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# Mechanisms of Reference Posture Correction in the System of Upright Posture Control

**A. V. Terekhov[a,b], Yu. S. Levik[c], and I. A. Solopova[c]**

[a] *Moscow State University, Vorob'evy gory, Moscow, 119899 Russia*
[b] *Collége de France, Paris, France*
[c] *Institute of Problems of Data Transmission, Russian Academy of Sciences, Moscow, 101447 Russia*

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**Abstract**—It was earlier shown that ultraslow tilts of the support under quiet standing conditions evoke an unusual response reflecting the operation of compensatory mechanisms: postural sway is a superposition of postural oscillations typical of quiet standing and greater, slower inclinations of the body caused by the tilt. This may be explained by the presence of two hierarchical levels of upright posture control: *real-time control* compensates for small deviations of the body from the reference posture prescribed by *presetting control.* Mathematical simulation methods have been used to study the mechanisms of reference posture control. The results are compared with available experimental data. It is demonstrated that the reference posture can be corrected according to the gravitational vertical with the use of a kinesthetic reference alone. It is hypothesized that, when correcting the reference posture, the nervous system "assumes" the support to be immobile. The afferent input from sole pressure receptors is an important factor in reference posture correction. The advantages of the putative two-level control over control based on an explicit internal model are discussed.

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## INTRODUCTION

The erect or upright posture inherent to humans is one of the common characters distinguishing humans from related mammals. The orthograde posture, which determined the divergence of humans from apes and relieved the forelimbs of locomotor functions, formed as early as several million years ago, which is reflected in the name of one of our ancestral species, *Homo erectus* (upright man). It should be emphasized that the conditions of maintaining the upright posture in humans are especially difficult: the support area is small, articulate joints are numerous, and the center of gravity is elevated. Humans spend much time in an upright position, which requires the optimization of energy expenditure on its maintenance and preparedness to withstand perturbations. Therefore, the system of upright posture control should be reliable and suitable for various conditions (different tilts and instabilities of the support, the presence or absence of an additional support, etc.).

Since the upright posture implies a definite orientation of the body in the gravitational field, it could be suggested that its control is based on the body tilt relative to the vertical; i.e., the vertical direction forms a natural frame of reference. However, the vestibular apparatus, which is the main source of such information, has a relatively large zone of insensitivity. According to Fitzpatrick and McCloskey [1], vestibular thresholds in a vertical posture are about 1° with respect to tilt and 1°/s with respect to velocity. However, the posture control system is known to operate considerably more accurately: postural sway amplitudes in quiet standing are as small as fractions of an angular degree [2]. This suggests sources of considerably more precise information on the tilt.

Kinesthesia is the only source meeting this requirement [1, 3]. The threshold of kinesthetic sensitivity is substantially lowered in the case of upright posture control compared to a similar task that does not require active correction [3], which indicates a special importance of the kinesthetic reference. However, precise as it might be, kinesthesia only signals relative changes in the body configuration and does not indicate explicitly the orientation in the gravitational field. How then does kinesthesia allow deviations from the vertical to be compensated and the upright posture to be maintained?

Gurfinkel' et al. [4] hypothesized that the posture control system requires an internal reference vertical or reference posture relative to which kinesthetic data are "measured." In other words, the control is assumed to be hierarchical, including at least two levels: the upper, presetting level determines the reference position corresponding to the desired posture, while the lower, real-time control level ensures stabilization of the posture in the frame of reference determined by the presetting control. This differentiation compensates for the absence of precise information on the deviations from the gravitational vertical at the level of real-time control. Indeed, if the reference position corresponds to the vertical orientation, the compensation based on kines-

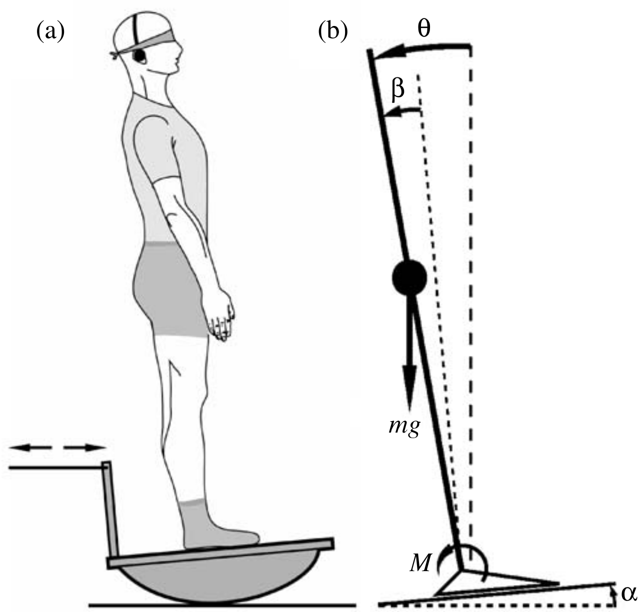


**Fig. 1.** The scheme of the experiment and the mathematical model. (a) The experimental installation; (b) the upturned pendulum model for a nonhorizontal support.

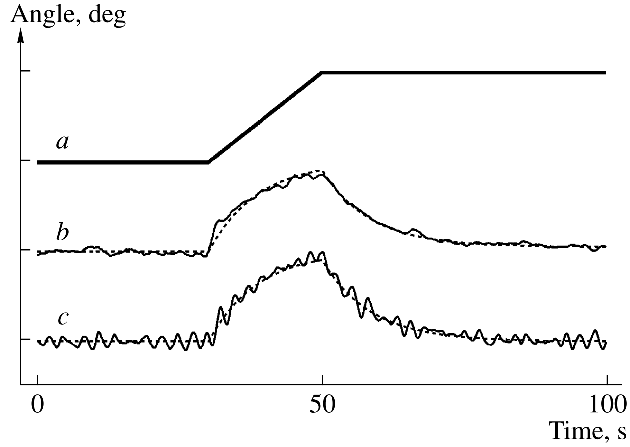


**Fig. 2.** The response to a linear perturbation. (*a*) The support tilt; (*b*) the averaged curve of the body tilt in response to the stimulus (the solid line) and its approximation with exponential functions (the dashed line); (*c*) the response of the model to the stimulus (the solid line) and its approximation with exponential functions (the dashed line).

thetic data measured relative to this position will guarantee that deviations from the vertical are compensated. Experiments with ultraslow support tilts yielded much evidence in favor of this hypothesis [4].

The mechanisms of correction of the reference posture in response to changes in the support tilt were beyond the scope of the cited study [4]. Although the authors demonstrated that kinesthesia was the main source of information, it is unclear how it can be used to form a reference position *corresponding to the gravitational vertical.* We believe that this problem calls for mathematical simulation based on physiologically correct assumptions and taking into account the structure of posture control suggested in [4]. The results of mathematical simulation could either confirm the interpretation suggested in that study or show the necessity of another interpretation of the available experimental data. We performed such a mathematical simulation and describe its results below.

## METHODS

**Experimental.** The experimental installation used in [4] included a movable support in the form of a paperweight (Fig. 1a) with a radius of 25 cm and a height of 16 cm. This support was driven by an electric motor. A stabilograph was set on the base of the platform. The subjects were instructed to stand on the stabilograph in a comfortable posture; the positions of the feet were such that the "paperweight" rotation axis corresponded to the axes of the ankle joints as precisely as possible. We recorded the sagittal stabilogram, the ankle joint angle, and the angle of tilt. The angles were calculated from the linear shifts of characteristic points on the ankle and chest measured by wire strain gauges. Simultaneously, the tilt of the support was recorded. The readings of all gauges were digitized with a discretization frequency of 5 Hz.

Two laws of movement of the support were used, with sinusoidal and linear changes in the tilt. In experiments with a linear law of movement (Fig. 2, curve *a*), the recording duration was 100 s. During the first 30 s, the support was immobile; then, it was tilted by 1° during 20 s with a constant angular velocity of 0.05°/s. The direction of the support movement corresponded to the plantar flexion. In the case of sinusoidal movement, the support tilt varied according to a sinusoidal law with a range of 3° and a period of 155 s (Fig. 3, curve *a*). The duration of the recording was 360 s, the support beginning to move 80 s before the recording started. In both cases, the subjects wore glasses with frosted lenses to exclude visual information on the tilt and a headset to prevent them from determining the start of movement by the sound of the motor.

Twelve subjects aged 20–70 years participated in the experiments. Each subject performed six tests with sinusoidal variation of the tilt and eight tests with linear variation. There were 5- to 10-min breaks between the tests. The experiments lasted for several days, so that a subject performed no more than 12 tests a day.

**The mathematical model.** We constructed a model of the stabilization of the upright posture in the sagittal plane. To describe the mechanics of the human body, we used an upturned pendulum model (see, e.g., [5]). The body was represented as a two-link system (Fig. 1b), the lower link corresponding to a foot, which was assumed to be fixed on the support, and the upper link corresponding to the suprapedal part of the body.

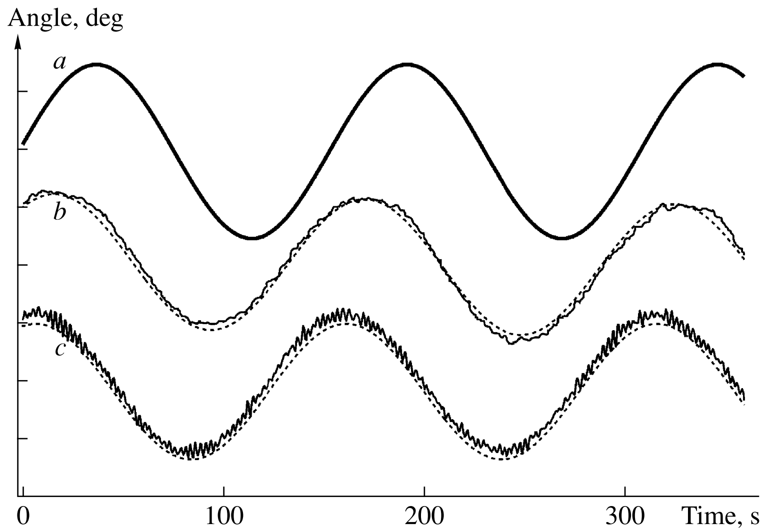


**Fig. 3.** The response to a sinusoidal perturbation. (*a*) The support tilt; (*b*) the averaged curve of the body tilt in response to the stimulus (the solid line) and its approximation with the sum of a sinusoidal function and a small linear trend (the dashed line); (*c*) the response of the model to the stimulus (the solid line) and its approximation with a sinusoidal function (the dashed line, slightly lowered to make it more illustrative).

Free rotation of the upper part relative to the joint between the links was allowed. The equation of motion of the upturned pendulum has the form

$$I\ddot{\theta} = mgh\theta - M, \tag{1}$$

where $\theta$ is the tilt angle; $I$, $m$, and $h$ are the moment of inertia, mass, and center of mass of the human body relative to the ankle joint; and $mgh\theta$ and $M$ are the moments of force of gravity and the muscles, respectively. We assumed that the upright posture corresponded to a zero tilt, which was unessential for the model but allowed us to simplify the equations considerably.

According to the two-level structure of control in the ankle joint suggested in [4], we assumed that posture stabilization was mediated by feedbacks from the deviation and velocity of deviation of the ankle joint angle $\beta$ from a certain value $\beta^*$ presetting the reference posture:

$$M = K(\beta - \beta^*) + R\dot{\beta}. \tag{2}$$

This feedback could be ensured by both the stiffness of active muscles and reflex signals from the CNS. Note that Eq. (2) entirely corresponds to Fel'dman's $\lambda$ model [6].

It was assumed that the support could deviate from the horizontal ($\theta \neq \beta$). The slope of the support relative to the horizontal was denoted $\alpha$. There was a simple relationship (Fig. 1b):

$$\theta = \beta + \alpha. \tag{3}$$

Combination of Eqs. (1)–(3) yields

$$I\ddot{\theta} + R\dot{\theta} + (K - mgh)\theta = K\alpha + K\beta^* + R\dot{\alpha}. \tag{4}$$

The posture is upright if the right side of Eq. (4) is zero; hence, in the case of an immobile support, the presetting level problem is reduced to the equation

$$\beta^* = -\alpha. \tag{5}$$

We assumed that the main source of information used to form the reference posture $\beta^*$ is kinesthesia, i.e., the angle $\beta$ and angular velocity $\dot{\beta}$ measured by the I*a* and II afferents, the moment $M$ measured by the I*b* afferents, and the position of the center of pressure $CoP = h\theta - [I/(mg)]\ddot{\theta}$ determined from the afferent signals from the foot pressure receptors. The last two inputs are equivalent in terms of upturned pendulum model (1).

We solved the problem of ensuring equality (5) with the use of kinesthetic signals alone. The main difficulty is that the kinesthetic input does not carry explicit information on either the vertical $\theta$ or the tilt of the support $\alpha$. However, the value $\alpha$ can be reconstructed. Since the angle $\alpha$ affects the equilibrium position of system (4) and postural sway, according to Eq. (4), occurs about the equilibrium position, we may attempt to estimate $\alpha$ by comparing the actual signals of kinesthetic inputs and their expected values obtained with the use of an internal model. In automatic control theory, this approach is referred to as adaptive control [7]. Application of methods for constructing adaptive control yields the following law of change in $\beta^*$ (see [8] for more detail):

$$\dot{\beta}^* = \frac{1}{T}\left(\frac{K}{K - mgh}\right)\frac{CoP}{h}. \tag{6}$$

This law of control is intended for the correction of the reference posture by its continual adjustment to the support tilt, which is unknown but is assumed to be constant. The time required for this operation is determined by the parameter $T$. The ability of the presetting control to solve this problem is illustrated under Results. Here, it should be noted that correction at the presetting level should not interfere with the real-time control; i.e., the general system (4), (6) should be stable. The conditions of stability are the following:

$$\begin{gathered} T > \frac{1}{R}\frac{IK}{mgh} \\ R > 0 \\ K > mgh. \end{gathered} \tag{7}$$

**The conditions of the numerical experiment.** The behavior of mathematical model (4), (6) was compared with experimental data obtained in tests with the same laws of perturbation of the support movement $\alpha$. The mass–inertia characteristics $I$, $m$, and $h$ were determined according to [9] for a "standard" subject with a body height of 1.7 m and a body weight $m$ of 70 kg: $I$ = 80 kg m and $h$ = 1 m. The rigidity $K$ was chosen so that, in the case of an immobile support, system (4) was oscillatory with an oscillation frequency of 0.3 Hz, which agreed with experimental data [2, 10]. The value of the damping parameter $R$ affected the pattern of slow processes in the system insignificantly provided that conditions of stability (7) were met. The parameter $R$ was assigned values small enough for the condition of stability to be satisfied at $T$ values of about 10 s. Finally, we set $R$ = 40 N m/s. Noise was added to the right sides of Eqs. (4) and (6) to approximate the model to a real situation.

## RESULTS

**Experimental results.** The qualitative pattern of the response to perturbation can be most clearly seen in curves averaged over all tests and all subjects. Figures 2 and 3 show averaged curves of the tilt angle for the sinusoidal and linear tilts, respectively. The tilt was a resultant of two processes: slow deviations from the vertical axis and small, frequent oscillations, which were apparently indistinguishable from the postural sway in quiet standing. We observed a paradoxical situation: small (about 0.3°) body tilts characteristic of postural sway (they are barely visible in the averaged curves) were compensated almost instantly, whereas the compensation of substantially greater inclinations (on average, 3° in the case of a sinusoidal tilt) was obviously insufficient.

This insufficient compensation had a stereotypic structure determined by the stimulus type. In the case of linear perturbation (Fig. 2, curve $a$), the start of support movement initiated a slow deviation from the vertical in the direction of the support inclination, which was followed by a slow return immediately after the support stopped (Fig. 2, curve $b$). Both phases of slow movement were adequately approximated by an exponential relationship (cf. the solid and dashed lines in Fig. 2, curve $b$). On average, the tilt angle practically returned to the initial value (the difference was about 0.05°). The characteristic times of both exponential curves were almost equal; for the average curve, this value was 8.5 s (the dashed line in Fig. 2, curve $b$).

In the case of a sinusoidal tilt (Fig. 3, curve $a$), slow inclinations were close to sinusoidal with a perturbation period (the solid line in Fig. 3, curve $b$). The dashed line in Fig. 3, curve $b$ shows the approximation of the experimental curve by a superposition of a sinusoid with a period of 155 s and a slight linear trend (0.2° over 360 s). The enhancement coefficient (the ratio of the signal amplitude to the tilt amplitude) and the phase shift were determined for each subject in each test in [4]. The enhancement coefficient was 0.92 ± 0.43, and the phase shift was 55 ± 19° (phase advance).

The changes in the ankle joint angle had similar structures in both cases (data not shown; see [4]) and were adequately approximated by the difference between the angle relative to the vertical and the tilt of the support. The stabilogram was almost indistinguishable from the tilt curve.

**Simulation results.** We have constructed a mathematical model (4), (6) describing the correction of human upright posture on a rotating support. The model is based on the hypothesis of two levels of human upright posture control: real-time control and presetting control levels. We suggest an algorithm of operation of the presetting control level (6) using only a kinesthetic reference (the position of the center of pressure) for correcting the reference posture.

The model was subjected to perturbations simulating the perturbations used in the real experiment. Figures 2 and 3 show the summary plots of changes in the upright posture characteristics in the real experiment and the simulation. In both the experimental and model curves, there were explicit slow and fast components, the patterns of the slow components being qualitatively identical (cf. curves $b$ and $c$ in Figs. 2 and 3). In the case of a linear law of support movement, the tilt was adequately approximated by two exponential functions (Fig. 2, curve $c$). The choice of the proper parameter $T$ of the presetting level ensured similarity of the slow components of the model and experimental curves. In the model, the tilt angle completely returned to its initial value, which was the only difference between approximating exponential curves $b$ and $c$ in Fig. 2.

Figure 3 shows the averaged experimental and model curves for the case of sinusoidal perturbation. The model curve was obtained at the same values of parameters as that shown in Fig. 2. One may notice some discordance between the experimental and model curves, which is mainly explained by the difference in the phase shift (72° in the model vs. 55 ± 19° in the experiment). The enhancement coefficient in the model

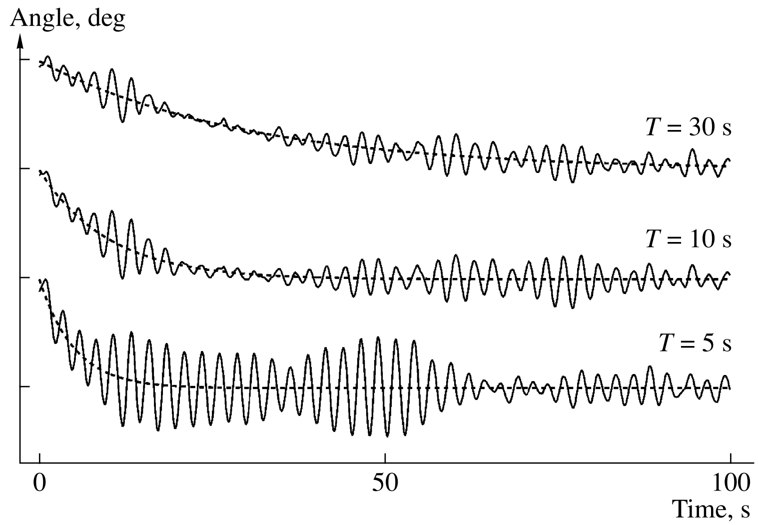


**Fig. 4.** Upright posture correction curves in the case of an initially incorrect reference posture for different values of the correction time parameter $T$ (the solid lines) and their approximation with exponential functions (the dotted lines). A decrease in the correction time was accompanied by an increase in the postural sway amplitude.

was closer to the experimental one (0.79 vs. 0.92 ± 0.43). In general, the model values differed from the experimental ones by less than the value of the mean square deviation of the experimental values; i.e., the difference was nonsignificant. Moreover, a small variation of system parameters (less than 20%) was enough for the model enhancement coefficient and phase shift to fit the respective mean experimental parameters precisely (data not shown). Taking into account that, generally speaking, the subjects differed in their mass/inertia, geometric, and other parameters included in model (4), (6), the slight quantitative discordance between the model and experiment is quite explainable.

The suggested algorithm ensured slow reference posture correction toward the vertical (Fig. 4). The kinetic curves of the restoration of the upright posture were close to exponential. Varying the parameter $T$ of algorithm (6) made it possible to obtain different characteristic times of slow processes (Fig. 4). However, if the dissipation coefficient (the parameter $R$ in Eq. (4)) was fixed, a decrease in the time of correction was accompanied by an increase in the postural sway amplitude because the state approached the limit of stability determined by condition (7).

Note that the suggested model is resistant to the variation of its parameters and the introduction of a small nonlinearity; i.e., such perturbations did not substantially affect the behavior of the model, including the shape of the curves shown in Figs. 2 (curve *c*), 3 (curve *c*), and 4.

## DISCUSSION

In this study, we have constructed a mathematical model of human upright posture control on the basis of the earlier [4] assumption on two hierarchical levels of control. In the model, the real-time control consists of a stabilizing linear feedback from the deviation and velocity of deviation of the ankle joint angle from a certain value. This assumption is traditional for the mathematical simulation of upright posture stabilization in humans. According to different authors, this feedback reflects the viscoelastic characteristics of the innervated muscles [10, 11], probably combined with similar characteristics of the postsynaptic stretch reflex loop [6, 12] or a more complex reflex loop [13, 14]. Probably, the feedback uses internal estimates of the tilt obtained from an internal model, rather than direct signals from receptors of some modality [15]. In contrast to literature data on the stabilization mechanisms, literature data on the time course of correction of the system of reference (reference posture) in maintaining the position of the body are scarce. The most relevant are the results of [16] on the aftereffect of body tilt caused by a rapid inclination of the support by 5° in the absence of visual input. The subjects were instructed not to counteract the tilt. The restoration of the upright posture was slow and approximately exponential. The subjects clustered into two groups, in which the characteristic time of posture restoration after the perturbation was 5–10 and 30–60 s, respectively. The authors explained this difference in response by assuming that the former subjects mainly relied on the frame of reference related to the vertical and the latter on that related to the support. Note that the perturbation parameters used in [16] were superthreshold for the vestibular apparatus, which probably allowed the subjects to use it to form the frame of reference related to the vertical.

A fundamental difference of our study from the others is that we analyzed the ability of the posture control system to bring the reference posture into correspondence with the vertical position *using a kinesthetic ref-*

*erence alone*. Indeed, the inclination velocity (no more than 0.05°/s) was subthreshold for all modalities [1, 17]; however, the posture control system responded to the tilt and attempted to compensate it, although it was tens of seconds behind (Fig. 3). Experiments with a linear inclination of the support (Fig. 2) showed that the correction became noticeable almost simultaneously with the start of the perturbation. The slow component of the movement in the entire range between the 30th and 50th seconds shown in Fig. 2 (curve *b*) is approximately exponential, whereas it would be close to linear if there were no correction. It is noteworthy that, in psychophysiological experiments [17], subjects did not notice the inclination of the support (with parameters close to those in [4]) until about 10 s after the inclination began. The reports of subjects in [4] indicate that they perceived the support to be immobile throughout the experiment.

The nervous system seems to overlook such slow inclinations of a support. But then it is unclear what triggers the correction of the reference posture. Probably, the correction mechanism functions throughout the time of standing; however, it only becomes apparent if the body tilts, where this mechanism, for some reason, fails to compensate the perturbation completely, which gives rise to stereotypic slow processes (Figs. 3, 4). This interpretation is supported by observations [18] showing that the equilibrium position of a standing subject is continually varying.

Since kinesthesia, the main source of information in quiet standing, does not signal directly either the inclination of a support or the orientation relative to the vertical, it is unclear how it can ensure reference posture correction according to the vertical. We have demonstrated that, in theory, this problem can be solved if the support is immobile, although not necessarily horizontal. The algorithm described here ensures reference posture correction even if the orientation of the support is unknown (Fig. 4). If the support changes position, the imperfection of the algorithm leads to the same slow sway pattern that is observed when similar perturbations are applied to a quietly standing subject (Figs. 2, 3).

The only parameter of this algorithm is the coefficient of proportionality between the shift of the center of pressure and the velocity of the change in the reference posture. This parameter may be conventionally called the averaging time. As can be seen in Fig. 4, a decrease in this parameter results in an increase in postural sway, this increase being markedly nonlinear: the amplitude increases less than 1.5-fold as $T$ decreases from 30 to 10 s but more than threefold as $T$ decreases from 10 to 5 s. Apparently, the nervous system chooses a $T$ of about 8.5 s as a compromise between the postural sway amplitude and the velocity of reference posture correction. A decrease in $T$ would have resulted in a drastic increase in the oscillation amplitude and decrease in stability.

Earlier, an attempt was made to reconstruct a stochastic model of unperturbed posture control based on the deviation of the center of masses in standing [15]. The system's characteristics were determined, including a periodic component with an oscillation frequency of about 0.3–0.5 Hz and an aperiodic component with a characteristic time of 8–10 s. According to the authors [15], the oscillatory component reflected the functioning of feedback loops, and the aperiodic one, the dynamics of an internal estimator monitoring the velocity and position of the body with an internal model. It was assumed that such a large time constant resulted from solving the optimal estimation task under conditions where not only measurements and output signals to muscles but also the sensory integration within the nervous system is subject to noise. Note that deviation of the support from the horizontal position was not allowed and the sensitivity thresholds of the vestibular apparatus were not taken into account.

Our data agree with the results of [15] in that we also assume that the dynamic system reflecting the unperturbed posture control has periodic and aperiodic components. The numerical estimates of the frequency and characteristic time reported in [15] and obtained in our study are also practically equal to each other. However, we put forward an alternative interpretation of the slow aperiodic component. We assume that it corresponds to the loop of reference posture correction according to the vertical. This explanation seems most probable. Indeed, it is reasonable, instead of using a complex internal model for combined processing of information with different modalities, to adjust the kinesthetic input so that deviations in the ankle joint themselves correspond to the deviation from the vertical. This adjustment seems all the more preferable as it permits using quick proprioceptor reflexes to stabilize posture (at the real-time control level) instead of waiting for the estimator located in supraspinal structures to respond. Moreover, since the estimator compares afferent information with simulation data provided by the internal model of the human body dynamics, its efficiency largely depends on the accuracy of the internal model. For example, addition of a small nonlinearity or variation of parameters may considerably distort the result of estimation, which, in turn, will lead to errors in stabilization signals and, hence, loss of equilibrium. Conversely, the algorithm suggested here does not contain an internal model explicitly and is resistant to its possible inaccuracy. If the algorithm operates incorrectly, this will little affect the real-time control level and will only result in a stationary tilt without loss of equilibrium. In addition, the suggested algorithm is "undemanding" in terms of the "calculations" performed by the system. Direct integration of the data from the receptors of the sole of the foot is substantially less complicated than simulation of the behavior of a complex system with several degrees of freedom. Such a simple algorithm is possible due to the hypothesis on the support immobility that we believe to be "accepted" by the posture control system. There is experimental evidence that, in the case of slow perturbations, the support is indeed perceived to be immobile at both the conscious and postural reflex levels [19, 20].

It should be emphasized that the mechanism suggested here can only correct the reference position. The initial condition for its normal operation is a reference posture little differing from that corresponding to a vertical orientation of the body (according to experimental data [16], a discordance of several angular degrees is acceptable). Apparently, this initial condition cannot be met without a more complex analysis of all afferent information and previous experiences.

## CONCLUSIONS

In this study, we have further developed the hypothesis on two hierarchical levels of unperturbed posture control that was first put forward in [4]. We have constructed a mathematical model demonstrating that the reference position can be corrected according to the vertical with the use of information from the kinesthetic input alone. The results of numerical integration of the equations of this model agree with experimental data. We hypothesize that an a priori presumption that the support is immobile is crucial for the nervous system to correct the reference posture. The advantage of the two-level control compared to an internal estimator has been demonstrated.

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