

Physiological Adaptations to Weightlessness: The Contractile Properties and Fatiguability of the Human Triceps Surae Muscle After Exposure to Simulated Microgravity Environments

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ARTICLE INFO

Received: 📅 August 30, 2024

Published: 📅 September 06, 2024

Citation: Yuri A Koryak. Physiological Adaptations to Weightlessness: The Contractile Properties and Fatiguability of the Human Triceps Surae Muscle After Exposure to Simulated Microgravity Environments. Biomed J Sci & Tech Res 58(3)-2024. BJSTR. MS.ID.009167.

ABSTRACT

Abbreviations: MVC: Maximal Voluntary Contraction; TPT: Time-To-Peak Tension; TCT: Total Contraction Time; SAP: Surface Action Potential; EMG: Electromyography

Introduction

This study examined the effects of short- (1-, and 3-day) and long-term (7-day) 'dry' immersion (DI) on neuromuscular function of human the triceps surae muscle.

1. The isometric twitch tension (P_o) decreased by 8.7% after 1-days but increased by 11.5% and 9.8% after 3- and 7-days DI, respectively. Maximal voluntary contraction (MVC) decreased by 13.6%, 19.7%, 33.8% after 1-, 3-, and 7-days DI, respectively ($P < 0.05-0.01$), electrically evoked (frequency of 150 impulses·s⁻¹) tetanic tension (P_o) reduced by 1.8%, 5.3%, 8.2%, respectively, (nonsignificant). The difference between P_o and MVC expressed as a percentage of P_o and referred to as force deficiency (F_d) was also

calculated. F_d increased by 23.4%, 20.2%, 78.7% after 1-, 3-, and 7-days, respectively ($P < 0.05-0.001$).

2. After DI, the time-to-peak tension (TPT), half-relaxation time (1/2RT), and total contraction time (TCT) was reduced. The TPT decreased by a mean of 8.5%, 3.3% after 1- and 3-days, respectively, and after 7-day did not reveal significant changes in the curve of the TPT. 1/2RT and TCT was shorter in the post-immersion condition than in the control value.

3. The rate of increase of voluntary contraction calculated according to an relative scale had significantly reduced after DI ($P < 0.05-0.001$), but for the electrically evoked contraction (frequency of 150 impulses·s⁻¹) no substantial changes from the initial physiological state.

4. A standard 2-min fatigue of electrically-induced intermittent test (frequency of 50 impulses·s⁻¹) did not differ substantially from the initial physiological state, but the electrical M-waves reduced significantly. The relative extent of the decline in either of these two parameters can be determined from the change in the relation of the electrical M-wave to the contractile response (the E/C ratio).

5. After long-term DI (7 day) of muscle a significantly greater decline of electrical waves is observed as compared to contractile response by a short-term DI (1-, and 3-day), respectively.

The neuromuscular system of humans and/or mammals is continuously exposed to gravity. Unfortunately, there are few data concerning the influence of spaceflight, and therefore, lack or attenuation of these factors on the neuromuscular system. The limited data from spaceflight shows decrease in contractile properties muscle. Elucidation of the mechanism(s) underlying this effect is essential to understanding the role of gravity on the neuromuscular system. This paper will focus on neuromuscular function from Earth-based studies of simulated microgravity in humans. From the onset of manned spaceflight, it has been assumed that neuromuscular function would deteriorate as a result of prolonged periods in space. Numerous observations have supported these initial expectations. It was clear from the earliest short-term flights that neuromuscular function was negatively affected by flight [1-6]. Similar neuromuscular functional tests were performed during long-term spaceflights [7-12]. None of these studies, however, provide any insight as to whether the spaceflight-induced decrements in neuromuscular function were of a neural or a muscular origin. Immersion has been used extensively as a model for studying the effects of eliminating postural activity on human limb muscles. The consequences of microgravity on the contractile properties of skeletal muscles have stimulated much interest in the factors controlling muscle function.

Unfortunately, in man, few comparable investigations have been undertaken regarding the time course of muscle disfunction following disuse. In the previous study [13] we have shown that long-term (a 120-day) voluntary disuse (controlled period of voluntary strict bed rest) of the extensor muscle groups (the triceps surae muscle) or spaceflights (a 118-days) produced a significant increase in the

time-to-peak tension (TPT) of the isometric twitch tension (P_t) and a reduction in maximal voluntary contraction (MVC) and a electrically evoked (frequency of 150 impulses·s⁻¹) tetanic tension (P_o). We postulated that the changes in twitch mechanics may have been due to altered Ca²⁺ release and re-uptake by the sarcoplasmic reticulum, whilst the decrease in MVC relative to the electrically evoked maximal tetanic tension may reflect a reduction in central neural drive resulting from the voluntary inactivity. The purpose of the present investigation was

1. To examine the contractile properties (during twitch, voluntary contraction, and tetanic contractions) and the fatigability slow-twitch skeletal (the triceps surae-TS) muscle from humans exposed to 'dry' immersion (DI) for a period of 1-, 3-, and 7-days, and
2. To determine the specificity of these responses to the muscle.

Methods

The experimental protocol procedures for this study were reviewed and approved by the Russian National Committee on Bioethics of the Russian Academy of Sciences and was in compliance with the principles set forth in the Declaration of Helsinki.

Subjects

Twenty men served as subjects. Age, height, and body mass of all subjects are shown in Table 1. The subjects were assigned at random into three groups and were horizontally put for 1-day (members of group I; n = 8), for 3-days (members of group II; n= 6), and on 7-days (members of group III; n = 6) in a special bath on fabric film. Each subject served as his own control. All subjects volunteered for the study and signed a form giving informed consent. Selection of subjects was based on a screening evaluation that consisted of a detailed medical history, physical examination, complete blood count, urinalysis, resting and cycle ergometer electrocardiogram, and a panel of blood chemistry analysis. All of the subjects were evaluated clinically and considered to be in good physical condition. No subject was taking medication at the time of the study, and all subjects were nonsmokers. After an intensive familiarization period, subjects entered the Human Research Facility of the Health Ministry Institute of Biomedical Problems.

Table 1: Physical characteristics of the subjects [mean (± SEM)].

	Age, years	Height, cm	Body mass, kg		
			Before	After	Δ, %
I groups (1-day; n = 8)	27.9 ± 2.2 (21 - 39)	177.8 ± 2.6 (168 - 189)	69.3 ± 1.7 (64.5 - 77.0)	67.9 ± 2.1 (61.1 - 77.0)	2
II groups (3-day; n = 6)	28.0 ± 3.7 (17 - 40)	172.7 ± 2.5 (168 - 180)	66.3 ± 1.5 (62.0 - 71.0)	64.3 ± 1.3 (60.2 - 68.5)	3
III groups (7-day; n = 6)	22.7 ± 3.5 (18 - 40)	176.3 ± 2.5 (168 - 180)	68.5 ± 2.4 (64.0 - 80.0)	66.6 ± 2.3 (61.5 - 76.8)	3.1

'Dry' Water Immersion

To simulate microgravity the DI model has been used [14]. This model seems to be a useful method for ground based investigations. As it has been shown in previous studies [15,16] a close similarity exists between the effects of short time real microgravity and immersion. However, the dimension of these changes is different. The alterations during and after immersion are more marked than those of equal duration spaceflights. The subject was positioned horizontally in a special bath on fabric film that separated him from the fluid. Water temperature was constant ($\sim 33.4^{\circ}\text{C}$) and maintained automatically at this level throughout the experiment. The duration of the immersion was 1-, 3-, and 7-days. The subjects were kept under medical observation. The functional properties of the neuromuscular system were evaluated twice: before and after it ended. The test protocol was identical for both pre-immersion and post-immersion tests.

Experimental Procedure

The dynamometer, regarding system, and the methods and procedures used to measure the electrically evoked and voluntary isometric contractions of the triceps surae muscle were similar to those described in detail Koryak [17,18]. The subjects were required to sit on a specially designed leg dynamometer with the thigh horizontal and the knee and ankle fixed at the angle set at $85\text{-}90^{\circ}$. Electrical stimulation of the tibial nerve was applied through an active monopolar electrode (1 cm diameter) which was placed in the popliteal fossa and a passive one placed on the lower third of the thigh. Because of the influence of temperature on neuromuscular transmission, the temperature of the muscle was maintained at a constant level. Skin temperature was 35°C , corresponding to an intramuscular temperature of 37°C . Skin temperature was 35°C , maintained by a lamp and a sensor on the skin over the TS muscle. Isometric twitches were elicited with brief rectangular wave pulses (1 ms) at 30-s interval and by progressively increasing voltage until maximal force (P_v) was obtained. The criteria for the determination of P_v as voltage 30%-40% greater than minimal voltage at which a maximal M-wave of the muscle had been obtained for the first time.

The time-to-peak tension (TPT), half-relaxation time ($1/2\text{RT}$), and total contraction time (TCT) of P_v defined as the time elapsed from the moment of stimulation to peak force, the time from peak to half-force, and the time from the moment of stimulation to the total muscle relaxation. Isometric tetanic contraction (P_o) were measured at frequencies of $150\text{ impulses}\cdot\text{s}^{-1}$ [17,18]. After an appropriate period of rest subjects performed a maximal voluntary contraction (MVC) of the triceps surae muscle. During the contractions, the subjects were verbally encouraged and visual feedback was provided. The greatest force of 3 attempts (1 min rest interval) was recorded. The difference between P_o and MVC expressed as a percentage of the P_o value and referred to as force deficiency (F_d) has also been calculated. The subjects were carefully instructed to respond to an auditory signal by exerting maximal force as rapidly as possible. In the force-time curves analysis,

the times taken to increase the force from a level initial to 25%, 50%, 75%, and 90% of the maximum were calculated [17,18]. Similarly, the rate of rise of the evoked contraction, in response to electrical stimulation of the nerve with a frequency of $150\text{ impulses}\cdot\text{s}^{-1}$ [17,18] was measured.

After an appropriate rest the motor nerve stimulated at various intervals. Time course of active state of muscle fibers in skeletal muscle determine methods double stimulation [19]. Two supramaximal stimuli at 330, 250, 200, 100, 50, and 20 Hz were studied [17]. On double stimulation, the maximum amplitude (strength) of the muscle contraction was determined. The maximal strength (amplitude) of the muscle contraction was determined and expressed as a percentage of the twitch contraction. The final measure, a 2 min intermittent test of muscular endurance via electrical stimulation motor nerve was conducted. Fatigue was tested in the TS muscle of intact humans during intermittent contraction. Fatiguability was studied during a standard series of 60 1-s intermittent isometric electrically evoked contractions separated by 1-s intervals for 2 min as has been described by Koryak et al. [20], and Koryak [21]. The stimulation frequency was $50\text{ impulses}\cdot\text{s}^{-1}$ (rectangular pulses of 1 ms duration) during the fatigue tests, because it has been found that this is within the physiological frequency range of activation of muscle cells during the initial part of strong voluntary contractions [22,23] on the one hand, and estimated to elicit maximal isometric tetanic contraction in response to an electric tetanic stimulation of the nerve, innervating the TS muscle [17,18], on the other.

These results is associated with alteration of membrane ionic processes and appear to play the dominant role in the mechanical impairment recorded in disused muscles. An index of fatigability was calculated as ratio of the average force produced during the final 5 contractions and the average force of the initial 5 contractions [20]. Recording of muscle electrical activity, called electromyography (EMG) or surface action potential (SAP) in the test, was achieved by means of Ag-AgCl surface electrodes (0.8 cm diameter) attached to the skin over the soleus muscle belly, their centres 23 mm apart. The pass band of the recording system was 10 Hz-1kHz. The EMG was analyzed from the amplitude of the electrical responses - M-waves at end of the 1-, 3-, 5-, 31-, 61-, 91-, and 121-s of the intermittent muscular contraction. To determine the relative extent of change in contractile (C) responses and electrical (E) waves (M-waves) the E/C ratio was calculated where is the amplitude of the M-wave and C the mechanical response of the triceps surae muscle. The E/C ratio was calculated at the end of contractions at 1-, 3-, 5-, 31-, 61-, 91-, and 121-s during the electrical fatigue test. The results of the experiment were simultaneously recorded on magnetic tape and the SAP was also recorded on a storage oscilloscope.

Statistics

All values reported are the mean \pm SEM. Intergroup differences pre- and post-immersion data were compared using repeated mea-

asures analysis of variance or a paired t-test. Relative changes were calculated by [(before value-after value) / before value] x 100. In each analysis the level of significance was set at $P < 0.05$.

Results

At the end of the experimental period, the average value body mass of the control groups were similar. In contrast, the average value body mass after DI in 1, 2, and 3 groups was decreased by 2.0%, 3.0%, and 3.1%, respectively (Table 1), but the differences between the groups were not significant.

Immersion and Strength, and Velocity, and Force-Velocity Relationship

Force Properties: Mean data of the changes in the TS muscle tension properties are shown in Figure 1. The analysis of the results obtained revealed a significant decrease in tension properties of the muscle. Thus, isometric P_t decreased by a mean of 8.7% [pre 124.6

(SEM 14.7) N compared to post 113.8 (SEM 18.6) N] after 1-days and increased by a mean of 10.9% [pre 125.6 (SEM 13.7) N compared to post 139.3 (SEM 18.6) N] and 11.5% [pre 112.8 (SEM 9.8) N compared to post 127.5 (SEM 10.7) N] after 7- and 3-days DI; MVC by a mean of 11.5% [pre 417.9 (SEM 48.1) N compared to post 369.8 (SEM 42.1) N], 16.5% [pre 398.3 (SEM 54.9) N compared to post 332.6 (SEM 54.0) N], and 33.8% [pre 481.7 (SEM 35.3) N compared to post 318.8 (SEM 33.4) N] ($P < 0.05-0.01$), respectively, and P_o by a mean of 1.8% [pre 602.3 (SEM 58.9) N compared to post 591.5 (SEM 64.7) N], 5.3% [pre 628.8 (SEM 59.8) N compared to post 595.5 (SEM 53.7) N], and 8.2% [pre 643.5 (SEM 34.3) N compared to post 590.5 (SEM 56.8) N], respectively, ($P > 0.05$). The F_d increased significantly by a mean of 23.4% [pre 30.4 (SEM 4.8) % compared to post 37.5 (SEM 3.5) %], 20.2% [pre 36.7 (SEM 6.7) % compared to post 44.1 (SEM 3.7) %], and 78.7% [pre 25.4 (SEM 3.1) % compared to post 45.4 (SEM 4.9) %], respectively, ($P < 0.05-0.001$), after 1-, 3-, and 7-days DI (Figure 1).

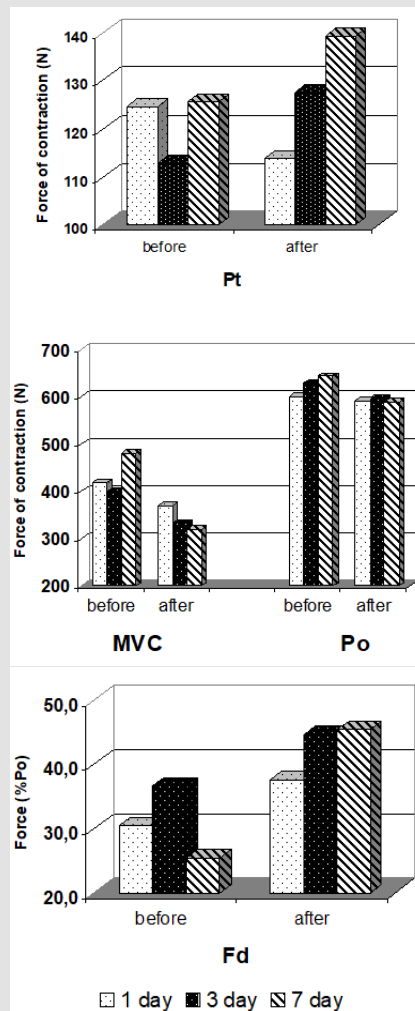


Figure 1: The effects of voluntary "dry" water immersion on the maximal twitch tension (P_t), maximal voluntary contraction (MVC), and maximal electrically evoked tetanic contraction (P_o , recorded at 150 impulses $\cdot s^{-1}$) before and after immersion, and force of MVC as percentage (force deficiency - F_d) after of immersion in control and disused muscle.

Mean data of the changes in isometric force of the TS muscle under paired stimulation of maximum intensity when the twin stimuli was applied at 3, 4, 5, 10, 20, 50 ms after first impinging are presented in graph form in Figure 2. As is seen from the analysis of the data, the greatest force of contraction under these conditions is noted at the intervals between the impulses of 4-20 ms and the decrease or increase of interpulsing interval of

above-mentioned levels is accompanied by its considerable decline ($P < 0.05$) not changing the general trend of the developing tension of the muscle. At the same time, there are changes patterning the curvies at one and the same interpulse interval: a relative increase in force of contraction after DI effect was more by comparison with the control value ($P < 0.01$).

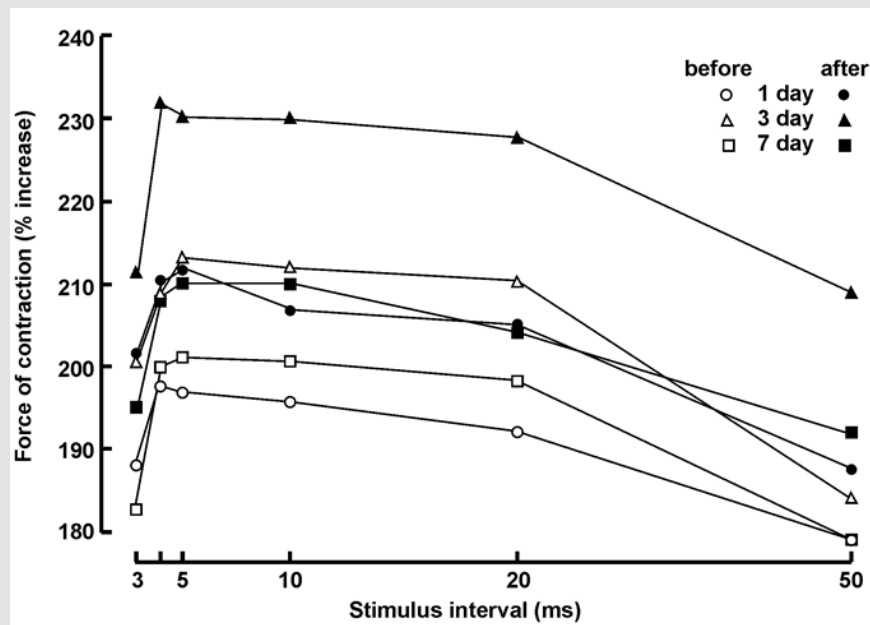


Figure 2: Mean value of the maximal force of isometric contraction of the triceps surae muscle with doublet stimulation with varying intervals between impulses before and after immersion.

Velocity Properties: The data of the change of mean time of isometric twitch contraction for the TS muscle after a short- and long-term DI effect, are given in graph form in Figure 3. As is seen from the analysis of the data, remaining exposed to DI conditions was accompanied by a statistically significant increase of the muscle contraction and relaxation velocity. Thus, TPT decreased by a mean of 8.5% [pre 129 (SEM 5) ms compared to post 118 (SEM 4) ms], and 3.3% [pre 122 (SEM 4) ms compared to post 118 (SEM 3) ms] after 1- and 3-days DI. The concomitantly recorded mechanical twitch of the TS muscle after 7-day DI did not reveal significant changes in the curve of the TPT. Thus, TPT increased by a mean of 0.9% [pre 118 (SEM 5)

ms compared to post 119 (SEM 4) ms]. 1/2RT and TCT was shorter in the post-immersion condition than in the control value. Thus, 1/2RT decreased by a mean of 13.8% [pre 108 (SEM 5) ms compared to post 94 (SEM 5) ms], and 4.0% [pre 100 (SEM 6) ms compared to post 96 (SEM 5) ms], and 5.3% [pre 94 (SEM 3) ms compared to post 89 (SEM 4) ms], respectively, after 1-, 3-, and 7-days DI. The TCT reduced by a mean of 10.2% [pre 560 (SEM 18) ms compared to post 503 (SEM 22) ms], and 11.3% [pre 515 (SEM 28) ms compared to post 457 (SEM 32) ms], and 2.8% [pre 504 (SEM 10) ms compared to post 490 (SEM 16) ms], respectively, after 1-, 3-, and 7-days DI.

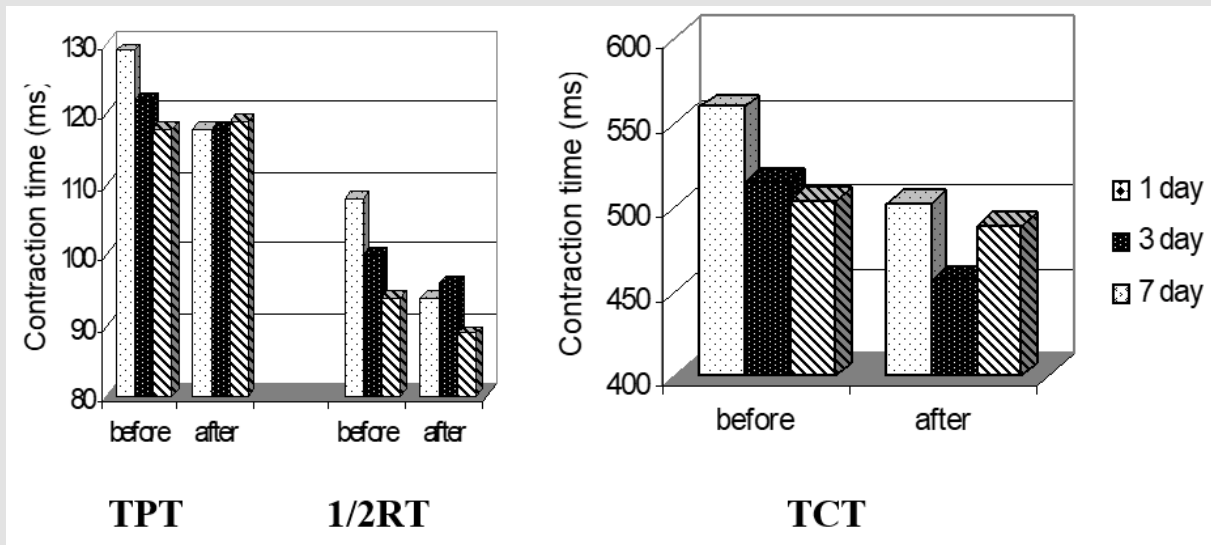


Figure 3: Effects of voluntary “dry” water immersion on the isometric of contraction times of the triceps surae muscle.

Force-Velocity Properties: Mean data of the changes in the development rate of the TS muscle isometric tension are given in Figure 4. The analysis of the data gives evidence of the decrease in the rate of rise in isometric voluntary tension development of the TS muscle.

However, in the assessment of the force-velocity muscle properties on electrically evoked tetanic development no substantial changes were observed.

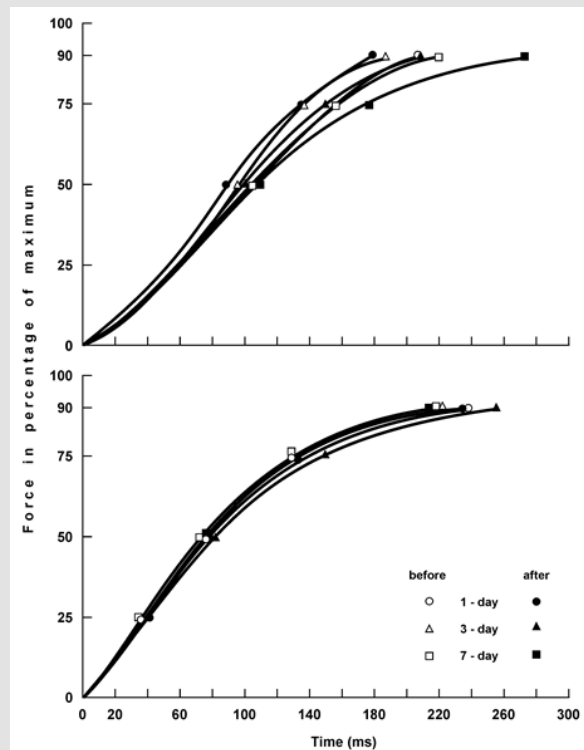


Figure 4: Average force-time curves for triceps surae muscle expressed on a relative scale while executing explosive voluntary contraction (top panel) and as a result of electrical stimulation at 150 impulses s⁻¹ (bottom panel) before and after immersion.

Immersion and Capacity for Work: The effects of DI on the evoked electrically intermittent contractions, stimulated at frequency of 50 impulses·s⁻¹ is illustrated in Figure 5. In this example, tetanic force decrease gradually to about 55-56% - 56-59%, respectively, before and after DI of its initial value. An index of fatigue ability was 20-39% vs. 36-43%, respectively, before and after DI ($P > 0.05$). Considerable distinctions over a length of the entire curve before and after disuse are not found. The reduction of muscle force output could be explained by a decrease of electrical activity. Figure 6 compares the muscle SAP measurements recorded during intermittent contractions separated by 1-s intervals and shows that the electrical processes changes differently in the control and disused muscles. After a DI

the amplitude of the negative SAP phase was reduced, whereas duration was increased. These changes developed with the occurrence of the first M-wave and increased at the end of 1-s, 5-s and particularly by the end of the test contractions (Figure 6). After disuse with fatigability both the force of electrically-induced contraction and the electrical M-waves reduce significantly. The relative extent of the decline in either of these two parameters can be determined from the change in the relation of the electrical M-wave to the contractile response of the TS muscle (the E/C ratio). The post-immersion analysis of the time course of a change in the E/C ratio has revealed the distinction (Figure 7).

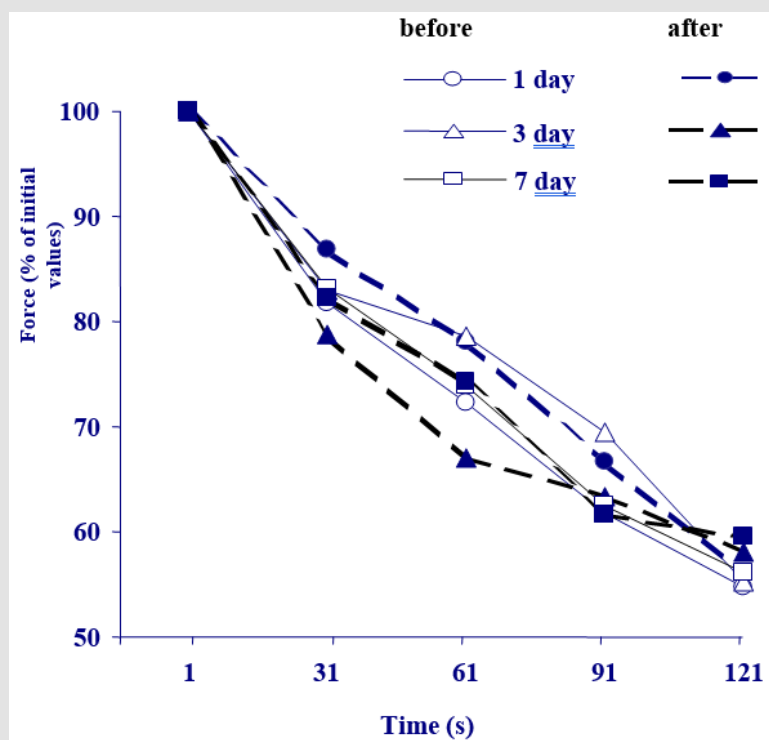


Figure 5: Changes in force during 60 intermittent (1 s duration) electrically evoked contractions, separated by intervals of 1 s, in control conditions and after 1, 3, and 7 days of “dry” water immersion. Values expressed as percentage of initial force during tetanus (50 impulses s⁻¹).

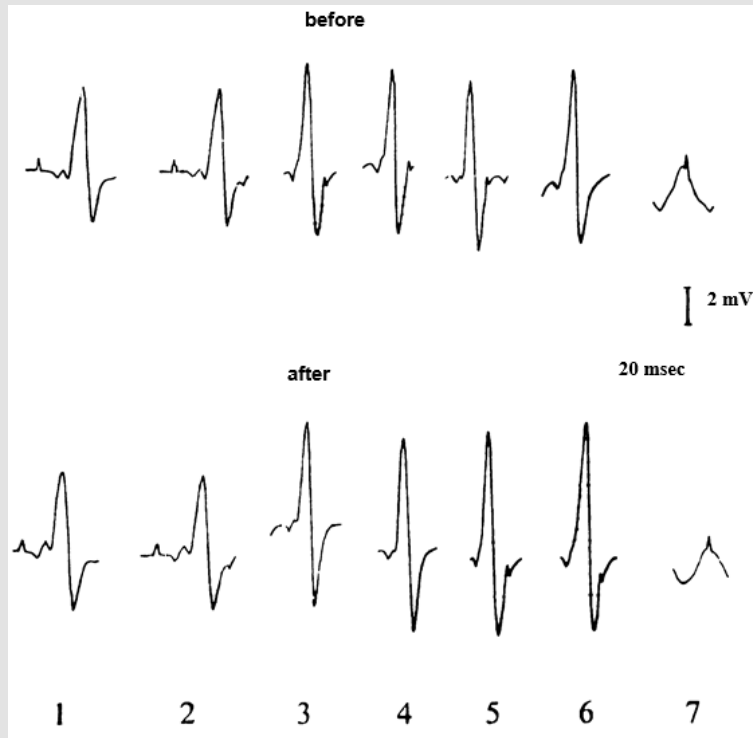


Figure 6: Typical record of surface action potentials (SAP) at one subject. 1 - maximum SAP (M-wave), 2 - first SAP in the rhythmic tetanic (50 Hz) series of contractions; 3-7 - registered at the end of 1, 3, 5, 7, and 121 s before and after “dry” water immersion.

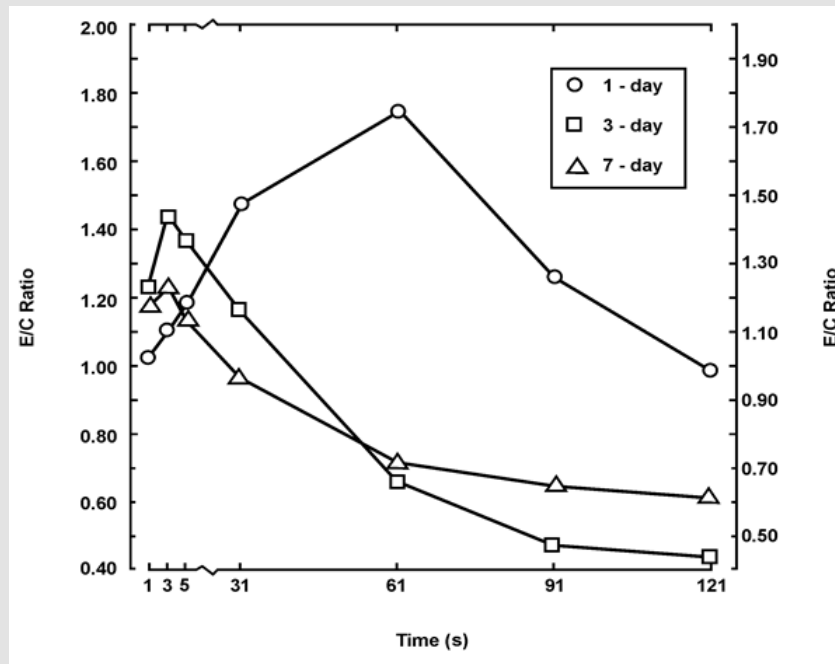


Figure 7: Changes of the ratio of electrical responses to force muscle contraction (the E/C ratio) during 60 intermittent (1 s duration) electrically evoked contractions (50 impulses-s⁻¹) after 1, 3, and 7 days of voluntary “dry” water immersion.

As the analysis by this ratio showed, during muscle work of the same intensity there may be different changes in the status of the “contractile” and “electrogenic” elements of the peripheral neuromuscular system. After long-term disuse (7-day DI) of muscle significantly greater decline of electrical waves is observed as compared with contractile responses by a short-term disuse (1-day DI). Thus, after disuse during the initial 5-sec of the test contraction, there is a relatively more marked decrease in contraction force than that of electrical *M*-waves. With increasing duration of disuse a relatively more marked decrease of the muscle electrical responses occur.

Discussion

The first objective of this study was to use a noninvasive procedure of reducing the muscle activity to determine the effect of the short- and long-term disuse (DI) on the contractile properties and fatigability the TS muscle. The results of the present study confirm and extend our previous findings [23] concerning the effects of voluntary disuse on the mechanical characteristics of the TS muscle. The results show that a slow contracting muscle group [24] was rapidly affected by disuse. The P_t decreased after 1-day of voluntary DI. It was suggested that the most likely explanation of these findings be explained the tendency for P_t to decrease in this study may be in outlined above, a reduction in the rate at which Ca^{2+} is dissociated from the myofibrillar proteins [25]. Dissociation would occur more fast if the rate of Ca^{2+} re-uptake by the sarcoplasmic reticulum (SR) increased as a result of immersion. A increased rate of Ca^{2+} dissociation from myofibrillar proteins might be expected due to not only decrease the time course of the twitch response but also allow less force to generated, since cross-bridges will continue to be formed while Ca^{2+} is available in the sarcoplasm. An increase in the uptake of Ca^{2+} will not enhance cross-bridge formation, and thus the generation of reduction force. The tendency for P_t to increase in this study during 3-day and 7-day DI, cannot be explained. This of interest since, assuming the twitch changes are due to not only SR alterations, but they must be reflect the alteration in muscle enzyme systems [26]. Significant decrease in maximal isometric twitch TPT and 1/2RT were produced after of voluntary DI, and these effects were maintained during the TCT. These data are in agreement with other reports on the responses of the slow-twitch muscle to disuse [27].

The reduced twitch duration in the TS muscle might in part result from the lower P_t obtained in this muscle. However, an increase of contraction speed can be perhaps explained by at least one of two mechanisms:

- 1) The rate of Ca^{2+} binding was changes and/or
- 2) Some kinetic parameter of the acto-myosin cross-bridges cycle was modified. According to the data obtained, an intensity of developing an active state after DI was considerably increased (cf. Figure 3); this in turn presupposes a increased capacity of the contractile apparatus to mobilize the reserves of SR [28]. Results reported

earlier clearly showed that the beginning of the contractile process was more dependent on the Ca^{2+} concentration [29]. The reduced TPT may indicate a shift in the fibre population of the TS muscle towards a faster contractile speed. According to Edgerton et al. post-flight (space Shuttle flight 5-day) biopsies from the vastus lateralis muscle had 14 % fewer type I fibers than pre-flight. The reduction in the percentage of type I fibers be accompanied by an increase by 11 % in the percentage of type II fibers. A further possible cause of a decrease in TPT is decreased compliance of the system after disuse [30], which might also explain the increased tetanus-to-twitch ratio observed, though 1/2 RT also decrease. A more likely explanation of the TPT change in the immersion limb is a relatively greater atrophy of slower motor units, which make up the majority of the TS muscle [31]. A loss of force attributable to slow motor units will reduce P_t and thus increase the relative contribution of faster firing units to force production and result in a decreased TPT. Alternatively, the observed change in the twitch duration may result from an altered SR as the functional capacity of the SR shows a high inverse correlation with twitch duration [25].

The changes in maximal tetanic isometric tension (P_o) were small compared to those described for the twitch. The mean changes during the DI period were -1.8, -5.3, and -8.2 % after 1-, 3-, and 7-day, respectively (cf. Figure 1). P_o is a direct measure of the force-generating capacity of a muscle and is thought to reflect the number of active interactions between actin and myosin [32]. Our results showed, that immersion short- and long-term produced a non significant decline in P_o in the slow-twitch the TS muscle. This would indicate, that the total number of active cross-bridges and in density of cross-bridges was none reduced after disuse. The greater change in MVC compared with P_o during the period of DI (cf. Figure 1) is consistent with earlier findings and suggests either unwillingness or inability of the subjects to perform a normal MVC. The much larger and progressive reduction in MVC compared to the insignificant change in P_o after DI may indicate an inability of the central nervous system to activate the TS muscle normally. The increase in F_d (cf. Figure 1) suggests a decline in central drive in the control of voluntary muscle by the motor nervous system. Whether this is due to a lack of motivation on the part of the subject, or an involuntary reduction in neural drive, is difficult to distinguish. The subjects certainly appeared well motivated and had no discomfort or foot stiffness before performing the tests, which could account for the low MVC.

The time course of force development of the TS muscle were determined by tetanic and voluntary contractions as described previously. Our findings found that the rate of force development is a measure of the time at which force is developed, slow on isometric voluntary tension development and no substantial changes on electrically evoked tetanic development after short- (a 1-, 3-day) and long-term (a 7-days) DI. Simmons & Jewell [33] have proposed that the rising phase of an isometric tetanus is determined by the net rate of cross-bridges attachment, and that the rate constant for the exponen-

tial phase of relaxation is equal to that of cross-bridge detachment. The shape of the force-time curve is thus probably governed by the ratio of attachment and detachment of cross-bridges [33,34]. It, therefore, seems reasonable to conclude that the short- and long-term DI (disuse) in man effect has no or very little influence on the cycles of cross-bridges formation. The greater change in the development rate of the TS muscle voluntary isometric tension compared with electrically evoked contractions during the period of immersion (see Figure 4) directly show that the ability of the central nervous system to activate the TS muscle declines. One possibility is that immersion affects the character of the central drive.

The maximal firing rate decreased after disuse without change in the firing rate at recruitment may indicate that the motor unit frequency modulation is narrowed in disused muscles [35]. Decrease in maximal firing rate could be explained by changes in proprioceptive afferents on the motoneurons [36] and/or reduced ability to activate motor units [37]. This last point was suggested by the finding after immobilization of a smaller reflex potentiation which is closely controlled by the central drive [38]. In addition, data reported by Antonutto et al. showed a larger fall in maximal power during maximal pushes (of ~250 ms) on force platforms after spaceflights, suggests that a fraction of the former (especially relevant for maximal explosive power) is due to the effects of weightlessness on the motor unit recruitment pattern. Interestingly, it has been shown that the recruitment order of low- and high- frequency motor units can be altered by blockades of proprioceptive afferent activity [39].

Changes in the recruitment threshold of motor units during voluntary contraction have also been demonstrated by cutaneous electrical stimulation [40]. These data suggest that the proprioceptive afferent inputs can play an important role in motor unit recruitment during both voluntary (strong) contraction and voluntary (explosive) contractions. It can be speculated that the pattern of afferent input to the motoneuron pool may become altered during immersion and that this alteration could be in part responsible for the progressive reduction in motor unit firing frequency. Our results mechanical failure (fatigue) during intermittent contractions show that:

- 1) The rate of decrease in the force of muscle contraction during rhythmic fatigue stimulation does not vary in control and after disuse;
- 2) A correlation between the electrical and mechanical responses of the muscle indicates that the specific role of fatigue of "electrogenic" and "contractile" elements of the neuromuscular system is changed during the development of peripheral fatigue. Our previous findings concerning the effects of long-term voluntary DI on the electrical waves of the TS muscle show that on stimulation (frequency of 50 impulses·s⁻¹) the action potentials showed a marked decline in amplitude and increase in duration reflecting changes in the peripheral generation of the action potentials by the muscular fibers.

Our findings do not reveal difference in the reduction of the working capacity before and after disuse which is in good agreement with previously obtained data [41] and confirm Merton's point of view [42] that peripheral mechanisms play an important role in force reduction. Peripheral fatigue probably results from a deterioration the excitability of the muscle fibers. Failure of propagation of action potentials may occur: Along the terminal branches of motor nerves [43], At the neuromuscular junction [44], Along the surface of muscle fibers [43,44], and along the T-tubules [45]. The blocking of the fiber action potentials during stimulation indicates a failure of excitation, but the location cannot be determined. Blocking of an action potentials was invariably preceded by a major change in the amplitude and duration of the fiber action potential. As is evident from the present findings, the reduction in the contraction force of the muscle during the intermittent fatigue test was similar in control and after disuse suggesting, on the one hand, that the fatigue developed cannot be explained by the changes in the contractile apparatus itself as a result of an active factor and, on the other, that one of the components (if not the only cause) of developing peripheral fatigue could be a disorder in the "electrogenic" element of the neuromuscular system, The comparison of the changes in mechanical response with the corresponding alteration of electrical response (the E/C ratio) enables the determination of the specific role of the "electrogenic" and "contractile" elements in the development of peripheral fatigue.

Analysis of the E/C ratio before and after immersion indicated that there occurred different dynamics of changes in the state of contractile and electrical elements of the peripheral neuromuscular system (cf. Figure 7). These results do not contradict the above discussions because an interpretation of the E/C ratio suggests a linear relationship between mechanical responses of muscle, but the relationship between the EMG and fatigue has remained unclear [46], especially when developing fatigue can be impaired. During contraction triggered by electrical stimulation of motor nerve, the decrease in the contractile force of the muscle cannot be compensated by a modulation of the motor unit firing frequency [47]. The study of electrically evoked fatigue shows that the decrease in force observed during of intermittent contractions is not different in control and disused muscles and indicates that fatigue is now larger after immersion. Besides, the normal action potential of muscle fiber is several times higher than the threshold value required for an activation of the contractile apparatus [48], due to this even reduced action potentials are capable of triggering normal contraction of muscle fibers [49-51].

Conclusion

In conclusion, the present experiments suggested that the contractile properties of antigravity muscles loss which develops of the DI is associated with not only alters the peripheral electrical and mechanical processes, but also similarly changes the neural command. The present data demonstrate that neuromotor functions are affected adversely after immersion and that the neural component is certainly

a contributor to the observed decrement in voluntary performance (MVC). Furthermore, the comparison of peripheral electrical and mechanical changes during intermittent electrically triggered contractions, recorded before and after long-term immersion muscles, supports the proposition that the electrical changes do not closely control the mechanical failure, and that at peripheral sites electrical failures are larger after inactivity. These results is associated with alteration of membrane ionic processes and appear to play the dominant role in the mechanical impairment recorded in disused muscles.

Acknowledgements

The author wishes to express his appreciation to all persons who contributed to the successful performance of the experiment. He is also very thankful to Mr. Vladimir Gratchev the technical design of the work, and also very thankful to Mr. Yuri Voronkov, Ph.D., D.Sci. manager of the Department of Medical Clinic, and Mrs. Elena Dobrokvashena, Ph.D. physician of the Department of Medical Clinic for monitoring of the subjects. He gratefully acknowledges the subjects who participated in this study. The author also thank two anonymous reviewers for their insightful critiques of the manuscript. This work was supported by the SRC-Institute of Biomedical Problems RAS.

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ISSN: 2574-1241

DOI: 10.26717/BJSTR.2024.58.009167

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