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CONTRACTILE CHANGES ON SKELETAL MUSCLE ASSOCIATED WITH THE MEN STRUAL CYCLE AFTER THE 3-DAY '*DRY*' IMMERSION AS MICROGRAVITY SIMU LATION IN WOMEN

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Abstract

Purpose: The study aimed to investigate the changes in muscle architecture (lengths and angles of fascicles) of the female medial gastrocnemius muscle (MG) in vivo and the changes in biomechanical properties of muscles after 3 days of 'dry' water immersion (DI) with respect to the menstrual cycle.

Methods: Young healthy females (n = 6, age 28.4 ± 1.4 yr, body length 1.7 ± 0.1 m, body weight 60.2 ± 3.8 kg) volunteered to participate in the study. The subjects had a moderate physical activity level and a normal menstrual cycle 26-32 days, (mean 28 days) and did not receive any hormonal treatment. The isometric maximum voluntary contraction (MVC) of the plantar flexor muscles was measured using a isokinetic dynamometer (Biodex, USA) at an ankle angle of 0º. The subjects performed drop jumps (DJs) from drop heights of 20 (DJ_{20}), 40 (DJ_{40}) and 60 (DJ_{60}) cm on a contact plate. Statistical comparisons of the vertical ground reaction force (vGRF), impulse, moment, power, and work were made between different DJ heights. A real-time B-mode ultrasound system (Edge, USA) and a linear 7.5-MHz electronic transducer with a 60-mm field of view were used to obtain MG images (to measure the fascicle length and angle) at rest and during MVC (100 %). Additional images were taken at 20 and 80 % of MVC at an ankle angle of 0º. The internal architecture of the MG was determined at ankle angles of -15º (dorsiflexion), 0º(a neutral anatomical position), and +30º (plantarflexion) and a knee angle of 0º. In each position, longitudinal ultrasound images of the MG were obtained at the proximal level corresponding to 30 % of the distance between the popliteal crease and the center of the lateral malleolus. The images obtained at rest for each ankle position were used to measure, the fiber length (L_f) and pennation angle (Θ_f) relative to the aponeurosis. The cycle phases considered were menstrual early follicular (when the estradiol concentration is low) and late follicular (when estradiol is elevated). Three sets of experiments (Isokinetic, Jumping, and Architecture) were performed following. The Jumping experiment were performed the before the start of the subject's exposure to the DI conditions (BDC –2) and after the rise (R) from the bath (R +2). The Architecture experiment was performed directly on the day of exposure (BDC -0) of the subject and immediately after from the bath (R +0).

Results: Significant changes in MVC, muscle architecture, and mechanical properties of the human muscle were observed in the late follicular phase. MVC increased significantly (by approximately 11%) in the late follicular phase. DJ performance in the late follicular phase was better than in the early follicular phase.

Conclusion: Changes in female steroid hormones during the menstrual cycle were concluded to increase the muscle strength and to affect the mechanical properties of human muscles in the follicular phase. The finding supports the idea that the hormones influence the regulation of the parameters under study in conditions of unloading of the muscular apparatus.

Key words: Unloading, pennate muscle, muscle fascicle and angles behavior, ultrasonography, drop jumps, voluntary contractions

Introduction

At present, the participation of women in manned space flights has increased. So, if, as of June 2013 into space 57 women [4], then as of April 2025 already 105 space travelers were women [18, 126]. Therefore, to ensure the safety of female astronauts during long-term space flights, it is necessary to study and understand the mechanisms of changes in the contractile properties of skeletal muscles. The study of the contractile function of skeletal muscles in women exposed to space flight factors is increasing in importance. On the Earth, 6° head-down tilt bed rest is an accepted model of real long-term microgravity and is used in musculoskeletal studies. The model has been successfully used in studies with the participation of men as subjects [34, 69, 70, 85, 87], as well as in groups of subjects with gender differences disregarded [5, 26, 27, 70, 71, 72, 87]. In the latter case, researchers apparently proceed from the conventional assumption that adaptations to training and reactions to physical activity are the same in men and women [17, 116]. However, a growing body of evidence points to cyclic changes in steroid hormone (e.g., estrogen) levels during the ovulatory menstrual cycle [17, 117]. The menstrual cycle is a complex physiological phenomenon and includes both physical and physiological changes [65]. A decrease in muscle strength during menstruation was first reported over 50 years ago [22]. 'Dry' water immersion (DI) provides another model that reproduces the conditions of unloading [113]. Surprisingly, we did not find in the literature studies involving women as subjects and addressing the DI effect on muscle contractile properties and architectonics. We understand that it is extremely difficult to women to participate in the DI model, given the physiological characteristics of the female body. Nevertheless, it is critical to determine whether the menstrual cycle affects the muscle strength, internal structure, and mechanical properties of muscles in order to plan more efficient training and rehabilitation protocols for women after a long space flight.

It is well known that men and women differ in many aspects of the musculoskeletal system, with men generally having greater muscle mass and strength. In this regard, an important question arises: space flight of the same duration is accompanied by an equal loss of muscle strength in men and women. If this is indeed the case, then it is a strong argument in favor of the development of separate preventive measures for women and men. The problem is of immense importance. However, a problem of no less importance stems from the differences in the physiological functions of the body between men and women and must be taken into account in the training process.

Due to their short and painstaking reproductive age, women are more vulnerable physically during different phases of the menstrual cycle. Understanding the physiological effects of sex hormones on various systems of the body is crucial for sound scientific design [116]. Fluctuations in certain physiological parameters of various systems may be related to oscillations in the hormonal levels in different phases of the menstrual cycle. Physical performance may vary with variations in sex hormone secretion during the menstrual cycle. Motor functions are affected, in fact, by the oscillations in female steroid hormone levels [49, 87]. Fluctuations in estrogen potentially affect physical performance in females [88]. Apart from their reproductive function, the female sex hormones affect various physiological systems and have a role in exercise performance [100]. The phases of the menstrual cycle are influenced by alterations in the concentrations of hormones, such as estrogen and progesterone [15, 97]. Certain physiological parameters, including athletic performance, could change along with the phases of the menstrual cycle [7]. Fluctuating levels of sex steroids across the normal menstrual cycle affect sensorimotor association of an individual [98]. Maximum muscle strength in the follicular phase and at ovulation is greater than in the luteal phase in both untrained [103, 108] and trained [100] females. Recovery and reconstruction of muscle fibers after eccentric exercise have been shown to be faster in the mid follicular phase compared with the luteal phase [50, 52]. This confirms that estrogen exerts a positive effect on skeletal muscles. Studies have not been done as of yet to evaluate the influence of the menstrual cycle on the mechanical properties of female muscle in DI conditions.

Vertical jumping has been described as a complex human movement that requires a high degree of motor coordination between the upper- and lower body segments [86]. Vertical jumps are often used as a performance test to assess the individual potential, to identify athletes' strengths and weaknesses, and to measure the efficiency of training programs [36]. The maximum jump height achieved by an individual, is an indicator of the power of leg muscles and, can provide key information about their functional capacity and performance [109]. In fact, vertical jumping is considered to provide an essential functional performance of the neuromuscular system in humans. The vertical jump performance is determined by a complex interaction of several factors, including the maximum force developed by the musculature involved, the rate at which force can be developed, and the neuromuscular coordination of the upper- and lower -body segments [48, 89]. Various devices, including contact mats and force plate, have been used to measure the contributions of the factors [64]. Common performance measures calculated from the device data are flight time, vertical ground reaction force, vertical velocity at take-off, and peak power.

The architecture of a skeletal muscle is an important determinant of its functional characteristics [40, 41, 42]. Muscle strength and power are determinants of successful performance in a motor task. Gravitational loading appears to be necessary for the maintenance of human lower limb skeletal muscle size and force [45, 75]. A decrease or complete absence of muscle loading leads to a decrease in the function and size of skeletal muscles [45, 71]. Greater loss in muscle strength than in mass is the best-known phenomenon in the effect of actual (a space flight) or simulated (prolonged bed rest) microgravity [60]. The phenomenon directly indicates that factors other than atrophy additionally contribute to muscle weakness. Muscle architecture has been known to be associated with performance [23]. Increases in fascicle thickness strongly correlate with the ability to produce force [94, 95]. An increase in pennation allows for a greater number of fibers to be present within a given cross-sectional area and thus is often associated with an increased muscle and fascicle thickness and a higher strength [85]. However, when the cross-sectional area is constant, but the pennation angle changes, a deficit in strength can be observed with the increasing pennation angle [55]. This is because the angle of pull of the fibers is indirect to the pull of the total muscle, and the pull of the muscle is thus diminished by the cosine of the pennation angle. Fascicle length depends on both pennation angle and fascicle thickness. A the pennation angle decreases or the fascicle thickness increases, the fascicle length will also increase. A greater fascicle length suggests either longer sarcomeres or more sarcomeres in line. Thus, as the length of the contractile element increases, so does the velocity of contraction and the force that can be applied at a high velocity.

In this work, the relationship between muscle architecture (the lengths and angles of fascicles) and the force of contraction was studied in the human medial gastrocnemius muscles (MG) in vivo in passive (relaxed) and active (contracting) conditions by means of ultrasonography. Information about the skeletal muscle function in simulated microgravity may help elucidate the etiology of a decrease in force during spaceflights. In view of this, the objectives of the study were, first, to investigate the changes in internal architecture of the MG as a function of the ankle and, second, to evaluate the change in the mechanical efficiency of lower limb extension muscles a drop jump (DJ) test in young females after DI. We studied how the biomechanical properties change with the increasing drop height. We aimed to investigate how the main determinants of a maximum voluntary contraction in young healthy females are affected by 3 days of DI during the menstrual cycle. We hypothesized that the kinematic and kinetic parameters of vertical jumps would be reduced following unloading in the late follicular phase.

Methods

Overall Study Design

The overall design of this investigation integrated several experiments that examined the physiologic, responses to simulated weightlessness (i.e. 3-day DI) in young healthy females. In view of this, the objectives of the study were, first, to investigate the changes in internal architecture as a function of the ankle joint angle for of the MG and, second, to evaluate the change in the mechanical efficiency of lower limb extension muscles during DJ in young females after DI (Fig. 1, *top panel*). The study was conducted at the Institute of Biomedical Problems (Moscow, Russia).

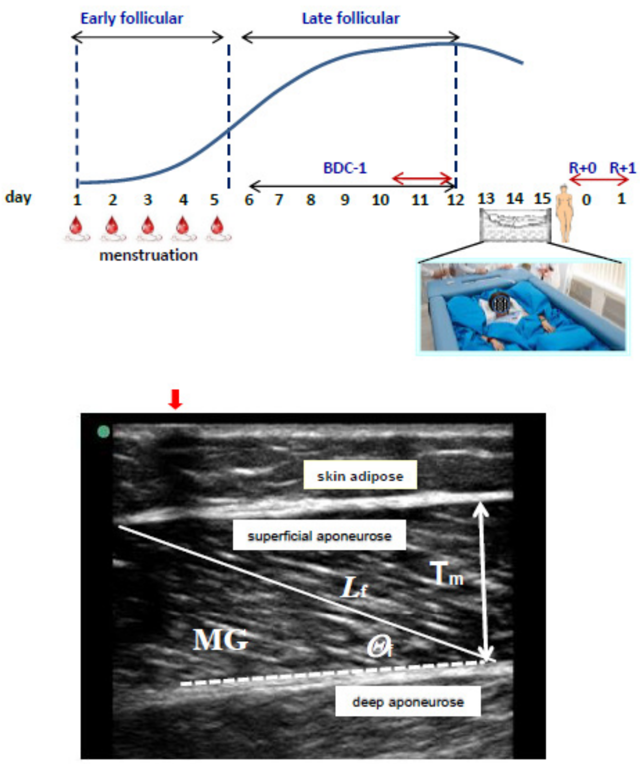


Figure. 1. Experimental design (*top panel).* Schematic displaying the hormonal fluctuations across an idealised 28-day menstrual cycle. Adapted from McNulty et al. (88). A marker (↔) indicates of BDC days for the Isokinetic, Jumping and Architecture experiments. **A standard ultrasound image of a muscle** (*botton panel*). Sagittal ultrasound image of the medial gastrocnemius (MG). 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 (L_f) was measured along an ultrasound signal line drawn parallel to a fiber measured as an angle of the line drawn parallel to a fiber between the deep and superficial aponeuroses. A diagonal white line superimposed on the ultrasound image shows the path of a fiber between the superficial and deep aponeuroses. Muscle thickness (T_m) was obtained by measuring the distance between the superficial and deep aponeuroses. A marker (⬇) between the deep and superficial aponeuroses (horizontal white line). The pennation angle (Θ_f) was) was placed between the skin and the ultrasonic probe as the landmark to confirm that the probe did not move during measurements.

Participants

The study was conducted in the Department of Sensorimotor Physiology and Countermeasures, Laboratory of Gravitational Physiology of Sensorimotor System, Institute of Biomedical Problems of the Russian Academy of Sciences after obtaining an Ethical Clearance Certificate from the Bioethical Commission of the Institute of Biomedical Problems in accordance with the latest update of the Declaration of Helsinki.

Six young female volunteers who were menstruating regularly were recruited through local advertisements and the subjects had never been involved in microgravity model studies. It was considered that the participation of six subjects would be sufficient for this study if significant changes were found in the group of foot extensors and the general functional capabilities of the subjects. Descriptive physiological data are reported in Table 1. All participants had a regular menstrual cycles for (28 ± 2 days) for 4 months prior to the experiment. A prestudy physical examination showed that none had any evidence of menstrual disorders. The subjects did not take oral contraceptives or other hormones for at least 6 months before or during the study. The subject' characteristics are presented in Table 1.

Table 1. Anthropometric data for subjects (n = 6).

Age, yr	Height, cm		Weight, kg		BMI⁺, kg/m²	
	Before	After	Before	After	Before	After
30.2	166.3	166.5	62.1	60.5	22.4	21.8
2.1	3.1	3.1	3.1	3.2	0.8	0.9

$^{+}$-body mass index

The participants did not use any form of hormonal contraception for at least 6 months prior to the experiment. All participants were free from any type of menstrual disorders (e.g., dysmenorrhea, amenorrhea, or heavy symptoms associated with pre-menstrual syndrome), had no musculoskeletal injuries within 3 months prior to the investigation and were not taking drugs or dietary supplements during the study. Selection of the subjects was based on a screening evaluation which consisted of a detailed medical history, complete blood count, urinalysis, resting electrocardiogram, and a panel of blood chemistry tests (fasting blood glucose, blood urea nitrogen, creatinine, lactic dehydrogenase, bilirubin, uric acid, and cholesterol).

All of the participants were physically active, but not specifically trained (moderate aerobic physical activity ≤3 times a week). The subjects were not engaged in any strength training program within for at least 6 months prior to the study. The subjects did not take medications at the time of the study, and all subjects were nonsmokers, and lacked neurological disorders. Informed consent was obtained from each participant 2 weeks before the study.

The subjects performed three sets of experiments (Isokinetic, Jumping, and Architecture). The study included 2 days of baseline data collection (BDC). The Jumping experiment were performed the before the start of the subject's exposure to the DI conditions (BDC –2) and after the rise (R) from the bath (R +2). The Architecture and Isokinetic experiments were performed directly on the day of exposure (BDC -0) of the subject and immediately after from the bath (R +0). The subjects were familiarized with the experiment during a preliminary session before starting the tests. Each subject served as her own control.

Body Temperature Measurements

The subjects measured their basal body temperature (BBT) orally for 20 seconds, immediately upon awakening in the morning, using a digital thermometer (C-531; TERUMO Co. Ltd., Tokyo, Japan) with scale steps of 0.018 C. BBT were recorded in a logbook. We confirmed the biphasic characteristics of BBT. BBT was used to predict the cycle phases. The phases of the menstrual cycle were determined by counting days [108]. Hormone tests were not performed.

'Dry' Water Immersion

'*Dry*' water immersion (DI) was used to simulate microgravity as described by Shulzhenko & Vil-Villiams [113]. A subject was positioned horizontally in a special bath on a fabric film, which separated her from the water. During DI, the subjects remained in a horizontal position (with a angle which make the body and a horizontal line, i.e. 5^0 head-up position) continuously, including excretory functions and eating. The water temperature was constant (33.4 ± 2^0 C) and was maintained automatically throughout the experiment. The DI duration was 3 days. The 20-10 days before exposure the participants in the experiment were familiarized with the experimental procedures. The subjects were allowed to leave the immersion bath for hygiene procedures and examinations. The average time spent by the subjects outside the immersion bath was ~ 28 min, 22 and 18 min on days 1-3, respectively. Every evening, the subjects were raised from the bath for an average of 15–20 min to carry out hygiene procedures, but most hygiene procedures were performed in the supine position. All baseline data of the subjects were collected 4-3 days before exposure, and subsequent measurements were performed on the day of subjects' awakening. Nursing staff was present for the subjects' transportation, hygiene procedures (including toilet), provision of food, and medical care, and support of the subjects' needs within the constraints of the protocol. The subjects were under medical observation for 24 $h.d^{-1}$.

Procedures

Measurement of Maximum Voluntary Isokinetic Contraction

Before starting muscle strength measurements, a subject lay on her back in a supine position to reduce the effect of prior activity, as an exogenous factor [24]. All subjects were instructed to abstain from food for 2 hours before testing, from caffeine for 4 hours before testing, and from exercise for 12 hours before testing. Standard joint-specific warm-up procedures were followed and consisted of five submaximal repetitions and two to three maximal repetitions. After the warm-up, the subjects rested for at least 2 min. Strength tests were performed so that the subject exerted a maximal effort in only one direction for each set of repetitions.

After a full warm-up, the isometric ankle extension torque of the subject's right legs was tested at joint angular velocities of $0^0/s^{-1}$, using a Biodex Isokinetic Dynamometer (Biodex System 4 PRO™, Biodex Medical Systems, Shirley, New-York, United States). The participants was seated upright in the Biodex dynamometer chair with her trunk positioned and secured to the seatback with waist and shoulder belts to ensure consistent positioning and minimal movement. The hips were positioned to 90^0 with the thigh, and the knee angles were 45^0 (flexed) and the ankle angle was 90° to determine the plantarflexion torque. The lateral malleolus of the right foot was aligned with the axis of rotation on the Biodex dynamometer. The foot was fastened to the footplate with inelastic straps, which were firmly secured behind and on the underside of the footplate to prevent heel lift. When heel lift occurred or the torque did not return to baseline, the protocol was stopped and repeated after 3– to 5-min rest. The subject performed three sets of four repetitions of maximal isometric ankle extension at an angular velocity of $0^0/s^{-1}$ with a 2-min resting period between contractions unless the third trial exceeded one of the two first ones by more than 10 %. In that case an additional trial was performed. The participants was instructed to grip the side handles to help stabilize the trunk.

Each subject was instructed to exert maximal effort in only one direction and in every movement when performing the test; no verbal instruction was provided during testing. Two-min rest separated the sets. The peak isometric torque at $0^{o0}/s^{-1}$ (maximum voluntary contraction (MVC) was recorded for each subject. The contractile properties of muscles were determined 2 days before the start of DI and 1 day after the end of DI.

Measurement of Maximal Rate of Force Development

All subjects performed at least 2 familiarization sessions with submaximal and maximal isometric foot press efforts in the laboratory set up used for testing. The day after subjects came to the laboratory for the assessment of maximum isometric force, and architecture and the rate of force development during foot press. Subjects were instructed to apply their maximum force as fast as possible for 2 seconds. Two maximum trials were performed with 3 minutes interval. Subjects were vocally encouraged to perform their best effort during the measurement. Variables calculated from the *force-time* curve included the maximum isometric peak force, the rate of force development (RFD), and the impulse. Maximum MVC was calculated as the greater force generated from the force-time curve. The RED of increased muscle tension was calculated from of the force-time curve 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 [70, 71, 73].

Measurement of Jump Performance

Jump Test

Jump heights and contact times of the jumps described below were detected using a contact mat measuring system (Ergojump-Skurvydas, Lithuanian Sports University Kaunas, Lithuania).

Drop Jump

A second testing session was performed by subjects within 24 hours of the first. The drop-jump (DJ) a custom-built steel staircase with 5 step dimensions were used to collect the fast-reactive strength and their height were 20 mm (height), 40, 60, 80 and 100 mm. The subjects performed vertical jump after dropping from heights of 20 (DJ_{20}), and 40 (DJ_{40}), and 60 (DJ_{60}) cm. The subjects landed on both feet on a contact platform (70 x 70 cm), which was placed approximately 20 cm in front of the staircase edge. To ensure safety of the subjects during the DJ landing phase, the force platform was placed in a foam surr (40 cm x 40 cm). In three jumps subjects were asked to immediately jump off the ground after landing with maximum effort and jump as high as possible [10, 11]. In the starting position, a subject stand upright on a custom-built steel staircase with hands were placed on waists to restrict arm movements during DJs. The subjects were allowed to practice several times before data collection. As in the first testing session, the subjects were required to refrain from exercise for at least 24 hours. Before testing, the subjects performed a standardized warm-up consisting of dynamic lower-body stretches. No static stretching was done because of its known possible interference with power production and disruption of the elastic component. The dynamic stretches included body weight squats, knee hugs, walking lunges, walking quadriceps stretches, high kicks, and lateral lunges.

All 3 jump types were performed in 2 consecutive sets of 3 jumps in set in both jumps; the instructions were to jump as high as possible. The subjects were allowed to practice several times before data collection. The subjects rested for 3 minutes between sets to allow complete recovery [31]. The subjects were told to drop to the most natural position before jumping. All jumps were performed with the hands on the waist to limit any upper body influence on the jumps.

All jumps were performed on a calibrated contact platform [64]. From this position, the subject started with a forward swing of a leg from the steel staircase and aimed to jump as high as possible after a short contact with the ground, paying attention to a bouncing jump execution. Ground contact times of ≥ 200 ms, disengagement of the hands from the hips, ground contact of the heels during the takeoff, or excessive joint angle enlargement in the knee and hip joints made a jump invalid. Verbal encouragement was received by the subjects during testing and remained consistent across all subjects and trials.

The contact platform with an electronic timer was synchronized to a vertical jump meter to measure the flight time of jumps (H-Matis, Institute of Sports, Kaunas, Lithuania). Time counting was triggered as the subject's feet left the platform and stopped at the moment of touch down. The method assumes that the jumper's position on the mat is the same in take-off and landing. The best performance in terms of jump height was used for further analysis. The flight time, the height of the jump, and the force ("*explosive*" force) and time of take-off from the platform were determined. The flight time (t_f, s) measured from the sound signal was used by H-Matis to automatically calculate the height h (m) gained by the center of mass each jump. The rise in the body's centre of mass above the ground (h in meters) was automatically calculated by the H-Matis from the flight time (t_f in seconds) applying the following formula, where *g* is the acceleration due to gravity (9.81 m x s^{-2}):

$$h = t_f^2 \text{ x } (g \text{ x } 8^{-1})$$

The vertical velocity the rise in the body's centre of mass above the ground (V_v in m/sec) was calculated from the ground contact time (t_c in seconds) applying the following formula, where g is the acceleration due to gravity (9.81 m x s^{-2}):

$$V_v = g \text{ x } t_c/2.$$

Ultrasound Scanning

A subject was seated as convenient in a chair of the Biodex isokinetic dynamometer. The trunk was fixed to the back of the chair with shoulder and waist belts to ensure a constant position and minimal movements. The hip joint was fixed relatively rigidly at an angle of 120°; the knee joint, at an angle of ~90°; and the ankle joint, at a plantarflexion angle of 20°. The configuration of joint positions was explained by the fact that the gastrocnemius muscle–tendon complex is relatively weak when the knee angle is 90°, and a 20° plantarflexion angle was used to compensate for this effect at the ankle joint. The lateral malleolus of the right foot was aligned with the rotation axis of the isokinetic dynamometer, and the center of the knee joint was thoroughly aligned with the rotation axis of the detector of the dynamometer. The subject was allowed to hold side handles to stabilize the trunk position. Each subject's right foot was relatively rigidly fixed on a special platform of the Biodex isokinetic dynamometer so that the ankle angle could to be set passively at -15^0 (plantar flexion), 0^0 (a neutral position), $+15^0$, and $+30^0$ (plantar extension).

Real-time evaluation of the MG architecture in vivo at rest was performed using ultrasound scanner (Edge, *SonoSite*, United States) with a 7.5-MHz linear electronic transducer in the B mode. To improve acoustic coupling, special gel was applied onto the scanning surface of the transducer and the skin over the target muscle. The transducer was oriented along the middle sagittal axis of the muscle and arranged along the plane of muscle bundles so that all bundles visible in the scanning window were accessible for examination. A part visualized in the scanning window was measured for each bundle, and the invisible part was evaluated via linear extrapolation of bundles and aponeuroses. The measurement error was ~ 4 % with this approach [104]. The lengths and pennation angle of muscle fibers were measured on images. In each angular position, longitudinal ultrasonic images of the triceps surae (medial (MG) gastrocnemius muscle) were obtained at the proximal levels 30 % of the distance between the popliteal crease and the center of the lateral malleolus [61]. Each level is where the anatomic cross-sectional area of the respective muscle is maximal [39]. At that level, mediolateral widths of MG were determined over the skin surface, and the position of one-half of the width was used as a measurement site for each muscle. The scanning head was coated with water-soluble transmission gel, which provided for acoustic contact without depressing the dermal surface. The transducer pressure on the skin was kept minimal during scanning in order to avoid pressing the muscle. By visualizing the fascicles along their lengths from the superficial to the deep aponeuroses, one can be convinced that the plane of the ultrasonogram is parallel to the fascicles [58]. Otherwise, the fascicle length would be overestimated and the fascicle angle would be underestimated [111]. The echoes from interspaces of the fascicles were sometimes imaged more clearly along the fascicle length when the plane was changed to be slightly diagonal to the longitudinal line of each the muscle, in which cases the recreated image was used. The images were saved as files on a hard disk for further analysis. The participants of the experiment was instructed to relax the ankle extensor muscles during measurement, and the fiber length and angle were measured 20 min after to allow bodily liquids to achieve a steady state [6, 73].

The length of a fascicles (L_f) across the deep and superficial aponeurosis was measured as a straight line [39, 58] (Fig. 1, *botton panel*). To determine (L_f), the visible part of fibers was measured directly in an ultrasound window. A minor part of the bundle was outside of the window in some cases and was therefore estimated via linear extrapolation of the fibers and aponeuroses [1]. The method adequately measures the muscle fiber (bundle) length [25] and is highly reliable, showing a within-class correlation coefficient of 0.99. A linear extrapolation error is no more than 2–7% [10]. The fascicle pennation angle (Θ_f) was measured from the angles between the echo of the deep aponeurosis of each muscle and interspaces among the fascicles of that muscle [39, 59] (Fig. 1).

The distance between aponeuroses (muscle thickness - T_m) was estimated from the fascicle length and pennation angle using the following equation:

$$T_m = L_f \text{ x } \sin\dot{\alpha}, \qquad \text{where}$$

L_f, and $\dot{\alpha}$ are, recpectively, the fascicle length and pennation angle as determined by ultrasound.

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

The physiological cross-sectional area (PCSA) was estimated in the present study by the following equation [10]:

$$\text{PCSA index} = T_m^2 / L_f$$

Statistics

Conventional statistical methods were used for to calculate the mean, standard error (± SE), and coefficients of correlation. Differences between baseline and post-exposure (background) values of the same subject were tested for significance by Student's paired t-test. Data are reported in text and displayed in Figs. 2–6 as mean ± SE. Percentage changes were calculated for pre- and post-exposure values. The level of significance was set at $p < 0.05$ in all analyses.

Results

All of the subjects belonged to an age group of 24 to 39 years; the mean age was 30.2 ± 2.1 years. The mean body mass index (BMI) was 22.4 ± 0.8 kg/m^2 before unloading and 21.8 ± 0.9 kg/m^2 after 3-day unloading (Table 1). All the subjects could be characterized by as healthy people who lacked neuromuscular disorders and had a common lifestyle with respect to exercise. The subjects had never been subjected to microgravity model studies. Changes in both contractile functions of the extensor muscles and the internal architecture of the MG were observed after 3-day unloading.

Changes in Muscle Function

Plantarflexor Torque

The changes maximum voluntary plantarflexion torque after 3-day unloading is shown in Fig. 2. The maximum voluntary torque measured at $0^{\circ 0}/s^{-1}$ increased significantly from 106.2 ± 3.1 N*m to 117.4 ± 5.2 N*m ($p < 0.05$), corresponding to a relative change of 10.5 % (*left panel*). All subjects reported an increase in maximum voluntary torque moment, and only two subjects showed a decrease in the muscle strength (Fig. 2, *right panel*).

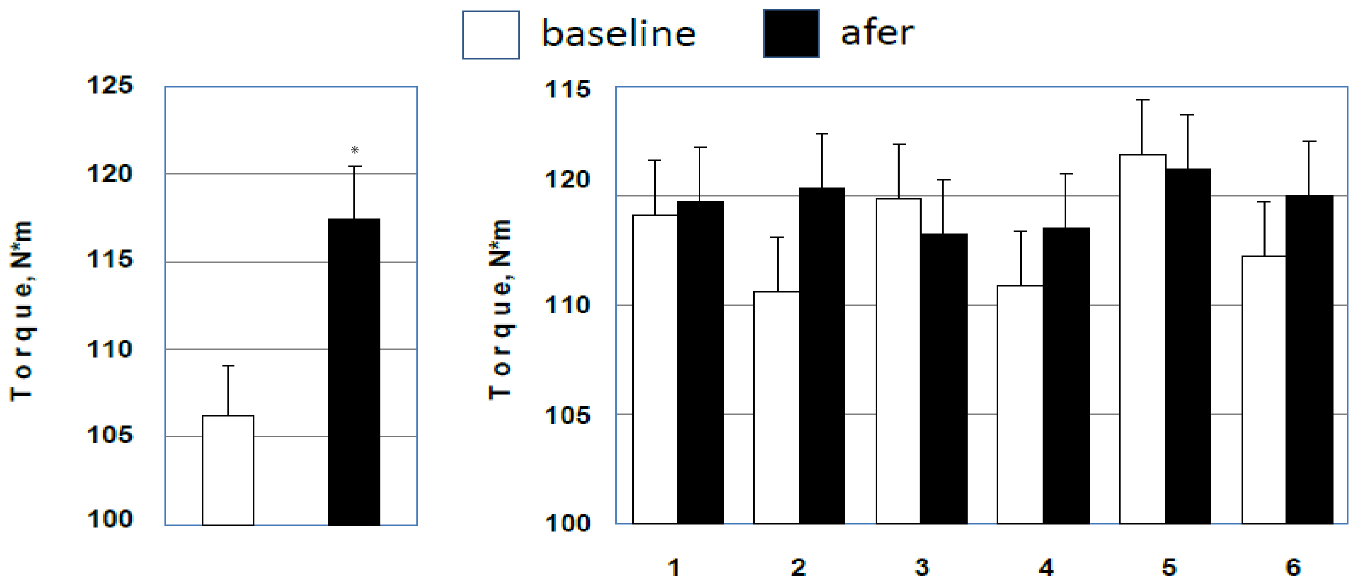


Figure. 2. Effects of 3-day DI on the contractile properties.
The maximum joint moment of the ankle extensor muscles was measured during voluntary contractions at an angular velocity of 0°/s with the ankle in a neutral position before and after unloading (*left panel*) and individual data of subjects after of 3-day unloading (*right panel*). Differences were significant at (*) $p < 0.05$

Rate of force development

RFD and impulse increased after 3 days of unloading. The mean changes in RDF of isometric tension and impulse of the TS muscle are shown in Fig. 3. The increase in MVC (on average ~11) after 3 days of unloading was associated with a significant increase in the velocity, or gradient, of development of isometric voluntary muscle contraction (Fig. 3, $p < 0.01$–0.001); the maximum dP/dt was significantly increased (on average 74.4%) when expressed in relative units, i.e. as a percentage of MVC (Fig. 3, inset, $p < 0.001$). Analysis of impulse demonstrated greater increases after DI at 100, 150, 200, and 300 milliseconds (Fig. 3, *bottom panel*).

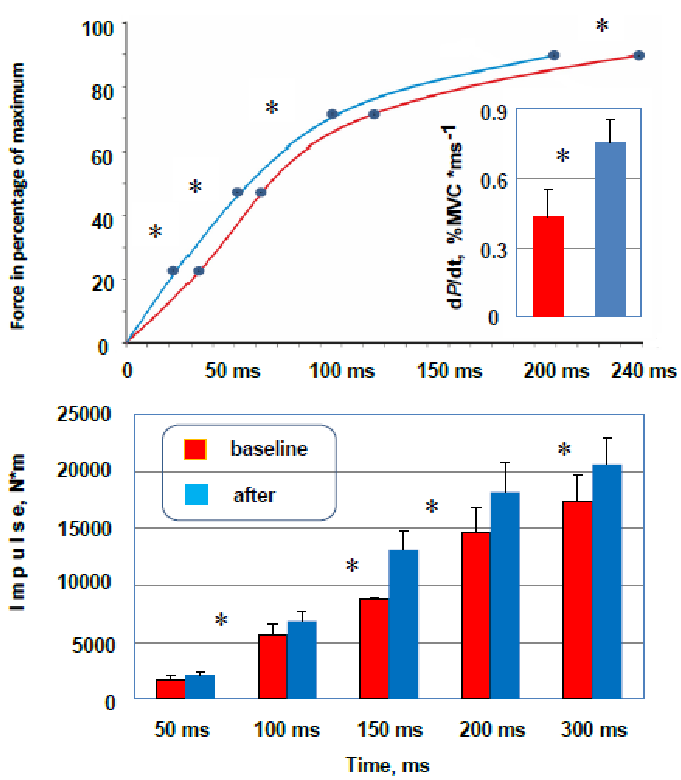


Figure. 3. The effects of 3-day DI on rate of force development of the triceps surae muscle expressed relative to the maximal force (*top panel*), and the maximal rate of rise of tension development (*insert*), and impulse force (*bottom panel*). Significant increases between before and after unloading (*$p < 0.05$).

Jump Performance

The DJ test with a dropping height of 20 cm, 40 cm and 60 cm showed all participants. The flight time, vertical ground reaction force, ground contact time, peak vertical ground reaction force, and vertical take-off velocity were determined in jumps (Fig. 4). Differences were between days BDC1 and R+1. DI was found to significantly affect the jump height, flight time, vertical ground reaction force, ground contact time, peak vertical ground reaction force, and vertical take-off velocity. By day R+1, the jump height increased from 25 ± 2 cm to 27 ± 1.4 cm (corresponding to a relative change of 8 %), flight time from 450 ± 20 ms to 470 ± 10 ms (corresponding to a relative change of 4.4 %), ground contact time from 360 ± 50 ms to 490 ± 80 ms, vertical take-off velocity from 2.20 ± 9 m/s to 2.31 ± 5 m/s (corresponding to a relative change of 5 %). Peak vertical ground reaction force did not change significantly in DJ_{20} cm (Fig. 4; *top panel*). At the same time, in DJ_{60} cm the jump height, flight time, ground contact time, and vertical take-off velocity during maximum jumps increased by 12 %, 7 %, 6 %, and 17 %, respectively, while peak vertical ground reaction force did not change significantly (Fig. 4; *lower panel*).

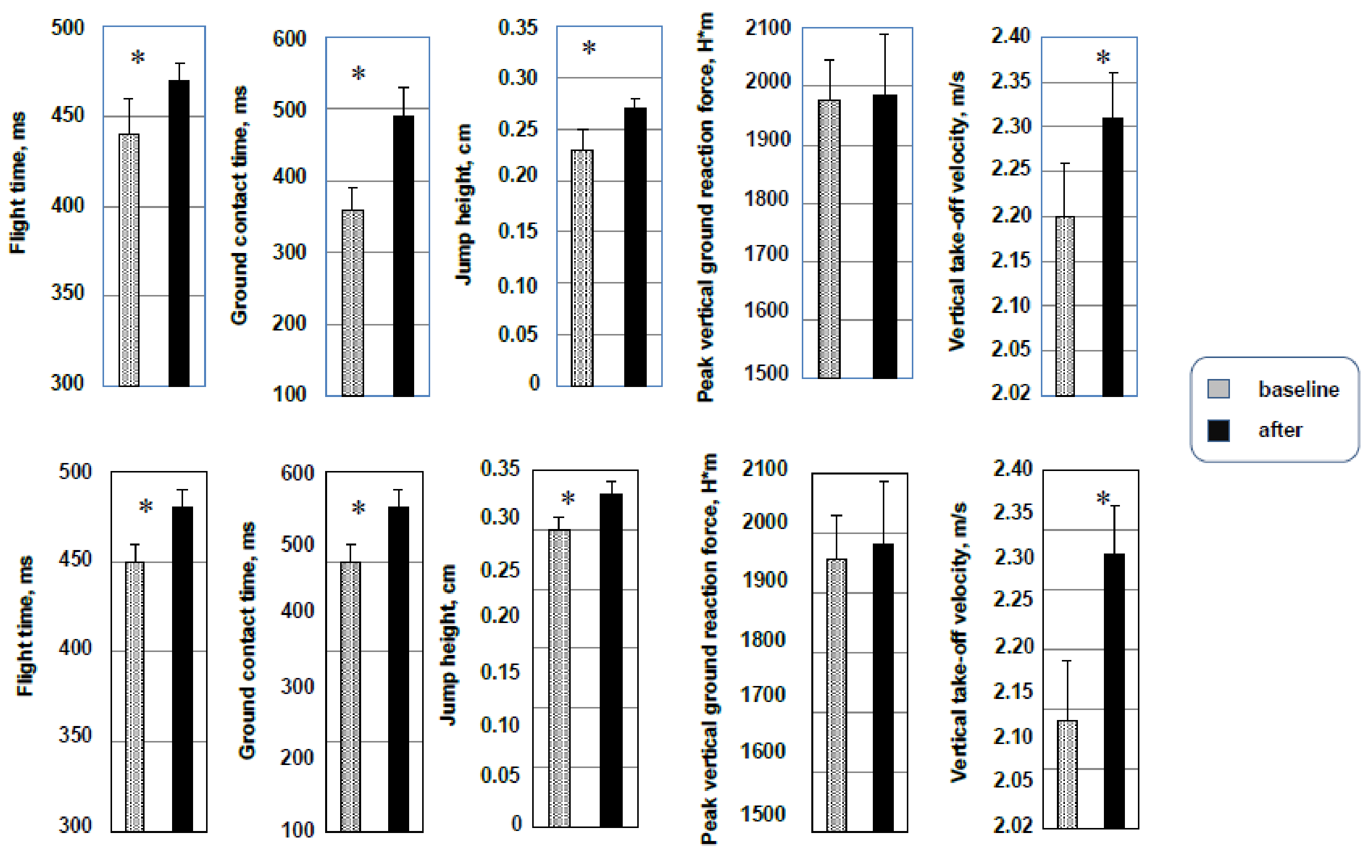


Figure. 4. Changes in biomechanical properties during drop jumps of incremental height by young girls after a 3-day DI. *Represents a significant difference to drop jumps performance. Values are reported mean ± SE.

Architectural Characteristics Before Unloading

Architectural Characteristics at Rest

T_m of the MG at rest (~14 mm) did not change significantly in response to changes in muscle length resulting from changes in ankle joint angle (Fig. 5). In muscle at rest, pennation angle and fibre length were ankle angle dependent. In muscle, as ankle angle increased from -15⁰ to +30⁰, the pennation angle increased from 18.1 ± 2.0 to 25.5 ± 1.7 deg (40.9 %, p < 0·01). In muscle, as ankle angle increased from -15⁰ to +30⁰, fibre length decreased in MG from 38.2 ± 2,1 to 34 ± 1.8 mm (11 %, *p* < 0·01).

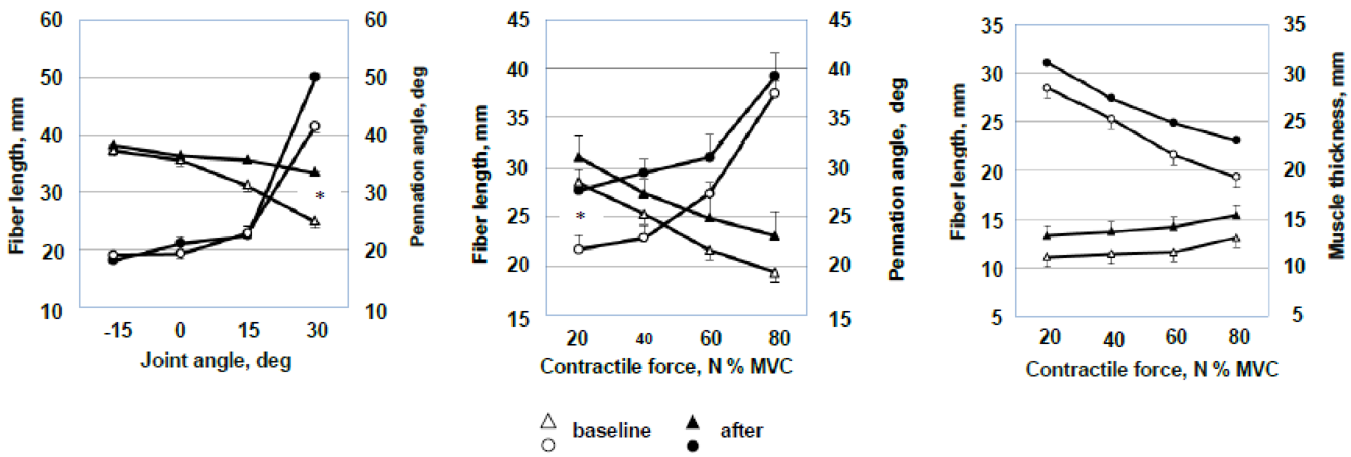


Figure. 5. Architecture of the medial gastrocnemius muscle.
Changes in the fiber length (L_f) and pennation angle (Θ_f) as functions of the ankle joint angle in the medial gastrocnemius (MG) as a result of a long-term DI. Differences were significant at (*) p < 0.05 or (**) p < 0.01

Architectural Characteristics during MVC

T_m of the MG during MVC (~16 mm) did not change significantly in response to changes in muscle length (Fig. 5). In muscle during MVC, pennation angle and fibre length were ankle angle dependent. In muscle, as ankle angle increased by 32º (when -15º; 63.9 %, *p* < 0·01), by 27.6º (when +15º; 55.1 %, *p* < 0·01) and by 24.6º (when +30º; 49.1 %, *p* < 0·01). In muscle, as ankle angle increased from -15 to +30 deg, fibre length decreased by 16 mm (when -15º; 72 %, *p* < 0.01), by 13 mm (when +15º; 60 %, *p* < 0.01) and by 11 mm (when +30º; 50 %, *p* < 0.01), respectively.

T_m of the MG (~16 mm) at any given ankle angle was not significantly different between rest and MVC.

Architectural Characteristics during Graded Isometric Force

During graded isometric force up to 100% of MVC at the neutral ankle position, the thickness of MG remained constant (Fig. 5). Pennation angle increased and fibre length decreased as a function of contraction intensity in muscles. Pennation angle in MG gradually increased на 22º (44.7 % при 20 %, *p* < 0·01), на 20º (40.1 %, при 40 %, *p* < 0.01), на 21º (41.1 %, при 60 %, *p* < 0.01) и на 13º (25.1 %, при 80 %, *p* < 0·01), respectively. Fibre length in MG decreased gradually на 8.8 mm (39.6 %, при 20 %, p < 0·01), на 5.2 mm (23.4 %, 40 %, *p* < 0·01), на 2.7 мм (12.2 %, 60 %, *p* < 0·01) и на 0.8 mm (3.6 %, 80 %, *p* < 0·01), respectively.

Architectural Characteristics after Unloading

Architectural characteristics at rest

T_m of the MG at rest (~ 4 mm) did not change significantly in response to changes in muscle length resulting from changes in ankle joint angle (Fig. 5). In muscle at rest, pennation angle and fibre length were ankle angle dependent. In muscle, as ankle angle increased from -15 ⁰ to +30 ⁰, the pennation angle increased from 19.0 ± 2.0 to 28.5 ± 1.7 deg (50 %, *p* < 0·01). In muscle, as ankle angle increased from -15 ⁰ to +30 ⁰, fibre length decreased in MG from 37.3 ± 2.1 to 24.9 ± 1.8 mm (33.3 %, *p* < 0·01).

Architectural Characteristics during MVC

T_m of the MG during MVC (~ 16 mm) did not change significantly in response to changes in muscle length (Fig. 5). In muscle during MVC, Θ_f and L_f were ankle angle dependent. In muscle, as ankle angle increased from -15º to +30º, the Θ_f increased by 23º (when -15º; 54.3 %, p < 0·01), by 18.7 º (when +15º; 45.1 %, *p* < 0·01) and by 13.4º (when +30º; 32.2 %, *p* < 0·01), In muscles, as ankle angle increased from -15 to +30 deg, Lf decreased by 18.4 mm (when -15º; 72 %, *p* < 0.·01), by 13 mm (when +15º; 60 %, *p* < 0·01) and by 11 mm (when +30º; 50 %, *p* < 0·01), respectively.

T_m of the MG (~ 14 mm) at any given ankle angle was not significantly different between rest and MVC.

Architectural Characteristics during Graded Isometric Force

During graded isometric force up to 100 % of MVC at the neutral ankle position, the thickness of MG remained constant (Fig. 5). Θ_f increased and L_f decreased as a function of contraction intensity in muscles. Θ_f in MG gradually increased by 22º (44.7 % when 20 %, *p* < 0·01), by 20º (40.1 %, when 40 %, *p* < 0·01), by 21º (41.1 %, when 60 %, *p* < 0·01) and by 13 º(25.1 %, when 80 %, *p* < 0·01), respectively. L_f in MG decreased gradually by 8.8 mm (39.6 %, when 20 %, *p* < 0·01), by 5,2 mm (23.4 %, when 40 %, *p* < 0.01), by 2.7 mm (12.2 %, when 60 %, *p* < 0·01) and by 0.8 mm (3.6 %, when 80 %, *p* < 0·01), respectively.

Discussion

The present study was planned as a study of the degree of adaptation of the contractile functions of the foot extensor muscles (triceps surae, TS) and the internal architecture of the MG, as one of the three heads of the TS complex that contributes to the generation of MVC, in a 3-day unloading (DI) in a group of healthy young females with regular menstruation. The main results show that prior unloading resulted in changes both muscle contractility and muscle architecture. This is the first study to describe the *in vivo* architecture of the human MG at rest and during isometric plantar flexion to full contractile state (MVC) after 3-days of unloading. The study showed the reconstruction of the architecture of one of the main locomotor muscles caused by unloading. The main conclusion of the study are as follows. First, the MG architecture of the (the lengths and angles of fascicles) changed in response to changes in the position of the ankle joint and the force developed. Second, the MG thickness did not change depending on the intensity of muscle contraction. Third, 3-day unloading of the muscular apparatus under DI conditions was accompanied by an increase in the maximum voluntary torque (MVC) and the biomechanical properties of the leg muscles lower as measured in the DJ test. Contrary to our expectations, the isometric MVC of the foot extensor muscles increased, rather than decreasing after 3 days of unloading. Prolonged mechanical unloading of muscles is well known to cause significant maladjustment of the musculoskeletal system [82]. However, changes in maximal foot extensor activation appear to be in conflict with the above disuse paradigms in our study. The main findings confirmed our initial hypothesis that, explosive movements (i.e., jumps requiring the stretch-shortening cycle (SSC) of muscles) and MVC change significantly in women exposed to 3-day unloading in the follicular phase.

Muscle Performance

Menstrual Cycle Effect on Strength

Given the lack of studies using similar performance tests, and involving as subjects exposed to DI conditions, it is extremely difficult to compare the results presented here with data from other studies. Nonetheless, our results support the data from previous studies (using isometric or isokinetic tests with voluntary contractions) that phases of the menstrual cycle affect the muscle strength. Our results indicate that endogenous reproductive hormonal fluctuations characteristic of the menstrual cycle in women cause significant changes in jumping performance (jump height and flight time) and maximum effort (MVC).

Our study is the first to examine the changes in the muscle strength of plantar flexors and vertical jumping performance in the late follicular phase of the menstrual cycle in healthy young women. The main finding of this study is that the mechanical properties of muscles ware affected by the phase of the menstrual cycle. A higher muscle strength and endurance usually attributed to high estrogen levels in the follicular phase [56, 57, 66, 88]. An increase in estrogen and levels is associated with improved performance in the postmenstrual phase [43]. Estrogen has been assumed to exert a profound effect on the muscle strength [102, 103]. An inotropic effect of estrogen on muscles has been reported [103], peaking just before ovulation, and reaching 10-11 % in magnitude [110], and a switching of muscle cross-bridges from low- to high-force generation has been postulated. Moreover, apart from exercise, estradiol is known to modify growth hormone secretion and metabolism [79]. The anabolic effects of this hormone may promote the maximal muscle gain and, accordingly, the force of contraction at certain times during the menstrual cycle in women [7, 8, 9] The variations in muscle strength may largely be attributed to metabolic changes that are due to oscillations in the concentrations of ovarian hormones. Based the literature, estrogen, which peaks during the follicular phase, may promote a higher muscle strength by modulating carbohydrate, protein, and fat metabolism in the body [21]. Estrogen levels observed in the late follicular and early luteal phases stimulate glucose availability and glucose uptake in type I muscle fibers, and glucose acts as fuel during short duration exercise [97].

An increased in muscle strength in terms of time to fatigue at 30% of MVC has been observes between the menstrual and follicular phase [9, 119]. Another study has explored the effects of training during the follicular phase vs. the luteal phase on muscle strength, muscle volume and microscopic parameters. An increase in muscle strength and muscle diameter was detected in the follicular phase at higher concentrations of testosterone and free testosterone [106]. Moreover, it reported that females feel improvments in the first 14 days following the menstrual phase, compared to the subsequent 14 days [65]. Sarwar et al. [108, 109] have reported significantly higher values of maximum voluntary isometric force in quadriceps and handgrip during ovulation compared with the other phases. Phillips et al. [103] have similarly observed a higher adductor pollicis strength during the follicular phase than during the luteal phase. Our findings are consistent with outcomes of previous studies [21, 100, 101, 103, 109] in which researchers reported of an effect of the menstrual cycle on muscle performance. Petrofsky et al. [101] have reported greater strength endurance in the late follicular phase compared with the luteal phase. Our findings concerning isometric strength agree with the data. The phase at testing was determined only by counting the days in the menstrual cycle in our work, like in all of the above studies. The ideal menstrual cycle is 28 days long, with ovulation at cycle day 14, but the range of a normal cycle length is between 22 and 36 days [63]. Ronkainen et al. [107] have compared 15 postmenopausal monozygotic twin pairs in which one twin had been using hormone replacement therapy for an average of approximately 7 years while the other had no history of use. They concluded that long-term hormone replacement therapy use was associated with better mobility, greater muscle power, and favorable body and muscle. Moreover, Dieli-Conwright et al. [28] have compared postmenopausal females with or without hormone replacement therapy use and reported that the women using hormone replacement therapy had significantly greater upregulation of proanabolic gene expression both at rest and following exercise. Studies using transcranial magnetic stimulation [115] indicate that the later follicular phase, when estradiol reaches its peak concentration, is associated with enhanced cortical excitation, in contrast to the early follicular phase, which is characterized by cortical inhibition [116]. This may be important to emphasize given the clear positive association between excitability and muscle strength [34]. It is therefore logical to hypothesize that muscle strength increase in the late follicular phase due to the increase in excitation and is reduced in the early follicular phase due to cortical inhibition. The results obtained in the present study support this hypothesis. Force production was higher after unloading, which is comparable with the late follicular phase of the menstrual cycle. A higher muscle strength is attributed to high estrogen levels, especially in the late follicular phase [57]. A remarkable difference in muscle strength was observed during the late follicular phase in our study and is probably explained by higher estrogen concentrations after unloading.

The shape of mean changes in the rate of force development of isometric tension of the TS muscle are given in Fig. 3. MVC (~11 %) was associated with a significant increasing of the rate of rise of development of isometric voluntary tension of the TS muscle (Fig. 3, *top panel*; $p < 0.01$-0.001). is little affected, which is in agreement with the observations [127] of relatively constant mechanics of contraction and the present-day cross bridge theory of muscle contraction [114]. Reasoning from the statement that the shape of the force-time curve is determined by the net rate of formation and disruption of relation of the cross bridges [114] which is proportional to the activity of myosin-ATP-ase [26] then it may be assumed that the cycling of cross-bridges and activity of myosin-ATP-ase varies slightly (or not at all) under the effects of unloading. The increase of the normalized rate of tension development (dP/dt), that we recorded during disuse is in line with the finding that myosin-ATP-ase activity and maximal velocity of shortening are enhanced during unloading [120].

At the same time, there is an increase in the rate of increase in muscle force when performing isometric voluntary explosive contractions in the initial phase of contractions (<100 ms). This is the first study to show differences in the rate of voluntary force development during the first 50 ms of force onset. We are not aware of any previous studies that have compared the effect of muscle unloading on the rate of force development in the first 50 ms of force onset. The results show that 3 days of DI causes an increase in MVC and varying degrees of adaptation of contractile properties in the early and late phases of fast voluntary explosive muscle contractions. The increase in the maximum voluntary F_{50} gradient appears to be primarily due to increased neural activity of the movement agonist muscles, while the increase in voluntary F_{100} and F_{150} is likely due to a proportional increase in MVC [33].

The present study we note an increase in MVC. It appears that the increase in MVC was largely associated with increased activation of movement agonist muscles. The latter, apparently, can be achieved by increasing the excitatory afferent input into the pool of motoneurons of muscles-agonists of voluntary movement, which will lead to an increase in the initial frequency of impulses and, accordingly, a higher rate of recruitment of motor units [24]. Previous studies have shown that during unloading, despite a decrease in muscle activation, there is an increase in reflex excitability [23, 112], suggesting that unloading causes plastic changes in neural function at the level of the spinal cord [21]. An increase in the excitability of spinal motoneurons under resting conditions with disuse has been observed in both humans and animal models, and a number of authors generally attribute this to a decrease in presynaptic inhibition of I-a afferents and/or an increase in motoneuron excitability [118]. A decrease in presynaptic inhibition of spinal motor neurons and/or suppression of postsynaptic inhibitory pathways may determine the overall observed increase in the rate of force development [2]. Increased excitability of spinal motor neurons is possibly associated with a decrease in motor units recruitment thresholds and an increase in the magnitude of the efferent nerve impulse to active muscle fibers [123]. Moreover, as noted previously, a decrease in load is accompanied by a change in the order of motor units recruitment during isometric contractions, thus facilitating the recruitment of large motor units, which exhibit the highest rate of force development [123].

On the other hand, it is known, that skeletal muscles are plastic and capable of adapting their contractile phenotype in response to physiological stress, including physical exertion and hormonal changes [59]. Unloading of the female muscular system promotes physiological adaptation throughout the body, mediated by female sex hormones and, in particular, estrogen. Changes in the metabolic properties of skeletal muscles as a result of unloading allow the female body to cope with physiological problems when performing motor tasks. Estradiol affects various tissues through receptors and, in particular, the contractile functions of muscles. It should be noted that the kinetics of myosin-actin cross-bridges, which determine the dynamics of muscle contractile properties, depends on the estrogen content. It was noted that the kinetics of myosin-actin cross-bridges were higher in fast-twitch muscle fibers compared to slow-twitch fibers, indicating that contractile velocity may be dependent on estrogen content and, secondly, that different fiber types in human skeletal muscle respond to changes in estrogen hormone [99]. Moreover measures of ATPase rates indicate that the cycling between weak and strong binding for myosin-actin cross-bridges is slowed with ovariectomy but restored with estrogen [125]. The latter is supported by a meta-analysis of data obtained from women who received hormone replacement therapy [55]. The authors showed that specific strength (strength normalized for muscle size) was approximately 10 % greater compared to those who did not receive treatment [55]. These results indicate that muscle function, but not necessarily muscle size, is improved by estrogen treatment [100].

Menstrual Cycle Effect on Jumping Performance

We hypothesized that biomechanical variables at different drop heights would be reduced after unloading. Differences between drop heights were observed and found to increase with the increasing drop height. However, all parameter values were better after unloading regardless of the drop height.

In the force-velocity tests (e.g., DJs), the main muscular activity is concentric contractions [20, 122]. The jump can be considered a ballistic type movement, in which the SSC is very important [67]. The mechanical power achieved in a jump depends on both neuromuscular coordination and the elastic energy stored in series of elastic components in active muscles and tendons (37, 67), especially tendons [76]. Both tendons and ligaments are built of collagen as a structural protein. Estradiol-17b, which is the main and most active hormone of the group of estrogens, is known to inhibit the collagen synthesis in ligaments [81] and consequently increases the ligament stiffness. The data suggest that changes in female steroid hormones during the menstrual cycle affect the mechanical properties of human muscles and tendons [43].

Lower-limb ballistic movements, or SSC muscle actions, have been identified as key determinants of physical performance in women [53, 68]. Jumping tests are widely used to assess the mechanical capabilities of the lower-limb and the efficiency of the SSC [53, 74]. In this study, we examined the effects of 3-day DI and the late follicular phase of the menstrual cycle on vertical jumping in young women. The findings contradict our initial hypothesis, i.e., 'athletic' performance in the explosive task (vertical jumping) requiring SSC muscle actions changed significantly after unloading in subjects over the course of their ovarian. Estrogen has been assumed to exert a profound inotropic effect on muscles [103], peaking just before ovulation by 11 % in magnitude [109]. A switching of muscle cross-bridges from low- to high-force generation has been postulated in some studies. Moreover estradiol modifies hormone secretion and metabolism [79]. The anabolic effects of estradiol may promote maximum muscle gain and thus increase the force of contraction at certain period during the menstrual cycle in women [8]. Estrogen improves glucose availability and uptake in type I muscle fibers, providing the fuel of choice during short-duration voluntary movements (MVC), and increases free fatty acid availability and oxidative capacity, favoring endurance performance [9, 98].

Investigations of the force and power output during DJ have shown that these variables may reach larger values after unloading. We assume that improvements in jumping technique might act as an additional factor in performing high jumps [12, 13, 14]. The jumping technique might influence the efficiency of DJ.

Available data indicate that the mechanical impact energy may be absorbed with dissipation during the landing. Our findings suggest that dropping from a higher height may decrease the contact time and increase the leg, knee, and ankle stiffness. That is subjects may manipulate the knee and ankle joint angles upon contact (and the contact time) to modulate the leg, knee, and ankle joint stiffness with different drop heights. This should facilitate the release of more elastic energy during takeoff. Our findings agree with data reported by Farley et al. [32] that altered body geometry may affect the leg stiffness and knee angle upon landing. The changes were observed when the drop height was 60 cm. The drop height may elicit changes in lower-limb geometry before impact to assist in controlling the movement. Our findings suggest that the leg and joint stiffness might be increased in the young females after 3 days of unloading in DI conditions in the late follicular phase of the menstrual cycle. The increased leg stiffness allows for a greater storage and release of elastic energy based on the SSC [40, 64] and is associated with an economy of voluntary motion [44].

Muscle Architecture

Consequences of Unloading for Muscle Architecture

The present study showed that a remodeling of muscle architecture is induced in main locomotor muscles by prolonged (3-day) unloading. Morphological adaptation of skeletal muscles to unloading is the focus of many studies and is achieved via a structural remodeling of contractile machinery. A remodeling of sarcomeres, that is, the addition or removal of sarcomeres in series and in parallel, is generally believed to result from alterations in structures involved in mechanical transduction [96]. The remodeling is possible to assess at a gross level by evaluating the changes in muscle architecture (that is, fiber length and pennation angle) [38, 104]. The length of muscle fibers strongly affects their contraction velocity [12, 78] 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 [80, 94]. 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 is possible to consider as a factor when explaining muscle tissue "weakness" [2]. In this study, a decrease in fiber length upon passive plantar flexion from –15 ⁰ to +30 ⁰ suggests that muscle fibers became progressively "*weaker*" with the increasing ankle angle. Changes in ankle angle suggest changes in muscle length [77]. It is of interest that the fiber length and pennation angle decreased after unloading, but the decrease in fiber length was lower.

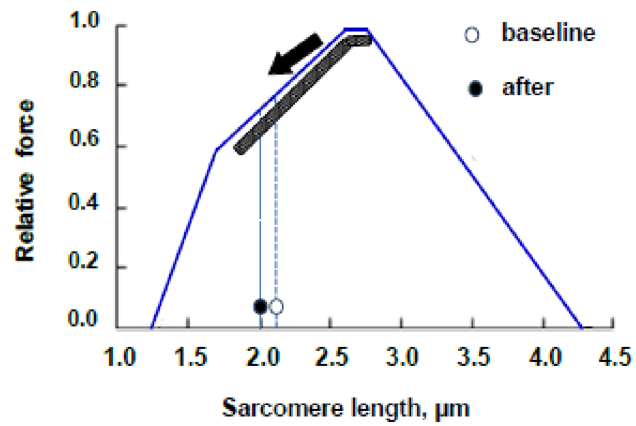
The fiber length was measured at three different joint angles in view of the following. If the fiber lengths before and after unloading (particular DI) are compared at only one particular joint angle and a difference in length is not confirmed, there are chances that the fiber length was initially the same. On the other hand, if the fiber length–joint angle ratio differs between pre- and post-DI measurements, it is impossible to judge about fiber length changes assessed at only one joint angle. The fiber length was therefore 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 post-unloading conditions.

A main finding of the study is that the MVC of the TS muscle increased (+11 %) after 3-day unloading. 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. Given that the majority of human muscles are pennate, changes in the internal organization of a muscle, which is known as muscle architecture, are important to consider in order to correctly interpret the functional consequences of unloading.

Together with internal muscle properties, such as fiber composition, muscle architecture affects the functional characteristics of a muscle (e.g., the maximum force and shortening velocity) [15, 16, 93, 95]. Changes in force-generating capacity depend on the differences in internal architecture to a greater extent than on the differences in fiber composition [15, 19]. This study is the first to assess the changes in the architectural parameters of the MG in young females with a normal menstrual cycle after short-term unloading with the use of ultrasound and to correlate the architectural changes with the contractile function and joint position.

Our study showed that 3-day unloading decreased L_f by 2.2 % and Θ_f by 8.5 % in the MG, respectively. The MG thickness did not change in response to contraction intensity. Consistency in MG thickness was confirmed by comparing the resting state with MVC or comparing different contraction intensities observed during gradual isometric plantar flexion with the ankle in a neutral position. Our finding that thickness of the human MG remains constant at different muscle lengths and different contraction stages is line with *in vivo* ultrasound observations of the same human by Narici et al. [93]. Kawakami et al. [61, 62] have reported that Θ_f of the MG was reduced by 7 %, respectively after 20 days of bed rest. Interestingly, Reeves et al. [105] and Maganaris et al. [85] have reported only 10 % and 13 % reductions in L_f and Θ_f of the MG, respectively, after 90 days of bed-rest. Moreover, a decrease in pennation angle must make the muscle relatively weaker because, first, parallel sarcomeres are lost. Second, a decrease in fiber length makes sarcomeres function at greater lengths, thus jeopardizing general force production. A greater number of motor units has to be recruited to maintain the absolute force constant, potentially leading to rapid muscle fatigue.

Fascicle length has been linked to muscle contraction properties [111]. Differences in fiber length correspond to differences in the length of sarcomeres, which are located sequentially within the fiber, respectively. It is well known additionally that the length of sarcomeres in striated muscles influences the force that can be generated by the respective muscle fiber [46]. Sarcomere lengths can be estimated by dividing the fascicle length by the average number of sarcomeres in series in fascicles [12]. The sarcomere length is a major determinant of muscle force generation potential [39]. To estimate the sarcomere length at maximum force, we divided the fiber length by the number of sarcomeres connected in series in the MG fiber (17,600 [54]) and superimposed the result on the sarcomere length-force relationship of human muscles [124] (Fig. 6). The results indicate that the working range of sarcomere length during voluntary contraction of foot extensors corresponded to an upper region of the ascending part of the length-force relationship both before and after unloading, indicating that a relatively large force could be generated after unloading.



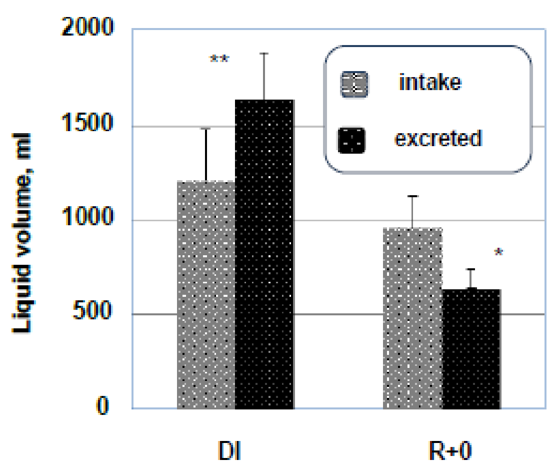


Figure. 6. Average sarcomere length-fascicle force relationship during MVC. Calculated MG sarcomere length were obtained by dividing the fiber length by the mean sarcomere number in a fiber series (46) and collated with a force–length relationship of human muscles (124). Cross points with the force–length curve and vertical lines show the force-generating potential or a sarcomere at various lengths. A crosshatched line under the ascending part and a plateau region of the curve shows the working range observed for MG sarcomeres in this work, assuming that the ankle angle optimal for force production corresponds to a sarcomere length of 2.6 µm

(*top panel*) and changes in the daily volume of fluid consumed and excreted during unloading (*bottom panel*). Differences were significant at (*) $p < 0.05$; (**) $p < 0.01$.

There was no significant change in muscle thickness in our study. However, given the relationship of fascicle length and angle with muscle thickness, a decrease in muscle thickness can occur when fascicle angles, fascicle length, or both of the parameters decrease (e.g. minor changes in fascicle length and angle may be reflected in a great change in muscle thickness). A decrease in fascicle length and angle might accompany a decrease in muscle size. However, other factors probably caused the changes length in our study. The mechanism where by female sex hormones (especially estrogen) could cause architectural changes in muscles is unclear. The subjects showed a greater reduction in fascicles angle and a smaller reduction in fascicle lengths after unloading in our study. The changes are likely to result in a similar decrease in muscle thickness.

Fluid (water) retention in muscles might be among the above factors. Water retention might occur due to dehydration after the of DI exposure (Fig. 6, *top panel*), increasing the muscle fibers. The released fluid volume is known to increase during unloading and decrease after the end of exposure [91]. Incorporation of water into muscles would enlarge of the muscle fibers, leading to changes in strength. Thus, architectural changes may have preceded a strength gain.

Alternatively, a lower decrease in fiber length might be a muscle adaptation to unloading in the subjects. A decrease in muscle thickness and fiber angle with a slight decrease in fiber length means that part of the force developed a muscle fiber will be transmitted in this case because, fibers are oriented at a certain angle ($Cos\Theta_f$) relative to the force generation axis. A slight decrease in fiber length partly compensates for the loss of force vie more efficient force transmission to the tendon, $Cos\Theta_f$ increases by 13 % after unloading. Larger angles of fascicles in muscles aid strength development by allowing more contractile tissue to attach to the tendon [57]. Tendon excursion is greater for a given length of fiber shortening when the angle between the fascicles and the tendon is greater [92]. This is because fibers in pennate muscles not only shorten, but they also undergo tremendous rotation during shortening [11, 109]. Thus, fibers are able to produce a greater force depending on their length-tension and force-velocity properties. Moreover, muscle contraction creates intramuscular pressure, which increases with muscle contraction, and there is a positive relationship between contraction intensity and intramuscular pressure [3]. An increased intramuscular pressure leads to a curvature in muscle fibers [121]. The difference between the pennation angles measured and after unloading under isometric conditions with increasing contraction intensity, and the percentage difference in the slope of the angle - contraction intensity curve (Fig. 6, *bottom panel*) suggest a curved shape of fibers in the muscle.

Our results conflict with data of Aratow et al. [3] and Maganaris et al. [85], who habe determined the *in vivo* changes in pennation angle and fiber length of the MG a functions of ankle angle during isometric ankle plantar flexion under normal gravity conditions. A similarity has been observed between the change in MG fiber curvature (percentage difference between pennation values) as a function of isometric contraction intensity and the change in intramuscular pressure as a function of isometric contraction intensity. Our study did not find similarity between the change in fiber curvature (percentage difference between slope values) depending on the intensity of isometric muscle contraction and the change in intramuscular pressure depending on the intensity of isometric contraction. Intramuscular pressure decreases with the increasing contraction intensity. Fluid is known to create pressure. Because unloading is accompanied by a loss of fluid, the intramuscular pressure decreases accordingly. This decreases the bending of fibers, thus ensuring efficient transfer of the developed force to the tendon.

To our knowledge, our study is the first to demonstrate a linear relationship between the muscle architecture variables (Fig. 7, *bottom panel*). A In high correlation was observed between PCSA index and fiber pennation angle ($r^2 = 0.61$, $p < 0.01$) after unloading. The relationship between PCSA index and fiber pennation angle was relatively weak before unloading ($r^2 = 0.29$, $p < 0.05$). The MG pennation angle increased to a greater extent with the increasing PCSA index before unloading. A different pattern was observed after unloading; i.e., the pennation angle increased to a lesser extent increasing PCSA index. We believe that the increase in correlation after unloading is associated with the important role of sex hormones produced in the late follicular phase of the menstrual cycle, that is, the sex hormones change the mechanical properties of the muscle tendon and musculotendinous complex. Thus, changes in muscle architecture can explain, at least partly, the differences in functional properties observed in our study.

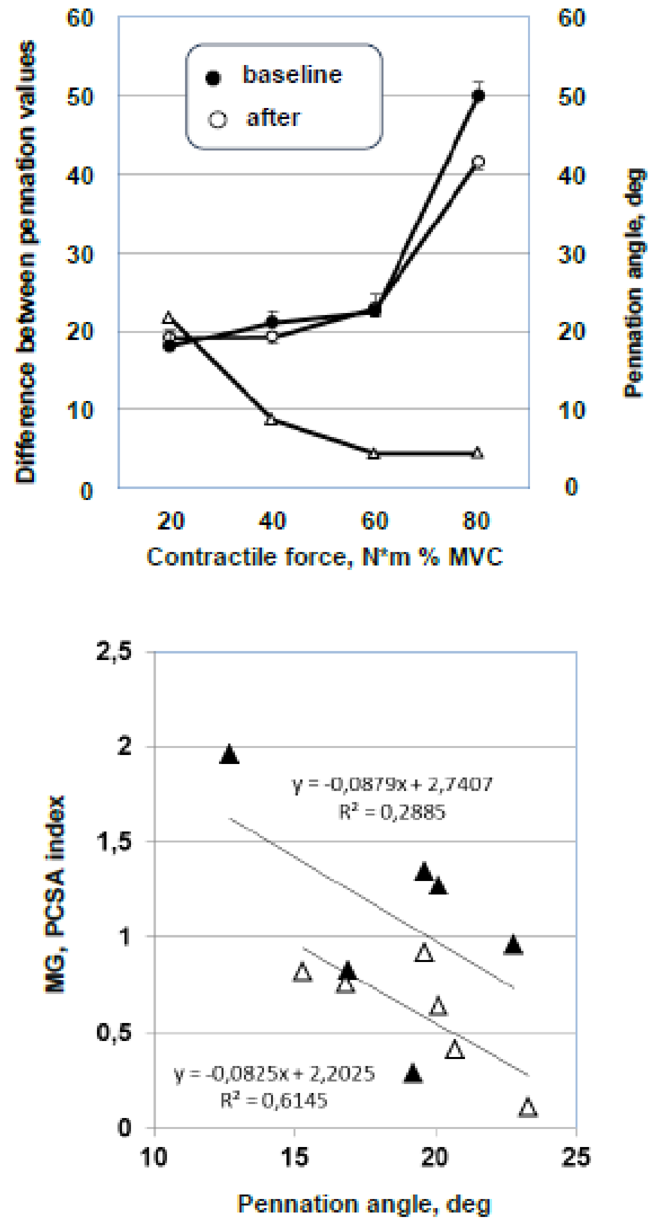


Figure. 7. Percentage difference between the angles of fascicles values obtained before and after unloading depending on the intensity of contraction in the neutral ankle position.
Note the similarity between the change in fiber pennation depending on the intensity of isometric contraction in the muscle in the subjects of the

present study and the change in fiber curvature (percentage difference between the inclination values) (*top panel*) and relationship between PCSA and pennation angle in the medial gastrocnemius muscle studied (*bottom panel*). Open circles: before; filled circles: after. PCSA, physiological cross-sectional area.

A role of neural activation in the control of voluntary movements cannot be excluded. Two studies postulated that the main mechanism responsible for the increase in neural activation following unloading may be increased spinal excitability [20, 112], and point of view was confirmed experimentally [84]. Lundbye-Jensen and Nielsen [84] have demonstrated that increase in reflex excitability (increased H-reflex amplitude) after unloading is caused by both presynaptic inhibition and homosynaptic postactivation depression. Because a main contribution to the work performed is made by the TS muscle during locomotion [83], an increase in neural activity might be an additional factor in the increase in muscle functions.

Conclusion

The muscle contractions (MVC and vertical jumping requiring SSC muscle actions) were studied in relation to the menstrual cycle and proved to be significantly higher and forceful during the late follicular phase. Changes occurring during the normal menstrual cycle can affect the voluntary movements and must therefore be taken into account during the preparation and selection of experimental programs.

This study demonstrated that muscle strength and biomechanical efficiency of muscles change between different menstrual cycle phases in young women exposed to unloading. Our findings disagree with data from other studies, which involved only men as subjects and showed a decrease in strength after unloading [71, 73]. However, this is the first study in young women, and further research is necessary to perform in order to elucidate the interactions and consequences of unloading and the functional effects associated with hormonal changes during the menstrual cycle.

Limitations

We acknowledge that the present study has some limitations.

First, this study is limited by the small size, and we did not recruit a control group. Second, the phases of the menstrual cycle were assessed by counting from the first day of bleeding and noninvasively measuring the basal body temperature. In addition, we also used hormone urine test strips. This is a valid methodology and was used in previous studies [100]; however, there was no measurement of serum female sex hormones to confirm the cycle length and the beginning/end of each phase. Third, the concentrations of sex hormones [82], were not assessed in the study, but would have been much more relevant in classifying the phases of the menstrual cycle. However, despite these limitations, muscle strength, velocity-force, and power performance were higher to the end of experimental period.

Considering results of the findings of our study, it seems the improved contraction properties adaptations observed in this study are the result of the anabolic effect of estrogen in the late follicular phase.

Lastly, we did not investigate either neural or tendon adaptations to the experiment protocol used.

Practical Applications

The menstrual cycle affects the mental and physical state in young women, and female hormones influence skeletal muscle metabolism. We postulated that changes in women hormones during the menstrual cycle affect the outcomes of biomechanical properties during DJs and voluntary contractions. The menstrual cycle is a key element contributing to the change in functions in women, and this should be taken into account when planning studies with unloading of the muscular apparatus.

The overall results of this study have important implications for astronaut/cosmonaut coaches. From the practical viewpoint, it important to allow for the menstrual phase when programming training sessions for female astronauts/cosmonauts and to decrease the training load in the postmenstrual phase to limit neuromuscular fatigue accumulation. Additionally, the follicular phase appears to be the best time for high-intensity training to improve performance and productivity, especially in periods of critical operator activity. This indicates that the frequency, volume and intensity of training should be selected individually based on the biological potential of the menstrual phase. Future investigations should focus on the concept of training programs tailored to different phases of the menstrual cycle.

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The author have made a contribution to this study in terms of the study design and data analysis, writing and revision of the manuscript, and providing final approval of the submitted material and agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. All of the experiments described in this manuscript were performed at Institute of Biomedical Problems of the Russian Academy of Sciences in Russia. The author are most grateful to all the participants the research for their contributions to this study and also the medical and engineering staff for their attention to detail and hard work during the study; doctors of the clinical department of the Institute of Biomedical Problems of the Russian Academy of Sciences for participation in the selection of volunteers; I. Ponomarev for technical assistance during data collection and had no role in the design of the study, the analysis of the data, or the decision to publish. The author expresses special gratitude to G. Vasil'yeva for collecting water balance data, preliminary analysis and kindly providing material on water balance. The author wish to acknowledge the project management contribution of E. Tomilovskaya.

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The author confirm that no artificial intelligence tools were used at any stage of the research development, design, data collection, analysis, or manuscript preparation for this study.

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