

ORIGINAL ARTICLE

Yuri Koryak

The effects of long-term simulated microgravity on neuromuscular performance in men and women

Accepted: 18 June 1998

Abstract The effects are reported of prolonged exposure to simulated microgravity (strict bed rest in an antiorthostatic position – -6° head-down tilt, HDT) on voluntary and electrically evoked contractions of the triceps surae muscle in men ($n = 6$) and women ($n = 4$). The subjects served as their own controls. Bed rest is a model that has commonly been used to simulate spaceflight. Measurements made in the control condition (10–8 days before the beginning of HDT) and after 120-days of HDT (on the 3rd day after it ended) included examination of the properties of isometric maximal voluntary contractions (MVC), isometric twitch contractions (P_t) and tetanic contractions (P_o). After HDT, the MVC decreased by means of 44% and 33%, P_t by means of 36% and 11%, P_o by means of 34% and 24%, in the men and the women, respectively. The difference between P_o and MVC, expressed as a percentage of P_o and referred to as force deficiency (FD), has also been calculated. The FD increased by means of 60% and 28.8% in the men and the women, respectively. Time-to-peak tension of the triceps surae muscle increased by means of 12% and 14% in the men and the women, respectively, but half-relaxation time decreased by means of 9% and 19%. Total contraction time increased by a mean of 23% in the men and decreased by a mean of 17% in the women. Force-velocity of properties of the triceps surae muscle calculated according to a relative scale of voluntary contraction development significantly decreased more in the women than the men. The calculations of the same properties of electrically evoked contraction development did not differ substantially from the initial physiological state. It can be concluded that not only were the contractile properties of the triceps surae muscle significantly different in the men and the women, but that the effects of exposure to

simulated microgravity on these properties were also different. These differences may be explained by sex differences in the muscle tissue itself and in its maximal neural activation.

Key words Simulated weightlessness by bed rest · Sex difference · Triceps surae muscle

Introduction

Space exploration of the past 30 years, and particularly the Soviet Space Station MIR and the US Space Shuttle, has identified the occurrences of major physiological changes due to weightlessness in a variety of organ systems, in particular the neuromuscular system (Kozlovskaya et al. 1981; West 1984; Kozlovskaya 1991; Day et al. 1995). Weightlessness has been shown to cause considerable functional changes with the greatest change observed in antigravity muscles such as the triceps surae muscle (Grigor'eva and Kozlovskaya 1987; Martin et al. 1988; Riley et al. 1990). Progressive weakness of the antigravity skeletal muscles remains a risk, particularly during missions by cosmonauts/astro-nauts for the construction and operation of a Space Station, or on a voyage to another planet. Therefore, exposure of humans to simulated microgravity is required to understand better the basic mechanism(s) of activity related muscle remodelling as they occur on Earth and in Space.

The effect of exposure to stimulated microgravity on the functional properties of human skeletal muscle has been extensively studied. Numerous previous observations have described neuromuscular adaptations to microgravity occurring mainly in men (Dudley et al. 1989; Koryak 1994, 1995a, b) or conjointly in men and women (Dudley et al. 1994; Suzuki et al. 1994a, b; Ja-weed et al. 1995; Day et al. 1995). However in women, the effects of muscle exposure to weightlessness are not well known.

Y. Koryak (✉)
Department of Neurophysiology,
Institute of Biomedical Problems,
76-A Khoroshevskoye Shosse
123007 Moscow D-7, Russia

It seems to have been well established that women may adapt better than men to the performance of endurance exercise (Nygaard 1981). These sex-related differences may be a result of differences in the metabolic characteristics of skeletal muscle, as Nygaard (1981) has reported that a higher proportion of muscle cross-sectional area is occupied by type I fibres in women. In contrast to studies involving relatively high-intensity dynamic or isometric exercise, absolute values of muscle strength measured as the maximal voluntary contraction (MVC) force produced during an isometric contraction, have been shown to be greater for men than for women (Petrofsky et al. 1975). If muscle dimensions increase in a geometrically proportional manner (Asmussen 1974), then greater absolute changes would be expected to occur in men because of their substantially greater initial muscle size. It would seem that relative strength increases are similar in men and women, but the relative degree of muscle hypertrophy is less in women. This indicates that neural adaptations are greater in women. However, others authors have reported that the relative contributions of nerve and muscle adaptations to strength changes in men and women are similar (Moritani and DeVries 1979). In addition, human skeletal muscle metabolism is under hormone control, in particular by testosterone concentration which plays an important role in muscle hypertrophy, and strength development has been shown to remain smaller in women than in men (Häkkinen 1994).

Up to now, due to methodological difficulties, examination of the intrinsic contractile properties of human skeletal muscles in a true weightless environment and/or during its simulation has been beyond the capability of scientists who have therefore concentrated mostly on investigating the mechanical features of the voluntary muscle contractions. The natural contractile properties of skeletal muscles in men, and ever more so in women, have not been a subject for systematic and independent study. As a result, it is still unknown:

1. To what degree functional peculiarities of the neuromuscular system of women are determined by the contractile properties of muscles themselves
2. What is the role of central command in determining muscle contractile properties
3. The effect of microgravity on neuromuscular system functional properties in women and the relative role of central command and peripheral sites in determining the functional properties of the neuromuscular system.

The purpose of this study was firstly to compare the effects of exposure to simulated microgravity on the contractile properties of the triceps surae muscle after of a 120-days -6° head down tilt (HDT) in normal adult subjects – men and women, and, secondly, to investigate the extent of muscle adaptations in women and men following a long-term exposure to weightlessness.

Methods

Subjects

A total of ten healthy volunteers were recruited to participate in this present study after explanation of the experiment protocol, which had been approved by the Human Ethics Committee at the Institute of Biomedical Problems. Each subject was informed of the purpose and the method of the study before signing the required consent form. Selection of subjects was based on a screening evaluation that consisted of a detailed medical history, physical examination, complete blood count, urine analysis, resting electrocardiogram, and a selection of blood chemistry analyses, which included concentrations of fasting blood glucose, blood urea nitrogen, creatinine, lactic dehydrogenase, serum transaminase, bilirubin, uric acid, and cholesterol. The subjects were divided into two groups – one group of men ($n = 6$), and the second group of women ($n = 4$). The subjects served as their own controls. The physical characteristics of the subjects are shown in Table 1. The subjects underwent 120-days in an antiorthostatic position (-6° HDT) of the body. All were non-smokers, and none took non-prescribed medication, and were recreationally active but not especially well trained. No adverse health problems were observed or reported during the study.

Isometric dynamometry

The subjects were carefully familiarized with the test procedures of voluntary force production during several warm-up contractions preceding the actual maximal contractions. They were allowed to habituate to the electrical stimulation procedures during preliminary visits to the laboratory before definitive control measurements were taken. In addition, the subjects were trained to perform a voluntary contraction and to relax during electrically elicited contractions of their dominant foot (the triceps surae muscle). On each occasion the subjects were required to sit in a specially designed leg tendometrical setup in a standard position (knee joint angle between tibia and sole of foot of 90° ; see Koryak 1995a, Fig. 1). The dynamometer and recording system used to measure the forces produced by electrical and voluntary contractions of the triceps surae muscle have previously been described in detail (Koryak 1992, 1994, 1995a, 1996). Contractile properties of the triceps surae muscle were tested twice: 10–8 days before the beginning of bed rest and 3-days after it ended. The test protocol was identical for both pre-bed rest and post-bed rest tests.

The subjects were instructed to respond to an auditory signal by exerting maximal force. Usually three to five contractions were required from each subject until maximal voluntary force (MVC)

Table 1 Physical characteristics of the subjects

| | Age (years) | | Height (cm) | | Body mass (kg) | |
|-------------------|-------------|-----|-------------|-----|----------------|-----|
| | Mean | SEM | Mean | SEM | Mean | SEM |
| Women ($n = 4$) | 32 | 2 | 162 | 2 | 55.0 | 1.8 |
| Range | 28–36 | | 158–167 | | 51–59 | |
| Men ($n = 6$) | 38 | 2 | 179 | 2 | 79.5 | 2.8 |
| Range | 31–45 | | 164–182 | | 69–91 | |

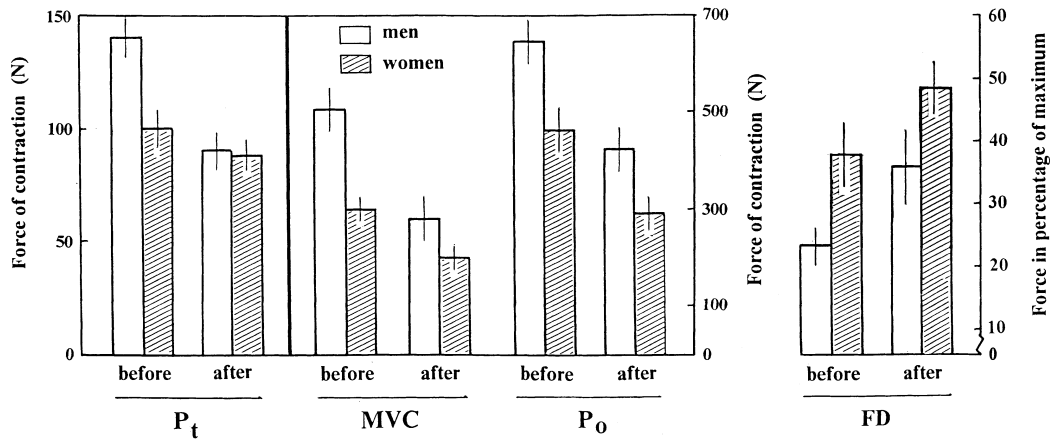


Fig. 1 The effect of 120-day 6° head-down tilt on maximal voluntary contraction (*MVC*), evoked tetanic tension at 150 Hz (P_0), and on tension of the maximal twitch (P_t) of the triceps surae muscle (*left panel*), and force deficiency (*right panel*)

was obtained. The subjects were also carefully instructed to respond to the auditory signal by exerting maximal force as rapidly as possible, and to maintain that force as long as the signal was audible (1.5–2.0 s). In the force-time curves, the times taken to increase the force to 25%, 50%, 75%, and 90% of the maximum were calculated (Koryak 1992, 1995a).

Electrical stimulation was applied through monopolar electrodes, one (the cathode) 1 cm in diameter was located in the popliteal fossa (tibialis nerve) which is the place of the lowest resistance, and the other electrode (the anode) 6 cm × 4 cm in size was positioned on the lower one-third of the surface of the thigh. The large earthed electrode (7.5 cm × 6.5 cm) was located on the proximal portion of the leg between the pick-up and the stimulating electrodes. The voltage was increased in a stepwise manner until maximal twitch responses were evoked. A single stimulus was given every 30 s. From the maximal twitch response the force (P_t), time-to-peak tension (TPT), half-relaxation time (1/2RT), and total contraction time (TCT) were measured.

After an appropriate rest the motor nerve was stimulated at various intervals. Supramaximal twin stimuli at 330, 250, 200, 100, 50, and 20 Hz were studied (Koryak 1992). On double stimulation, the maximal amplitude (strength) of the muscle contraction was determined.

The muscle tetanus (P_0) was evoked by delivering supramaximal (+40%) voltage rectangular electrical pulses of 1-ms duration at a frequency of 150 Hz (Koryak 1992, 1994, 1995a). The difference between P_0 and MVC expressed as a percentage of the P_0 value and referred to as force deficiency (FD) was also calculated (Koryak 1992, 1995a).

Strict bed rest

After an intensive familiarization period for 3 months before bed rest, the subjects entered the Human Research Facility of the Health Ministry Institute of Biomedical Problems. During this 120-day experiment, the subjects were housed 24 h day⁻¹ in this Facility. During bed rest, the subjects remained in the HDT position continuously for all activities including excretory functions, showering, and eating. The -6° HDT position was chosen since various physiological alterations induced by actual spaceflight are similar to those which has been reported in ground-based studies using this model (Convertino et al. 1981; Sandler and Vernikos 1986).

Statistical analysis

Standard statistical methods were used for the calculation of means and standard errors (SEM). Differences between the baseline values

of the subject and those after HDT effect were tested for significance by Students *t*-test. A difference was considered significant at $P < 0.05$. The percentage changes from pre-bed rest to post-bed rest were calculated.

Results

Isometric evoked and voluntary strength

Isometric twitch tension (for both groups combined) was less post-HDT than before (by a mean of 27.8%) [pre 122.6 (SEM 9.8) N compared to post 87.3 (SEM 6.8) N; $P < 0.01$]. The men and women were different in the relationship between the control and post-HDT tests. Mean data for the changes in the triceps surae muscle tension properties following the HDT effect are shown in Fig. 1 (left panel). In the men, the mean post-HDT value for P_t was 35.7% lower than the control value ($P < 0.01$) whereas in the women the post-HDT value was only 11.2% lower, ($P < 0.05$).

In the combined results for both groups the post-HDT value for the reduction in MVC was a mean of 40.5% [pre 404.2 (SEM 35.3) N compared to post 240.3 (SEM 30.4) N; $P < 0.01$], whereas for the men and women separately the post-HDT value was 44.4% [pre 485.6 (SEM 38.3) N compared to post 269.8 (SEM 47.1) N; $P < 0.01$] and 32.9% [pre 307.1 (SEM 21.6) N compared to post 196.2 (SEM 22.6) N; $P < 0.01$], respectively, less than the control value (Fig. 1, left panel).

The isometric muscle tetanus – P_0 (for both groups combined) was less post-HDT than in the control (by a mean of 29.6%) [pre 570.1 (SEM 37.3) N compared to post 401.2 (SEM 26.5) N; $P < 0.01$]. The men and women were different in the relationship between the control and post-HDT measurements. Mean data for the changes in the tension properties of the triceps surae muscle after, HDT are shown in Fig. 1 (left panel). In the men, the mean post-HDT value for P_0 was 33.7% lower than the control value ($P < 0.01$) whereas in the women it was only 24.4% lower ($P < 0.01$).

The FD for both groups combined was increased post-HDT compared to control by a mean of 40.1% [pre 29.4 (SEM 3.4)% compared to post 41.2 (SEM 4.2)%;

$P < 0.001$]. The men and women separately showed similar results; there was a difference between the two groups in the relationship between the control and post-HDT values. In the men, the mean post-HDT value was 60.2% more than the control value ($P < 0.001$) whereas in the women the mean post-HDT value was only 28.8% ($P < 0.001$) more (Fig. 1, right panel).

The twitch-to-tetanus ratio was less in the men compared to the women (Fig. 3, right panel; $P < 0.05$). In women, before HDT, the twitch-to-tetanus ratio was 4.2% higher than the post-HDT ratio. In contrast, control and post-HDT values were equal in the men. The women's twitch-to-tetanus ratio exceeded the men's control and post-HDT values by 8.3% ($P < 0.001$) and 4.3% ($P < 0.01$), respectively.

The dynamics of the changes in amplitude of the triceps surae muscle response as a function of interpulse interval (in paired stimulation of the nerve) pre- and post-HDT is presented in Fig. 2. The results indicated that contraction force of the triceps surae muscle in response to the second stimulation with 4–10 ms intervals between pulses was, on average, about the same but an increase or decrease of interpulse interval over and above these values was accompanied by a substantial decline, not leading to a change in the general trend of developing the muscle tension. However, the curve location pattern at one and the same interpulse interval was changed: a relative rise of force contraction after 120-day HDT was significantly lower, but particularly in the women.

Isometric twitch

The data for the change in mean time of isometric twitch contraction for the triceps surae muscle after 120-day HDT, are given in Fig. 3 (left panel). In the combined results for the men and women the post-HDT value for TPT exceeded the control value by a mean of 8.9% [pre 124 (SEM 3.0) ms compared to post 135 (SEM 2) ms; $P < 0.05$]. The men and women separately presented similar results; however, there was a difference between the two groups in the relationship between the control and post-HDT values. In the men, the mean post-HDT

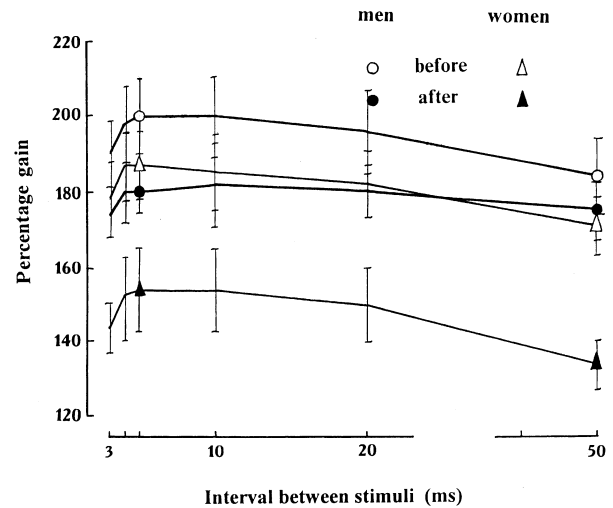


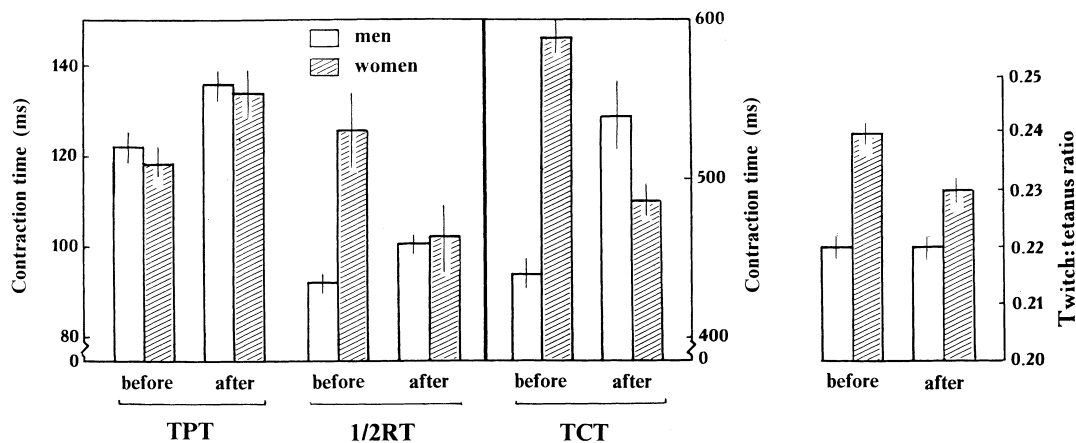
Fig. 2 The effect of 120-day 6° head-down tilt on the maximal force contraction of triceps surae muscle in response to supramaximal twin stimuli at 330, 250, 200, 100, 50, and 20 Hz

value was 11.5% more than the control value ($P < 0.05$) whereas in the women the mean post-HDT value was 13.6% more ($P < 0.01$).

The 1/2RT was shorter in the post-HDT condition than in the pre-HDT condition. The post-HDT value for 1/2RT was on average 5.7% [pre 106 (SEM 6) ms compared to post 100 (SEM 3) ms] less than the control value. In the men, the mean post-HDT value was 9.8% more than the control value ($P < 0.05$) whereas in the women the mean post-HDT value was 19.0% lower ($P < 0.01$).

In the combined results for men and women the post-HDT value for TCT exceeded the control value by a mean of 2.9% [pre 504.5 (SEM 24.6) ms compared to post 518.9 (SEM 14.4) ms; $P < 0.05$]. The men and women separately presented similar results; however, there was a difference between the two groups in the

Fig. 3 The effect of 120-day 6° head-down tilt on the isometric twitch time-to-peak tension (TPT), half-relaxation time (1/2RT), and total contraction time (TCT) of the triceps surae muscle (left panel) and twitch-to-tetanus ratio (right panel)



relationship between the control and post-HDT values. In the men, the mean post-HDT values was 22.9% more than the control value ($P < 0.05$) whereas in the women the mean post-HDT value was 16.5% less ($P < 0.01$).

Force-time curve

Mean data for the changes in the rate of development of isometric tension in the triceps surae muscle are given in Fig. 4. Analysis of the data gives evidence of a decrease in the rate of rise of development of isometric voluntary tension of the triceps surae muscle in the women (Fig. 4, upper panel). This may be seen as a decrease in convexity of the force-time curve estimated according to the relative scale. However, in the assessment of the force-velocity muscle properties of isometric electrically evoked tetanic development as a result of 120-day HDT no substantial changes were observed (Fig. 4, lower panel).

Discussion

The major aim of the present study was to examine the influence of simulated microgravity on the contractile responses of skeletal muscle in intact healthy men and women. In the present investigation the most striking influence was the change in skeletal muscle behaviour

after HDT in the men and women. The previous studies simulating microgravity have been limited to using only men (Dudley et al. 1989; Koryak, 1994, 1995a, b) or joint groups of men and women as test subjects (Dudley et al. 1994; Suzuki et al. 1994a, b; Jaweed et al. 1995; Day et al. 1995). The investigations dedicated to a comparative study of the extent of the microgravity-induced changes in the contractile properties of skeletal muscles of men and women followed by their quantitative analysis have not been done, particularly on a single muscle involving both voluntary and involuntary (electrically evoked) contractions. The question as to what extent microgravity influences the contractile properties of muscles in women and men is of great significance from at least two points of view. Firstly, it has been shown that the magnitude of muscle force produced during isometric contractions is greater in men than in women (Åstrand 1952). Secondly, the relative contributions of central command and peripheral sites to the functional properties of the neuromuscular system have been shown to differ significantly in women and men (Komi 1986a).

Our findings in all the subjects showed that the contractile properties of the triceps surae muscle differed considerably between the men and women which confirms the findings of previous observations (Åstrand 1952). With respect to sex differences, Sale et al. (1987) have observed that the peak force may differ significantly between men and women. Our data showed that the values of P_t and P_o in women differed by a means of 30% and 40% less compared to the men subjects, respectively. A major finding of this study was that the changes in the men were more marked compared to the women. The findings showed that during 120-day HDT, the MVC and P_o values had reduced in the male subjects by a mean of 44% and 34% and in the women group by 33% and 24%, respectively. This is an indication not only of changes in the contractile capacity of the muscle fibres, that is, of the peripheral nature of the changes in the recorded indices, but also of alterations in the central mechanism of voluntary control of movement.

What factors can determine these differences? On the one hand, it may be suggested that the differences in force properties of the muscles of men and women are determined by the muscle mass, which has been found to be greater in men (Hermansen and Dobein 1971). On the other hand, the differences can be conditioned by differing kinetics of developing an active state of the contractile elements of the muscle fibres in the triceps surae muscle. According to the findings of the present study, the intensity of developing an active state in the women was less than that in the men (Fig. 2), suggesting that the capacity of their contractile system for mobilizing the reserves of the contractile capacity of the muscle, especially after long-term HDT, was reduced. This assumption agrees with the relatively greater decrease of the contractile properties of the triceps surae muscle revealed in the women judging from the temporal parameters of developing the isometric twitch contraction.

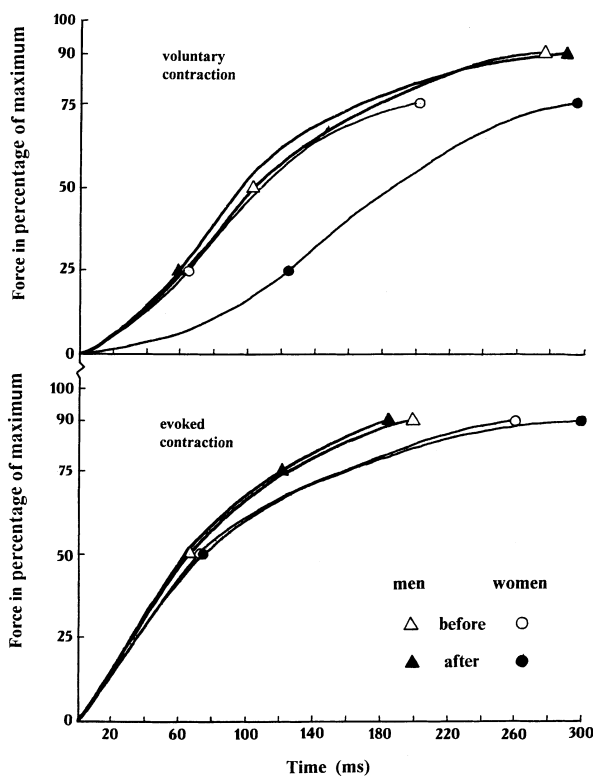


Fig. 4 The effect of 120-day 6° head-down tilt on the maximal isometric rate of voluntary force development (upper panel) and of electrically evoked tetanic force development (lower panel)

The greater change in MVC compared with P_o would suggest that the change in skeletal muscle behaviour reflects a neural adaptation to the experimental conditions (bed rest). The data would suggest that the women recruited more readily additional motor units and/or increased the discharges of the single motor units already firing at a high frequency, as well as allowing an increase in the relative level of synchronization of the motor units. There exist at least two possible explanations for the increase in synchronization of motor units. Firstly, α -motoneurons gain an increased input of impulses from the sensory fibres. Because during HDT a redistribution of the support area (in the direction of its increase) does occur, by and large one might expect an increased afferent input of impulses to the central nervous system (CNS). The increase of the impulse frequency can be compared to the effect of recruiting the motor units.

As is clear from the results shown in Fig. 3 (right panel) the value of the twitch-to-tetanus ratio was higher in the women compared to the men. Hence the change in frequency of α -motoneuron (the triceps surae) in the women was greater than in the men. Secondly, the higher motor centres increase their descending activity and, in particular, reduce the inhibitory processes. This allows one to suggest that the short-term synchronization of motor units that has been shown to develop as a result of disuse (Kirenskaya et al. 1985) has a beneficial effect on muscle function and it should be considered as a side effect of the divergence of nerve fibres coming to the motoneurons (Freund 1983). From the present point of view, the evidence presented here provides reason enough to consider that in the women with lack of use both these mechanisms were obviously present to a greater extent compared to the men.

A key element which determined the difference in contractile properties of the triceps surae muscle between two groups of subjects could be the qualitative aspects of the skeletal muscle. Muscle biopsy samples were not taken in this study so the precise influence of these possible factors could not be assessed. The activity and training status of the two groups was similar. It has been shown that not only the percentage of the type II fibres and their individual variation but the selective hypertrophy of type II fibres as well are relatively higher in men compared to women (Komi and Karlsson 1978).

The difference in muscle fibre number is probably an intrinsic, genetically based sex difference, whereas the difference in muscle fibre cross-sectional area may reflect both a genetic sex difference and a behavioural difference in physical activity patterns. Besides, which it has been found that the fast twitch motor units are preferentially recruited at high force levels (Milner-Brown et al. 1973) and require an increase in motor neuron firing frequency for their full activation. The analysis of the present data would suggest that in response to a decreased gravity-force load in the men, the large fast twitch motor units, apparently suffered to a greater extent the contribution of which to developing strength

has been suggested as being significant (Burke 1981). However, the decrease in maximal firing rate and the reduced ability to activate motor units compared to the women confirms the significance of the nerve component in the development of slow force (Häkkinen and Komi 1983; Komi 1986b). The latter is supported by the greater increase in the magnitude of FD in the men compared to the women (Fig. 1, right panel) being indicative of the relatively retained capacity of CNS to activate the muscular system.

The analysis of the force-time curve of voluntary contractions (Fig. 4) allows one to suggest that the observed differences can be explained by factors other than the more qualitative distinctions of the skeletal muscles. Difference in the force-time curve in the relative scale supports the earlier observations of Komi and Karlsson (1978) that the rate of force development in women is much lower than in men. What is more, the comparisons of the force-time curve of voluntary contractions and electrically evoked contractions due to microgravity were indicative of the great changes in the motor control mechanisms in the women compared to the men. This latter was evidently dictated both by the character and the intensity of descending voluntary (cortical) effects and the passivity of spinal systems. In any event, on the basis of data that has been previously obtained on the increase of the contractile capacities of the skeletal muscles as a result of additionally induced afferent effects (Martyanov and Koryak 1973) the availability of a low intensity of the afferent input the impulses towards the muscle-agonist of the movement and, apparently, increasing under disuse effect. Also it cannot be ignored that the relatively low intensity of the descending supramaximal voluntary commands affects the activation of the high-threshold motor units involved in the action when the muscular intensity augments (see Henneman et al. 1965), and a longer period of time is required.

It has been suggested that the deficit of afferent impulses during weightlessness/simulated microgravity (Kozlovskaya et al. 1981; Kozlovskaya 1991) could be one of the factors in the conflicting sensory situation between the controlling system (properties of neuromuscular system) and the controllable system (motor command). On the one hand, it has been indicated, that disuse increases the reflex excitability of motoneurons conditioned both by the decreased afferent input from mechanoreceptors of the "support" area of the foot (Magnus 1924) and the reduced input of muscle afferents in connection with the discharge of muscle receptors (Kozlovskaya 1991; Koryak and Kozlovskaya 1994). On the other hand, explosive voluntary contractions depend on the optimal combination of manifestations of the force and velocity of muscle contraction per unit of time and this requires an integration of the proprioceptive information. The disorder for the mechanisms for integrating proprioceptive information has been shown to be accompanied by a decrease in gradation of the force to control precisely the voluntary movements (Simard et al. 1968). However, the deficit of

input from the mechanoreceptors has been found to determine not only the deterioration of descending inhibitory effects from the cortex of the cerebral hemispheres and reticular formation on the activity of γ -motoneurons (Magoun and Rhines 1946) but can also improve the conditions of afferents entering CNS from the other receptive fields. Carlsöö and Edfeld (1963) and Wagman et al. (1965) have taken the exteroceptive stimuli as being at least auxiliary ones for the proprioception in controlling exactly voluntary movements. The present experimental data would suggest that the men had a better capacity for integrating information coming from a variety of other sensory systems when performing an explosive force type of motor task compared to the women.

The concavity of the force-velocity curve is dimensionless and, for isolated muscle, its magnitude has been shown to be dependent on the fibre type distribution, that is the concavity of the force-velocity curve has been shown to be smaller for slow twitch than for fast twitch muscle (Close 1972). If this were true for the concavity of the force-velocity curve of in situ muscle, no difference would be expected in the concavity of the force-velocity curve between men and women, since no substantial differences in the histochemically determined muscle fibre composition have been found so far (Komi and Karlsson 1978; Nygaard et al. 1983; Schantz et al. 1983). This is consistent with the observed relative constancy of the mechanics of the tetanus and current (cross-bridge) theories of muscle contraction. Simmons and Jewell (1974) have proposed that the rising phase of an isometric tetanus is determined by the net rate of cross-bridge attachment and the values of the maximal velocity of shortening at zero load have been described as being directly proportional to the myosin adenosine triphosphatase activity (Close 1972). It, therefore, seems reasonable to conclude that long-term HDT in men and women has no or very little influence on either cross-bridge cycles or myosin activity.

In summary, the results showed on the one hand that after prolonged HDT, contractile properties of the human triceps surae muscle are reduced, and on the other hand, the data demonstrated sex differences in the contractile properties of the ankle plantarflexor muscles. The magnitude of the changes in the contractile properties of the neuromuscular system in men and women under conditions simulating microgravity were shown to differ markedly. These data would suggest different effects of HDT on neural command and on peripheral sites (fibre function) determining functional properties of the neuromuscular system in men and women. This should be taken into consideration when employing women and men in professional operations on Space missions. Finally, these differences should be taken into consideration both in developing and recommending countermeasures aboard an orbital Space Station.

Acknowledgements The author wishes to express his appreciation to all those who contributed to the success of the experiment. He is

especially grateful to Miss Lyudmila Prokopenkova and Mr. Anatoli Dotsenko for technical assistance in the preparation on the manuscript. The author gratefully acknowledges the contribution made by the four women subjects who endured the 120-day confinement. This work was supported by the Founds Institute of Biomedical Problems.

References

- Asmussen E (1974) Development patterns in physical performance capacity. In: Larsson L (ed) *Fitness, health and work capacity: international standards for assessment*. MacMillan New York, pp 435–438
- Åstrand P -O (1952) *Experimental studies of physical working capacity in relation to sex and age*. Munksgaard Copenhagen
- Burke RE (1981) Motor units: anatomy, physiology, and functional organization. In: Brooks VB (ed) *Handbook of physiology, section 1. The nervous system, vol II. Motor control, part 1*. pp 345–422
- Carlsöö S, Edfeld AW (1963) Attempts at muscle control with visual and auditory impulses a auxiliary stimuli. *Scand J Psychol* 4:231–235
- Close RI (1972) Dynamic properties of mammalian skeletal muscle. *Physiol Rev* 52:129–197
- Convertino VA, Bisson R, Bates R, Goldwater D, Sandler H (1981) Effects of antiorthostatic bedrest on the cardiorespiratory responses to exercise. *Aviat Space Environ Med* 52:251–255
- Day MK, Allan DL, Mohajerani L, Greenisen MC, Roy RR, Edgerton VR (1995) Adaptations of human skeletal muscle fibers to spaceflight. *J Gravit Physiol* 2:P47–P50
- Dudley GA, Duvoisin MR, Convertino VA, Buchanan P (1989) Alterations of the in vivo torque-velocity relationship of human skeletal muscle following 30 days exposure to simulated microgravity. *Avia Space Environ Med* 60:659–663
- Dudley GA, Duvoisin MR, Adams GR, Meyer RA, Belew AH, Buchanan P (1994) Adaptations to unilateral lower limb suspension in humans. *Aviat Space Environ Med* 63:678–683
- Freund HJ (1983) Motor unit and muscle activity in voluntary motor control. *Physiol Rev* 63:387–436
- Grigor'yeva LS, Kozlovskaya IB (1987) Effects of weightlessness and hypokinesia on velocity and strength properties of human muscles. *Kosm Biol Aviakosm Med* 21:27–30
- Häkkinen K (1994) Neuromuscular adaptation during strength training, aging, detraining, and immobilization. *Crit Rev Phys Rehabil Med* 6:161–198
- Häkkinen K, Komi PV (1983) Electromyographic changes during strength training and detraining. *Med Sci Sports Exerc* 15:445–460
- Henneman E, Somjen G, Carpenter DO (1965) Functional significance of cell size in spinal motoneurons. *J Neurophysiol* 28:560–580
- Hermansen L, Döbeln W von (1971) Body fat and skinfold measurements. *Scand J Clin Lab Invest* 27:316–319
- Jaweed MM, Grana EA, Glennon TP, Monga TN, Mirabi B (1995) Neuromuscular adaptations during 30 days of cast-immobilization and head-down bedrest. *J Gravit Physiol* 2:P72–P73
- Kirenskaya AV, Kozlovskaya IB, Sirota MG (1985) Effect of immersion hypokinesia on the characteristics of the rhythmic activity of the motor units of the soleus muscle. *Kosm Biol Aviakosm Med* 19:27–32
- Komi PV (1986a) Training of muscle strength and power: interaction of neuromotoric, hypertrophic, and mechanical factors. *Int J Sports Med [Suppl]* 7:10–15
- Komi PV (1986b) How important is neural drive for strength and power development in human skeletal muscle? In: Saltin B (ed) *Biochemistry of exercise. VI. International Series on Sports Science vol. 16. Human Kinetics, Champaign, Ill.*, pp 515–529
- Komi PV, Karlsson J (1978) Skeletal muscle fibre types, enzyme activities and physical performance in young men and women. *Acta Physiol Scand* 103:210–218
- Koryak Y (1992) *Methods of investigation of neuromuscular system of athlete*. Institute Park Press, Moscow

- Koryak Y (1994) Contractile characteristics of the triceps surae muscle in healthy men during 120-days head-down tilt (HDT) and countermeasure. *J Gravit Physiol* 1:P141–P143
- Koryak Y (1995a) Contractile properties of the human triceps surae muscle during simulated weightlessness. *Eur J Appl Physiol* 70:344–350
- Koryak Y (1995b) Mechanical and electrical adaptation of skeletal muscle to gravitational unloading. *J Gravit Physiol* 2:P76–P79
- Koryak Y (1996) Changes in action potential and contractile properties of skeletal muscle in human's with repetitive stimulation after long-term dry immersion. *Eur J Appl Physiol* 74:496–503
- Koryak Y, Kozlovskaya IB (1994) The excitability of motoneuron pool in man under long-term antiorthostatic hypokinesia. In: Agadzhanian N (ed) *Proceedings of VIIIth All-Russian Symposium: Ecologo-physiol problems of adaptation*. Academic Press, Moscow, pp 127–128
- Kozlovskaya IB (1991) Neurophysiological effects caused by short- and long-term exposures to microgravity. In: Yajima K (ed) *Aerospace Science*. Nihon University, Tokyo, pp 145–150
- Kozlovskaya IB, Kreidich YV, Rakhmanov AS (1981) Mechanisms of the effects of weightlessness on the motor system of man. *Physiologist* 24:S59–S64
- Magnus R (1924) *Korpersfelling*. Springer, Berlin Heidelberg New York
- Magoun HW, Rhines R (1946) An inhibitory mechanism in the bulbar reticular formation. *J Neurophysiol* 9:165–171
- Martin TP, Edgerton VR, Grindeland RE (1988) Influence of spaceflight on rat skeletal muscle. *J Appl Physiol* 65:2318–2325
- Martyanov VA, Koryak YA (1973) Increase of a voluntary strength effort due to additional afferent effects. *Sechenov Physiol J (USSR)* 59:1756–1760
- Milner-Brown HS, Stein RB, Yemm K (1973) The orderly recruitment of human motor units during voluntary isometric contraction. *J Physiol (Lond)* 230:359–370
- Moritani T, DeVries HA (1979) Neural factors versus hypertrophy in the time course of muscle strength gain. *Am J Phys Med* 58:115–130
- Nygaard E (1981) Women and exercise – with special reference to muscle morphology and metabolism. In: Poortmans J, Niset G (eds) *Biochemistry of exercise*. IVB. University Park Press, Baltimore, pp 161–175
- Nygaard E, Houston M, Suzuki Y, Jorgensen K, Saltin B (1983) Morphology of the brachial biceps muscle and elbow flexion in man. *Acta Physiol Scand* 117:287–292
- Petrofsky JS, Burse RL, Lind AR (1975) Comparison of physiological responses of women and men to isometric exercise. *J Appl Physiol* 38:863–868
- Riley DR, Slocum GR, Bain JLW, Sedlak FR, Soma TE, Mellender JW (1990) Rat hindlimb unloading: soleus histochemistry, ultrastructure, and electromyography. *J Appl Physiol* 69:58–66
- Sale DG, MacDougall JD, Alway SE, Sutton JR (1987) Voluntary strength and muscle characteristics in untrained men and women and bodybuilders. *J Appl Physiol* 62:1786–1793
- Sandler H, Vernikos J (1986) *Inactivity: physiological effects*. Academic Press, Orlando, Fla, pp 1–9
- Schantz P, Randall-Fox E, Hutchison W, Tyden A, Astrand P-O (1983) Muscle fibre type distribution, muscle cross-sectional area and maximal voluntary strength in humans. *Acta Physiol Scand* 117:219–226
- Simard T, Basmajian JV, Janda V (1968) Effects of ischemia on trained motor units. *Am J Phys Med* 47:64–71
- Simmons RM, Jewell BR (1974) Mechanics and models of muscular contraction. *Rec Adv Physiol* 9:87–147
- Suzuki Y, Murakami T, Haruna Y, Kawakuba K, Goto S, Makita Y, Ikawa S, Gunji A (1994a) Effects of 10 and 20 days bed rest on leg muscle mass and strength in young subjects. *Acta Physiol Scand* 150 [Suppl 616]:5–18
- Suzuki Y, Kashihara H, Takenaka K, Kawakubo K, Makita Y, Goto S, Ikawa S, Gunji A (1994b) Effects of daily mild supine exercise on physical performance after 20 days bed rest in young persons. *Acta Astron* 33:101–111
- Wagman IN, Pierce DS, Burger RE (1965) Proprioceptive influence in volitional control of individual motor units. *Nature* 207:957–958
- West JB (1984) Spacelab – the coming of age of space physiology research. *J Appl Physiol* 57:1625–1631