Resistance training preserves skeletal muscle function during unloading in humans

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ABSTRACT

SCHULZE, K., P. GALLAGHER, and S. TRAPPE. Resistance training preserves skeletal muscle function during unloading in humans. *Med. Sci. Sports Exerc.*, Vol. 34, No. 2, pp. 303–313, 2002. **Purpose:** The intent of this investigation was to design and evaluate a low-volume, high-intensity resistance-training program to preserve knee extensor (KE) and plantar flexor (PF) size as measured by cross-sectional area (CSA), strength, and neuromuscular function (IEMG) with unloading. **Methods:** Thirty-two men (age = 30 ± 3 yr; weight = 80 ± 4 kg; height = 181 ± 2 cm) participated. Sixteen men underwent 21 d of unilateral lower-limb suspension (ULLS) and were assigned to control (ULLS-CON, $N = 8$) or countermeasures (ULLS-CM, $N = 8$). The remaining subjects were ambulatory for 21 d and were assigned to control (AMB-CON, $N = 8$) or countermeasures (AMB-CM, $N = 8$). Countermeasure subjects performed resistance training every third day during the 21-d period. **Results:** KE and PF CSA decreased ($P < 0.05$) 7% in the ULLS-CON, whereas no changes occurred in ULLS-CM, AMB-CON, and AMB-CM. ULLS-CON maximal voluntary contraction (MVC) decreased 17% ($P < 0.05$) in the KE and PF. ULLS-CON torque-velocity characteristics (concentric and eccentric) decreased ($P < 0.05$), 22% to 12% and 20% to 14% (slow to fast) in the KE and PF, respectively. ULLS-CM PF increased ($P < 0.05$) in MVC and eccentric contractions, whereas no other changes occurred in MVC or torque-velocity characteristics in the KE or PF of the ULLS-CM, AMB-CON, and AMB-CM subjects. Submaximal IEMG increased ($P < 0.05$) whereas maximal IEMG decreased ($P < 0.05$) in the KE and PF of the ULLS-CON group. However, no change or slight improvements in IEMG activity were found in the KE and PF of the ULLS-CM, AMB-CON, and AMB-CM. **Conclusion:** These results indicate that a resistance-training paradigm employed every third day during 21 d of unloading was effective in maintaining skeletal muscle strength (static and dynamic) and size of the KE and PF. **Key Words:** UNILATERAL LOWER-LIMB SUSPENSION, SIMULATED WEIGHTLESSNESS, MUSCLE STRENGTH, CROSS-SECTIONAL AREA, ELECTROMYOGRAPHY

As the National Aeronautics and Space Administration (NASA) enters a new era of long-term space exploration, decrements to the musculoskeletal system are of considerable concern for long-duration spaceflights (1). As a result, the introduction of appropriate countermeasure exercise protocols will become essential for prevention of skeletal muscle deconditioning. The primary obstacle facing NASA is the identification and development of realistic countermeasures that can be employed to effectively maintain muscle strength and size.

Most in-flight countermeasure programs primarily involve aerobic exercise protocols that have demonstrated the ability to attenuate alterations of aerobic fitness and help maintain cardiovascular function (22). However, these programs have proven to be relatively ineffective in maintaining skeletal muscle size and strength (4). This is important because skeletal muscle unloading elicits deleterious effects on both skeletal muscle strength and size in humans (3,14,20,23,28,29) and animals (18,34). Human muscle strength has been shown to decline in as little as 7 d and continue to decline with the length of exposure (9,10,19,26,28). This reduction in strength is associated with concomitant decreases in muscle cross-sectional area after periods of bed rest (16,29) and space flight (20,28). Furthermore, the reduction in strength may also be due, in part, to alterations in neural drive (30).

Resistance training in a 1-G environment (Earth) is known to evoke increases in muscle size and strength and an improved neural drive (32). As a result, resistance training offers promise as an effective countermeasure to attenuate the muscular deconditioning induced by microgravity exposure (4,33). Recently, it was found that resistance training every other day during 14 d of bedrest was sufficient to maintain muscle strength in humans (5,6). This is encouraging; however, it would be beneficial to know if the frequency and volume of resistance training could be reduced and still preserve muscle function and size. Moreover, this is of practical importance because the space program is interested in knowing the minimal amount of exercise

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TABLE 1. Subject characteristics, including age (yr), weight (kg), height (cm), and percent body fat determined from seven-site skin fold measurements.

Group	Age (yr)	Weight (kg)	Height (cm)	% Body Fat
ULLS—CON	27.1 ± 3.0	77.3 ± 5.3	181 ± 2	14.1 ± 1.9
ULLS—CM	29.5 ± 2.9	86.0 ± 2.5	183 ± 2	22.1 ± 1.8
AMB—CON	31.4 ± 2.9	78.8 ± 4.3	178 ± 2	16.5 ± 2.5
AMB—CM	32.5 ± 3.9	79.3 ± 3.1	180 ± 3	15.4 ± 2.0

ULLS—CON, unilateral lower-limb suspension control group ($N = 8$); ULLS—CM, unilateral lower-limb suspension countermeasure group ($N = 8$); AMB—CON, ambulatory control group ($N = 8$); AMB—CM, ambulatory countermeasure group ($N = 8$).

needed to maintain astronaut health and safety while in space and upon return to Earth (4).

The purpose of this study was to determine whether a high-intensity program of isometric and isotonic (dynamic) resistance training was effective in maintaining size, strength, and neuromuscular function of the knee extensor and plantar flexor muscles during 21 d of unloading using the unilateral lower-limb suspension (ULLS) model. A secondary purpose of this investigation was to compare the knee extensor and plantar flexor muscle groups on the effects of unloading and the effects of the countermeasures program. The addition of ambulatory groups permitted the evaluation of this resistance protocol on muscle size and function in free-living subjects. When designing this program, the intention was to create an effective exercise protocol in terms of the time and energy that it would require to complete. It is important to emphasize that the goal of this countermeasure-training program was not to promote gains in muscle strength and/or size but to prevent the loss of muscular size and function.

METHODS

Subjects

A total of 32 men were selected to participate in this study and were randomly assigned to either ULLS ($N = 16$) or ambulatory (AMB; $N = 16$) groups. Subjects were 20–50 yr of age, healthy, normoactive nonsmokers who were free of any previous lower-limb pathology and who had not been involved in any physical training program for 6 months before the start of the study. Subject characteristics are presented in Table 1. ULLS subjects completed 21 d of lower-limb suspension whereas ambulatory subjects were permitted uncontrolled ambulation for the 21-d period. All subjects completed identical pre- and post-testing of the reference leg (left leg). Subjects in each of these two main groups were then randomly assigned to either control (ULLS-CON; $N = 8$ or AMB-CON; $N = 8$) or countermeasure groups (ULLS-CM; $N = 8$ or AMB-CM; $N = 8$). Control subjects did not engage in any resistance exercise. Countermeasure subjects participated in an isometric and isotonic (concentric and eccentric) resistance-training protocol with the reference leg every third day throughout the suspension period, for a total of 6 sessions over the 21-d treatment period. All subjects gave written informed consent in accordance with the University Institutional Review Board before participation in the study.

Experimental Protocol

Pretesting data collection involved four sessions for each subject: 1) an orientation session where subjects were familiarized with the Cybex Norm dynamometer (Ronkonkoma, NY) and the complete strength testing protocol; 2) pretest 1 where they completed the entire strength testing protocol with the addition of electromyography (EMG) measurements (BIOPAC Systems Inc., Santa Barbara, CA); 3) thigh and calf whole-muscle cross-sectional area (CSA) evaluation via computed tomography (CT; General Electric CT/I, Milwaukee, WI) and within 2 d of the CT scan; and 4) pretest 2 where anthropometric measurements were made in addition to the strength testing protocol and EMG measurements.

The 21-d evaluation period began the morning after pretest 2. The ULLS subjects were fitted with crutches and the suspension apparatus. Computed tomography evaluation for determination of posttesting whole-muscle CSA was completed on the 20th day of the 21-d period. Posttesting muscle strength and EMG evaluation took place on day 21 at approximately the same time of day as the pretesting sessions. Immediately after the cessation of the posttesting protocol, ULLS subjects were unweighted and allowed uncontrolled ambulatory activity.

Unilateral Lower-Limb Suspension (ULLS)

The subjects in the ULLS group conducted all ambulatory activity on crutches while wearing a suspension harness. The harness was made of tubular nylon strips that had been sewn together and allowed for suspension of one limb by means of a strap secured around the shoulder and attached to the foot. The harness was fastened so that the subject's toes were lifted approximately 10 cm above ground level with the knee angle between 90 and 120°. The foot strap served a dual purpose in that it eliminated weight bearing of the left leg and placed the left foot in a toe-down orientation. The toe-down orientation slightly stretched the knee extensor group and shortened the plantar flexor muscle group, thus replicating the natural lower-limb position in space. Subjects were allowed free movement about the hip, knee, and ankle joints, and were instructed to manually assist any movement of the nonambulatory limb. To help minimize joint stiffness, subjects were encouraged to manipulate their leg musculature early in the morning and also in the evening before going to bed. In an attempt to ensure compliance, subjects were closely monitored and were required to report to the laboratory every day. In addition, subjects were contacted by telephone on a regular basis, at least once per day, by one of the investigators throughout the suspension period.

Whole-Muscle Cross-Sectional Area

Computed tomography (CT) was performed before and after the 21-d period for the determination of any relative change in thigh and calf whole-muscle size (CTI Helical Scanner, General Electric). Before all CT scans, the subjects were placed in a supine position with their left foot slightly elevated for 15 min to minimize the influence of fluid shifts on cross-sectional area measurements (8). Subjects were oriented feet first and remained supine for the duration of the scan. The left foot remained elevated during the scan to prevent compression of the leg musculature. Each scan was done for a 3-s period, utilizing a 5-mm slice. The precise location of the scan slice was standardized for the pre- and post-testing measurements by using measured distances from bony landmarks identified on the scout scans and images.

Knee extensors. The scan was performed halfway between the superior aspect of the greater trochanter and the distal portion of the medial epicondyle.

Plantar flexors. The measurement was made between the tibial plateau and the talofibular joint (top of the talus), the scan performed at one third of that distance below the tibial plateau.

The CT images were obtained using a 512 × 512 reconstruction matrix. The images and associated scale were filmed on Kodak MNB film and were manually scanned to a personal computer, and the determination of cross-sectional area was made using NIH Image software (version 1.60). Cross-sectional area of the bone was then subtracted from that of the muscle plus bone area to arrive at the whole-muscle cross-sectional area in cm^2.

Subject Positioning for Muscle Function Tests

Maximal isometric, isokinetic, and isotonic knee extensor and plantar flexor strength were evaluated on the Cybex Norm Dynamometer. All knee extensor muscle function tests were completed first, followed by all plantar flexor muscle function tests.

Knee extensors. Subjects sat upright with a hip angle set at 85° of hip flexion. A seat belt was secured across the subject's chest and lower abdomen. The subject's left knee joint axis was aligned with the axis of the dynamometer with the shin pad located slightly above the left lateral malleolus. The subject's anatomical zero was set at full extension of the left leg. The range of knee extensor motion was set at a knee extension of 15° to a knee flexion of 95–100°. The subjects' right legs were placed behind the leg support, and they were instructed to grip the handles located along the side of their seat.

Plantar flexors. Subjects were placed in a supine position with their left foot strapped into a footplate and left knee secured into a leg support strap. The height of the knee support rest and footplate were adjusted until the angle of the knee was 160° (35). Subjects were strapped to the dynamometer table with chest and lower abdominal straps and their left ankle joint axis aligned with the axis of the dynamometer. The anatomical zero was set at the point where the foot was at a 90° angle to the tibial shaft. The ankle joint range of motion was set from −10° dorsiflexion to 30° plantar flexion. To ensure proper form, the subjects were instructed to drive their knee up into the pads, push their toes around their ankle joint, and told to hold onto their chest straps during each set of contractions.

Isometric Evaluation

The isometric evaluation consisted of two submaximal contractions followed by two maximum voluntary contractions (MVC), of which the highest torque achieved was recorded. For the submaximal contractions, visual feedback was employed, and the subjects were instructed to apply a constant force for 5 s by tracing a predetermined force output line. Two repetitions were completed at each submaximal load, and each contraction was separated by a 20-s rest period. This was followed by two maximum voluntary contractions where subjects were instructed to carefully move their leg or foot to the testing angle, then to quickly produce a maximal force and maintain the contraction for 5 s. Peak force was defined as the highest force recorded during this contraction period. If the difference between the torque from the two MVCs was greater than 5%, subjects were required to complete a third maximal isometric contraction. Subjects were given 60 s of rest between MVCs.

Knee extensors. All isometric contractions were performed at a knee joint angle of 60° below horizontal. The two submaximal forces were 100 and 150 Nm.

Plantar flexors. Plantar flexor contractions were performed at −10° joint angle. The two submaximal contractions were 60 and 100 Nm.

Isokinetic Evaluation

The subjects completed maximal concentric and eccentric isokinetic torque measurements for both the knee extensors and plantar flexors. At each angular velocity subjects performed four submaximal "warm-up" contractions, at approximately 50% of their maximal torque, followed by 20-s rest, then four maximal contractions. The highest torque achieved during each maximal set was recorded as the maximal torque. All maximal sets were followed by a 90-s rest period.

The ambulatory control data illustrated the inherent variability of the strength testing procedures. On average, the coefficient of variation within our entire knee extensor protocol was approximately 3%. This variability, which was independent of testing velocity, appeared to be greater when evaluating the eccentric velocities (mean = 5.5%) than the concentric velocities (mean = 2.3%).

Knee extensors. Concentric knee extensor torque was assessed at 1.05, 2.09, 3.14, 5.24, 6.98, and 8.73 rad·s^{-1}, followed by eccentric isokinetic evaluation at 1.05, 1.57, 2.09, 3.14, 4.19, and 5.24 rad·s^{-1}.

Plantar flexors. Subjects performed concentric contractions at the following velocities: 0.52, 1.05, 2.09, 3.14, 4.19, and 5.24 rad·s^{-1} and the following eccentric velocities: 1.05, 1.57, 2.09, 3.14, 4.19, and 5.24 rad·s^{-1}.

Dynamic 1-RM Evaluation

Knee extensor and plantar flexor concentric isotonic 1RM was assessed on the Norm dynamometer. The 1 RM was recorded at the point where the subject could no longer move the lever arm through the set range of motion. In addition to the above 1 RM evaluation, subjects performed a second assessment of dynamic 1RM knee extensor strength on a Cybex Eagle, an isotonic free-weight leg extension machine. Single-leg Eagle isotonic 1 RM was recorded, for both the reference (left) and nonreference (right) legs, and represented the point at which the weight could no longer be lifted through the full range of motion.

Knee Extensor Work Capacity Evaluation

After isokinetic evaluation, subjects completed an isokinetic work capacity evaluation at 3.14 rad·s^{-1}. Subjects performed four submaximal contractions followed by 30 maximal concentric contractions, at approximately one contraction per second. They were instructed to put 100% effort into each contraction. The total work completed (kJ) was recorded. Due to the lack of repeatability, a work capacity evaluation on the plantar flexors was not performed.

Electromyography

Electromyography (EMG) recordings of vastus lateralis and vastus medialis muscle in the knee extensor muscle group and the gastrocnemius and soleus muscles in the plantar flexor muscle group were ascertained pre- and posttesting. The EMG was determined during the submaximal and maximal isometric contractions to measure any changes in neural activity associated with training or disuse.

Two active silver/silver chloride surface EMG electrodes (BIOPAC Systems Inc.), with a contact area diameter of 11.4 mm separated by 20 mm were positioned at the site of detection on the left leg. A third silver/silver chloride disposable electrode was positioned on the right tibia approximately 5 cm distal to the tibial tuberosity. Before electrode placement, the placement areas were shaved, lightly abraded, and thoroughly cleaned with isopropyl alcohol. Water-soluble conducting gel was then applied to the electrodes to reduce electrical impedance. The electrodes were fixed to the skin with a double-sided adhesive washer (Model #4416, Tape Shapers by Converters Inc., Huntington Valley, PA), which was first affixed to the electrode and then placed over the muscle.

The EMG signal was sampled at 1024 Hz, and the raw signal was filtered with low and high cut-off frequencies of 12 and 500, respectively, full-wave rectified and integrated using AcqKnowledge III for the MP100WS (BIOPAC Systems Inc.). EMG data, along with the isometric force/voltage recordings, were stored on a computer disk for later analysis. For the standardized submaximal workloads, average integrated EMG (IEMG) and torque were calculated over a 1-s window. For the MVCs, a 500-ms window on either side of the peak torque achieved (1 s total) was analyzed and the peak IEMG and torque calculated. Finally, all IEMG signals were multiplied by a constant of 1000 to permit ease of comparison.

Knee extensors. The site of electrode placement on the vastus lateralis was 10 cm proximal to the lateral aspect of the patella. The site of electrode placement on the vastus medialis was 7 cm above the medial aspect of the patella.

Plantar flexors. The sites of detection for each muscle in the plantar flexor muscle group were as follows: medial gastrocnemius at 10 cm below the medial area of the popliteal crease and the soleus at 2 cm below the distal medial gastrocnemius muscle belly. All placement markings were examined at the specific isometric angle of contraction to verify proper positioning and adjusted accordingly.

To standardize electrode placement within subjects, the sites of EMG measurements on both the knee extensors and plantar flexors was marked with indelible ink and then transferred onto an overhead transparency that was also marked with the anatomical and skin landmarks. This transparency was used to properly position the electrodes during the posttesting measurements.

Countermeasure Resistance Training

The countermeasure resistance-training program consisted of isometric and concentric/eccentric isotonic knee extensions. Subjects were monitored and supervised during all training and testing sessions. These exercises were designed to minimize the potential losses in whole-muscle size and strength associated with simulated weightlessness as well as the time required to complete them. Countermeasure subjects were required to report to the Human Performance Laboratory every third day, i.e., six times during the 3-wk suspension period, to perform the protocol. After each training session, the total concentric and eccentric work performed was recorded (kJ). Subjects in the control group did not complete any of the following countermeasure training.

Knee extensors. After a warm-up set of 10 isotonic contractions completed at 40% of 1RM, the subjects completed the following knee extensor training protocol: 1) two maximal voluntary isometric contractions of 5 s in duration at 60° knee extension, 2) one set of 10 isotonic repetitions at 80% of 1RM, and 3) one set of isotonic repetitions at 80% of 1RM to volitional failure. The total protocol time, including rest time, was approximately 6.5 min. Total knee extensor work time averaged 2 min, depending upon the number of contractions that the subjects were able to complete during the final set to exhaustion.

Plantar flexors. After a warm-up set of 10 contractions completed at 40% of 1RM, the subjects completed the following training protocol: 1) two maximal 5-s isometric contractions at −10° of plantar flexion, 2) one set of 10 isotonic repetitions at 80–85% of 1RM, and 3) one set of isotonic contractions to volitional failure. The total work time averaged 2 min, depending upon the number of contractions that the subjects were able to complete during the final set to exhaustion. The total time (work and rest) for completion of the plantar flexor protocol was approximately 7 min.

Protocol Justification

This specific protocol was implemented with the goal of maintaining knee extensor muscle size and strength. Maximal voluntary isometric contractions were employed to promote the development of maximal voluntary muscle tension. In 1G environments, isotonic training loads of 80–85% of 1RM optimize both hypertrophic and neural gains in skeletal muscle (5,11). The addition of an eccentric resistance component has been shown to greatly enhance strength gains without appreciably increasing the metabolic cost of the exercise (12,16). Thus, the present protocol employed a combination of maximal voluntary isometric contractions and high-intensity (80% of 1RM) concentric/eccentric isotonic contractions in the attempt to maximally stimulate the muscle to maintain size and strength during a period of muscular unloading.

The types of muscular activity employed in this investigation are in agreement with a recent NASA roundtable report (4). The committee recommended that resistance muscle training should provide a combination of isometric, eccentric, and concentric contractions to attenuate muscle atrophy and strength loss during exposure to weightless environments.

Dietary Analysis

A 3-d dietary analysis was completed three separate times by all ULLS subjects: before the suspension period, during the first week of suspension, and during the final week of suspension. All subjects were encouraged to consume their "normal" habitual diet throughout the study. Dietary analysis was conducted to monitor the nutritional status of the subjects to ensure that there was no marked change in dietary intake that could potentially have affected the test results. All dietary information was analyzed by the same investigator and was evaluated using Food Processor Nutrition and Fitness software version 7.0 (Escha Research, Salem, OR).

Statistical Analysis

All data are presented as means ± standard errors. The data were analyzed using the SPSS for windows statistical program (v. 10.0.5). A general linear model (ANOVA) with repeated measures was performed on all variables with the within- and between-subject factors being time and group, respectively. The alpha level was set at $P < 0.05$. Values found to be significantly different were compared using the Bonferroni *post hoc* test.

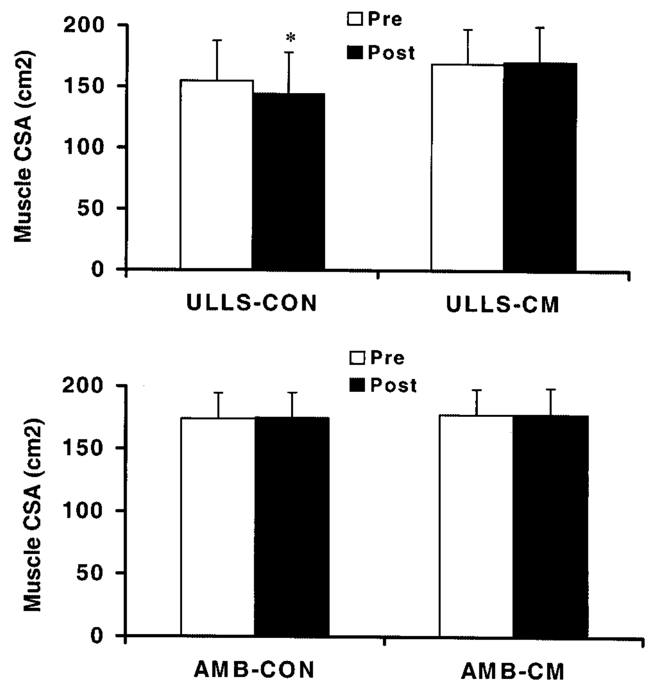

FIGURE 1—Whole-muscle cross-sectional area of the thigh, as determined from computer tomography, before (pre) and after (post) 21 d of unilateral lower-limb suspension (ULLS) or normal ambulation (AMB). ULLS-CON represents unilateral lower-limb suspension control group, ULLS-CM represents unilateral lower-limb suspension countermeasures group, AMB-CON represents normal ambulation control group, and AMB-CM represents normal ambulation countermeasures group. * Significant decrease from pre- to post-unloading for the ULLS-CON group ($P < 0.05$).

RESULTS

Whole-Muscle Cross-Sectional Area

The muscle CSA of the thigh and calf are presented in Figures 1 and 2, respectively. The ULLS-CON group demonstrated a 7% decrease in CSA of the thigh and lower leg muscles after the 21-d unloading period ($P < 0.05$, time). The muscle CSA of the ULLS-CM group was unchanged. Thigh and calf muscle size of the AMB-CON and AMB-CM groups was unaltered after the 21-d period.

Muscle Strength

Force-velocity characteristics of the knee extensor and plantar flexor muscles of the ULLS-CON and ULLS-CM groups are illustrated in Figure 3.

Knee extensors ULLS.

ULLS-CON subjects displayed a 17% decrease in maximal voluntary isometric strength of the knee extensors ($P < 0.05$, time). An average decrease in knee extensor isokinetic strength of 19% across concentric (range: 12–23%) and eccentric isokinetic speeds (range: 19–24%) ($P < 0.05$, time) was observed for the ULLS-CON. The maximal force was lower ($P < 0.05$, time) at every velocity except 5.25 rad·s^{-1} ($P = 0.053$, time) after the suspension period (Fig. 3). Concentric isotonic 1RM strength evaluated on the Cybex Eagle was 24% lower in the suspended leg of

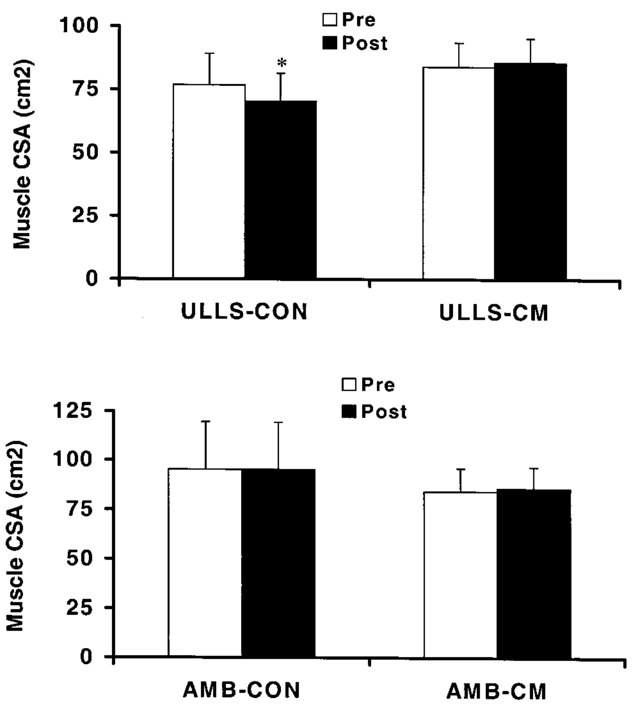

FIGURE 2—Whole-muscle cross-sectional area of the lower leg, as determined from computer tomography, before (pre) and after (post) 21 d of unilateral lower-limb suspension (ULLS) or normal ambulation (AMB). ULLS-CON represents unilateral lower-limb suspension control group, ULLS-CM represents unilateral lower-limb suspension countermeasures group, AMB-CON represents normal ambulation control group, and AMB-CM represents normal ambulation countermeasures group. * Significant decrease from pre- to post-unloading for the ULLS-CON group ($P < 0.05$).

ULLS-CON subjects ($P < 0.05$, time), with no change in 1-RM strength of the nonsuspended leg (Table 2). Conversely, results from the ULLS-CM group showed no changes at any of the concentric or eccentric isokinetic speeds (Fig. 3) or in the isotonic 1-RM (Table 2).

Plantar flexors ULLS. ULLS-CON showed decrements in maximal isometric strength (17%) ($P < 0.05$, time), and across all concentric (range: 15 to 22%) and eccentric (range: 15 to 19%) angular velocities ($P < 0.05$, time) (Fig. 3). The ULLS-CM group had no change at any concentric velocities except for an increase ($P < 0.05$, time) at 1.05 rad·s^{-1}. The ULLS-CM had an increase in maximal isometric strength ($P < 0.05$, time) and an increase in eccentric peak torque at all velocities ($P < 0.05$, time). The 1-RM of the ULLS-CON decreased 16% from 94 to 79 Nm ($P < 0.05$, time), whereas the ULLS-CM group increased ($P < 0.05$, time) 9% from 96 to 106 Nm (Fig. 4).

Force-velocity characteristics of the knee extensor and plantar flexor muscles of both AMB-CON and AMB-CM groups are illustrated in Figure 4.

Knee extensors ambulatory. AMB-CON subjects showed no change in maximal isometric or concentric and eccentric isokinetic strength at any of the angular velocities tested except 5.25 rad·s^{-1} ($P < 0.05$, time) (Fig. 5). In addition, the AMB-CON group had no change in 1-RM strength (Table 2). Similarly, maximal isometric and isokinetic strength was unchanged in AMB-CM. However, AMB-CM did show increases in isotonic 1RM strength of the training leg of 8% ($P < 0.05$, time) (Table 2).

Plantar flexors ambulatory. There was no change in the AMB-CON group with respect to maximal isometric plantar flexion strength or across any of the concentric or eccentric angular velocities tested (Fig. 5). However, the AMB-CM group increased in maximal isometric strength, concentric peak torque at 0.75 and 1.05 rad·s^{-1}, and eccentric peak torque at 1.57 and 5.24 rad·s^{-1} ($P < 0.05$, time). The AMB-CON had no change in concentric 1RM, whereas the AMB-CM group had a 14% increase ($P < 0.05$, time) in 1 RM strength (92–105 Nm).

Muscle Work Capacity

ULLS-CON knee extensor work capacity, as measured by the total work done in 30 isokinetic contractions at 3.14 rad·s^{-1}, decreased 13% (5108 ± 516 J to 4471 ± 495 J) ($P < 0.05$, time). No significant change was found in ULLS-CM or in either ambulatory group.

Electromyography

Knee extensors. IEMG activity during submaximal isometric contractions increased in the vastus lateralis (23%) and vastus medialis (28%) muscles for the ULLS-CON group ($P < 0.05$, time). Furthermore, the maximal neural activation of the vastus lateralis and vastus medialis decreased 20% and 26%, respectively, in the ULLS-CON group ($P < 0.05$, time). ULLS-CM experienced no significant alteration in neural activation during either submaximal or maximal torque loads.

In the AMB-CON group, no change in IEMG activity of either the vastus lateralis and vastus medialis was noted

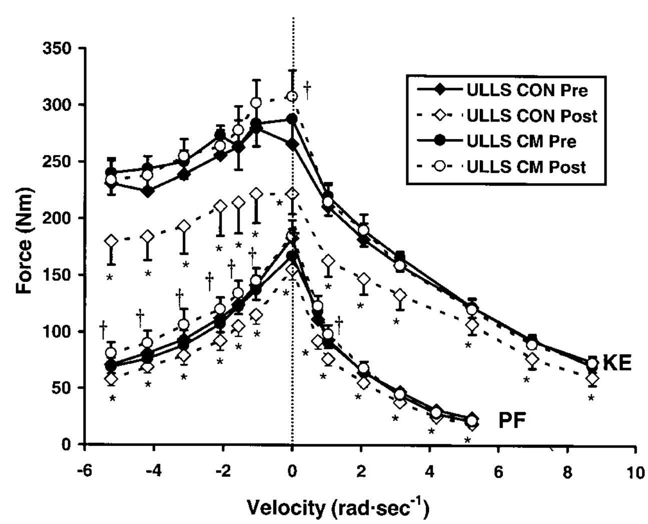

FIGURE 3—Torque-velocity characteristics of the left knee extensor (KE) and plantar flexor (PF) muscle groups of the unilateral lower-limb suspension control group (ULLS-CON) and unilateral lower-limb suspension countermeasures group (ULLS-CM) after 21 d of unloading. Each point represents group means ± standard error. * Significant decrease from pre- to post-unloading for the ULLS-CON group ($P < 0.05$). † Significant increase from pre to post for the ULLS-CM group ($P < 0.05$).

TABLE 2. One-repetition maximum strength evaluated on the Cybex Norm (Norm) dynamometer and Cybex Eagle (Eagle) dynamic leg extension (total weight lifted) devices.

Group	Norm 1RM (Nm)		Eagle L - 1RM (kg)		Eagle R - 1RM (kg)	
	Pre	Post	Pre	Post	Pre	Post
ULLS—CON	156 ± 11	131 ± 11*	45.5 ± 4.8	34.5 ± 4.1*	46.5 ± 5.0	47.1 ± 5.2
ULLS—CM	165 ± 12	166 ± 13	45.7 ± 3.4	45.6 ± 3.1	46.0 ± 3.6	50.1 ± 4.3
AMB—CON	166 ± 11	166 ± 11	49.2 ± 5.4	48.9 ± 6.0	51.4 ± 6.1	50.3 ± 1.5
AMB—CM	148 ± 12	160 ± 14*	41.9 ± 4.2	45.0 ± 4.6	43.3 ± 3.8	44.4 ± 4.1

1 RM, one-repetition maximum; L, left; R, right; ULLS—CON, unilateral lower-limb suspension control group ($N = 8$); ULLS—CM, unilateral lower-limb suspension countermeasure group ($N = 8$); AMB—CON, ambulatory control group ($N = 8$); AMB—CM, ambulatory countermeasure group ($N = 8$).
* $P < 0.05$ pre to post.

during submaximal or maximal loads. AMB-CM subjects' neural activation was unaltered in the vastus lateralis and vastus medialis at either submaximal workload. However, there was an increased IEMG activity after the 21-d period of both the vastus lateralis (29%) and medialis muscles (23%) during the MVC ($P < 0.05$, time).

Plantar flexors. ULLS-CON had no change in gastrocnemius IEMG activity at 60 Nm; however, at the 100-Nm load, IEMG activity increased 24% ($P < 0.05$, time). Additionally, MVC IEMG activity decreased 28% in the gastrocnemius ($P < 0.05$, time). ULLS-CON soleus IEMG increased 24% at 60 Nm and 22% at 100 Nm ($P < 0.05$, time). Furthermore, a 31% decrease in IEMG activity occurred during the MVC for the soleus of the ULLS-CON group ($P < 0.05$, time). The ULLS-CM group showed no significant change in gastrocnemius activation during either the submaximal or maximal contractions. Likewise, ULLS-CM soleus had no alteration in neural activation at either 60 or 100 Nm or in maximal IEMG activity. No significant change was found in AMB-CON submaximal or maximal IEMG activity of either muscle group. Furthermore, no change was observed for the AMB-CM group in IEMG activity of the gastrocnemius or soleus muscle during the submaximal isometric contractions. Although no change IEMG activity was observed in the gastrocnemius muscle during the MVC of the AMB-CM, the IEMG activity of the soleus was 20% greater after the 21-d period ($P < 0.05$, time).

Countermeasure Resistance Training

Both muscle groups (knee extensors and planar flexors) were trained in succession, and, including equipment maneuvering, the total training session time for both muscle groups was about 20 min. Training of each muscle group required approximately 7 min to complete, including work and rest time. The total work time for each muscle group was, on average, about 2 min. However, this time was dependent upon how many repetitions were completed in the final set to failure. Most subjects were able to complete a greater number of plantar flexor contractions than knee extensions in this final set. The mean number of contractions and mean work performed for each muscle action is reported in Table 3.

Dietary Analysis

Three-day dietary recall analysis revealed no interaction between or within suspension groups at any time point. The control group consumed an average of 2739 ± 231 calories per day; the countermeasures consumed an average of

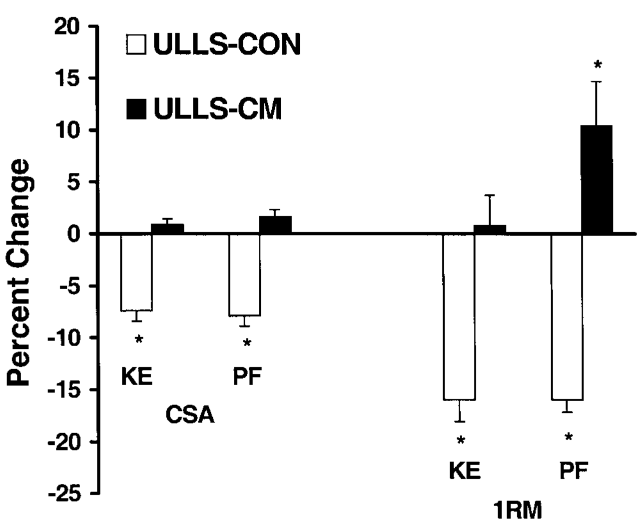

FIGURE 4—Comparison of percent change in cross-sectional area and one-repetition maximum strength of the knee extensor (KE) and plantar flexor (PF) muscle groups for the unilateral lower-limb suspension control (ULLS-CON) and countermeasures (ULLS-CM) groups after 21 d of unloading. CSA, cross-sectional area; 1 RM, one-repetition maximum. * $P < 0.05$.

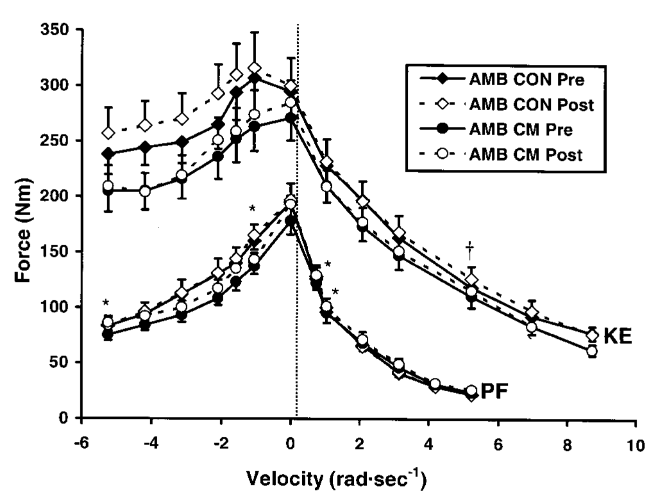

FIGURE 5—Torque-velocity characteristics of the left knee extensor (KE) and plantar flexor (PF) muscle groups of the ambulatory control group (AMB-CON) and unilateral lower-limb suspension countermeasures group (AMB-CM) after 21 d of unloading. Each point represents group means ± standard error. * Significant increase during 21 d of normal ambulation for the AMB-CM group ($P < 0.05$). † Significant increase from pre to post for the AMB-CON group ($P < 0.05$).

TABLE 3. Summary of the average number of contractions and work performed for the knee extensor and plantar flexor muscle groups during each countermeasure training session.

	Knee Extensors		Plantar Flexors	
Variable	ULLS	AMB	ULLS	AMB
Total number of contractions	36	39	50	50
Contractions at 80% 1RM	24	27	38	38
Contractions at 40% 1RM	10	10	10	10
Maximum isometric contractions	2	2	2	2
Mean work done (J)	8578	7546	3443	2870

ULLS, unilateral lower-limb suspension; AMB, ambulatory; 1RM, one-repetition maximum.

2875 ± 136 calories per day. Dietary analysis was not performed with ambulatory subjects.

DISCUSSION

The aim of this investigation was to develop and test a countermeasure program of resistance exercise to attenuate the loss in skeletal muscle function and size that occurs in humans with unloading. One of our primary considerations when designing the countermeasure activity was to implement a preventive strategy that could be conducted quickly and efficiently, while maintaining the integrity of the skeletal muscle. The major finding from this investigation was that the high-intensity resistance training employed every third day was effective in preserving muscle size, strength (static and dynamic), and neuromuscular function in the knee extensor and plantar flexor muscle groups during 21 d of unilateral limb unloading. Each muscle group (knee extensors and plantar flexors) subjected to the countermeasures program consisted of a warm-up and one isometric and two isotonic sets, and required approximately 2 min of actual work time to complete.

Muscle Cross-Sectional Area

Muscle cross-sectional area data from this investigation indicate that significant atrophy occurred in the thigh and calf muscles of the ULLS-CON subjects with no corresponding decrease in CSA of the countermeasure exercise group (ULLS-CM). The reduction in muscle size (7%) was the same for both the upper leg and lower leg (see Fig. 4). This decline in ULLS-CON muscle size of the present investigation parallels data from a number of bed rest and ULLS studies that report decreases from 7 to 16% after 28–42 d of unloading (9,24,31).

At the present time, no other unloading investigations have examined the impact of isotonic countermeasure training on whole-muscle cross-sectional area. Akima et al. (2) found that whole-muscle CSA is preserved during 20 d of bed rest with daily isometric exercise. Furthermore, Bamman et al. (5) reported no change in Type I and II muscle fiber CSA of the vastus lateralis in their exercise group. Whole-muscle size of the countermeasure subjects in the present investigation did not change, thereby supporting the idea that the resistance-training protocol prevented decrements in whole-muscle size. The fact that there were no alterations in whole-muscle size in the ambulatory countermeasure group suggests that our training protocol did not promote muscle growth. This result is upheld by the observation that short-term resistance-training programs do not typically result in muscle hypertrophy (32). Therefore, although the countermeasure protocol did not induce hypertrophy in ambulatory subjects, it was an effective measure for preventing muscle disuse atrophy in unloaded subjects.

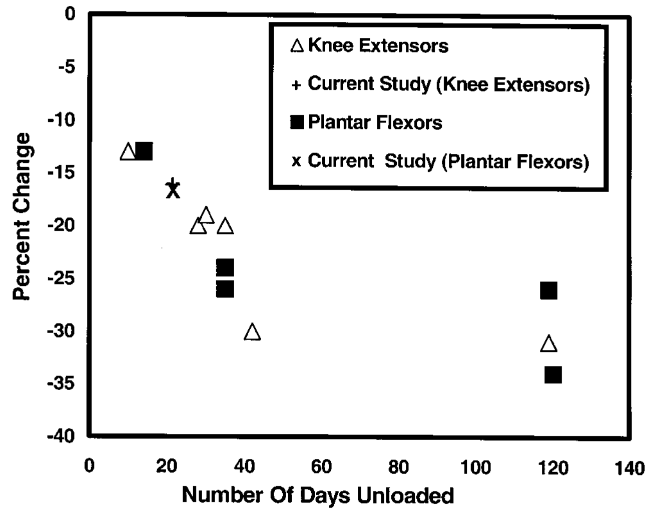

FIGURE 6—Relationship of strength decreases to duration unloaded for the knee extensor (KE) and plantar flexor (PF) muscle groups reported in previous investigations (5,9,10,15,26,27), including mean strength loss of current 21-d unloaded period.

Muscle Strength

The resistance-training protocol utilized in the present investigation was effective in maintaining whole-muscle static and dynamic (concentric and eccentric) strength in both the knee extensor and plantar flexor muscle groups. The observation that the plantar flexors increased in strength but the knee extensors did not in the ULLS-CM group may be due to the fact that the initial relative strength of plantar flexors was lower than the knee extensors. This premise is supported by the fact that during the training sessions, subjects were able to perform a greater number of plantar flexor contractions compared with knee extensor contractions at 80% of their initial 1RM. Conversely, an average 18% decline in maximal knee extensor strength and 17% decline in maximal plantar flexor strength was observed in the ULLS-CON group after 21 d of unloading without countermeasures (Fig. 6). Data from ground-based studies with no countermeasure exercise have provided comparable reductions in knee extensor muscle strength to those found in the current study. Investigations of 10–120 d report losses in concentric knee extensor and/or triceps surae strength ranging from 9 to 36% (7,10,19,26,29). Thus, the majority of ground-based unloading studies supports the results from the current investigation and shows a linear decline in strength with duration of unloading (see Fig. 6).

From the torque-velocity data, the ULLS-CON group displayed a significant decrease in torque production in the knee extensors (slow to fast velocity ranged from −22% to

−12%) and plantar flexors (slow to fast velocity ranged from −20% to −14%). Thus, it appears that concentric torque production was more affected at the slower speeds. This may be due, in part, to muscle atrophy, but the correlation between CSA and MVC is not significant for either muscle group (0.192 and 0.168 for knee extensors and planter flexors, respectively). Other characteristics of muscle contractions, such as intrinsic changes in the muscle cell (36) and/or alterations in neuromuscular recruitment, may be responsible for the variation in muscle performance at slow versus fast movements. In the current study, the 12% decrease at the higher velocities ($>$3.14 rad·s^{-1}) was equivalent to 5–10 Nm, whereas the 20% decrease at the slower speeds was equivalent to 17 Nm for the calf and 48 Nm for the quadriceps. Thus, from a whole-muscle performance standpoint, muscle actions requiring large loads at slower movements may be much more problematic compared with tasks requiring low loads and fast movements. However, other investigations have not observed differences in the reduction of strength at different contraction velocities after unloading (1,7,9,14). Differences between the current study and previous investigations may be due to the fact that we tested subject's strength at faster velocities (8.73 vs 3.14 rad·s^{-1}) than previous investigations. In the current study, there were no differences in the decrease in strength between 0.57 and 3.14 rad·s^{-1} for the ULLS-CON group. Without the faster velocities (i.e., $>$ 3.14 rad·s^{-1}), we would obtain the same conclusion as previous investigations.

Although the concentric torque-velocity relationship was more affected at the slow speeds, the eccentric torque-velocity relationship demonstrated a drop-off in torque production that ranged 17–20% regardless of speed. This is in contrast to *in vivo* muscle preparations (17) but in agreement with several *in vitro* human studies (12,13,25). Muscle preload, the amount of preload, and the strength dynamometer used have all been shown to greatly affect eccentric force production (25). The dynamometer used in this study (Cybex Norm) with a preload phase indicates that eccentric torque production gradually decreases with increasing speed and that eccentric force production is reduced with unloading. However, when resistance training is employed during unloading, pre-unloading eccentric torque values are attained.

Data from the ULLS and ambulatory countermeasure groups showed no significant change in any of the dynamic strength parameters tested. Thus, although the present resistance protocol was effective in preventing strength decrements, it did not serve as an effective stimulus to promote improvements in muscle strength over a 21-d period. An exception to this was the increase in ULLS countermeasure MVC ($P < 0.05$) and increase ($P < 0.05$) in some of the concentric and eccentric force-velocity parameters of the ambulatory countermeasure group. These results are most likely due to the fact that neural adaptations to maximal isometric resistance training have been found to occur more rapidly than with dynamic exercise (32). The isometric contractions in the current protocol made up only a small component of the total number of contractions (2 isometrics vs ~45 dynamic contractions). Akima et al. (2) found that 30 isometric contractions per day was sufficient to maintain muscle strength and size during 20 d of bed rest.

The total work completed during 30 maximal continuous isokinetic contractions (3.14 rad·s^{-1}) was unchanged in the countermeasure exercise group (ULLS-CM) but was considerably reduced (13%) in the no exercise ULLS-CON group ($P < 0.05$). This outcome is analogous to that of Berg et al. (8), who reported a 17% decrease in the muscle's work capacity as measured by an identical testing protocol after 28 d of ULLS.

Motor Unit Recruitment

The current 21-d investigation of uninterrupted ULLS led to an altered knee extensor and plantar flexor motor unit recruitment. The alterations in neural drive were equivalent among the four muscles that were studies (i.e., v. lat, v. med., gastrocnemius, and soleus). IEMG activity increased in all four muscles at submaximal intensities except for the gastrocnemius at 60 Nm. Diminished IEMG activity was observed for all muscle groups during the MVC contraction, suggesting either a decrease in activation, a change in antagonist coactivation, or an inhibition in neural drive. These data indicate that the neuromuscular adaptations of the two muscle groups are similar with unloading.

The large increases in submaximal IEMG in the ULLS control group corresponds to previously reported increases with unloading (10,14). The ULLS-CM group displayed no change in submaximal IEMG, suggesting that the present resistance-training protocol sufficiently stimulated the nervous system, thus preventing the need for an increase in activity to maintain the same absolute submaximal torque load. Furthermore, the minor change in the ambulatory countermeasure group indicates that the training succeeded only in prevention of the need for additional recruitment of motor units.

The reduction in habitual motor unit recruitment that occurs after periods of injury, inactivity, and/or detraining leads to decreases in maximal EMG activity (21,30). With muscle unloading, Berg and Tesch (10) found a nonsignificant increase in maximal neural activation after 10 d of ULLS, although the authors did not report absolute or percent change. It is possible that this discrepancy in outcome arose because the suspension period of only 10 d was not of sufficient length to alter maximal neural activation pattern of the knee extensor muscles. The increases in maximal IEMG activity seen in muscles (v. lat, v. med., gastrocnemius, and soleus) of the ambulatory countermeasure groups in the current investigation suggest that the resistance protocol may alter neural recruitment patterns by stimulating high-threshold motor units, increasing maximal firing frequency (30).

Practical Implications

The current study design was based on previous ground-based resistance-training programs (11,12,33) and a countermeasure program used in two previous unloading studies

(5,6). Although the current investigation does not establish the minimum resistance training required to preserve muscle strength and size, it does decrease the volume from previous unloading studies. However, it should be noted that the effects of periodization and individual variations to training-induced adaptations were not investigated in the present or previous investigations.

In 14-d bed rest study, Bamman et al. utilized a concentric/eccentric isotonic resistance-training protocol performed every other day that was effective in maintaining muscle strength of the knee extensors (5) and plantar flexors (6). During the training sessions, subjects performed concentric and eccentric muscle contractions (5 sets, 6–10 reps) at 80% of maximum. Each training session subjects performed ~50 contractions (40 at 80% 1RM and 10 warm-up). Overall, subjects performed approximately 350 contractions for each muscle group (~700 total, knee extensors and plantar flexors) during the 14-d bed rest. In the current investigation, subjects averaged ~38 and ~50 contractions for the knee extensors and plantar flexors, respectively (see Table 3). During the entire 21-d unloading period, subjects performed between 225 and 300 muscle contractions per muscle group (~525 total). Thus, the current investigation employed fewer muscle contractions over a longer period of time (21 d vs 14 d) and was still effective in maintaining muscle strength and size in both the knee extensors and plantar flexors. The studies by Bamman et al. (5,6) and the current investigation provide a baseline of information from which future protocols can be used to establish if fewer muscle contractions are effective for people living in space.

SUMMARY

In summary, a program of maximal isometric, and concentric and eccentric isotonic contractions performed every third day provided enough stimuli to attenuate the loss of knee extensor and plantar flexor muscle size, strength, and neuromuscular function during 21 d of muscle unloading. However, due to the relatively short period of unloading, slight losses in strength may not have been detected. The present resistance-training protocol did not promote increases in strength and size in ambulatory subjects. In addition, these data suggest that the knee extensor and plantar flexor muscle groups respond similarly to the unloading and resistance-training countermeasures employed in this investigation. Although this protocol was effective, further investigation is warranted to establish the minimum stimulus (volume, frequency, intensity, and periodization) required to attenuate the observed losses in human skeletal muscle strength and size with unloading.

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