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Maintaining an Upright Posture with Different Sizes of the Object Providing Visual Feedback on Rigid and Compliant Supports

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Abstract—It was previously shown that the size of the visible object (sphere) providing visual feedback significantly influenced the maintenance of the vertical posture while standing on a rigid support. Thus, an increase in the size of a stationary sphere led to a decrease in body sway, and the same increase in the size of a moving sphere, on the contrary, increased oscillations. The frequency of oscillations of the center of gravity of the body (CoG) with a stationary sphere tended to increase with increasing size of the sphere, and with a moving one, it decreased. We tried to find out whether the relative contribution of the amplitude and frequency components of body oscillations to maintenance of a vertical posture will change on a compliant support. The subjects stood in stereo glasses in front of the screen, onto which a three-dimensional image of a sphere painted dark gray was projected. Three spheres covering visual fields of 4.5, 18, and 36 degrees, respectively, were used. The amplitude-frequency characteristics of two elementary variables were estimated: the trajectory of the projection of the body CoG on the support and the difference between the trajectories of the center of pressure (CoP) and the CoG (variable CoP–CoG). In the control, the sphere was motionless; under test conditions, the displacements of the sphere were in-phase or out-of-phase with the fluctuations of the CoG. The amplitude of the sphere's oscillations was two times higher than the amplitude of oscillations of the CoG. On a compliant support, a more significant destabilization of the vertical posture was observed (about 1.5-fold with an immovable object and twofold with a movable one). The deterioration of standing on a compliant support occurred not only due to an increase in amplitudes, but also due to more significant (than with a rigid support) changes in the frequency characteristics of the CoP and CoP–CoG variables. Just as when standing on a rigid support, an increase in the size of the stationary sphere led to a decrease in the amplitude of the oscillations of the body, and an increase in the size of the movable sphere to its increase. On a compliant support with a stationary visual environment, the oscillations frequency of the CoG decreased with increasing size of the sphere. With a movable sphere and a compliant support, it practically did not change, and with a rigid it decreased. On the other hand, on a compliant support, the oscillation frequency of the variable CoP–CoG with a stationary environment clearly increased with the sphere, and with a moving environment it decreased, and on a rigid support the changes in this variable were slightly expressed. Thus, the dependence of the amplitude and frequency characteristics of body oscillations on visual conditions during standing on a rigid and compliant support was different. It can be assumed that these differences are associated with changes in the relative contributions of visual and proprioceptive sources of information to maintaining balance on a compliant support.

Keywords: vertical posture, visual destabilization, virtual visual environment, sensorimotor conflict, stabilography, compliant support

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While maintaining an upright posture, the nervous system of a healthy individual integrates information from several sensory sources at once: from the eyes, vestibular organs, muscles and joints. The study of the interaction between these sensory inputs during standing was initiated a long time ago [1–5]. On the basis of these works and other later studies [6–10], the idea was formed that the ratio of the contributions of visual, vestibular, and somatosensory information in the construction of postural corrections may change in response to changes in the conditions of the external environment or the state of the nervous system. It has been shown, e.g., that the transition from light to dark or the change in the properties of a support (transition from a stationary to a moving track) is accompanied by sensory reweighting through which the nervous system regulates the relative contribution from various sensory sources used to control the vertical posture. This ultimately leads to the alignment of muscle commands based on new, more accurate sensory information [2, 10, 11].

In some studies of the relative contribution of various sensory sources to vertical posture control, techniques were used to remove or attenuate any sensory source, e.g., by closing the eyes [12–14] or changing the properties of the support surface [14]. Studies were also carried out in situations in which it was possible to assume the presence of adaptation to neurological deficits, such as partial or complete loss of vestibular function [7, 15, 16].

The efforts of a number of other researchers have focused on the properties of motor reactions that occur, in particular, when a particular sensory input is impaired in healthy individuals. For example, it has been shown that with a gradual increase in the strength of sensory perturbation, the amplitude of body oscillations may not correspond to the degree of this increase, which indicates a change in the coupling coefficient between the magnitude of perturbations and the amplitude of oscillations [5, 6]. In order to focus on the transitional moments of sensory reweighting, in a number of works, the dynamics of contributions from individual sensory sources was investigated by changing the relative strength of various influences, simultaneously disturbing the vertical posture [7, 17, 18]. In particular, a combination of two stimuli was simultaneously used [7]: rotation of the support surface and rotation of a virtual visual environment. It was shown that a change in the amplitude of platform movement caused comparable changes in the magnitude of responses to both platform rotation and rotation of the visual environment, while a change in the amplitude of rotation of the visual environment changed motor responses to this rotation, but did not significantly affect the responses from rotations of the platform. This indicates that the scheme of integration of somatosensory and visual signals can be asymmetric.

Previously, it was shown [19] that the size of the virtual visible object (sphere) providing visual feedback significantly affects the maintenance of an upright posture when standing on a conventional rigid support. Thus, an increase in the size of a stationary sphere led to a decrease in vibrations of the body, and the same increase in the size of a movable sphere (the movement of which was coupled with vibrations of the body) caused, on the contrary, an increase in these vibrations. At the same time, the oscillation frequency of the body center of gravity (CoG) with a stationary sphere tended to increase with an increase in the size of the sphere, and with a movable one, to decrease.

In the present study, using the same experimental model with a change in the size of the visible object, the authors tried to find out how the amplitude and frequency parameters of body oscillations behave under different conditions of the virtual visual environment during the transition from standing on a rigid support to standing on a compliant support.

METHODS

The study involved 17 healthy subjects: nine men (mean age, 64.3 ± 7.6 years) and eight women (67.0 ± 4.8 years). The subjects who took part in the experimental study were apparently healthy and, according to the survey data, previously did not experience neurological complaints and diseases of the vestibular and muscular systems. During the study, the subjects stood in comfortable shoes on a square platform of a Stabilan-01-2 stabilograph (RITM, Russia). It was used to record changes in the position of the sole center of pressure (CoP) on the support. The subjects' feet were in a comfortable position, with the heels spaced 6–10 cm apart and the toes spaced 18–22 cm apart.

During vertical posture control, the subjects looked at a screen (1.5 m high and 2 m wide) made of a fabric that depolarizes the incident light to a minimum (silverscreen). A three-dimensional stereo image of the sphere was formed on the screen using the so-called passive method [20]. For this purpose, two images of the same sphere were simultaneously projected onto the screen from two projectors (Sharp XR-10X, Japan) equipped with polarizing filters oriented orthogonally relative to each other. The subjects and the projectors were on one side of the screen. The subjects wore glasses with Panorama 3DS-GS polarizing filters (Stel—Computer Systems, Russia; alternation frequency, 120 Hz) oriented parallel to the corresponding filters of the projectors, which provided a three-dimensional perception of the virtual visual environment. The subjects' field of view was limited by glasses, approximately 60° vertically and 80° horizontally, and did not go beyond the screen. The subjects stood in a darkened room and saw only a virtual three-dimensional image of the sphere colored dark gray.

Three sphere sizes with diameters of 8.75, 35, and 70 cm were used. Spheres with these sizes covered fields of view of 4.5, 18 and 36 degrees, respectively. In the control, the visible sphere was motionless (immobile visual environment, IVE), and under testing conditions it continuously shifted, since it was coupled with in-phase or antiphase (IP and AP) oscillations of the body CoG in the anteroposterior and lateral directions. The sphere oscillation amplitude was twice as high as the amplitude of oscillations of the CoG.

In the course of the experimental study, the subjects first maintained a quiet vertical posture standing on an ordinary rigid support (RS) surface of the stabilograph and then on a compliant support (CS). A compliant support was created using a 10-cm thick square foam rubber plate, which was placed on the stabilograph platform and covered from above with a 10 mm-thick plywood plate; the plate dimensions were identical to the size of the platform. The foam rubber compliance was about 3 cm at a pressure of 0.5 N/cm^2.

During the experiment, the subjects performed 72 trials: 36 trials on a rigid support and 36 trials on a compliant support. The duration of each trial was 40 s. During the trials, the subjects looked at the sphere and tried to stand quietly on the stabilograph. When standing both on a rigid support and on a compliant support, all trials were divided into three blocks, each of which included four control trials with an immobile sphere and eight trials in which the sphere movement was coupled antiphase or in-phase with the body CoG oscillations. Trials were made at intervals of 30–40 s. In each block of trials, the sphere was of the same size. After each block, the subject rested sitting for 4–5 min. Trial blocks with spheres of different sizes were alternated in random order. The amplitude–frequency characteristics of two elementary variables calculated from the trajectories of the center of pressure of the feet (CoP) in the anteroposterior and lateral directions, including the trajectories of the projection of the body's CoG on the support (CoG variable) and the difference between the trajectories of CoP and CoG (CoP–CoG variable), were estimated.

Body vibration analysis. The trajectory of the sole center of pressure (CoP) obtained using the stabilograph pressure sensors was converted from analog to digital form with a digitization frequency of 50 Hz and then recorded on a personal computer. In the subsequent analysis, it was expanded as the sum of two time functions along each (lateral and anteroposterior) of the axes. The maintenance of the vertical posture was estimated by analyzing the changes in the amplitude-frequency characteristics of two elementary variables calculated from CoP displacements on the support. One of them was the vertical projection trajectory of the center of gravity (CoG variable), and the second was the difference between the CoP and CoG trajectories (CoP–CoG variable). To calculate them, we used the approach proposed in [20] and described in detail and used in a number of works [21–23]. In this regard, only its main provisions will be given below.

The method for calculating these elementary variables is based on the fact that there is a clear dependence of changes in the amplitude of CoG and CoP oscillations on the oscillation frequency. In particular, it was shown [21, 24] that the ratio of the amplitudes of these variables (CoG/CoP) is the highest, approaching 1.0, at minimum vibration frequencies (close to 0.0 Hz) and the lowest, approaching 0.0, at maximum frequencies (more than 3 Hz). From this it can be concluded that relatively high-frequency oscillations of the SCoP do not affect the magnitude of fluctuations of the CoG. Indeed, in the cited works, it was experimentally shown that, in fact, CoP oscillations at frequencies above 0.5 Hz practically do not affect the magnitude of CoG oscillations. Based on this understanding, in order to obtain elementary variables, we used the low-frequency filtering method, which expresses the ratio of the amplitude of CoG and CoP oscillations and reflects connection of the frequency of CoP oscillations with the movements of the body [21, 24]. Later, during the analysis of the testing results, the movement of CoG was considered as a controlled variable, and the CoP–CoG difference was considered as a variable coupled with body acceleration and reflecting changes in the resultant muscle stiffness in the ankles [19, 22, 23, 25].

The program for frequency filtering of CoP oscillations with the aim of separating the CoG and CoP–CoG variables from it and the subsequent calculation on their basis of the MF and RMS of the oscillation spectra was written in the Matlab environment.

The influence of different sphere sizes on maintaining an upright posture under control and test conditions was assessed by analyzing the changes in the median frequency (MF) and root-mean-square value (RMS) of the amplitude spectra of the studied variables in the ranges of 0–0.5 Hz for the CoG variable and 0–3.0 Hz for the CoP–CoG variable. For this purpose, we compared the spectral MF and RMS means obtained for different sphere sizes in the control and test trials.

Statistical processing. The influence of "the visual control conditions" (IVE, AP, and IP), "the support surface conditions" (RS, CS), and "the size of the observed sphere" on postural responses was revealed using analysis of variance (ANOVA). During the study of the influence of the sphere size (8.75, 35, and 70 cm), the significance of differences in the RMS and MF of the spectra of both variables was also determined, if necessary, when comparing the data obtained under control (IVE) and test conditions (AP and IP) depending on the size of the sphere using a paired two-sample *t* test for the means.

RESULTS

Analysis of the RMS and MF of the oscillation spectra of the studied variables calculated from the CoP oscillations in the anteroposterior direction when standing on RS and CS. Figure 1 shows the RMS values of the amplitude spectra averaged over all subjects for the CoG and CoP–CoG variables calculated from the results of the analysis of maintaining an upright posture on a rigid and compliable support under conditions when the visible three-dimensional image of the sphere was motionless and when it shifted due to the presence of antiphase or in-phase coupling between the position of the sphere and body oscillations. As seen from Fig. 1, the RMS values of the spectra of the studied variables in the RS condition were lower than in the CS condition. Analysis of variance revealed the global influence of the "support surface conditions" factor: for the CoG variable in the IVE condition, $F_{1,101} = 18.495$, $p < 3.968E\text{-}05$; in the AP condition, $F_{1,101} = 39.844$, $p < 7.605E\text{-}09$; in the IP condition, $F_{1,101} = 63.156$, $p < 2.954E\text{-}12$. For the CoP–CoG variable, the following estimates of the significance of the differences were obtained: in the IVE condition, $F_{1,101} = 25.117$, $p < 2.334E\text{-}06$; in the AP condition,

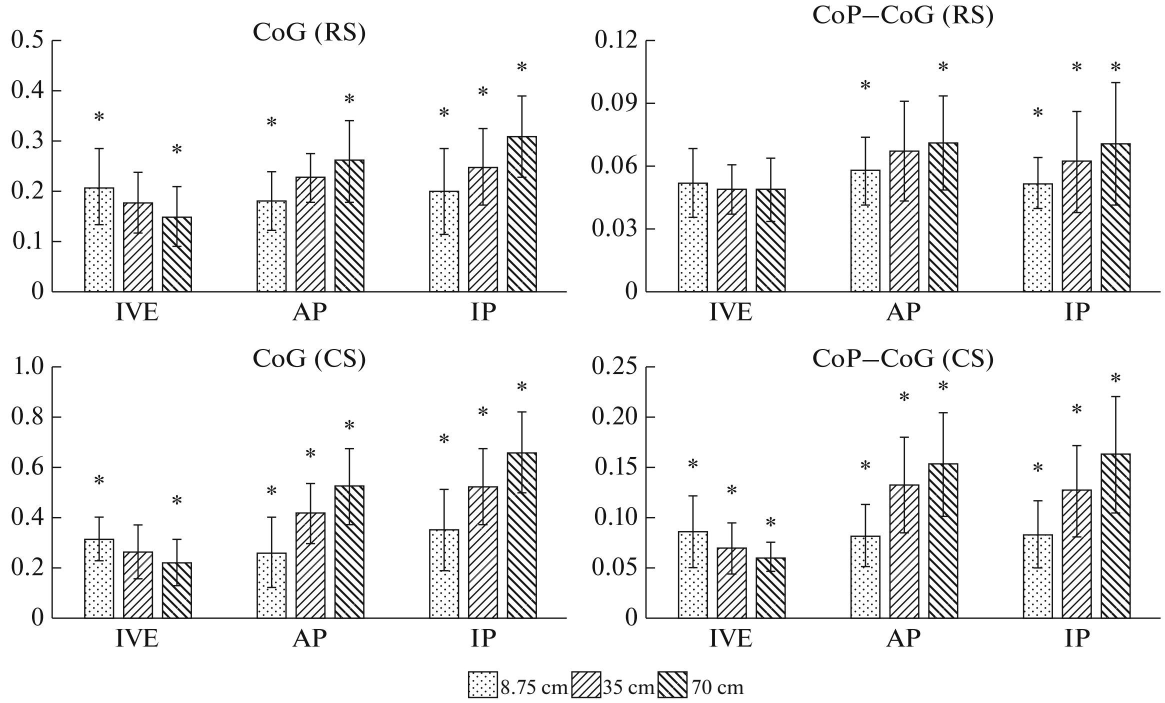

Fig. 1. RMS (mm) of the spectra of the CoG and CoP–CoG variables and their standard errors in control trials (immobile visual environment, IVE) and in test trials during antiphase (AP) and in-phase (IP) coupling of the sphere position with body oscillations. The abscissa shows the size of the sphere on the screen in centimeters. RS is a rigid support; CS is a compliant support. Asterisks indicate significant differences depending on the size of the sphere.

$F_{1,101}$ = 51.981, $p <$ 1.087E-10; in the IP condition, $F_{1,101}$ = 56.481, $p <$ 2.465E-11.

The results of analysis of variance also showed the presence of a global influence of the “visual control conditions” factor during posture control on RS in different visual conditions (IVE, AP, and IP) on the RMS of the spectra of the studied variables: for CoG, $F_{2,152}$ = 10.906, $p < 0.000038$; for CoP–CoG, $F_{2,152}$ = 7.563, $p < 0.00074$.

As also seen from Fig. 1, the RMS values of the amplitude spectra of the CoG variable during posture control in standing position on RS depended on the “sphere size” factor regardless of visual conditions. Under the IVE condition, with an increase in the size of the presented sphere, the RMS value decreased ($F_{2,50}$ = 3.391, $p < 0.0419$), and under the AP and IP conditions, on the contrary, it increased (for AP, $F_{2,50}$ = 6.213, $p < 0.00399$; for IP, $F_{2,50}$ = 7.346, $p <$ 0.0016). As for the changes in the amplitude spectra of the CoP–CoG variable, no significant dependence of the RMS value on the size of the presented sphere was revealed under any of the visual conditions.

The results of analysis of variance for CS also revealed a significant influence of the “visual control conditions: IVE, AP, and IP” factor on the RMS of the spectra of the studied variables (for CoG, $F_{2,152}$ = 31.858, $p <$ 1.86E-12; and for CoP–CoG, $F_{2,152}$ = 20.422, $p <$ 1.276E-08).

During posture control on standing on CS under all visual conditions, the RMS values of the amplitude spectra of the CoG variable, as well as during standing on RS, *depended on the sphere size*, while under the AP and IP conditions this dependence was significantly greater than under the IVE condition. In particular, if in the IVE condition of the RMS value of the spectra decreased with an increase in the size of the presented sphere approximately in the same way as in the RS condition ($F_{2,50}$ = 3.664, $p < 0.0322$), then under the AP and IP conditions, dependence on the sphere size significantly increased (for AP, $F_{2,50}$ = 17.455, $p <$ 1.422E-06; for IP, $F_{2,50}$ = 17.842, $p <$ 1.125E-06). In contrast to this variable, the RMS values of the amplitude spectra of the CoP–CoG variable when standing on a rigid support did not depend on changes in the size of the presented sphere under all visual conditions (for IVE, $F_{2,50}$ = 0.256, $p < 0.774$; for AP, $F_{2,50}$ = 1.709, $p < 0.192$ and for IP, $F_{2,50}$ = 2.866, $p < 0.067$). On the other hand, during posture control in standing position on a compliant support, the RMS of the spectra of the CoP–CoG variable, on the contrary, changed significantly as a function of the size of the sphere (for IVE, $F_{2,50}$ = 4.085, $p < 0.023$; for AP, $F_{2,50}$ = 11.447, $p <$ 7.823E-05 and for IP, $F_{2,50}$ = 12.595, $p <$ 3.584E-05).

Figure 2 shows the *spectral MF* values averaged over all subjects for the CoG and CoP–CoG variables cal-

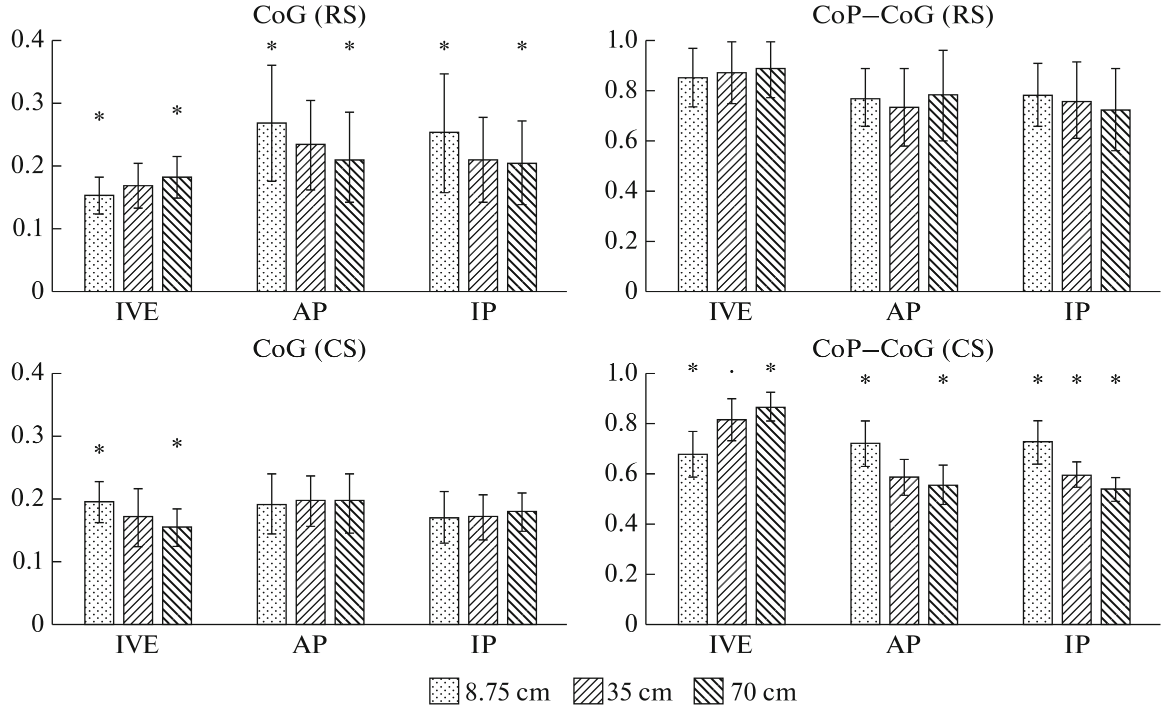

Fig. 2. MF (Hz) of the spectra of the CoG and CoP–CoG variables and their standard errors calculated from the stabilograms of the anteroposterior direction in control trials (immobile visual environment, IVE) and in test trials with antiphase (AP) and in-phase coupling (IP) of the position of the sphere with body oscillations. See Fig. 1 for designations.

culated from the results of analysis of maintaining an upright posture on a rigid and compliant support.

As seen from Fig. 2, in comparison with the amplitude spectra under these conditions, the MF values of the spectra of the studied variables in the RS condition did not substantially differ (in absolute values) from the values obtained in the CS condition. At the same time, the changes coupled with the size of the presented sphere tended to differ under different supports conditions.

Analysis of variance did not reveal a statistically significant effect of the "support surface conditions" factor on the MF of the spectra of the CoG variable in the IVE condition, $F_{1,101} = 0.8507, p < 0.358$; however, the influence of this factor in two other visual conditions was significant: in the AP condition, $F_{1,101} = 6.5627, p < 0.0119$; in the IP condition, $F_{1,101} = 13.423$, $p < 0.00039$. In contrast to the CoG variable, the influence of this factor on the CoP–CoG variable was very strong. In particular, the following estimates of the significance of differences in the MF of the spectra were obtained for the "support surface conditions" factor: in the IVE condition, $F_{1,101} = 15.723$, $p < 0.00014$; in the AP condition, $F_{1,101} = 25.03, p < 2.419\text{E-}06$; in the IP condition, $F_{1,101} = 32.394, p < 1.261\text{E-}07$.

The results of analysis of variance showed the presence of a global influence of the "visual control conditions: IVE, AP, and IP" factor on the median frequencies of the studied spectra obtained under RS conditions (for CoG, $F_{2,152} = 11.123$, $p < 3.130\text{E-}05$; for CoP–CoG, $F_{2,152} = 7.307, p < 0.00094$). During postural control on CS, the influence of this factor was slightly different. For example, the MF spectra of the CoG variable changed to a lesser degree than on standing on a rigid support ($F_{2,152} = 3.757, p < 0.0256$) and the MF of the spectra of the CoP–CoG variable, on the contrary, to a much greater degree, $F_{2,152} = 36.347, p < 1.345\text{E-}13$.

The nature of the influence of the "size of the visible object (sphere)" factor on the studied variables under different supports conditions was not always similar under the same visual conditions. Thus, during posture control on RS in the IVE condition, a statistically significant increase in the MF spectra of CoG was observed in response to an increase in the size of the sphere ($F_{2,50} = 3.322, p < 0.0445$), while under the RS conditions in the same visual condition, on the contrary, a decrease in MF was observed ($F_{2,50} = 3.237, p < 0.0486$). In two other visual conditions (AP and IP), a decrease in the MF of the spectra of the CoG variable was observed while standing on RS with an increase in the size of the sphere. In particular, although analysis of variance of globally (three conditions) significant changes did not reveal MF changes in the spectra of the CoG variable, paired comparison of frequencies showed the presence of differences in the AP condition when the spectral frequencies were

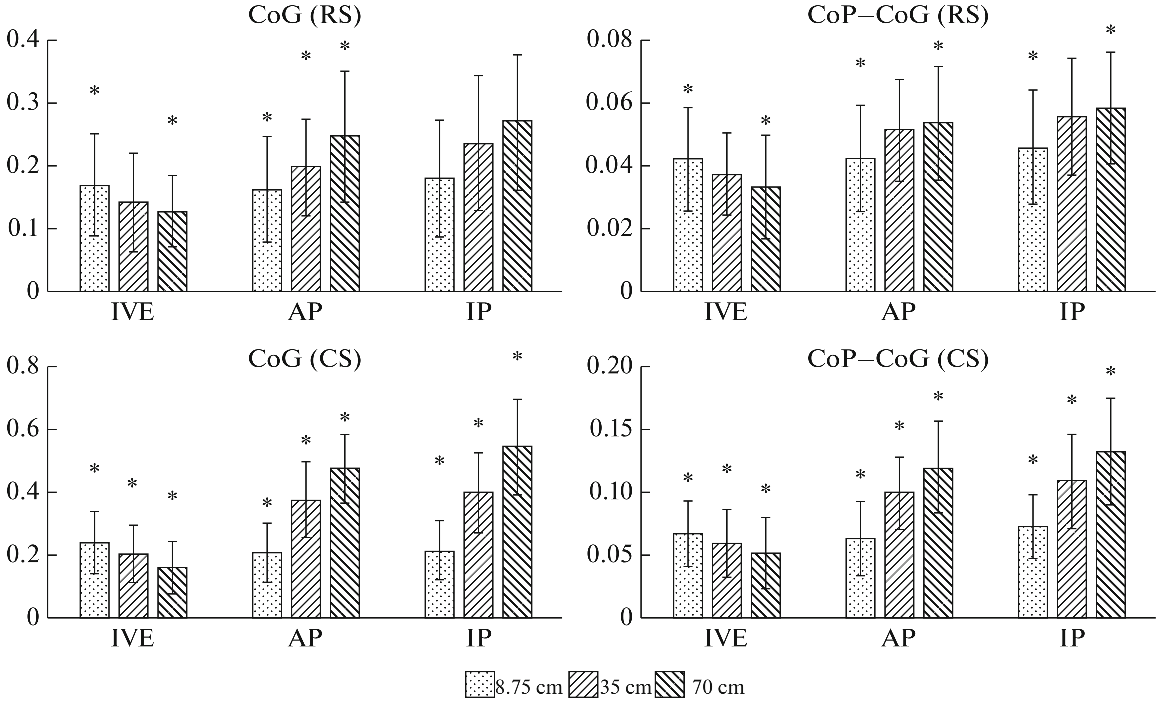

Fig. 3. RMS (mm) of the spectra of the CoG and CoP–CoG variables and their standard errors in control trials (immobile visual environment, IVE) and in test trials during antiphase (AP) and in-phase (IP) coupling of the position of the sphere with body oscillations. See Fig. 1 for designations.

compared separately for the sphere sizes 70 and 35 cm (*t Stat* = 4.569 at $p < 0.000157$) and for sizes of 70 and 8.75 cm (*t Stat* = 4.161 at $p < 0.000367$). Approximately the same differences were revealed for the IP condition: when comparing the spectral frequencies for the sphere sizes of 70 and 35 cm (*t Stat* = 5.361 at $p <$ 3.188E-05) and for the sizes of 70 and 8.75 cm (*t Stat* = 4.972 at $p <$ 6.9246E-05). At the same time, when standing on CS in the AP and IP conditions, no significant changes in the median frequency of this variable were observed.

As for the CoP–CoG variable, there was no significant similarity in the changes in the spectral MF in response to a change in the size of the observed object either: in particular, during posture control in standing position on CS in the AP condition, a statistically significant decrease in the MF of the spectra of the CoP–CoG variable was revealed in response to an increase in the size of the sphere ($F_{2,50} = 17.067$, $p <$ 2.519E-06), while on standing on RS in the same visual condition, no significant effects on MF were noted ($F_{2,50} = 0.305$, $p < 0.7386$). In two other visual conditions (IVE and IP), during posture control on different supports, more close changes (Fig. 2) were observed with an increase in the size of the sphere: under the IVE conditions both on RS and on CS, an increase in the MF of the CoP–CoG spectra was observed in response to an increase in the size of the sphere; in the IP condition, on the contrary, a decrease in the frequency of the spectra. However, analysis of variance revealed statistically significant changes only during standing on a compliant support. For the visual IVE condition on CS ($F_{2,50} = 19.996$, $p <$ 4.8209E-07); for the IVE condition on RS ($F_{2,50} = 0.986$, $p < 0.380$); for the visual IP condition with CS ($F_{2,50} = 32.296$, $p <$ 1.2986E-09) and for the visual IP condition with RS ($F_{2,50} = 1.321$, $p < 0.276$); for the visual AP condition with CS ($F_{2,50} = 17.067$, $p <$ 2.518E-06) and for the visual AP condition on RS ($F_{2,50} = 0.269$, $p <$ 0.765).

Analysis of the RMS and MF of the oscillation spectra of the studied variables calculated from the oscillations of the center of pressure in the lateral direction when standing on RS and CS. Figure 3 shows the RMS values of the amplitude spectra averaged over all subjects for the CoG and CoP–CoG variables calculated from the results of the analysis of vertical posture control in the lateral direction on a rigid and compliant support.

In this lateral plane of fluctuations, the RMS value of the spectra of the CoG and CoP–CoG variables varied for different sizes of the observed sphere in approximately the same way as it varied with the body fluctuations in the anteroposterior direction.

The RMS values of the spectra of the studied CoG and CoP–CoG variables in the RS condition were lower than in the CS condition. Analysis of variance unambiguously confirmed these differences, i.e., revealed the influence of the “support surface conditions” factor: for the CoG variable the IVE condition, $F_{1,101} = 13.716$, $p < 0.000348$; in the AP condition, $F_{1,101} = 36.828$, $p < 2.323E\text{-}08$; in the IP condition, $F_{1,\,101} = 27.601$, $p < 8.440E\text{-}07$. For the CoP–CoG variable, the following estimates of the significance of differences were obtained: in the IVE condition, $F_{1,101} = 27.408$, $p < 9.125E\text{-}07$; in the AP condition, $F_{1,101} = 49.445$, $p < 2.563E\text{-}10$; in the IP condition, $F_{1,101} = 53.621$, $p < 6.298E\text{-}11$.

The results of analysis of variance for RS showed the presence of a global influence of the “visual control conditions: IVE, AP, and IP” factor on the RMS of the spectra of the studied variables (for CoG, $F_{2,152} = 10.481$, $p < 5.489E\text{-}05$; for CoP–CoG, $F_{2,152} = 6.589$, $p < 0.00181$). The results of analysis of variance for CS also revealed a significant influence of the “visual control conditions: IVE, AP, and IP” factor on the RMS of the spectra of the studied variables (for CoG, $F_{2,152} = 23.968$, $p < 9.279E\text{-}10$; for CoP–CoG, $F_{2,152} = 20.686$, $p < 1.164E\text{-}08$).

As seen from Fig. 3, the RMS values of the amplitude spectra of the CoG variable in standing posture on RS under all visual conditions changed in response to a **change in the size of the sphere**. However, with an increase in the size of the presented sphere in the IVE condition, analysis of variance did not reveal the significance of these changes ($F_{2,50} = 1.511$, $p < 0.2309$), although the spectral RMS value tended to decrease. At the same time, analysis of variance for the AP and IP conditions confirmed the significance of the observed increase in the RMS value of the spectra of the CoG variable in response to an increase in the size of the sphere (for AP, $F_{2,50} = 3.589$, $p < 0.0353$; for IP, $F_{2,50} = 3.664$, $p < 0.033$).

During posture control in standing on CS under all visual conditions, the RMS values of the amplitude spectra of the CoG variable, as well as during standing on RS, varied with a change in the size of the sphere. Note that under the AP and IP conditions, this dependence was significantly stronger than under the IVE condition. In particular, the RMS values of the spectra decreased significantly with an increase in the size of the presented sphere in the IVE condition ($F_{2,50} = 4.855$, $p < 0.012$), i.e., more substantially than during standing on RS. Under the AP and IP conditions, the RMS of the spectra increased with an increase in the size of the sphere, and this increase was also more significant than under the RS conditions (for AP, $F_{2,\,50} = 26.759$, $p < 1.558E\text{-}08$; for IP, $F_{2,50} = 31.133$, $p < 2.144E\text{-}09$).

The influence of the “sphere size” factor on the RMS of the amplitude spectra of the CoP–CoG variable during standing on RS was insignificant. Thus, for the IVE condition, analysis of variance revealed that $F_{2,50} = 1.272$ at $p < 0.291$; for the AP condition, $F_{2,50} = 0.923$ at $p < 0.404$; for the IP condition, $F_{2,50} = 0.913$ at $p < 0.408$. During vertical posture control on CS, the influence of the “sphere size” factor was significant only under the AP and IP conditions: $F_{2,50} = 14.701$ at $p < 8.00E\text{-}06$ and $F_{2,50} = 14.462$ at $p < 9.33E\text{-}06$. During posture control under IVE conditions, no dependence of the RMS of the spectra of the CoP–CoG variable on the size of the sphere was found ($F_{2,50} = 1.959$ at $p < 0.310$).

Figure 4 shows the spectral MF values averaged over all subjects for the CoG and CoP–CoG variables calculated from the results of the analysis of vertical posture control on a rigid and compliant support **in the lateral plane**.

It is seen from Fig. 4 that, compared with the amplitude spectra, the absolute MF values of the spectra of both variables under the RS and CS conditions did not differ greatly from each other. Indeed, analysis of variance did not reveal a statistically significant influence of “the support surface conditions” on the MF of the spectra of the CoG variable during posture control under the IVE conditions, $F_{1,101} = 2.719$, $p < 0.102$. However, the influence of this factor in two other visual conditions was significant, although not very strong: in the AP condition, $F_{1,101} = 6.001$, $p < 0.016$; in the IP condition, $F_{1,101} = 6.992$, $p < 0.0095$. Approximately the same was evidenced by the estimation of the significance of differences in the MF of the spectra for CoP–CoG in the study of the influence of this factor: under the IVE condition, this variable had no differences in the oscillation frequency on different supports: $F_{1,101} = 0.219$, $p < 0.641$; and in two other visual conditions they were revealed: for the AP condition, $F_{1,101} = 4.885$, $p < 0.0294$; for the IP condition, $F_{1,101} = 13.379$, $p < 0.00041$.

The results of analysis of variance of the global influence of the “visual control conditions: IVE, AP, and IP” factor on the median frequencies of the studied spectra in the frontal plane significantly differed from the results obtained under RS conditions in the sagittal plane. In particular, there was no effect on the MF of the spectra of the CoG variable ($F_{2,152} = 0.205$, $p < 0.814$), and a weaker effect of this factor on the medial frequencies of the CoP–CoG variable was found ($F_{2,152} = 5.949$, $p < 0.003$). During posture control on RS, the influence of the “visual control conditions” on the MF of the spectra of the CoP–CoG variable was very significant ($F_{2,152} = 31.372$, $p < 4.145E\text{-}12$), but similarly to the RS condition, no significant changes were revealed in the MF spectra of the CoG variable ($F_{2,152} = 0.184$, $p < 0.832$).

The influence of the “size of the visible object (sphere)” factor on the studied variables under different supports conditions was not always close under the same visual conditions. For example, during posture control on RS under the IVE condition, a statistically significant increase in the MF of the CoG spectra was observed in response to an increase in the size of the sphere ($F_{2,50} = 6.217$, $p < 0.004$). However, during

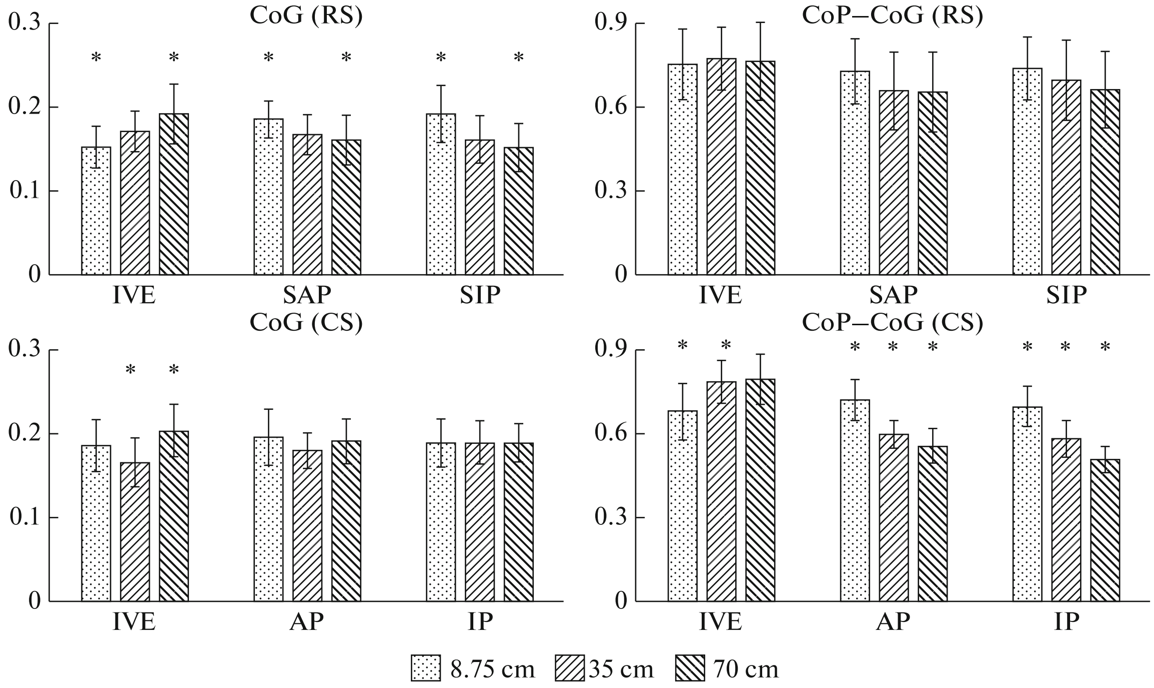

Fig. 4. MF (Hz) of the spectra of the CoG and CoP–CoG variables and their standard errors calculated from stabilograms in the lateral plane obtained in control trials (immobile visual environment, IVE) and in test trials during antiphase (AP) and in-phase (IP) coupling of the sphere with body oscillations. See Fig. 1 for designations.

standing on CS in the same visual condition, although analysis of variance revealed significant changes in MF ($F_{2,50} = 4.706$, $p < 0.014$), they were associated with diametrically opposite changes in MF with medium and large sphere sizes. In particular, at a sphere size of 35 cm, the MF of the CoG spectra significantly decreased relative to MF at a sphere size of 8.5 cm (paired *t*-test for the means: $t_{16} = 2.652$, $p < 0.0087$) and at a large size (70 cm), on the contrary, increased and were significantly larger than at a size of 35 cm ($t_{16} = 3.172$, $p < 0.0029$). During posture control on RS under the condition of antiphase oscillations of the sphere and human body (AP), a statistically significant decrease in the MF of the CoG spectra was revealed in response to an increase in the size of the sphere ($F_{2,50} = 3.534$, $p < 0.037$). Under the in-phase oscillation conditions (IP), a significant decrease in the MF of the CoG spectra was also found with an increase in the size of the observed sphere ($F_{2,50} = 8.981$, $p < 0.0005$). It can be seen from Fig. 4 that under the conditions of standing on CS during antiphase and in-phase oscillations of the sphere and human body (AP and IP), no significant changes in the MF of the CoG spectra occurred in response to changes in the size of the sphere, which was confirmed by analysis of variance (for AP, $F_{2,\ 50} = 0.944$, $p < 0.396$, and for IP, $F_{2,50} = 0.0022$, $p < 0.998$).

The influence of the "size of the visible object (sphere)" factor on the MF of the spectra of the CoP–CoG variable under different supports conditions was noted in the same visual conditions. Thus, during posture control on RS under the IVE condition, no statistically significant changes in the MF of the spectra of CoP–CoG were observed in response to an increase in the size of the sphere ($F_{2,50} = 0.129$, $p < 0.878$), and in standing on CS, the median frequencies of this variable increased with an increase in the size of the sphere ($F_{2,50} = 9.88$, $p < 0.0003$). A similar pattern of changes in the MF of the spectra of CoP–CoG was also observed in response to an increase in the size of the sphere in other visual conditions: in the AP and IP conditions, analysis of variance did not reveal statistically significant changes during posture control on RS ($F_{2,50} = 0.028$, $p < 1.624$ and $F_{2,50} = 0.281$, $p < 1.305$, respectively). However, during posture control in quiet standing on CS, a statistically significant decrease in the MF of the CoP–CoG spectra was found with both AP and IP oscillations of the sphere and the human body ($F_{2,50} = 30.864$, $p < 2.409\text{E-}09$; $F_{2,50} = 23.709$, $p < 6.895\text{E-}08$, respectively).

DISCUSSION

Balance control is based on extremely reliable neuronal mechanisms that are able to quickly compensate for sudden changes or loss of orientation information from one or even two sensory sources. Such a loss of sensory information is common in everyday life, e.g., for the visual system when closing the eyes or entering a dark room, and for proprioceptive sources of spatial information, in particular during transition from movement on a rigid surface to movement on a compliant surface and vice versa. Untimely and inadequate readjustment of the balance control mechanism makes a person vulnerable to falls and injuries in unexpectedly changing environments [7, 26]. Nashner and Berthoz [27], apparently, were among the first researchers to suggest that the contribution of individual sensory systems may change in response to changes in the available sensory information. Subsequently, the possibility of changing the contributions of individual sensory sources (so-called "sensory reweighting") was confirmed by quantitative indicators when the effect of the support surface tilt [6], galvanic vestibular stimulation [28], and/or changes in the visible visual environment [28, 29] on the vertical posture was studied.

This study is a continuation of our earlier work [19], in which it was found how the size of the visible object (sphere), which provides visual feedback, influences vertical posture control during standing on a conventional rigid support.

In this study, we investigated the effect of changes in the size of a three-dimensional object (sphere), which provides visual feedback in a virtual visual environment, on the amplitude and frequency characteristics of body oscillations after the transition of vertical posture control from a rigid to a compliant support. *The main task in this case was to find out whether the relative "contributions" of visual and proprioceptive information flows to body balance control would change after the transition from maintaining a posture on a rigid support to standing on a compliant support.* We estimated the amplitude-frequency characteristics of two elementary variables calculated from the trajectories of the sole center of pressure (CoP) in the anteroposterior and lateral directions: the projection trajectories of the CoP (variable CoG) of the body and the difference between the CoP and CoG trajectories (variable CoP–CoG). During the analysis of the testing results, CoG displacement was considered as a controlled variable, and the CoG-CoG difference was considered as a variable associated with body acceleration and reflecting changes in the resulting muscle and joint stiffness in the ankles [30, 31]. It should be noted that under control the sphere was motionless, while under test conditions the sphere, on the contrary, was mobile due to its being coupled with oscillations of the CoG of the body.

Analysis of body oscillations in the anteroposterior and lateral directions (Figs. 1, 3) showed that the RMS values of the amplitude spectra of the CoG variable when standing on RS under most visual conditions depended on the size of the sphere. In the IVE condition, with an increase in the size of the presented sphere, the RMS value either significantly decreased (Fig. 1, anteroposterior direction) or only tended to decrease (Fig. 3, lateral direction). Under the AP and IP conditions, the RMS of the amplitude spectra of the CoG variable, on the contrary, increased in both planes.

After transition to postural control in standing position on CS, the RMS of the amplitude spectra of the CoG variable increased approximately 1.5-fold in the IVE condition and twofold in the AP and IP conditions. Note that the degree of dependence on the size of the sphere in a stationary and mobile visual environment also changed. In particular, under the IVE conditions in standing posture on CS, the RMS value of the amplitude spectra decreased with an increase in the size of the sphere approximately to the same extent as under the RS conditions. However, under the AP and IP conditions, the dependence of changes in the RMS of the CoG spectra on the size of the sphere under CS conditions increased by far more, which is clearly seen in Figs. 1 and 3 and confirmed by the results of analysis of variance. To summarize, we can say that the relative "contribution" of visual and proprioceptive information flows to control of body CoG oscillations after the transition from standing on RS to standing on CS increased significantly, but only under the conditions of antiphase and in-phase coupling of the sphere with body oscillations.

It can be seen from Fig. 1 (anteroposterior body vibrations) that the RMS values of the amplitude spectra of the CoP–CoG variable during standing on RS changed moderately and nonsignificantly in response to an increase in the size of the sphere presented to the subjects under all visual conditions. During posture control in quiet standing on CS, the RMS of the spectra of the CoP–CoG variable in absolute values increased moderately and statistically significantly: 1.5-fold for the IVE condition and twofold for AP and IP. Statistical analysis showed that the nature of these changes substantially depended on the size of the sphere: under the IVE condition, the RMS values of the spectra significantly decreased with an increase in size, and under the AP and IP conditions they increased. In the study of lateral vibrations of the body (Fig. 3), the influence of the "sphere size" factor on the RMS of the amplitude spectra of the CoP–CoG variable during standing on RS was also insignificant. During vertical posture control on CS, the absolute values increased approximately in the same way as under the conditions of oscillations in the anteroposterior direction; however, the influence of the "sphere size" factor was statistically significant under the AP and IP conditions only. During posture control under the IVE conditions, no dependence of the RMS of the CoP–CoG spectra on the size of the sphere was revealed. Thus, the results of the analysis of changes in the RMS spectra of the CoP–CoG variable show that the relative "contribution" of visual and proprioceptive information flows to postural control by influencing muscle stiffness after the transition of standing from RS to CS significantly increased under the AP and IP conditions in both planes and in the IVE condition during balance control in the anteroposterior plane.

The relative contribution of the “size of the visible object (sphere)” factor to *the frequency characteristics* of oscillations in the *anteroposterior direction* was different under the same visual conditions during standing on RS and CS (Fig. 2). Thus, when standing on RS in the IVE condition, a statistically significant increase in the MF of the CoG spectra was observed in response to an increase in the size of the sphere, whereas during standing on CS in the same visual condition, on the contrary, MF was shown to decrease. In two other visual conditions (AP and IP), a decrease in the MF spectra of the CoG variable was revealed when standing on RS with an increase in the size of the sphere. In particular, the pairwise comparison of frequencies showed the presence of differences in the AP and IP conditions when the spectral frequencies were compared separately for the sphere sizes 70 and 35 cm and for the sizes 70 and 8.75 cm. At the same time, during posture control in quiet position on CS in the AP and IP conditions, no significant changes in the median frequency of this variable were observed.

The influence of the “size of the visible object (sphere)” factor on the MF of the CoG spectra calculated under different supports conditions (RS and CS) based on body oscillations *in the lateral plane* (Fig. 4) was not always close under the same visual conditions with different supports either. During posture control in quiet standing on RS in the IVE condition, a statistically significant increase in the MF of the CoG spectra was observed in response to an increase in the size of the sphere. Although analysis of variance revealed significant changes in MFs upon standing on CS in the same visual condition, they were associated with diametrically opposite changes in the MF of the CoG spectra with medium and large sphere sizes: at a sphere size of 35 cm, the MFs of the CoG spectra decreased relative to frequencies at a sphere size of 8.5 cm, and at a large size (70 cm), on the contrary, increased and were significantly higher than at a sphere size of 35 cm. Significant differences were also revealed in maintaining the posture on RS and CS under conditions of antiphase and in-phase oscillations of the sphere and the human body: on the one hand, in a standing posture on RS, a significant decrease in the MF of the CoG spectra was revealed in response to an increase in the size of the sphere, and, on the other hand, no significant changes in the MF of the spectra of CoG were found under CS conditions. As for the CoP–CoG variable, there was no significant similarity of changes in the MF of the spectra in response to a change in the size of the observed object upon standing on different supports. The analysis of changes in the spectra of this variable revealed its statistically significant contribution only when posture was maintained under the CS conditions. The severity of these changes revealed from the vibrations of the body in the anteroposterior and lateral directions was approximately the same.

Studies in which immersion in a virtual visual environment was combined with a change in the support characteristics are of great interest. Here we should note the contribution of the recently deceased outstanding Russian physiologist Kozlovskaya, who actually discovered a new sensory system, the support afferentation system, which affects motor functions both directly and indirectly through the integrative multisensory structures of the central nervous system. She showed that by disrupting the activity of the main proprioceptive systems, primarily the vestibular and support systems, weightlessness creates conditions for transformations in motor control systems expressed in the reorientation of motion control systems to more reliable sensory sources in new conditions, in changes in tactics and coordination structure of movements, as well as in changes in the nature of motor synergies [32–36]. In our experiments, changes in the support characteristics significantly influenced the stability indicators in the virtual visual environment, and these changes were not only qualitative, but also quantitative in nature.

CONCLUSIONS

Changes in the support characteristics have a significant effect on the stability of standing in a virtual visual environment. A more significant destabilization of a vertical posture was observed on CS. The deterioration of the quality of standing in the CS conditions occurred not only due to the increase in amplitudes, but also due to changes in the frequency characteristics of the variables, more significant than during standing on RS. Just as in standing on RS, an increase in the size of a stationary sphere led to a decrease in the amplitude of body oscillations, an increase in the size of a mobile sphere led to its increase. On CS, the frequency of CoG oscillations in an immobile visual environment decreased rather than increased with an increase in the size of the sphere. With a movable sphere and CS, it virtually did not change; with RS, it decreased. On the other hand, on CS, the oscillation frequency of the CoP–CoG variable with a immobile environment clearly increased with an increase in the sphere and decreased in a moving environment; on RS, the changes in this variable were marked, but slightly. Thus, the dependence of the amplitude and frequency characteristics of body oscillations on the visual conditions during standing on RS and CS was different. It is suggested that these differences may be linked to a change in the relative contributions of visual and proprioceptive sources of information to balance control on CS.

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COMPLIANCE WITH ETHICAL STANDARDS

All procedures performed in studies involving human participants were in accordance with the biomedical ethics principles formulated in the 1964 Helsinki Declaration and its later amendments and approved by the local bioethical committee of the Kharkevich Institute for Information Transmission Problems, Russian Academy of Sciences (Moscow).

INFORMED CONSENT

Each study participant provided a voluntary written informed consent signed by him after explaining to him the potential risks and benefits, as well as the nature of the upcoming study.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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