Biol. Cybern. 80, 299–308 (1999)

Biological Cybernetics

A multisensory integration model of human stance control

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Received: 25 August 1997 / Accepted in revised form: 8 December 1998

Abstract. A model is presented to study and quantify the contribution of all available sensory information to human standing based on optimal estimation theory. In the model, delayed sensory information is integrated in such a way that a best estimate of body orientation is obtained. The model approach agrees with the present theory of the goal of human balance control. The model is not based on purely inverted pendulum body dynamics, but rather on a three-link segment model of a standing human on a movable support base. In addition, the model is non-linear and explicitly addresses the problem of multisensory integration and neural time delays. A predictive element is included in the controller to compensate for time delays, necessary to maintain erect body orientation. Model results of sensory perturbations on total body sway closely resemble experimental results. Despite internal and external perturbations, the controller is able to stabilise the model of an inherently unstable standing human with neural time delays of 100 ms. It is concluded, that the model is capable of studying and quantifying multisensory integration in human stance control. We aim to apply the model in (1) the design and development of prostheses and orthoses and (2) the diagnosis of neurological balance disorders.

1 Introduction

Humans perform a seemingly simple task, such as standing, more or less automatically. Sometimes we forget how hard we have worked to establish stable standing. Only after a disabling event (e.g. stroke or amputation) or during ageing are we reminded about the complexity of this seemingly simple motor task. Studying human stance control is not only important from a scientific point of view to unfold the mysteries of motor control but ultimately leads to new designs of prostheses and orthoses and rehabilitation approaches. In human stance control, the nervous system receives delayed information from a multisensory system. Using this delayed information, the nervous system estimates body orientation relative to an a priori unknown environment. With this estimate, the nervous system then controls a skeletal structure powered by muscles to maintain or achieve a desired orientation in this unknown environment. Standing is not an easy and straightforward task for the nervous system since:

1. In an a priori unknown environment, exact estimation of body orientation is not possible because the nervous system receives all sensory information with a certain time delay (Kleinman 1969). Thus, the nervous system can only provide a best possible estimate.
2. The estimation of body orientation involves an integration of different sensory systems each with its own coordinate frame (Mergner et al. 1997).
3. The sensory signals may not always be reliable as, for instance, in patients with sensory deficits (Horak et al. 1990) or in sensory illusion situations (Bles and Dewitt 1976).

In an experimental setting, multisensory integration is studied by using patients with sensory deficits (Horak and Macpherson 1996) or by manipulating sensory systems (Black et al. 1988). Unfortunately, manipulation of sensory system(s) and quantifying of sensory deficits are difficult to accomplish and cannot always be well-defined. An additional problem is that experimental results can be confounded by the subject's intent and experience (Jacobs and Burleigh-Jacobs 1998). Arguments for using mathematical modelling are that models (1) provide a systematic framework, (2) allow systematic manipulation of parameters and (3) assist the experimenter to define experimental conditions and explain experimental results. In this paper, we present a model to study and quantify the contribution of the available sensory information to human standing based on

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optimal estimation theory (Gelb 1974). Optimal estimation theory has proven its power in modelling man-machine systems (Kleinman et al. 1970), the optokinetic system and vestibulo-ocular reflex (Robinson 1977) and human spatial orientation (Borah et al. 1988).

2 Model

The model consists of a person standing on a movable support base (Fig. 1). The support base can rotate and/or translate. Two types of perturbations can be simulated and applied to the model: internal and external. Examples of the former are breathing, heart rate or muscle tremor. Examples of the latter are sudden bus stops, platform perturbation experiments or simply a push applied to the body. Given these perturbations, it is the controller's goal to maintain erect standing.

The structure of the model is subdivided into four parts (Fig. 2; details in the following sections):

1. Body dynamics – a three-link segment model representing a standing person on a movable support base;
2. Sensor dynamics – transfer functions representing input-output relations of five different sensory systems;
3. Sensory integration centre – optimal estimation model representing the integration of all available multisensory information providing a best estimate of body orientation;
4. Action control centre – controller representing the selection of muscle actions based on the best estimate of body orientation as provided by the sensory integration center.

2.1 Body dynamics

A standing person on a movable support base is modelled by a three-link segment model in the sagittal plane. The three segments represent the shank, thigh and trunk. The segments are connected by friction-free hinge joints. The muscle actions are modelled as a torque actuator at each individual joint. The inputs to the segment model are muscle actions (u_{st}) and optional internal and external perturbations (w_{st}). The outputs of the segment model (y_{st}) are the kinematics and dynamics of the three linked segments. The equations of motion are derived following Euler-Lagrange formalism and written as a set of coupled first-order differential equations (Appendix A):

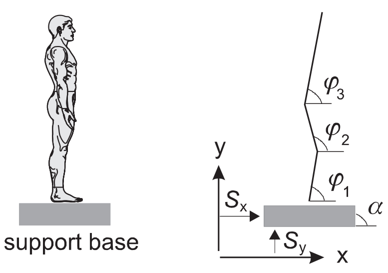

Fig. 1. A three-link segment model attached to a movable support base. The model consists of shank, thigh and trunk $\varphi_i (i = 1..3)$ is the segment angle, $[s_x\, s_y]$ is the position of the support base, and α is the support base angle

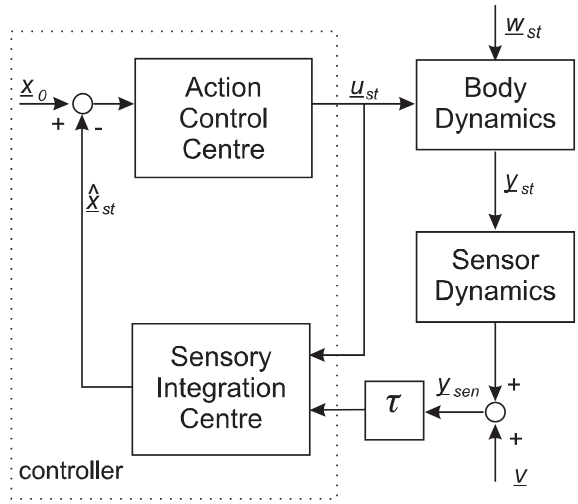

Fig. 2. Flow diagram of the human stance control model. Body dynamics describes a standing person controlled by muscle actions (u_{st}) and exposed to unknown perturbations (w_{st}). Sensor dynamics relates the sensory input (y_{st}) to the sensory output (y_{sen}). The delayed sensory output distorted by noise (v) and the muscle actions are input to the sensory integration centre which makes a best estimate of body orientation ($\hat{x}_{st}$). Based on this estimate the action control centre selects muscle actions in order to maintain standing and to achieve a desired orientation of the body (x_0)

$$\dot{x}_{st}(t) = f_{st}(x_{st}(t), u_{st}(t), w_{st}(t), t) \tag{1}$$

where f_s is a non-linear function of the system states (x_{st}, i.e. segment angles and angular velocities), the muscle actions (u_{st}), unknown disturbances (w_{st}) and time (t). The output of the segment model contains the physical quantities which are used as input to the model of sensor dynamics (Appendix B):

$$y_{st}(t) = g_{st}(x_{st}(t), u_{st}(t), a(t), t) \tag{2}$$

where g_{st} is a non-linear function of the system states (x_{st}), the muscle actions (u_{st}), time (t) and a vector a representing the platform kinematics and disturbances other than support base accelerations (w^*_{st}):

$$a(t) = \left[s_x(t); \dot{s}_x(t); \ddot{s}_x(t); s_y(t); \dot{s}_y(t); \ddot{s}_y(t); \alpha; \dot{\alpha}; w^*_{st}(t)\right] \tag{3}$$

2.2 Sensor dynamics

Five different sensory systems are modelled:

1. Muscle spindles are assumed to sense the joint angles and joint angular velocities.
2. Otolith organs are assumed to sense translational accelerations of the head.

3. Semicircular canals are assumed to sense rotational accelerations of the head.
4. Skin afferents are assumed to sense the shear and pressure forces in the sole of the foot.
5. The visual system is assumed to sense the position and the velocity of the head.

Each sensory system is characterised by its own specific dynamics (Borah et al. 1988) and is expressed by:

$$\dot{x}_{\mathrm{sen}} = f_{\mathrm{sen}}(x_{\mathrm{sen}}(t), y_{\mathrm{st}}(t), t) \tag{4}$$

and

$$y_{\mathrm{sen}} = g_{\mathrm{sen}}(x_{\mathrm{sen}}(t), y_{\mathrm{st}}(t), t) + v(t) \tag{5}$$

where f_{sen} and g_{sen} are functions of the sensor states (x_{sen}) and the sensory input (y_{st}), y_{sen} is the sensory output, and $v(t)$ is the sensory signal noise. The sensory signal noise ($v(t)$) is modelled as zero mean Gaussian noise with spectral density matrix $V(t)$ [denoted by $v(t) \approx N(0, V(t))$].

2.3 Sensory integration centre

Kleinman (1969) proved that the best estimate of the system states for a linear system, with time delay and signal noise, is obtained by the cascade combination of a Kalman filter and a linear predictor. The Kalman filter produces a best estimate of the system states of a linear model by using both the motor outflow ('efference copy') and the sensory output ('afference copy') with a model of the motor system ('internal representation'). These sensory and motor signals are integrated in such a way that the overall uncertainty in the state estimates is minimised. The working of the Kalman filter is a combination of two processes, which together contribute to the state estimate (Wolpert et al. 1995). The first process uses the current state estimate and motor commands (muscle actions) to predict the next state by simulating the movement dynamics with a forward internal model. The second process uses a model of the sensory dynamics to predict the sensory output corresponding to this predicted next state estimate. The sensory error, the difference between actual and predicted sensory output, is weighted by the Kalman gain to drive the state estimate resulting from the first process to its true value. Sensory errors arise when the internal representation is not an exact copy of the motor system, because of mechanical disturbances or when the efference/afference copies are distorted by noise. The relative contributions of both processes to the final estimate are modulated by the Kalman gain so as to provide optimal state estimates. The elements of the Kalman filter are the ratios between statistical measures of the uncertainty in the predicted next state (caused by an imperfect internal representation, an imperfect copy of motor commands or external mechanical disturbances) and the uncertainty in a sensory output signal. Thus, the Kalman gain is 'proportional' to the uncertainty in the estimate and 'inversely proportion' to the sensory signal noise reflecting the precision or reliability of a sensory signal. If the sensory signal noise is large and the uncertainty in the predicted state is small, then the sensory error is due chiefly to the sensory signal noise, and only small changes in the state estimate should be made. On the other hand, small sensory signal noise and large uncertainty in the state estimates suggest that the sensory errors contain considerable information about errors in the estimate. Therefore, the difference between the actual and the predicted measurement will be used as a basis for strong correction of the state estimates. Hence, the Kalman gain is specified in a way which agrees with an intuitive approach to improving the estimate.

In the absence of sensory output, in our case due to time delays, the predicted next state estimate (made by the first process) cannot be corrected by sensory feedback, and the Kalman filter reduces to an optimal predictor. A best state estimate of a system with sensory delays is to first make a best estimate of the states for which sensory information is available (Kalman filter) and then use this estimate of a delayed state as a basis to make a prediction (predictor) of the current state to compensate for the time delays.

In our model, the linear case is extended to the non-linear case by the cascade combination of an extended Kalman filter and a non-linear predictor (Fig. 3). The difference from the linear case is that the internal representation is no longer linear, and although the mathematics becomes more complex, the principle remains the same. In order to use the extended Kalman filter equations, (1–4) need to be rewritten to obtain the correct form of the system states equation:

$$\dot{\mathrm{x}}(t) = \begin{bmatrix} \dot{x}_{\mathrm{st}}(t) \\ \dot{x}_{\mathrm{sen}}(t) \\ \dot{a}(t) \end{bmatrix} = \begin{bmatrix} f_{\mathrm{st}}(x_{\mathrm{st}}(t), u_{\mathrm{st}}(t), a(t), t) \\ f_{\mathrm{sen}}(x_{\mathrm{sen}}(t), g_{\mathrm{st}}(x_{\mathrm{st}}(t), u_{\mathrm{st}}(t), a(t), t), t) \\ A_a a(t) \end{bmatrix} + \begin{bmatrix} 0 \\ 0 \\ G_a w_a(t) \end{bmatrix} = f(x(t), u_{\mathrm{st}}(t), t) + Gw(t) \tag{6}$$

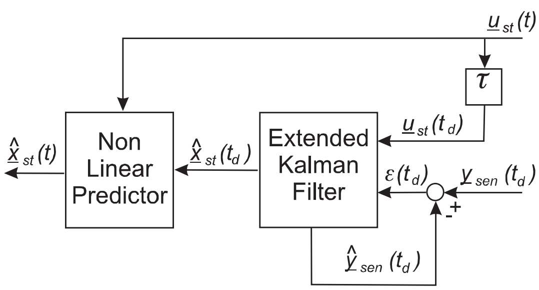

Fig. 3. Flow diagram of the sensory integration centre. The extended Kalman filter generates a best estimate of the delayed system state ($\hat{x}_{\mathrm{st}}(t_{\mathrm{d}})$) based on the synchronised muscle actions ($u_{\mathrm{st}}(t_{\mathrm{d}})$) and the delayed sensory output ($y_{\mathrm{sen}}(t_{\mathrm{d}})$). The difference ($\varepsilon(t_{\mathrm{d}})$) between the real sensory output and the estimated sensory output is used to correct the estimate of the delayed state. The non-linear predictor generates the best estimate of the current state ($\hat{x}_{\mathrm{st}}(t)$) from the estimate of the delayed state based on known muscle actions ($u_{\mathrm{st}}(t)$)

where $x(t)$ is the extended state vector, and $a(t)$ is expressed as a stochastic differential equation (Appendix C), A_a and G_a are time-invariant matrices and $w_a \approx N(0, W_a)$. The strength of the noise, w_a, corresponds roughly to the possible range of variation in support base accelerations $(\ddot{s}_x, \ddot{s}_y)$, the support base angular velocity $(\dot{\alpha})$ and disturbances other than support base accelerations (w^*_{st}). In order to use the extended Kalman filter equations, (5) needs to be rewritten to obtain the correct form of the sensory output equation:

$$y_{sen} = g(x(t), u_{st}(t), t) + v(t) \tag{7}$$

Finally, given (6) and (7), the extended Kalman filter obtains a minimum variance estimate of the delayed state, $\hat{x}(t - \tau)$:

$$\dot{\hat{x}}(t_d) = f(\hat{x}(t_d), u_{st}(t_d), t_d) + K(t_d)\varepsilon(t_d) \tag{8}$$

where $t_d = t - \tau$, $K(t_d)$ is the Kalman gain (see Appendix D), and $\varepsilon(t_d)$ is the difference between the real sensory output and the estimated or predicted sensory output:

$$\varepsilon(t_d) = y_{sen}(t_d) - \hat{y}_{sen}(t_d) \tag{9}$$

where the estimated sensory output is a function of the estimated state and muscle actions:

$$\hat{y}_{sen}(t_d) = g(\hat{x}(t_d), u_{st}(t_d), t_d) \tag{10}$$

The non-linear predictor obtains the best estimate of the current system state $\hat{x}_{st}(t)$ from the summation of $\hat{x}_{st}(t_d)$ and the time integral of body dynamics according to:

$$\hat{x}_{st}(t) = \hat{x}_{st}(t_d) + \int_{t_d}^{t} f_{st}(\hat{x}_{st}(\xi), u_{st}(\xi), \xi)\, d\xi \tag{11}$$

2.4 Action control centre

The action control centre selects the muscle actions in order to maintain erect standing based on the best estimate of body orientation as provided by the sensory integration centre. The muscle actions are obtained by a regulator that minimises the objective function:

$$J = \int_0^\infty \left((\hat{x}_{st} - x_0)^T Q_r (\hat{x}_{st} - x_0) + u_{st}^T R_r u_{st} \right) \mathrm{d}t \tag{12}$$

where R_r and Q_r are weighting matrices, penalising muscle actions and deviations from the desired position, respectively. Segment angles and angular velocities, corresponding to erect body orientation, are grouped in a vector x_0. After linearizing the body dynamics (1) around the desired orientation (x_0), the linear quadratic regulator minimises this objective function (Kwakernaak and Sivan 1982) and is given in state feedback form by:

$$u_{st}(t) = -L(\hat{x}_{st}(t) - x_0) \tag{13}$$

where L is the feedback gain. This linearization is allowed since small deviations from the desired orientation occur (Khang and Zajac 1989).

3 Results

The influence of sensory manipulation on total body sway during quiet stance is studied by changing the reliability of individual sensory systems (Fig. 4). In the model, this is accomplished by calculating the centre of mass distribution for different spectral density matrices, $V(t)$ (Appendix E). A high value of $V(t)$ corresponds to an unreliable/perturbed sensory system. The model results show that perturbation of one sensory system results in an increase in total body sway. In addition, the increase in sway is different for each sensory system that is perturbed. Combined effects of perturbing two or more systems are more than the sum of the individual effects of sensory perturbations. For all simulations of sensory perturbations, the model remained standing.

It is important to note that the model results closely resemble the experimental results of sensory perturbations on total body sway (Fig. 4; Simoneau et al. 1995). These results lend confidence in the capability of the model to study and quantify multisensory integration in human stance control.

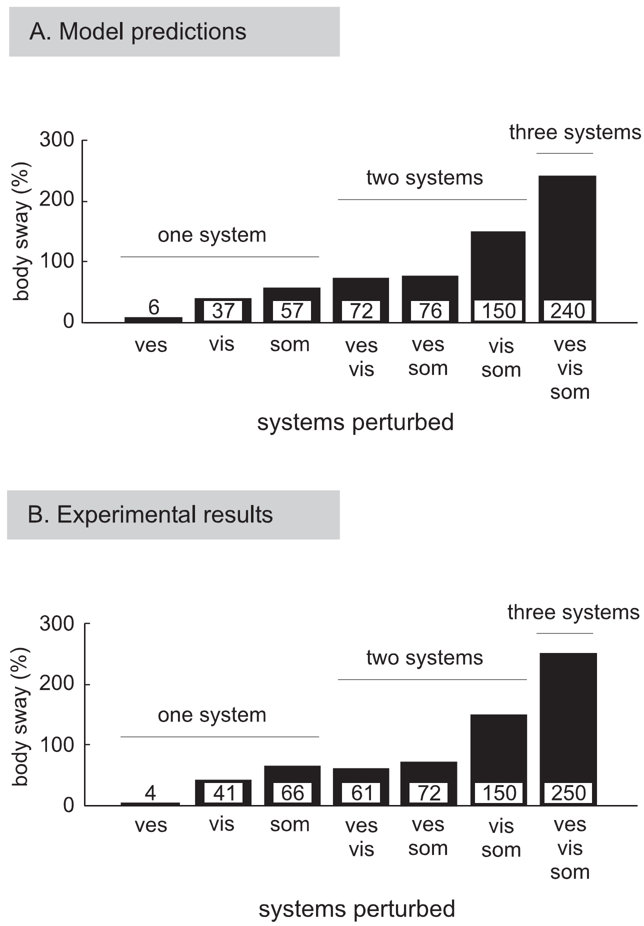

Fig. 4. The effect of sensory perturbations on total body sway (expressed as percentage increase of body sway compared with the body sway when no sensory system is perturbed): model predictions (**A**) and experimental results (**B**) (adopted from Simoneau et al. 1995) [*ves* vestibular system, *vis* visual system, *som* somatosensory system (skin afferents in soles of the feet)]

The stability of the controller is studied by applying quasi-random internal perturbations at each individual joint (Fig. 5). Despite these perturbations, the controller is able to stabilise the model of an inherently unstable standing human with a neural time delay of 100 ms. However, applying the same internal perturbations after removing the predictive element from the sensory integration centre results in unstable standing, i.e. the person falls down (not shown).

Applying external perturbations, here a horizontal support base acceleration, the controller stabilises the model of a standing human (Fig. 6). The model remains standing during the perturbation and returns back to the erect position when the perturbation stops. The corrective response is mainly accomplished by muscle actions around the ankle joint.

The sensory output (Fig. 7) that results from this horizontal perturbation is integrated in such a way that a best estimate of body orientation is obtained. When the model returned to the erect position, the sensory output returns to its stationary value. Only an offset in the horizontal position of the head corresponding to the support base displacement remains.

Again, removing the predictive element from the sensory integration centre causes the person to fall. Apparently, the predictive element plays a crucial role in the human stance control model. In general, time delays have a destabilising effect on model performance (Palmor 1996). The role of the predictive element is to

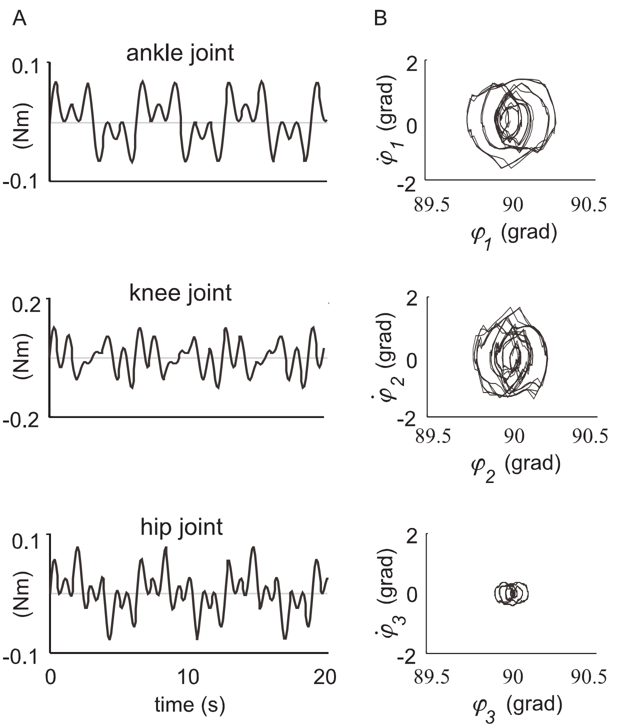

Fig. 5A,B. Results of a 20 s simulation during which the three-segment model was exposed to internal perturbations. The internal disturbances (**A**) were modelled as the sum of three sinuses with different frequencies and applied as additive joint torques. The model remains standing as is shown by the phase portraits (**B**)

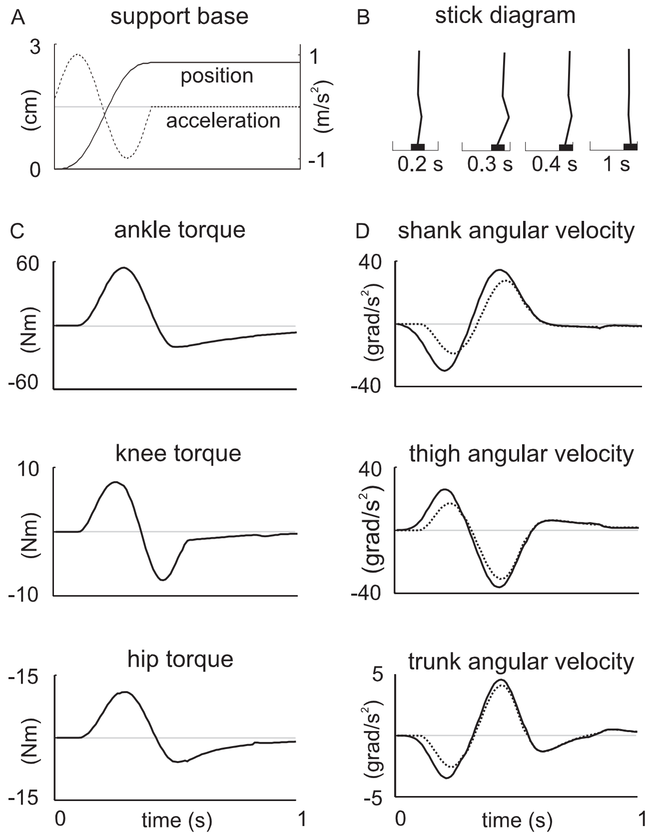

Fig. 6A–D. Results of a 1 s simulation during which a three-segment model was exposed to an external perturbation, namely a horizontal support base displacement (**A**). Despite the perturbation, the controller is able to stabilise the model of an inherently unstable standing human with a neural time delay of 100 ms. The model remains standing during the perturbation and returns back to the erect position when the perturbation stops (**B**). The predictive element compensates for neural time delays: actual (*solid*) and predicted (*dotted*) segment angular velocities are shown (**D**)

compensate for neural time delays. This compensation is perfect in the absence of perturbations; the actual and predicted segment angular velocities coincide (Fig. 6). However, this compensation is not perfect in the presence of unknown perturbations; the actual and predicted segment angles and angular velocities exhibit a significant phase lag (Fig. 6).

4 Discussion

An important aspect of the model is the use of optimal estimation theory, which enables us to model multisensory integration in human stance control. In the model, all delayed sensory information is integrated in such a way that a best estimate of body orientation is obtained. This model approach agrees with the present theory of the goal of human balance control, i.e. to achieve effective weighting of all sensory information to maintain a stable vertical and horizontal alignment of the body with respect to the individual's intent, experience, instruction and environment (Jacobs and

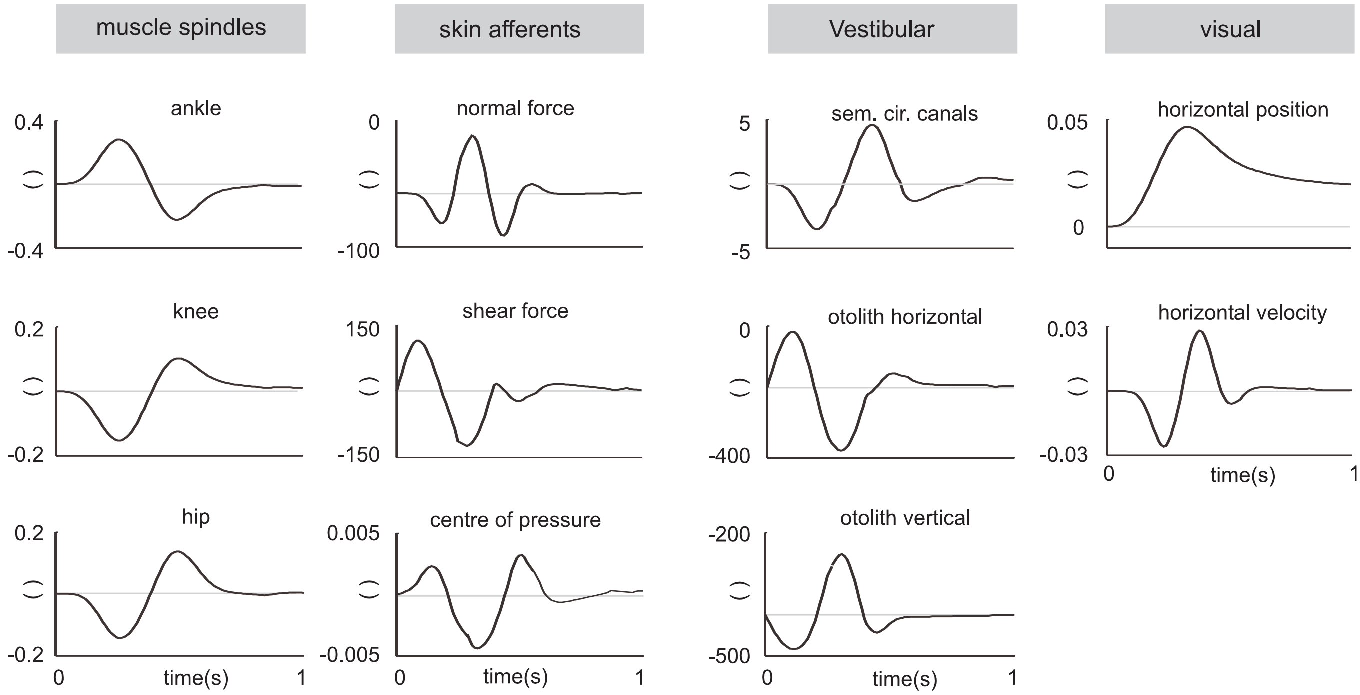

Fig. 7. Selection of the sensory output of a 1 s simulation during which the three-segment model was perturbed by a horizontal support base displacement (same as in Fig. 6). Shown are the sensory output signals of the different sensory systems used by the sensory integration centre to obtain a best estimate of body orientation

Burleigh-Jacobs 1998). In addition, the use of optimal estimation theory enables us to quantify the effects of sensory manipulations and/or deficits.

The presented multi-segment control model of human stance is non-linear and explicitly addresses the problem of multisensory integration. This is in contrast to other models which are linear and do not explicitly address the problem of multisensory integration (e.g., Barin 1989; Iqbal et al. 1993; Johanson and Magnusson 1991; Kuo 1995). These models have in common that they utilise a form of state feedback, assuming that the nervous system is able to derive the exact system states from sensory information. This is not a realistic assumption, since neural time delays and noisy sensory signals make an exact state reconstruction practically impossible (Kleinman 1969). In addition, sensory dynamics is not included in these models. However, the present model results show the importance of sensory dynamics as is nicely demonstrated by the influence of sensory manipulation on total body sway.

The use of the Kalman filtering theory assumes that the control model would have some knowledge of body and sensory dynamics, precision of the different sensory systems and a representation of the environment. Thus, the control model 'knows', for example, that activating the soleus will result in backward body movement and that the muscle spindles are sensitive to muscle stretching and shortening. Note that within the Kalman theory this knowledge does not have to be perfect since the Kalman filter also corrects for deviations of the internal representation from the true motor system. For an optimal estimate, the control model should also have knowledge about the environment. Interestingly, the control model has only 'knowledge' of the environment through its senses. To study this problem, one can make use of adaptive filtering theory (Myers and Taply 1976).

In the future, we intend to apply the model to the design and development of prostheses and orthoses. Here it is important to study the effect of sensory loss on the stability of a standing person with a prosthesis or orthosis. In addition, the contribution of added artificial sensory feedback from the prosthesis/orthosis on the stability of the patient will be investigated. Secondly, the model could be useful in the diagnosis of neurological balance disorders. Here experiments with different patient populations will provide important parameters that quantify their stability in standing. These parameters will be used by the model to quantify the contribution of different sensory systems in standing. The model will be extended with models of muscle dynamics and models of passive joint structures to create a more realistic musculo skeletal model. In this paper, the simulations performed did not produce hyperextension of the joints. Therefore, the results are not influenced by neglecting the passive joint structures. In the more general case, these structures can play an essential role, e.g. by backward translation of the support base. Inclusion of these passive structures will also have implications for the modelled action control centre, since the body dynamics are no longer linear around the erect posture. In this case the linear quadratic controller has to be replaced with a non-linear control scheme. However, in this paper, our focus has been on developing a model for multi-sensory integration and not on studying the role of non-linear effects and non-linear control schemes.

The model will also be extended to three dimensions and to more body segments, for instance, including head-neck mechanics and sensory interactions (Peng et al. 1996). Finally, the current model predicts the effects of sensory manipulations during quiet stance very nicely. However, to apply the model for diagnosis, new experiments have to be designed to validate it for a wide variety of different balance disorders and perturbations.

Acknowledgements. We would like to thank our colleagues of the Man-Machine-Systems Group, Delft University of Technology, Drs. Henk Stassen, Frans van der Helm, and Ton van Lunteren for stimulating discussions and suggestions; and Dr. Anne Burleigh-Jacobs for suggestions and review of the manuscript.

Appendix A. The equations of motion

The model of the human body consists of three linked segments (shank, thigh and trunk). The segments are connected by friction-free hinge joints. The model is planar and accounts only for anteroposterior motion of the body. It also assumes that the mass centre of each segment lies on the line connecting the two adjacent joints. The foot is assumed to be flat on the ground. The equations of motions are derived by means of the Euler-Lagrange method. The equation can be written in compact form as:

$$M(\mathbf{\Theta})\ddot{\Theta} = B(\mathbf{\Theta})\dot{\Theta}^2 + G(\mathbf{\Theta}) + R(u_{\mathrm{st}} + w^*_{\mathrm{st}}) + D(\mathbf{\Theta})S \quad (14)$$

where

$\Theta =$	$[\varphi_1, \varphi_2, \varphi_3]$ is a vector with segmental angles (3×1)
$M(\Theta)$:	is a symmetric inertia matrix (3×3)
$B(\Theta)$	is an anti-symmetric matrix (3×3)
$G(\Theta)$	is the gravitation vector (3×1)
R	is a transformation matrix relating joint torque to segmental torque (3×3)
u_{st}	vector with control joint torques (3×1)
w^*_{st}	vector with disturbance joint torques (3×1)
$D(\Theta)$	support base disturbance matrix
$S = [\ddot{s}_x, \ddot{s}_y]$	vector with platform accelerations

The elements of vectors and matrix in (14) are given below. $I_i(i = 1..3)$ is the moment of inertia of the ith segment relative to the centre of the corresponding segment, $m_i(i = 1..3)$ is its mass and $L_i(i = 1..3)$ is its length.

$$M(1,1) = (\tfrac{1}{4}m_1 + m_2 + m_3)L_1^2 + I_1$$
$$M(1,2) = M(2,1) = (\tfrac{1}{2}m_2 + 2m_3)L_1L_2\cos(\varphi_1 - \varphi_2)$$
$$M(1,3) = M(3,1) = \tfrac{1}{2}m_3L_1L_3\cos(\varphi_1 - \varphi_3)$$
$$M(2,2) = (\tfrac{1}{4}m_2 + m_3)L_2^2 + I_2$$
$$M(2,3) = M(3,2) = \tfrac{1}{2}m_3L_2L_3\cos(\varphi_2 - \varphi_3)$$
$$M(3,3) = \tfrac{1}{4}m_3L_3^2 + I_3$$
$$B(1,2) = -B(2,1) = \tfrac{1}{2}(m_2 + 2m_3)L_1L_2\sin(\varphi_1 - \varphi_2)$$
$$B(1,3) = -B(3,1) = \tfrac{1}{2}m_3L_1L_3\sin(\varphi_1 - \varphi_3)$$
$$B(2,3) = -B(3,2) = \tfrac{1}{2}m_3L_3L_2\sin(\varphi_2 - \varphi_3)$$
$$G(1,1) = -(\tfrac{1}{2}m_1 + m_2 + m_3)gL_1\cos(\varphi_1)$$
$$G(2,1) = -(\tfrac{1}{2}m_2 + m_3)gL_2\cos(\varphi_2)$$
$$G(3,1) = -\tfrac{1}{2}m_3L_3g\cos(\varphi_3)$$
$$D(1,2) = \tfrac{1}{2}(m_1 + 2m_2 + 2m_3)L_1\cos(\varphi_1)$$
$$D(1,1) = -\tfrac{1}{2}(m_1 + 2m_2 + 2m_3)L_1\sin(\varphi_1)$$
$$D(2,2) = \tfrac{1}{2}(m_2 + 2m_3)L_2\cos(\varphi_2)$$
$$D(2,1) = -\tfrac{1}{2}(m_2 + 2m_3)L_2\sin(\varphi_2)$$
$$D(3,2) = \tfrac{1}{2}m_3L_3\cos(\varphi_3)$$
$$D(3,1) = -\tfrac{1}{2}m_3L_3\sin(\varphi_3)$$

$$R = \begin{bmatrix} 1 & -1 & 0 \\ 0 & 1 & -1 \\ 0 & 0 & 1 \end{bmatrix}$$

Equation (1) is obtained by substitution of $x_{\mathrm{st}}(i) = \varphi_i \ (i = 1{:}3)$, $x_{\mathrm{st}}(i+3) = \dot{\varphi}_i(i = 1{:}3)$ and $w_{\mathrm{st}} = [w^{*T}_{\mathrm{st}}\ \ddot{s}_x\ \ddot{s}_y]^T$ in (14).

Appendix B. The sensory input

The sensory input is lumped in the vector $\mathbf{y}_{\mathrm{st}}$ which contains: the ankle, knee and hip angles $(\theta_1, \theta_2, \theta_3)$, the ground reactions force in the normal direction (F_{gn}) and in the tangential direction (F_{gt}) to the sole, the centre of pressure (***CoP***), the rotational (vb_1) and translation (vb_2, vb_3) accelerations sensed by the semicircular canals and the otolith organs, the position $(x_{\mathrm{head}}, y_{\mathrm{head}})$ and velocity $(\dot{x}_{\mathrm{head}}, \dot{y}_{\mathrm{head}})$ of the head in relation to a visual reference frame. Two visual reference frames are defined, one relative to the support base and one relative to the fixed world.

$$\begin{aligned} y_{\mathrm{st}} = [&\theta_1, \theta_2, \theta_3, F_{\mathrm{gn}}, F_{\mathrm{gt}}, CoP, vb_1, vb_2, vb_3, \\ &x_{\mathrm{head},1}, y_{\mathrm{head},1}, \dot{x}_{\mathrm{head},1}, \dot{y}_{\mathrm{head},1}, x_{\mathrm{head},2}, \\ &y_{\mathrm{head},2}, \dot{x}_{\mathrm{head},2}, \dot{y}_{\mathrm{head},2}] \end{aligned} \quad (15)$$

B.1 Joint angles

$$\theta_1 = \varphi_1 - \alpha \qquad \theta_2 = \varphi_2 - \varphi_1 \qquad \theta_3 = \varphi_3 - \varphi_2 \quad (16)$$

B.2 Ground reaction forces and the centre of pressure

$$\begin{aligned} F_{\mathrm{gn}} &= (m_{\mathrm{tot}})((\ddot{y}_{\mathrm{m}} + \ddot{s}_y - g)\cos(\alpha) + (\ddot{x}_{\mathrm{m}} + \ddot{s}_x)\sin(\alpha)) \\ F_{\mathrm{gt}} &= (m_{\mathrm{tot}})(-(\ddot{y}_{\mathrm{m}} + \ddot{s}_y - g)\sin(\alpha) + (\ddot{x}_{\mathrm{m}} + \ddot{s}_x)\cos(\alpha)) \end{aligned} \quad (17)$$

$$CoP = \left(gx_{\mathrm{m}} + \sum_{i=1}^{n_{\mathrm{seg}}} I_i^* \ddot{\varphi}_i\right) \Big/ F_{\mathrm{gn}}$$

where m_{tot} is the total mass of the segment model, $I_i^*(i = 1..3)$ is the moment of inertia of the ith segment relatively to the ankle joint, $\ddot{\varphi}_i$ is the rotational acceleration of the ith segment, α is the support base angle, $\ddot{u}_x, \ddot{u}_y$ are the support base accelerations, $(x_{\mathrm{m}}, y_{\mathrm{m}})$ are the centre of mass coordinates relative to the support base:

$$x_{\mathrm{m}} = \sum_{i=1}^{n_{\mathrm{seg}}} C_i\cos(\varphi_i), \qquad y_{\mathrm{m}} = \sum_{i=1}^{n_{\mathrm{seg}}} C_i\sin(\varphi_i) \quad (18)$$

and $(\ddot{x}_{\mathrm{m}}, \ddot{y}_{\mathrm{m}})$ are the accelerations of the centre of mass relative to the support base:

$$\begin{aligned} \ddot{x}_{\mathrm{m}} &= \sum_{i=1}^{n_{\mathrm{seg}}} -C_i(\cos(\varphi_i)\dot{\varphi}_i^2 + \sin(\varphi_i)\ddot{\varphi}_i) \\ \ddot{y}_{\mathrm{m}} &= \sum_{i=1}^{n_{\mathrm{seg}}} C_i(-\sin(\varphi_i)\dot{\varphi}_i^2 + \cos(\varphi_i)\ddot{\varphi}_i) \end{aligned} \quad (19)$$

with $C_i(i = 1 : n_{\mathrm{seg}})$ are constants:

$$C_i = \left(\frac{1}{2}m_iL_i + \sum_{j=i+1}^{n_{\mathrm{seg}}} m_iL_j\right) \Big/ m_{\mathrm{tot}} \quad (20)$$

B.3 Accelerations sensed by the vestibular system

$$
\begin{aligned}
vb_1 &= \ddot{\varphi}_3 \\
vb_2 &= (\ddot{x}_{\text{head}} + \ddot{s}_x)\sin(\varphi_3 + 25^\circ) - (\ddot{y}_{\text{head}} + \ddot{s}_y - g)\cos(\varphi_3 + 25^\circ) \\
vb_3 &= (\ddot{x}_{\text{head}} + \ddot{s}_x)\cos(\varphi_3 + 25^\circ) + (\ddot{y}_{\text{head}} + \ddot{s}_y - g)\sin(\varphi_3 + 25^\circ)
\end{aligned}
\tag{21}
$$

where $\ddot{x}_{\text{head}}, \ddot{y}_{\text{head}}$ are the accelerations of the head relative to the support base:

$$
\begin{aligned}
\ddot{x}_{\text{head}} &= \sum_{i=1}^{n_{\text{seg}}} -L_i(\cos(\varphi_i)\dot{\varphi}_i^2 + \sin(\varphi_i)\ddot{\varphi}_i), \\
\ddot{y}_{\text{head}} &= \sum_{i=1}^{n_{\text{seg}}} L_i(-\sin(\varphi_i)\dot{\varphi}_i^2 + \cos(\varphi_i)\ddot{\varphi}_i)
\end{aligned}
\tag{22}
$$

B.4 Vision relative to the support base

$$
x_{\text{head},1} = \sum_{i=1}^{n_{\text{seg}}} L_i\cos(\varphi_i) \qquad y_{\text{head},1} = \sum_{i=1}^{n_{\text{seg}}} L_i\sin(\varphi_i) \tag{23}
$$

$$
\dot{x}_{\text{head},1} = \sum_{i=1}^{n_{\text{seg}}} -L_i\sin(\varphi_i)\dot{\varphi}_i \qquad \dot{y}_{\text{head},1} = \sum_{i=1}^{n_{\text{seg}}} L_i\cos(\varphi_i)\dot{\varphi}_i \tag{24}
$$

B.5 Vision relative to the fixed world

$$
x_{\text{head},2} = x_{\text{head},1} + s_x \quad y_{\text{head},2} = y_{\text{head},1} + s_y \tag{25}
$$

$$
\dot{x}_{\text{head},2} = \dot{x}_{\text{head},1} + \dot{s}_x \quad \dot{y}_{\text{head},2} = \dot{y}_{\text{head},1} + \dot{s}_y \tag{26}
$$

where (s_x, s_y) is the support base position and $(\dot{s}_x, \dot{s}_y)$ the support base velocity.

Appendix C. Vector a expressed as a stochastic differential equation

Since support base kinematics and the unknown disturbances are a priori unknown and can vary in time, these variables can be expressed as a stochastic differential equation (Gelb 1974):

$$
\dot{a} = \begin{bmatrix} \dot{s}_x \\ \ddot{s}_x \\ \dddot{s}_x \\ \dot{s}_y \\ \ddot{s}_y \\ \dddot{s}_y \\ \dot{\alpha} \\ \ddot{\alpha} \\ \dot{w}^*_{\text{st}}(1) \\ \dot{w}^*_{\text{st}}(2) \\ \dot{w}^*_{\text{st}}(3) \end{bmatrix}
= \begin{bmatrix}
0&1&0&0&0&0&0&0&0&0&0 \\
0&0&1&0&0&0&0&0&0&0&0 \\
0&0&0&0&0&0&0&0&0&0&0 \\
0&0&0&0&1&0&0&0&0&0&0 \\
0&0&0&0&0&1&0&0&0&0&0 \\
0&0&0&0&0&0&0&0&0&0&0 \\
0&0&0&0&0&0&0&1&0&0&0 \\
0&0&0&0&0&0&0&0&0&0&0 \\
0&0&0&0&0&0&0&0&0&0&0 \\
0&0&0&0&0&0&0&0&0&0&0 \\
0&0&0&0&0&0&0&0&0&0&0
\end{bmatrix}
\begin{bmatrix} s_x \\ \dot{s}_x \\ \ddot{s}_x \\ s_y \\ \dot{s}_y \\ \ddot{s}_y \\ \alpha \\ \dot{\alpha} \\ w^*_{\text{st}}(1) \\ w^*_{\text{st}}(2) \\ w^*_{\text{st}}(3) \end{bmatrix}
+ \begin{bmatrix}
0&0&0&0&0&0 \\
0&0&0&0&0&0 \\
1&0&0&0&0&0 \\
0&0&0&0&0&0 \\
0&0&0&0&0&0 \\
0&1&0&0&0&0 \\
0&0&0&0&0&0 \\
0&0&1&0&0&0 \\
0&0&0&1&0&0 \\
0&0&0&0&1&0 \\
0&0&0&0&0&1
\end{bmatrix} w_{\text{a}} = A_{\text{a}} + G_{\text{a}} w_{\text{a}}
\tag{27}
$$

where A_{a} and G_{a} are time-invariant matrices and $w_{\text{a}} \approx N(0, W_{\text{a}})$. The strength of the noise, w_{a}, should correspond roughly to the possible range of variation in support base accelerations $(\ddot{s}_x, \ddot{s}_y)$ and other disturbances (w^*_{st}).

Appendix D. The Kalman filter equations

The Kalman gain which the drives the estimated state to the true state is expressed by:

$$
K(t_d) = P(t_d)H^T(\hat{x}(t_d), u_{\text{st}}(t_d))V^{-1}(t_d)) \tag{28}
$$

where P is the error covariance matrix, $E\{\hat{x}(t_d)\hat{x}^T(t_d)\}$, given by the differential equation:

$$
\begin{aligned}
\dot{P}(t_d) =& F(\hat{x}(t_d), u_{\text{st}}(t_d), t_d)P(t_d) + P(t_d)F^T(\hat{x}(t_d), u_{\text{st}}(t_d), t_d) \\
&+ GW(t_d)G^T - K(t_d)V(t_d)K^T(t_d)
\end{aligned}
\tag{29}
$$

where

$$
F(\hat{x}(t_d), u_{\text{st}}(t_d), t_d) \equiv \left.\frac{\partial f(x(t_d), u_{\text{st}}(t_d), t_d)}{\partial x(t_d)}\right|_{x(t_d)=\hat{x}(t_d)} \tag{30}
$$

and

$$
H(\hat{x}(t_d), u_{\text{st}}(t_d), t_d) \equiv \left.\frac{\partial g(x(t_d), u_{\text{st}}(t_d), t_d)}{\partial x(t_d)}\right|_{x(t_d)=\hat{x}(t_d)} \tag{31}
$$

Appendix E. The covariance of the center of mass

A closed form expression for the centre of mass distribution is obtained by linearizing the human stance control model around erect position (x_0). When F and H are linear time-invariant matrices and V and W are time- invariant spectral density matrices, (28) and (29) reduce to:

$$
K(t_d) = P(t_d)H_0^T V^{-1} \tag{32}
$$

and

$$
\dot{P}(t_d) = F_0P(t_d) + P(t_d)F_0^T + GWG^T - K(t_d)VK^T(t_d) \tag{33}
$$

where

$$
F_0 = F(x_0, 0) \; H_0 = H(x_0, 0) \tag{34}
$$

For $t_d \Rightarrow \infty$, the error covariance matrix reaches a steady-state value, P_∞, and therefore:

$$
F_0P_\infty + P_\infty F_0^T + GWG^T - P_\infty H_0^{TVH}0P_\infty^T = 0 \tag{35}
$$

which is an algebraic Ricatti equation and can be solved for P_∞. The steady state Kalman Gain is:

$$K_\infty = P_\infty H_0^T V^{-1} \tag{36}$$

By linearizing the human stance model around the desired orientation, a closed-form expression for the covariance of the centre of mass is obtained. Unknown disturbances (w_{st}) are zero mean Gaussian noise with spectral density matrix W_{st}. The covariance matrix of the system states is (Kleinman 1969):

$$\begin{aligned} E\{x_{st}(t)x_{st}^T\} &= \exp(A\tau)P_\infty^* \exp(A^T\tau) \\ &+ \int_o^\tau \exp(A\sigma)G_{st}W_{st}G_{st}^T \exp(A^T\sigma)d\,\sigma \\ &+ \int_0^\infty \exp(\bar{A}\sigma)\exp(A\tau)P_\infty^* H^{*T}V^{-1}H^*P_\infty^* \\ &\times \exp(A^T\tau)\exp(\bar{A}^T\sigma)d\sigma \end{aligned} \tag{37}$$

where P^* and H^* denote, respectively, the elements of P and H corresponding to the system states (x_{st}), and sensor states (x_{sen}) and:

$$\bar{A} = A - BL$$

$$A \equiv \left.\frac{\partial f_{st}(x_{st}, u_{st}, w_{st})}{\partial x_{st}}\right|_{x_{st}=x_{st}^0, u_{st}=0, w_{st}=0}$$

$$G_{st} \equiv \left.\frac{\partial f_{st}(x_{st}, u_{st}, w_{st}t)}{\partial w_{st}}\right|_{x_{st}=x_{st}^0, u_{st}=0, w_{st}=0}$$

$$B \equiv \left.\frac{\partial f_s(x_{st}, u_{st}, w_{st})}{\partial u_{st}}\right|_{x_{xt}=x_{st}^0, u_{st}=0, w_{st}=0}$$

A closed form expression for the covariance of the centre of mass is:

$$\begin{aligned} E\{x_m^2\} &= E\Big\{[C_1 \quad C_2 \quad C_3]x_{st}\,x_{st}^T[C_1 \quad C_2 \quad C_3]^T\Big\} \\ &= [C_1 \quad C_2 \quad C_3]E\{x_{st}\,x_{st}^T\}[C_1 \quad C_2 \quad C_3]^T \end{aligned} \tag{38}$$

where $C_i\,(i = 1 : n_{seg})$ are constants, see (20).

Appendix F. Simulation parameters

All simulations were performed in Matlab (Mathworks). Parameters of the segmental model in the simulation are: m is the mass of a segment, L is the length of a segment, and I is the moment of inertia of a segment relative to the centre of the corresponding segment. Segment 1 is shank, 2 is thigh and 3 is trunk. Parameter values are: $m_1 = 4\,\mathrm{kg}$, $m_2 = 7\,\mathrm{kg}$ and $m_3 = 48\,\mathrm{kg}$; $L_1 = 0.6\,\mathrm{m}$, $L_2 = 0.5\,\mathrm{m}$ and $L_3 = 0.8\,\mathrm{m}$; $I_1 = 0.12\,\mathrm{kgm}^2$, $I_2 = 0.1458\,\mathrm{kgm}^2$ and $I_3 = 2.26\,\mathrm{kgm}^2$; and $g = 9.81\,\mathrm{ms}^{-2}$. The neural time delay (τ) is 100 ms. Parameters for the Kalman filter equations are the spectral density matrices V and W_a. All non-diagonal elements of V are zero and the diagonal entries are:

$$V(1,1) = V(2,2) = V(3,3) = 0.22\text{e-}5$$

$$V(4,4) = V(5,5) = V(6,6) = 0.76$$

$$V(7,7) = V(8,8) = V(9,9) = 2$$

$$V(10,10) = V(11,11) = V(14,14) = V(15,15) = 4.9\text{e-}5 \text{ and}$$

$$V(12,12) = V(13,13) = V(16,16) = V(17,17) = 3.7\text{e-}5$$

In the case of a sensory perturbation, the corresponding diagonal element of V was set to 1 e6. All non-diagonal elements of W_a are zero. In the case of internal perturbations, the diagonal entries are:

$$W_a(1,1) = W_a(2,2) = W_a(3,3) = 1.6\text{e-}3 \qquad \text{and}$$
$$W_a(4,4) = W_a(5,5) = W_a(6,6) = 1\text{e-}29$$

In the case of a horizontal support base perturbation, the diagonal entries are:

$$W_a(1,1) = W_a(2,2) = W_a(3,3) = 1.6\text{e-}3 \qquad \text{and}$$
$$W_a(4,4) = 1\text{e-}29, W_a(5,5) = 1\text{and } W(6,6) = 1\text{e-}29$$

The spectral density matrix W_{st} used in the expression for the covariance of the centre of mass (37) is a diagonal matrix where in the case of internal perturbations:

$$W_{st}(1,1) = W_{st}(2,2) = W_{st}(3,3) = 0.11 \qquad \text{and}$$
$$W_{st}(4,4) = W_{st}(5,5) = 0$$

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