Effects of Manipulations with Visual Feedback on Postural Responses in Humans Maintaining an Upright Stance

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We studied postural reactions evoked by vibrational stimulation of the anterior tibial and posterior neck muscles under three different conditions of visual control (in a darkened room): (i) upon standing with the eyes open, EO, with perception of a stationary 2D image of the visual environment on the screen, (ii) under conditions of perception of a 3D virtual visual environment, VVE, and (iii) upon standing with the eyes closed, EC. Vibrational stimulation of both muscle groups evoked forward inclinations of the body; average values of the latter under control conditions (EC) were close to each other. The VVE mimicking a real visual environment possessed two planes, a mobile foreground one, whose shifts were programmed in such a manner that they correlated with oscillations of the body, and a stable background one. The tested subjects were asked to use the latter as a visual reference. Under VVE conditions, the amplitude of postural reactions depended on the feedback coefficient between the body movements and shifts of the VVE foreground and the direction of this feedback (its synphase or antiphase, sph or aph, mode). Postural responses at the feedback sph direction became greater with increase in the feedback coefficient (i.e., with increases in the magnitude of shifts of the VVE foreground) and reached values typical of standing under EC conditions. In the case of the aph type of feedback, the responses changed insignificantly. If the lowest feedback coefficient, 1.0, was used, the postural responses tended to decrease, as compared with those under EO conditions. The difference between the values observed at the sph and aph types of feedback with similar coefficients was manifested more intensely in the case of stimulation of the neck muscles. This fact shows that postural reactions triggered by afferent signals from the neck muscles depend more considerably on the ongoing visual afferentation.

Keywords: upright stance, postural reactions, 3D virtual visual environment, visual feedback.

INTRODUCTION

In the course of maintenance of an upright stance, a subject cannot stand absolutely stably even in the case of a very high level of motivation for such a task. The main reason for continuous postural corrections is fundamental. The human body in the vertical position corresponds to a reverse pendulum with the center of gravity, CG, situated about 1 m above the rotation axis (corresponding to the level of the ankle joints). Because of this, the subject inevitably inclines (begins to fall) upon minimum perturbations and must counteract such inclinations by activation of the corresponding muscles of the lower limbs. The contribution of different muscles and muscle groups to the maintenance of an upright stance are dissimilar. Most skeletal muscles are activated, first of all, in order to stabilize spatial positions of different body links [1], but two groups of muscles play a special,

crucial role in the maintenance of body equilibrium in the standing position.

The shin muscles form one of the above groups. Precisely these muscles controlling the ankle joints, i.e., axes of rotation of the entire body in an upright stance, create resulting (with respect to the body mass) force moments that interact with the supports and counteract falling. Afferent signals from proprioceptors of the shin muscles are addressed to neuronal structures localized at different CNS levels; they exert the most powerful direct influences on spinal motoneurons [1, 2].

In addition to initiation of segmental reflexes, signals from shin muscle afferents and, in general, from lower limb muscles come via the spino-cerebellar tract to the cerebellum. After being integrated with the activity of cerebral mechanisms, they allow the subject to adequately realize accurate sensorimotor coordination and to maintain muscle tone and posture [3]. At the brainstem level, the above-mentioned ascending pathways give collaterals projecting to a few cerebral structures playing the key role in planning and control of movements and posture. These are the primary motor cortex, supplementary (secondary) motor cortex, and basal ganglia [4, 5]. Afferentation from these muscles

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also influences the brain neuronal structures related to perception of the position of the body and its separate parts in the surrounding space [5]. This circumstance provides the possibility of initiating both real spatially oriented postural reactions and illusions of changes in the posture upon selective stimulation of shin muscle proprioceptors (e.g., using vibration) [6, 7].

In addition to the shin muscles, the neck muscles play a special role in the maintenance of upright stance. The ascending pathways transmitting information from the above muscles, when coming to the spinal cord, also bifurcate. Some of their branches form the components of local reflex networks, while others ascend to the dorsal column nuclei. This ascending pathway, via the medial lemniscus, comes to the thalamus and terminates in its posteroventral nucleus [3]. From this structure, neck muscle-born information comes to the cortex, where, probably, there are specific regions related to the involvement of these muscles in stabilization of the head position with respect to the body [8, 9]. Results of modern studies based on the techniques of brain scanning (PET and MRI) allowed researchers to interpret in more detail the data obtained earlier in experiments on animals and in neurological practice, which are related to localization of the brain regions obtaining afferentation from the neck muscles in humans [10, 11]. In the mentioned works, an extensive complex of primary and secondary cerebral regions activated by neck afferentation was identified. First of all, these are cortical zones receiving mostly direct proprioceptive inputs from the thalamus, namely the somatosensory fields 3a, 2, and S2, the parietal/insular part of the vestibular cortex (PIVC), and also the motor and premotor cortical regions. In addition, such a target for afferentation from the neck muscles as the posterior parietal cortex, PPC, should be specially mentioned. This area plays a critically important role in the current regulation of targeted (first of all, grasping) upper limb movements, which need integration of efferent motor commands and feedback influences from the visual organs and from proprioceptors of the hand and neck muscles [12]. As is believed, the PPC is one of the brain regions where primary processing of sensory information, which finally results in the creation of an egocentric notion on the position of the body in the external space (internal body model), is performed. It seems quite possible that, precisely, close interrelations of afferent flows from the neck muscles and organs of vision determining the formation of the internal spatial body model represent the main factor responsible for the appearance of postural reactions triggered by selective stimulation of the above muscles and looking like body inclinations.

Differences in the structure of central connections of the ascending pathways transmitting sensory information from muscles of the shins and the neck may be the reason why patterns of motor reactions (including postural ones) elicited by stimulation of these muscle groups differ from each other even in the case of their biomechanical identity. Differences between the patterns of the dependence of the formation and dynamics of these reactions in the case of arrival of information of other modalities (e.g., coming from visual receptors) may explain the adequacy of this supposition.

To test this hypothesis, we carried out a comparative study of the dependence of postural reactions evoked by vibrational stimulation of the posterior neck and anterior tibial muscles on the parameters of visual feedback (VFb). The selection of the above muscle groups was related to the fact that their vibrational stimulations induce forward inclinations of the body biomechanically similar to each other. In the course of initiation of postural reactions, we manipulated with the parameters of VFb by changing the direction of the latter and the level of correspondence of body shifts and shifts of the observed visual surroundings that were unexpected for the tested subject.

METHODS

Experimental Procedures. Eleven healthy persons, 5 men (mean age, 46.6 ± 9.6 years) and 6 women (54.0 ± 6.2 years, $M \pm s.d.$) took part in the tests. All participants obtained detailed information on the content and procedure of the experiments and gave their informed consent. In the course of the tests, the subjects stood on a rigid horizontal force platform ($40 \times \times 40$ cm), which allowed us to record changes in the position of the center of feet pressure (CFP) on the platform surface. The feet of the subjects were in a subjectively comfortable position; the heels and toes were 8 to 12 cm and 23 to 28 cm apart, respectively. The subjects were asked to maintain an adequate vertical posture by minimizing, as possible, both spontaneous and muscle stimulation-induced inclinations of the body from the gravitational vertical.

Visual Conditions. The subjects were in a darkened room; their postural reactions to vibrational stimulation of the shin and neck muscles were examined under three different conditions of visual control. These were: (i) standing with the eyes open (EO) and looking for a stationary 2D image on the screen, (ii) standing under conditions of perception of a 3D virtual visual environment (VVE), and (iii) standing with the eyes closed (EC). The reactions observed under the two former
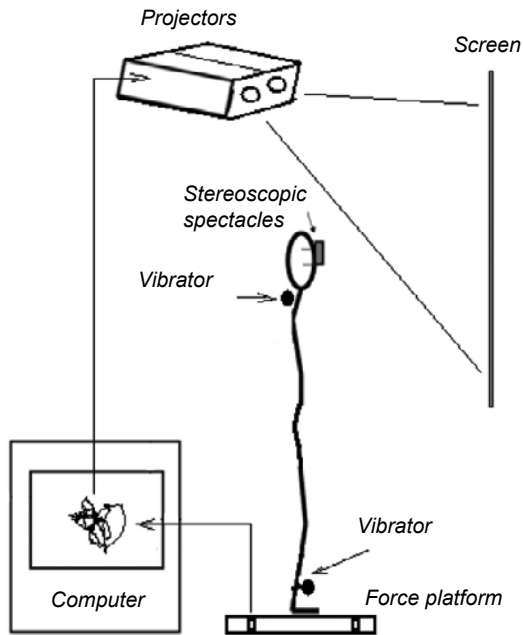
Fig. 1. Scheme of the position of the tested subject and details of the experimental setup under conditions of virtual visual envitonment.

visual conditions were compared with each other, while reactions under EC conditions were used as the control.

To create the VVE, we used the so-called passive method of formation of a 3D stereoscopic image based on the effect of light polarization [13, 14]. With the use of two projectors supplied with polarization filters orthogonally oriented with respect to each other, two images of one and the same picture (in our case, this was an urban landscape seen through the window) were simultaneously projected on the screen made from a special material characterized by a minimum level of depolarization (the so-called silver screen). The subject and projectors were at the same side with respect to the screen (Fig. 1). Under conditions of creation of a 3D visual environment, the subjects saw a picture including two plans. The first one looked like a window with adjacent walls, while the second plan was a part of the urban landscape (neighboring buildings seen through the window). The distance to the image of the first (foreground) plan from the subject corresponded to 1.2 m, while the distance to the second (background) plan was about 20 m. The subjects wore special spectacles. The latter were supplied with polarization filters oriented in a parallel manner with respect to the corresponding filters of the projectors; this situation provided 3D perception of the VVE. The field of vision for the subjects was limited and equal to about 80 and 90 deg from the vertical and horizontal axes, respectively. Because of this, the subjects could provide their visual orientation only within the limits of the presented virtual visual picture. To support

the feeling of a more complete immersion in the virtual reality, shifts of the foreground of the VVE were "tied" to horizontal oscillations of the center of gravity (CG) of the body. Shifts of the CG related to inclinations of the body were estimated according to filtered oscillations of the CFP position. For this purpose, we used special software allowing us to smooth out high-frequency oscillations of CFP components and to detect only oscillations of the frequency range corresponding to that of CG oscillations. This aspect was described earlier in more detail [15, 16]. The frequency of filtration of the CFP oscillations was chosen according to the results of a number of analytical studies [17, 18]. It was demonstrated that oscillations of the CFP of a standing subject with frequencies below 1 Hz practically coincide with oscillations of the body CG, while higher frequencies of CFP oscillations are not reproduced by CG shifts. Correlation of the VVE with CG oscillations was provided in the following way. In some tests with vibration of the muscles, the pattern of body oscillations and shifts of the VVE foreground was antiphase (aph), while in other tests it was synphase (sph).

In this situation, the ratio (feedback coefficient) between the VVE and CG shifts in the course of stimulation could be equal to 1.0 (K1; fluctuations of the perceived visual image corresponded in magnitude to those of the body CG), or 2.0 (K2; oscillations of the visualized picture were two times greater in amplitude than in the case of K1), or 4.0 (K4; oscillations of the visualized picture were four times greater, as compared to those at K1). To standardize the conditions of the background stance and to avoid the effects of these conditions on postural reactions, the minimum feedback coefficient K1 was used in all tests with VVE preceding muscle stimulation. Movements of the VVE were reproduced with a small delay (20 msec) with respect to inclinations of the body; this delay appeared in the course of filtration of CFP oscillations and "fastening" of the VVE foreground to CG oscillations in an online mode. Due to "fastening" of the VVE foreground to oscillations of the body CG, the visual environment was, in general, perceived by the subjects as nonstationary, despite the fact that the background remained immobile and the instruction that the subject should fix his/her eyes on some object within this background.

Under VVE conditions, 24 trials with vibration of each muscle group were performed (four trials under each of the three different conditions with sph and aph relations for VVE shifts). Under EO conditions, the subjects stood with the same spectacles on, and their field of vision was limited by the same borders as under VVE conditions. In front of them, the subjects saw the screen with the same image, but the latter was stationary and
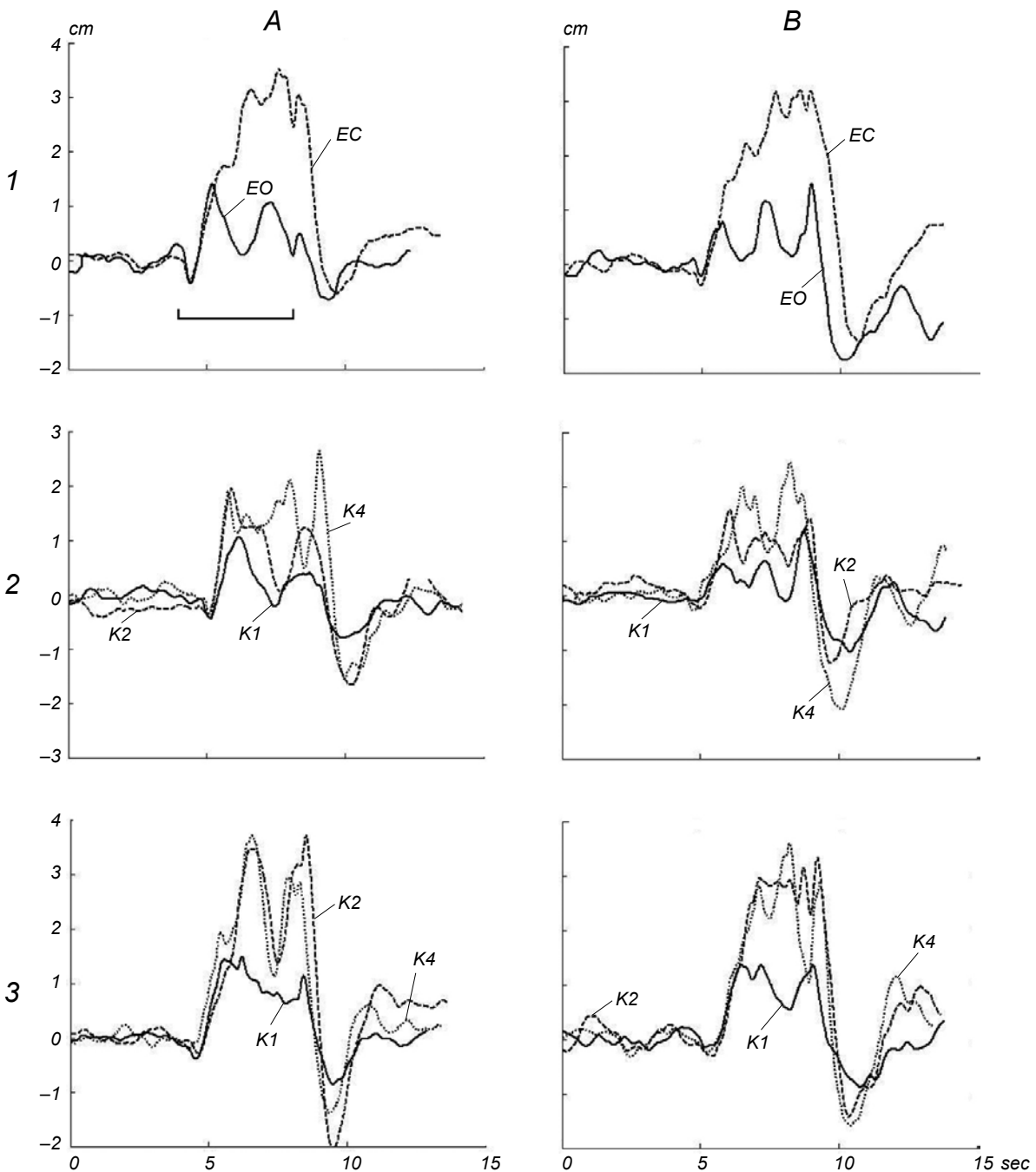
Fig. 2. Postural responses to vibrational stimulation of the neck muscles (A) and anterior tibial muscles (B) recorded in an upright stance of one of the subjects under different visual conditions. Abscissa) Time, sec; ordinate) displacements of the feet pressure center, cm. Upward shifts in the graphs correspond to forward inclinations of the body. 1) Postural responses upon standing with the eyes closed and open (EC and EO, respectively) under conditions of a stationary visual environment. In A, 1, a 4-sec-long period of action of vibration is shown by a horizontal bar below the graph. 2) Postural responses under conditions of antiphase feedback between inclinations of the body and shifts of the virtual visualized environment, VVE, with different feedback coefficients, K1, K2, and K4. 3) Postural responses under conditions of synphase feedback between body inclinations and VVE shifts with different coefficients.

flat. Thus, the tested subjects maintained the standing position under conditions corresponding, in general, to normal visual perception, but their field of vision was limited to some extent. Under EO conditions, similarly to the EC conditions, postural reactions were tested 12 times (6 and 6 trials with vibrational stimulation of the neck and tibial muscles).

Recording and Estimation of Postural Reactions. Postural reactions were elicited by vibrational stimulation either of the regions of tendons of both
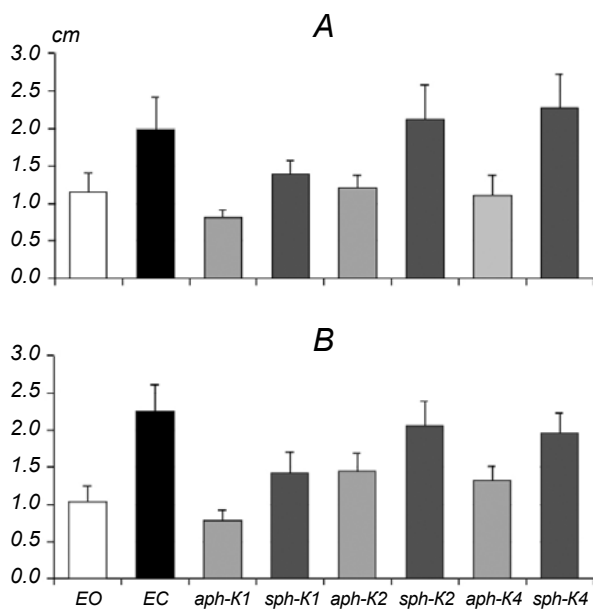
mm. tibialis anterior or of the muscles of the neck back surface (mostly of the trapezoidal and belt muscles). The stimulation frequency, amplitude, and duration were 70 to 100 Hz, 1.0 mm, and 4.0 sec, respectively. In both cases, we used vibrators constructed on the basis of DC electric motors with eccentrics fixed on their axes. To provide simultaneous activation of both shin muscles, the vibrator was rigidly fixed to the middle part of a wooden lath (40 × 3 × 1 cm) softly positioned by elastic bandages across the tendons of *mm. tibialis anterior*. Such a mode of fixation of the vibrator allowed us to synchronously stimulate the right and left muscles. For stimulation of the neck muscles, a shorter lath with the vibrator was positioned across the back neck surface at the level of the cervical vertebrae 5 and 6 and pressed by a special fixing bandage.

Initially (before the beginning of the experiment), we selected, by varying the vibration frequency, the levels of stimulation of the shin and neck muscles such that the evoked postural responses (forward inclinations of the body) were approximately equal to each other.

In the course of trials, we recorded frontal and sagittal components (along the *x* and *y* coordinates) of the CFP position onto the support surface. Signals from the force platform were digitized at a 100 sec^{-1} frequency and entered into a PC for subsequent analysis. The duration of a trial under each visual condition was 20 sec. The trials included an interval of background tranquil upright stance (9 to 10 sec long), an interval of the postural reaction to vibrational stimulation of the muscles (4.0 sec), and a period of return to the initial position (Fig. 2). In the course of analysis of

postural responses, the average value of the shifts along the *y* axis (inclinations of the body in a forward/ backward direction within the interval of vibrational stimulation) was measured. The value of this shift along the *y* coordinate was estimated with respect to the mean level of body oscillations within the background period during the last 4-sec-long segment before the beginning of vibrational stimulation.

For each visual condition, four trials with vibration of the neck muscles and also four trails with vibration of the anterior tibial muscles were performed. Trials with activation of the neck and shin muscles under different visual conditions were alternated in a randomized order. In the cases of vibrational stimulation of both the neck and shin muscles, shifts of the body in lateral directions were relatively small and demonstrated no systematic pattern; this is why estimates of such shifts along the *x* axis have not been analyzed and presented in this publication. On the whole, each tested subject realized 72 experimental trials in the course of the experiment (2 muscle groups × × 4 repetitions × 3 visual conditions × 3 feedback coefficients) including 60 trials under VVE conditions and 12 control trials under EO and EC conditions.

Statistical Processing. The effects of the conditions of visual control on postural reactions were revealed using ANOVA dispersion analysis. The "feedback coefficient" (K1, K2, and K4) and "feedback direction" with respect to oscillations of the body and shifts of the visual environment (sph and aph) were considered the factors. The significance of differences between the results of measurements of the magnitude of postural responses observed under separate visual conditions was estimated using the *t*-test for samplings with dissimilar dispersions. As was mentioned above, no systematic inclinations of the body within the frontal plane were found; this is why only results of analysis of the shifts of the CFP along the *y* coordinate calculated for the sagittal component of the postural reaction will be described below.

RESULTS

Figure 2 illustrates postural responses (four similar trials averaged) to vibrational stimulation of the neck
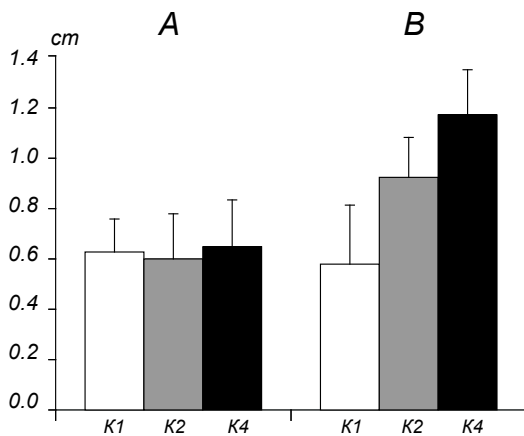
Fig. 4. Differences, cm, between the magnitudes of the postural responses upon synphase and antiphase directions of feedback between the shifts of the virtual visual environment and body inclinations. The differences were calculated for the cases of stimulation of the shin (A) and neck (B) muscles with different feedback coefficients, K1, K2, and K4.

muscles (A) and anterior tibial muscles (B) in one of the examined subjects.

Vibrational stimulation of both muscle groups evoked forward inclinations of the body, which, under similar visual conditions, demonstrated mean values rather close to each other. As can be seen in Fig. 2, postural responses to vibration of both muscle groups were, at the feedback coefficient K1, somewhat smaller in the aph feedback direction and greater in the sph direction than those under EO conditions. Recall that the subject observed a stationary 2D image under the latter conditions. At the coefficients K2 and K4, postural responses increased; in the case of the sph relations between the body and CFP oscillations, such responses became close in amplitude to the responses observed under EC conditions. Similar dependencies of the postural responses under different visual conditions were observed in other tested subjects. Results of statistical processing of the data for the entire examined group are shown in Fig. 3.

Vibrational Stimulation of the Neck Muscles. Dispersion analysis demonstrated the existence of a global influence of the "feedback direction" factor on the magnitude of postural responses induced by stimulation of the neck muscles ($F_{1.63} = 9.17$, $P < 0.005$). The subsequent two-sampling t-test allowed us to find significant statistical differences between the postural responses for the conditions of aph-K1 vs sph-K1 ($t = 2.63$, $P < 0.02$), aph-K2 vs sph-K2 ($t = 1.95$, $P < 0.05$), and aph-K4 vs sph-K4 ($t = 2.94$, $P < 0.01$). At the same time, dispersion analysis showed the absence of a global influence of the "feedback coefficient" factor on the magnitude of the postural responses

under both aph and sph conditions for relations between the body oscillations and the VVE shifts. Comparison of the data samplings obtained in the case of the aph relations showed, however, the presence of significant differences between the magnitudes of the postural responses for aph-K1 vs aph-K2 conditions ($t = 2.06$, $P < 0.05$), while comparison of the data samplings obtained at the sph relations showed that there are significant differences for cases of sph-K1 vs sph-K2 ($t = 1.94$, $P < 0.05$) and for sph-K1 vs sph-K4 cases ($t = 1.84$, $P < 0.05$).

Results obtained with the two-sampling t-test showed that postural responses observed under EO conditions were significantly greater than those in the aph-K1 case ($t = 1.91$, $P < 0.05$) and significantly smaller than under sph-K2 and sph-K4 conditions ($t = 2.84$, $P < 0.01$ and $t = 2.46$, $P < 0.01$, respectively). Postural responses under EC conditions were significantly greater than those under nearly all visual conditions except for sph-K2 and sph-K4.

Vibrational Stimulation of the Shin Muscles. Dispersion analysis showed the existence of a global effect of the "feedback direction" factor upon the magnitude of the postural responses evoked by vibration of the anterior tibial muscles ($F_{1.63} = 7.22$, $P < 0.01$). The subsequent two-sampling t-test allowed us to reveal significant statistical differences between the postural responses under aph-K1 conditions vs sph-K1 ($t = 1.99$, $P < 0.05$), aph-K2 vs sph-K2 ($t = 3.35$, $P < 0.01$), and aph-K4 vs sph-K4 conditions ($t = 2.34$, $P < 0.05$).

Similarly to the analysis of postural responses to vibrational stimulation of the neck muscles, dispersion analysis of changes in the magnitudes of the postural responses to shin muscle stimulation demonstrated no global influence of the "feedback coefficient" factor. At the same time, comparison of the data samplings obtained in the case of aph feedback showed the presence of significant differences between the postural responses for aph-K1 vs aph-K2 ($t = 2.49$, $P < 0.03$) and aph-K1 vs aph-K4 ($t = 2.25$, $P < 0.05$). In the case of sph feedback, significant differences were found for sph-K1 conditions vs sph-K2 ($t = 3.13$, $P < 0.01$) and sph-K1 vs sph-K4 ($t = 2.34$, $P < 0.05$).

The two-sampling t-test showed that the postural responses elicited by vibration of the shin muscles under EO conditions were significantly smaller than those in the aph case ($t = 2.09$, $P < 0.05$) but did not differ considerably from those under aph-K1 and aph-K4 conditions. At the same time, the use of the above test showed that, similarly to what was observed in the case of vibrational stimulation of the

neck muscles, the responses to vibration of the lower limb muscles under EO conditions were significantly smaller than those under conditions of sph-K1 ($t = 1.91$, $P < 0.05$), sph-K2 ($t = 2.71$, $P < 0.01$), and sph-K4 ($t = 2.42$, $P < 0.01$). Postural responses induced by vibration of the anterior tibial muscles in the EC cases were significantly greater than the responses observed under nearly all other visual conditions except for sph-K2 and sph-K4.

Despite the fact that the patterns of influences of changes in visual conditions on postural responses elicited by vibrational stimulation of both muscle groups are rather similar to each other, there is also an important difference between these patterns. Such a difference is related to the dissimilarity of the response magnitudes obtained at sph and aph modes of relations between oscillations of the body and changes in the VVE upon one and the same value of the feedback coefficient. Figure 4 graphically illustrates this difference for all the three feedback coefficients. These differences were approximately equal to each other at all feedback coefficients for the responses to stimulation of the anterior tibial muscles. At the same time, this difference demonstrated a nearly linear dependence on the feedback coefficient in the case of postural responses evoked by stimulation of the neck muscles. Its value was the smallest at coefficient K1 (differing only insignificantly from the dissimilarity between the "sph" and "aph" responses to vibration of the shin muscles), increased noticeably at coefficient K2, and reached the greatest value at K4. Comparison of this index for the two muscle groups demonstrated significant intergroup differences in the cases of coefficients K2 ($t = 2.27$, $P < 0.05$) and K4 ($t = 2.05$, $P < 0.05$).

DISCUSSION

Our tests demonstrated that the magnitudes of the postural responses under conditions of perception of the 3D VVE were, as a rule, greater than those upon standing with the EO and that this parameter depended on both the direction and the value of the feedback coefficient between the body shifts and VVE displacements. In the case of sph feedback between the postural rearrangements and VVE shifts, the vibration-induced postural responses increased with rise in the above coefficient and became nearly equal to those under EC conditions. This fact indicates that the subjects actively used the data of visual perception as the main reference until the moment where the set of input influences used for postural corrections was supplemented by signals of

other modalities (similarly to what occurred under EC conditions, i.e., a complete absence of visual information). Under conditions of aph shifts of the VVE, the intensity of responses to vibrational stimulation of both muscle groups depended on visual conditions to a lesser extent and was close to the control in the case of EO, i.e., upon perception of a stationary 2D image. Nonetheless, certain specificities of the effects of visual conditions on the postural responses elicited by stimulation of different muscle groups can be noticed. In the case where we used vibration of the shin muscles under conditions of aph feedback and coefficient K1 (i.e., 1.0), the postural responses only mildly tended toward a decrease. In the case of other feedback coefficients, these responses were significantly greater than under EO conditions (but considerably smaller than under EC conditions). At the same time, when vibrational stimulation of the neck muscles was used, and the feedback coefficient was equal to 1.0, the postural responses were significantly smaller than those under EO conditions; at other values of the coefficient, the responses did not differ from the latter ones. Therefore, the aph movement of visual environment promoted a decrease in postural responses to vibrostimulation (especially in the responses to neck muscle stimulation). Based on these data, we can conclude that body oscillation-correlated shifts in the VVE can either destabilize the maintenance of the vertical posture and, therefore, intensify postural reactions to the effect of vibrational stimulation or can help in stabilization of the above posture. It should be noted that in both cases these effects resulted from active estimation of the direction and value of the VVE shifts by the subjects.

Despite the fact that the patterns of visual condition-dependent changes in the postural responses were, in general, similar to each other (in the case where we used stimulation of both tested muscle groups), the difference between the values of such responses obtained at sph and aph correlations with similar coefficients of the latter was found to be noticeably greater when we used vibrational stimulation of the neck muscles (Fig. 4). This fact indicates that the effect of visual information on the postural responses was expressed more strongly when just these muscles were stimulated. This fact also confirms the supposition mentioned in the Introduction: Afferentation from the neck muscles more effectively (as compared with that from the lower limb muscles), influences the cerebral structures responsible for both the formation of a spatial model of the subject's body and postural reactions corresponding to the mentioned model and current visual environment.

In general, the results obtained confirmed the statements on the special, predominant, role of vision

in the control of upright stance in humans proposed by a number of researchers [19, 20]. Studies of Lee and co-authors [21, 22] especially help one to form such a viewpoint on the role of vision. These authors, in particular, demonstrated that mild (about 6 mm) oscillations of the experimental surrounding (walls and ceiling of the room where the subject stood on a stable floor) resulted in synphase inclinations of his/her body. These inclinations induced in such a mode were especially significant (up to initiation of falling) in small children. As the authors commented, the subjects in such a case did not even understand what factor induces destabilization of their posture.

Our study discovered additional facts confirming the above-mentioned point of view. We demonstrated that the direction and magnitude of shifts of the visualized environment directly influence rapid and significant (in their magnitude) correcting postural reactions. Under most special visual conditions, the process of postural correction is worsened, although signals from receptors of the lower limb muscles (except for those subjected to vibration), feet, and vestibular organs continue to carry undistorted and adequate information about changes in the spatial position of the body. This worsening is especially intensely manifested under conditions of sph correlation between body inclinations and shifts of the VVE in the case of greater values of the feedback coefficient. In general, our results allow us to conclude that the visual system plays a predominant role during conflict between visual information and information from other sensory systems. Signals coming from the visual system are actively used as the reference for postural corrections until the moment when other sensory systems begin to produce signals stemming from a danger of loss of body equilibrium.

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