Isokinetic Force and Work Capacity After Long-Duration Space Station Mir and Short-Term International Space Station Missions

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INTRODUCTION: The effects of long-duration (213.0 ± 30.5 d) stays aboard the orbital station Mir and short-term (∼10 d) spaceflights aboard the International Space Station (ISS) on the joint torques of various muscles and work capacity of knee extensors were studied in male cosmonauts.

METHODS: Joint torque and muscle endurance testing was performed 30 d before and 3–5 d after a spaceflight, using a LIDO® Multi-Joint Isokinetic Rehabilitation System (USA).

RESULTS: Greater postflight changes in maximal joint torque were observed for back, knee, and ankle extensors compared with flexors, and the difference was especially clearly seen after long-term spaceflights. The decrease in maximal joint torque of hip extensors substantially varied, being the greatest in voluntary concentric movements in a low-velocity high-force mode at angular velocities of 30 and $60° \cdot s^{-1}$ (by 16 and 13%, respectively) and the lowest in high-velocity modes at velocities of 120 and $180° \cdot s^{-1}$ (by 9 and 11%, respectively). Muscle work capacity was inferred from the gradient of declining muscle force produced in a series of rhythmic voluntary concentric movements and was found to decrease after both short- and long-term spaceflights. The area under the muscle contraction curve decreased to a greater extent and in all regions of the curve after long-term spaceflights. The fatigue index averaged 0.90 ± 0.03 at baseline and remained much the same, 0.90 ± 0.04, after a short-term spaceflight. However, after a long-duration spaceflight, the fatigue index increased 14.1%.

DISCUSSION: The finding that the contractile functions and work capacity of muscles decrease more after long-term than after short-term spaceflights in spite of the physical training program of a certain type gave grounds to assume that physical training employed in long-term spaceflights were insufficient to simulate the daily mechanical load that the cosmonauts had before a spaceflight.

KEYWORDS: real microgravity, spaceflight, contractile properties, isokinetic dynamometry.

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Astronauts and cosmonauts undergo important physiological deconditioning in space due to the weightless environment. Bone loss, muscle atrophy, cardiovascular deconditioning, and neurovestibular and muscle alterations are some of the most common issues experienced during space missions. The loss of skeletal muscle mass and functions in response to microgravity exposure has been a medical and physiological concern since the early Gemini, Soyuz and Skylab missions, and, together with changes in neural drive, is a main determinant of the decline in muscle strength and power.[6] Extremely complex changes arise in muscle mass and contractile function in microgravity in spite of physical training (PT) employed during long-duration spaceflights, as has been demonstrated in many studies. The loss of skeletal muscle mass[28] and concomitant changes in muscle function[42] induced by prolonged sojourns in microgravity environments can adversely affect the performance of astronauts during routine mission-related activities and upon their return to Earth.

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Muscle mass loss of 4–10% has been observed in astronauts after an 8-d Shuttle mission.[28] The muscle volume has been reported to decrease to a somewhat greater extent, by 6–16%, with the spaceflight duration increasing from 9 to 16 d.[1] Moreover, muscle fiber atrophy of 16–36% has been found in m. vastus lateralis after an 11-d spaceflight.[7]

Greater losses of muscle mass occur during longer spaceflights in spite of employing physical training (PT) programs. For instance, a decrease of 10–24% in muscle volume has been observed in astronauts after missions of approximately 6 mo to the Mir Space Station and the International Space Station (ISS).[8,28,42] However, the muscle mass has been found to stabilize to a certain extent or to achieve a new stable level in humans exposed to 120-d antiorthostatic bed rest,[28] which is used as a main ground-based model of long-duration spaceflights to study the long-term effects of microgravity.[8]

The strength of muscle contraction decreases in parallel with muscle volume loss, but the changes in strength are somewhat greater.[4] For instance, a substantial (up to 14%) decrease in hand muscle contraction strength has been observed after short-term (2–5 d) spaceflights aboard Soyuz spacecrafts,[12] and decreases of 12% in the strength of hip extensors, 23% in the strength of hip flexors,[9] and up to 16% in muscle work capacity[28] have been reported for astronauts after Shuttle missions of 5–17 d.

Studies of the force–velocity characteristics of ankle extensors and flexors by conventional isokinetic dynamometry after a 7-d spaceflight have shown a decrease in the strength of ankle extensors throughout the velocity range examined, including an isokinetic regimen, the decrease amounting to 20–30% of the baseline in all but the isometric mode and being somewhat lower, ~15%, in the isometric regimen.[26]

Postflight measurements in crewmembers after missions of 16–28 wk to the Mir Space Station have shown a decrease of up to 48% in the force of maximal voluntary contraction (MVC) of ankle flexors[42] and a 31% increase in the maximal shortening velocity of muscle fibers.[27] The contraction force of knee extensors and the endurance of knee flexors have been found to decrease by approximately 26% after a mission of 129–145 d to the ISS.[27] Trappe et al.[40] have reported decreases in maximal power (by 32%) and maximal force (by 20–29%) of ankle extensors in voluntary movements in a broad isokinetic velocity range after a mission of approximately 6 mo to the ISS. It is commonly accepted that major losses affect trunk and lower limb muscles, which are highly active under normal Earth's gravity (1 G). Muscle strength in the upper limbs is affected to a lesser extent than that in the lower limbs.[26]

The fact that losses in muscle strength are greater than losses in muscle mass (volume) after both spaceflights and model exposures (immersion, bed rest, or limb suspension) has prompted a hypothesis that the motor control is basically affected in microgravity.[22,24] For instance, a 45% decrease in power produced by hip extensors after a 180-d spaceflight is considerably greater than can be explained solely by muscle mass loss.[24] A decrease in power produced by hip extensors during explosive voluntary contractions is accompanied by a substantial decrease in their electromyographic (EMG) activity.[24] Zange et al.[42] have observed a greater percent change in force (by 20–48%) than in muscle volume (by 6–20%) for knee extensor by magnetic resonance imaging (MRI). Lambertz et al.[27] have similarly reported a 17% decrease in isometric force after 90–180 d.

A decrease in muscle contraction force has been accompanied by a decrease in EMG activity of ankle extensors, averaging 39%.[27] Concomitant changes observed after spaceflights have similarly been detected in ground-based model studies simulating muscle unloading. For instance, Hather et al.[11] have shown using MRI that a 6-wk unilateral unloading of the left leg reduced the cross-sectional area (CSA) of its hip extensors by 12% relative to the right leg, which was not unloaded. The total muscle CSA of the left leg was 14% lower than that of the right leg. MRI showed irregular reduction of the CSA for thigh muscles. The CSA reduction in hip extensors (−16%) was twice greater than in hip flexors (–7%). Interestingly, the rectus femoris muscle of the knee extensors showed no change in CSA, whereas the vastus lateralis, and vastus medialis muscles showed similar decreases of approximately 16%. The total CSA reduction in the unloaded limb was assumed to be due mostly to the CSA reduction in m. soleus (–17%) and m. gastrocnemius (–26%). Berg et al.[4] have observed that the isometric MVC and concentric forces of hip extensors were reduced by 25–30% after bed rest for 42 d, while the CSA decreased only by 14%; and maximal EMG activity, by 19%.

Greater changes in muscle strength than in CSA suggest changes in internal properties[19,20,43] and of motor units, their recruitment, or neural drive.[17,36] The last assumption is supported by a lower electromechanical efficiency, which is evident from the finding that higher EMG activity (+44%) is involved in generating the same isometric force (100 Nm) after 6-wk bed rest.[34] Therefore, changes in muscle activation may substantially affect the operational ability of crewmembers upon landing after exposure to microgravity.

Here are reported the changes observed in the maximal joint torques of several muscle groups and the muscle work capacity of nine crewmembers after Mir missions of 213.0 ± 30.5 d and five visiting crewmembers after ISS missions of 7–10 d.

Although all of the spaceflight crewmembers did the training during the flight, the prolonged impact of weightlessness had a detrimental effect on the human neuromuscular system.[10,16] However, detailed information on the actual exercise programs performed during long-duration space missions is sparse, thus making it difficult to quantitatively assess the effectiveness of the exercise countermeasures to protect against skeletal muscle atrophy and function.

A unique feature of this study is that changes in contractile properties are directly compared for spaceflights of different durations and muscular alterations are considered in the context of using or not using PT during a spaceflight.

The objective of the study was to quantitatively estimate the changes in contractile functions and work capacity of muscles in cosmonauts after short-term and long-duration spaceflights by using isokinetic dynamometry during voluntary contractions. In the current study, we report changes in the skeletal muscle strength and endurance (performance) in nine crewmembers' missions to the Mir Orbital Station and in five crewmembers' missions to the ISS. We assumed that large changes will be observed after long-duration spaceflights and to a greater degree in the extensors muscles.

METHODS

The cosmonauts reported to the laboratory twice. During the first visit, they were only familiarized with the experimental set-up and procedures during a preliminary session before starting the preflight tests [~60 d preflight (L-60)]. On a subsequent visit the cosmonauts performed two sets of experiments: ~40-30 d before spaceflight baseline data collections and immediately after spaceflight [return (+R); +R5/+R7]. The cosmonauts gave their written informed consent to participate in this study.

The study was approved by the Biomedical Ethics Committee at the Institute of Biomedical Problems (Russian Academy of Sciences) and Yu.A. Gagarin Cosmonauts Training Centre (Star City, Moscow region, Russia).

Subjects

Two groups of male cosmonauts participated in the study. Group 1 ($N = 9$; 45.1 ± 2.0 yr, 176.0 ± 2.3 cm, 79.9 ± 2.0 kg) included prime crewmembers from long-duration missions (209.8 ± 30.4 d) to the Mir Space Station; group 2 ($N = 5$; 37.6 ± 2.8 yr, 177.0 ± 1.8 cm, 74.0 ± 2.8 kg) included visiting crewmembers from short-term missions (9.4 ± 0.2 d) to the ISS. All crewmembers were informed about the goals and methods of the study of muscle contractile functions, the study procedures, risks, and significance, and gave their written informed consent to voluntarily participate in the study.

The cosmonauts did not do PT during short-term missions and followed a standard Russian PT program during long-duration spaceflights.[38]

Procedure

Torques of extensor and flexor muscles of the back, knee, and ankle were measured during voluntary movements of back, knee, and ankle flexion and extension. All testing was conducted on the right limbs. Peak torques and joint angle at peak torque of various muscles were measured with a LIDO® Active Multi-Joint Isokinetic Rehabilitation System (Loredan Biomedical, Davis, CA, USA), which was modified to measure the maximal joint torque during concentric muscle contractions of more than 400 Nm.

Before isokinetic testing was conducted, subjects pedaled a cycle ergometer at a workload of 25–50 W at a cadence of 60–80 rpm for 5 min. Standard joint-specific warm-up procedures were followed and consisted of five submaximal repetitions and two to three maximal repetitions. After the warm-up, subjects rested at least 2 min. Strength tests were performed such that subjects exerted a maximal effort in only one direction for each set of repetitions.

The protocol and procedures of testing muscle functions with a LIDO® system were explained to the subjects 30 ± 5 d before the spaceflight.

A subject sat comfortably on the special universal table of a LIDO® isokinetic dynamometer. The LIDO® dynamometer was calibrated externally and internally (electronically) before each test session, and a gravity correction procedure was performed to eliminate the effect of the limb weight on joint torque measurements. The subjects familiarized themselves with each angular test velocity by performing three to five movements, from which the maximum value from either of the two preflight baseline sessions was selected. Data were collected after 2–3 min rest.

Each subject was instructed to exert maximal effort in only one direction and in every movement when performing a test; no verbal instruction was provided during testing.

Three protocols were employed in pre- and postflight testing for maximal voluntary joint torques produced by various muscles.

In Protocol 1, joint torques were measured during voluntary concentric movements with various angular velocities when flexing and extending back, knee, and ankle muscles.

In Protocol 2, joint torques were measured during voluntary eccentric movements with various angular velocities when flexing and extending back, knee, and ankle muscles.

In Protocol 3, repetitions of voluntary concentric movements were assessed upon ankle extension at a velocity of $60° \cdot s^{-1}$ in cycles of 1-s contraction and 1-s relaxation.

Each subject performed three movements at a given velocity in a given movement mode with at least 1 min rest between movements.

Muscle strength was measured as a peak joint torque produced in the total range of concentric (**Fig. 1**, upper panel) or eccentric (Fig. 1, middle panel) movements, and the highest value obtained in consecutive voluntary contractions for both flexor and extensor muscles was taken as a maximal joint torque.

Testing the flexors and extensors of the back of the subject was carried out in a sitting position and angle of the hip joint was ~130–140° and hip axis coincided with the axis of rotation of the recording device of the isokinetic dynamometer (Fig. 1, top panel). The range of motion in trunk flexion and extension was 75–130° at angular velocities of 30 and $75° \cdot s^{-1}$.

Testing the extensor muscles and the hip flexors of the subject was carried out in a sitting position and angle of the knee joint was ~90°, and the axis of the knee joint coincided with the axis of rotation of the recording device of the dynamometer. The range of motion in flexion and extension was 90–60° in tests for maximal joint torque during concentric movements and work capacity and 33–90° in tests for maximal joint torque during eccentric movements. Angular velocities of thigh muscle contractions were 30, 60, 120, and $180° \cdot s^{-1}$ in concentric movements and 30, 60, 90, and $120° \cdot s^{-1}$ in eccentric movements.

Testing muscles, the extensor and flexor of the foot, was performed in the test position "kneeling" and the angle of the knee and ankle joint was ~90° and the ankle joint axis coincided with the axis of rotation of the recording device of the dynamometer. The range of motion in ankle flexion and extension was ~25° in

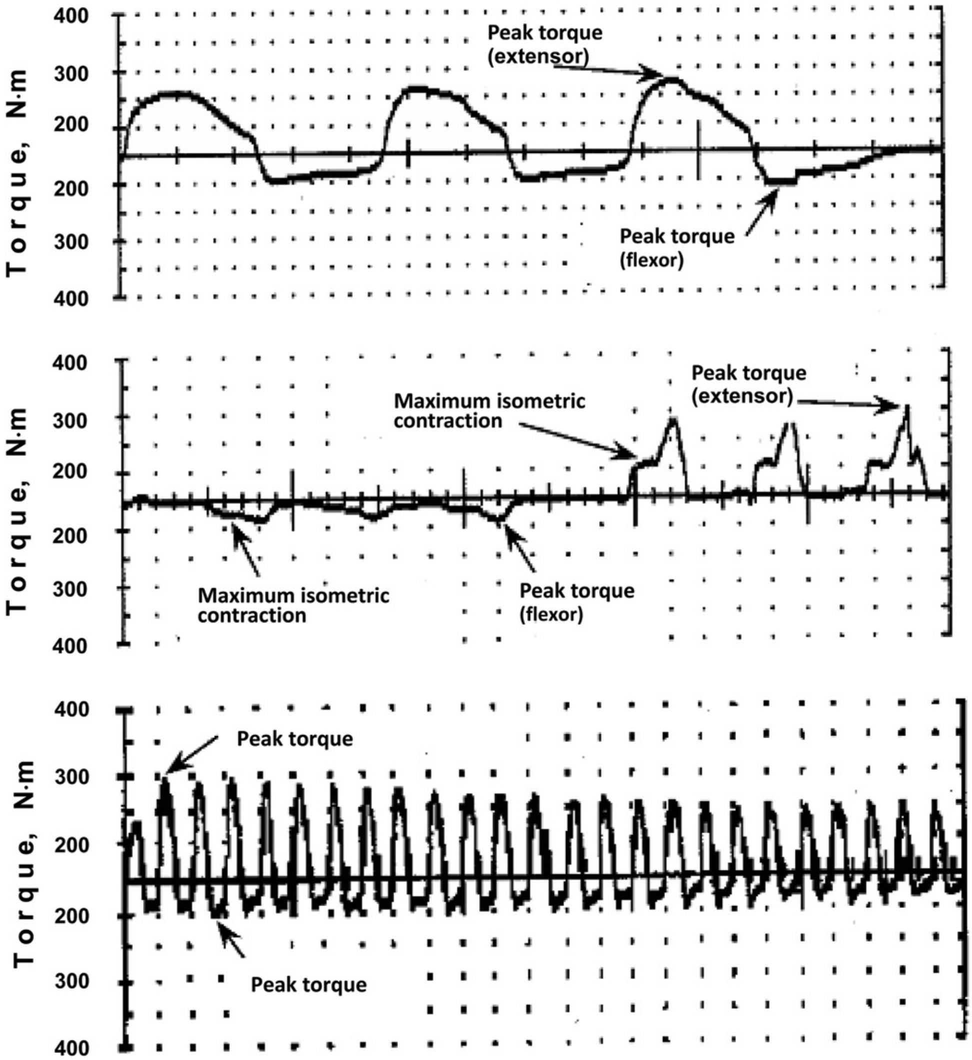

Fig. 1. Examples of three concentric (upper panel) and eccentric (middle panel) isokinetic voluntary contractions and during 25 repetitions of isokinetic voluntary contractions (lower panel). (From Greenisen et al., 1995).[9]

the case of maximal extension and 20° in the case of minimal flexion in both concentric and eccentric movements (Fig. 1, lower panel). Angular velocities of ankle muscle contractions were 60, 120, and $180° \cdot s^{-1}$ in concentric movements and 30, 60, 90, and $120° \cdot s^{-1}$ in eccentric movements.

After voluntary testing, the subjects proceeded with the fatigue test. Skeletal muscle endurance was defined as the total work generated during 25 repetitions of voluntary concentric knee extension at an angular velocity of $60° \cdot s^{-1}$ in cycles of 1-s contraction and 1-s relaxation (Fig. 1, lower panel). The angle between the thigh and shin was 90° in the starting position. Prior to performing local dosed muscle work, the subject was instructed to exert maximal effort in every movement.

Peak torque values were used as measures of knee extensor/flexor strengths in pre- and postspaceflight sessions. For each joint movement, peak torque was defined as the highest torque value achieved across each of the repetitions. For knee extensor and flexor tests, isokinetic endurance was defined as the total work performed during 25 repetitions of concentric knee exercise. The first prespaceflight test was considered a familiarization session and was not used for subsequent analyses.

The degree of fatigue, or performance, was evaluated in terms of fatigue index (FI), which was calculated as a ratio of the maximal joint torque averaged over the five last contractions in a series of voluntary 25 repetitions of concentric muscle contractions to the maximal joint torque averaged over the five first contractions.[23]

The leading (right) limb was examined in all testing procedures (excepting the trunk), if not medically contraindicated. Joint positions (configurations) and ranges of motion were recorded for each subject and reproduced upon testing on day 3 (± 1) after landing.

All subjects were instructed to abstain from food for 2 h before testing, from caffeine for 4 h before testing, and from exercise for 12 h before testing.

To preserve the muscle contractile properties in long-term space missions, cosmonauts used PT, which were mostly of a locomotor type and were performed for 1.5–2 h. Four-day microcycles, each including 3 d with PT and 1 d of rest, were followed in the PT program.[12]

A treadmill and a cycle ergometer were the main PT tools, training the cardiovascular and respiratory systems.[34] The treadmill device could be used in a passive (subject driven) or active (motorized) mode of operation, which was selected by the crewmember during each exercise session. Crewmembers used a subject-loading device to fix themselves to the treadmill, which provided varying levels of loading relative to body weight (typical load was ~70% of body weight) during use. In this way, the crewmembers could complete running or walking exercise while partially loaded. The cycle ergometer provided a load of 50–225 W at a pedaling rate of 40–80 rpm. The crewmembers also had access to bungee cords, which they could use to provide resistance-type exercise for various muscle groups.

Statistical Analysis

The effect of spaceflight on function [all isokinetic speeds and maximal voluntary contraction (MVC) angles] was analyzed using a one-way repeated-measures ANOVA for each variable. A significant time effect was interpreted using pairwise comparisons combined with the Bonferroni adjustment. For all strength measurements, data were collected at 500 Hz. From these data, peak torque, for any given measurement, was taken as the highest recorded value. Any record showing an artifact or torque spike was discarded and not used for analysis. During the maximal isokinetic contraction, the record with the greatest value was used. In addition, the angle-specific torque at 90° was recorded for all contractions. Differences between preflight (baseline) and postflight parameters were checked for significance by the parametric Student *t*-test and were considered significant at $P < 0.05$. Values are given as mean ± SEM in the text. The percentage changes for pre- and postspaceflight was also calculated.

RESULTS

Our analysis of the functional changes in muscles showed that the maximal joint torques of flexor muscles were consistently lower than baseline in both concentric and eccentric voluntary movements at all angular velocities.

However, the decrease in maximal joint torque of hip extensors substantially varied (**Fig. 2**, upper panel), being the greatest in voluntary concentric movements in a low-velocity high-force mode at angular velocities of $30° \cdot s^{-1}$ (from 153.4 ± 15.7 N to 129.2 ± 17.0 N, corresponding to a relative change of 16%; $P < 0.05$) and $60° \cdot s^{-1}$ (from 82.4 ± 2.2 N to 79.8 ± 11.6 N, corresponding to a relative change of 13%) and the lowest in high-velocity modes at velocities of $120° \cdot s^{-1}$ (from 128.8 ± 18.1 N to 118.2 ± 16.2 N, corresponding to a relative change of 9.0%) and $180° \cdot s^{-1}$ (from 78.4 ± 10.6 N to 69.6 ± 11.4 N, corresponding to a relative change of 11.2%). In the case of hip flexors, the maximal joint torque decreased insignificantly throughout the angular velocity range, by 3, 8, 11, and 6% at angular velocities of 30, 60, 120, and $180° \cdot s^{-1}$, respectively.

When analyzing the maximal joint torques produced by knee muscles during voluntary eccentric isokinetic movements, similar decreases (approximately 14%; $P < 0.05$) in contractile potential were observed at angular velocities of 60, 90, and $120° \cdot s^{-1}$ and an insignificant increase (9% on average) was only detected a low-velocity (high-frequency) regime.

Decreases in maximal joint torque of ankle extensors (**Fig. 3**, lower panel) were much the same (approximately 13%; $P < 0.05$) in eccentric isokinetic voluntary movements at angular velocities of 30, 90, and $120° \cdot s^{-1}$. In the case of ankle flexors, the lowest changes (~6%) were observed for low-velocity (high-force) movements ($30° \cdot s^{-1}$).

A greater effect of spaceflights on muscle strength was observed for back muscles in both concentric and eccentric movements at all angular velocities. A decrease in strength of trunk extensors was maximal (from 285.0 ± 63.2 N to 192.3 ± 43.5 N, corresponding to a relative change of 32.5%) in high-velocity movements and lower (from 277.3 ± 59.6 N to 201.8 ± 44.9 N, corresponding to a relative change of 27.2%) in low-velocity (high-force) movements. In the case of back flexors, a decrease in maximal joint torque was greater (from 204.0 ± 7.9 N to 171.9 ± 3.8 N, corresponding to a relative change of 16.2%) at high velocities than at low velocities (high force) (from 210.0 ± 10.0 N to 197.6 ± 14.1 N, corresponding to a relative change of 5.7%).

Fig. 4 (upper panel) shows how the maximal joint torque of hip extensor muscles changed during rhythmic dynamic concentric movements (contractions) at a constant angular velocity of $60° \cdot s^{-1}$ before and after a short-term space mission. A data analysis demonstrated that the maximal joint torque of knee extensor muscles generally decreased during rhythmic movements, but the kinetics of changes in torque did not significantly differ between pre- and postflight tests; i.e., work capacity of hip extensors, or their fatigue, did not significantly change after a spaceflight. The FI averaged 0.90 ± 0.03 at baseline and remained much the same, 0.90 ± 0.04, after a spaceflight (Fig. 4, upper panel, insert).

An analysis of changes in the force–velocity parameters of knee flexors and extensors (Fig. 2, upper panel) showed, first, that the maximal joint torques of the muscles in eccentric movements were substantially higher than in concentric movements. Second, the maximal joint torque of thigh muscles decreased considerably in all crewmembers at all angular velocities both before and after a spaceflight according to isokinetic dynamometry data. The extensor muscles showed significant changes in both concentric and eccentric movement modes. The changes differed in extent between the modes, being greater in concentric than in eccentric movements. In the case of hip flexors, similar decreases in force properties (approximately 20%) were observed at different angular velocities in both concentric and eccentric movements. In the case of hip extensors, such a pattern was not observed, and the changes varied. Substantial changes in maximal joint torque were detected during concentric movements in high-velocity ($180° \cdot s^{-1}$; from 106.7 ± 6.5 N to 80.3 ± 4.3 N, corresponding to a relative change of 24.7%; $P < 0.05$) and high-force ($60° \cdot s^{-1}$; from 153.1 ± 11.8 N to 118.0 ± 9.2 N, corresponding to a relative change of 22.9%; $P < 0.05$) modes, while similar decreases in the parameter were seen at angular velocities of $120° \cdot s^{-1}$ (from 118.0 ± 6.4 N to 96.0 ± 6.2 N, corresponding to a relative change of 18.6%) and $30° \cdot s^{-1}$ (from 137.3 ± 15.6 N to 112.0 ± 9.8 N, corresponding to a relative change of 18.4%).

A similar time course of changes in force–velocity properties was observed for ankle flexors and extensors (Fig. 3, lower panel). It should be noted that the maximal joint torques of ankle flexors and extensors changed to a greater extent than those of hip flexors and extensors. Greater changes were observed during movements in both concentric and low-velocity ($30° \cdot s^{-1}$; $P < 0.05$) high-force eccentric modes, especially in the latter. At higher velocities ($120° \cdot s^{-1}$ and $180° \cdot s^{-1}$; $P < 0.05$), greater changes were detected in eccentric movements. Ankle flexors showed unidirectional changes, decreasing in maximal joint torque in both concentric and eccentric movements throughout the angular velocity range examined. The changes in maximal joint torque were somewhat greater in concentric voluntary movements.

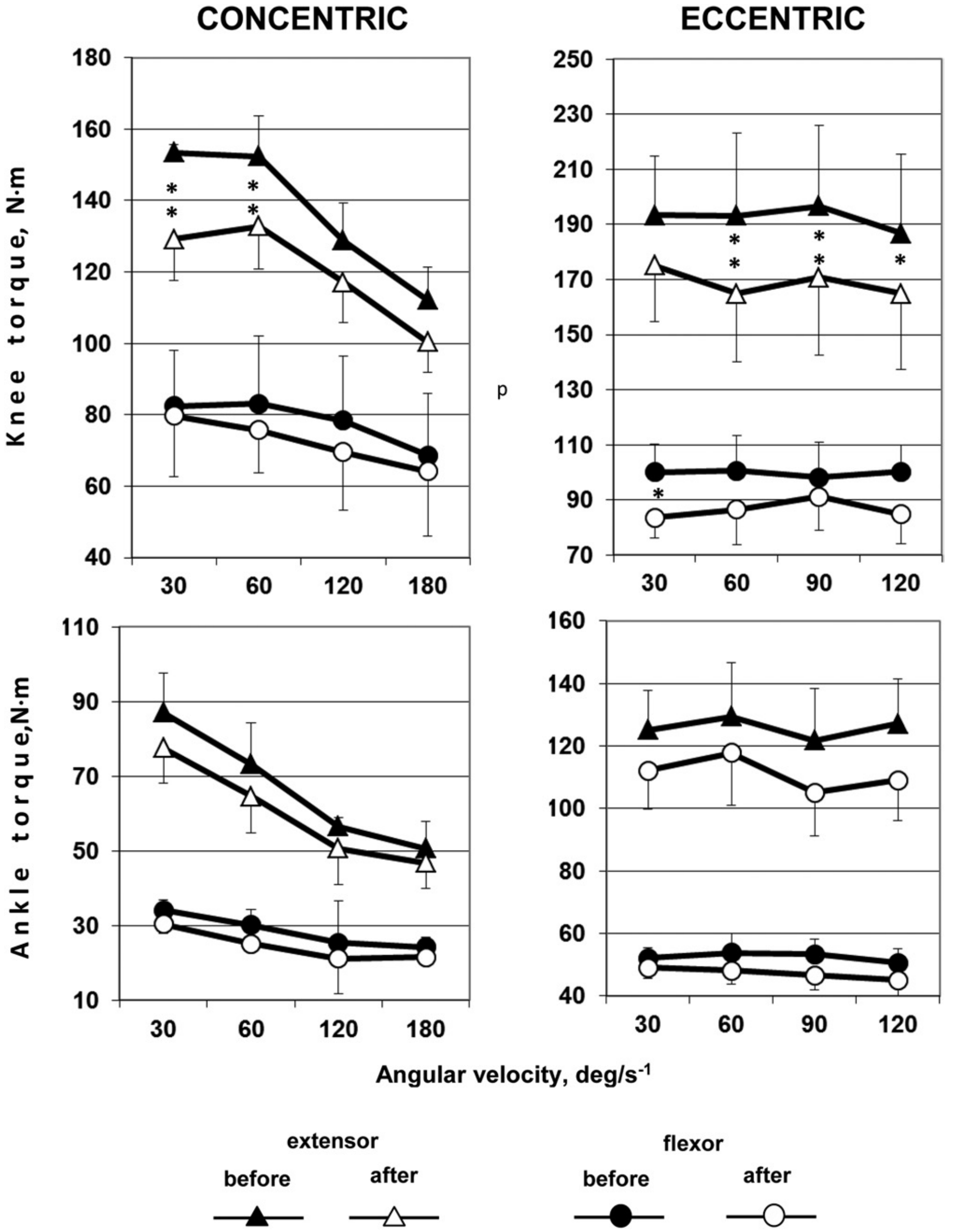

Fig. 2. Knee (upper panel) and ankle (lower panel) extensors (two upper curves) and flexors (two lower curves) were tested for maximal joint torque during concentric and eccentric voluntary contractions at various angular velocities before and after a short-time spaceflight. ***$P < 0.05$; ** $P < 0.01$.

An analysis of the changes in maximal joint torques produced by back flexors and extensors during eccentric and concentric movements showed, first, that the maximal joint torques produced by back flexors and extensors in eccentric contractions were significantly higher than in concentric contractions both before and after a spaceflight. Second, dissimilar muscle responses to unloading were observed during concentric and eccentric voluntary movements. Changes detected during low-velocity concentric contractions of back flexors were significantly lower than during eccentric movements. Back flexors showed opposite changes. At the same time, concentric voluntary movements at a greater angular velocity ($75° \cdot s^{-1}$) revealed an opposite pattern. The greatest changes in flexors were observed during concentric movements compared with eccentric ones, while back extensors displayed the greatest changes during eccentric movements compared with concentric ones.

The time course of changes in the force of knee extensor contractions was analyzed in crewmembers involved in long-duration space missions. Tests for dynamic concentric rhythmic movements (contractions) at a constant angular velocity of $60° \cdot s^{-1}$ were performed before and after a spaceflight (Fig. 4, lower panel). The analysis showed a decrease in contraction force over 25 rhythmic contractions. In other words, the work capacity of knee extensors substantially decreased; i.e., fatigue of the muscular system increased after a spaceflight ($P < 0.05$–0.001). The FI averaged 0.71 ± 0.04 at the baseline and increased to 0.81 ± 0.02 ($P < 0.01$) after a spaceflight (Fig. 4, lower panel, insert).

DISCUSSION

Three primary findings resulted from this study. First, the results of this study contribute to the literature describing the effects of spaceflight on the strength of various muscles. Second, our results supplement the literature data on the effects of short-term and long-duration spaceflights on the contractile properties of human muscles. A general trend observed in our study is that the maximal joint torques developed by lower-extremity muscles during concentric and eccentric isokinetic contractions decreased both after short-term and long-duration space missions. A time course of functional changes arising in various muscle groups was inferred from the experimental findings. Third, we observed that muscles respond to unloading in a nonlinear manner in humans exposed to microgravity, contractile properties decreasing to a greater extent in the flexor muscles that are involved in maintaining vertical posture under normal Earth's gravity (1 G). Changes in extensor muscles were similar, but lesser in extent.

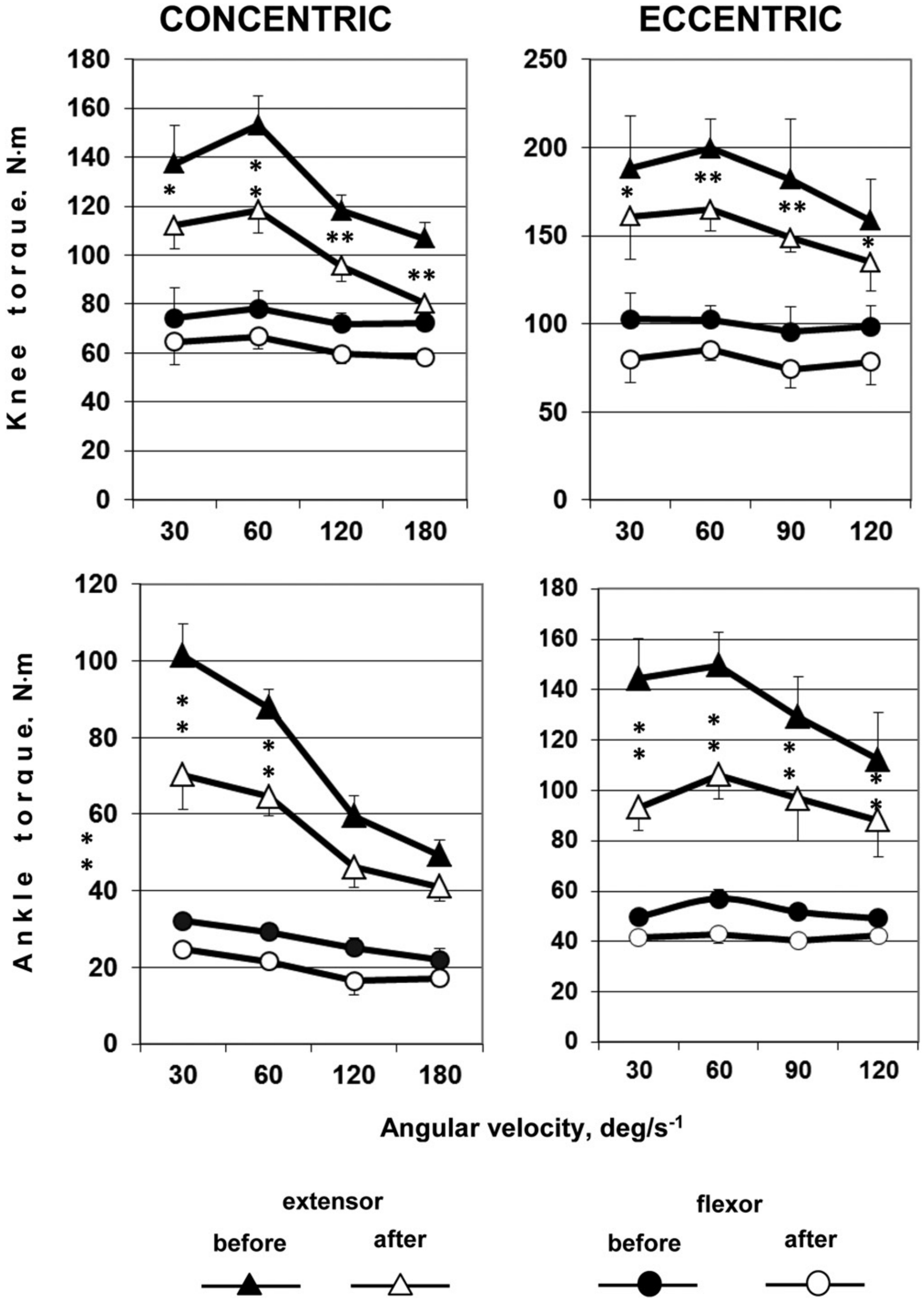

Fig. 3. Knee (upper panel) and ankle (lower panel) extensors (two upper curves) and flexors (two lower curves) were tested for maximal joint torque during concentric and eccentric voluntary movements at various angular velocities before and after a long-term spaceflight. ***** $P < 0.05$; ****** $P < 0.01$.

A direct strength comparison after a long-term spaceflight revealed certain differences for muscle groups involved in locomotion.

As demonstrated in earlier studies focusing on the characteristics of voluntary and electrically induced tetanic contractions of m. triceps surae, a short-term spaceflight causes a slight decrease in the forces of MVC (by ~9%) and electrically evoked tetanic contractions (by ~8%) and an increase in force deficiency (by 12% on average).[21] Long-duration spaceflights lead to a substantial decrease in MVC force (by 22%) and, of principal importance, muscle intrinsic force properties measured by the force of electrically evoked tetanic contractions (by 16%), causing almost a twofold increase in force deficiency.[17,18] The findings directly indicate that a predominantly central mechanism determines a decrease in muscle contractile properties in a short-duration spaceflight (in early exposure to microgravity), while a predominantly peripheral (intramuscular) mechanism comes into play at the next stage. The finding that force deficiency further increases after a long-duration spaceflight indicates that the central mechanisms continue contributing to the decrease in muscle contractile properties.

A decrement in peripheral local muscle work capacity may be due to both a decrease in muscle strength because the total area under the work capacity curve depends on the force of contraction and a poorer ability to maintain (produce) high tension in muscle contraction, that is, a decrease in endurance. The area under the curve decreased substantially for all regions of the contraction curve obtained for a test contraction after a spaceflight. The finding indicates that muscle work capacity was reduced not only because the force decreased, but also because endurance grew lower as well. It is not feasible to determine the specific contribution to work capacity for each particular factor because dynamic voluntary contractions were used to measure the work capacity, and these contractions provide an integral characteristic for both the contractile properties of the muscles involved (a peripheral factor) and their central nervous regulation (a central factor). Changes in the peripheral (contractile) component of the neuromuscular system cannot alone explain the decrease in muscle work capacity, although their contribution is major. A role is also played by alterations of the electrogenic component, including lower propagation velocities of

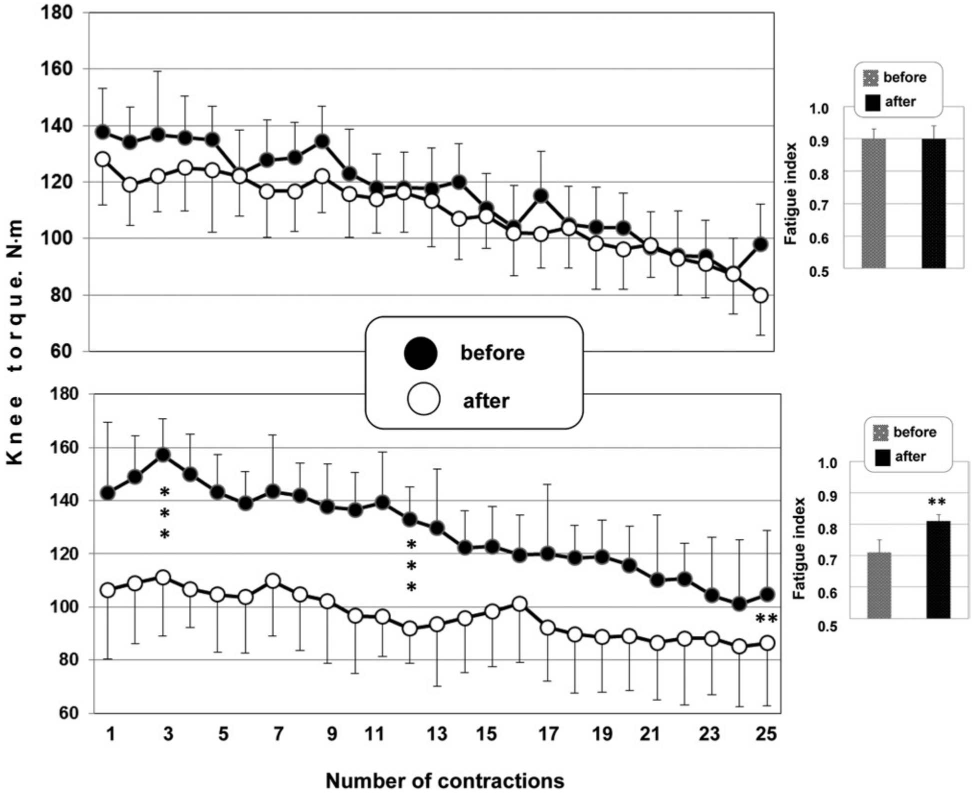

Fig. 4. Time course of the maximal joint torque of knee extensors during 25 rhythmic concentric movements (velocity 60° · s^{-1}) was studied before and after short-term (upper panel) and long-term (lower panel) spaceflight. **$P < 0.01$; ***$P < 0.001$.

action potentials in motoneuron terminals, neuromuscular synapses,[13] and electrogenic membranes of muscle fibers.[5] As we have shown previously, more prolonged exposure to mechanical unloading of the muscular system leads to a relatively higher contribution of the electrogenic component to peripheral fatigue.[17]

Greater changes in contractile properties have been observed by isokinetic dynamometry, wherein many muscles are involved in a given movement, as compared with tendon dynamometry,[17,18] wherein only one muscle is assessed. The finding suggests activation of antagonist muscles[29] and a role of efferent input to these muscles.[30,31] This input has a relatively low intensity, but seems to increase in microgravity, where support load as a factor that triggers important events in the locomotor system is absent, automatically suppressing (up to complete inhibition?) tonic activity and subsequently causing a number of physiological and structural secondary effects.

Another concept discussed in the spaceflight context is that mechanical unloading changes the activation and pattern of recruited motor units, the change affecting the muscle output in movement tests. The simplest conditions for evaluating adaptation of the muscle contractile function are provided by isometric contractions, wherein the muscle length remains constant. However, the muscle length and loading may decrease or increase depending on the external conditions during movements in vivo. In spite of its complexity, the relationship between force and speed at a particular activation level is predictable for many skeletal muscles, given that the muscle architecture and movement mechanics are known. Although the function and work capacity of muscles change in microgravity, basic mechanisms generating muscle force are preserved. The force potential is somewhat higher when an activated muscle elongates at a zero speed. It should also be noted that the force decreases with the increasing contraction speed, and, vice versa, the maximal speed increases when a minimal load is imposed on contractile elements of the muscle.

Our findings show that greater unloading-induced changes in contractile functions occur in extensors compared with other muscles[2,26] after a long-duration space mission in spite of regular PT. The finding indicates that PT is not intense enough to preserve the muscle system.[41]

It follows that the contractile properties of a muscle depend on its activity history in addition to other factors. The cosmonaut training process was therefore analyzed, and the analysis showed that cyclic exercises were mostly employed in training crewmembers for long-duration space missions. Such training seems insufficient for preserving the muscle function during a spaceflight. Hence, the training process should be planned with due regard for the functional potential of the neuromuscular system as a leading physiological system of the body.

The fact that muscle contractile functions decrease during space missions supports the idea that more efficient training programs are needed to protect skeletal muscles in long-term spaceflights. The majority of the PT programs used during spaceflights utilize a treadmill and a cycle ergometer, providing mostly cardiovascular and respiratory training[25,26] and improving aerobic capacity, but not power properties of the muscle system. However, the programs have been found to be less efficient not only in maintaining muscle mass and functions, but also in regulating mineral turnover.[32,33] As has been observed, the MVC force is already dramatically reduced (40%) after 7-d unloading without PT and continues to decrease with increasing exposure duration.[13,14] Changes in neural drive may act as an MVC-limiting factor because muscle contractile properties have been found to decline greater than muscle mass, volume, or CSA in both model exposures (bed rest[15,22]) and spaceflights.[28]

Power (resistance) training in 1 G conditions is known to increase muscle strength, muscle size, and neural drive.[3] Power training is therefore a promising means to alleviate muscle disadaptation in microgravity.[39] At any rate, observations have shown that, to maintain the mass and dynamic and isometric forces of hip and ankle extensors, it is enough to do resistance exercises every other day during a 14-d bed rest[3] or every third day during a 21-d unilateral limb unloading (suspension).[37]

Therefore, the fact that muscle contractile functions decrease, especially in long-term spaceflights, supports the idea that muscle protection during long-duration missions warrants a training program that includes high-intensity exercises to improve the power properties of muscles.[41] Power exercises seem promising for preventing muscle atrophy and weakness. Moreover, to make resistance training maximally efficient, a PT program should include both concentric and eccentric muscle contractions performed with a high intensity.[3,40]

Recent improvements in the exercise hardware on the ISS (the Advanced Resistance Exercise Device - ARED) may provide enhanced loading potential. This information is critical to guide the countermeasure program forward for future long-duration space missions. The use of resistive exercises (ARED) in the training process really improved, but did not completely eliminate, the loss of functions. The training process is a pedagogical process with its own laws. It is not enough only to use resistive exercises in the training process. It is necessary to take into account the volume of exercises performed, the number of repetitions and the number of approaches, as well as the intensity of the exercises. A recent study by Rittweger et al.[35] supports our point of view. Two crewmembers (A and B) spent 6 mo in space on ISS. Crewmember A performed fewer treadmill sessions than B (90 vs. 114), ran with lower pull-down force (median 55.9 vs. 85.6% of body weight), ran at slower speed (median 11.3 vs. 12.9 km/h), and covered a shorter distance than B per running session (median 4.7 vs. 5.8 km). Crewmember A also trained less with ARED, performing fewer heel raise sessions (54 vs. 98) with fewer repetitions (30 vs. 48) and at lower resistive force (median 122 vs. 221% of body weight). Thus, findings showed that the program of PT and the exercise devices available on the ISS (the treadmill, the cycle ergometer, and the advanced resistive exercise device) were not able to elicit loads comparable to exercise on Earth. This is confirmed by other authors.[10] To summarize, our experimental analysis confirmed again that certain phenomena are seen after short-term and long-duration spaceflights, that is, exposure to real microgravity. We quantitatively described the postflight changes and assumed that at least two mechanisms are responsible for the decrease in muscle contractile functions, determining its two stages. A central mechanism mostly contributes to the decrease in contractile functions in early exposure to microgravity (short-time spaceflights), while a peripheral mechanism plays a major role at the second stage (long-duration spaceflights).

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