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Changes in human skeletal muscle architecture and function induced by extended spaceflight

Yuri A. Koryak *

State Scientific Center of the Russian Federation – Institute of Biomedical Problems of the Russian Academy of Sciences, Russia

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ABSTRACT

The aim of this study was to quantitatively describe the relationships between joint angles and muscle architecture (lengths (L_f) and angles (Θ_f) of fascicles) of human triceps surae [medial (MG) and lateral (LG) gastrocnemius and soleus (SOL) muscles] *in vivo* for three men-cosmonaut after long-duration spaceflight. Sagittal sonographs of MG, LG, SOL were taken at ankle was positioned at 15° (dorsiflexion), 0° (neutral position), +15°, and +30° (plantarflexion), with the knee at 90° at rest and after a long-duration spaceflight. At each position, longitudinal ultrasonic images of the MG and LG and SOL were obtained while the cosmonauts was relaxed from which fascicle lengths and angles with respect to the aponeuroses were determined. After space flight plantarflexor force declined significantly (26%; $p < 0.001$). The internal architecture of the GM, and LG, and SOL muscle was significantly altered. In the passive condition, L_f changed from 45, 53, and 39 mm (knee, 0°, ankle, −15°) to 26, 33, and 28 mm (knee, 90° ankle, 30°) for MG, LG, and SOL, respectively. Different lengths and angles of fascicles, and their changes by contraction, might be related to differences in force-producing capabilities of the muscles and elastic characteristics of tendons and aponeuroses. The three heads of the triceps surae muscle substantially differ in architecture, which probably reflects their functional roles. Differences in fiber length and pennation angle that were observed among the muscles and could be associated with differences in force production and in elastic properties of musculo-tendinous complex and aponeuroses.

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1. Introduction

Architecture of a muscle is an important determinant of its functional characteristics (Gans and Bock, 1965; Gans, 1982; Gans and Gaunt, 1991). The muscle architecture may be studied noninvasively *in vivo* by using real-time ultrasonography (Huijing, 1985; Rutherford, Jones, 1992; Fukunaga et al., 1997; Kawakami et al., 2001).

Gravitational loading appears to be necessary for the maintenance of human lower limb skeletal muscle size and force (Narici and Cerretelli, 1998; Kubo et al., 2000; Gopalakrishnan et al., 2010). A decrease of muscle loading leads to a decrease in the function and size of muscles (Berg et al., 1998; Gopalakrishnan et al., 2010; Koryak, 2014). Studies simulating microgravity have shown that exercise countermeasures can attenuate, but not completely prevent the loss of muscle mass and force (Kawakami et al., 2000; Koryak, 2014, 2015a,b). It should be noted that knee and ankle extensors are affected to the greatest extent in this case (LeBlanc et al., 1988; Akima et al., 2002). Greater loss in muscle strength than in mass is the best-known phenomenon in the effect of actual (a space-flight—SF) or simulated (bed rest) microgravity (Kawakami et al., 2001). √ The phenomenon directly indicates that factors other (e.g., architecture) than atrophy additionally contribute to muscle weakness. Most affected is the TSM, where 20% fiber atrophy occurs after 6 months of SF (Fitts et al., 2010). In ground-based models (e.g. bed rest, "dry" immersion), muscle atrophy is associated with decreases in fascicle pennation angle and length (Kawakami et al., 2001; de Boer et al., 2008; Koryak et al., 2010). Alterations of muscle architecture are expected to affect the mechanical output, thereby contributing to muscle weakness (Wilson and Lichtwark, 2011). Moreover, muscle unloading also leads to reductions in the fibers "specific force and power", and in myosin heavy chain concentration (Hvid et al., 2017). All these factors can independently alter the mechanical capabilities of muscles.

The size of a human muscle is conventionally assessed in terms of a cross-sectional area, which is measured by computed tomography, magnetic resonance imaging, or ultrasonography. The last method allows real-time measurements of the pennation angle *in vivo* (Kawakami et al., 1993, 1995; Kuno and Fukunaga, 1995).

* Address: SSC – Institute of Biomedical Problems of RAS, Khoroshevskoye Shosse 76-A, 123007 Moscow, Russia.
E-mail address: yurikoryak@mail.ru

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The majority of human muscles (Gans and Bock, 1965) are pennate muscles; i.e., their fibers are at an angle to the axis of muscle action. The pennation angle is an important architectural parameter of a muscle and affects its force production (Gans and Bock, 1965; Gans, 1982; Gans and Gaunt, 1991; Narici et al., 1992; Kawakami et al., 1993, 1995; Fukunaga et al., 1997). The pennation angle is a component of the force that acts through muscle fibers horizontally and perpendicularly to the tendon, thus affecting kinetic force transmission from muscle fibers to the bone (Lieber, 1992; Kawakami et al., 1993).

For a given muscle, its size, a greater pennation angle, and a lower fiber length jeopardize the shortening velocity and the range of motion, but a greater amount of contractile material arranged in parallel facilitates the maximal force production (Gans, 1982; Muhl, 1982). It should be noted that the muscle architecture has been studied in experiments with muscle *disuse* or unloading (bed rest or "*dry*" water immersion) (Maganaris et al., 1998; Kawakami et al., 2000; Koryak et al., 2010), while data on the effect of actual microgravity are absent in the literature.

The purpose of this study was to quantify first, to investigate the changes in architecture as a function of the ankle joint angle for the three heads of the human triceps surae muscle (TSM) (medial (MG) and lateral (LG) gastrocnemius and soleus (SOL) muscles] after long-duration SF and, second, to quantitate the changes in functional characteristics of the human TSM after a long-duration SF. We hypothesized that changes in the length of fascicles and the fascicle pennation angle of fibers will reflect the effect of unloading the muscle during SF.

2. Methods

2.1. Subject

The experiments were performed on three male-cosmonauts. The cosmonauts spent >180 days aboard to the ISS. Cosmonauts gave their informed, written consent, and experiments were carried out according to the guidelines of the Declaration of Helsinki and were approved by the Biomedical Ethics Committee at the IMBP and Yu.A. Gagarin GCTC at Star City, Moscow.

2.2. Procedures

2.2.1. Isometric set-ut

The mechanical responses of the human TSM were recorded by method tendometry (59) which made it possible to measure the force of a single muscle contraction by the degree of tension change in muscle distal tendon. 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. 1, *top left panel, insert).* If a strain-gauge transducer is pressed to the tendon, the transducer causes it to bend at an angle. The force ($\mathbf{F_1}$) 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 ($\mathbf{F_2}$) that is directed to the distal point of the tendon attachment. $\mathbf{F_1}$ 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 $\mathbf{F_1}$ (or $\mathbf{F_2}$). 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. A rigid fixation of the leg joints ensured the isometric mode of muscle contractions.

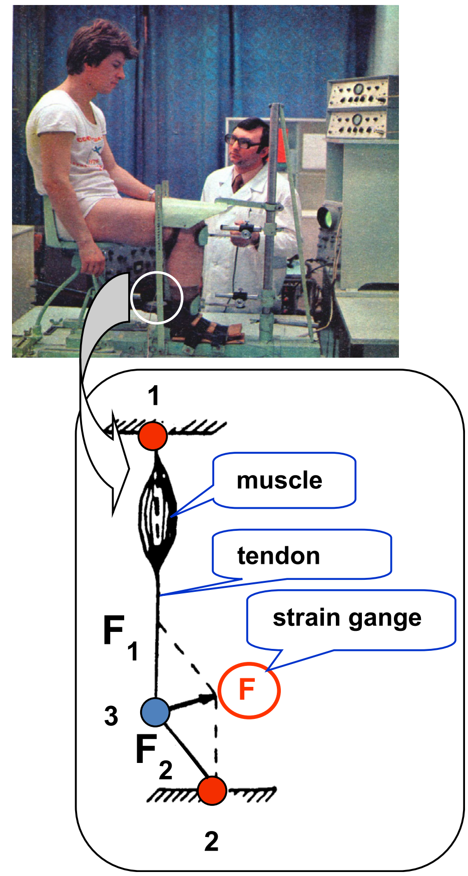


Fig. 1. Experimental set-up and scheme the principle of tendometry method.

Subject was seated comfortably on a special chair a custom built dynamometer [Koryak, see Ref. Kots et al., 1976] in a standard position (knee joint angle between tibia 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.

2.2.2. Isometric force measurements

The whole protocol was executed by one investigator. For all cosmonauts, the right leg was studied. The contractile properties of the TSM were estimated according to the mechanical parameters of a 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 approximately 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 isometric voluntary contraction performed, on instruction, «*to exert a maximal contraction*». 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 maximal voluntary contraction (MVC). During the contractions, the subjects were verbally encouraged and a visual feedback was provided.

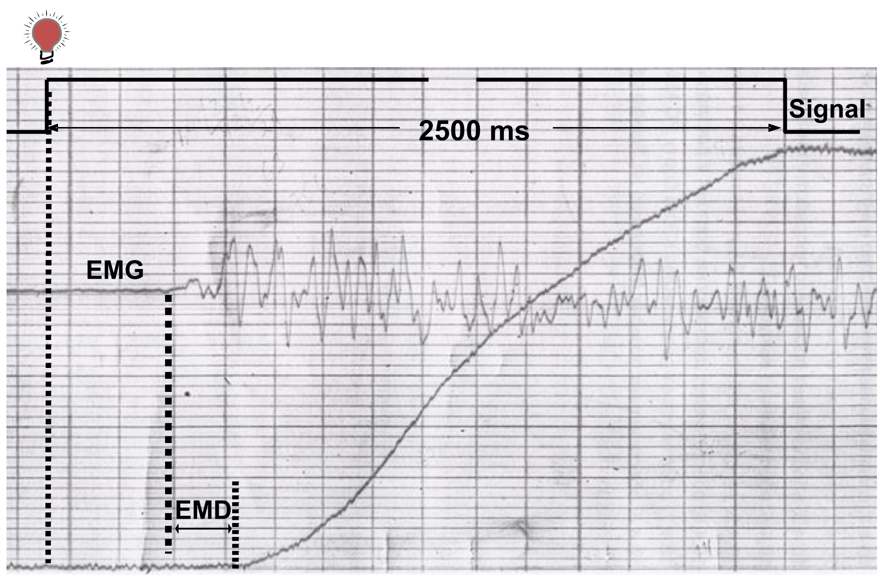
The mechanical responses of the human TSM were recorded by ~30 days before and ~5–7 days after a SF.

2.2.3. Electromechanical delay

On a light signal the cosmonaut carried out plantar flexor under condition of "*contracting as quickly and as strongly possible*" The signal to movement of «*explosive*» character was the visual diode (Ø 7 mm, 1 W)—was placed at eye level 1 m in front of the cosmonaut. Lasted signal were 2.5 s and the pause between the signal was random ranging from 1.4 to 5.0 s. A mechanogram was used to measure the electromechanical delay (EMD) as a time between the onset of electrical activity in the movement agonist muscle and the onset of its tension (Cavanagh and Komi, 1979; Koryak, 2014, 2015a,b) (Fig. 2, *top panel*). Cosmonaut were permitted three practice trials separated by 30 s and the best of the three readings was used to determine the EMD.

2.2.4. Ultrasound scanning

Each subject's right foot was firmly attached to special platform dynamometer. Resting fibre fascicle length (L_f) and pennation angle (Θ) were measured using B-Mode, real time ultrasonography, as shown in Fig. 2, *lower panel*. Ultrasonographic images of the MG and LG in vivo and its change from of one cosmonaut before (a) and after (b) long-duration space flight show in Fig. 3. The ankle joint was fixed at −15° (plantar flexion), 0° (a neutral position), +15°, or +30° (plantar extension). The knee joint was positioned at 0° (full extension). In each position, longitudinal ultrasonic images of the TSM [medial (MG) and lateral (LG)



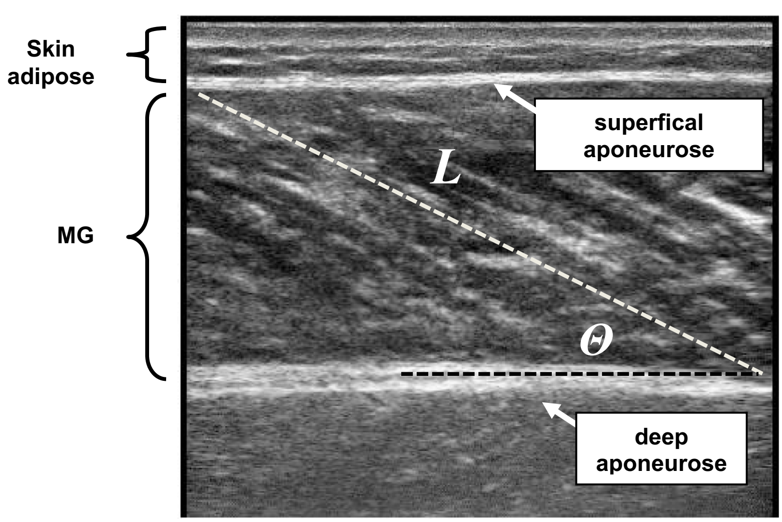


Fig. 2. Schematic presentation of a sample showing motor time or electromechanical delay (EMD) and electromyogram (EMG) of the soleus (SOL) muscle (*top panel*). Ultrasonic images of longitudinal sectional of medial (MG) gastrocnemius muscle. Ultrasonic transducer was placed on skin over the muscle at 30% distance between the popliteal crease and the center of the lateral malleolus. Fascicles length (L) was determined as length of a line drawn along ultrasonic echo parallel to fascicles. Fascicles angles (Θ) was determined as angle between echoes obtained from fascicles and deep aponeurosis in ultrasonic image (*lower panel*).

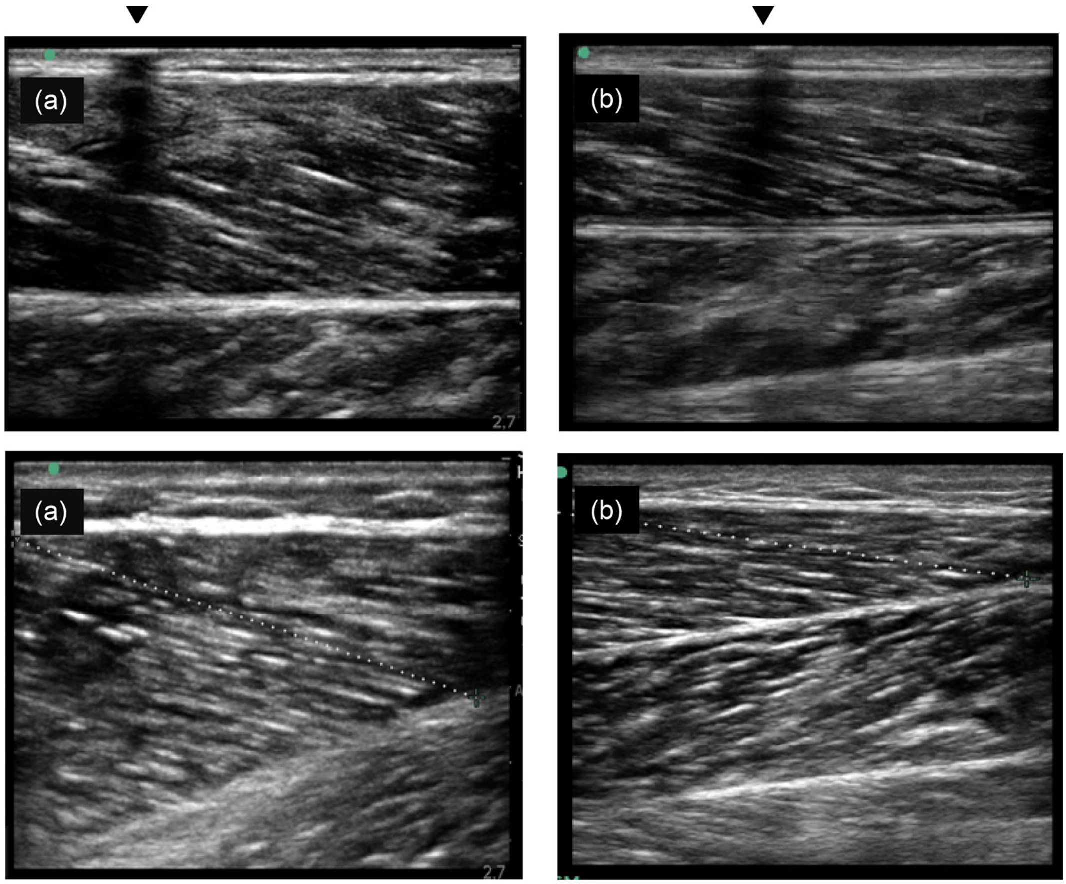


Fig. 3. Ultrasonographic image of the MG (*top panel*) and LG (*lower panel*) from of one cosmonaut before (a) and after (b) long-duration space flight. ▼, marker between skin and ultrasonic probe.

gastrocnemius and soleus (SOL) muscles] were obtained (Edge, SonoSite, USA; a linear 7.5-MHz electronic transducer with a 60-mm field of view) at the proximal levels 30% (MG and LG) and 50% (SOL) of the distance between the popliteal crease and the center of the lateral malleolus (Kawakami et al., 1998). The transducer was arranged along the plane of muscle bundles so that all bundles visible in the scanning window were accessible for examination. The measurement error was ~4% with this approach (Reeves et al., 2004). The whole protocol was executed by one investigator.

The length of fascicles (L_f) across the deep and superficial aponeurosis was measured as a straight line (Kawakami et al., 1993; Fukunaga et al., 1997) (Fig. 2, *lower panel*). The fascicles pennation angle (Θ) was measured from the angles between the echo of the deep aponeurosis of each muscle and interspaces among the fascicles of that muscle (Kawakami et al., 1993; Fukunaga et al., 1997) (Fig. 2, *lower panel*).

Muscle thickness (H) was estimated from using the following equation:

$$H = L_f \times \sin\alpha,$$

where L_f, and α is the pennation angle of each muscle determined by ultrasound.

2.3. Statistics

Differences between baseline (background) values of pre- and post SF were tested for significance by Student's paired *t* test. Values are given as means ± s.e.m. in the text. Significance was accepted at the $p < 0.05$ level.

3. Results

3.1. Effect of unloading on mechanical properties

Contraction force. The MVC of the TSM decreased from 456.9 to 338.4 N after the SF corresponding to a relative change of 26.0% ($p < 0.05$).

Electromechanical delay. The EMD increased from 31.4 to 42.1 ms after the SF corresponding to a relative change of 34.1% ($p < 0.01$).

3.2. Effect of unloading on internal architecture

Fascicles length before the SF. With the ankle angle increasing from −15° to +30°, L_f decreased from 45.2 ± 1.2 to 26.1 ± 2.1 mm (42,3%) in the MG, from 53.1 ± 0.5 to 33.2 ± 1.3 mm (37%) in the LG, and from 39.2 ± 1.2 to 28.2 ± 2.0 mm (28%) in the SOL (Fig. 4, *top panel*).

Pennation angle before the SF. With the ankle angle increasing from −15° to +30°, Θ increased from 18.8° ± 2.1° to 25.2° ± 2.0° by 34%) in the MG, from 11.4° ± 2.1° to 18.2° ± 1.6° (by 59.6%) in the LG, and from 21.7° ± 1.4° to 30.3° ± 2.2° (by 39.5%) in the SOL (Fig. 4, *lower panel*).

Muscle thickness before the SF. With the ankle angle increasing from −15° to +30°, H decreased from 14.5 to 11.2 mm (by 22.8%) in the MG, from 10.5 to 10.4 mm (by 0.9%) in the LG, and from 14.5 to 14.2 mm (by 2.1%) in the SOL.

Fascicles length after the SF. With the ankle angle increasing from −15° to +30°, L_f decreased from 26.9 ± 1.7 to 17.8 ± 1.9 mm (34%) in the MG, from 42.7 ± 0.4 to 25.2 ± 2.4 mm (by 40.8%) in

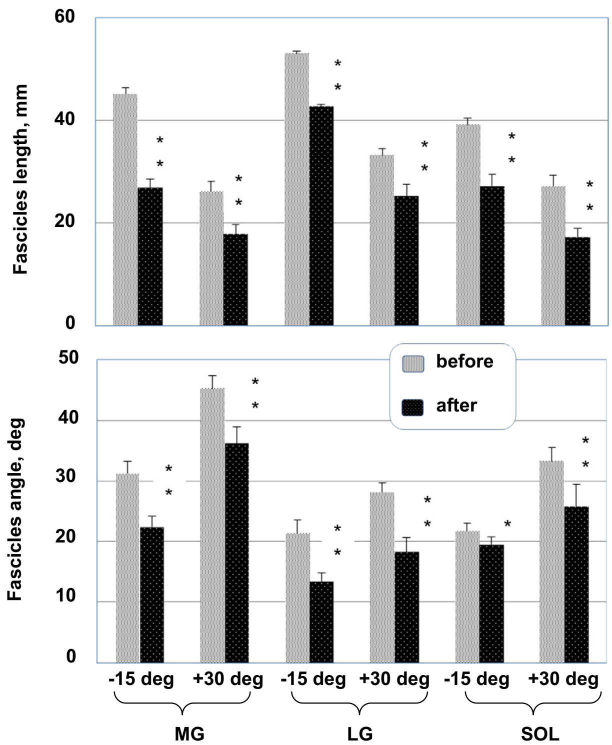


Fig. 4. Architecture of the triceps surae muscle. Changes in the fiber length and pennation angle as functions of the ankle joint angle in the MG, LG, and SOL as a result of a long-duration space flight. *p < 0.05; **p < 0.01.

the LG, and from 27.2 ± 2.3 to 18.2 ± 1.8 mm (by 33.1%) in the SOL (Fig. 4, *top panel*).

Pennation angle after the SF. With the ankle angle increasing from −15° to +30°, Θ increased from 26.6° ± 1.8° to 22.3° ± 2.7° (by 16.2%) in the MG, from 10.4° ± 1.4° to 9.3° ± 2.3° (by 10.6%) in the LG, and from 19.5° ± 1.3° to 15.8° ± 1.7° (by 18.9%) in the SOL (Fig. 4, *lower panel*).

Muscle thickness after the SF. With the ankle angle increasing from −15° to +30°, H decreased from 11.9 to 6.8 mm (by 42.9%) in the MG, from 7.7 to 4.1 mm (by 46.8%) in the LG, and from 9.1 to 4.9 mm (by 46.2%) in the SOL.

4. Discussion

The present study shows significant remodelling of muscle architecture and of the muscle–tendon complex (MTC) induced by prolonged (>180-day) a SF. This is the first study wherein muscle–tendon adaptation of human skeletal muscles to a SF was quantitatively evaluated and changes in function, rigidity, and architecture as main determinants of mechanical force generation were assessed simultaneously *in vivo* after a SF, using MG, LG, and SOL. In addition, the study is unique in terms of the unloading duration (>180 days) in estimating the effect on muscle architecture because many earlier reports have been based on model studies (Kubo et al., 2000; Kawakami et al., 2001; Reeves et al., 2005; Koryak et al., 2010).

As a main result, the study showed a decrease in MVC (−26%) and an increase in EMD (34%) of the TSM after a SF. The changes that arise in muscle functions on exposure to external factors result from changes in either contractile processes or neural (motor) drive. In fact, the MVC of a muscle is affected by its force–fiber length relationship, its geometric position relative to its joint, and its architectural characteristics. The majority of human muscles are pennate muscles, and a correct interpretation of data on the functional consequences of muscle unloading should consider the changes in the muscle internal organization known as the muscle architecture. The architecture of a muscle, along with its intrinsic properties such as the fiber composition, affects its functional characteristics (Bodine et al., 1982; Powell et al., 1984). Differences in architecture exert a greater effect on force production as compared with differences in fiber composition (Bodine et al., 1982; Burkholder et al., 1994). In this study, ultrasound examination was for the first time employed in evaluating the changes in architectural characteristics of the three heads of the TSM after SF, and architectural changes were related to the contractile functions and joint position.

The LG has the longest fibers in the TSM, and the sarcomere number in a fiber is consequently the highest, providing for a high speed potential (Wickiewicz et al., 1983; Huijing, 1985). In contrast, the MG has shorter fibers and greater pennation angles to allow more fibers to be packed, thus having a greater force production potential. The data are supported by the fact that the cross-sectional area of the MG is 2.5-fold greater than that of the LG, while the difference in muscle volume is only 1.7 fold (Fukunaga et al., 1992). As it is known, EMD is a peripheral component of human motor reaction embracing the lag from the onset of muscle-agonist electromyography till actual motion or, in other words, time of stretching the series viscoelastic component by the contractile elements (Cavanagh and Komi, 1979), which, in its turn, is dependent on force generation rate (Cavanagh and Komi, 1979). Consequently, EMD increase/reduction can be an indirect indicator of changed MTC stiffness (Mora et al., 2003). Changes in stiffness of the MTC have impacts for motion control as stiffness dictates mechanics of the interaction between the system and its environment. The present study has shown that EMD response to long-term mG suggests changes in the TSM properties. Previous results demonstrated convincingly that unloading can alter mechanic behavior of the muscle tendon, and that tendon extension results in decrease of tendon stiffness (De Boer et al., 2007; Kubo et al., 2004; Mora et al., 2003; Koryak, 2014, 2015). This loss in tendon stiffness may amplify its deformation in the course of force generation. According to our data, post-space flight EMD increased 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. (2004). It should be noted that EMD prolongs substantially in consequence of gross loss in tendon stiffness (Costa et al., 2010), however, EMD does not alter in the event when “weak tendon is raised” (Muraoka et al., 2004) and extends the MTC (Mora et al., 2003).

Both fiber length and pennation angle were lower after a SF, suggesting losses of both consecutive and parallel sarcomeres, respectively. The observation agrees with earlier findings (Narici and Cerretelli, 1998). 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 (Gordon and Huxley, 1966). 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 (Narici and Maganaris, 2007). 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. In the present experiment show that changes after long-duration SF L_f decreased in MG, LG and SOL by 33,8%, 40,9% and by 36,8% and Θ_f by 52,7%, 36,6% and by 32,5%, respectively, while before to SF

L_f decreased in MG, LG and SOL by 42,3%, 37,5% and by 30,6% and Θ_f by 44,9%, 31,8% and by 34,8%, respectively.

A lower pennation angle observed after a SF partly compensates for loss of force because the force transmission to the tendon becomes more efficient in spite of the decreased stiffness of the MTC, the EMD increases. This assumption is supported by the reports that a decrease in structural rigidity of a tendon has been observed in subjects after prolonged bed rest (Kubo et al., 2000, 2004; Reeves et al., 2005). A decrease in tendon rigidity after SF indicates that the tendon would experience a greater deformation as any contraction force is generated after a SF. A lower tendon rigidity would shift the *length–tension* ratio to the left, thus reducing the force of muscle contraction. Changes in the number of consecutive sarcomeres may affect the angle at which muscle fibers shorten during contraction (Reeves et al., 2004). Thus, adaptations to muscle unloading that arise in the muscle and MTC compensate for each other to maintain the functional range of the muscle at a constant level.

To summarize, a long-duration SF decreased the rigidity of the MTC of the TSM and changed the architecture of the MG, LG, and SOL. Differences in fiber length and pennation angle that were observed among the muscles and could be associated with differences in force production and in elastic properties of tendons and aponeuroses.

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Declaration of Competing Interest

The author declare that they have no competing interests.

References

Akima, H., Foley, J.M., Prior, B.M., Dudley, G.A., Meyer, R.A., 2002. Vastus lateralis fatigue alters recruitment of musculus quadriceps femoris in humans. J. Appl. Physiol. 92, 679–684.

Berg, H.E., Larsson, L., Tesch, P.A., 1998. Lower limb skeletal muscle function after 6 weeks of bed rest. J. Appl. Physiol. 82, 182–188.

Bodine, S.C., Roy, R.R., Meadows, D.A., Zernicke, R.F., Sacks, R.D., Fonrnier, M., Edgerton, V.R., 1982. Architectural, histochemical, and contractile characteristics of a unique biarticular muscle: the cat semitendinosus. J. Neurophysiol. 48, 192–201.

Burkholder, T.J., Fingado, B., Baron, S., Lieber, R.L., 1994. Relationship between muscle fiber types and sizes and muscle architectural properties in the mouse hindlimb. J. Morphol. 221, 177–190.

Costa, P.B., Ryan, E.D., Herda, T.J., Walter, A.A., Hoge, K.M., Cramer, J.T., 2010. Acute effects of passive stretching on the electromechanical delay and evoked twitch properties. European Journal of Applied Physiology 108, 301–310. Submitted for publication.

De Boer, M., Maganaris, C.N., Seynnes, O.R., Rennie, M., Narici, M., 2007. Time course of muscular, neural and tendinous adaptations to 23 day unilateral lower-limb suspension in young men. Journal of Physiology 583, 1079–1091. Submitted for publication.

de Boer, M.D., Seynnes, O.R., di Prampero, P.E., Pisot, R., Mekjavic, I.B., Biolo, G., Narici, M.V., 2008. Effect of 5 weeks horizontal bed rest on human muscle thickness and architecture of weight bearing and non-weight bearing muscles. Eur. J. Appl. Physiol. 104, 401–407.

Cavanagh, P.R., Komi, P.V., 1979. Electromechanical delay in human skeletal muscle under concentric and eccentric contractions. Eur. J. Appl. Physiol. 42, 159–163.

Fitts, R.H., Trappe, S.W., Costill, D.L., Gallagher, P.M., Creer, A.C., Colloton, P.A., Peters, J.R., Romatowski, J.G., Bain, J.L., Riley, D.A., 2010. Prolonged space flight-induced alterations in the structure and function of human skeletal muscle fibres. Journal of Physiology 588, 3567–3592. Submitted for publication.

Fukunaga, T., Roy, R.R., Shellock, F.G., Hodgson, J.A., Day, M.K., Lee, P.L., Kwong-Fu, H., Edgerton, V.R., 1992. Physiological cross-sectional area of human leg muscles based on magnetic resonance imaging. J. Orthop. Res. 10, 926–934.

Fukunaga, T., Ichinose, Y., Ito, M., Kawakami, Y., Fukashiro, S., 1997. Determination of fascicle length and pennation in a contracting human muscle in vivo. J. Appl. Physiol. 82, 354–358.

Gans, C., 1982. Fiber architecture and muscle function. Exerc. Sport Sci. Rev. 10, 160–207.

Gans, C., Bock, W.J., 1965. The functional significance of muscle architecture — a theoretical analysis. Ergebnisse der Anatomie und Entwicklungsgeschichte 38, 115–142.

Gans, C., Gaunt, A.S., 1991. Muscle architecture in relation to function. J. Biomech. 24 (53–65), 1991.

Gordon, A.M., Huxley, A.F., Jullian, F.J., 1966. The variation in isometric tension with sarcomere length in vertebrate muscle fibres. J. Physiol. 184, 170–192.

Gopalakrishnan, R., Gencenc, K.O., Rice, A.J., Lee, S.M.C., Evans, H.J., Maender, C.C., Ilaslan, H., Cavanagh, P.R., 2010. Muscle volume, strength, endurance, and exercise loads during 6-month missions in space. Aviat. Space Environ. Med. 81, 91–102.

Huijing, P.A., 1985. Architecture of the human gastrocnemius muscle and some functional consequences. Acta Anatomica 123, 101–107.

Hvid, L.G., Brocca, L., Qrtenblad, N., Suetta, G., Aagaard, P., Kjaer, M., Bottinalli, R., Pellegrino, M.A., 2017. Myosin content of single muscle fibers following short-term disuse and active recovery in young and old healthy men. Exp. Gerontol. 87, 100–107.

Kawakami, Y., Abe, T., Fukunaga, T., 1993. Muscle-fiber pennation angles are greater in hypertrophied than in normal muscles. J. Appl. Physiol. 74, 2740–2744.

Kawakami, Y., Abe, T., Kuno, S.Y., Fukunaga, T., 1995. Training-induced changes in muscle architecture and specific tension. Eur. J. Appl. Physiol. 72, 37–43.

Kawakami, Y., Ichinose, Y., Fukunaga, T., 1998. Architectural and functional features of human triceps surae muscles during contraction. J. Appl. Physiol. 85, 398–404.

Kawakami, Y., Akima, H., Kubo, K., Muraoka, Y., Hasegawa, H., Kouzaki, M., Imai, M., Suzuki, Y., Gunji, A., Kanehisa, H., Fukunaga, T., 2001. Changes in muscle size, architecture, and neural activation after 20 days of bed rest with and without resistance exercise. Eur. J. Appl. Physiol. 84, 7–12.

Kawakami, Y., Muraoka, Y., Kubo, K., Suzuki, Y., Fukunaga, T., 2000. Changes in muscle size and architecture following 20 days of bed rest. J. Gravitat. Physiol. 7, 53–60.

Kots, Ya. M., Absalyamov, T.M., Zorin, V.P., Koryak, Yu.A., Kuznetsov, S.P., Sin, L.D., 1976. Modification of the tendometric method to measure the force contraction for individual human muscles. Human Physiol. 2, 1045–1048.

Koryak, Yu.A., 2014. Influence of simulated microgravity on mechanical properties in the human triceps surae muscle in vivo. I: Effect of 120 days of bed-rest without physical training on human muscle musculo-tendinous stiffness and contractile properties in young women. Eur. J. Appl. Physiol. 114, 1025–1036.

Koryak, Yu.A., 2015a. Influence of simulated microgravity on mechanical properties in the human triceps surae muscle in vivo. II. Effect of 120-days of bed rest with physical training on human muscle contractile properties and musculo-tendinous stiffness in young women. Central Europ. J. Sport Sci. Med. 11, 125–143.

Koryak, Yu.A., 2015b. Influence of 120-day stimulated microgravity with countermeasures on human muscle musculo-tendinous stiffness and contractile properties. Int. J. Sports Exercise Med. 1, 1–8.

Koryak, Yu.A., Kuz'mina, M.M., Berezhinskiy, I.V., Kovalenko, V.M., 2010. Long-term electrical stimulation-based muscle training in humans exposed to unloading of the locomotor system and its effect on the architecture and function of the triceps surae muscle. Fundament. Res. 3, 69–87.

Kubo, K., Akima, H., Kouzaki, M., Ito, M., Kawakami, Y., Kanehisa, H., Fukunaga, T., 2000a. Changes in the elastic properties of tendon structures following 20 days bed-rest in humans. Eur. J. Appl. Physiol. 83, 463–468.

Kubo, K., Akima, H., Ushiyama, J., Tabata, I., Fukuoka, H., Kanehisa, H., Fukunaga, T., 2004. Effects of resistance training during bed rest on the viscoelastic properties of tendon structures in the lower limb. Scand. J. Med. Sci. Sports 14, 296–302.

Kubo, K., Akima, H., Kouzaki, M., Ito, M., Kawakami, Y., Kanehisa, H., Fukunaga, T., 2000b. Changes in the elastic properties of tendon structures following 20 days bed rest in humans. Eur. J. Appl. Physiol. 83, 463–468.

Kuno, S., Fukunaga, T., 1995. Measurement of muscle fibre displacement during contraction by real-time ultrasonography in humans. Eur. J. Appl. Physiol. 70, 45–48.

LeBlanc, A., Gogia, P., Schneider, V., Krebs, J., Schonfeld, E., Evans, H., 1988. Calf muscle area and strength changes after five weeks of horizontal bed rest. Am. J. Sport Med. 16, 624–629.

Lieber, R.L., 1992. Skeletal muscle structure and function Implications for rehabilitation and sports medicine. Williams and Wilkins, Baltimore. Md.

Maganaris, C.N., Baltzopoulos, V., Sargeant, A.J., 1998. Changes in Achilles tendon moment arm from rest to maximum isometric plantarflexion: observations in man. J. Physiol. 510, 977–985.

Mora, I., Quintero, S., Pérot, C., 2003. Electromechanical assessment of ankle stability. European Journal of Applied Physiology 88, 558–564. Submitted for publication.

Muhl, Z.F., 1982. Active length-tension relation and the effect of muscle pennation on fiber lengthening. J. Morphol. 173, 285–292.

Muraoka, T., Muramatsu, T., Fukunaga, T., Kanehisa, H., 2004. Influence of tendon slack on electromechanical delay in the human medial gastrocnemius in vivo. Journal of Applied Physiology 96, 540–544. Submitted for publication.

Narici, M.V., Cerretelli, P., 1998a. Changes in human skeletal muscle architecture induced by disuse atrophy. J. Physiol. 506, 59.
Narici, M.V., Landoni, L., Minetti, A.E., 1992. Assessment of human knee extensor muscles stress from in vivo physiological cross-sectional area and strength measurements. Eur. J. Appl. Physiol. 65, 438–444.
Narici, M., Cerretelli, P., 1998b. Changes in human muscle architecture in disuse-atrophy evaluated by ultrasound imaging. J. Gravitat. Physiol. 5, P73–P74.
Narici, M.V., Maganaris, C.N., 2007. Plasticity of the muscle-tendon complex with disuse and aging. Exerc. Sport Sci. Rev. 35, 126–134.
Powell, P., Roy, R.R., Kanim, P., Bello, M.A., Edgerton, V.R., 1984. Predictability of skeletal muscle tension from architectural determinations in guinea pig hindlimbs. J. Appl. Physiol. 57, 1715–1721.
Reeves, N.D., Narici, M.V., Maganaris, C.N., 2004. In vivo human muscle structure and function: adaptations to resistance training in old age. Exp. Physiol. 89, 675–689.
Reeves, N.D., Maganaris, C.N., Ferretti, G., Narici, M.V., 2005. Influence of 90-day simulated microgravity on human tendon mechanical properties and the effect of resistive countermeasures. J. Appl. Physiol. 98, 2278–2286.
Rutherford, O.M., Jones, D.A., 1992. Measurement of fibre pennation using ultrasound in the human quadriceps in vivo. Eur. J. Appl. Physiol. 65, 433–437.
Wickiewicz, T.L., Roy, R.R., Powell, P.L., Edgerton, V.R., 1983. Muscle architecture of the human lower limb. Clin. Orthop. Relat. Res. 179, 275–283.
Wilson, A., Lichtwark, G., 2011. The anatomical arrangement of muscle and tendon enhances limb versatility and locomotor performance. Philos. Trans. Roy. Soc. London. Ser. B Biol. Sci. 366, 1540–1553.