RESEARCH ARTICLE

Architectural and functional specifics of the human triceps surae muscle in vivo and its adaptation to microgravity

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Koryak Yu. A. Architectural and functional specifics of the human triceps surae muscle in vivo and its adaptation to microgravity. J Appl Physiol 126: 880–893, 2019. First published December 20, 2018; doi:10.1152/japplphysiol.00634.2018.—Long-term exposure to microgravity (μG) is known to reduce the strength of a skeletal muscle contraction and the level of general physical performance in humans, while little is known about its effect on muscle architecture. Architectural and contractile properties of the triceps surae (TS) muscle were determined in vivo for male cosmonauts in response (n = 8) to a spaceflight (213.0 ± 30.5 days). The maximal voluntary contraction (MVC), tetanic tension (P₀), and voluntary and electrically evoked contraction times and force deficiency (P₉) were determined. The ankle was positioned at 15° dorsiflexion (−15°) and 0, 15, and 30° plantar flexion, with the knee set at 90°. At each position, longitudinal ultrasonic images of the medial (MG) and lateral (LG) gastrocnemius and soleus (SOL) muscles were obtained while the subject was relaxed. After a spaceflight, MVC and P₀ decreased by 42 and 26%, respectively, and P₉ increased by 50%. The rate of tension of a voluntary contraction substantially reduced but evoked contractions remained unchanged. In the passive condition, fiber length (Lₐ) changed from 43, 57, and 35 mm (knee, 0°; ankle, −15°) to 34, 38, and 25 mm (knee, 0°; ankle, 30°) for MG, LG, and SOL, respectively, and θ₀ changed from 27, 21, and 23° (knee, 0°; ankle, −15°) to 43, 29, and 34° (knee, 0°; ankle, 30°) for MG, LG, and SOL, respectively. Different Lₐ and θ₀, and their changes after spaceflight, might be related to differences in force-producing capabilities of the muscles and elastic characteristics of tendons and aponeuroses.

NEW & NOTEWORTHY The present work was the first to combine measuring the fiber length and pennation angle (ultrasound imaging) as main determinants of mechanical force production and evaluating the muscle function after a long-duration spaceflight. The results demonstrate that muscles with different functional roles may differently respond to unloading, and this circumstance is important to consider when planning rehabilitation after unloading of any kind, paying particular attention to postural muscles.

INTRODUCTION

The effects of long-duration exposure to microgravity (μG) on the human body are well known. The effects arise as the human body adapts to its new environment (81, 82, 94) and include decreases in muscle volume, strength of contractions, bone mass, and aerobic capacity (31, 81). Decreases in muscle strength and stability impair the general physical performance and lead to several sequelae observed in crew members upon their return to Earth and during rehabilitation (81). Knee and ankle extensors act as antigravity muscles and experience the greatest effect of μG in (1, 4). Of these, the triceps surae (TS) muscle is the most affected (1, 4), the circumstance being possibly related to the extent of TS muscle loading during normal daily activities, such as maintaining posture or pushing off during locomotion.

The TS muscle acts as a main synergist in plantar flexion and thus plays a key role in locomotion and postural control (67) because TS muscle activation results in ankle extension and forward displacement of the center of plantar pressure within the base of support (67). Therefore, the TS muscle is of importance not only for regulating the anteroposterior body position as dependent on the actual position of the center of mass to maintain postural balance but also for a transition from standing to walking or running (96). In this context, any change in plantar pressure within the base of support or in force transmission may adversely affect the postural balance and increase risk of falling from a purely biomechanical point of view (92). Moreover, the internal architecture (muscle length, fiber length, and pennation angle) differs among the medialis gastrocnemius (MG), lateralis gastrocnemius (LG), and soleus (SOL), which form the TS muscle (22).

Losses in muscle strength are greater than losses in muscle dimensions (4), indicating that atrophy is not the only factor that contributes to muscle weakness. Magnetic resonance imaging and computed tomography provide conventional gold-standard tests to measure the muscle dimensions in humans (75, 91), producing images with a high contrast between tissues differing in molecular properties. However, the tests are extremely expensive and impose stringent clinical requirements. Ultrasound imaging is therefore used now as an available noninvasive method to evaluate the architectural properties of muscles (23, 40, 89). Ultrasound is relatively inexpensive, provides a relatively high time resolution, produces clear muscle images, and involves low risk for patient. The last circumstance makes it possible to employ ultrasound in vivo to investigate the muscle architecture, that is, the geometrical arrangement of fibers within a muscle (28, 29). The fiber arrangement substantially affects the force generation potential of a muscle (39, 63).

Many, if not the majority, of human muscles are pennate; i.e., muscle fibers are oblique and insert at a certain angle into
an aponeurosis or a tendon (27, 39a). The angular geometry substantially affects the force transmission from muscle fibers to the tendon (23, 24, 25, 27, 40). The angle of muscle fibers to the line of action of the tendon is an important functional characteristic of a muscle (e.g., see 23, 26, 27). In a given muscle, a higher pennation angle, first, results in a shorter fiber length, thus reducing the shortening velocity and the range of reciprocating motion, and, second, allows a greater amount of contractile material to be arranged along the tendon, thus increasing the force production (e.g., see Refs. 3, 26, 72). The pennation angle is a component of the force that acts through muscle fibers horizontally and orthogonally to the tendon, thus affecting the kinetic force transmission from muscle fibers to the bone (39, 63, 64, 65, 66). The geometric arrangement of fibers within a muscle is a main determinant of its functional properties (26, 27, 29, 89). The fiber length reflects the number of sarcomeres in series in a muscle fiber and is therefore proportional to the contraction velocity and excursion range.

Attempts have been made to determine the geometric arrangement of muscle fibers or fascicles (muscle architecture) in humans, and many attempts have been based on measurements of cadaver specimens (22, 37, 39). However, available data on human muscle architecture based on human cadaver or simulated μG exposure, i.e., bed rest or dry immersion in water (41, 43, 44, 55, 56), specimens might not accurately represent the profile of changes muscles; consequently, there are particular advantages in using noninvasive techniques to determine the muscle architecture in living subjects and especially after spaceflight (58). The data on the effects of actual μG are absent in the available literature.

Hitherto, however, no studies have investigated the extent of muscular architecture and contractile adaptations to long-duration spaceflight simultaneously and the impact there of on muscle function. The hypothesis of the present study was that changes in fascicle length and fascicle angle of the beam will reflect the degree of change in the functional characteristics of the muscles.

The present study is the first to quantitatively describe the relationships between joint angles and muscle architecture (lengths and angles of fascicles) of the human TS muscles and to determine architecture of a human muscle, both at rest and after long duration spaceflights. We employed real-time ultrasonography to visualize fascicles in vivo. The second purpose of the present work was to determine contractile properties the human TS muscles and their changes after a long-duration spaceflight. The second purpose of the present work was to determine contractile function the human TS muscles and their changes after a long-duration spaceflight.

METHODS

The experimental protocol was approved by the committee ethics at the Institute of Biomedical Problems of the Russian Academy of Sciences and by the medical boards of the International Space Station (ISS) missions the Yu. A. Gagarin Cosmonauts Training Center at Star City and was in compliance with the principles set forth in the Declaration of Helsinki.

Experimental Design

Cosmonauts were informed about the experimental procedures ~50–60 days before the spaceflight. Baseline data collections were performed ~30 days before flight and immediately after spaceflight by 3–5 days.

Participants

The subjects in this study were eight male cosmonauts who participated in ISS missions. Before the flight, their average age, height, and body mass were 45.7 ± 0.9 yr (range 43–52), 1.76 ± 2.3 m (range 1.67–1.82), and 79.9 ± 2.0 kg (range 70–86), respectively. Long-duration missions on board the ISS were by mean 213.0 ± 30.5 days (range 115–380). Each subject performed one set of experiments 30 days before spaceflight (baseline data collections) and immediately after spaceflight of 3–5 days.

Familiarization

The cosmonauts reported to the laboratory twice. During the first visit, the cosmonauts were familiarized with the experimental setup and procedures. The cosmonauts gave their written informed consent to participate in this study. On a subsequent day, the cosmonauts were involved in testing contraction properties of the ankle extensor muscles. Each subject served as his own control.

Testing Procedure and Measurement

Isometric setup. The mechanical responses of the human TS muscle were recorded by method tendometry (Fig. 1A), which made it possible to measure the force of a single muscle contraction by the degree of tension change in muscle distal tendon (59). Measurement of muscle tension using a strain-gauge transducer is based on the physical law of the resolution of forces according to the parallelogram principle (Fig. 1A, inset). If a strain-gauge transducer is pressed to the tendon, the transducer causes it to bend at an angle. The force (F1) that is directed along the muscle axis to the proximal point of attaching and originates during the muscle contraction is oppositely directed and equal to the force (F2) that is directed to the distal point of the tendon attachment. F1, which is directed across the tendon, operates at the point of the transducer and tendon contraction. If the angle at which the tendon bends is constant, the force (F) recorded by the strain-gauge dynamometer is proportional to F1 (or F2). A rigid dynamometer is needed for recording the muscle force using a strain-gauge transducer, because any deformation under tendon pressure will change the transducer position and alter the tendon angle. A steel dynamometer ring was used in our transducer.

Subject was seated comfortably on a special chair in a standard position (knee joint angle betweenibia and sole of foot at ~90° and a trunk-thigh angle of ~100°). The position of the seat was adjusted to the individual and then firmly secured. The limb was rigidly fixed, creating thus an isometric regime of muscle contraction.

The dynamometer that is a steel ring with a saddle-shaped special block was tightly attached to support the Achilles tendon of the muscle. The degree of pressure between the tendometrical sensor and the tendon was constant for all the subjects and amounted to 49 N.

Surface electromyography. After careful preparation of the skin including shaving excess hair, abrading the skin with fine sandpaper, and cleaning the skin with an isopropyl alcohol swab to reduce impedance, pairs of surface Ag–AgCl electrodes (Ø 8 mm, center to center distance 25 mm and a recording area of 50 mm²) were placed of 6 cm below the insertion of the gastrocnemii on the Achilles tendon for the SOL. Electrode gel was used with all surface electrodes. The electrodes were placed longitudinally with respect to the underlying muscle fiber arrangement and located according to the recommendations by surface EMG for noninvasive assessment of muscles (SENIAM). The large grounding electrode (7.5 × 6.5 cm) was located on the proximal portion of the leg between the upper recording electrode and the stimulating electrodes. Recordings of the electrical responses (EMG) of the skeletal muscle during slow maximal voluntary isometric contraction

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(MVIC) were made during for a short period (~0.2 s). EMG signals were amplified (×1,000) and digitized (bandwidth of 0–2,000 Hz) at a sampling rate of 5 kHz. During contraction the EMG signal was recorded on FM tape and simultaneously displayed on an oscilloscope to assess its quality. EMG signals were bandpass filtered between 20 and 500 Hz and smoothed using a moving root-mean-square filter with a time constant of 50 ms.

Electrical stimulation. A single, square-wave, supramaximal transcutaneous electrical stimulus of a 1-ms duration was delivered to the tibial nerve. Transcutaneous electrical stimuli were administered to the tibial nerve using supramaximal rectangular pulses with a frequency of 150 impulses/s (46, 49, 50). All the recordings were made in a room at constant temperature (~22 ± 1°C). The contractile properties of the TS muscle were tested twice: pre (~30 days) and postmission (~3–4 days), and the test protocols were identical for both pre- and postmission tests.

Fig. 1. Experimental setup and scheme estimated of parameters. A: experimental setup and scheme the principle of tendometry method. F, force. B: examples measurements of mechanical response parameters in isometric twitch contraction curve (left) and in electrically evoked tetanic tension and voluntary muscle tension development (right), and measurements electromechanical delay (inset). TPT, a time-to-peak; 1/2 RT, a half-relaxation time; TCT, a total contraction time; Pt, a twitch force. C: schematic representation of a sample contraction showing electromechanical delay (EMD), force time curve, and EMG recorded from soleus. D: sagittal ultrasound images of the medialis gastrocnemius (MG) head. The ultrasound transducer was placed over the muscle at the level of 30% of the distance between the popliteal fold and the center of the lateral malleolus. The fiber length was measured along an ultrasound signal line drawn parallel to a fiber between the deep and superficial aponeuroses. The pennation angle was measured as an angle of the line drawn parallel to a fiber between the deep and superficial aponeuroses. A white line superimposed on the ultrasound image shows the path of a fiber between the superficial and deep aponeuroses. θ, Pennation angle; L, fiber length.
**Tension properties.** The whole protocol was executed by one investigator. For all cosmonauts, the right leg was studied. The contractile properties of the TS muscle were estimated according to the mechanical parameters of a voluntary and electrically evoked contraction (maximal isometric twitch and tetanic contractions).

**Voluntary contraction.** Before the measurement, several warm-up ankle extensions and one to two near maximal ankle voluntary isometric plantar flexions were performed. During the measurement, the subjects were instructed to perform maximal isometric voluntary isometric plantar flexions for ~2–3 s. Measurements were performed a total of three times and the peak force was used in data analysis. The maximal voluntary contraction was measured from the tendogram of an isotonic voluntary contraction performed, on instruction, to exert a maximal contraction (Fig. 1B). Two separate efforts were made routinely, and a third extension was performed if more than a 5% difference existed. The highest peak voluntary contraction was adopted as MVIC. During the contractions, the subjects were verbally encouraged and a visual feedback was provided.

**Evoked (tetanic) contraction.** The maximal strength was measured from the tendogram from the evoked contraction (Pevoked, Fig. 1B) in response to an electric tetanic stimulation of the nerve, innervating the TS muscle, with a frequency of 150 impulses/s (45, 48, 50).

The difference between Pevoked and MVIC expressed as a percentage of the Pt value and referred to as force deficit (Pd) has also been calculated (46, 51) (Fig. 1B).

**Velocity properties.** The maximal isometric peak twitch force (Pt) was measured from the tendogram of the TS muscle isometric twitch response to a single electrical stimulus applied to the tibial nerve. The time from the moment of stimulation to peak twitch (TPt) and the time from contraction peak to half-relaxation (1/2 RT) were calculated from the tendogram of the isometric twitch (Fig. 1B). The accuracy of measurement was 1 ms.

**Rate of force development.** The rate of development of increased muscle tension was calculated from the tendogram by the isometric voluntary contraction after the instruction to exert the fastest and greatest tension using a relative scale, i.e., the time of reaching 25, 50, 75, and 90% of maximum tension (46, 49, 50). Similarly, the rate of rise of the evoked contraction, in response to electrical stimulation of the tibial nerve with a frequency of 150 impulses/s, was calculated (46, 49, 50) (Fig. 1B). The accuracy of measurement was 1 ms.

**Electromechanical delay.** The experiments were divided into two protocols.

**Protocol 1: voluntary contraction.** On a light signal, the subject carried out plantar flexor under condition of to contract as it is possible quickly and strongly (Fig. 1C). Voluntary contraction in response to a visual stimulus (flash lamp) was adopted as a rapid "explosive" movement. The signal to movement of explosive character, the visual diode lamp (Ø 7 mm, 1 W), was placed at eye level 1 m in front of the subject. Lasted signals were 2.5 s, and the pause between the signals was random ranging from 1.4 to 5.0 s. The threshold for force was 49 N.

A separate timer was used to record the time interval from the presentation of the light signal to movement. The special timer allowing synchronously with presentation of a light signal to the beginning of movement to carry out record of development of mechanical answer of the human TS muscle was used.

Electromechanical delay (EMD) was determined from the time lag between the onset of dorsiflexion force and surface EMG in the SOL muscle (108). The force thresholds were also taken as relative values of 2% from the maximum isometric force level of each contraction. Subjects were permitted three practice trials separated by 30 s and in most cases the mean of three readings was used to determine EMD.

**Protocol 2: twitch contraction.** To evaluate time of involuntary (evoked twitch contraction) EMD, rectangular electrical pulses were applied to the tibial nerve. The active electrode was placed over the popliteal space. Four single supramaximal stimuli were delivered to the tibial nerve, and a maximal M-wave was recorded. The rest interval between stimuli was no less than 30 s. The EMD was determined as a time interval between stimulation artifact and the onset of the twitch response (Fig. 1B, inset). The results of the experiment were simultaneously recorded on magnetic tape and simultaneously displayed on an oscilloscope to assess its quality. The accuracy of measurement was 1 ms.

**Ultrasound scanning.** To perform TS muscle ultrasound, a cosmonaut’s foot was relatively rigidly fixed to a special platform, which allowed the ankle angle to be set at ~15° (plantar flexion), 0° (neutral anatomical position), +15°, or +30° (plantar extension). The cosmonaut lay prone special a bed. At each ankle angle, longitudinal ultrasonic images of the TS muscle (MG, LG, and SOL) were obtained (Edge, SonoSite) at the proximal levels of SOL (MG and LG) or 50% (SOL) of the distance between the popliteal fold and the center of the lateral malleolus as measured in the neutral ankle position (42). Each level corresponded to the maximal anatomical cross-sectional area of the respective muscle (25). A marker was placed at each level to serve as a landmark and to prevent sensor displacement during testing. Panoramic B-mode ultrasonic images of the MG, LG, and SOL muscle in vivo were obtained at rest, using ultrasound system (Edge) and a linear 7.5-MHz electronic transducer with a 60-mm field of view.

Before spaceflight, the distance between the popliteal crease and the center of the lateral malleolus was found for each cosmonaut. After the spaceflight, the procedure was repeated with the determination of the proximal levels 30% (MG and LG) and 50% (SOL).

To improve the acoustic contact and prevent skin injury over the muscle, water-soluble gel was applied onto the skin area of the transducer. The transducer was oriented along the sagittal plane of the muscle and orthogonally to the skin surface. The transducer was aligned with the muscle bundle plane so that the total accessible portion of a muscle bundles could be examined in the scanning window. The intensity and brightness of ultrasonic signals were adjusted to improve image quality.

The transducer was pressed as lightly as possible against the skin during scanning to prevent any pressure on the muscle. The cosmonaut was instructed to relax ankle extensor muscles during measurement, and the fiber length and angle were measured 20 min after to allow the bodily liquid medium to achieve a steady state (8). Images were saved to the hard drive to obtain a file for subsequent analysis of the fiber length and fiber angle.

The fiber length (Lf) of a muscle was measured as a distance between the sites where a fiber is attached to the surface aponeurosis and inserts into the deep aponeurosis (39) (Fig. 1A). The pennation angle (θf) was determined using the line between the sites where a fiber is attached to the surface aponeurosis and inserts into the deep aponeurosis (24) (Fig. 1A).

The distance between aponeuroses [muscle thickness (Hm)] was estimated from the fascicle length and pennation angle using the following equation: muscle thickness = Lf × sin θf, where Lf and θf are the pennation angles of each muscle determined by ultrasound.

In the present study, ultrasonic measurement was repeated three times for each individual and averaged values were used. The coefficients of variation of three measurements were in the range of 0–2%.

**Exercise regimens.** Details of the training program and performance tests have been provided elsewhere (98). Briefly, subjects were accustomed to training using bilateral supine leg press and arm press. The physical training (PT) consisted of three regimes: on the first day a force-velocity regime was carried out (70% of the training was force-velocity exercise, and 15% a velocity and force requiring exercise); on the second day a velocity regime (70% of the training was velocity required exercise, while 15% was force and force-velocity requiring exercise); and on third day a force regime (70% was force exercise, and 15% velocity and force-velocity requiring exercise).

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The PT was scheduled over a 4-day cycle: 3 days of training and 1 day of rest. PT used during long-term spaceflights included a warm-up (walking on a treadmill for 5 min), and low (2 min), moderate (2 min), and maximum (1 min)-intensity running. The training sessions were conducted for 60 min each day for 6 days/wk for 14 wk and 30/40 min twice a day for 2 wk under the experimental conditions. The recommended workload and intensities of exercises on treadmill varied from 3,100 to 4400 m, performed with an average rate of 117–135 m (60). It is known that intensity of loads set up by the subject’s level of work load, durations of high-intensity intervals, and subsequent pauses give a fairly correct notion about working abilities. In addition, taking into consideration the anatomical and physiological specificities of a woman’s body, the total physical load was reduced to 70% of that usually exposed to by men, and when the expanders were used for muscle-strengthening exercises, the load was reduced by 25–30%.

Statistics

Conventional statistical methods were used for the calculation of means ± SE. Values are given as means ± SE in the text. In addition, a paired t-test was performed for two measurements in each condition and at each joint angle to test their statistical difference. To investigate the effect of the conditions (rest and after spaceflight) and ankle joint angles on the lengths and angles of the fascicles, a two-way ANOVA with repeated measures was used. Relationships of two variables were tested with Pearson’s product moment correlation coefficient. Significant differences between means were set at the \( P < 0.05 \) level.

RESULTS

A baseline evaluation showed that the TS muscle contractile properties were within the physiologically normal ranges and the subjects could be characterized by their functional potential as healthy people who lacked neuromuscular disorders and had a common lifestyle with respect to exercise. A postspaceflight evaluation showed substantial changes in both contractile functions of the TS muscle and internal architecture of the MG, LG, and SOL.

Effect of Unloading on Mechanical Properties

Changes in maximal muscle strength. The mean changes in TS muscle tension under long-duration spaceflight are shown in Fig. 2, A and C, and reveal a significant decrease. The MVIC decreased 41.7% from 520.0 ± 66.7 to 303.1 ± 50.0 N (\( P < 0.05 \)), and isometric muscle tetanic (\( P_o \)) decreased 25.6% from 738.6 ± 65.7 to 549.4 ± 37.3 N (\( P < 0.05 \)) after spaceflight, respectively (Fig. 2, A and C).

The \( P_d \) increased prespaceflight to postspaceflight from 32.2 ± 4.6 to 46.7 ± 5.4% (Fig. 2; \( P < 0.01 \)), corresponding to a relative change of 49.7% (Fig. 2B).

Changes in velocity properties. The change in mean time of isometric twitch contraction, as the opposite value to contraction velocity for the TS muscle after a long-duration spaceflight.
effect, is given in Table 1. TPT the TS muscle increase 4.0% from 126 ± 3.6 to 131 ± 6.2 ms after spaceflight (P < 0.05), and 1/2 RT reduced 17.6% from 102 ± 5.4 to 84 ± 13.2 ms (P < 0.05).

Changes in rate of force development. Mean changes in the rate of development of isometric tension of the TS muscle are given in Fig. 3. MVIC (42%) was associated with a significant slowing of the rate of rise of development of isometric voluntary tension of the TS muscle (Fig. 3, P < 0.01-0.001). However, in the assessment of the force-velocity muscle properties of isometric electrically evoked tetanic development as a result of long-duration spaceflight, no substantial changes were observed (Fig. 3, P > 0.05).

Changes in EMD. The mean changes in EMD under long-duration spaceflight are shown in Table 1. EMD increased 34% pre- to postspaceflight from 31.4 ± 2.8 to 42.1 ± 3.4 ms (P < 0.05; Table 1), corresponding to a relative change of 34.1 ± 1.3%.

The coefficients of correlation between the EMD and MVIC before spaceflight were −0.68 (P < 0.05), and strongest correlations were found between EMD and explosive voluntary force (r = 0.90; P < 0.01). The coefficients of correlation decreased between the EMD and MVIC after spaceflight (r = −0.56; P = 0.05) and between the EMD and explosive voluntary force (r = −0.72; P = 0.07).

The mean changes in EMD during a twitch contraction did not differ significantly pre- to postspaceflight (Table 1).

Effect of Unloading on Internal Architecture

The length fibers and fascicle angle before to the spaceflight. Table 2 shows average Lf of MG, LG, and SOL as a function of the ankle joint angle (are shown in Fig. 4). In all three muscles, Lf depended on the ankle joint angle and Lf were longest when the ankle joint angle was −15° and shortest at the ankle joint angle was +30°. As the ankle angle changed from −15 to +30°, Lf decreased from 43 ± 1 to 34 ± 1 mm (20.9%, P < 0.01) in the MG, from 57 ± 2 to 38 ± 2 mm (33.3%, P < 0.01) in the LG, and from 35 ± 2 to 25 ± 1 mm (28.6%, P < 0.01) in the SOL. The highest Lf was observed for the LG at an ankle angle of −15°.

The degree of Lf change was not identical for the three muscles. The effects of ankle joint positions on fascicle lengths were significant for MG and LG. In other words, the MG and LG showed the greatest changes in Lf with the changing ankle joint position. In all of the three muscles, Θf depended on the ankle joint angle and the effect of the ankle joint position was significant (Fig. 4). The Θf of MG demonstrated the greatest variation in three muscles. As the ankle joint angle changed from −15 to +30°, increased from 27 ± 1 to 43 ± 2° (59%, P < 0.01) in the MG, from 21 ± 1 to 29 ± 2° (38.1%, P < 0.05) in the LG, and from 23 ± 1 to 34 ± 2° (47.8%, P < 0.01) in the SOL.

The length fibers and fascicle angle after the spaceflight. In all of the three muscles, Lf depended on the ankle joint angle. As the ankle joint angle changed from −15 to +30°, Lf decreased from 40 ± 1 to 31 ± 1 mm (22.5%, P < 0.01) in the MG, from 54 ± 1 to 35 ± 3 mm (35.2%, P < 0.01) in the LG, and from 32 ± 2 to 23 ± 1 mm (28.1%, P < 0.01) in the SOL (Fig. 4). The Lf changes due to changes in ankle joint position were significant in the case of the LG.

In all of the three muscles, Θf depended on the ankle joint angle. As the ankle joint angle changed from −15 to +30°, Θf decreased by 16.2% (from 24 ± 1 to 37 ± 2°) in the MG, 38.9% (from 18 ± 1 to 25 ± 1°) in the LG, and 45.7% (from 20 ± 1 to 29 ± 1°) in the SOL. The lowest spaceflight effect on Θf as a function of the ankle joint angle was observed in the case of the LG.

Muscle thickness before and after a spaceflight. Before spaceflight no significant difference in the Hm was found among the MG, LG, and SOL. Therefore, Hm was 2.1 ± 0.06 cm in the MG, 1.8 ± 0.10 cm in the LG, and 1.5 ± 0.12 cm in the SOL (Fig. 5). A decrease in Hm was observed after a spaceflight for all of the three muscles. Compared with the prespaceflight baseline, Hm decreased by 18.9% in the MG, 19.8% in the LG, and 18.8% in the SOL.

Table 1. The mechanical and time characteristics of the human triceps muscle after a long-duration spaceflight

|             | Before       | After        | Δ, % |
|-------------|--------------|--------------|------|
| MVIC, N     | 520.0 ± 66.7 | 303.1 ± 50.0 | 41.1†|
| Pa, N       | 738.6 ± 65.7 | 549.4 ± 37.3 | 25.6†|
| Pa, %       | 32.2 ± 4.6   | 46.7 ± 5.4   | 49.7†|
| TPT, ms     | 126 ± 3.6    | 131 ± 6.2    | 4.0  |
| 1/2 RT, ms  | 102 ± 5.4    | 84 ± 13.2    | 17.6†|
| EMDiso, ms  | 31.4 ± 2.8   | 42.1 ± 3.4   | 34.1†|
| EMD, ms     | 10.3 ± 0.4   | 12.4 ± 0.3   | 20.4  |

Values are means ± SE; n = 8. EMDiso, electromechanical delay voluntary contraction; EMD, electromechanical delay twitch; MVIC, maximal voluntary isometric contraction; Pa, force deficiency; Pd, tetanic tension; 1/2 RT, time from contraction peak to half-relaxation; TPT, time-to-peak. †P < 0.05.

Fig. 3. The effects of long-duration spaceflights on development of force of the triceps surae muscle express relative to the maximal force. Average curves showing the development of force while executing explosive voluntary contraction and as a result of electrical stimulation at 150 impulses/s. Values are means ± SE. **P < 0.05; ***P < 0.01.
spaceflight-induced decrease in lower extent in the LG and significantly in the SOL; and greater deformation of the tendon is necessary for generating the functional potential of a muscle and to preserve its force. These changes possibly compensate for each other to maintain 1 length. The main new findings of the study are the following:

1. Muscles cannot remain constant upon changes in muscle length. The main new findings of the study are the following:

| Muscles/Ankle Position | Before | After | Δ, % |
|------------------------|--------|-------|------|
| MG                     |        |       |      |
| −15                    | 43 ± 1 | 40 ± 1 | 15   |
| 0                      | 39 ± 2 | 37 ± 1 | 12   |
| 15                     | 37 ± 1 | 35 ± 1 | 13   |
| 30                     | 34 ± 1 | 31 ± 1 | 5    |
| LG                     |        |       |      |
| −15                    | 57 ± 2 | 54 ± 1 | 14   |
| 0                      | 45 ± 1 | 41 ± 1 | 13   |
| 15                     | 39 ± 1 | 36 ± 1 | 22   |
| 30                     | 38 ± 2 | 35 ± 3 | 19   |
| SOL                    |        |       |      |
| −15                    | 35 ± 2 | 32 ± 2 | 26   |
| 0                      | 33 ± 2 | 30 ± 1 | 13   |
| 15                     | 31 ± 2 | 28 ± 2 | 17   |
| 30                     | 25 ± 1 | 23 ± 1 | 21   |
| Fascicle angles, °     |        |       |      |
| MG                     |        |       |      |
| −15                    | 27 ± 2 | 24 ± 4 | 15   |
| 0                      | 32 ± 2 | 28 ± 4 | 22   |
| 15                     | 42 ± 3 | 32 ± 4 | 25   |
| 30                     | 43 ± 3 | 37 ± 5 | 26   |
| LG                     |        |       |      |
| −15                    | 21 ± 2 | 18 ± 1 | 24   |
| 0                      | 23 ± 1 | 20 ± 2 | 20   |
| 15                     | 24 ± 2 | 21 ± 2 | 19   |
| 30                     | 29 ± 2 | 25 ± 2 | 29   |
| SOL                    |        |       |      |
| −15                    | 23 ± 3 | 20 ± 2 | 19   |
| 0                      | 28 ± 3 | 24 ± 2 | 16   |
| 15                     | 30 ± 3 | 26 ± 3 | 26   |
| 30                     | 34 ± 3 | 29 ± 3 | 27   |

Values are means ± SE. Lg, lateral gastrocnemius; MG, medial gastrocnemius; SOL, soleus.

**DISCUSSION**

This study for the first time, to our knowledge, to describe the internal architecture of the human MG, LG, and SOL in vivo changes at rest and after a long-duration spaceflight (>180 days). We present simultaneous data on the time course of deterioration of the main determinants of skeletal muscle mechanical output after spaceflight. The data show significant losses in force in MVIC plantar flexors and muscle-tendon complex (MTC) stiffness and architecture muscle after of prolonged exposure to μG. In addition, this study is unique in terms of the duration of unloading because model conditions have been used to study the changes in internal architecture of muscles in many earlier works (41, 43, 55, 88). Our findings showed that the fiber length and pennation angle of human muscles cannot remain constant upon changes in muscle length. The main new findings of the study are the following: 1) $\Theta_i$ and $H_{mo}$ of all muscles decreased after a spaceflight; 2) $L_f$ of the LG decreased after a spaceflight to a greater extent than the $L_f$ values of the other muscles, while $\Theta_i$ decreased to a lower extent in the LG and significantly in the SOL; and 3) a spaceflight-induced decrease in $\Theta_i$ was lower than in $L_f$, and these changes possibly compensate for each other to maintain the functional potential of a muscle and to preserve its force generating capacity. Finally, a decrease in the rigidity of a MTC (an increase in EMD) after a spaceflight means that a greater deformation of the tendon is necessary for generating force, i.e., the length-tension ratio is consequently shifted to the left, and the muscle force is reduced.

**Effects of Spaceflight on Force Properties**

After prolonged spaceflight, the electrically evoked contractions ($P_o$) decreased significantly at a rate of 26% of preflight testing. The $P_o$ is a direct measure of the force-generating capacity of a muscle and has been considered to reflect the number of active interactions between actin and myosin (16). Disuse produced a decline in $P_o$ (20, 46). This decline could reflect a decrease in the number of active cross bridges and be expected to decrease the work capacity. Two hypotheses may be suggested to account for the observation. First, the total number of cross bridges could have been smaller after the period of spaceflight. Second, the force output per cross bridge could have been decreased. However, Steven and Mounie (102) have shown that when it was expressed per cross-sectional area, the force was unchanged after disuse (99). This would indicate that the first hypothesis of a decrease in the maximal number of cross bridges was more appropriate to our results, rather than a change in density.

Potentially contributing to the disproportionate loss of muscle strength compared with muscle size is a reduction in single fiber specific tension. Although not assessed in the present study, this has been found after bed rest (94, 105) due to a decrease in the number of active cross bridges, as suggested by a decrease in myofibrillar density, rather than in the force per cross bridge (18, 94). A decrease in thin filament density observed in astronauts after spaceflight (94) has also been proposed as a cause of this phenomenon. Last but not least are the changes in tendon tensile properties since tendons influence the length at which muscle fibers operate (78) and thus, ultimately, influence force production.

As a whole the mechanisms responsible for the force loss with μG are not well understood. However, changes in the force might have been caused by changes in different architectural properties, such as muscle length, fascicle length, and pennation angles (22, 111). Consequently, the relationships among joint angles, muscle lengths, and pennation angles are highly specific to muscle. Muscle architecture, together with intrinsic properties such as fiber composition, also affects functional characteristics of muscle, e.g., maximal shortening velocity and $P_o$ (83). In addition, considering that the TS muscle our experimental environment was not extended and was, which makes possible the associated of such a condition with physiological shortening, it may be assumed that the total number of successively sarcomeres in series was considerably decreased (21). These may have contributed to the reduced in muscle layer thickness and fascicle angles. In fact, according to Clément et al. (15), it seems that cosmonauts adopt a dorsiflexion position during spaceflight. Then, in post-flight, a shortening of the plantar flexors will occur when the preflight neutral position is reached.

The much larger reduction in MVIC when compared with changes in $P_o$ after a prolonged spaceflight may indicate an inability of the central nervous system to activate the TS muscle normally. Whether this was due to a lack of motivation on the part of the subjects or to an involuntary reduction in neural drive is difficult to distinguish. Additionally, a decline in maximal power was also proved by Antonutto et al. (6) after...
long-duration spaceflight and was attributed to a decrease in neural input. The increase in \( P_d \) would suggest a decline in central drive in the control of voluntary muscle by the motor nervous system. In fact, this decrease in maximal firing rate should imply the recruitment of a larger number of motor units to develop the same target strength in preflight and postflight conditions.

On the other hand, a decrease in maximal firing rate could be explained by changes in proprioceptive afferents on the motoneurons (69). Additionally, the data of Antonutto et al. (5, 6) suggest that \( \mu \)G causes a fundamental alteration in motor control. The data of Recktenwald et al. (85) also suggest that \( \mu \)G induced a reorganization of motor recruitment motor units. These changes of motor control may be one contributing factor of \( \mu \)G to the reduced extensor muscle torque and maximal power previously experienced by cosmonauts/astronauts after spaceflight (6, 34) and to the change in architecture of muscle (a decrease in muscle \( L_f \) and \( \Theta_f \) as observed in this study) and MTC, as previously is shown in astronauts after spaceflight (51, 62). In addition, considering that the TS muscle in spaceflight was not extended and tensed (“fetal” posture), which makes possible the association of such a condition with physiological shortening, it may be assumed that the total number of successively sarcomeres in series was considerably decreased (103). We may surmise that this ankle joint position added to the reduction of fiber length.

Effects of Spaceflight on Velocity Properties

In the present study, the difference between the post- and preflight the TS muscles was ~4%. The underlying mechanisms basis of TPT and 1/2 RT involve the competitive interaction of factors involved with activation (\( \text{Ca}^{2+} \) release kinetics), cross-bridge cycling, \( \text{Ca}^{2+} \) uptake by the sarcoplasmic reticulum (SR), and changes the active fraction (muscle fibers) or the passive fraction (tendons) of the series-elastic component.

The rapid nature of the isometric changes, i.e., twitch duration, may be related to alterations in SR function (10). The primary factor (mechanism) of the explanation for these the changes may be a reduction in the rate at which \( \text{Ca}^{2+} \) is dissociated from the myofibrillar proteins (10). Dissociation would occur more slowly if the rate of \( \text{Ca}^{2+} \) reuptake by the SR was decreased. Such a decrease has been found following disuse (40). A reduced rate of \( \text{Ca}^{2+} \) dissociation from myofibrillar proteins might be expected due not only to increase the time course of the twitch response but also to allow more force to be generated, since cross bridges will continue to be formed while \( \text{Ca}^{2+} \) is available in the sarcoplasm (100). These effects on the SR would be difficult to observe as the effects on \( P_t \) would be masked by atrophy but are of interest on the assump-
tion that the twitch changes are due to SR alterations. The changes in the kinetics the mechanical responses at paired stimulation (46, 47) might also be explained by altered development of Ca2+ kinetics in the muscle used in the experiment. At any given interpulse interval, the relative increase in force of contraction after long-term spaceflight effect was significantly less compared with the preflight value.

Effects of Spaceflight on Force-Velocity Relationship

The rate of rise of evoked contraction in response to electrical stimulation of the nerve with a frequency of 150 impulses/s calculated according to a relative scale showed only minor changes due to μG, which agrees with the data obtained earlier (48, 113). Witzmann et al. (113) have shown that there were no significant changes in the force-velocity characteristics of rat SOL, extensor digitorum longus or superior, and vastus lateralis muscles after 21 days of immobilization or in the human TS muscle after 120 days of head-down tilt (46, 48), which is consistent with the observed relative constancy of the mechanics of the tetanus and current (cross bridge) theories of muscle contraction (84, 95). It would therefore seem reasonable to conclude that disuse (for example, head-down tilt) in women patients has little effect on either cross-bridge cycling or myosin activity (16).

Effects of Spaceflight on EMD

As it is known, EMD is a peripheral component of human motor reaction embracing the lag from the onset of muscle-agonist EMG until actual motion or, in other words, time of stretching the series viscoelastic component by the contractile element (14), which, in turn, is dependent on force generation rate (14, 107). Consequently, EMD increase/reduction can be an indirect indicator of changed MTC stiffness (70, 71). Changes in stiffness of the MTC have an impact on motion control as stiffness dictates the mechanics of the interaction between the system and its environment.

The present study has shown that EMD response to long-term μG suggests changes in the TS muscle properties. Previous results demonstrated convincingly that unloading can alter mechanistic behavior of the muscle tendon and that tendon extension results in decrease of tendon stiffness (19, 61, 68, 70, 71). This loss in tendon stiffness may amplify its deformation in the course of force generation. As a result, muscle fibers shift in the nonoptimal zone of the tension-length relation. Earlier it was shown that the greatest contraction force is determined on the tension-length plateau (90). Therefore, exaggerated shortening of contracting muscle fibers due to increased tendon deformation makes sarcomeres work at shortened, far from optimal, lengths and consequently lower force production.

Changes in muscle MTC stiffness influence the rate of contractile force transfer to the bone system. In this investigation, we explored two variables associated with the rate of force transfer from muscle to the skeleton (i.e., the time required to transmit contraction forces to bones and rate of tension rise). The latter is dependent on tendon stiffness and the contraction rate at which force is transferred to the bone system, whereas EMD is dependent on the propagation of action potential along on muscle membrane, the excitation-contraction coupling processes, and the stretching of the series elastic component by the contractile element (112). Since it is known that unloading inhibits the rate of excitation transfer along the membrane of any type of muscle fiber (12), this may contribute to EMD prolongation. According to our data, post-spaceflight EMD increased (34%) with reduction of the voluntary contraction rate suggesting a significant prolongation of the time of communication between excitation contraction and viscoelastic series components, which can be a result of tendon stiffness reduction. These data are in good agreement with data Kubo et al. (61). It should be noted that EMD prolongs substantially in consequence of gross loss in tendon stiffness (17); however, EMD does not alter in the event when “weak tendon is raised” (73) and extends the MTC (71).

As shown in this study, EMD found a negative relationship with the MVC, i.e., the shorter the EMD, the higher the MVC. This means that subjects with higher MVIC have a high content of fiber type II. Interestingly, this relationship varies with the experimental conditions. Therefore, after unloading there is a weakening of the connection; in other words, there is less dependence on the proportion of EMD type II fibers in the muscle. This may be due to differences in recruitment strategy motor unit, i.e., less type II fibers active at a lower rate of force development and therefore a lesser dependence of the EMD on the proportion of this type of fibers in the muscle (30). These data are comparable with previous studies that found a negative correlation between EMD and in type II fibers (80, 106) and a positive correlation between the proportion of type II fibers and MVC (45).

Spaceflight and Countermeasures

It is well known that long-duration exposure to μG has detrimental effects on the human neuromuscular system (31, 104, 109, 110). The reduction of contractile functions in space mission crewmembers supports the idea that “protection” of skeletal muscles during long-term spaceflight requires PT with more effective program. The program of PT with the use of such means of training process as a treadmill and bicycle ergometer improves aerobe capacity by providing of training of the cardiovascular and respiratory systems (34) but not power characteristics of muscle apparatus. Our findings showed that the program of PT and the exercise devices available on the ISS (the treadmill, and 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 (31, 32). Moreover, the duration and/or loading proved insufficient to prevent bone loss (13). That is why the reduction of contractile functions of muscles after spaceflight supports the idea that “protection” of muscles during spaceflight requires PT with a more effective training program including in particular high-intensive and/or explosive exercises, which increase power characteristics of muscles (31, 35, 104) and are promising for avoiding muscle atrophy and “weakness.” In addition, analysis of training process used in spaceflight has not revealed specific exercises aimed at the training of plantar flexors that could be additional factor in the reduction of contractile functions of muscles.

Effect of a Spaceflight on Muscle Architecture

The present study shows that significant remodeling of muscle architecture of the main locomotor muscles was in-
duced by prolonged (>180 days) spaceflight. Morphological skeletal muscle adaptation to unloading can be assessed by evaluating the changes in fiber length and pennation angle (26, 65, 66, 74, 87). The length of muscle fibers strongly affects their contraction velocity (9) and is important for improving the kinematic efficiency. It is of immense importance to deeply understand muscle architecture when interpreting the changes that unloading induces in muscle function because architecture plays a key role in determining the mechanical properties of muscles (65, 77). The understanding is additionally important for improving the kinematic efficiency of human movements. A decrease in fiber length and an increase in pennation angle with the increasing muscle length are possible factors to consider while explaining muscle tissue “weakness” (2). In this study, a decrease in fiber length upon passive plantar flexion from –15 to +30 ° suggests that muscle fibers became progressively “weaker” with the increasing ankle joint angle. It is of interest that the fiber length and pennation angle decreased after a spaceflight, but the decrease in fiber length was greater.

The fiber length was measured at three different joint angles because of the following. If the fiber lengths before and after a spaceflight were compared at only one particular joint angle and a difference in length was not confirmed, there are chances that the fiber length was initially the same. On the other hand, if the fiber length-joint angle ratio differs between pre- and postspaceflight measurements, it is impossible to judge about fiber length changes assessed at only one joint angle. In view of this, the fiber length was measured at three different joint angles, including those associated with longer or shorter fibers. Differences in fiber length were observed at all joint angles. It is therefore possible to conclude that the fiber length differed in fact between pre- and postspaceflight conditions.

A main finding of the study is that the MVC of the TS muscle decreased (~42%) after a spaceflight. Changes induced in muscle functions by external factors may be due to changes in contraction processes or changes in nervous (motor) control. In fact, the MVC of a muscle is affected by its force-length relationship, the geometric position of the muscle relative to its joint, and the architectural characteristics of the muscle. Since the majority of human muscles are pennate, changes in the internal muscle organization are important to consider to correctly interpret the functional consequences of unloading.

Muscle architecture, together with internal muscle properties such as fiber composition, affects the functional characteristics of a muscle (e.g., the maximal force and shortening velocity) (9, 83). Changes in force-generating capacity depend on differences in internal architecture to a greater extent than on differences in fiber composition (9, 11). This study is a first attempt to evaluate, by means of ultrasound, the changes in architectural parameters of the TS muscle (MG, LG, and SOL) in humans after a long-duration spaceflight and to correlate the architectural changes with contractile functions and joint positions.

The MG was characterized by shorter fascicle lengths and larger fascicle angles. The MG can thus pack more fibers within a certain volume and hence would have a greater force potential. On the other hand, the LG had the longest fascicle lengths in the TS muscle. This means that the number of sarcomeres in series is the largest for this muscle, which illustrates the eminent velocity potential of the LG, as has been suggested previously (36, 111). These results are in accordance with the previous report that the physiological cross-sectional area of the MG is 2.5 times greater than that of the LG, while the muscle volume difference between them is only 1.7 times (25). The maximal shortening velocity of a muscle is additionally influenced by the fiber type composition (101). However, because the fiber type composition is similar in the MG and LG (38), the maximal shortening velocity and maximal force are principally determined by their architectural properties.

The fiber length, pennation angle, and muscle thickness changed to a lesser extent in the SOL, although the muscle thickness and fiber length tended to decrease. In addition, a “flexor” position observed in μG conditions (15) determined a slightly plantar-flexed position of the ankle, and this circumstance might enhance the effect observed in the MG and might contribute to the fiber length reduction.

Both fiber length and pennation angle were lower after a spaceflight, suggesting losses of both consecutive and parallel sarcomeres, respectively. The observation agrees with earlier findings (76). Loss sarcomeres of series suggests that the working range of each sarcomere becomes too great. When the working range of a sarcomere exceeds 3.65 μm, actin and myosin cease to interact (33). This circumstance probably affects the length-force and velocity-force relationships. A decrease in fiber length will change the length at which a sarcomere works at any muscle–tendon length (79). As a result, sarcomeres may have to function at greater lengths, the characteristic length-tension curve will change, and a shift from the optimal sarcomere length in the length-tension ratio will reduce the active strain for these sarcomeres, thus decreasing the total force of muscle contraction.

The present experiment shows that changes after 180 days spaceflight, $L_f$ decreased in MG, LG, and SOL by 23, 35, and 28% and $\Theta_f$ by 16, 39, and 46%, respectively. Following 23 days of unilateral lower limb suspension, Seynnes et al. (93) reported that $\Theta_f$ and $L_f$ of the LG were reduced by 5 and 4%, respectively. After a similar duration of bed rest, Kawakami et al. (41) reported that $\Theta_f$ of the MG, LG and SOL were reduced by 7, 5, and 4%, respectively. Interestingly, Reeves et al. (86) reported 10 and 13% reductions, respectively, in $L_f$ and $\Theta_f$ of the MG muscle after 90 days of bed rest. The relatively small alteration in muscle architecture reported by these authors after unloading suggests that model conditions have significantly less impact than real μG.

This reflects the number of sarcomeres in-series and therefore the contractile velocity; in addition, it should be noted that muscle contraction velocity is not only dependent on $L_f$ (i.e., total number of in-series sarcomeres) but also on myosin heavy chain $L_s$ isofrom composition and on the intrinsic speed of the myosin molecule. A slow-to-fast myosin heavy chain shift is typically reported after spaceflight (114) and in some bed rest studies (105), yet not all (7), and is likely to attenuate the negative effect of a reduction in the number of in-series sarcomeres on power production.

Moreover, a decrease in pennation angle must make the muscle relatively weaker because, first, parallel sarcomeres are lost and, second, a decrease in fiber length makes sarcomeres function at greater lengths, thus jeopardizing general force production. A greater number of motor units will have to be recruited to maintain the absolute force constant, potentially leading to rapid muscle fatigue.
A lower Θ\textsubscript{t} observed after a spaceflight (54, 57) partly compensates for the loss of force because the force transmission to the tendon becomes more efficient in spite of the decreased stiffness of the MTC (51). Such a decrease in stiffness has been observed, in subject after a long-term exposure to μG-simulating conditions and in cosmonauts after a long-duration spaceflight (51, 52, 53). The fact that the stiffness of the MTC decreases upon unloading (a spaceflight in our case) indicates that far greater tendon deformation is necessary for generating contraction force of any magnitude after a spaceflight. This circumstance will change the length-tension ratio, shifting it to the left, and the force of muscle contraction will thus be reduced (32).

A change in the number of sarcomeres in series may affect the angle at which muscle fibers shorten during contraction (89, 90). Thus this circumstance indicates that the changes that occur in the muscle and MTC during their adaptation to unloading compensate for each other to maintain the functional range of the muscle at a constant level. To summarize, the results showed that long-term exposure to μG rapidly leads to changes in structural and functional characteristics of muscles and the MTC, while force characteristics of muscles remain almost unchanged. Exposure to μG is accompanied by a decrease in the force of muscle contraction and changes in the TS muscle (muscle thickness, fiber length, and pennation angle) in the TS muscle, which acts as an antagonist muscle. Differences in the changes in fiber length and pennation angle among the muscles under study may be associated with differences in force generating capacity of the muscles and elastic characteristics of their tendons and aponeuroses.

Architecture substantially differs among different human TS muscle heads, possibly reflecting their different functional roles. The results demonstrate that muscles with different functional roles may respond differently to unloading, and this circumstance is important to consider when planning rehabilitation after unloading of any kind, paying particular attention to postural muscles.

The above conclusions are of clinical significance in terms of rehabilitation of the locomotor system after unloading in land-based models or in μG conditions. It is highly recommended that the tendon, in addition to the muscle, receives more attention in rehabilitation programs, which preferably to unloading compensation for each other to maintain the functional range of the muscle at a constant level.
Human Triceps Adaptsions to Microgravity

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