META LEVEL CONCEPT VERSUS CLASSIC REFLEX CONCEPT FOR THE CONTROL OF POSTURE AND MOVEMENT

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INTRODUCTION

The control of posture is traditionally thought to be based upon simple sensory feedback mechanisms known as the postural reflexes. The reflexes consist of highly stereotype postural reactions which are observed in response to sensory stimuli. This concept received support from basic research in that electrophysiological and anatomical studies demonstrated neuronal connections between the corresponding sensors, their central relays and motor output centres. Postural reflexes can be evoked not only in primitive animals, but also in mammals and man. This applies, however, only as long as the central nervous system of mammals and man is still in an immature state, or if it is damaged during later life. In the intact and adult individual, in contrast, the postural responses are no longer stereotype and therefore cannot be termed reflexes. Yet, they still represent highly automatized reactions and certain body postures adopted during spontaneous behaviour are reminiscent of the reflexes (38). It is generally believed that the postural reflexes come under the control of higher brain centres soon after birth with maturation of the brain. This would then allow volition and cognition to control the postural mechanisms. How this control is achieved is still an enigma, however. A simple and straight forward assumption would be a control that modulates the gain of the reflexes – an often adopted notion. The present study suggests an alternative.

The alternative we suggest is that posture control of the adult and intact individual is no longer based directly on the sensory signals, but on centrally processed sensory information. Thus, we assume an interruption of the tight sensor-actuator coupling of the reflex loops, postulating an interposition of a sensory processing level on which the brain reconstructs the physical stimuli that evoke the sensory signals (meta level). For example, it tries to identify the cause of a given vestibular signal by reconstructing, by way of interaction of the vestibular signal with other sensory signals, whether the underlying head rotation stems from a head, torso (trunk), or support surface rotation. The resultant estimate of the stimulus is then used for the sensory control of the response, instead of the original vestibular signal. By this, the response becomes more specific than a stereotype vestibulo-spinal reflex would be.

Our concept is in the tradition of earlier attempts to overcome the classic reflex concept. Most of these earlier attempts focused on a particular aspect. They dealt

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with the question how the brain overcomes the problem that reflexive stabilisation of a given limb or body position tends to prevent or distort voluntary movements. This posture-movement problem or paradox, as it is sometimes called, is still debated to date (e.g. Ostry and Feldman) (30). Notably, however, with the sensorimotor control mechanism envisaged here, this problem does not arise. Rather, we can make it quite obvious that compensation of external stimuli represents a prerequisite for a successful performance of goal directed movements.

In the following we briefly consider the classical literature on sensory control of posture and on related own findings. We then provide support for the new concept of internal stimulus reconstruction by showing that it can be implemented into a simple posture control model. This model is then compared to one that represents the classical concept of direct sensor-actuator coupling. The stimulus reconstruction model has been presented under different aspects already in a previous study (25) in which we showed that it is able to mimic certain dynamic transfer characteristics of human postural responses obtained under a variety of different experimental conditions. This is similar to the study of Peterka (33) which was the first to demonstrate in a detailed and comprehensive way that the most essential aspects of human postural behaviour can be simulated with a simple sensory feedback control model.

The classical concept of postural reflexes and the posture-movement problem.
The early literature of postural reflexes distinguished mainly between two sets of reflexes, the vestibular and neck *positional* reflexes ("tonische Labyrinth- und Hals-Reflexe" of Magnus, 15) and *righting* reflexes ("Labyrinth- und Hals-Stellreflexe"). The positional reflexes tend to maintain body equilibrium during stance against external perturbations. They can be evoked in a stereotype way in the decerebrate cat, i.e. after removal of the upper midbrain structures and above. Animals in which the damage is restricted to centres above the midbrain are capable of producing a more complex chain of reactions by which they may restore primary (upright) head and body position in space even from a lying starting position after a fall, for instance (righting reflexes). Comparable positional and righting reflexes are found in man in the newborn state, while during later life they are observed only after large cerebral lesions (8, 31, 41, 45). Focusing on stance control, we will consider in the following exclusively the positional reflexes. Furthermore, we will disregard earlier attempts that tried to distinguish between static versus dynamic reflexes, or otolith versus canal reflexes, or rescue reactions for large and fast stimuli etc.

Among the positional reflexes, the vestibular reflex acting on the limbs (the vestibulo-spinal reflex, VSR) is generally considered to play a decisive role (for literature of its anatomical connections and electrophysiological characteristics, see 38, 47; also Manzoni, this issue). In vertebrates in which the head can be moved independently of the trunk, a functionally similar reflex is evoked by neck proprioceptive stimulation during neck excursion (cervico-spinal reflex, CSR). Both, the VSR and the CSR are shown in schematic form in most textbook chapters on posture control. A version of the scheme is given in Figure 1A. It goes back to a study of von Holst and Mittelstaedt (44) in which they suggested that the VSR is asym-

metric (one leg extending, the other flexing), while Magnus (15) originally had considered it symmetric. Now the VSR was regarded a functional counter-part to the CSR which was known to be asymmetric. The authors suggested that the two reflexes interact such that they both counteract trunk excursions in space, but cancel each other when only the head is moved on stationary trunk (for details, see Figs. 1Aa-c, 37). Later work then provided experimental evidence for such a VSR-CSR interaction in the decerebrate cat (13, 16).

In their study, von Holst and Mittelstaedt (44) pointed out that this vestibular-neck interaction allows the brain to behave as if the vestibular system were located in the trunk. This is highly relevant since most of the body weight is located in the trunk and the imaginary point called centre of (whole body) mass, COM, is normally located there too. Hence, motion of the trunk mechanically disturbs postural stability of the COM, while that of the head hardly does, and it is thus the stabilisation of the trunk which is instrumental for equilibrium control.

The study of von Holst and Mittelstaedt (44) was meant as an argument against the classic reflex concept and the general notion at that time that the reflexes are shut off by inhibition during voluntary movements. The just described vestibular-neck interaction was one of several mechanisms by which they tried to overcome this concept and the related posture-movement problem. The particular argument here was that, by way of the VSR-CSR interaction, head movements would not interfer with trunk stability, be they active or passive (compare Fig. 1a-c). But, notably, the head movement would activate, in addition, a vestibular reflex that tries to stabilise the head in space, the vestibulo-collic reflex (VCR). How to prevent that the VCR hinders the voluntary head movements? In another part of their paper (their Fig. 3), von Holst and Mittelstaedt (44) offered a solution also for this problem. They assumed that the corresponding voluntary command signal, stemming from higher brain centres, feeds into the lower-level reflex centre and makes this centre produce the voluntary movement. In today's terminology of feedback control systems, we would refer to this as a simple kind of servo control (see below).

Not considered by von Holst and Mittelstaedt (44) was, however, that head stabilisation is achieved not only by the VCR, but in addition by a local proprioceptive reflex of the neck muscles, the cervico-collic reflex (CCR), as we know meanwhile. It sums additively with the VCR during head rotation on the stationary trunk (9). Based on similar or related aspects, other researchers considered that these concepts of von Holst and Mittelstaedt (44) did not fully resolve the posture-movement problem and therefore searched for other solutions. Roberts (37), for instance, assumed that a voluntary head and trunk movement of an intact animal usually does not lead to postural reflexes, because "anticipatory pre-emptive actions" (learned patterns of postural actions) take over before the sensory thresholds of the reflexes are reached.

We like to mention here two more concepts, by which von Holst and Mittelstaedt (44) aimed to overcome the posture-movement problem. One concept, the "reafference principle", relates to the question how the brain distinguishes during voluntary movements between sensory signals which are self produced (reafferent) and those which stem from external stimuli (exafferent). They suggested that this distinction is

made on the basis of a comparison between an "expected" sensory signal, derived from a "copy" of the voluntary command signal ("efference copy"), and the actual sensory signal. Any component of the sensory signal which is not explained by the efference copy must represent an exafferent signal (potentially an external perturbation that requires a compensatory response). They applied the principle to visual control of eye movements, where an efference copy-like signal had been postulated before by Helmholtz and others and where it still can be found in contemporary concepts (e.g. 40). Furthermore, it is contained in very general form in sensorimotor control models in which feed forward control from central command signals is combined with sensory feedback control (e.g. 42).

Another solution of the posture-movement problem envisaged by von Holst and Mittelstaedt (44) concerns the interaction of voluntary limb movements with the stretch reflex. The reflex is evoked by passive muscle stretch that activates muscle spindle afferents, which in turn activate alpha-motoneurons and by this lead to a muscle contraction that counteracts the stretch. Summarising findings from the literature of their times, the authors presented a scheme in which they postulated how a voluntary movement may be generated despite this reflex. The corresponding voluntary command signal would not only activate the alpha-motoneurons, but also the gamma-motoneurons (alpha-gamma co-activation). This then leads to a contraction of intrafusal muscle fibres, which in turn tend to stretch the muscle spindles and thereby neutralises spindle relaxation from extrafusal muscle fibre contraction. The result is that, overall, the spindle afferent signal is not changed during the voluntary contraction. A further aspect anticipated by these authors is that the alpha motoneurons might be driven via gamma motoneuron activation and spindle afferent input, so that the voluntary movement may actually arise from a pre-stretch of the spindles. This would represent a servo control mechanism which is more complex than the aforementioned one. The concept is still contained in similar form in contemporary schemes of limb movement control (e.g. Fig. 8.14 of 5).

These concepts represent historically important steps in our understanding of how voluntary movements and the various postural control mechanisms (e.g. vestibular and proprioceptive) combine in spatially oriented behaviour. However, an implementation of these concepts into a posture control model for comparison with experimental data has not been attempted so far, to our knowledge.

Vestibular-proprioceptive interaction in gaze stabilisation and self-motion perception.

In their example of the cat's responses during tilt, von Holst and Mittelstaedt (44) also considered effects on the eyes. They assumed that vestibular and neck proprioceptive reflexes on the eyes combine such that they synergistically stabilise eye position in space in the head-only tilt situation. However, later work showed that the neck reflex on the eyes (cervico-ocular reflex, COR) shows a considerable amplitude only shortly after birth in both cat and man, and that in the adult individual the vestibulo-ocular reflex (VOR) clearly dominates (27). This is what one would expect theoretically; for eye stabilisation in space it suffices to react to any head-in-

space movement by a corresponding eye-in-head counter-movement. In contrast, the relative excursion of the head with respect to the trunk (neck deflection) should remain without effect on the eyes. On this background, oculomotor physiologist relate eye-in-space (gaze) stabilisation primarily to the vestibular signal arising during head movements and usually do not consider the behavioural context in which the head movement is generated. The situation is quite different, however, with posture control, i.e. with stabilisation of the body in space on its support base. Here it matters whether the vestibular signal arises from a head movement on stationary trunk, a whole-body movement on stationary feet and foot support, or a whole-body excursion through support surface rotation: The postural reactions, conceivably, should differ accordingly.

One may think that this problem is already solved by the above described vestibular-neck interaction, which yields a postural mechanism for the trunk as the most relevant body part that is to be stabilised (see above). It was therefore a surprise when we observed in psychophysical studies on self-motion perception a set of rules which appeared to be in conflict with this notion. The rules may be summarised in the following way: When the brain tries to differentiate to what extent a vestibular signal stems from a head-on-trunk, body-on-feet or foot support-in-space motion, it uses neck and leg proprioceptive signals. A corresponding neck signal indicates a head-on-trunk motion, a corresponding leg proprioceptive signal a body-on-feet motion. Finally, any component in the vestibular signal that is not explained by the neck and leg proprioceptive signals must stem from a rotation of the support surface in space. In other words: Within the functional context of self-motion perception, at least, an isolated vestibular signal is taken to indicate motion of the support surface. In the above described context of the VSR, by contrast, we assumed that it indicates motion of the trunk. Before we try to resolve this apparent discrepancy, we briefly explain the psychophysical findings.

In our psychophysical work on self-motion perception (26, 39) we seated normal subjects and patients with loss of vestibular function on a rotation chair and applied whole-body rotations in space in the horizontal plane (semicircular canal stimulation). In addition, we rotated the subjects' heads independently of their trunks (with the help of a head rotation device). The patients perceived only the head-on-trunk rotation. The normal subjects, in contrast, were able to estimate, in addition, the trunk-in-space and head-in-space rotations. The data of the normal subjects could be simulated by a model of vestibular-neck interaction. In the model, the interaction is performed in two steps: (1) First, an internal estimate of trunk-in-space rotation is obtained; to this end, the vestibular head-in-space signal is summed with a neck signal of trunk-to-head rotation. (2) In the second step, the perception of head-in-space rotation is obtained, by summing the trunk-in-space estimate with a neck signal of head-on-trunk rotation. This head-in-space estimate was clearly distinguishable from the vestibular head-in-space signal (e.g. when comparing detection thresholds).

However, introspective reports in these studies suggested that one perceives in this experimental situation the trunk rotation only as a consequence of the chair rotation and that it is primarily the chair (body support) which is experienced as rotat-

ing. This led us to place in a subsequent study subjects' feet on a rotatable support and to study the interaction between vestibular and leg proprioceptive inputs (22). The results were analogous to the previous findings on vestibular-neck interaction. We therefore concluded that the space reference in the vestibular head-in-space signal is transferred via the trunk to the feet or, generally, to the body segment which is resting on the body support, yielding ultimately an internal representation of support motion in space. Furthermore, analogous findings were obtained when we studied self-motion perception during translatory trunk and leg motion in the horizontal plane (interaction between otolith and leg proprioceptive inputs; 11).

Together, these findings led us to formulate a more general concept of vestibular-proprioceptive interaction: We assume that the sensory signals internally interact such as to reconstruct the physical stimuli having impact on the body. During stance, the multi-segment structure of the human body can be viewed as a stack of several superimposed motion platforms (legs, trunk, head), which are anchored by gravity one upon the other, with the lowest one resting on a support surface. Each lower segment in the stack and ultimately the support surface serve as buttress when body segments are moved (19, 23). Our notion of an internal reconstruction of the physical stimuli complies with the earlier notion of experimental psychology according to which perception aims to reflect the 'distal' stimulus (physical stimulus) rather than the 'proximal' stimulus (specific impact on receptors; physiological stimulus or stimulus dimension).

The internal multisensory reconstruction of the physics appears to be advantageous for the individual because of several reasons. For instance, when the individual organises the sensorimotor control of its body, it has a natural basis to deal with the high complexity of the body in terms of its many segments and thus the many degrees of freedom (20). Furthermore, we have shown that, by way of the afore described vestibular-proprioceptive interaction, the internal estimate of body motion shows a minimum of signal noise whenever the support surface is stationary, i.e. in the normally prevailing situation of firm ground. The reason is that the estimate is then determined by the proprioceptive input alone, which shows much lower noise than the vestibular signal (24). This is analogous to the estimation of body motion during vestibular-visual interaction; it also becomes determined by visual input alone when the visual scene is stationary and then no longer bears the high noise of the vestibular signal (28). In the present context, we would assume that the internal multisensory reconstruction of the physics is advantageous also for posture control. A single sensory signal fed into a postural reflex usually is insufficient to represent the physical stimulus that evoked the signal (see above). Therefore, a multisensory reconstruction is required, and the more accurate the stimulus reconstruction, the higher the chance that the response is adequate, accurate and successful.

A framework for a revised posture control concept

We have considered above on one hand the vestibular-proprioceptive interaction in the context of VSR and CSR. We took it as instrumental to transfer the vestibular reference from the head to the trunk for a mechanism that tries to stabilise the COM

in space. On the other hand, we presented psychophysical evidence for a vestibular-proprioceptive interaction that registers motion of the body support in space by transferring the vestibular reference from the head via the trunk to the feet. In the following, we postulate that both interaction mechanisms exist in parallel and serve different functions. To explain this view, we reconsider the classic VSR-CSR interaction scheme after revising it in several respects.

We revise the scheme by placing the cat's feet on a support surface, on which it becomes anchored by gravitational reaction forces (Fig. 1Ba-f). Furthermore, we assume that the cat balances actively on the support and produces for some reason the shown trunk tilt in space in terms of a voluntary lean (panels a, b, d-f). An argument for the revision comes from a study of Britton et al. (3). In this study, galvanic vestibular stimulation in human subjects yielded a response in their leg muscles only when they used these muscles for equilibrium control. In contrast, when subjects grabbed with their hands a ground-fixed hold for balancing, the vestibular response occurred no longer in the leg muscles, but in the arm muscles, although the legs were still bearing essentially all of the body weight. We therefore assume that some high-level mechanism decides which body segment disposes of a buttress appropriate for equilibrium control. The situation for the cat here would be that it is to use the support surface as buttress.

In the following we consider three different physical stimuli which we assume to represent the relevant external perturbations of body equilibrium. They would have to be compensated for by the cat in order to allow it the voluntary lean towards the intended position in space. Having obtained in our psychophysical studies (see above) ample evidence for intersensory interactions between vestibular, proprioceptive and other sensory signals and the existence of internal estimates of external motion stimuli, we assume that these or analogous estimates are used in the sensory control of the corresponding postural responses.

The first external stimulus we consider is gravity. During the trunk lean together with the head in panel Ba, and similarly during the trunk-only lean with the head remaining upright in panel Bb, the cat's COM becomes tilted and shifted in space with respect to the support base given by the legs. This entails a change in the geometry of the ground reaction forces and requires a modification of the 'antigravity' muscle tone in the legs, as indicated schematically by the filled arrows within the legs in these panels (but no change in the length of the limbs). In contrast, hardly any change of the COM occurs with the head-only tilt in panel Bc and, correspondingly, no considerable modification of the antigravity tone in the leg muscles is required. Note that the cat's head and trunk excursions in panels Ba-c resembles those in Figure 1Aa-c. We take this similarity to assume that a vestibular-neck proprioceptive interaction analogous to the VSR-CSR interaction is evoking the change in antigravity muscle tone. In contradistinction to the classic reflex concept, however, we assume here that the response evoked by the vestibular-neck interaction aims *not* to restore the body's starting position, but rather tries to compensate the gravitational effects during the lean (thus preventing gravity from accelerating the COM off its desired position). In the following we term this presumed mechanism '*vestibular gravity compensation*'.
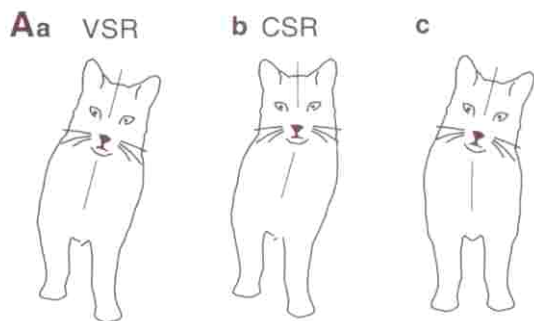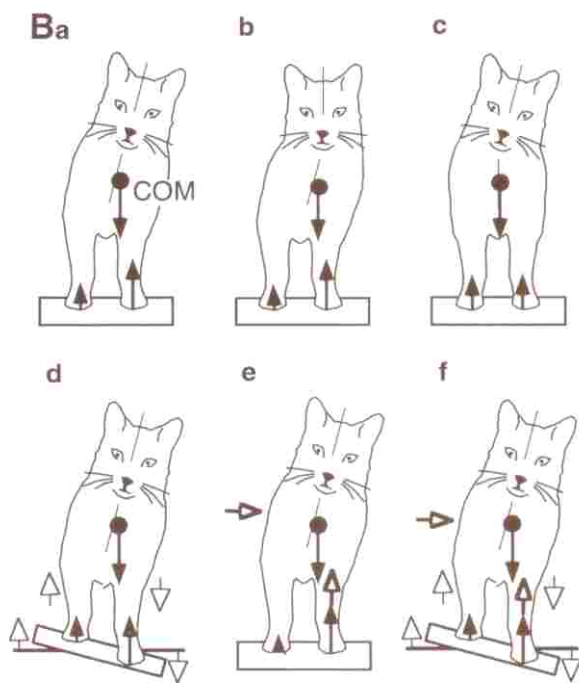
Fig. 1A,B. - *Schematic presentation of postural reflexes.*

A: Classical scheme of vestibulo-spinal reflex (VSR, a), cervico-spinal reflex (CSR, b), and of VSR-CSR interaction with mutual reflex cancellation during head tilt on stationary trunk (c). The VSR is evoked by head-in-space rotation during the whole-body tilt and the CSR is evoked by neck deflection during trunk tilt with the head remaining stationary. Both reflexes lead to leg extension on the shoulder-down side and flexion on the opposite side, thought to counter-act the trunk excursions. B: Modified version of the classical reflex scheme. a-c Body postures are same as in Aa-c, but all are actively adopted on a support surface. The voluntary body leans in panels a and b lead to a shift of the centre of mass (COM) with respect to the foot support base. This is compensated for by appropriate changes in limb muscle tone (filled arrows in legs). d Superposition of support tilt on lean; it requires an additional change in the length of the limbs (thin open arrows). e Superposition of a contact force in the form of a push against right shoulder; it requires an additional change in limb muscle tone (bold open arrows). f Superposition of stimuli of panels d and f. Further descriptions in text.

The second external stimulus is a tilt of the support surface. In the situation shown in Figure 1Bd, the stimulus is superimposed on the cat's active lean movement. Note from the figure that a successful performance of the lean requires not only the afore described gravity compensation, but in addition a change in limb length (thin open arrows in the Figure). Since we have described in the previous section that the brain disposes of an internal estimate of support surface motion from vestibular-proprioceptive interactions, we assume here that the cat uses an analogous estimate to produce the required response in terms of a compensatory change in limb length. This produces a body-on-support excursion counter to the support-in-space tilt, thus trying to maintain or restore the body's starting position (*'vestibular support tilt compensation'*).

The third external stimulus which we consider is an external contact force having impact on the cat's body during the voluntary lean. Let the behavioural situation here be that of a push which is exerted against the cat's shoulder in the direction of the lean (open arrow at right shoulder of the cat in Figure 1Be). We assume that the cat disposes of an internal estimate of the effect which the stimulus exerts on the postural system. The push is mechanically transmitted to the feet where it adds to the gravitational ground reaction forces and the forces actively produced by the cat during the balancing. The sum of these forces is registered by plantar pressure receptors and the brain extracts from the corresponding sensor signal by means of central intersensory interactions an estimate of the contact force component, as we will explain in more detail below. It then uses this estimate to produce a compensatory change in leg muscle tone (panel e, open arrow in left leg). Given this *'contact force compensation'* is successful, the cat is able to achieve and maintain the desired lean position despite the push.

We conceive that the estimates of these physical stimuli are generated on a sensory processing level (meta level) which becomes interposed in the sensor-to-actuator coupling of the reflex loops, possibly some time after birth when the individual is learning from active confrontation with the external world. What is then replaced in the sensory control loop by these internal estimates of the physical stimuli? It is the receptor effect of the physiological stimulus, the direct sensory signal, which in the classic concept evokes the reflex. Applied to the situations shown in Figure 1B, one may note that, actually, all three stimuli may lead to a body excursion off the desired position in space: In panel d, it represents a primary effect upon support tilt, and in panels a, b and e it may represent a secondary effect upon body acceleration by the gravitational force or contact force, if these are not sufficiently compensated for. In fact, the classic reflex concept took body excursion in space as the relevant stimulus for the positional reflexes on the limbs, and it took the associated vestibular input as the relevant sensory feedback signal or, in vertebrates with mobile neck, feedback from a hypothetical graviceptive sensor in the trunk. The view of a transformation of the vestibular reference to the trunk, which became popular after the work of von Holst and Mittelstaedt (44), did not really change the classic reflex concept, since it can be explained by an interaction of the reflexes rather than of sensory signals.

In the following we compare the new concept with the classic reflex concept. We do so in a theoretical approach by implementing both concepts into simple postural control models and compare the results of model simulations. One model contains the meta level with the presumed internal reconstruction of the physical stimuli (*'stimulus reconstruction' model*), while the other model assumes direct couplings between sensors and actuator (*'direct coupling' model*). In the simulations we test the three physical stimuli used in Figure 1B in superposition with the voluntary lean. Finally, a superposition of all three physical stimuli as in Figure 1Bf results (combination of panels *d* and *e*). We assume that such a complex situation and continuous shifts between the different situations are realistic and may well occur in the normal behavioural repertoire of a cat, for instance when it is fighting against another cat on a swaying branch of a tree.

The models we present in the following represent a biped (human) rather than a quadruped, however. One reason is that we try to remain for the moment as simple as possible. Therefore, it is easier to deal with the fore-aft angular body-to-foot motion of a biped (in terms of an 'inverted pendulum') than with the more complex motion of a quadruped. Another reason is that control models and many experimental data became available recently for human subjects from a number of laboratories (e.g. 7, 33, 43) including our own (25). By using an 'inverted pendulum' model, we avoid complications from the multi-body dynamics of a body that contains several moving segments. This simplification entails that we do not consider in the following independent head and trunk movements, but rather take head and trunk as a rigid 'body' which contains the vestibular systems (thus, no vestibular-neck interaction is considered).

METHODS

The two postural control models were implemented in Simulink/Matlab (The MathWorks Inc., Natick, MA, USA). The physics (mechanics) part is identical in both models. It is shown in Figure 2, both schematically as an inverted pendulum stick figure (inset) and as a wiring diagram. The main inputs into the PHYSICS part consist of MUSCLE TORQUE generated by the SUBJECT (on top of the diagram) at the ANKLE JOINT and of the physical stimuli (see below). The outputs are given by the inputs into the SENSORS of the individual, as described later. The physics basically consists of vertical rotations of two segments about the ankle joint in the sagittal plane (inset). One segment comprises the head, trunk and legs (forming together the 'body', B), with the primary position of B being upright in space (S). The other segment consists of the foot and the foot support surface ('foot' segment, F), with the primary position of this segment being horizontal. With both segments in primary position, the body's weight presses the foot firmly on the support surface, by which the foot becomes fixated on its support. In the following, only small angular excursions about the ankle joint axis of the body in space and the foot in space are considered (angles BS and FS, respectively), a fact which will allow us to use small-angle approximations (e.g. $BS \approx \sin(BS)$). Angles in the model are given by full lines, while dashed lines indicate torque.

The effect of the muscle torque via the ankle joint on the body is shaped by the body's moment-of-inertia, which we represent in the model by the box 'Inertia'. The torque tends to move the body with respect to the foot segment which serves as buttress. In the box Inertia the torque, T, leads to a rotational acceleration of the body in space, which is inversely proportional to the moment-of-inertia, J, of the body about the ankle joint axis ($d^2BS/dt^2 = T/J$). The value of J in the model was taken from our recent experimental study (25; calculated from our subjects' mean COM value and mean COM height above ankle joint). BS, resulting then from d^2BS/dt^2 by double integration, is taken as the output of the Inertia box.

The effect of gravity on the body is given by the box 'Gravity' and its positive feedback on the ankle joint. The input to this box is BS. With the body perfectly upright such that the body's COM is exactly located above the ankle joint, the gravitational acceleration of the COM would be essentially zero, since it is oriented in the direction of the rigid support of the COM by the skeletal system. Off the vertical, the effect of the gravitational acceleration of the COM increases and generates an ankle joint torque depending on the sine of BS times the height above the ankle joint, h. The torque furthermore depends on the mass of the COM, m, and g (the value of the gravitational torque was taken from our previous work, see above). The output of this box in terms of gravitational ankle joint torque is taken to represent the first of the three external physical stimuli which we consider.

The second external stimulus is given by a tilt of the foot support surface, represented in the Figure by an input into the FS line. FS changes the foot-to-body angle FB depending on BS. The
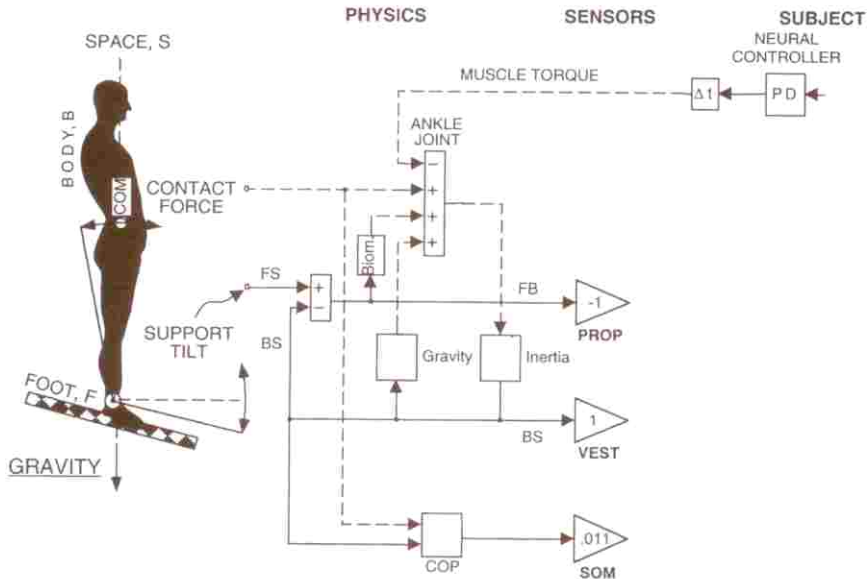
Fig. 2. - *'PHYSICS' part of our posture control models.*

The inset (left) defines the 'inverted pendulum' consisting of two segments (B, body segment: head, trunk, and legs; F, foot segment which includes support base) which both can pivot about the ankle joint. External stimuli are gravity, support tilt (rotating platform with axis through ankle joint), and contact force (horizontal pull on centre of mass, COM).

The wiring diagram (right) describes the signal flow. Torque in the ankle joint stems from 'muscle torque' (produced by neural controller, box PD) and the contact force. Furthermore, it may arise from platform tilt (input FS, foot-in-space angle). FS sums with BS, the body-in-space angle, yielding FB, the foot-to-body angle. Box Biom. (for biomechanics) transforms FB into ankle torque. Finally, torque in the ankle joint is produced by the contact force and the gravitational acceleration of the body (box Gravity), depending on BS. The ankle joint torque, in turn, accelerates the body, which changes BS depending on the body's inertia (box Inertia). Generally, dashed lines represent torque and solid lines angles. All delays in the system are represented as one dead time (Δt). BS excursion leads to a shift of the centre of pressure (box COP; also affected by the contact force stimulus).

PROP, proprioceptive sensor; VEST, vestibular sensor; SOM, somatosensory sensor in terms of plantar pressure cue. This and the following wiring diagrams were directly taken from the simulation program and thus do not strictly follow the conventions of how engineers present sensory feedback models.

change in FB evokes a torque in the ankle joint via the passive viscous and elastic elements of the ankle joint (in the muscles and ligaments; for the moment we take these to be very small as compared to the active elements, i.e. 1 in the box Biom., for biomechanics; compare Results). Furthermore, FB is fed via a proprioceptive sensor into a feedback loop that stabilises the ankle joint (see below).

The third physical stimulus, the external contact force, is taken to stem from a horizontal pull exerted on the COM (trunk), which is mechanically transmitted to the ankle joint and adds there to the other torques considered so far. Furthermore, to the extent that the ankle joint is stabilised, the contact force is mechanically transmitted to the foot and it sole (further details below). At the ankle joint the contact force is, overall, the fourth torque input (one being the active one by the muscles, while three are passive, stemming from gravity, support tilt, and contact force). Conceivably, BS will be stabilised (remain constant) only to the extent that the sum of these four torques becomes zero.

We conceive that the three physical stimuli can be internally reconstructed by the brain with the help of the following *three sensors*:

1. *Ankle joint proprioception* (PROP). We assume that mainly muscle spindle receptors from the ankle joint muscles inform the brain about the angle of BF. The proprioceptive signal is taken to show broad band pass frequency characteristics (box PROP is given ideal transfer characteristics; the sign reversal, -1, changes FB into BF). The internal representation of BF, the signal bf, will be used as a sensory feedback signal in a local control loop for ankle joint stabilisation. In addition, bf will be used for an internal reconstruction of the support tilt stimulus (see below).

2. *The vestibular system* (VEST). It is thought to provide an internal estimate of BS, bs. In particular, the signal bs is taken from an internal interaction mechanism which processes information of angular head velocity provided by the semicircular canal receptors and of linear head acceleration provided by the otolith organs (21; 47). In the present context it suffices to assume that bs shows broad band pass characteristics (we therefore simplify and give the box VEST ideal transfer characteristics, 1). A version of the bs signal will be used in the model as an estimate of the body's COM angular excursion with respect to the gravitational vector. Another version of bs will be used to derive, by way of vestibular-proprioceptive interaction, an estimate of support surface tilt (see below).

3. *Plantar somatosensory receptors (SOM)*. Information about this sensor system can be found in previous studies from this laboratory (17, 18). In short, one function of the system during stance is to inform, with the help of somatosensory receptors in the foot soles and of proprioception, the brain about the properties and the geometry of the foot support base. Furthermore, there exists another function which is more relevant here. The studies showed that the system provides graviceptive information in the low frequency range; it allows patients with complete vestibular loss to balance, with eyes closed, on a support surface that is slowly tilted. It does so by providing an estimate of how the centre of pressure (COP) is shifted under the feet. A low-pass filtered version of the COP signal reflects rather well the excursions of the COM in space on stationary support, here corresponding to BS (the low pass filtering removes contributions from active torque to the COP). It appears that the patients may use the internal estimate of it to some extent as a substitute for the vestibular bs signal.

We assume, however, that normal subjects use the plantar somatosensory system mainly for a different purpose. For them, this cue is instrumental for estimating external contact forces which have impact on body posture. As mentioned above, the contact force is to a large extent mechanically transmitted to the plantar soles, since the ankle joint is stabilised by the aforementioned local proprioceptive mechanism. This transmission is reflected in the model by a direct input from the contact force into the box 'COP'. In this box the input combines with the gravitational effect which the COM exerts on the plantar soles (note that also BS, which in addition contains the effects of the active muscle torque, is fed into the box). In the box these signals are transformed into one representing linear COP shift on the support surface (in cm). This shift is then registered by the plantar somatosensory system (SOM). SOM transforms the COP shift signal back into a signal of angular COM excursion (re-scaling factor 0.11 in the box SOM; a subsequent low-pass filter helps to suppress high frequency components which stem mainly from active torque). Not shown here is a subsequent intersensory interaction at the meta level; it compares the somatosensory estimate of BS (i.e., of the COM angular excursion) with the corresponding vestibular estimate of BS and takes any component of the signal which is not explained by the vestibular estimate as a measure of the external contact force.

The ankle joint and its muscles are taken here to represent an ideal angular actuator, assuming that the brain has found ways during phylogenesis and ontogenesis to deal with the joint and muscle properties on a global control level in some simplifying way (the one chosen here in the modelling follows largely the engineers' control theory). In this view, the actuator receives its input from a "neural controller" that performs the neuromuscular processing. It transforms a neural command signal (or error signal in a simple feedback system) into the torque. Stabilisation of an invert-

ed pendulum is known to require not only a proportional transformation ("stiffness" or propor-tionality factor, K_P), but in addition a time derivative version ("damping" factor, K_D). K_D is required to deal with body inertia; it does so by accounting for the forth coming kinematic and kinetic effects (without us having to invoke in the system an explicit feed forward predictor with an internal model of the physics and a shaping of the controller signal in terms of 'inverse kine-matics', for instance). Another simplification is that we implement into the model only a single delay time (box Δt; 100 ms), by which we assume that the brain has found ways to overcome the problem that is given by the fact that the various receptor systems, the central and peripheral path-ways, etc. each have different delay or processing times.

The model is highly simplified not only by considering solely two body segments, but also by restricting the motion to only the anterior-posterior (sagittal) rotational plane. Furthermore, we assume that the subject's eyes are closed (no visual orientation cues) and restrict the number of sensors to the minimum we consider necessary for an internal representation of the three physical stimuli. We avoided even to implement specific transfer functions for the proprioceptive and vestibular sensors, trying to chose the simplest presumption, which would be that these sensors have ideal transfer characteristics over the frequency range considered. By this we followed the premise of parsimony for using dynamic control models (generally called "Occam's Razor"). Generally, we address here a posture control system which deals with relatively small perturba-tions as they normally occur during standing, sitting etc. We assume that we have to distinguish this from other control systems which specifically deal with very large and rapid stimuli and gen-erate rescue reactions, for instance.

Descriptions of the intersensory interactions at the presumed meta level and of the feedback sig-nals are given in the Results section. Simulations of the models were performed using a smoothed ramp (derived from a 'raised cosine function') (24) and sinusoids (f = 0.01-1.6 Hz).

R E S U L T S

With the just described physics part of the model and the sensors as framework, we design now the postural control models by adding the sensory feedback loops. For both the stimulus reconstruction model and the direct coupling model we pro-ceed in four steps, starting from a situation in which a voluntary command signal is used to produce an active body lean, before then adding in the subsequent steps the three physical stimuli gravity, support tilt, and contact force. In model simulations we test to what extent the stimuli are successfully compensated and the voluntary lean is correctly performed. Different stimulus waveforms are used for the stimuli and the lean, so that they can easily be distinguished in the simulation results.

Stimulus reconstruction model.

1. *Voluntary body lean.* The situation is shown in Figure 3Aa. The physics part of the model contains here so far only the active muscle torque, the ankle joint, and the 'body' of the inverted pendulum with its mass inertia (the foot support surface is level and fixed; no gravity, no contact force). The muscle torque is applied to the joint and tries to move the body with respect to the foot. The movement is measured by the leg proprioceptive sensor, PROP, which yields an internal estimate of the body-to-foot angle BF. The internal estimate of BF, the signal bf, is implemented in a negative feedback control via the neural controller and the delay time. Into this loop we feed, as a set point signal, a voluntary command signal for the body lean (the latter is given a negative sign in order to account for the negative sign of the
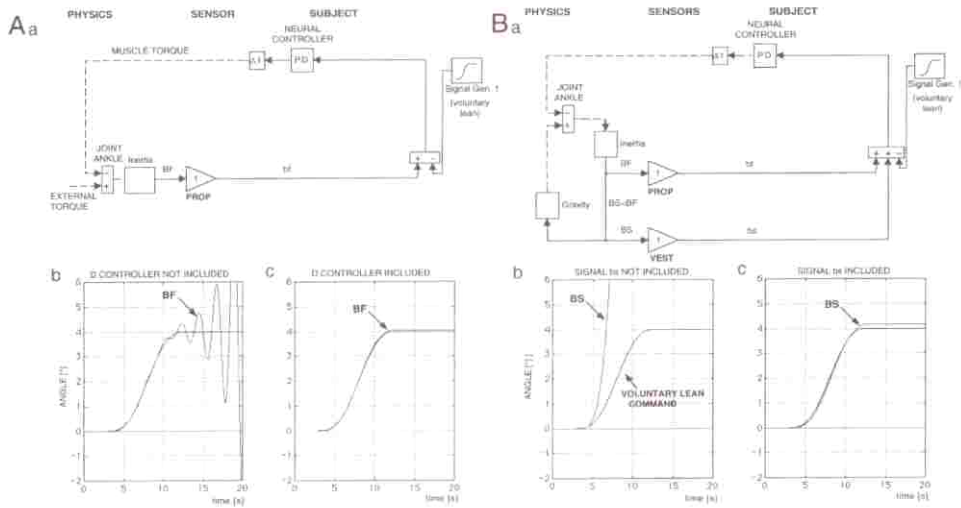
Fig. 3A,B. - *The first two steps in the design of the stimulus reconstruction model.*

A: Implementing a sensorimotor control of a voluntary body lean movement (gravity omitted, body support surface stationary; panel a). The control is based on a proprioceptive (sensor PROP) negative feedback loop by which the ankle joint is stabilised. Upon an EXTERNAL TORQUE, the loop produces a compensatory muscle torque at the ankle joint (note negative sign), in order to restore and maintain the body-to-foot angle (BF). The command signal for the lean (smoothed ramp from Signal Generator 1 on the 'SUBJECT' side of the model, to the right) is fed into the loop as a set point signal (servo control principle). The muscle torque is produced by means of the neural controller. If the 'damping' (or D, for derivative) part of the controller is missing, the control tends to be unstable (simulation curve in panel b). With both, the P (proportional) and D parts of the controller, in contrast, a stable and adequate movement control is obtained (panel c).
B: Addition of gravity to the control system (panel a). When gravity is added and no adjustment of the control loop is made, the 'inverted pendulum falls over' (panel b). A successful control is achieved (panel c) when an estimate of body-in-space excursion (BS), derived from a vestibular sensor (VEST), is added to the internal summing junction. bs and bf, internal estimates of BS and BF, respectively.

feedback loop at the joint). The waveform of the command signal consists here of the smoothed position ramp. With the appropriate K_P and K_D values in the controller (12 Nm/° and 4.4 Nm•s/°, respectively), BF is obeying closely the lean command (Fig. 3Ac). Noticeably, without the "damping" factor K_D the control of the lean would not be stable, but start to oscillate (Fig. 3Ab). The frequency characteristics of the lean, tested with sinusoidal stimulation and plotted in Bode diagrams, showed a gain of ≈ 1 and a phase of $\approx 0°$ at frequencies < 0.2 Hz, a resonance peak at about 0.4 Hz, and a drop in gain and lag in phase at higher frequencies.

We like to add here a few points. Note that, without the bf feedback, the command signal, transformed into a torque, continuously accelerates the body, so that BF does not follow the command (not shown). Furthermore, in the here presented form with the bf feedback, the system represents a local stabilisation of the ankle joint, in the sense of a proprioceptive stretch reflex, to which the lean command signal is added. The command serves as a set point signal for this loop and makes the system a simple servo control mechanism. If we add to the loop an external perturbation in the

form of a torque (as indicated), the stimulus is largely, although not completely compensated for (> 90%; see below, contact force). Finally, a hindrance of the voluntary lean by the local joint stabilisation does not occur, as is clear from Figure 3Ac.

2. *Adding gravity as an external stimulus.* We add gravity to the physics part of the model (Fig. 3Ba) and then perform a first simulation of the model without an internal estimate of this stimulus. The results is that gravity accelerates the body during the lean, bringing it far off the intended position (Fig. 3Bb). In contrast, when using an internal estimate of BS (the signal bs derived from the vestibular sensor, VEST), as a feedback signal in addition to the proprioceptive bf feedback, the effect of gravity is compensated for and the lean now follows closely the command signal (Fig. 3Bc; *vestibular gravity compensation*). The frequency characteristics of the lean responses in the Bode diagrams (not shown) displayed a gain and phase behaviour similar as before, but noticeably without the resonance peak at 0.4 Hz.

Note that the bs signal in the model is simply added to the summing junction of bf and the lean command signal. It can be viewed as a further set point signal of the local proprioceptive loop. Or, expressed in other words: bs represents a signal that is enhancing the gain of the local loop during the lean such that the effect of gravity is always neutralised (with the small-angle approximation bs ≈ sin (bs)). Therefore, the lean exactly follows the command signal. The bs signal is used directly as a feedback signal without intersensory interaction. However, as will be discussed later, bs is actually derived from canal-otolith and vestibular-neck interactions.

3. *Adding support surface tilt.* Support surface tilt is represented in the model, as mentioned before, by a change in the angle FS (Fig. 4Aa). FS changes the foot-to-body angle FB depending on BS (FB = FS - BS). The change of FB is registered by PROP (the negative sign in the PROP box indicates a sign reversal, so that PROP yields an estimate of BF, as before). In addition, the change of FB creates a torque in the ankle joint where it adds to the actively produced torque and the torque resulting from gravity. In the model simulations, we used for the tilt a sinusoidal waveform with a frequency of 0.6 Hz and an amplitude of ± 1°. In a first simulation without internal tilt compensation, the sinusoidal modulation of FS is superimposed on BS almost 1:1 (although with a slight phase lag), which brings the voluntary lean off the intended trajectory (Fig. 4Ab). In contrast, in a second simulation, in which an internal estimate of the FS stimulus was created (fs) and used as additional feedback signal, the lean trajectory is almost ideally following the command (Fig. 4Ac; *support tilt compensation*). The estimate fs is created by internally summing versions of the bs and bf signals (fs = bs - bf).

The frequency characteristics of the voluntary body lean response were essentially unchanged by concurrent support tilt. The frequency characteristics of the support tilt responses in the absence of voluntary lean were essentially ideal (gain of BS approximately zero over the frequency range of 0.01-1.6 Hz).

The signal fs can be viewed as another set point signal for the local (proprioceptive) ankle joint stabilisation, which is simply added to the two other set point signals. Still another aspect is that the summation of bf with fs at the following sum-
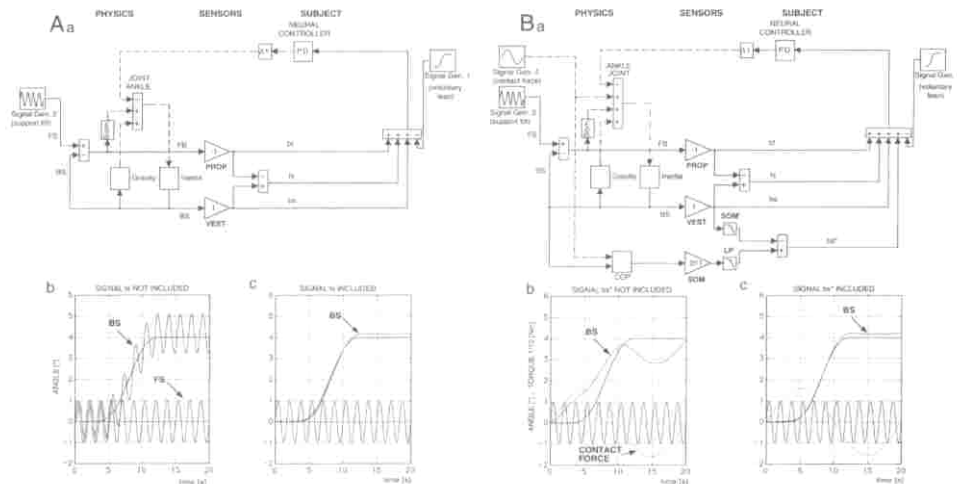
Fig. 4A,B. - *The last two steps in the model design (stimulus reconstruction model).*

A: Addition of the support tilt stimulus (sinusoid, 0.6 Hz, ± 1°). The stimulus, a foot-in-space excursion (FS), changes the foot-to-body angle (FB; BF after sign reversal in PROP, -1), depending on concurrent body-in-space motion (BS). Without an internal estimate of the FS stimulus, the lean movement becomes distorted by FS (panel b), while it is essentially unperturbed (panel c) when this estimate (fs) is added to the internal summing junction. The fs estimate is obtained by combining the estimates bf and bs (fs = bs - bf).
B: Addition of the contact force stimulus (sinusoid, 0.05 Hz, ± 16 Nm). The stimulus generates torque in the ankle joint, but in addition has impact on the centre of pressure (COP, which also receives input from BS). Without internal estimate of this stimulus, it distorts the lean movement, although considerably diminished by the bf and the bs feedback control (panel b). In contrast, with such an internal estimate in the feedback loop, derived mainly from a somatosensory measurement of the COP by means of plantar pressure receptors (SOM), the voluntary lean becomes essentially unperturbed (panel c). The estimate requires an interaction with vestibular signals (via the box SOM', see text).

ming junction can be viewed as an upgrading of the body-to-foot stabilisation (local loop) to a body-in-space stabilisation (fs + bf = bs'). Finally, one could object that the transformation of FB into torque is unrealistically small (1 in box Biom. for both the viscous and the elastic elements). However, when we increased these values to 10% of the K_D and K_P values in the controller, respectively, as suggested in the study of Peterka (33), and accounted for this change in the feedback by decreasing the gain of the bf signal by 10%, essentially the same simulation curves as the one in Figure 4Ac were obtained.

4. *Adding a contact force.* As described before, the contact force is taken to result from a pull on the COM. It yields an external torque input to the ankle joint as well as a torque that is transmitted to the plantar soles and there represents a component of the COP (Fig. 4Ba). Here we give the stimulus a sinusoidal waveform with a frequency of 0.05 Hz and an amplitude of ± 16 Nm. The stimulus is superimposed on the ramp-shaped voluntary lean and the sinusoidal support tilt stimulus. In a first simulation, without internal representation in the feedback, the stimulus distorts the

lean movement (Fig. 4Bb). However, the distortion is relatively small, because it is reduced to a large degree by the local proprioceptive joint stabilisation and the vestibular gravity compensation. When we included in the following simulation an internal estimate of the contact force into the feedback, the lean became essentially free of the perturbation (Fig. 4Bc). In the model, this stimulus estimate is obtained by subtracting from the plantar somatosensory signal a version of the bs signal, which is fed through an internal model of the SOM sensor (SOM') to mimic the low pass filter characteristics of this sensor. Thus, we subtract from the SOM signal an internal 'prediction' of how much of it is caused by a COM shift. Furthermore, we added via the box SOM' a signal that neutralises the high-frequency components of the SOM signal which stem from the active torque (a second derivative of bs with a factor of 0.11)[1].

The frequency characteristics of the body lean response were again essentially unchanged by the pull stimulus. The frequency characteristics of the pull responses in the absence of voluntary lean were essentially ideal in that the gain of BS excursion was < 0.02. Further simulations confirmed that the body lean is essentially unperturbed in a situation where the contact force stimulus is applied in the absence of the support tilt, as well as in all other stimulus combinations we tested.

Direct coupling model.

The model in Figure 3Ba (voluntary lean in the presence of gravity) can be viewed as a direct coupling model (compare Discussion). We therefore start our considerations with this model, extend it in the following by adding first the support tilt and then the contact force, and modify it, if necessary.

We take up our considerations with the simulation results in Figure 4Ab, i.e. with the simulation of the model in which the support tilt was applied, but the internal estimate of the tilt was not yet added to the proprioceptive and vestibular feedback signals. As described before, the lean movement was clearly distorted by the tilt stimulus. This can be explained by the fact that the bf signal tends to stabilise the body with respect to the tilting support, while the bs signal is neutralising the effect of gravity. Thus, the control with the proprioceptive and vestibular feedback, which

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1 The active torque component in the COP represents a major problem for the stability of the sensory feedback control loop, as we explain with the help of the folliwing example. The component can be identified in the COP trace during a voluntary lean. Let the lean be forward from an upright position, for instance. The main response of the COP is then a forward shift, stemming from the forward excursion of the COM. This response is preceded by a small backward shift of the COP. It stems from a backward thrust against the ground, which is actively produced to set the COM into forward motion. This active component is derived in the box COP of the model from the COM input (BS signal) to this box by branching off a version of it, taking the second derivative of this signal and giving it a negative sign ((before summing it with the COM's gravitational effect on the COP). Noticeably, if the active component in the COP would be allowed to contribute via the SOM sensor to the control loop, it would be sign reversed once more by the negative feedback (see negative sign of muscle torque at the ankle joint) and thus, overall, yield a positive feedback. This would make the control unstable. Therefore, the active component is to be removed from the feedback if the plantar pressure cues are used for sensory feedback of posture control. It is neutralised in the model centrally with the help of the vestibular bs signal, but other solutions may be possible, as well. Here, the removal mechanism represents another "vestibular function" in postural control ("active torque compensation", in addition to the vestibular gravity compensation and support tilt compensation).

is adequate for a level and stationary support (since the effect of two feedback sig-
nals combine synergistically in this situation), fails when the support moves. A
straight forward solution of this problem would be to decrease the gain of the bf sig-
nal (making it 0) and increase the gain of the bs signal (2). This modified model with
a G = 2 vestibular feedback (not shown) functions equally well in the two support
surface conditions. The simulation results for the tilting support condition were iden-
tical to those obtained with the stimulus reconstruction model shown in Figure 4Ac.
This is not surprising, because the two models are equivalent during tilt; the fs sig-
nal in the reconstruction model (Fig. 4Aa) has the effect that, at the common sum-
ming junction of bf and bs, bf becomes zero and the bs signal doubled, since fs = bs
- bf. Thus, the effect we just have achieved explicitly by interfering with the model
(in terms of a sensory re-weighting) occurs in the reconstruction model implicitly by
the fs signal.

The next step is to apply to the direct coupling model with the G = 2 vestibular
feedback, in addition to the tilt stimulus, also the pull (contact force) stimulus. The
simulation results obtained without further changes of the model are identical to
those in Figure 4Bb; although there is compensation of this stimulus by the feed-
back, the lean movement is considerably distorted. Noticeably, the compensation
cannot be improved by adjusting bs gain (nor by implementing anew the bf signal,
since this would degrade the tilt compensation). However, implementation of a con-
tact force compensation by means of the afore described SOM sensor yields a model
that is able to cope with the superposition of all three physical stimuli and the vol-
untary lean.

The final version of the direct coupling model is shown in Figure 5. Note that, in
comparison to the model in Figure 4Ba, the proprioceptive bf signal is omitted, fur-
thermore the interaction between the bs signal and the SOM signal. The latter was
achieved by removing the SOM' box (which contains a vestibular prediction of how
the COM affects the COP, i.e. a -bs signal; see above) in exchange to a reduction of
the VEST (bs) gain to 1. (A suppression of the high-frequency components of the
SOM signal was obtained here by means of a low pass filtering of the acceleration
signal in the box COP, taken to represent a mechanical filtering in the foot soles).
Thus, we arrive at a direct coupling model with the two sensors VEST and SOM.
The simulation results for the situation with a superposition of all three stimuli and
the lean, shown as inset in Figure 5, are essentially identical to those in Figure 4Bc.
When determining the frequency response characteristics, also these results were
similar to those described before for the reconstruction model, apart from a small
overshoot of the lean response at high frequencies (which is due to the fact that the
-bs signal in the SOM' box, which is now missing, was low-pass filtered).

DISCUSSION

The results show that it is possible to implement our stimulus reconstruction con-
cept into a simple postural control model which allows to apply the three physical
stimuli (external perturbations) at the same time and, in addition, a voluntary lean

movement. The lean movement is not hampered by the perturbations. Just the oppo-
site: It is the postural stimulus compensation which makes that the lean movement
is not perturbed. Noticeably, this concept is different from most of the previous con-
cepts of postural control in so far that these assumed a vestibular mechanism which
tries to maintain a given body position, or to restore this position upon excursion,
independent of the underlying physical stimulus. In our reconstruction model, in
contrast, the feedback is thought to be detached from the direct sensor signals and
determined by the estimates of the underlying physical stimuli.

Our results show furthermore that the stimulus reconstruction model can be trans-
formed into a more simple, direct coupling model with two sensors only (VEST and
SOM), which functionally is equivalent to a large degree. Also this extremely sim-
ple model is able to cope with superposition of the three stimuli and the lean in all
possible combinations without requiring a sensory re-weighting. Interestingly, in a
global sense, there is a parallel between this direct coupling model with VEST and
SOM and the classic reflex concept, in so far that Roberts (38), for instance,
assumed that the vestibular mechanism (vestibular-neck interaction for trunk stabil-
isation) is complemented by a "somatosensory buttressing".

However, the equivalence between the reconstruction model and the direct cou-
pling model does not hold if we go beyond the simplifications we made in the mod-
elling and, in addition, take into account previous experimental findings. There are
several points to be considered. One point concerns the vestibular-neck interaction
which is required for trunk stabilisation. Experimental evidence indicates that this
interaction occurs at sensory processing levels, starting already in the vestibular
nuclei, rather than at the motor output (decerebrate cat, 2,46; see also Manzoni this
issue; intact cat, 1). Thus, the bs signal in our models must be considered the result
of an intersensory interaction. Actually, the vestibular signal itself, i.e. the signal that
codes orientation of the head with respect to the gravitational vertical, appears to
results from a sensory interaction. The reason for this assumption is that the brain
cannot decide from an otolith signal alone whether this stems from a change in angu-
lar head position or from a linear head acceleration. Therefore, it is generally
assumed that the brain resorts to additional sensory signals, such as canal signals
(see canal-otolith interaction) (21, 48).

Interestingly, we have reasons to assume that the two bs signals in the recon-
struction model differ in their origins (i.e. the bs signal used for gravity compensa-
tion and the bs signal used for the fs signal and the support tilt compensation in the
model of Figure 4Ba). The evidence for this assumption comes from postural
responses of human subjects obtained in a recent study from this laboratory (25). It
showed that the responses are non-linear in the sense that gain decreased with
increasing amplitude of pull and support tilt stimuli (see also 33). Using a version of
our reconstruction model, we were able to simulate these effects by introducing
detection thresholds for the internal stimulus estimates. For the fs signal, we
required a velocity threshold, while it was a position threshold for the bs signal of
the gravity compensation. We take this as evidence that the vestibular source of fs is
an angular velocity signal (primarily derived from the canals which represent angu-
lar speedometers), while that of the bs signal for gravity compensation is an angular
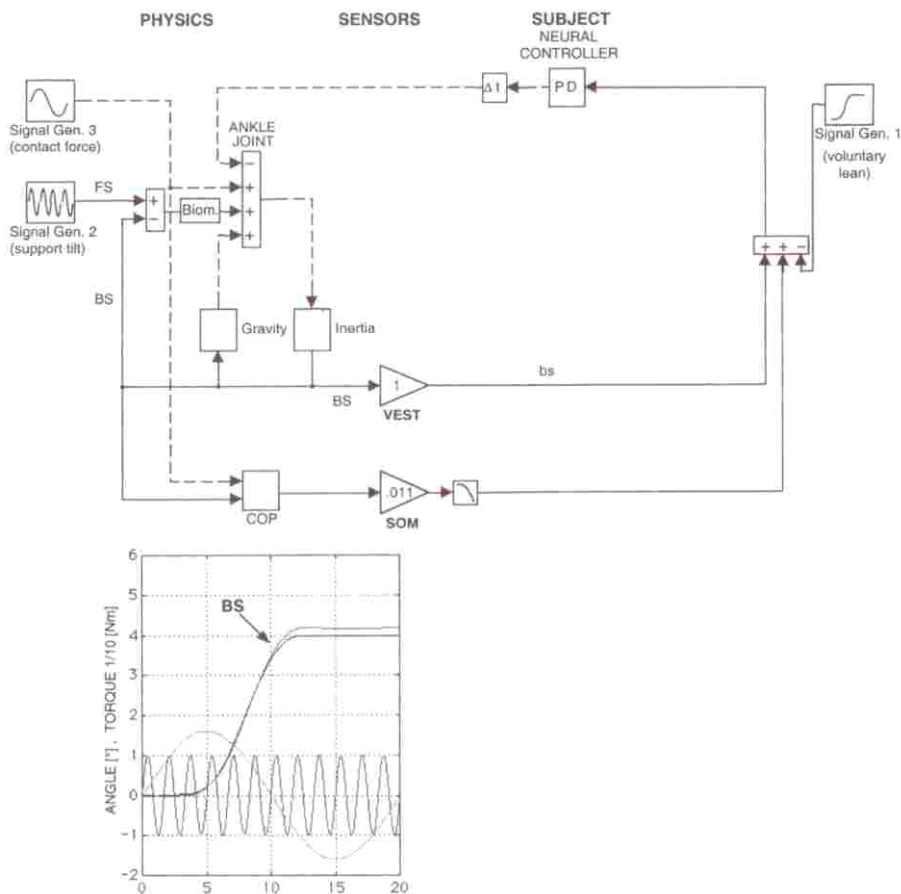
Fig. 5. - *The direct coupling model.*

It was obtained by simplifying and modifying the stimulus reconstruction model in Figure 4Ba (details in text). The simulation below the wiring diagram shows the result of a superposition of all three external stimuli and the lean (compare Fig. 4Bc).

position signal (primarily derived from the otoliths; but both signals are taken to involve the canal-otolith interaction). The presumed threshold-like mechanisms appear to be related to a suppression of noise. The noise appears to be high in the vestibular signals and considerably lower in the proprioceptive signals (24, 35, 43). These and other differences between the vestibular and the proprioceptive signals, neglected here, may turn out to be instrumental in future comparisons between experimental results and model simulations, when it comes to distinguish between different model topologies.

A severe problem with the direct coupling model is that it does not integrate the local proprioceptive stabilisation of the ankle joint into the postural mechanism. This is in conflict with experimental evidence which indicates that ankle proprioceptive

input is involved in postural control. For instance, it is known that leg propriocep-tive stimulation by vibration of the joint's muscles leads to a postural response (6) and that this response combines linearly with vestibular responses (10). As men-tioned before, the problem cannot be solved simply by adding a proprioceptive feed-back to the direct coupling model. Rather, the use of a proprioceptive feedback in this model would require a mechanism that re-weights the sensory signals depend-ing on the behavioural situation.

In recent papers, Peterka (33, 34) succeeded to describe postural responses of human subjects to a variety of different external perturbations using simulations of a direct coupling model. He did so by adjusting the gain of the sensory signals for each behavioural situation and stimulus amplitude, assuming that subjects are nor-mally performing such sensory re-weightings. In a subsequent paper (36), he pro-vided experimental evidence for such a re-weighting, but the experiment involved a special support surface condition (a position coupling of the support to the body). We hold that our internal stimulus reconstruction represents or yields such a senso-ry re-weighting. We conceive that it represents an integral part of the posture con-trol mechanism of the adult individual, while very special circumstances such as the just mentioned support surface condition require additional adjustments of the pos-tural mechanism (compare 25).

Basically, we proceeded here from the assumption that sensory feedback repre-sents an essential part of the human postural control mechanism, in line with Johannsson and Magnusson (12) and Peterka (33, 34, 36). But we cannot exclude that feed forward (open loop) mechanisms are involved as well, as suggested before by other authors (e.g. 7, 14, 29, 42). We like to point out, however, that previous evi-dence for open-loop control in the system (4) have later been explained by a closed loop feedback system containing noise and delay time (32). The situation becomes even more complicated if we include non-linear elements into the models such as the afore mentioned threshold-like mechanisms (25).

Finally, we like to come back to the classic reflex concept and to the anatomical and electrophysiological studies which demonstrated rather direct connections between sensory and motor centres, such as the vestibulo-spinal pathways, for instance. These pathways outlast the modification of the postural mechanisms from reflexes to reactions, which occurs with maturation of the brain after birth. This rais-es the question which function they serve after the modification. Our speculation would be that they represent in certain situations short latency starter mechanisms for the postural reactions, or yield early components of rescue reactions, before the meta level with the sensory reconstruction of the physical stimuli takes over. Given such a co-existence of the classical direct with the here postulated more complex postural mechanisms, one would expect a certain degree of functional equivalence between them. A high degree of functional equivalence was noted, in fact, in the Results section between the stimulus reconstruction model and the direct coupling model. An alternative explanation would be that the direct connections, originally representing a simple neural network of their own, later become some part in a more complex network of distributed processing, in which they no longer serve a defined function.

SUMMARY

Postural reflexes are replaced soon after birth by automatic reactions that allow for volition and cognition. It is still an enigma how this change in postural control is achieved. We suggest that the change involves the formation of a sensory processing level (meta level) that becomes interleaved in between the tight sensor-actuator coupling of the classic reflexes. We assume that the brain applies at this level intersensory interactions to reconstruct the physical stimuli which are causing the physiological stimuli and sensory signals. The thus derived estimates of the physical stimuli are then used as feedback signals in the posture control system. We present this concept on the background of the classic reflex concept and earlier attempts in the literature to overcome it. The earlier attempts were often motivated by the question how the brain prevents voluntary movements from being hampered by reflexive stabilisation of posture (so-called posture-movement problem). We compare our new concept with the classic reflex concept in a theoretical approach, by implementing both concepts into simple postural control models. In simulations of the two models we superimpose external perturbations (the physical stimuli) and a voluntary body lean movement. We show that it is possible to achieve successful stimulus compensation and unperturbed lean movement with both, the model derived from the new concept and the one of the classic reflex concept. With both approaches, the posture-movement problem does not arise. Based on preliminary considerations that include experimental findings from the literature, however, we conclude that the new concept provides more explanatory power than the classic reflex concept.

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