sensor signals yield estimates of the four disturbances. The estimates are fed into a proprioceptive ankle angle feedback loop for disturbance rejections. The result is a purely sensor-based disturbance estimation and compensation (DEC) mechanism.

4. Volitional effects

The following section deals with the human ability to exert voluntary control over the reactive stance control, i.e. with fusion of the 'proactive' and reactive controls. To the best of my knowledge, there are hardly any human system identification studies of this fusion currently available in the literature. Therefore, this section presents mainly novel concepts and results. It uses model simulations to explore whether and how the DEC mechanism may be used for the fusion. The simulations are aimed to derive hypotheses and guidelines for future human experiments.

In previous works, we have shown that the DEC model can be used to generate voluntary lean movements without interfering with the reactive disturbance compensation (Mergner, 2004; Mergner, Schweigart, & Fennell, 2009; an old debate on such an interference is briefly outlined in Appendix E). To generate the voluntary lean, a desired movement signal may be fed into the

model's set point input (see this input in Fig. 3, which 'servoes' the reactive control loop to perform the voluntary movement). However, the previous work left open several aspects such as the question how to deal with self-produced disturbances arising from the movement. Prediction and anticipation of the self-produced disturbances, but also of external disturbances are considered in the following. Furthermore, volitional modification of the external disturbance compensations is included (addressed as control policy). These three aspects of voluntary control (see illustrations in Fig. 4B–D) directly profit from the meta level of the DEC model, i.e. from the explicit internal representation of the disturbances generated or arising in the outside world. This form of representation facilitates context-dependent prediction and anticipation.

4.1. Disturbance compensation policy

Humans are able to switch the compensation of each disturbance on and off. A 'sensory reweighting switch' for the FS compensation was identified in humans in a study by Schweigart and Mergner (2008). It was found that humans, who stand on a support that first is stationary for a while and then is tilted, switch from a body-support stabilization to a body-space stabilization strategy when the body-space excursion exceeds a certain value (approx. 1° forward and 0.5° backward). The findings could be mimicked using the DEC model in software and robot simulations (also Mergner, Schweigart, & Fennell, 2009). Other intuitive examples of voluntary changes in disturbance compensation policy would be to giving way to an external push or pull stimulus, instead of resisting it, or to allowing gravity to tip the body over. The repertoire of policies reflects the four disturbance estimates of the meta level.

There exist also possibilities other than switching the estimate on or off. For example, fall due to gravity can voluntarily be slowed. In software and robot simulations, one can mimic such graded compensations by changing the scaling factors of the disturbance estimates (not shown). Furthermore, humans have the ability to modify the compensations by internally tracking through the set point input a foreseen or expected external disturbance (example below).

Two additional aspects may be considered in this context. First, if an estimate is not functioning for some reason or is switched off, its job is taken over partially or fully by the other estimates (e.g. if \hat{x}_{FS} is switched off, its job is taken over by \hat{T}_{ext} ; above, Section 3.4). Second, humans also have the ability to modify the proprioceptive joint angle stabilization (α_{bf} signal of local loop; modification mechanisms not considered in Fig. 3). This applies, for instance, when a neurologist assesses the 'muscle tone' of a patient's limb by moving it periodically while instructing the patient to relax. A form of pathological resistance, called rigidity, is found in patients with Parkinson's disease, a basal ganglia disease. In a recent study (Anastasopoulos, Maurer, Nasios, & Mergner, 2009), Parkinson disease rigidity could be attributed to patients' inability to efficiently neutralize the reflexive joint stabilization. This is in contrast to healthy subjects who neutralize it by internally predicting and tracking the periodic external passive limb motion. The finding suggests that voluntary or, more general, predictive context-dependent interference with the reactive control involves the basal ganglia (compare Appendix D).

4.2. Anticipation of self-produced disturbances

Here, the question is addressed how the DEC model deals with self-produced disturbances that arise during voluntary movements (compare gravity effect in Fig. 4C).

Generally, such preparatory activities are called postural adjustments (PAs; overview, Bouisset & Do, 2008). During

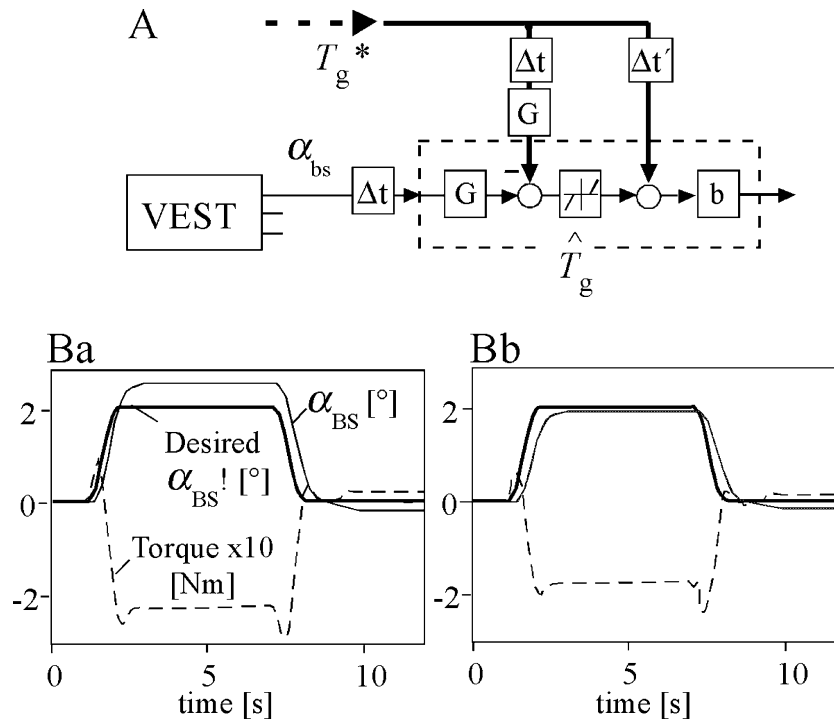


Fig. 5. (A) Estimate of gravitational torque disturbance \hat{T}_g and its prediction signal T_g^* that arises with a proactive body-space lean. (Box b, angle-to-torque conversion). (B) Software simulation results for a 2° voluntary lean forward and back. (Ba) Without prediction. (Bb) With prediction.

voluntary movements, they often are identified on the basis that they involve muscles other than the primary mover muscles, for which they may provide the postural platform. Different types of PAs may be distinguished. For instance, they may either be anticipatory, synchronous, or consecutive. With multi-link postural control, PAs may occur as ‘chains’ (in sequence) and appear to help in coping with inter-link force couplings. It is also known that they are adaptable to changes in functional state (fatigue, growth, structural impairment, microgravity, etc.). But it is still open how they are generated and controlled.

In the following, a mechanism for anticipatory disturbance compensation with the DEC model is suggested and its effect on accuracy and movement effort is explored using software simulations.

Referring to the example of Fig. 4C, the increase of gravitational torque T_g during a voluntary body-space lean is simulated.² First, an unforeseen passive lean is considered (no prediction; dominant frequency $f_d = 0.4$ Hz, $A = 2^\circ$). The reactive compensation through the sensory estimate \hat{T}_g is shown in Fig. 5Ba. COM displacement overshoots the desired lean angle. This is mainly due to the nonideal scaling and the threshold of \hat{T}_g (compare Section 3.2 and Fig. 5A; $G = 0.8$; threshold, $\pm 0.1^\circ$; sensory delay, $\Delta t = 100$ ms). The below-unity scaling, the threshold, and the resulting under-compensation of the gravity compensation are attributed here mainly to noisy and inaccurate information in the sensory signals (Section 3.1).

With prediction of T_g during proactive lean, the signal T_g^* is streamed from a hypothetical stored central representation into the estimate \hat{T}_g , thereby replacing the sensory estimate. To this end, two versions of T_g^* are summed with \hat{T}_g . The first version closely resembles the sensory estimate (same afferent sensory transport and processing delay and scaling factor, similarity acquired through learning). It is subtracted and therefore tends to

cancel \hat{T}_g . The second version is assumed to be closer to ideal, in that it carries a shorter delay ($\Delta t' = 10$ ms), due to its central origin, a scaling of unity, and no threshold (due to repeated improvements of the stored representation by learning). The second version is added. The result is that the lean now meets better the desired value and timing is better (Fig. 5Bb; note that the earlier response in panel Ba owes to a partial ‘falling’ towards the desired value). Furthermore, less torque is required for the movement.

This concept resembles the Smith predictor method (Smith, 1959; compare Miall, Weir, Wolpert, & Stein, 1993 for another sensorimotor application of this method). It *directly* uses learned information on sensory delays and scaling factors. In contrast to observer methods, for example, it does not require a continuous generation of internal information by feeding a motor *command* efference copy through internal models (compare above, Section 3). The T_g^* signal is generated in relation to the *desired* body-space lean, representing the predicted *external disturbance*. In the literature, other and possibly complementary ways to make the desired movement signal reach its goal are the adding of some form of inverse dynamics or using robust tracking (e.g. Johansson, Fransson, & Magnusson, 2009; Tahboub, 2009). It remains to be evaluated to what extent these can be replaced by the here posited prediction.

With fast voluntary movements (e.g. upper body-on-hip or head-on-trunk movements), prediction may include in addition movement-contingent centrifugal and Coriolis forces. These may possibly be covered by the prediction T_g^* as well, in the same or some analogous form. Furthermore, humans may predict self-produced impacts on their bodies also from the other three disturbances. For instance, this may be a contact force when hitting an obstacle or a support surface rotation when stepping on a seesaw or on compliant ground. In these situations, the disturbance may not be fully predictable, so that a mixture between self-produced and unforeseen external disturbance (or disturbance parameters) arises. Humans usually are able to cope with such situations without catastrophe. This ability is attributed here to

² Here and in the following model and robot simulations, the stimulus waveform was a ‘raised cosine velocity function’ (characteristics are defined by amplitude A and dominant frequency f_d (details in Appendix F).

fusing the prediction of the self-produced and external disturbances with the disturbance estimations.

4.3. Anticipation of external disturbances

Humans often perceive the external disturbances as outside world events that may be learned and predicted in some context dependent way (compare 'long latency reflexes' in Appendix D). Furthermore, external disturbances may arise to various extents in combination with self-produced disturbances during voluntary movements (Section 4.2). For anticipating the external disturbance (example in Fig. 4D), the DEC model assumes again that a stored disturbance representation is streamed from high centers (e.g. cerebral cortex) via intermediate processing stages (e.g. cerebellum) to the disturbance estimation mechanism. There, it tends to cancel the sensory estimation by replacing it with a 'better' signal (shorter delay, no threshold, and scaling closer to unity) in the same way as described above (Section 4.2).

Simulations of support surface tilt responses without and with prediction of $\hat{\alpha}_{FS}$ are shown in Fig. 6 ($f_d = 0.2$ Hz, $A = 2^\circ$). Again, two versions of the prediction signal (α_{FS}^*) are summed with the sensory estimate (Fig. 6A). The first version closely resembles the sensory input (same delay, $\Delta t = 100$ ms, and scaling factor, $G = 0.75$), and hence cancels it. The second version, representing the original prediction (short delay, $\Delta t' = 10$ ms, unity scaling), is added after the threshold and substitutes the sensory estimate.

Fig. 6B gives simulation results for the COM responses ($\alpha_{COM} = \alpha_{BS}$) and active torques in panels Ba and Bb, respective-

ly. The responses obtained with prediction (curves 2) yield better tilt compensation than without prediction (curves 1), in that α_{COM} and torque are smaller. The response differences between (2) and (1) owe mainly to the better scaling of the prediction signal. To illustrate this point, a simulation is shown (curves 2') where the scaling was not improved. If the prediction is made to start earlier or later than the tilt onset (e.g. 300 ms or more; not shown), there is still a clear benefit as compared to the situation without the prediction, which also is mainly due to the better scaling. Unexpected failure of tilt occurrence leads to α_{COM} response and torque in the 'wrong' directions (curves 3). However, these 'errors' are remarkably small compared to the responses that result if $\hat{\alpha}_{FS}$ is completely missing (e.g. switched off, curves 1'). The reason is that the two α_{FS}^* prediction versions then partially cancel each other. Thus, by using this prediction method, even a completely erroneous prediction is not disastrous.

Also, the responses to external contact forces and support surface translational acceleration profit from prediction. Fig. 7B gives the results obtained with a forward pull stimulus ($f_d = 0.2$ Hz, $T_{ext} = 8$ Nm). Without prediction (panel Ba), the pull leads to a small forward COM lean (α_{COM}). Active ankle torque is backward, compensating for both the stimulus and the COM's gravitational torque. With prediction (Bb), there is a small COM lean backwards, so that the COM's gravitational torque 'helps' compensating the pull stimulus. If \hat{T}_{ext} and T_{ext}^* are entirely omitted, there is a COM response forward, which is somewhat larger than in Ba (not shown). If only \hat{T}_{ext} is omitted, leaving T_{ext}^* (its second part in panel

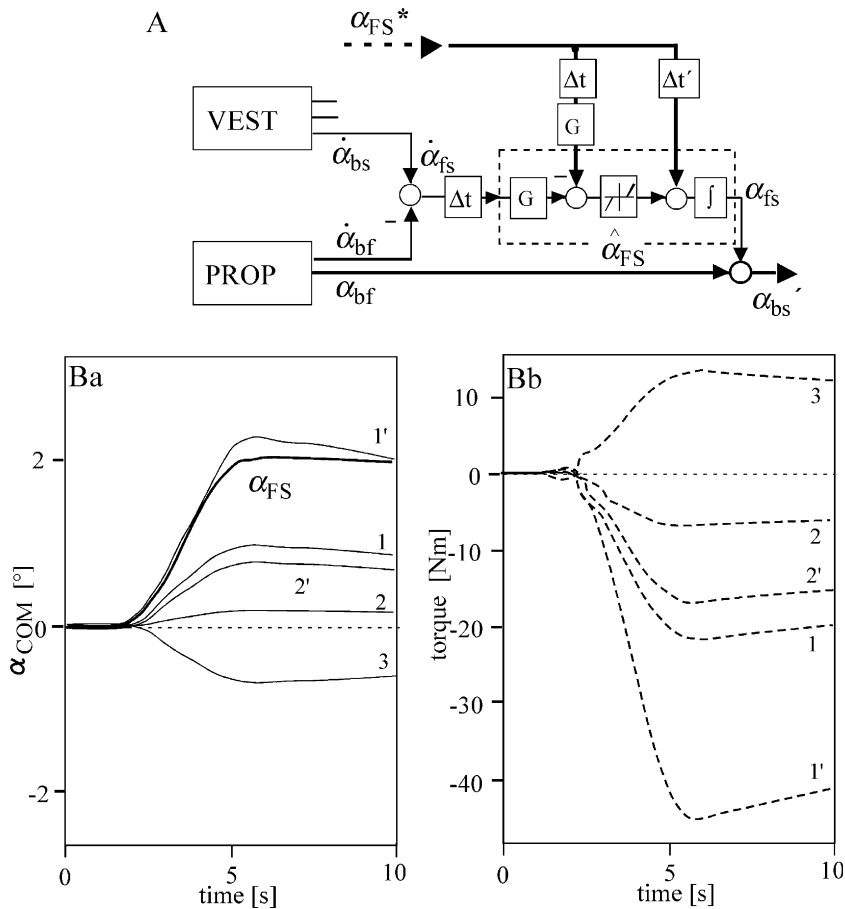


Fig. 6. (A) Estimate of foot-space rotation disturbance $\hat{\alpha}_{FS}$ and its prediction signal α_{FS}^* . (B) Software simulation results for a 2° forward support surface tilt. Ba gives α_{BS} ($= \alpha_{COM}$) responses and tilt stimulus α_{FS} , Bb corresponding active ankle torques. Curves 1, no prediction (1', for comparison estimate $\hat{\alpha}_{FS}$ in addition disabled). 2, with prediction (2', timing and threshold effects only, scaling effect omitted). 3, prediction as 2, but disturbance (tilt) fails to occur ('sham trial').

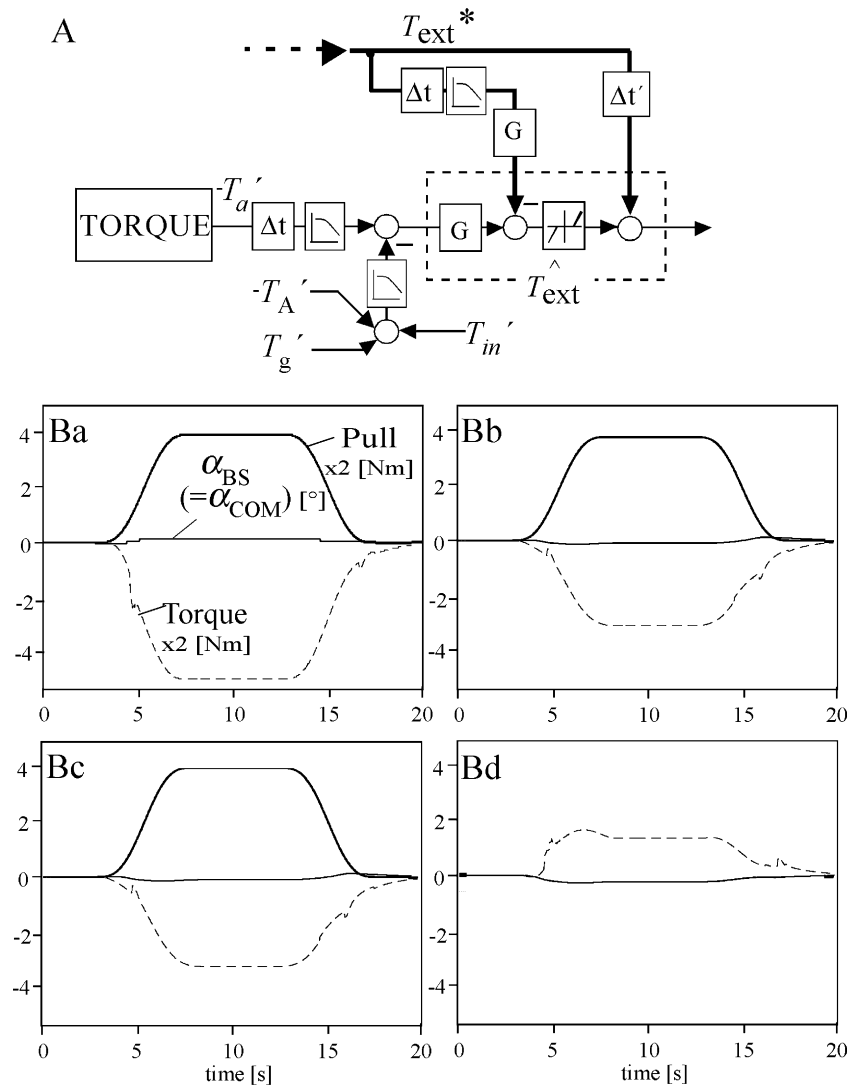


Fig. 7. (A) External contact force estimate \hat{T}_{ext} and its prediction signal T_{ext}^* . (B) Software simulation results for a forward pull stimulus showing COM angular displacement (α_{COM}) and active ankle torque responses. (Ba) Without prediction. (Bb) With prediction. (Bc) Prediction only (\hat{T}_{ext} switched off at threshold). (Bd) With prediction, but here pull stimulus fails to occur ('sham trial').

A), the response (Bc) is the same as in panel Bb, confirming that there the first part of the prediction completely cancelled the sensory estimate. With a sham trial (with \hat{T}_{ext} and its prediction active, but stimulus not occurring), a small anticipatory COM backwards lean results (Bd). The reason that the sham trial effect is so small is again that the two parts of the prediction signal then partially cancel each other.

Fig. 8B shows prediction results obtained with a foot-space translational acceleration disturbance forward and back (\ddot{x}_{FS} ; translation $x = 0.2$ m, $f_d = 0.2$ Hz, peak accelerations, ± 0.05 m/s²). Upon the initial forward acceleration, there results a COM excursion (α_{COM}) backwards followed by a forward excursion upon deceleration (simulation without prediction; Ba). With prediction \ddot{x}_{FS}^* (Bb), the initial backward COM excursion is soon cancelled and then replaced by a forward excursion, with less torque being produced. Retesting with wrong prediction timing (500 ms delayed) still led to a small improvement of the response (Bc). In a sham trial, solely some predictive COM response resulted (Bd; not disastrous). With complete omission of \ddot{x}_{FS} (Be), the COM response is basically similar to the one without prediction in panel Ba (as predicted; compare Section 3.4). When omitting in addition to \ddot{x}_{FS} also \hat{T}_{ext} , the COM responses and the torques are clearly larger (Bf).

Predictions of \hat{T}_g are assumed to arise mainly in relation to proactive movements (generally, of torques evoked by gravity, centrifugal forces, and Coriolis forces; see above, Section 3.2).

In the previous section (Section 3), it was pointed out that humans possibly use only two of the four disturbance estimates most of the time for their reactive stance control (\hat{T}_g and $\hat{\alpha}_{FS}$, together with local loop), making the other two (\hat{T}_{ext} , $\hat{\alpha}_{FS}$) largely redundant. This section provided an argument not to completely omit the latter, since the control appears to profit from the specific prediction of each of the four disturbances. It remains to be evaluated to what extent also the system's stability profits from the predictions due to shorter time delays.

In summary, the DEC model easily lends itself to include volitional control in terms of control policy and disturbance prediction. In model simulations, a method is demonstrated which replaces the sensory derived disturbance estimates by predicted ones with shorter time delays and better scaling. The method leads to more accurate balancing and this with less effort for both, self-produced and external disturbances. Erroneous anticipatory disturbance compensations in sham trials are small and not disastrous, because two components of the predictions then partially cancel each other. These simulations together with

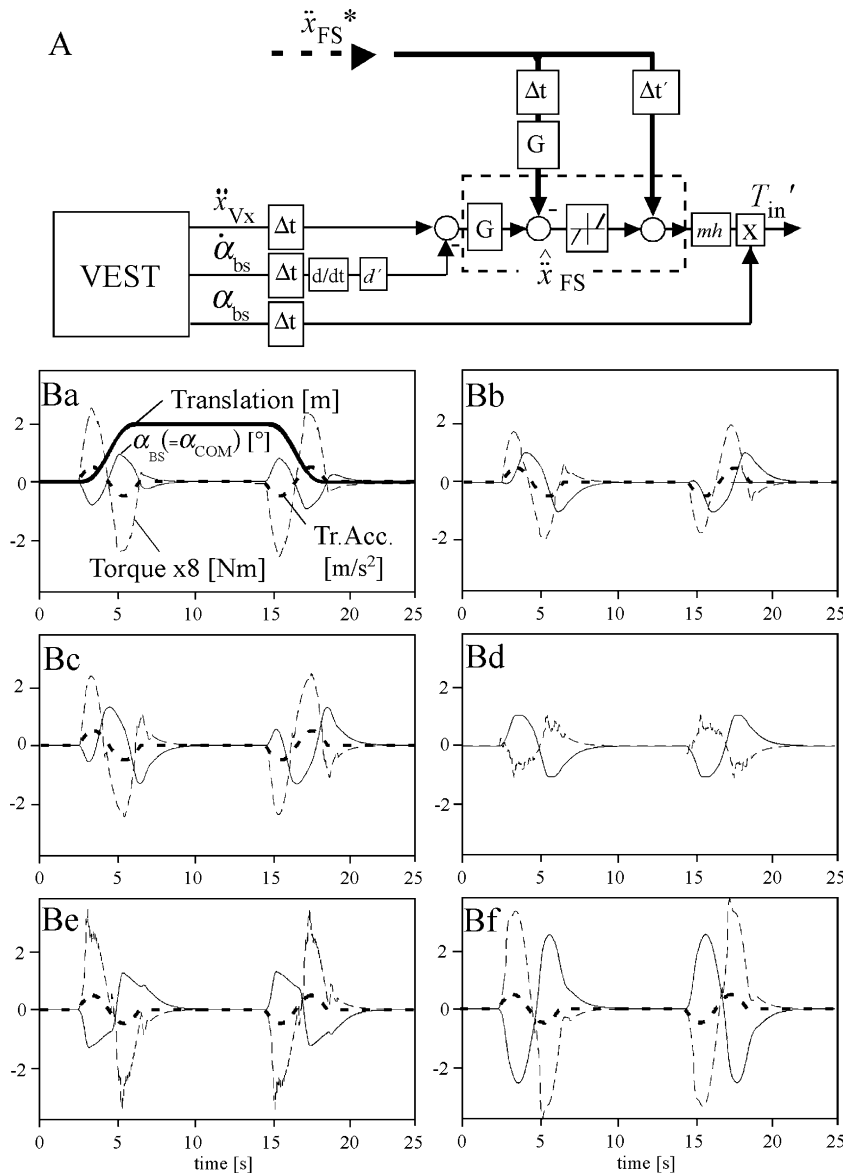


Fig. 8. (A) Estimate of foot-space translational acceleration \hat{x}_{FS} and its prediction signal \hat{x}_{FS}^* . (B) Simulation results for a forth-back translation. Shown are the translation, the translational accelerations (Tr. Acc.), COM angular position (α_{COM}), and active ankle torques. (Ba) Without prediction. (Bb) With prediction. (Bc) With prediction, delayed by 500 ms. (Bd) Sham trial. (Be) Complete omission of \hat{x}_{FS} and its prediction. (Bf) Omission of both, \hat{x}_{FS} and \hat{T}_{ext} .

corresponding future human experiments may help the identification of the human control system, which is hampered by multisensory redundancy as well as free-choice omissions (of estimates when not needed) and additions (not considered so far, such as loop gain adjustment or modification of joint impedance by agonist–antagonist co-contraction).

5. Augmenting modelling by robot simulations

Analysis, abstraction, and modelling of sensorimotor functions are often performed in an iterative back and forth between modelling and experiment using engineering tools. For many years, however, results stayed behind expectations. There were exceptions such as modelling of basic oculomotor functions (Robinson, 1987) and vestibular self-motion perception (Young, 1981). Contributing to these exceptions were that eyeball mechanics are relatively simple and that self-motion psychophysics may be studied under open loop conditions, i.e. such that subjects' verbal or indication responses are not interfering with stimulation. Difficulties in modelling include that biological

systems are often complex and non-linear, calling for a holistic systems approach where the main tenet is that system properties may arise in an unforeseen way from interplays of the parts of a whole. This idea is considered nowadays across the many layers of life sciences from the behavioural levels considered here down to molecular and genetics levels (Chong & Ray, 2002). An important guideline often used in the modelling is the Occam's razor rule that demands to search for the simplest possible solution in order not to be arbitrary (Gibbs & Sugihara, 1996/1997). This goes well together with the notion that biological evolution has established computational parsimony for many brain functions (below, Section 6).

Including a robot as a re-embodied model into the iterations between experiments and modelling may enhance this approach (Fig. 9). An argument for using the robot is that pure software modelling has its limitations, especially concerning the abstraction of environments and agent–environment interactions. Real environments tend to be rich, multimodal, and noisy and the interactions may introduce unforeseen biases. Also, the agent's mechanics may be more realistic than the ones in the software model. A further argument is that real world 'analog' sensors and

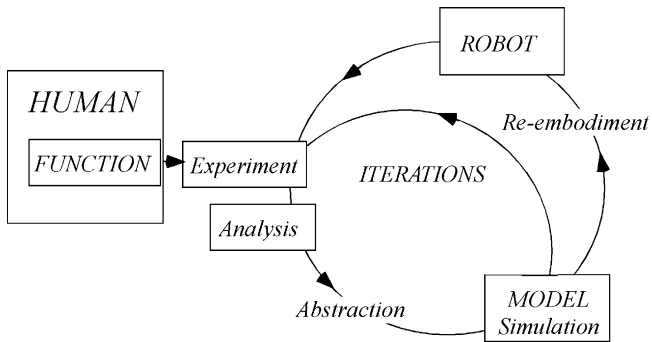


Fig. 9. Augmenting the iterative interplay between modeling and experiments by using robot simulations in addition.

actuators tend to be noisy and inaccurate, which makes them more human-like and the robot simulations a robustness test (in the general sense). Last not least, by using the robot for simulations, one may use one and the same testbed for the human-model comparisons (i.e. the posturography laboratory with all its equipment, see below).

For these reasons, we have embodied the DEC model into a biped robot (PostuRob, Fig. 10; Mergner, Huethe, Maurer, & Ament, 2006). Its anthropometric measures (height, weight, etc.) are human-inspired (Appendix F). The above described three sensor types are used: vestibular, body-foot (ankle joint) angle, and body-foot torque (details of the artificial vestibular sensor in Mergner, Schweigart, & Fennell, 2009). Freely standing on its feet, the robot's body is actuated about the ankle joints through leg (front and back) pneumatic 'muscles' that carry 'tendons' (springs) at their fixations (one DOF). Performance tests are obtained in a clinical posturography laboratory that includes a 6D motion platform, an optoelectronic motion capture device and a COP measuring platform.

PostuRob's reactive stance stabilization proved to be human-like (and thus was considered a 'proof of principle'). Video clips can be found at www.uniklinik-freiburg.de/neurologie/live/for-

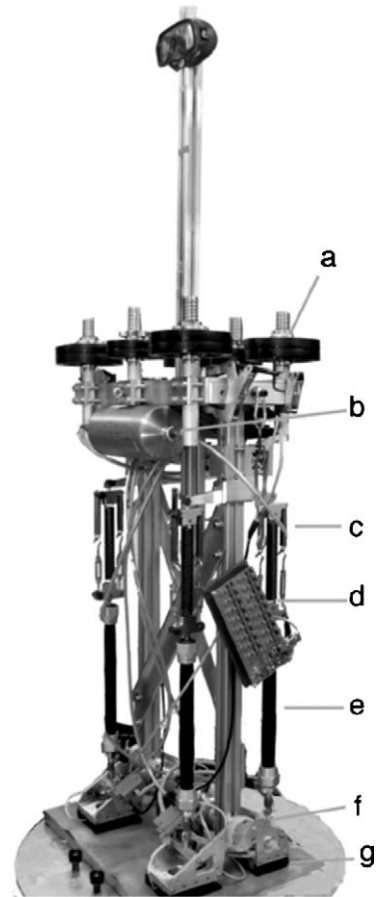


Fig. 10. PostuRob. a, weights; b, pneumatic system; c, springs ('tendons'); d, electronic sensor board with artificial vestibular system; e, pneumatic muscles; f, ankle potentiometers (joint angle proprioception); g, foot sole pressure sensors (force cues).

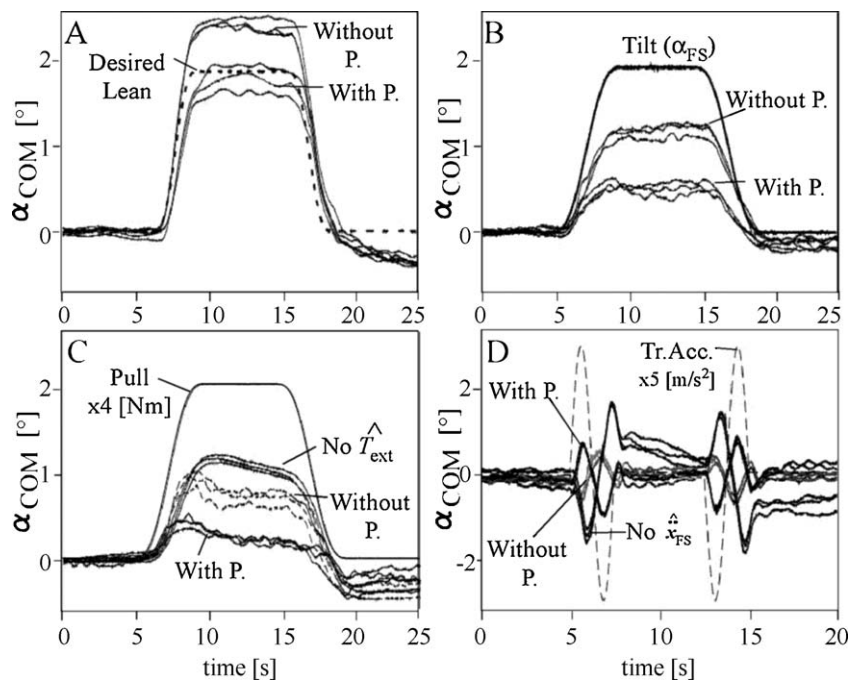


Fig. 11. Disturbance anticipation in robot simulations. (A) Proactive forward body lean (P., prediction). (B) Compensation of forward support surface tilt. (C) Compensation of forward pull stimulus (No \hat{T}_{ext} means omitting \hat{T}_{ext}). (D) Compensation during forward-back support surface translation. Always three response curves are superimposed.

schung/sensorfusion/posturob.html). So far, probing tests comprised pull stimuli with and without BSRP, tilt superimposed on voluntary lean, load compensation, tilt onset transients, dynamic tilts while standing on a statically inclined surface (e.g. hillside; see Schweigart & Mergner, 2008), and a change in control policy (switching off $\hat{\alpha}_{FS}$). More extensive tests comprised responses to tilt with and without BSRP, comparing between robot and humans, both either with or without vestibular sensor (see Mergner, Schweigart, & Fennell, 2009).

Here, we present robot simulations that repeat the software simulations of the disturbance predictions described in the previous section. Fig. 11A shows a proactive COM forward lean without and with prediction of the gravitational torque disturbance ($f_d = 0.4$ Hz, $A = 2^\circ$). Similar as before (Fig. 5Ba,b), the lean with prediction is closer to the desired lean than that without prediction (and the required torque is less, not shown). Fig. 11B shows the robot's compensations of support surface tilt without and with prediction ($f_d = 0.2$ Hz, $A = 2^\circ$), confirming a better compensation with prediction. Fig. 11C shows that compensation of a forward pull stimulus ($f_d = 0.2$ Hz, $T_{ext} = 8$ Nm) is better with prediction than without. Furthermore, it shows that omitting the external torque compensation (No \hat{T}_{ext}) yields a smoother, but less efficient compensation. Fig. 11D shows the results for the support surface translational acceleration ($f_d = 0.4$ Hz, $x = 0.14$ m; peak accelerations, ± 0.14 m/s²). Without prediction, the initial COM excursion is counter to the initial acceleration, whereas with prediction there is an anticipatory lean in the direction of the accelerations that helps stabilization. When the estimate \hat{x}_{FS} is switched off, there is a COM excursion counter to the acceleration, which is clearly larger than with \hat{x}_{FS} and no prediction (\hat{T}_{ext} takes over the T_{in} compensation, but less efficiently, because of its low pass filtering; compare Sections 3.4 and 4.3).

These simulations demonstrate that the method of disturbance prediction and anticipation, which before was implemented and tested in the model (section 4.), holds when it is applied to the robot. Using the robot simulations yielded several additional merits, which are described elsewhere (Mergner, Schweigart, & Fennell, 2009). They underline what often is captured by the slogan 'learning by doing' (e.g. Kawato, 2008).

In summary, the robot simulations demonstrate real world applicability of the disturbance prediction and anticipation method that builds on the framework of the DEC model.

6. Conclusions

A detailed system identification of human sensorimotor functions is more relevant for clinicians than for roboticists. Engineers who build humanoids may be satisfied with gross similarities to humans in form and behavior. Clinicians, in contrast, try to understand the human functions in depth to be able to interfere with them therapeutically (by using prostheses, brain and nerve stimulation, etc.). The more human-specific the therapeutic intervention or assistive device is, the better is the chance that it functions well in, and is accepted by the patients. For engineers interested in prostheses and assistive devices, adapted lectures and books of human anatomy, neurophysiology, and pathophysiology of sensorimotor impairments are available (e.g. Popovic & Sinkjaer, 2003; also for related sensorimotor control topics not covered in this article).

The system identification of human sensorimotor functions just started and still meets considerable problems. Approaches based solely on systems analysis are unlikely to suffice. To obtain more information on the underlying 'neural machine' one needs means to 'look into the brain'. Molecular research is too far away to help. Electrophysiological and imaging techniques do help, but interpretation of these findings is hampered by the distributed

processing principle that the brain is using (which appears to some extent reminiscent of that in artificial neural networks).

Our approach, which led us to the DEC model, proceeded from clinical evidence concerning the sensory modalities involved, from perception psychophysics (Appendices A and B), and from the dominant role of sensors in reactive balancing. The psychophysics suggests that humans use explicit sensory representations of the physical variables, from which they reconstruct then the interaction between the outside world and the own body mechanics. These findings were formalized in a meta level concept where sensory disturbance estimates are online calculated and then are used, instead of the sensors' variable measures, in a feedback control using the DEC method for disturbance rejection.

As described above (Section 3), the DEC model builds on previous system identification studies of reactive human stance, which suggest a PD controller and some form of multisensory integration. The human ability to immediately cope with changing external disturbance situations is mainly attributed to sensory reweightings. The DEC model performs these reweightings in an online and automatic way that includes thresholding. The model covers human experimental data across a large diversity of situations. Further work is required to evaluate its modularity in a multi-segment body.

In this article, we explored how the DEC model lends itself to a volitional control over the reactive balancing, which is an important aspect of the proactive-reactive fusion issue. The model simulations show that the DEC model lends itself easily to implementing control policy changes and the prediction and anticipation of disturbances, self-produced or external. As to the external disturbance predictions, the method posits context dependent recall of learned external events that are stored in look up tables. As a result of the anticipation, compensation is more accurate and requires less effort, as demonstrated in our software simulation. The robot experiments demonstrated then the method's applicability under real world conditions. The findings will be used as guidelines in future human experiments.

Some of the future work will focus on assistive devices for sensorimotor disabled patients. From the book of Popovic and Sinkjaer (2003) it becomes evident that many patients do not accept the currently available devices. One reason appears to be that these devices deal almost exclusively with mechanical and motor aspects and leave sensory aspects unconsidered. This reflects to some extent experience with patients who were provided, in addition, with sensor information and consider it not as helpful. The control method used in PostuRob provides an explanation and represents a kind of blueprint on how to include sensors and sensory processing in assistive devices for stance control. It demonstrates that humans perceive external disturbances from a specific composition of sensor signals, rather than perceiving individual sensor signals when balancing. This becomes especially relevant when humans predict the external disturbance and try to match predicted with actual perception (Section 4).

Therefore, in case of a spinal cord injury with the need for a functional electric muscle stimulation (FES) and its control through technical sensors, a full human-like disturbance reconstruction requires the processing of vestibular, ankle angle, and force sensor signals. It is possible to use less sensory information, but performance is then more limited. This is shown in the simulations where the estimates of external contact forces and translational accelerations of the support surfaces were omitted (\hat{T}_{ext} and \hat{x}_{FS} ; Section 4). Furthermore, it was shown that vestibular loss patients balance quite well with eyes closed on stable support, resorting to joint angle and force sensors, but fall on compliant support (stance control model in Mergner, Schweigart, & Fennell, 2009; robot simulations, Schweigart & Mergner, 2008).

The DEC model comes with flexibility, fault tolerance, and computational parsimony. These properties are typical of biologi-

cal systems, where they have been optimized over hundreds of millions of years of evolution. For example, the sensors represent stand-alone solutions with multipurpose functions, which in each vertebrate species and individual come 'from the shelf', and this already with some form of noise optimization (e.g. in the vestibular sensor; Mergner, Schweigart, & Fennell, 2009).

Flexibility and fault tolerance in biological systems appear to arise from interactions among relatively simple control mechanisms and between these and the physical laws of the outside world, as expressed in earlier visions of psychophysics (e.g. Wagemans, 1990) and robotics (e.g. Brooks, 1990). This notion is also reflected in the first autonomous robots with adaptive goal seeking and scanning behavior, an extremely simple artificial 'turtle' built by the neurologist Grey Walter around 1950 (Freeman, 2003). It is often viewed as an existence proof that brain functions may be simpler than often supposed. This view should be contrasted with recent attempts in computational neuroscience to combine many different sensorimotor control aspects in one powerful and complex algorithm. For example, it has been suggested that an optimal feedback control method may be used to adaptively correct the control for essentially all relevant interferences with task goals (Todorov, 2004; Todorov & Jordan, 2002). A warning from biologists is, however, that such methods come with a large computational price, this even for the simplest movement (Scott, 2002).

There is likely no controversy about computational parsimony being a goal of biological evolution. But still arguable is what makes, in brains, a high versus a low computational effort. Anyway, sensorimotor functions appear to belong to the more simple behavioral functions, if one considers that they are realized with surprising performance even in very small animals such as fruit flies (*Drosophila*; whole body size, 2–3 mm) that have only a few neurons at their disposal. Therefore, it does not come as surprise that some neuroscientists criticize the optimal control approach as too computationally demanding and conceptualize simpler motor control architectures (e.g. Andani, Bahrami, Maralani, & Ijspeert, 2009).

Authors of modeling studies often argue with supportive evidence from neural activities in brain structures reported in literature (e.g. Andani et al., 2009). This kind of biological inspiration is dangerous, however, since it may be selecting among a large diversity of findings and yield what is desired. Safer is the iterative back and forth between experiments and modeling (Fig. 9). In this article, function-to-structure assignments for the human nervous system were largely omitted, because they would still be rather general and hypothetical. We need more exact analyses of the stance control deficits in neurological patients (cerebellar impairments, Parkinson's disease, etc.) as well as corresponding databases. An important source of inspiration for assignments comes more and more from functional brain imaging. Inspirations also come from engineering control architectures (e.g. for the cerebellum; Ito, 2006, 2008) and will profit from the interdisciplinary research field neurorobotics (e.g. Mergner & Tahboub, 2009).

There has been impressive progress in the engineering evolution of humanoids over the last decades. In early simple humanoids, the robot's balance during walking often relied on pre-planned movements, guaranteeing that the COP remains within the base of foot support. They did not use reactive balancing with sensory feedback. More recent robots used online continuous or discontinuous force feedback for COP control (Caballero, Armada, & Alarcón, 2006; Prahla, Dip, & Meng-Hwee, 2008). Yet, their motor performance in stance still stays clearly behind that of humans (Mahboobin et al., 2008; Peterka, 2009). The most recent and advanced humanoids use, in addition, gyros and translational accelerometers for kinematic body-space sensors similar to the vestibular sensor, and their balancing performance comes closer to

that of humans (e.g. Löffler, Gienger, & Pfeiffer, 2003). Thus, sensors are instrumental for balance performance. Some of the most advanced robots are currently made by commercial companies (e.g. Asimo of Honda) that provide, however, only little information on the control methods used. More information is available on humanoids from universities such as the WABIAN robot (short for WAseda BIpeal HumANoid; see <http://www.takanishi.mech.waseda.ac.jp/top/research/index.htm>, also for scientific publications). Furthermore, there is published robotics work on balancing from neuroscience institutes such as the Computational Neuroscience Laboratories ATR in Japan. For example, using a commercial robot as platform (CB of SARCOS; Cheng et al., 2007), control methods are described that cover several behavioral aspects that are in common with those considered in this article for humans, such as balancing during external forces and on compliant body support surface (Hyon, 2009a,b; Hyon, Hale, & Cheng, 2007).

The balance control methods used in Asimo, WABIAN, and CB differ from each other, and these methods differ from the method described above for humans. Yet, certain basic aspects appear to be similar, such as a hierarchical architecture with reactive inverted single pendulum balancing at the basis, rescue reactions (e.g. preprogrammed stepping responses) attached, and proactive movement control (preprogrammed with fast walking, for example) superimposed.

Since robotics and neuroscience are facing related control problems, both will profit from interactions and collaborations. For example, roboticists designing humanoids may want to give them human-like behavioral flexibility and robustness, while neuroscientists may want to extend their systems identifications to include idiosyncrasies, learning of new solutions after brain damage, etc. This will help clinical neuroscientists to better understand sensorimotor pathologies. But they will also contribute to the system identification research by investigating and valuating impairments in patients as 'experiments by nature'.

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Appendix A. Sensors and sensor concept

From historical and evolutionary perspectives, intuitive analogies emerge when one compares evolution of biped stance control as depicted in ancient art with that in child development and in robotics and includes sensors and sensory processing in the consideration. Fig. 12 gives schematic examples of ancient Greek statues from the Old Period (a; 620–480 BC), the Classic Period (b; 480–320 BC), and the Hellenistic period (c; 320–30 BC). The statues of the Old Period show a static body-support control on firm and level support. Those in the Classic Period display more of an active body-support balancing, still on firm support. In the Hellenistic Period some statues appear as freed from the need of a firm support. Indeed, humans are capable of balancing on compliant or moving supports and of orienting in water immersion. Their control involves a body-space sensor (vestibular sensor, below, A.1) that evolved in sea-living animal ancestors. It allows already infants to swim and orient during water immersion. In childhood with its maturation of sensorimotor pathways and brain centres, balancing skills on firm support develop similar as in the old statues. It starts with stance, and then comes locomotion, before balancing on compliant surfaces can be performed. Humanoid robots' biped stance and locomotor skills show a similar

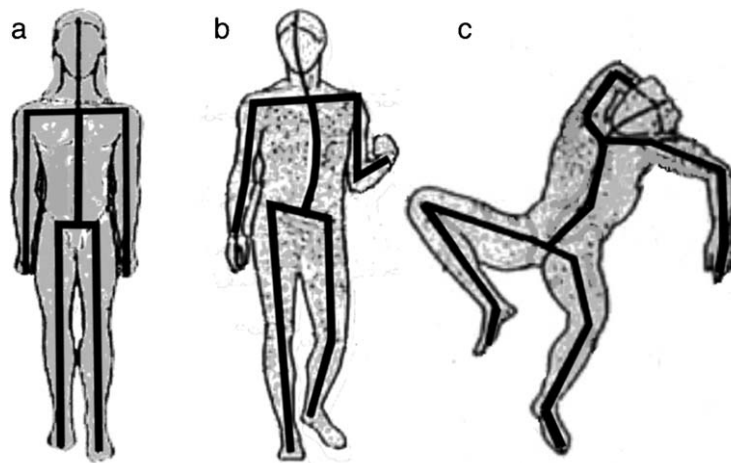


Fig. 12. Postures of life sized statues in ancient Greece. (a) Old period (statues are called Kouroi). (b) Classical period. (c) Hellenistic period.

development from passive towards active balancing and from a body-support towards a body-space control, this in relation to the use of more sensors and sophisticated sensor processing (above, Section 6; Bekey, 2005).

The sensors involved in the equilibrium control of adult humans are described below in abbreviated form (each of the following subchapters actually reflect large research areas in their own right). The term ‘sensor’ is used here for a chain of elements starting with receptors transducing physical events into neural signals, and terminating in an information processing network that outputs measures of kinematic and kinetic variables. Existence proof of this sensor concept, derived from psychophysics, will be described. Psychophysics may be used to characterize the variable measures in terms of transfer function, detection threshold, and noise (by analyzing response variability).

Disequilibrium and disorientation in patients with sensory loss indicate that mainly *vestibular*, *visual*, *joint angle proprioceptive*, and *force/torque sensors* are important, but vision is not instrumental (Horak & Macpherson, 1996).

A.1. Vestibular system

The vestibular system was the latest to be discovered among the human sensory systems (Breuer, 1874; Crum-Brown, 1874; Flourens, 1842; Goltz, 1870; Mach, 1875; Menière, 1861). It supports four physiological functions of spatially oriented behavior: perceptual orientation, body stabilization, retinal image stabilization (mainly via compensatory eye movements, the vestibulo-ocular reflex, VOR), and autonomic nervous functions that include reactive blood re-distribution upon changes in body orientation (Wilson & Melvill Jones, 1979).

The *vestibular organs* are located as a symmetric pair in the right and left inner ear. Encapsulated by bone, they encode field forces such as gravito-inertial forces (Wilson & Melvill Jones, 1979). Each organ comprises two receptor systems (transducers; engineering inspired reviews Mayne, 1974; Young, 1981). (1) In the *otolith transducer*, shear between a heavy membrane and its support bends sensory hair cells, yielding a neural signal of gravito-inertial acceleration. (2) The *semicircular canal transducers* comprise fluid filled circular tubes, one for each of the three orthogonal rotational planes. Upon angular acceleration, fluid inertia exerts pressure on hair cells embedded in a gelatinous membrane (cupula) that obstructs fluid rotation around the canal. This leads to a neural signal during head rotation, but not translation (Goldberg & Fernández, 1975). Due to its viscous-elastic properties, the transducer responds to angular accelerations at frequencies above 0.1 Hz with a 90° phase lag, i.e. with a velocity signal (thus, the

transducer can be viewed as an angular velocity meter with a decay time constant; canal time constant $T = 5$ s, see Mergner, Schweigart, & Fennell, 2009).

Vertigo and disequilibrium arises most often from *unilateral canal lesions* (Brandt, 1999). Underlying is that vestibular coding of rotation is a bilaterally distributed push-pull system that modulates activity about a resting level. Consequently, pathological firing reduction on one side leads to an imbalance of the push-pull system resulting in a self-rotation illusion (Mergner, 1982). The ensuing attempt to compensate for the apparent rotation destabilizes posture and gaze and induces nausea. Fortunately, the symptoms occur only transiently. Symmetry of ‘vestibular tone’ tends to become re-established within days and weeks by adaptive mechanisms.

Chronic *bilateral vestibular loss* hardly leads to clinical complaints (Mergner, Schweigart, Fennell, et al. 2009). However, closer scrutiny may reveal blurred vision during fast self-motion as well as postural instability when standing or walking on soft ground in the absence of a visual or tactile space reference. The impairments may be quantified by electro-oculography and posturography, respectively (compare Section 2.2.2). They witness the importance of the vestibular system for human gaze and body stabilization.

Concept of vestibular sensor. Each of the two vestibular transducers comes with a problem (details, Mergner, Schweigart, & Fennell, 2009). The *canal transducer problem* arises from integrations of the input signal (mathematical angular acceleration-to-velocity and velocity-to-position integrations). This processing emphasizes low-frequency components of noise (white noise would be transformed into $1/f$ and $1/f^2$ noise, respectively). The low-frequency components stand out as fluctuating drifts. Biological remedies are mainly high pass filtering (the above mentioned canal decay time constant, ≈ 5 s) and a velocity threshold at the cost of losing some low-frequency rotation information. The *otolith transducer problem* arises from the need to decompose the transducer’s gravito-inertial force (GIF) signal into its gravitational component produced by head tilt and its inertial component from head translational acceleration (GIF resolution). The inertial component may be reduced considerably by low pass filtering. Combining this low pass filtering with the high-pass filtering of the canal signal in a canal-otolith fusion overcomes the transducer problems (in engineering called complementary filter solution). The solution works, however, only within the normal human ecological framework and not during extremely strong and lasting accelerations. Remarkably, the vestibular organ was maintained in the phylogenesis of vertebrates over hundreds of millions of years after its origination in fishes. The canal diameter is surprisingly constant among animal species across many orders of

magnitude of body weight or size. The diameter has been related to the canal time constant of ≈ 5 s and this constant has been hypothesized to represent an optimal compromise in the selection of the complementary filters (Mergner, Schweigart, & Fennell, 2009).

There is further shaping of the vestibular signals in relation to their functions (details, Mergner et al., 1991; Mergner, Schweigart, & Fennell, 2009). For example, with *horizontal* rotation (no GIF signal), the canal decay time constant may be prolonged from a value of 5 s measured at the level of the nerve to a “behavioral” value of ≈ 20 s. Another example is a thresholding of noise in human perception of self-rotation, not to be mistaken as a transducer detection threshold. This thresholding in perception of horizontal body-space rotation is at $\approx 1^\circ/s$, whereas it is considerably lower in stance control, and virtually absent in gaze stabilization. Last not least, the vestibular sensor concept also comprises a fusion across the mirror symmetric pairs of transducers in the two inner ears.

A.2. Joint angle sensor

Muscle lengthening during a rotation of a joint leads to a firing increase of sensory endings in muscle receptors called muscle spindles. These spindles make a major contribution to the joint angle and movement sense (‘muscle proprioception’, ‘kinesthesia’). Since the muscle is elastic, however, the sense has to take into account in addition to muscle length also force, both in active and passive conditions. The force information appears to stem from transducers in the tendons (Golgi tendon organs, GTOs; see Duysens, Clarac, & Cruse, 2000). With active movements, there appears to exist also a contribution from central sources (‘effort’; Gandevia, 1987). Furthermore, transducers in the skin and in the joint capsules participate (Jones, 1972).

The joint angle sensor makes a major contribution to reactive balancing. This is witnessed by lean responses that result when spindles of ankle muscles are selectively activated through tendon vibration (Eklund, 1973; Hayashi, Miyake, Jijiwa, & Watanabe, 1981; Kavounoudias, Gilhodes, Roll, & Roll, 1999). Loss of large-diameter sensory nerve fibers stemming from the spindles dramatically degrades postural skills, although the effect may be obscured by visual control or mentally commanded postures (Cole & Sedgwick, 1992; <http://deafferented.apinc.org>). Without vision, such patients are able to perform some instructed movements under laboratory conditions, but these appear to play no functional role in everyday life.

A.3. Force/torque sensor

Mainly two transducer types are important, one being the aforementioned GTOs in the tendons. At the other end of the causal chain that links the force produced by the ankle muscles to the ground reaction force are pressure and tension transducers spatially distributed in the foot and its sole. From both transducers a measure of ankle torque may be derived (van der Kooij, van Asseldonk, & van der Helm, 2005). Related posturography studies mainly focused on the foot sole cues (“somatosensory graviception”, Kavounoudias, Roll, & Roll, 2001; Magnusson, Enbom, Johansson, & Pyykkö, 1990; Maurer, Mergner, Bolha, & Hlavacka, 2001; Meyer, Oddsson, & De Luca, 2004; Stal, Fransson, Magnusson, & Karlberg, 2003). The COP shift underlying these cues can be visualized in a posturographic laboratory by means of a force transducing platform. A ‘visceral graviception’ (Mittelstaedt, 1995) has so far been studied only psychophysically under static conditions.

Evidence for a role of force cues in stance control stems also from vestibular-loss patients. Standing with eyes closed on a tilted support surface, the patients are able to indicate the gravitational

vertical and tend to align their bodies with it (see Mergner, Schweigart, Fennell, et al. 2009). In vestibular-able subjects, it is difficult to provide *conclusive* evidence for a substantial contribution from force cues as long as vestibular and joint angle cues are available. Yet, such evidence was reported in system identification studies for tilt responses at low frequency (Peterka, 2003), for pull (contact force) stimuli at low frequency on body sway referenced platform, BSRP (Maurer et al., 2006), and in tilt experiments in which gravitational torque was varied (Cnyrim et al., 2009). The study of Maurer et al. (2006) indicated that the force contribution is given centrally low pass characteristics (corner frequency, 0.8 Hz; also Mergner, Schweigart, Fennell, et al. 2009).

It is often held that humans use force cues to maintain the COP within the base of the foot support (a popular notion also in robotics). A ‘tonic excursion limiter’ was identified in vestibular-able and vestibular-loss humans, but vestibular-able subjects appear to use vestibular cues for it (Schweigart & Mergner, 2008). A likely reason why they do not prioritize force cues is that these may become less reliable than vestibular body-space cues when standing or walking on compliant support surfaces (Mergner, Schweigart, Fennell, et al. 2009).

A.4. Psychophysical evidence for sensor concept

The concept of a *vestibular sensor* that arises from canal-otolith fusion is based on congruent evidence from psychophysics and VOR studies (Mergner, Schweigart, & Fennell, 2009). Two intuitive psychophysical observations on canal-otolith interaction are briefly described. First, the self-motion percept during passive whole-body rotation in the earth-horizontal plane shows the canals’ decay time constant, whereas it shows static (gravitational) sensitivity in the vertical planes. Second, unusual rapid and lasting horizontal translation, e.g. during aircraft catapult launch on a carrier ship, leads to a body-space tilt illusion, which is a typical feature of the complementary filter fusion method.

Also the concept of a *joint angle sensor* holds. Evidence from own work on proprioception of body-head rotation is given. This percept is essentially veridical over the human ecological frequency and amplitude ranges (Mergner et al., 1991, 2001). In subjective experience, the percept stems from a single joint and one transducer, although actually it stems from a large number of transducers and a mechanically complex structure (e.g. many cervical vertebral joints). Concerning the *force/torque sensor*, the intuitive example of a COP shift upon a body lean was mentioned above (Appendix A.3), but corresponding psychophysical studies are still missing to date.

In *summary*, canal and otolith transducer signals are fused in the brain, yielding a vestibular sensor that provides 3D information of head angular velocity, attitude, and translational acceleration in space. Furthermore, sensors of joint angle and angular velocity and of joint torque can be posited. The brain obviously makes an effort to derive from many transducer signals explicit measures of the relevant kinematic and kinetic variables (the same that are used in physics and engineering sciences). This makes it easy to implement human-like technical sensors in humanoids for balancing. The vestibular sensor may be mimicked, for example, by combining gyros and accelerometers, the ankle angle sensor by a goniometer, and the ankle torque sensor by force sensors in the ‘muscle tendons’ and/or by compression load cells under the feet.

Appendix B. Meta level concept

Psychophysics of human perception of passive self-motion provides information not only on how human fuse transducer signals to obtain physical variable measures (see above, sensor

concept), but also on how these measures are further used (in neuroscience, these aspects are often combined in the term 'multi-sensory integration'). Psychophysics provides here information that, to date is not directly available from single neuron recordings in animals nor from other electrophysiological or imaging data (psychophysics contributes to make the 'black box' system identification approach a 'grey box' approach). The psychophysical function principles are applied to reactive sensorimotor control with the argument that, there, basically the same variables are processed as in spatial orientation. This is a plausibility assumption that draws on a mostly valid action-perception congruency (Mergner, 2002).

An example of further processing of the vestibular sensor information was given in Section 2.1, where an interaction of the vestibular information with joint angle information was mentioned. It was explained that a neck proprioceptive body-head signal is used to transfer the vestibular space reference from the head to the trunk (to the COM) and further proprioceptive signals to transfer it to the foot (for the foot-space estimate).

Another important finding was that *conscious self-motion perception combines different sensor signals to reconstruct external stimuli* (overview Mergner, 2002). During passive body rotation on a platform, for example, subjects relate their sensation of self-motion not to the vestibular signal in the head, but to the physical stimulus, i.e. to the platform-space motion (and physically correct consider their body motion a consequence of the platform motion). They are not aware of the underlying sensory transformations of the space reference from the vestibular organs in the head via the body to the feet and their support.

The finding of an *online sensory reconstruction of the external stimuli* led to the *meta level concept*, which assumes that the sensor signals are not directly used for feedback in reactive stance control (Mergner, 2004). Rather, an interleaved processing level is assumed, at which the external disturbances are calculated (Sections 3.1–3.4).

Appendix C. Debate on neural controller

Early posturographic studies often applied rapid transient external perturbations (onset not foreseen by subjects) and interpreted initial parts of the postural responses as being sensory triggered and rapidly preprogrammed (i.e. as open loop controlled; overview Horak & Macpherson, 1996). Later response parts were considered to be determined mainly by volition and cognition. An instrumental role of continuous sensory feedback was considered unlikely, because peripheral plus central sensory transport delays were thought to be too long to be compatible with stability of the system. As described in Section 2.2, evidence from recent work is otherwise.

There also have been studies advocating an intermittent or predictive control on the basis of findings on 'spontaneous' sway during quiet stance. For example, an 'open-loop' and a 'closed-loop' region was identified in diffusion diagrams of COP (in a form of autocorrelation analysis; Collins & De Luca, 1993). Such regions, however, have meanwhile been mimicked in model simulations of an inverted pendulum stabilization using a continuous feedback with PID controller, random-plus-control torque, and time delay (Peterka, 2000). Predictive control was furthermore postulated in relation to the relatively low passive ankle stiffness (Loram & Lakie, 2002; Morasso & Sanguineti, 2002) and to an assumption of a long delay between ankle muscle EMG and COM (Gatev, Thomas, Kepple, & Hallet, 1999; for a critical consideration of using of autocorrelation methods in this and related studies, see Johansson & Magnusson, 1991; van der Kooij et al., 2005). In view of the studies of Peterka (2000, 2002) and Masani et al. (2006), however, there is no stringent evidence for a predictive

control beyond that provided by the derivative part of the PD controller (K_D).

The model depicted in Fig. 3 contains in addition to an inner feedback loop (the local proprioceptive loop) outer loops (disturbance estimations) and these contain nonlinearities in the form of thresholdings. As a result of these, the model shows limit cycles when, for example, noise is injected or very small disturbances are used. Possibly, these limit cycles can explain the occurrence of regular changes in neural output during quiet stance (Lakie & Loram, 2006) so that one would not need to postulate an intermittent PD controller that is actively switched on and off, as suggested by Bottaro, Yasutake, Nomura, Casidio, and Morasso (2008) for quiet stance.

Appendix D. Postural reflex concept

The basic neural feedback loop from a sensor via spinal cord back to a muscle (Sherrington, 1900) may clinically be tested using muscle stretch (muscle stretch reflex), e.g. in the form of the Achilles tendon tapping reflex. The reflex tends to be weakened with impaired nerve conduction or spinal transmission. An 'exaggerated' reflex response may result from lesions of higher control centers ('release from inhibition' effect). The reflex is involuntary and stereotypic and occasionally referred to as 'short latency reflex' (latency ≈ 20 –80 ms). It may represent the early part of a more complex response where the later parts, involving ascending loops in the spinal cord and brain, are called median-latency and long-latency reflexes. These arise in a context dependent way (Diener, Scholz, Guschlbauer, & Dichgans, 1987; Kurtzer, Pruszynski, & Scott, 2008; Marsden, Rothwell, & Day, 1983).

The stretch reflex uses the joint angle sensor and stabilizes a given desired segment (link) position. A local version of it is the neck-spinal (or cervico-spinal) reflex. These proprioceptive inter-segmental reflexes together with vestibulo-spinal reflexes represent the basis of the involuntary and stereotypical postural stabilizations that one may observe in newborn babies, brain injured human adults, and so-called reduced animal preparations (in which higher brain functions are eliminated; Magnus, 1924; Precht, 1977; Roberts, 1978; Walshe, 1923; Wilson & Melville Jones, 1979). In this *classical postural reflex concept*, reflex chains are assumed to explain more complex (multi-segmental) stabilizations such as the righting of a body from a horizontal to a vertical posture after falling down. A heavily debated notion was that all movements build in some way on reflexes that serve as a kind of motor primitives (Sherrington, 1900).

In intact and mature individuals, postural reflexes do not stand out anymore. They appear to be hidden (integrated) in more complex mechanisms that took over during childhood sensorimotor development with training and maturation of neural pathways and centers. But they may re-emerge in the adult upon large brain lesions (Walshe, 1923). How is their integration performed? Do the 'hidden' short latency reflex pathways in the intact adult still play a functional role, despite the fact that their selective lesion may remain unnoticed (in animal experiments; Wilson & Schor, 1999)? This issue is called in the following the *reflex integration problem*.

Two antithetic concepts to resolve the problem are briefly described. A recent concept of Konczak (2005) takes up the traditional notion of inhibition of the reflexes (compare Appendix E). It builds on the idea of motor primitives in the form that sets of 'basis force fields', generated in the spinal cord, serve as building blocks for voluntary movements (see Bizzi, Giszter, Loeb, Mussa-Ivaldi, & Saltiel, 1995; Giszter, Moxon, Rybak, & Chapin, 2000). These primitives govern the infants' reflex movements and come under the control of central commands from supra-spinal centers. However, this concept does not explain how reactive stabilization (e.g. of stance) is not inhibited, but rather maintained during voluntary movements.

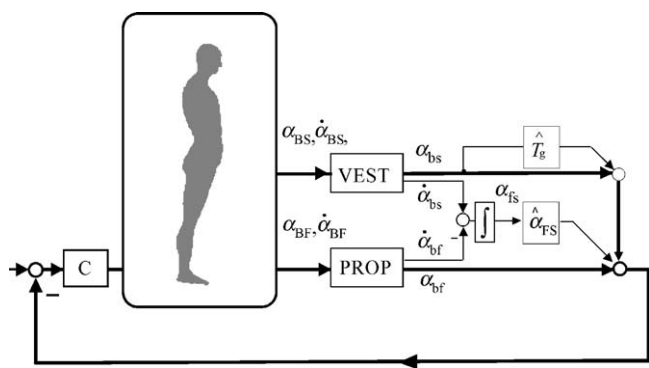


Fig. 13. Reflex integration concept. Short latency vestibular body-space and proprioceptive body-foot reflexes (bold α_{bs} and α_{bf} pathways, respectively) are complemented during childhood sensorimotor development by context dependent long-latency pathways that add to them estimates of the external disturbances (\hat{T}_g and $\hat{\alpha}_{FS}$).

An alternative novel concept is presented here. It builds on the DEC model (see Fig. 13). It suggests that the proprioceptive α_{bf} pathway (local loop) and the vestibular α_{bs} pathway (bold lines) represent short-latency reflexes, to which long-latency pathways that carry context dependent signals are added during childhood sensorimotor development (here depicted for the foot-space and gravitational torque estimation and compensation loops). In this concept, the short latency reflexes are not omitted. Rather, adding the context dependent long-latency control loops is used to provide the desired behavioral flexibility. (For literature of short-latency and long-latency vestibular responses and possible vestibular coordinate transformations at spinal levels, see discussion in Mergner et al., 1997).

Maintaining the short-latency reflexes explains their reoccurrence upon brain injury in adults. One may speculate that these reflexes serve as a kind of ‘spare tires’ (or ‘defaults’). Possibly more relevant is a stability aspect. With the short-latency loops present, the systems may tolerate better addition of long-latency pathways, which when used alone might endanger stability of the system (compare Section 2.2.1).

Appendix E. Posture-movement problem

In traditional reflex physiology, it was often assumed that the postural reflexes stabilize postures that *per definition* are static. It was believed that the reflexes would have to be suppressed during voluntary movements, so as not to hinder them. (A modern view would be that not only static postures, but also movements require stabilization against unforeseen or foreseen external disturbances, Section 4). Another concern was that the sensory inflow arising upon voluntary movement interferes with the sensory inflow that evokes the postural reflexes. These issues are still debated to date (e.g. Ostry & Feldman, 2003).

There were several suggestions of how to solve the problems, some being still influential to date. One suggestion was that, instead of reflex inhibition, reflex interactions might do the job (Roberts, 1978; von Holst & Mittelstaedt, 1950). The example considered was an interaction of the vestibulo-spinal and cervico-spinal reflexes. Each of them tries to stabilize the body when evoked in isolation (vestibular: whole body rotation; neck: trunk-only rotation). But when combined during head rotation, they are opposite in sign and tend to cancel each other. Therefore, so it was held, head movements can occur unhindered and furthermore do not endanger body stability. The flaw of this hypothesis is that the reflexes would still hinder active *body* movements. The idea of vestibular-proprioceptive interaction, however, is still present in the meta level concept.

Another influential suggestion was the efference copy principle of von Holst and Mittelstaedt (1950; analogous is ‘corollary discharge’; Sperry, 1950). It suggests that a copy of the motor command signal is used to cancel the self-produced part of the sensory inflow (‘re-afferents’), leaving untouched the part that stems from external stimuli (‘ex-afferents’). It draws on the intuitive notion that action-contingent expected sensory inflow is somehow matched with actual sensory inflow. It was considered to represent a functional scheme for causal physiological relationships that may exist in the animal world in various forms (von Holst, 1954), which appears to be true (e.g. Crapse & Sommer, 2008). In primates and humans, it is commonly applied in models of the visuo-oculomotor system, where eye muscle proprioception appears to play no considerable role and the eyeball mechanics and motor control is relatively simple (e.g. gravity can remain unconsidered). Concerning the human skeleton-motor system, evidence is still sparse and speculative, at least as concerns the efference copy of the motor command signal. In engineering, this is often used as a constituent of observer models (see Section 3). In contrast, the disturbance prediction and anticipation mechanism of the meta level concept

As mentioned in Section 4, a ‘servoing’ principle is used here to solve the posture-movement problem for stance control such that the DEC model simultaneously serves both, proactive (voluntary) movements and reactive stabilization. Interestingly, the original notion of reflexes serving as ‘primitives’ even for voluntary movements is realized in this solution, although in a form that probably was not foreseen by the discoverer of the reflexes (Sherrington, 1900).

Appendix F. Simulations and robot

The simulations in Sections 4.2 and 4.3 were performed using Simulink (MATLAB[®], The MathWorks Inc., Natick, MA, USA). The stimulus waveform used for these simulations and the robot was the ‘raised cosine velocity function’

$$v_{(t)} = -A f \cdot \cos(2\pi \cdot f \cdot t) + A \cdot f; \quad 0 < t < 1/f \quad (15)$$

where f is the dominant frequency and t is the time. When the signal is integrated, its waveform resembles a smoothed ramp and is similar to the waveform of many human skeleton-motor movements, which tend to show bell-shaped velocity profiles (Morasso, 1981).

The robot simulations were performed using PostuRob (Fig. 10). It consists of an aluminum skeleton body comprising two rigid legs, a pelvic girdle, and a spine torso (body mass, $m = 52$ kg (62 kg with feet); inertia, $J = 42$ kg m²; COM, mainly represented by metal weights mounted on the pelvis, is 0.9 m above ankle joint).

Freely standing on its feet, the body is actuated about the ankle joints through front and back pneumatic leg ‘muscles’ (Festo, Esslingen, Germany; Type MAS20; proportional-directional control valves, MPYE-5-1/4-010-B). The muscles carry ‘tendons’ at their fixations (springs, stiffness effect slightly below COM’s gravitational ankle torque that, using small angle simplification, is $mgh(\alpha_{BS})$, in Nm). The muscle-tendon system was designed to yield an essentially ideal actuator performance in the stance control context using an inner torque control (Mergner et al., 2006; Mergner, Schweigart, & Fennell, 2009; actuation dynamics below 3 Hz are almost ideal, see www.uniklinik-freiburg.de/neurologie/live/forschung/sensorfusion/posturob.html).

PostuRob’s controller values used for the simulations were $K_P = 470$ Nm/(rad s), $K_D = 162$ Nm s/rad, and $K_I = 12$ Nm/(rad s) (recall that the feedback gain during unperturbed stance comprises

both $G = 1$ of α_{bf} and $G = 0.8$ of \hat{f}_g , with the effect that reflexive stiffness suffices to stabilize the body). Times delays used in most recent experiments were 170 ms for the disturbance estimates and 80 ms for the proprioceptive α_{bf} loop.

PosturRob's sensors include an artificial vestibular system (details in Mergner, Schweigart, & Fennell, 2009). Furthermore, joint angular position and velocity measures are derived from the output of a rotatory potentiometer (placed in the robot's ankle joint axes) and its electronic differentiation. A measure of ankle joint torque is derived from a COP shift signal. It is calculated from pressure (normal force) signals recorded electronically under forefeet and heels of the two legs through compression load cells. Alternatively, a torque measure from force sensors in the 'tendons' may be used. The torque measure used for stance control was low pass filtered, unlike that used for linearizing muscle torque in the torque control.

The software environment for the robot was realized in MATLAB xPC technology (MATLAB[®], The MathWorks Inc., Natick, MA, USA). A target computer was equipped with data acquisition and control cards to communicate with the sensors and to command the actuators. It was under the control of a host computer that was used for designing and simulating the control scheme and for downloading this scheme to the target computer. The host computer was used in addition to monitor performance of the controlled system and to interactively pass parameters. In this setup, the plant (process) to be controlled is the robot with its sensors and actuators, whereas the control scheme was realized as a MATLAB/ Simulink model.

The testbed used for the robot simulation consisted of our posturography laboratory. It is supplied with a 6D motion platform that, under the control of a PC using custom made software, allowed us to apply platform tilts and translations. Furthermore, external force (pull) stimuli were applied using reciprocal action of two force-controlled cable winches (servo motors) under computer control. Captured were COP shifts (Kistler[®], platform type 9286, Winterthur, Switzerland), COM and platform positions in space (Optotrak 3020[®], Waterloo, Canada), and force stimulus magnitude. Stimulus applications and stimulus-response analyses were performed using custom made software.

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