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Role of support afferentation in control of the tonic muscle activity

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Abstract

The paper summarizes the results of experimental studies advocating for the leading role of support afferentation in control of the functional organization of the tonic muscle system. It is shown that transition to supportless conditions is followed by a significant decline of transverse stiffness and maximal voluntary force of postural (extensor) muscles limiting their participation in locomotion and increasing involvement of phasic muscles. Mechanical stimulation of the support zones of the soles under the supportless conditions eliminates all the above-mentioned effects, including changes in transverse stiffness and maximal voluntary forces of postural muscles, and consequent loss of influence of postural muscles in the locomotor activity. It is suggested that support afferentation, facilitating (support is present) or suppressing (support is absent) the tonic motor units (MUs) activities, defines the coordination patterns of postural synergies, and ensures the optimal strategy of corrective postural responses.

Keywords: Hypogravity; Support afferentation; Tonic muscle system; Muscle stiffness; Muscle force; Electromyography; Posture; Locomotions

1. Introduction

The results of studies performed in space flights (SF), in simulation investigations and animal experiments showed that removal of gravitational loading disturbs all mechanisms and structures of the motor system, giving rise to such developments as the "hypogravitational ataxia syndrome" and "hypogravitational muscle detraining syndrome" [1,2]. Analysis of nature of these alterations reveals the leading role of supportlessness in these syndromes. It was suggested that withdrawal of support in space and simulated weightlessness and ensuing decline of support afferentation can be a factor that suppresses the tonic muscle activity under the microgravity conditions; therefore, support afferentation can be a trigger for activation of the tonic muscle system [3,4].

This hypothesis was tested in a series of simulation studies directed to revealing the effects of hypogravity on different mechanisms and structures of the motor system. Results of these studies show that development of the flexor posture, i.e. prevalence of the flexor activity over the extensor one, is a consistent effect of transition to microgravity. Acquisition of flexor posture after support withdrawal was described by Russian and Italian authors who studied biomechanics of human locomotion under the conditions of moon gravity, which makes $\frac{1}{6}$ of the Earth's gravity [5,6].

Similar results were obtained later in experiments with primates [8] and also with human subjects, in

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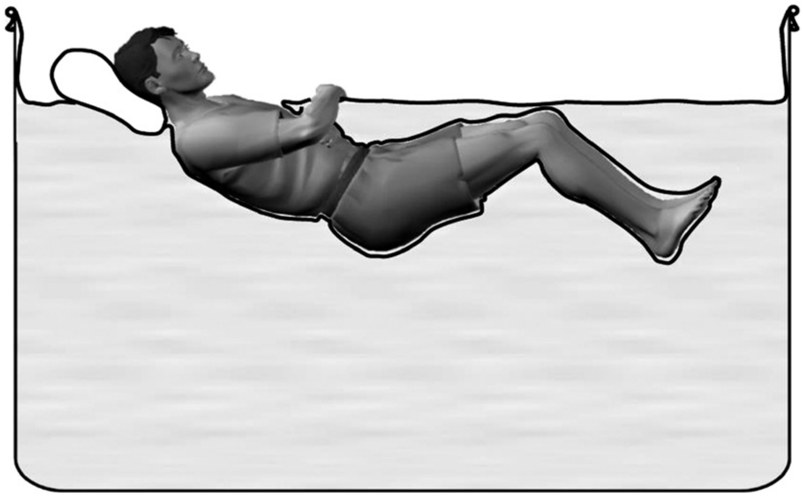

Fig. 1. Scheme of the dry immersion procedure. The picture shows a side view of the subject immersed in the water. The subject is in a supine horizontal position. The body is surrounded by the waterproof fabric.

which the flexor and extensor stiffness was measured in the experiments differing by the degree of support unloading, mainly: (1) immersion eliminating support completely; (2) bed rest when support loading still exists but is redistributed significantly falling mostly onto the large areas of the body unrelated to the vertical posture; (3) combination of 12 h of immersion and 12 h of bed rest every day of experiment [7] in each of the experimental groups support deprivation caused a dramatic impairment of postural muscles (extensors) stiffness. However, the depth of changes and speed of their development in the groups were far from uniform but correlated closely with a degree of support unloading, i.e. they were the largest in immersion, the lowest during bed rest and moderate in the group, in which these conditions alternated.

The reflex nature of atonia initiated by decrease of gravitational loading was revealed in studies on the precedence of recruitment of motor units (MUs) during performance of the task with maintenance of a small force (10–12% of the maximal voluntary force). Results of these studies showed that in immersion the mean duration of spike intervals (ISIs) increases pointing to the involvement of different, larger and stronger, units in task performance. Based on these results, the authors suggested that support unloading causes alteration in the order of MUs recruitment, suppressing the activity of small "tonic" units and enhancing the activity of the large "phasic" ones [9].

To test this hypothesis, a series of experiments with mechanical stimulation of the support zones of the soles was performed under the conditions of dry immersion (DI). In DI, proposed by E.B. Shulzenko and I.F. Vil-Villiams in 1973 [10], subject is isolated from water with a waterproof fabric so that the exposure can last for days and be of minimal discomfort (Fig. 1).

2. Material and methods

The studies were performed with participation of 18 volunteers (men) aged 22–30 who gave the written consent to the experiment and procedures. The experimental protocol was reviewed and approved by the RF SSC-IBMP Bioethics Board. All subjects were exposed to 7-h or 7 days DI twice. In the first series served as the control, immersion was not accompanied by support stimulation. In the other, mechanical stimulation of the soles support areas, i.e. the heel and the forefoot (Fig. 2A), in the regime of walking—10 min of slow pacing (75 steps/min) and 10 min of fast one (120 steps/min) with pressure of $0.5 \pm 0.1\,\text{kg/cm}^2$—was applied daily during 6 h for 20 min of every hour.

Resting EMG and transverse stiffness of *m. soleus* and *m. tibialis anterior*, the contractile properties of the leg and thigh muscles, EMG of *mm. soleus*, *gastrocnemius* and *tibialis anterior* during locomotion and kinematic characteristics of postural corrective responses were recorded before, during (except posture and locomotion) and after immersion.

Following the DI procedure, subject was placed afloat in a tub measuring 2.0 × 1.0 × 1.0 m. The tub filled with water that was kept at a constant temperature of

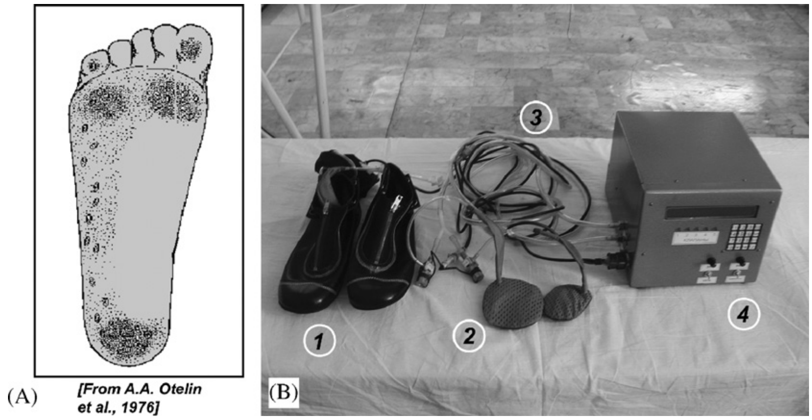

Fig. 2. Location of Fater–Paccinie' bodies in the human foot sole—A. The Paccinian corpusles are predominantly located in the support areas. B—Compensator of Support Unloading (CSU) consisting of footwear (1), compressed-air insoles (2), air tubes (3), compressor and control unit (4).

$33 \pm 0.5\,°C$. The subject was isolated from water by a free floating waterproof fabric and dressed in a comfortable training suit. By this means the subject was floating in water in the prone horizontal position for 7 h or 7 days.

Transverse stiffness of *mm. soleus* and *tibialis anterior* was determined with the help of resonance vibrography widely used for the assessment of visco-elastic properties of biological tissues [22]. According to this method, stiffness is assessed by the results of processing the data of acceleration (A) of the flat vibrating stamp pushed against the tested muscle and muscle resistance to deformation. Shear elasticity (E, in kPa) was registered in parallel with the other measurements. All recordings were performed in the supine and prone positions of subjects with the lower extremities relaxed as much as possible. Physiological feedback procedures were contingent on EMG recording of the tested muscle and consisted in visual or acoustic request to the patient—to keep the level of EMG activity low.

The force–velocity characteristics of the ankle extensors and flexors were assessed using the data of concentric isokinetic dynamometry at the speed of movements from $30°/s$ to $180°/s$. Three maximal movements were performed at each speed and the best measure was taken.

Locomotor tests consisting of quiet walking at 90 steps/min on a rigid and soft surface before and after 7-day immersion. The rate of locomotion was set by metronome. EMG of the shin muscles, i.e. *mm. gastrocnemius, soleus and tibialis anterior* was recorded in each of five sessions of registration bipolarly using silver-chloride electrodes of 10 mm in diameter spaced 20 mm apart. The obtained records were digitized, straightened, integrated with the steps of 25 ms, and smoothed. Maximal amplitudes and durations of the EMG bursts as well as the ratios of EMG amplitudes of the synergists and the antagonists during the locomotor movements were analyzed.

Postural testing was performed in the group without stimulation and only before and after 6 h of DI. During testing, the barefooted subject stood still on the dynamometric platform with the feet symmetrical relative to the center of the platform, and the toes turned slightly outward, eyes closed, and arms folded across the chest. A suspension system (harness) was used to protect the subject from a fall. Prior to testing, the subject was instructed to "stand quietly, not to anticipate perturbations, but to maintain equilibrium".

The tests were performed using a posturography system consisting of a dynamometric platform with three force sensors, a calibrated tensometric stick device that incorporated a force transducer to perform systematic pushes at the chest, and a video system. The video system was composed of a video camera and analyzer that included a video recorder, TV monitor, computer, and video frame digitizer. Only movements in the sagittal plane were recorded. Reflective markers (10 mm in diameter) were attached to the subject's foot in the area of the left *processus zygomaticus*, *acromion*, *trochanter major*, *epicondylus lateralis*, *malleolus lateralis*, *phalanx distalis* V and the posterior part of *calcaneus*. Stabilometric parameters and tensometer signals were sampled at 100 Hz, while video information was sampled at 25 Hz.

Pushes of various intensities (from threshold to maximum), driving the body backward around the ankles, were targeted at a plastic plate (10×15 cm) that was affixed to the chest. The calibrated pushes were delivered randomly at the intervals no shorter than 10 s. During each test session 10 to 15 pushes were given. The response to each push was recorded for 5 s.

Data analysis included examination of the following characteristics: center of pressure (COP) deviation in the sagittal plane (sagittal stabilogram), sagittal displacement of the body markers corresponding to endpoints of the major segments of the body, and changes of ankle, knee, and hip joints angles, as well as of the neck angle. Mean ± SD was calculated. A one-way repeated ANOVA measure was used to identify any changes before, during and after DI. Statistical significance was set at $p < 0.05$.

Mechanical stimulation in the regime of walking was performed using the Compensator of Support Unloading (CSU) developed by “Zvezda” Co in Moscow, Russia (Fig. 2B).

3. Results

3.1. Electromyographic activity and transverse stiffness

The EMG peak amplitude of *m. soleus* (8.81 ± 1.43 mkV) at rest was lower than that of *m. tibialis anterior* (11.46 ± 2.66 mkV). Under conditions of microgravity the trend *was* even more pronounced, since the *m. soleus* amplitude in DI gradually decreased to about 59%, whereas the *m. tibialis anterior* amplitude increased sharply during the very first hours of DI (Fig. 3). In the series with mechanical stimulation of the soles support zones the amplitude of *m. soleus* increased by 15% at the beginning and declined below control value at later stages. *M. tibialis anterior* amplitude increased significantly in the control group and did not change significantly in the experimental group (Fig. 4).

Transverse stiffness of *m. soleus* at rest was also lower as compared with *m. tibialis anterior*, i.e. 8.76 ± 3.79 kPa *m. soleus* vs. 10.3 ± 5.3 in *m. tibialis anterior*. During the initial 24 h in DI stiffness of *m. soleus* dropped sharply to 29% of baseline level and then stabilized (Fig. 4A). Stiffness of *m. tibialis anterior,* on the opposite, showed an upward trend during the first 24 h of immersion and later decreased slowly (Fig. 4B). Stimulation of the support zones reduced considerably the inhibitory effect of DI on the *m. soleus* activity: in this series of experiment the statistically significant inhibition was recorded only on the sixth day of immersion (Fig. 4A). Stimulation of the foot support zones suppressed also the initial increase of *m. tibialis anterior* stiffness at rest, further on muscle stiffness decreased gradually (Fig. 4B).

3.2. Contractile properties

Exposure to 7-day DI caused a significant decline of the force–velocity properties of leg muscles. During isokinetic testing the torque of *m. triceps surae* were lowered within the whole range of velocities (Fig. 5B). In the experimental group this effect was suppressed greatly. After 7 days in DI with stimulation the force–velocity curve did not differ significantly from the pre-DI one. Torque of the flexor muscle forces was also lowered by DI. This decline was the most prominent within the high velocity range (up to 20%)

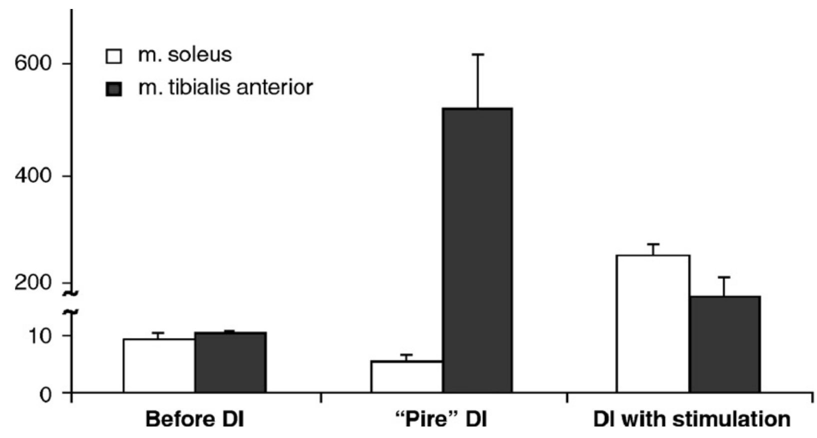

Fig. 3. EMG’ amplitudes of *m. soleus* (blank bars) and *m. tibialis anterior* (shadowed bars) before and after 7-h dry immersion in the control studies and DI with the stimulation of soles support zones. Ordinate shows EMG amplitude in mkv.

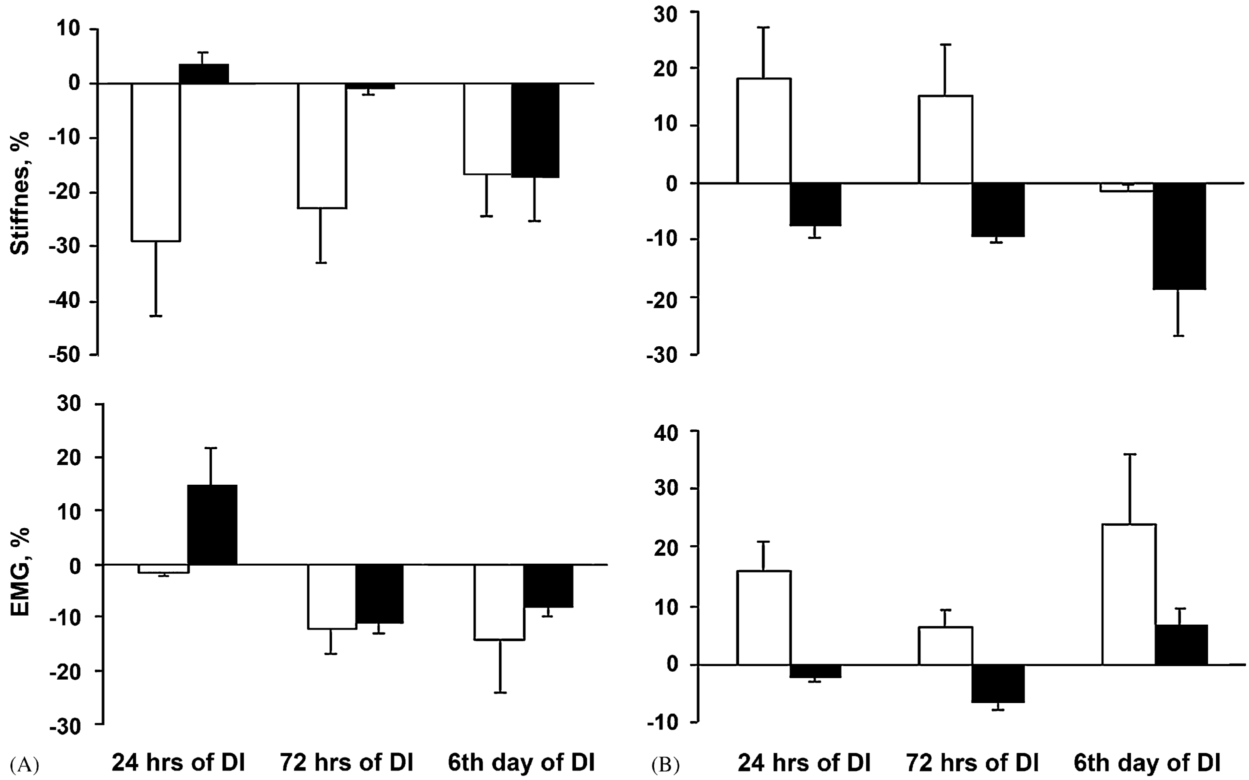

Fig. 4. Alteration of transverse stiffness (above) and amplitudes of EMG (below) of *m. soleus* (A) and *m. tibialis anterior* (B) after 6 days of dry immersion in control series (blank bars) and DI with the stimulation of soles support zones (shadowed bars). The ordinate shows the percentage of changes.

and the lowest (6–9%) within the low velocity range. Force values in the experimental group were changed slightly less reaching 13% only during the high velocity movements (180°/s) (Fig. 5B).

3.3. Electromyographic pattern of locomotions

After DI EMG amplitudes of both leg extensors increased significantly in the control series (Fig. 6). However, the amplitude of *m. gastrocnemius* grew considerably larger comparing with *m. soleus*. As a result, the ratio of *m. soleus* and *m. gastrocnemius* activities after immersion decreased. Application of mechanical soles stimulation during DI raised the *m. soleus* amplitudes higher than of *m. gastrocnemius*; correspondingly, the ratio of *mm. soleus/gastrocnemius* activities moved to the other direction. These data allowed the conclusion that participation of *m. soleus* in locomotor movements after exposure to "pure" DI become less active but this effect can be fully compensated by stimulation of the support zones.

The amplitude of EMG bursts in *m. tibialis anterior* after DI increased significantly reaching 1.4 mV (vs. 1.1 mV before DI). In the group with mechanical soles stimulation during DI the amplitude increase was negligible if any.

3.4. Vertical posture

In the control study (prior to immersion), intensity of the threshold, medium and submaximal stimuli were measured at 2.21±0.69, 5.65±1.02, and 8.65±1.29 kg, respectively. Deflections of the COP amplitudes at these push magnitudes were 38.83±16.11, 75.19±16.99, and 92.18 ± 12.72 mm, respectively (Fig. 7). The COP deviation amplitude was clearly dependent on the force of pushes. This dependence was close to linear considering that correlation coefficient (r) was 0.87 ($p < 0.05$).

The threshold push stimuli caused a reduction in the neck angle with a corresponding hip extension. The knee, as well as the ankle joints were flexed. The medium stimuli were followed by an increase of the

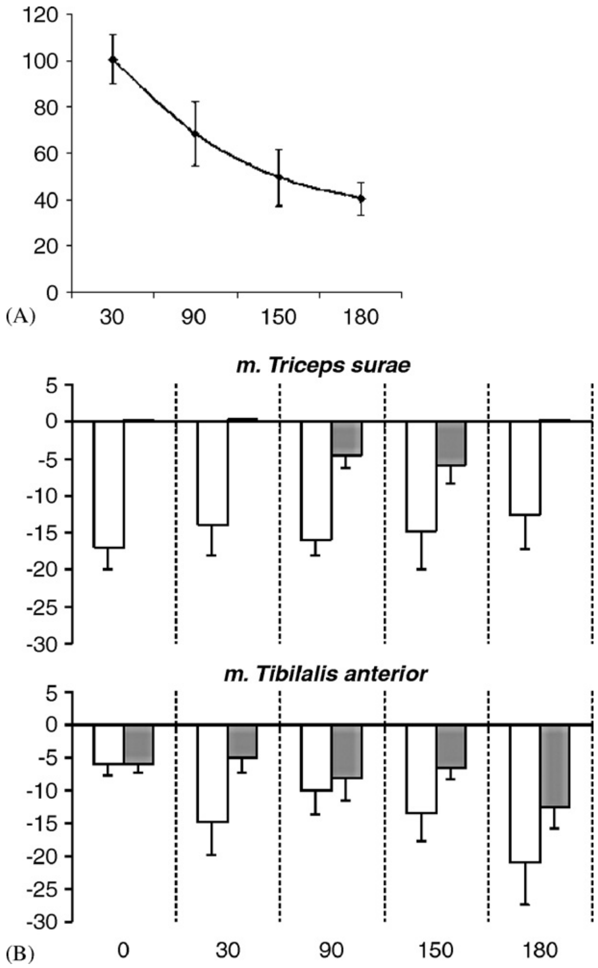

Fig. 5. A—Example of force–velocities curve. B—Alterations of leg muscles moments of force after exposure to dry immersion. Data obtained in the control series ("pure" DI) are shown by the blank bars, data of DI with the stimulation—by the shadowed bars. On the abscissas are shown the velocities of movements in deg/s; on the ordinates—the torques in N (A) and the values of changes in percent (B).

amplitudes of joints angular displacement in the same directions as mentioned above. When the submaximal stimuli were applied, the largest angular displacements in the joints were recorded (Table 1). Amplitude of the angular joints displacements highly correlated with the push intensities: correlation coefficients were equal to 0.73, 0.48, 0.68, and 0.60 ($p < 0.05$) in the neck angle, the hip, knee and ankle joints, respectively (Fig. 8).

Analysis of the stimuli intensities and stabilographic parameters of the corrective posture responses after 6 h in DI did not reveal any significant changes relative to control values. The dependence of the COP deviation amplitude on stimulus intensity was weakened, and the correlation coefficient declined was in the range of 0.64 ($p < 0.05$) (Fig. 8).

At the same time, changes in the magnitude of the joints angular displacements were prominent. The threshold stimulation increased the neck amplitude ($p < 0.05$); the hip, knee and ankle joints angles were slightly higher as compared with pre-DI testing ($p > 0.05$). As in the control study, increase of the push intensities to medium values was followed by the expected rise in angular displacements in the measured joints. However, amplitudes of the neck deflection were somewhat below control values ($p > 0.05$); the hip angle amplitude was slightly increased ($p > 0.05$), while those of the knee and ankle were significantly greater when compared with control values ($p < 0.05$). The most conspicuous differences in the magnitude of angular displacement were revealed when the submaximal pushes were used. Again, the neck deflection amplitude was below pre-DI values ($p > 0.05$); amplitude of the hip angular displacement was even lower than when the medium push amplitudes were used (amplitude values were less than half of those in the pre-DI investigations ($p < 0.05$). Amplitudes of the knee and ankle angular displacements were of the size similar to those after the medium intensity pushes ($p < 0.05$), that is much lower than before DI (Table 1). By and large, dependence of the amplitudes of angular displacements on push intensities was somewhat altered: the correlation coefficients for the neck angle slightly decreased (0.58($p < 0.05$)), and for the knee and ankle joints increased reaching 0.57 and 0.52 ($p < 0.05$), respectively. For the hip joint, this dependence was lost completely and the correlation coefficient dropped to 0.12 ($p > 0.05$) (Fig. 8).

4. Discussion and conclusions

The results of study show that support withdrawal leads to the development of significant changes in all parts of the tonic motor system. In full agreement with the earlier experimental data, transition to hypogravity was consistently followed by the significant decline of the force–velocities properties and electromyographic activity of all the extensors under study [7,11,12,23] and the increase of flexor muscles activity [13]. Suppression of the extensors activities in DI was immediate and persistent through the whole time of exposure independent of its duration (7 h or 7 days). Recovery of the activity was observed only in case of DI interruption or mechanical stimulation of soles support zones.

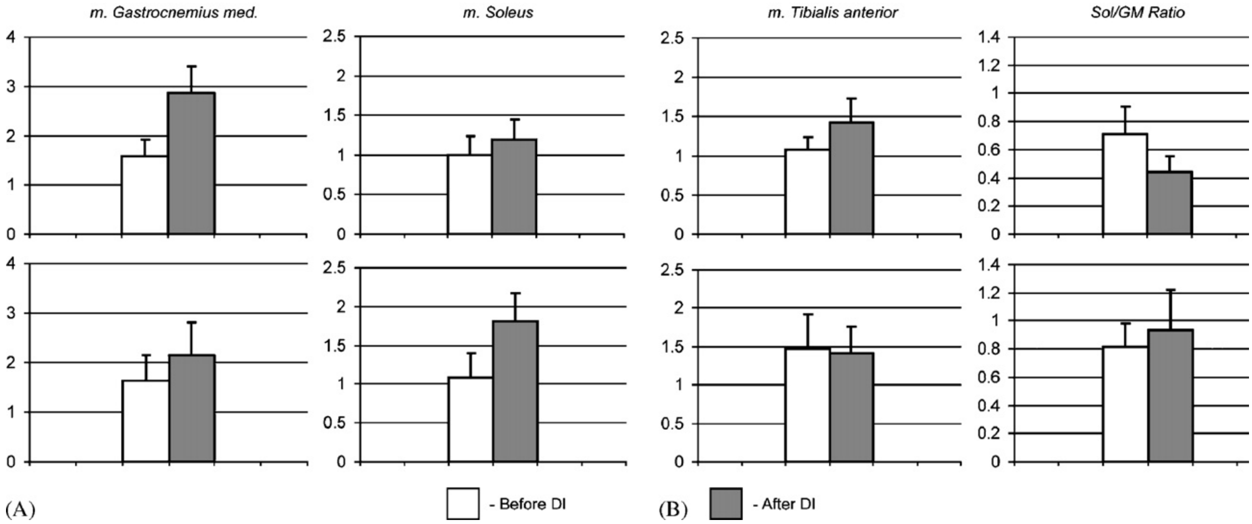

Fig. 6. Alterations of the amplitudes of EMG locomotor bursts of leg extensor and flexor muscles (shown in A), and the ratio of activities of *m. soleus* (Sol) and *m. gastrocnemius* (GM) (shown in B) before and after exposures to dry immersion (DI). The pre-DI data are shown by the blank bars. The post-immersion—by the shadowed bars. The data obtained in control series ("pure" DI) are presented in the upper row, the data of DI with the stimulation—in the lower one. On the ordinates—the amplitude in mv.

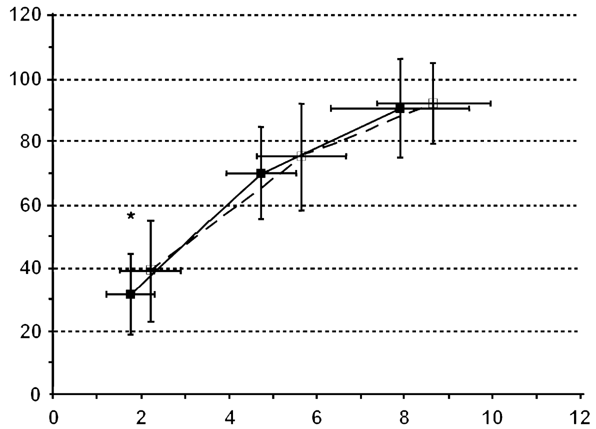

Fig. 7. Changes of the amplitude of COP deviations evoked by the threshold, medium and submaximal pushes to the chest before and following 6-h dry immersion (DI). Abscissa shows the stimulus intensity in kg; ordinate—the COP deviation amplitude in mm. Dotted line (empty circles) presents the data obtained before DI, the solid line (shadowed squares)—the data collected after 6-h DI. *—Statistical significance ($p < 0.05$) compared with the control data.

Table 1
The peak amplitudes of angular displacements in the joints before (Control) and after 6-h dry immersion (DI) (Explanation is in the text)

	Peak angular displacement, degree	
	Control	After 6-h DI
Neck		
Threshold	3.80 ± 2.11	6.51 ± 2.78
Medium	15.47 ± 6.25	13.97 ± 4.38
Submaximal	16.73 ± 2.99	15.12 ± 3.32
Hip		
Threshold	3.76 ± 1.07	4.38 ± 1.93
Medium	5.45 ± 2.71	6.57 ± 2.22
Submaximal	10.24 ± 4.07	6.62 ± 2.91
Knee		
Threshold	−3.42 ± 1.86	−5.33 ± 2.43
Medium	−7.84 ± 2.43	−12.03 ± 3.97
Submaximal	−12.21 ± 5.36	−13.36 ± 3.92
Ankle		
Threshold	−4.89 ± 0.89	−5.87 ± 2.09
Medium	−7.01 ± 1.41	−10.27 ± 2.54
Submaximal	−13.08 ± 3.50	−10.60 ± 2.03

Negative values mean flexion in joints.

It is important to emphasize that response to the mechanical stimulation of the support zones of the soles carried all features of systemic reactions. Stimulation of the fore foot provoked appreciable ankle contractions and sometimes even of the knee extensors. On the opposite, stimulation of the fore feet was followed by flexors contraction [13,14]. The analogous pattern of changes of the extensor-flexor couple EMG activity due to the gravitational unloading has been observed also in experiments in parabolic flights [15–17] and during vertical immersion with a gradual rise of water level to reduce the support loading [18]. In the latter case the gradual

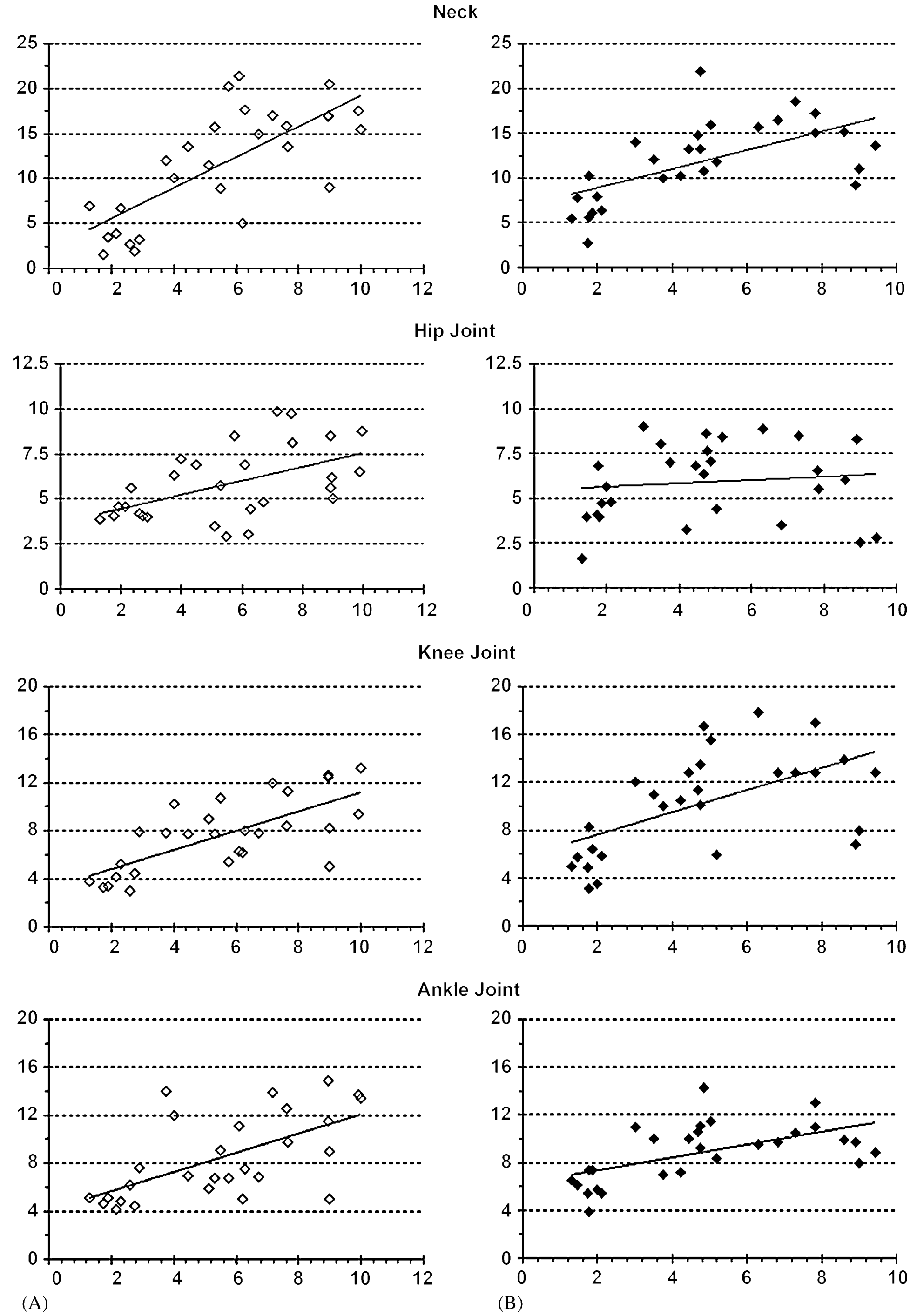

Fig. 8. Dependence of angular displacements in the joints on the stimuli intensities: A—the control study; B—the same following 6-h dry immersion (DI). Abscissa shows the stimuli intensity in kg; ordinate—the peak angular displacement in joints, with respect to the initial positions in degrees. Empty squares present the data obtained before DI and shadowed squares—the same after the 6-h DI.

character of muscles reactions to supportlessness and their strict dependence on the degree of support unloading was demonstrated clearly.

Along with the decline of the extensors muscles activity, the other consistent consequences of support withdrawal are as follows in the order of appearance:

a decline of maximal extensors force, alteration in the activity of spinal and supraspinal motor control mechanisms, slowed down by deep disturbances of the vertical posture, locomotions and voluntary movements. Timeline of these changes in the subjects varied but not the order of appearance. The timeline of recovery of the disturbed functions after completion of exposure to microgravity repeated to an extent that at the beginning of the exposure.

This study is particularly interesting and important as it demonstrated the method for full abolishment of all the effects of support unloading, as functional so also structural [4], by mechanical stimulation of the soles support zones. The fact supports directly the hypothesis about the leading role of support afferentation in control of the tonic muscle system offered at the beginning of this paper.

Results of this study together with the previous data on MUs and muscles groups allow to conclude that the primary response to withdrawal of support loading is suppression of the postural muscles (extensors) activity [19,20]. The other effects of support unloading, like the enhancement of flexor mechanisms revealing itself by the increased flexor muscles electromyographic activity at rest and during maintenance of the vertical posture as well as the higher amplitude of the *m. tibialis anterior* myographic response to support stimulation, the decline of force–velocity properties of extensors along with the alterations of associated mechanisms [12,21], and changed pattern of coordinated muscle recruitment [19], appear to be secondary as they are dependent on the mechanisms of central coupling (enhancement of the flexor activity) or learning (coordination reorganization).

References

[1] I.B. Kozlovskaya, I.F. Aslanova, V.L. Barmin, L.S. Grigorieva, The nature and characteristics of gravitational ataxia, Physiologist 26 (6, Suppl.) (1983) 108–109.

[2] I.B. Kozlovskaya, I.F. Aslanova, V.B. Barmin, L.S. Grigorieva, Gravitational mechanisms in the motor system, Studies in real and simulated weightlessness, in: V.S. Gurfinkel, M.Ye. Ioffe, J. Massion (Eds.), Stance and Motion, Plenum, New York, 1988, pp. 37–48.

[3] O.G. Gazenko, A.I. Grigoriev, I.B. Kozlovskaya, Mechanisms of acute and chronic effects of microgravity, Physiologist 29 (1986) S48–S50.

[4] A.I. Grigoriev, I.B. Kozlovskaya, B.S. Shenkman, The role of support afferents in organization of the tonic muscle system, Russian Journal of Physiology 90 (5) (2004) 37–43.

[5] V.A. Bogdanov, V.S. Gurfinkel, V.E. Panfilov, Human movements under conditions of moon gravity, Space Biology and Medicine 2 (3) (1971) 3–13 (in Russian).

[6] F. Margaria, G.A. Cavagna, Aerospace Medicine 35 (1964) 10–11.

[7] I.B. Kozlovskaya, L.S. Grigorieva, G.I. Gevlich, The comparative analysis of the effects of real and simulated weightlessness on strength-velocity characteristics and tone of human skeletal muscles, Space Biology and Medicine 18 (6) (1984) 22–26 (in Russian).

[8] G.S. Belkania, A.N. Razumeev, B.A. Lapin, Alterations of physiological functions in primates on the low gravity stand, Space Biology and Medicine 8 (5) (1974) 17–27 (in Russian).

[9] A.V. Kirenskaya, I.B. Kozlovskaya, L.I. Sirota, Effects of immersion hypokinesia on characteristics of rhythmic activity of *m. soleus* motor units, Physiology of Man 12 (1) (1986) 617–632 (in Russian).

[10] Ye.B. Shulzenko, I.F. Vil-Vilyams, Simulation of body detraining by method of “dry” immersion, in: 10th K.E. Tsiolkovsky Readings: Problems of Space Medicine Section, 1975, pp. 39–47 (in Russian).

[11] Yu.A. Korijak, I.B. Kozlovskaya, Influences of antiorthostatic bed rest on functional properties of the neuromuscular system in man, Physiologist 34 (1) (1991) 107–109.

[12] Y.A. Koryak, Electromyographic study of the contractile and electrical properties of human triceps surae muscle in a simulated microgravity environment, Journal of Physiology (London) 510 (1) (1998) 287–295.

[13] T.F. Miller, I. V Saenko, D.V. Popov, O.L. Vinogradova, I.B. Kozlovskaya, Effect of mechanical stimulation of the support zones of soles on the muscle stiffness in 7-day dry immersion, Journal of Gravitational Physiology 10 (1) (2003) 61–62.

[14] D.V. Popov, I.V. Saenko, O.L. Vinogradova, I.B. Kozlovskaya, Mechanical stimulation of foot support zones for preventing unfavorable effects of gravitational unloading, Journal of Gravitational Physiology 10 (1) (2003) 59–60.

[15] E.M. Yuganov, I.I. Kasian, B.F. Asyamolov, On some human reactions under conditions of decreased weight, Problems of Space Biology 2 (1962) 206–214.

[16] F. Kawano, T. Nomura, A. Ishihara, I. Nonaka, Y. Ohira, Afferent input—associated reduction of muscle activity in microgravity environment, Neuroscience 114 (4) (2002) 1133–1138.

[17] D. Leterme, M. Falempin, EMG activity of three rat hindlimb muscles during microgravity and hypergravity phase of parabolic flight, Aviat Space Environmental Medicine Nov 69 (11) (1998) 1065–1070.

[18] Mitarai, T. Mano, H. Mori, J. Jamasaka, Compensatory leg muscle function shift during adaptation to simulated weightlessness, Proceedings of 24 International Congress on Aerospace Medicine, London, vol. 48, 1978, pp. 1086.

[19] R.R. Roy, J.A. Hodgson, J. Aragon, M.K. Day, I.B. Kozlovskaya, V.R. Edgerton, Recruitment of rhesus soleus and medial gastrocnemius before, during and after spaceflight, Journal of Gravitational Phisiology 70 (1991) 222–2529.

[20] M.R. Recktenwald, J.A. Hodgson, R.R. Roy, S.N. Riazanskii, G.E. McCall, I.B. Kozlovskaya, D.A. Washburn, J.W. Fanton, V.R. Edgerton, Effect of spaceflight on rhesus quadrupedal locomotion after return to 1G, Journal of Neurophysiology 81 (5) (1999) 2451–2463.

[21] N. Bachl, R. Baron, M. Mossaheb, W. Bumba, R. Albreht, I. Kozlovskaya, N. Kharitonov, Specific strength diagnostic in long term spaceflight, in: Proceedings of Fifth European Symposium on Life Sciences Research in Space, Arcarshon, France, 1993, pp. 401–404.

[22] E.M. Timanin, On contribution of shear waves into a transverse stiffness of soft biological tissues in vibrating indenter investigations, 13th International Congress of Acoustics, Belgrade, 4, 1989, pp. 215–218.

[23] L.S. Grigorieva, I.B. Kozlovskaya, Effects of 7-days support unloading on force velocities properties of skeletal mussels, Space Biology and Medicine 4 (1983) 21–25 (in Russian).