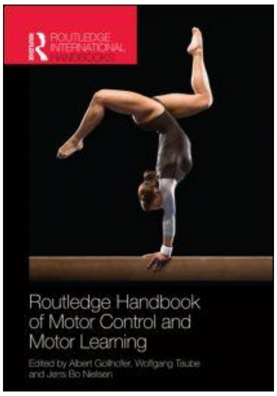

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POSTURAL CONTROL BY DISTURBANCE ESTIMATION AND COMPENSATION THROUGH LONG-LOOP RESPONSES

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Introduction

This chapter concentrates on the control of human biped stance and balancing as relatively simple prototypes of posture and movement control in general. The simplicity is mainly owing to the fact that the physics of the body sway resembles that of a single or double inverted pendulum. Clinically, postural control is often equated to equilibrium control of stance. However, posture control does not end with body-on-feet balancing. Rather, we balance the head on the trunk, the trunk on the hips, or make the trajectory of an arm during reaching movements resist gravity. Admittedly, there are differences among these tasks, depending on which muscle groups, joints, etc. are concerned. Yet, basic function principles resemble each other when viewed from a 'systems control perspective'. At this level, the muscles are abstracted as actuators. Furthermore the movements of body parts are formalized according to the rules of physics, and the balancing represents the neural control task. Such abstractions help to grasp the essence of the function principles.

The chapter includes a historical perspective on posture control research in the first half of the twentieth century. This perspective may help young scientists to appreciate that natural sciences tend to change over time, and is meant to encourage their own research. Before the twentieth century, scientists were unaware of the fact that humans use a special '*equilibrium sense*' for balancing. In the period 1840–1900, experimental and clinical scientists demonstrated that parts of the inner ears serve this function. Goltz (1870), for example, mechanically irritated these inner ear structures in frogs (nowadays known as the *vestibular organs*) and observed reflexive leg and body movements. These were later called postural reflexes. The first of the three sections of this chapter starts by explaining the reflex concept that then dominated the first half of the twentieth century. The second section covers approximately the second half of the twentieth century when posture control research profited from many important discoveries made in neuroanatomy and neurophysiology. Researchers started to conceptualize how voluntary movements are embedded in posture control. This was also the time when engineering sciences started to boom, and control and signal processing theories were developed. However, only in the last part of this period and the following decade were these theories successfully used for the modeling of sensorimotor control. The modeling will be described in the third part. It defines posture control as a context-dependent, yet mostly automatic disturbance compensation, by which the control of voluntary movements is freed from immense computational burdens. Although building on reflexes, the control principles provide the impressive human flexibility and richness of behavior, including cognitive aspects and voluntary control over the reflexes.

Fundamental levels of postural control research

The reflex concept originated mainly from the work of Sherrington (1900) on muscle function. He established the concept of a sensory feedback circuit, in which an external muscle stretch is sensed through muscle spindle receptors. These receptors then activate motoneurons in the spinal cord, which in turn command the muscle to counteract the stretch. The concept was later applied to postural control in special animal preparations (see Magnus 1924). One of the postural reflexes relates to Goltz's experiment and was called the *vestibulo-spinal reflex* (see Wilson and Melvill Jones 1979). The tonic components of these reflexes originate from activation of gravity-sensitive receptors in the vestibular otolith organs. The brain uses them to sense static body excursion with respect to the gravitational vertical and to adjust leg muscle activity to counteract the excursion. It was later noted that the vestibular canals contribute to the dynamics of the vestibulo-spinal reflexes. Furthermore, it was noted that the vestibulo-spinal reflexes have partners in the cervico(neck)-spinal reflexes, which arise when the head is deflected with respect to the trunk (i.e. they stem from neck muscle proprioception, as we know today). But the functional significance of this partnership remained unclear.

The postural reflexes were thought to cover even complex situations such as standing up following a fall (righting reflexes). This was attributed to a chain of reflexes, where the result of one reflex triggers the next. However, researchers were aware that the reflex concept does not explain the flexibility of human sensorimotor behavior. In this behavior, humans superimpose, for example, voluntary sensorimotor activities on balancing. Furthermore, we automatically adjust the balancing to changing external situations, whether it is a push against the body in a crowd or sequences of tilt and translation of the support surface when standing in a moving bus.

It was recognized that posture and movement should not be considered as two separate activities, even though posture is still often regarded as a static activity and movement as the dynamic counterpart. The control of both rather involves dynamic and static aspects and these two actually belong together functionally. Holmes (1922) conceived that 'the movement itself consists of a series of postures' and, similarly, Denny-Brown (1929) considered movement a modification of posture. In addition, Holmes (1922) extended his notion of posture control, stressing the need of a postural fixation of the moving limb on the body as a prerequisite for an accurate movement. Sherrington (1931) held that posture accompanies movement. This was later called coordination of movement with compensatory and anticipatory postural adjustments (see Gurfinkel 1994, and below).

The research of this period provided a number of 'postural control basics' that still hold today (a–f below). The paragraphs below draw mainly on a review by Hellebrandt and Franseen (1943).

(a) The balancing task

Balancing the inherently unstable body in biped stance usually means maintaining the body's center of mass (COM) over the relatively small supporting base given by the feet. In upright stance, the COM (sometimes also called COG, for center of gravity) is located in the trunk approximately at the 5th lumbar segment (Figure 3.1). With the COM above the feet in quiet stance, balancing is subjectively almost effortless. This applies, although the COM's gravitational vector points not exactly to the rotation axis passing through the two ankle joints, but slightly in front of it.

This COM location is essentially maintained when the body weight distribution is changed by a backpack, trunk bending, etc., in that the body configuration is adjusted accordingly. For example, a heavy backpack is compensated for by a forward body lean.

(b) Spontaneous body sway

In quiet stance, there is always some spontaneous sway. Closing the eyes increases sway amplitude (clinically performed with the feet placed side by side as 'Romberg test'). This suggests that the sway amplitude is related to how accurately our brain senses self-motion. But there exists also the possibility of active interference, for example by making joints stiffer by

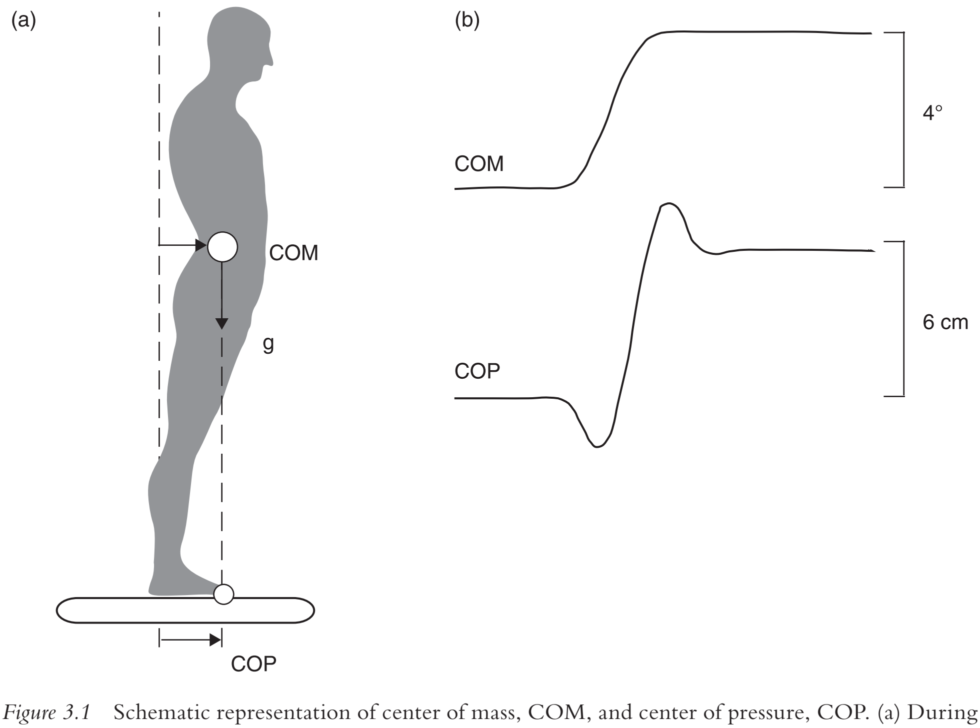

Figure 3.1 Schematic representation of center of mass, COM, and center of pressure, COP. (a) During a static body lean forward, the COM's projection to the support surface determines the COP. (b) During active lean (dynamic condition), the COP also contains the ground reaction force that is generated to accelerate and decelerate the COM.

co-contracting antagonistic muscles (see Nielsen 1998). Thus, sway amplitude should not be the only criterion for clinically diagnosing balancing problems.

(c) Multisensory control

The balancing control depends on co-operations of the muscle stretch reflex with activity arising from vestibular, proprioceptive (joint angle and torque), teleceptive (e.g. vision), and exteroceptive (e.g. touch) neural mechanisms. These mechanisms are usually not experienced consciously, although they involve the cerebral cortex in intact adult individuals, as suggested by lesion studies (Rademaker, 1931; Bard, 1933; Brooks, 1933).

The functional significance of the multisensory co-operations still remained open. The exception was a concept on a co-operation between the vestibulo-spinal and the cervico-spinal reflex (von Holst and Mittelstaedt, 1950; also Roberts, 1978). It suggested that the two reflexes combine in stabilizing the trunk and are not invoked during head rotation on the stationary trunk, in which case they cancel each other. This concept of vestibular–neck reflex interaction together with a modern view of vestibular–neck interaction (Lund and Broberg, 1983; Mergner et al., 1997) is illustrated in Figure 3.2.

(d) Function localization in the central nervous system (CNS)

In human babies, the primitive postural reflexes and their development within the first year of life are routinely tested for diagnostic purposes of brain maturation (Prechtl, 1977). They disappear with progressive maturation of the higher brain centers such as the cerebral cortex, the basal ganglia, and the cerebellum. From this and from comparisons with animal research it was concluded that the proprioceptive reflex mechanisms originate from the spinal cord, while the vestibulo-spinal reflex and its co-operation with the cervico-spinal reflex are processed in the brainstem (in particular the vestibular nuclei and the reticular formation) and the cerebellum. After these higher centers have taken over the control during maturation, the neural substrates of the reflexes remain, which explains why they may reappear upon lesions of these higher centers (Simons, 1923; Walshe, 1923).

(e) Orthostatic effects

Maintaining upright body posture is associated with a number of vegetative functions such as blood pressure control or the excretion of the hormone aldosterone that is related to blood pressure regulation. The need to compensate the hydrostatic effect of gravity, i.e. the return of venous blood to the heart, is quite intuitive. Failure may lead to 'orthostatic collapse'.

(f) Quantification, training and adaptation

Quantitative measurements of body posture and COM motion became possible through photography and film. Using these techniques it was shown that specific posture training tends to improve balancing. It also became evident that adaptation is an important feature of the postural control system, for example when an injury or disease makes it necessary that the neuro-muscular and skeletal systems change in order to regain sensorimotor functions like walking.

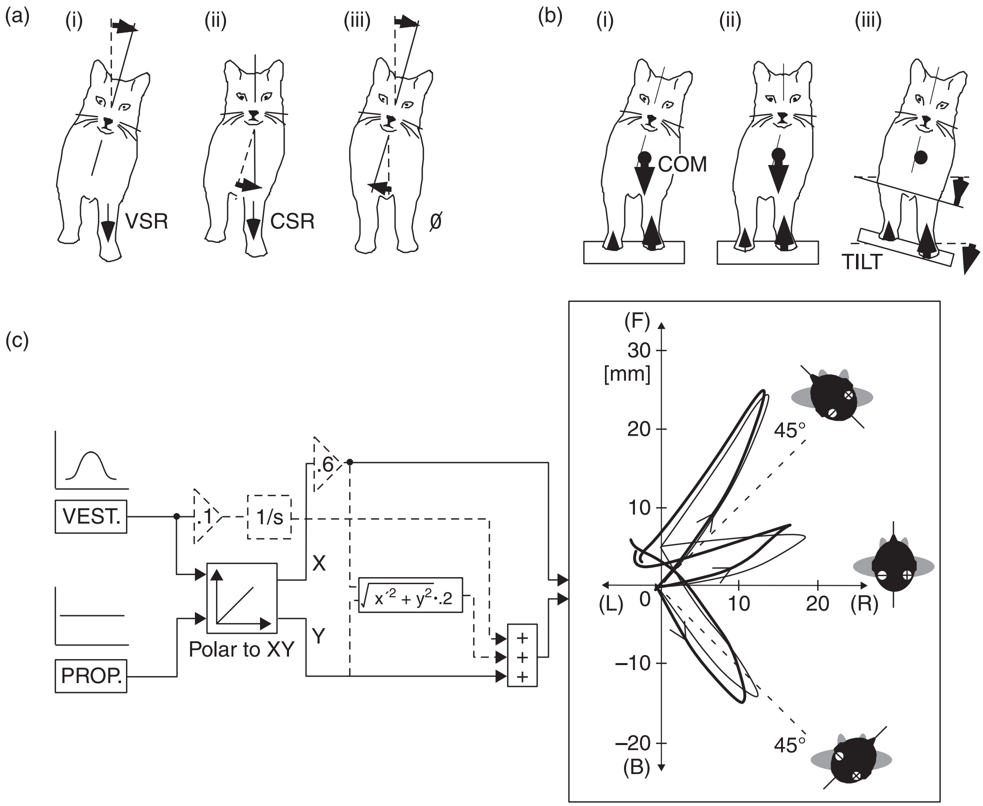

Figure 3.2 Vestibular–neck reflex interaction and re-interpretation in terms of coordinate transformation. (a) Classical view of vestibular–neck interaction in terms of vestibulo-spinal reflex (i, VSR; leg extension on one side and flexion on the other side upon head-in-space rotation) and cervico-spinal reflex (ii, CSR; evoked by trunk rotation with respect to the head). The signs of the two reflexes are such that they cancel each other during head rotation on stationary trunk (iii). (b) Re-interpretation. Tilt of trunk and head together, yielding vestibular head-in-space signal, is associated with COM shift to the same side. The vestibular signal evokes gravity-compensating changes in the leg muscle tone (i). Tilting the trunk with the head remaining vertical yields a similar effect, due to similar COM excursion in space (ii). But here, trunk orientation in space (TS) is perceived from the sum of the vestibular head-in-space signal (HS) and the proprioceptive trunk-to-head signal (TH; TS= HS + TH), which represents a coordinate transformation from body (TH) to space (TS) coordinates (adapted from Mergner 2004 and Mergner et al. 1997). Further down transformation allows estimation of foot-support-in-space tilt with the help of leg-to-trunk proprioceptive signals (iii). C Vestibular–neck coordinate transformation during horizontal head turns. The template shows original body lean response evoked by applying a trans-aural galvanic vestibular stimulus (cathode is at left ear) at different head orientations of a human subject (from above). Body lean results as compensatory reaction to illusory body lean. Direction of illusion turns with the horizontal head rotations due to neck proprioceptive coordinate transformation. (Original data, bold curves, and their model simulations, thin curves, adapted from Hlavacka et al., 1996.)

Emergence of numerous postural control concepts

In the second half of the twentieth century, electrical recordings of muscle and neuron activities and inferences on their relation to sensorimotor functions and behavior became popular in neurophysiology (review articles, Massion, 1992; Horak and Macpherson, 1996). This resulted in novel concepts in posture control research such as the *body schema*. It refers to the internal neural representations of body configuration and dynamic state which the system needs to know in postural control if an external disturbance such as a push against the body has to be compensated. The concepts of *muscle and movement synergies* refer to the fact that several muscles tend to cooperate during certain movements, and that the movements of several body-segments cooperate synergistically during motor behaviors such as walking. Since the movements tend to be structured spatially and in time, they appear to be generated on the basis of complex *central motor programs*. As will be explained below, spatial and temporal sequences of movements and their postural stabilization may as well emerge automatically from hierarchical sensorimotor control principles. Such emergences may also explain certain movement strategies and postural adjustments.

Motor strategies

The concept of motor strategies refers to the fact that a given motor goal may be achieved in different ways. In most situations, standing humans preferentially use the ankle joints for balancing (the 'ankle strategy') while in some special situations they also involve the hip joints ('hip strategy'; Nashner & McCollum, 1985; Nashner & Horak, 1986). Factors that favor the involvement of the hips are restriction of foot support base and fast disturbances (e.g. fast foot support motion; Allum et al., 1989). And involving the hips requires less effort (Kuo and Zajac, 1993b). The ankle strategy is favored at slow disturbance speed (Nashner and Horak, 1986) and sensory restrictions through disease or age (Horak & Macpherson, 1996). Contributions from the knee joints to the balancing are small (Alexandrov et al., 2001). They produce mainly vertical body accelerations, while balancing mostly deals with the compensation of horizontal accelerations of the body's COM (Kuo & Zajac, 1993a).

Postural adjustments

The concept of postural adjustments during voluntary movements was refined by recording electrical muscle activity (electromyogram, EMG) and using biomechanical measurements (overview, Bouisset & Do, 2008). Biomechanics furthermore differentiated the kinetic from the kinematic aspects. *Kinetics* refers to forces and torques. In posture control, it refers for example to adjustments of the ankle joint torque required to prevent an upright standing body from falling over. Superimposed may be a *kinematic* task, for example a righting movement of the trunk to maintain its vertical orientation in space in an attempt to stabilize the workspaces of the eyes and arms.

Quantitative measurements

In many of the above studies, the kinetic result of COM sway was measured using a 'posturographic platform'. It measures the COM-evoked ground reaction forces through a force transducing plate in terms of center of pressure (COP) shifts (Figure 3.1). Also, recordings of COM excursions became possible with the help of optoelectronic devices that measure movements of the body segments. The measurement of the COP provides more information than that of the COM, because it reflects in addition to the ground reaction force (which is holding the COM against gravity) also the joint torques (by which a subject actively moves the COM). Consider an active body lean movement forward (Figure 3.1b). In the beginning of the movement, the COP is transiently shifted backward by a ground reaction force that mirrors the force required to accelerate the COM forward. Then the COP shifts with the COM's projection, before finally an active body deceleration leads to a transient COP overshooting. In other words, in unperturbed stance, the COP measure reflects both the dynamic aspects of balancing, stemming from the ankle torque produced to overcome body inertia, and the static torque from the ankle joint that overcomes the gravity effect resulting from COM excursion. Recording EMG may provide additional information on the spatial distribution and timing of muscle activity during balancing.

Attempts to formalize conceptual frameworks

The recording of COP shifts, body segment and COM movements provides the information that is needed to develop system concepts on how the brain controls posture. The approach requires recording of balancing responses evoked by external disturbances such as translation or rotation of the support surface (e.g. on a motion platform) or well-controlled pushes and pulls acting on the body. In a so-called 'black box' approach of the systems analysis, the input stimuli (often having a sine wave form) are compared to the output response. From the relation between the two, inferences on the information processing in the 'box' can be made. However, this approach is not sufficient to infer the details of signal processing in the CNS and it does not allow a decision between several possible solutions. A variant of the black box approach is the 'grey box' approach. In this case, established knowledge from sensory and motor neurophysiology is included, allowing far-reaching conclusions as will been shown below. Further help comes from a simple scientific rule that demands a search for the simplest solution (Occam's razor rule; Gibbs & Sugihary 1996/97). This meets with nature's success to find simple, parsimonious solutions even for complex mechanisms.

In the further wake of cybernetics and control theory, new tools for control system identification, abstraction and simulation became available and inspired sensorimotor physiologists. Merton hypothesized that voluntary movements are initiated by the gamma motoneurons, setting an 'error' in the muscle spindle to drive the alpha motoneurons ('follow-up servo hypothesis'; Merton, 1953). This inspired others, leading to alternatives to or modifications of this hypothesis (e.g., 'alpha–gamma linkage' of Granit, 1955, and 'servo-assisted motor control' by Mathews, 1972). However, several researchers doubted that, apart from the short-latency primitive reflexes, sensory afferents from the periphery can contribute much to the control of movements. They favored therefore feed forward control and postulated that posture control in the adult individual is mainly centrally controlled (these protagonists were called the 'centralists' as compared to the 'peripheralists' by Mackay, 1980). The reason was that control theory asks for high gains in the control to achieve mechanical stability in the face of external disturbances, which seemed to be incompatible with the biological delay times that are long compared to those in technical systems and may lead to control instability (Rack, 1981). Engineering academia, on the other hand, provided mathematical control methods that required no sensory feedback, at least in their dogmatic forms, or only proprioceptive feedback on the state of the system. Other methods combined predictive fast feed forward control with slow sensory feedback (variants of the so-called Luenberger observer). Disputed observations, originally obtained in monkeys, lent support to this notion (Bizzi et al., 1978, 1984). This development fostered the question as to where the primitive reflexes remain during the development from birth to adulthood.

Developmental aspects

The primitive vestibular and proprioceptive reflexes get integrated into more flexible movement patterns approximately 3–8 months after birth, developing into righting reflexes (reactions) and positive support reactions (Magnus, 1924; Prechtl, 1977). Important in this period of child development is the development of anti-gravity extensor tone. The child starts balancing by learning to raise its head against gravity, before continuing to do so with the upper trunk etc. until it is able to stand upright, balancing by holding with the hands to some support. In this time, it learns to deal with the external field forces (gravity, centrifugal and Coriolis forces). Once learned, their impacts are no longer consciously perceived (for learning new Coriolis force effects in adults, see Lackner & DiZio, 1994).

The first period of child development includes the learning of a 'top-down' strategy (Massion, 1998). Vision helps balancing by fixating the eyes on items in the surroundings, thereby stabilizing gaze. Furthermore, when voluntarily moving in a goal-directed way in space, such a top-down strategy may be adopted so that, during body turns, gaze shifts occur first and are then followed by the body. For balancing with eyes closed or eyes open, however, a 'bottom-up' strategy must also be learned. In this strategy, the lowest joints (ankle joints) balance the body as a whole. This strategy compensates for self produced or externally applied disturbances, which can be support surface motion as well as field and contact forces having impact on the body.

Even though learning plays an important role in development, it was found that the initial responses to rapid perturbations (e.g. support surface translations) still reflect the primitive stereotype short-latency reflexes (SLR). This is in agreement with the observation that these reflexes persist and may re-emerge in adult humans and vertebrate animals after large brain lesions. Therefore, there was *agreement that the balancing responses to external disturbances initially stem from the primitive postural reflexes, after which a transition into voluntary feed forward control evolves* (although some authors were aware of the shortcomings of this notion and of pending new developments from systems analysis and modeling; e.g. Horak & Macpherson, 1996).

Long-latency reflexes

A revival of the reflex concept arose with the discovery of long-latency reflexes (LLR; the long latency originally referred to EMG responses upon electrical or rapid perturbing stimuli). Compared with the SLR, they occur in a context-dependent way and they act through supraspinal pathways to stabilize multiple joints in complex actions (Marsden et al., 1983; Kurtzer et al., 2008). The response and joint stiffness is modified by a subject's prior intentional or volitional set (Hammond, 1956; Marsden et al., 1976). The LLR represent a feedback control process that shares features of voluntary control (Pruszynski et al., 2011). They are affected in basal ganglia diseases, such as Parkinson's disease (PD), in which patients have difficulties in adjusting postural responses to behavioral contexts. The patients produce the responses even when body stability is not endangered, for example in response to a foot rotation stimulus while sitting (Diener et al., 1987).

An instructive example for the context dependency of the LLR in postural control has been reported for transient electrical vestibular stimulation in the adult human (Britton et al., 1993). In free stance, the stimulus evoked leg muscle activation in terms of an initial SLR response and a subsequent LLR response. In contrast, when equilibrium was maintained by the arms holding on to a firm support, the LLR disappeared in the leg muscles and emerged in the arm muscles. It appears that the LLR takes over postural control during development. In experiments on adult animals, for example, lesioning of the fast direct pathways from the vestibular nuclei in the brain stem to target motoneurons in the cervical spinal cord did not produce considerable functional impairment (Wilson & Schor, 1999). Although classical neurophysiology and neuroanatomy primarily focused their work on these direct pathways, their functional role in the adult individual is still open. Possibly, the SLR serves as a kind of 'spare tire' and, because of its short latency, contributes to overall stability of the feedback control loops. Concerning the LLR, they were only recently implemented in a postural control concept (see below).

Recent developments and postural control models

First attempts to describe human quiet stance and balancing with the help of control models reach back about half a century. As mentioned above, engineers' pleas for using high loop gains (which help to resist external disturbances) and their warnings in the face of biological time delays (because they may make the control unstable) prevented the implementation of LLR and favored mainly feed forward ideas of control (Rack, 1981). In a first comprehensive system identification study of human balancing by Fitzpatrick et al. (1996), however, it was shown that the loop gain of human stance control is rather low, which puzzled researchers about how the control might work. Even so, others have provided arguments against the notion that maintaining biped stance is mainly through passive stiffness (e.g., Morasso & Sanguineti, 2002).

Further work offered possible solutions. From a special analysis (stabilogram diffusion analysis) of COP time series, Collins & De Luca (1993) derived two different aspects of control, one called 'short range control' and the other 'long range control'. From this they inferred the existence of two control mechanisms operating during quiet stance, one open-loop and the other closed-loop. This COP behavior, however, can also be explained in terms of noise-related variations in the neural controller and time delay parameters rather than in terms of open-loop versus closed-loop behavior (Peterka, 2000). From observations of muscle length associated with spontaneous body sway during stance, Loram et al. (2005a,b; Lakie & Loram, 2006) hypothesized that stance is maintained by ballistic, catch and throw-like muscular activity with a cyclic pattern favoring a discontinuous control. Others, however, could explain these findings assuming a continuous control (Peterka, 2002; Masani et al., 2006). In the presence of very small activations, nonlinearities such as detection thresholds can, in fact, lead to such cyclic patterns (called limit cycles; compare below, thresholds in the DEC model).

An important aspect in the more recent modeling approaches is the combination of a derivative term with a proportional term in the feedback loop (PD controller). If the loop is used to control the body angle, this mechanism not only tries to minimize deviations of the body angle from the desired value (the P part), but uses in addition body angular velocity information, which precedes position (the D part). In addition, the D part helps to stabilize the system by 'damping' overshoots during rapid movements. Applying it to biological control loops does not necessarily imply that it is implemented in this form in the nervous system. It appears that biological loops tend to feed back both position and velocity sensor signals (as is true for muscle spindle afferents), which for certain purposes can be considered functionally equivalent to PD control. When using PD control and low loop gain, one can now build control loops that include LLR time delays. Interestingly, the low loop gain comes with compliant limbs, which is typical in humans (and is still an aim in robotics where humanoids show rigid limb behavior that may be dangerous to humans).

Another important aspect of human postural control is its multisensory nature, called 'multisensory integration'. This means that, during an external disturbance (e.g. a push having impact on the body), the control system combines proprioceptive joint position, vestibular, and visual signals for the balancing (a 'multisensory integration'). Changes in the relative contribution of the sensors across different disturbance scenarios are often termed 'sensory re-weighting'. In engineering modeling approaches, this was realized using an adaptive 'sensory integration center', in which the sensory signals are combined with additional information ('efference copy'). The approach aimed to find the most accurate sensory representation for a given environmental situation under noise optimization principles using Kalman filters with iterative processing (van der Kooij et al., 1999, 2001; also Kuo, 2005). A much simpler method is realized in the model of Peterka (2002). There, the sensory integration results from combining proprioceptive, vestibular, and visual reflex pathways ('independent channel model'). However, here the modeler performs the sensory re-weighting in relation to changes of the disturbances.

A third solution that combines simplicity in multisensory control and an automatic sensory re-weighting is presented below (DEC model). Before doing so, some building blocks are explained.

Sensor concept

The most relevant information for posture control stems from visual, vestibular, joint angle proprioceptive and joint torque proprioceptive sensors (Horak and Macpherson, 1996). In addition, haptic contact to the support surface has to be known for balance control. Vision improves stance stability, but is dispensable for principle considerations (Mergner et al., 2005). Therefore, the focus here is on the vestibular sensor and the joint angle and torque sensors. Noticeably, these sensors are not identical with the sensory organs (transducers).

For example, the information on self-motion in space and with respect to the gravitational vertical must be derived from combining signals from the vestibular canal and otolith organs, because each of them has flaws. The otolith organs react equally to both the inertial force during head translational acceleration and the gravitational force during head tilt. On the other hand, the canal organs provide information on head angular motion, but this information is not reliable during slow rotations for physical reasons. By way of interactions between canal and otolith signals, the nervous system improves the angular motion information and distinguishes between translation and tilt. The results are not ideal, still allowing self-motion illusions in special situations, but in concert with the other senses they suffice to provide a good estimation of self-orientation (overview in Mergner et al., 2009b).

Another example is the sensor of joint angle and angular velocity. Muscle lengthening during joint rotation leads to firing increase of sensory endings in muscle spindle receptors. These spindles make a major contribution to the joint angle and movement sense ('muscle proprioception', 'kinesthesia'). However, because the muscle is elastic, force signals need to be included in the sense to obtain reliable estimates in both active and passive conditions. The force information appears to stem from transducers in the tendons (Golgi tendon organs, GTOs; see Duysens et al., 2000). With active movements, a contribution from central sources ('effort'; Gandevia, 1987) also seems to play a role. Furthermore, transducers in the skin and in the joint capsules participate (Jones, 1972). Appropriate combinations of the transducer signals then provide estimates of the physical variables. These will from now on be called 'sensors'.

Thus, the sensors are virtual in that their signals arise from interactions within a distributed neural network. This network shows properties similar to artificial neural nets, where information on function typically cannot be drawn from a node within the net because the signal processing is distributed across many nodes. Functions can be inferred, however, from nodes at the input and output sites. An output into perception can be used to learn which information the sensors are providing. This has been done in human psychophysical experiments on conscious perception of self-motion with the help of open loop indication and estimation procedures (overview, Mergner, 2002). They showed that the percepts represent the physical variables such as position and velocity of joint angle or head rotation in space. In view of the mostly valid action–perception congruency in human behavior, it is plausible to assume that the sensors also feed into the sensorimotor systems.

Meta level concept

When subjects give verbal reports in psychophysical self-motion experiments, these typically do not reflect the sensor signals such as the vestibular head angular velocity. Rather, they reflect a reconstruction of the outside world event that was causing the self-motion, such as 'the chair I am sitting on was rotated first leftwards and then rightwards' (in psychological literature this is called 'distal stimulus', in contra-distinction to the 'proximal stimulus' that refers to the fluid pressure on a cupular receptor in the vestibular canals or a photon hitting a receptor cell in the retina). For the internal reconstruction of the outside events, typically several sensor signals are combined. This is performed by a continuous event 'estimation' from noisy sensory inputs, cognition and expectations.

The concept of perceptual reconstruction of external events from multisensory input was applied to the modeling of human balancing experiments, when it became clear that this required a novel concept of sensory processing (Mergner et al., 2003; Mergner, 2004). The question was, which external events in relation to balancing are perceptually reconstructed and from which sensors in which way. It was concluded on theoretical grounds that four external disturbances are reconstructed: support surface rotation and translational acceleration, field forces such as gravity, and contact forces such as a push against the body. Furthermore, it was identified which combinations of the vestibular, joint angle and joint torque sensor signal are required for the estimation of the four external disturbances (overview, Mergner, 2010).

Servo loop concept

Modeling of human stance control requires a concept of the underlying motor mechanism. As mentioned above, sensorimotor researchers were fascinated by engineering servo control (or *servomechanism*) because it shares essential points with the biological *reflex concept* in that it uses *automatic error-sensing negative feedback*. The technical concept is best known from effortlessly moving a steering wheel in a car, which makes the car wheels turn through some mechanical amplification (the car driver is serving as operator who first observes and then, based on certain intentions, etc., controls the servomechanism). In the version of the servo loop described below for stance control, movement performance by the mechanism is virtually without effort in that body inertia is accounted for by corresponding joint torque.

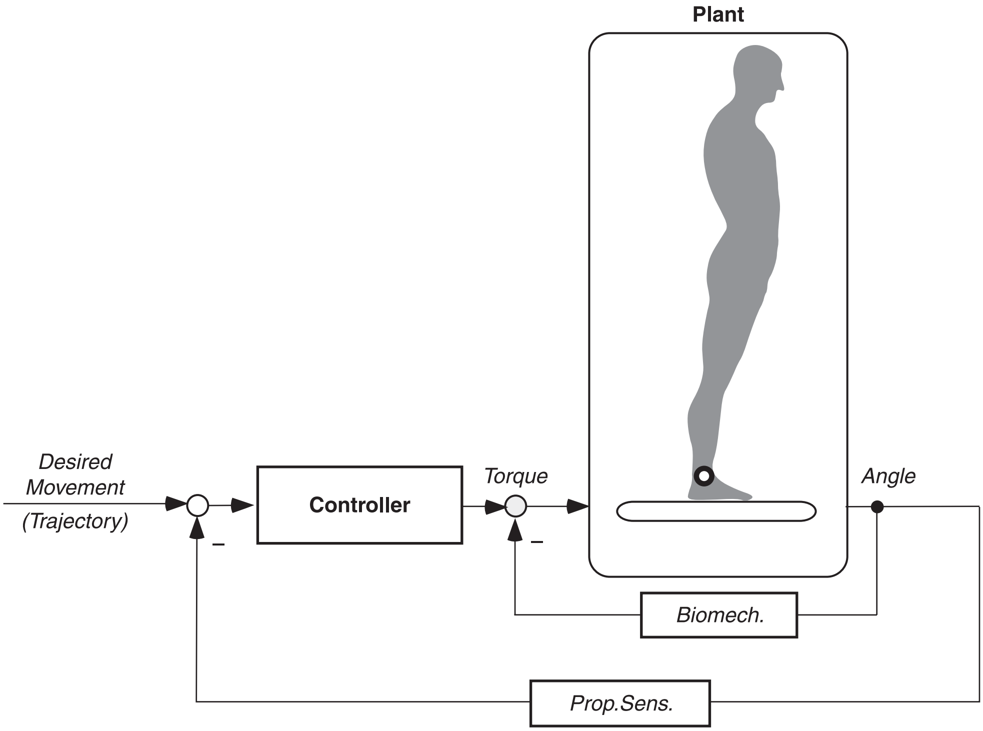

Figure 3.3 Servo control model. The desired movement is driven by error-sensing 'reflexive' negative feedback. Biomech., instrinsic (passive) muscle stiffness and damping. Prop.Sens., proprioceptive sensor of joint angle (here of ankle joint). Given feedback and controller parameters are adjusted to plant dynamics, the loop compensates for body inertia when performing the desired movement trajectory.

In this version, the input is a signal indicating the desired position or movement (displacement trajectory). The difference between the desired trajectory and the actual trajectory, reported by proprioceptive feedback of joint position, drives the movement via a controller (lower loop in Figure 3.3). The controller uses a proportional and a derivative term (PD controller) adjusted to yield a joint torque signal ('motor command') which is adapted to the plant dynamics. The command-to-movement transformation implies a joint actuator with an inner force control loop (not shown in the model). The negative proprioceptive feedback represents a short-latency reflex (SLR) that stabilizes the joint according to the desired position or rotates it according to the desired displacement (McIntyre & Bizzi, 1993, wrote of 'the beauty of movement from posture'). The generated reflexive stiffness combines with passive muscle stiffness (and damping) which provides additional negative feedback with virtually no time delay (box Biomech., for biomechanics; to some extent adjustable through co-contraction of agonist–antagonist muscle pairs).

An advantage of this mechanism is that it does not require an additional feed forward signal of inverse plant dynamics (this argument becomes relevant when additional mechanisms need to be added to the servo; see below). A problem with this mechanism is that the proprioceptive feedback is too weak to account sufficiently for the compensation of external disturbances such as gravity. However, this problem can be eliminated when one uses the estimations of the external disturbances from the meta-level to compensate them.

Disturbance estimation and compensation (DEC) model

Extending the servomechanism by the estimators of the four disturbances and feeding their signals with inversed signs into the input summing junction compensates for the disturbances (strongly simplified DEC model in Figure 3.4). Given full compensation, the servo can function and fulfill its task as if there was essentially no gravity or other external disturbance.

A more detailed picture of the DEC model is given in Figure 3.5 (for anterior–posterior balancing of the body around the ankle joints, biomechanically simplified as if the body was a single inverted pendulum). The fusion of the sensory transducer signals into the sensors is omitted. The figure shows the distributed network of sensor signals feeding into the disturbance estimators. Note that the vestibular sensor, for example, inputs into all four disturbance estimators (shown are actually two vestibular sensors, because the vestibular translation signal feeds into the support translation estimation, while the other vestibular signals deal with angular motion). Furthermore, note that each estimator receives a specific set of inputs, so that changes in the disturbances are automatically associated with changes in the contributions from each sensor – which represents a sensory re-weighting. Another type of the re-weighting comes from detection threshold mechanisms in the estimators. They are causing an amplitude non-linearity in the form that compensation of small disturbances is relatively weak and automatically gets more efficient when the disturbances get larger (in accordance with human behavior; Maurer et al., 2006). Additional effects of the two types of sensory re-weighting concern the reduction of sensor noise in the DEC loops (see Mergner et al., 2009b).

The DEC model was developed in an iterative back and forth between balancing experiments, modeling and model simulations. Eventually, the model described and predicted human balancing in a variety of external disturbance scenarios (Maurer et al., 2006; overview, Mergner et al., 2009b). It also covers the superposition of the different disturbances and of the disturbances and voluntary movements.

Furthermore, it has been extended to also include the hip joints in addition to the ankle joints (double inverted pendulum dynamics). Interconnections of sensors and estimators across the body segments lead to the emergence of human-like movement synergies and postural adjustments. In the example shown in Figure 3.6, trunk bending forward is automatically associated with a backward lean of the legs, because the DEC method tries to maintain the

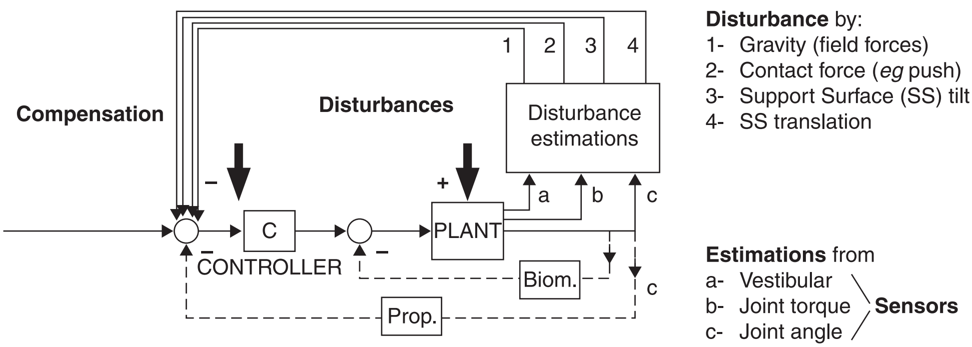

Figure 3.4 Servo control model extended by long latency reflex (LLR) loops for disturbance estimation and compensation ('DEC') model. Estimations of disturbances (1–4) receive multisensory input (a–c). Disturbance compensation occurs through feedback after sign reversal. Given ideal compensation, the servo loop performs the desired movement trajectory as if there were no disturbances.

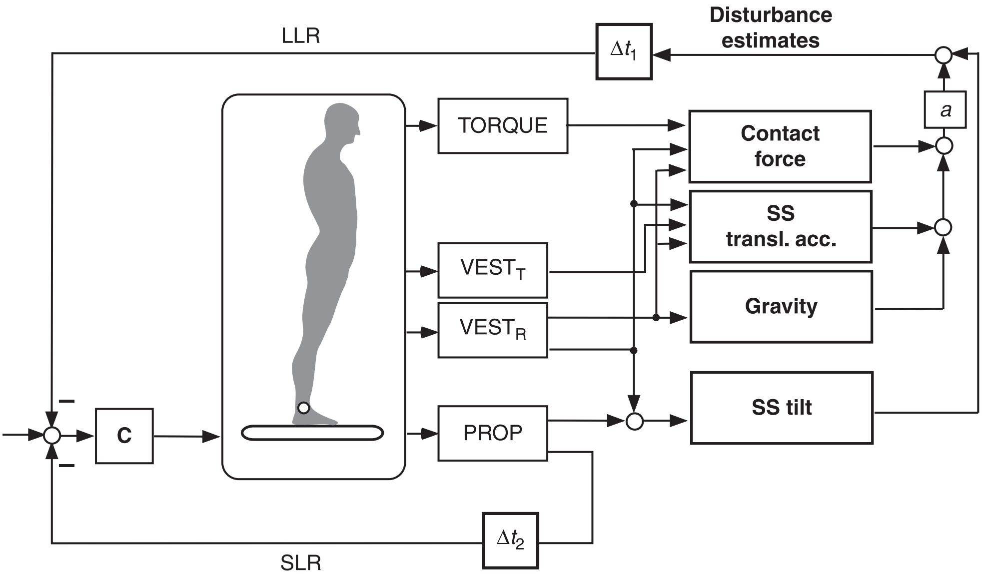

Figure 3.5 More detailed version of DEC model. It shows the network of sensor output signals that feed into the disturbance estimations ($VEST_T$ and $VEST_R$, vestibular sensors of head translation and rotation, respectively). The lower feedback loop represents the servomechanism in terms of short-latency reflex, SLR (lumped time delay is in the order of Δt_2 = 80 ms). The upper loop represents long latency reflexes, LLR (Δt_1 = 120–180 ms or more). The controlled variable is body-in-space angle. The torque signals in the LLR loops (upper three) are transformed into body-in-space angle equivalents (box *a*; e.g., estimate of COM gravitational torque, box Gravity, relates to body lean angle). Also, the support surface (SS) tilt estimate, a foot-in-space signal, is transformed into a body-in-space signal in that it combines with the body-to-foot signal from the proprioceptive SLR loop (this LLR loop is not shown separtely, for sinplicity).

COM of the body as a whole above the ankle joints. Together with simulations that included 4 DOF, Hettich et al. (2011) demonstrated modularity of the DEC method, meaning that the same control method can be applied as a module for each segment in a stack of segments. Control reconfiguration automatically occurs when a joint becomes fixed (e.g. by a plaster) or may be easily established for use of an additional segment (e.g., by handling a tool).

A basic constituent of the DEC model is the vestibular sensor. But human subjects without vestibular function are able to balance support surface tilts and pull stimuli, and this even with closed eyes (Maurer et al., 2006). When modeling this within the DEC framework, the postural responses of the vestibular loss subjects could be formally described and simulated in software simulations and robot experiments (Schweigart & Mergner, 2008; Mergner et al., 2009b). This implied the assumption that human subjects use force/torque cues to substitute the vestibular signals. However, this substitution endangers control stability and limits the working range of the balancing (Mergner et al., 2009a).

Cognitive aspects of the DEC model

The DEC loops represent LLR in that they perform context-dependent disturbance compensations involving loops through basal ganglia and the cerebral cortex. One aspect of this

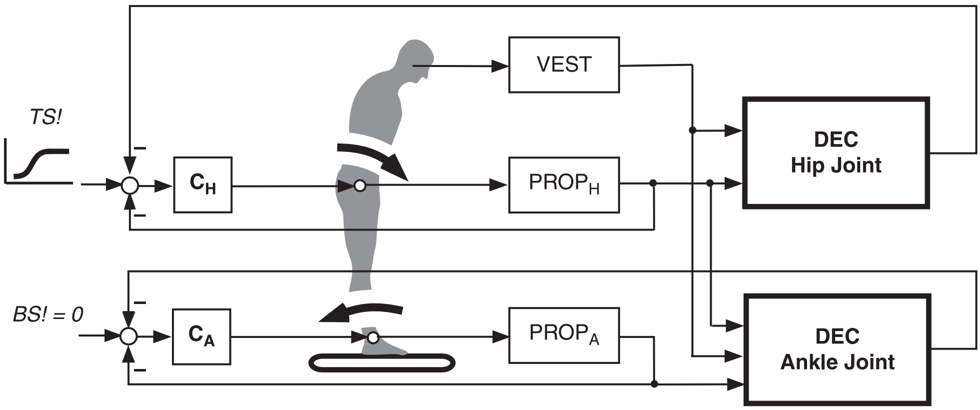

Figure 3.6 Emergence of movement synergy and postural adjustment from hierarchical DEC control (extended to include the hip joints in addition to the ankle joints). Trunk lean forward automatically leads to backward lean of legs. Simplified control model of corresponding double inverted pendulum biomechanics, where the desired trunk-in-space movement signal (*TS!*) is fed into hip control, while maintaining upright position of whole-body COM-in-space is desired for the ankle control (*BS!* = 0°). Ankle control takes into account the change in body geometry by including sensory information of trunk motion. Thus, the leg movement emerges from the DEC principle and does not necessarily require feed forward signals.

context dependency is that compensations are continuously adjusted to external disturbances. For example, when standing in a moving bus and the disturbances are changing from support surface tilt to translational acceleration, the type and strength of the compensations change accordingly. From the outside, the impression might be that an intelligent observer analyzes the scenario and adjusts the compensation accordingly. Actually, it is the DEC mechanism that in real-time automatically extracts the disturbances. The output mechanisms of the estimators then compute the disturbance compensations for the relevant joints (especially ankle, hip, and knee joints). This may involve motor learning and automating in the cerebellum.

Another aspect of the context dependency is that the compensation can voluntarily be influenced. For example, when standing on a tilting platform, an automatic response would be to compensate the tilt in order to remain upright, but it is also possible to voluntarily downscale the compensation and get rotated with the platform.

These two aspects make the DEC processing level an intermediate between the high level of cognition (with attention allocation, planning, reasoning, etc.) and the low levels of basic sensory processing and primitive reflex motor control. There may be even more intermediate level functions, *disturbance expectation and anticipation*, in addition to the context dependency of disturbance compensation.

One idea was that the cognitive level may associate objects and events in the outside world (ride in red bus) with typical disturbances in world or task coordinates. This may be advantageous compared to associations with patterns of muscle activities and joint torques in body coordinates as they change with body configuration. Having learned the associations between outside event and disturbance, a given event (red stop light) may invoke an *expected* disturbance (support surface deceleration) and predictive compensation (anticipatory postural adjustment). The expected disturbance signal would be fed forward from the cerebral cortex into the estimator and fused with sensory feedback estimates. Similarly, such expected disturbance signals can be thought to be derived from desired movement signals during voluntary movements, dealing then with the self-produced external disturbances (e.g., an increasing gravitational ankle torque with active body lean) or internal disturbances (inter-segmental torques).

Both ideas underwent proof-of-principle tests in experiments that used humanoid robots, in which the DEC model was implemented, in a human posture control laboratory for comparison with human subjects (see next section).

Robots and posture control research

Abstracting human experimental data into control models faces the problem that the models of complex mechanisms such as human sensorimotor control tend to be incomplete. For example, they do not usually contain 'real world' noisy and inaccurate sensors or non-linearities such as mechanical dead zones and thresholds. Some features such as foot friction on the support surface may even be very difficult to approximate in such models. Using robots in so-called 'hardware in the loop' simulations in addition to software computer simulation enhances the modeling. Benefits can be expected not only for sensorimotor research, but also for robotics where researchers would like to learn from biology human-like features such as failsafe robustness, flexibility, energy and processing efficiency, etc. (Mergner & Tahboub, 2009).

With this in mind, the DEC model was re-embodied in a humanoid robot (Figure 3.7) that was equipped with human-inspired mechatronic sensors and artificial muscles (Mergner et al., 2006). It was tested in the posture control laboratory in direct comparison with humans, demonstrating the validity of the DEC model (Figure 3.8; see Mergner et al., 2009b; Hettich et al., 2011). In a further step, it served the proof-of-principle tests for the predictive (feed

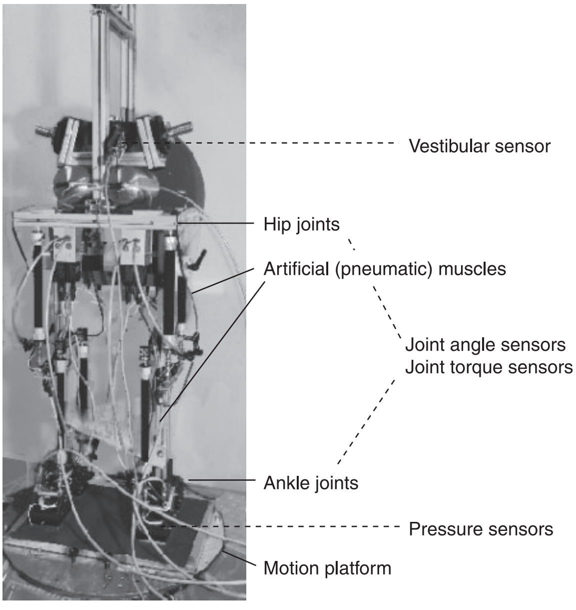

Figure 3.7 Picture of postural control robot Posturob II (2 DOF, hip and ankle joints). It is given human anthropometric parameters, uses artificial muscles and mechatronic artificial sensors and is controlled by the DEC algorithm. It serves as 'real world' model that is tested in the postural control laboratory in the same way as the human subjects.

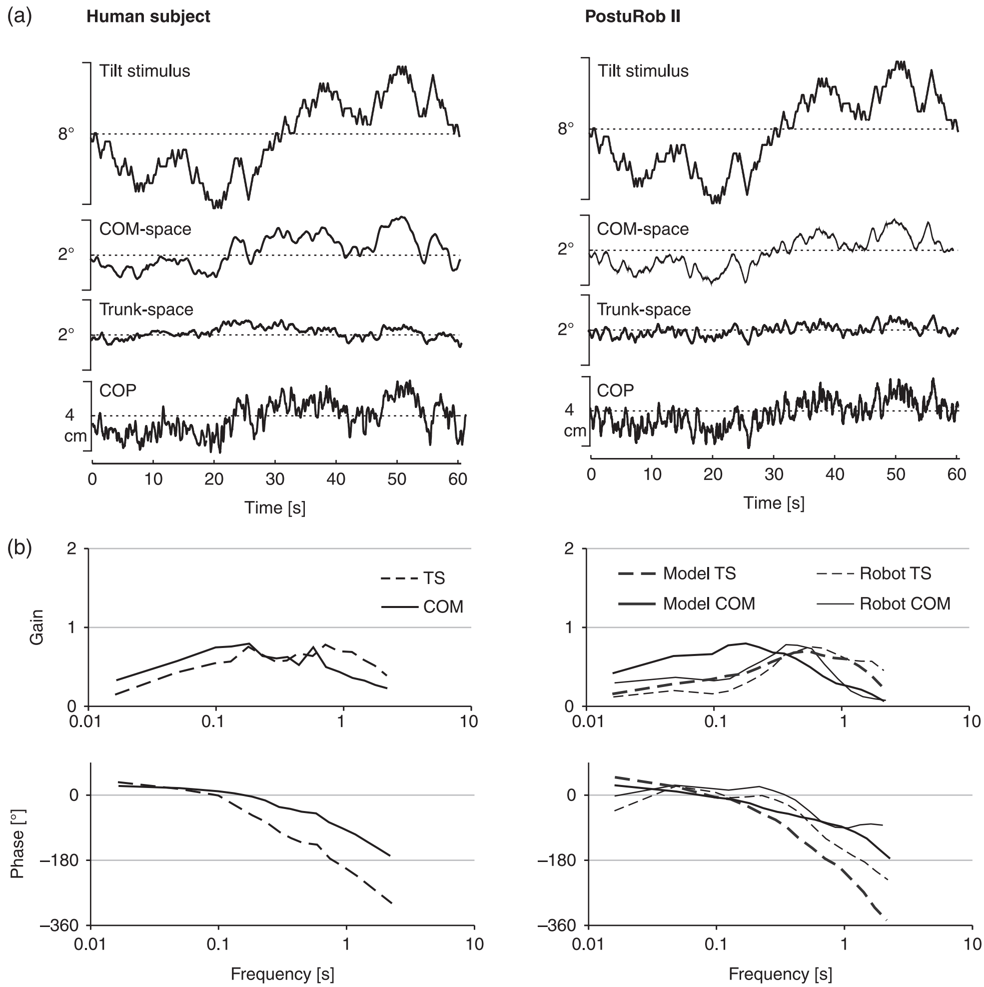

Figure 3.8 Comparison of postural responses between human and robot experiments. (a) Responses to pseudorandom sequence of anterior–posterior support surface tilts. Shown are angular wholebody COM and trunk excursions with respect to the gravitational space vertical and COP shifts (averages over five trials from one subject). (b) Gain and phase of the trunk and COM tilt responses plotted over frequency. Bode plots were calculated using cross-spectral analysis (Fourier transform; human data, averages of six subjects). Zero gain means that COM and trunk remain perfectly vertical, while unity gain means their rotation with the support surface (motion platform). The phase indicates the temporal relation between stimulus and response (adapted from Hettich et al., 2011).

forward) aspects of the DEC model (Mergner, 2010). The results of these robot experiments now provide the basis for future human experiments.

Further benefits obtained by including the robot into research were ‘learning by building’, making teaching more attractive, and better public reception for this research. Even more important, the robot with its human-like sensorimotor behavior represents a guideline for improving medical assistive devices such as prostheses and exoskeletons.

Summary

When we reach out with our arm or maintain a body posture, we compensate for mechanical disturbing factors such as gravity usually without being aware of it. The need to stabilize is more intuitive when we consider our activities during biped stance since we need to balance almost continuously. The balancing may be challenged not only by external factors such as gravity or compliant or rough terrain, but also by our own actions such as trunk bending or foot lifting. It has been known for a century that sensory feedback control is a key to understanding such stabilizations. Originally, it was thought to occur in the form of primitive postural reflexes. These reflexes, however, do not explain humans' rich and flexible sensorimotor behavior. Only recently have researchers discovered how the primitive reflexes become superseded by context-dependent sensory feedback in automated stabilizing reactions, which develop during sensorimotor maturation in childhood. These automated reactions provide the necessary behavioral flexibility. The underlying mechanisms have been abstracted and formalized for use in computer simulations and humanoid robots. This research helps to improve therapies and assistive devices for sensorimotor-impaired patients.

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