REPETITIVE ECCENTRIC STRAIN AT LONG MUSCLE LENGTH EVOKES THE REPEATED BOUT EFFECT

ROBERT W. PETTITT,¹ J. DAVID SYMONS,² PATRICIA A. EISENMAN,² JULIE E. TAYLOR,³ AND ANDREA T. WHITE²

¹Human Performance Research Laboratory, Mesa State College, Grand Junction, Colorado; ²Department of Exercise and Sport Science, University of Utah, Salt Lake City, Utah; ³Department of Physical Education, Southern Utah University, Cedar City, Utah.

ABSTRACT. Pettitt, R.W., J.D. Symons, P.A. Eisenman, J.E. Taylor, and A.T. White. Repetitive eccentric strain at long muscle length evokes the repeated bout effect. J. Strength Cond. Res. 19(4):918–924. 2005.—The repeated bout effect (RBE) is a phenomenon characterized by less delayed onset muscle soreness (DOMS) and torque deficit after the second of 2 separate eccentric exercise bouts. Previous investigators have reported that shifting of optimum angle after an initial bout of eccentric exercise mediates the RBE. We hypothesized that an RBE for elbow extensor exercise occurs after an initial bout performed at long (starting position of 50° to an end position of 130°) but not short (starting position of 0° to an end position of 80°) muscle length because strain at long length evokes a shifting of the optimum angle to a longer length. Untrained women performed an initial bout at either long or short length (n = 9 per group)followed 1 week later by a repeated bout (RB) through the full ROM (0-130°). Extensor torque and optimum angle was evaluated before, immediately after, and 2 days after each bout. A mechanical transducer depressed on the triceps brachii quantified DOMS. Torque deficits were 3% and 7% after exercise at short vs. long length, respectively. Two days after the RB, torque deficit was 8% and 1% for those previously exercising at short vs. long length (group \times bout, p < 0.05). Greater DOMS (N) was observed after exercise at long (16 ± 3) vs. short (23 ± 2) length; whereas greater DOMS occurred for the short-length (17 \pm 2) vs. long (26 \pm 3) group after the RB (group \times bout, p < 0.05). Optimum angle shifted to a longer length after exercise at long $(+10 \pm 4^{\circ})$ vs. short $(+1 \pm 3^{\circ})$ length (group × bout, p < 0.05). After the RB, those exercising previously at short length experienced a shift of $+15 \pm 4^{\circ}$ (main effect, p < 0.05). The findings of this study indicate that the repetitive strain at long but not short muscle length evokes both immediate and sustained shifts in optimum angle to longer lengths, and that this shifting mediates ($r^2 = 0.71$) the RBE.

KEY WORDS. delayed onset muscle soreness, eccentric exercise, popped sarcomere hypothesis, optimum angle

Introduction

hen previously untrained subjects perform 2 bouts of eccentric exercise more than 1 week apart, decrements in muscle force production (7, 10, 25) and eccentric-induced myofibril damage (13, 32) are diminished after the repeated bout (RB). This phenomenon is termed the repeated bout effect (RBE; Refs. 7, 29, 32). Although the mechanisms responsible for the RBE are unclear, 2 that have been proposed involve neuromuscular mediating factors (39) and structural changes (2, 26, 35). Findings from studies investigating potential neuromuscular me-

diating factors for the RBE are equivocal (25, 39). Con-

versely, independent research groups (2, 26, 35) have re-

ported that the RBE is mediated by structural changes

within skeletal muscle that affect length-tension relations.

Numerous factors potentially contributing to eccentric-induced muscle damage have been examined. The consensus of several research groups is that strain rate (i.e., speed of contraction) contributes little to damage, compared with percentage strain and muscle force (19, 20, 23). Between the 2 factors, strain and muscle force, separate groups (3, 18, 19) have concluded that strain percentage beyond optimum length (L_{\circ}) , as opposed to high muscle force (i.e., ripping from an isometric hold) causes the greatest magnitude of peak force reduction and histological damage. Further, eccentric-induced damage from active strain appears nonuniformly, rather than globally, and is prominent in fast- vs. slow-twitch muscle fibers (1, 17). Nonuniform damage was hypothesized by Morgan (27) to occur synonymously with a shift in L_0 to a length favoring force production at longer muscle

Both immediate and sustained shifts in optimum angle to angles favoring torque production at longer lengths have been observed for untrained humans performing RBs of hamstring exercise (2). Along with shifting of optimum angle or L_{\circ} , investigators have observed decreases in force (torque) production along the ascending limb of the length (angle)-tension (torque) curve in animal (1, 40) and human (2, 26, 35) models. However, investigators using both animal (16, 28) and human (5) models have reported that shifting of L_{\circ} (angle) only occurs after eccentric contractions performed at long and not short length (angle). Moreover, consistent with animal models (3, 18, 19), decrements in average joint torque production along with delayed onset muscle soreness (DOMS) is greater after exercise performed at long vs. short muscle length (30, 33). The question of whether exercise at short vs. long muscle length results in an RBE is unanswered (24). We tested the hypothesis that an RBE is observed after eccentric exercise at long but not short muscle length because strain at long length evokes a shifting of optimum angle to longer length.

METHODS

Experimental Approach to the Problem

Subjects performed an initial bout of eccentric exercise for the elbow extensors through partial range of motion (ROM) at either short (starting position of 0° to an end position of 80°) or long (starting position of 50° to an end position of 130°) muscle length (n=9 per group). After 1 week of rest, each group performed an RB of eccentric

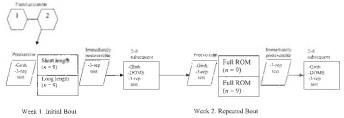


FIGURE 1. Flow diagram for eccentric exercise and testing. On the second of two familiarization days (1 and 2), subjects completed a 25 repetition test at 240°⋅s⁻¹. Subjects were then matched to either short (0-80°) or long (50-130°) length eccentric exercise conditions. One week later, subjects performed a repeated bout through full range of motion (0-130°). Upper arm girth was evaluated before exercise and 2 days after each bout. Delayed onset muscle soreness was also evaluated 2 days after each bout. Average extensor torque and optimum angle were determined from 3 repetition tests performed before exercise, immediately after exercise, and 2 days after each bout.

elbow extensions through full ROM (0-130°). We selected the isolated joint movement of elbow extension because the triceps brachii is the prime mover for this movement action at any joint angle (i.e., short or long length) and, therefore, this choice enabled us to compare our results with those from experiments using isolated muscle preparations. For each group, concentric elbow extensor torque was evaluated before, immediately after, and 2 days after each bout (Figure 1). As a measure of DOMS, the mechanical transducer force required to evoke tenderness in the triceps brachii was recorded 2 days after each bout (25, 31). Measures of torque deficit and DOMS determined whether an RBE occurred for the short- and long-length groups, respectively. Muscle volume was determined via girth measures of the upper arm (14) and was used to estimate muscle inflammation (36).

Subjects

Eighteen previously untrained women ([mean $\pm SD$] age, 26 ± 5 years; height, 170 ± 6 cm; weight, 69 ± 14 kg) participated in this study after approval from an Institutional Review Board. Subjects did not perform resistance training for 6 months before data collection and had no history of orthopedic injury/surgery involving the upper extremity. Subjects were matched to the short- and long-length groups based on their performance on a fatigue test (described in next paragraph). Investigators (39) have asserted that change in fast- vs. slow-twitch fiber recruitment occurs as a neuromuscular mediating factor to the RBE. Therefore, we matched on fatigability as a surrogate measure of fast- vs. slow-twitch fiber proportion (38), instead of other factors (e.g., body mass). We instructed subjects to refrain from using analysis and anti-inflammatory drugs while participating in the study and confirmed compliance of this verbally. Use of topical agents, consumption of antioxidant supplements, and conventional modalities were neither mentioned nor prohibited because the results of such interventions to attenuate the time course of DOMS at the time of this study were equivocal (8).

Familiarization

Before the initial bout, subjects for each group completed 2 familiarization concentric exercise sessions on an iso-

spring displacement gauge

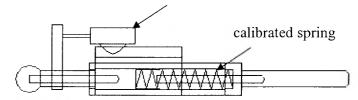


FIGURE 2. Illustration of transducer used to quantify delayed onset muscle soreness.

kinetic dynamometer (Kin-Com III, Chattecx, Inc., Chattanooga, TN) separated by 2 days of rest (11, 12). Each familiarization session consisted of 25 repetitions (reps) at 60, 180, and 240°⋅s⁻¹, respectively. A fatigue coefficient of 25 reps at 240°·s⁻¹ (15) was calculated from gravitycorrected data collected during the second day of familiarization. This coefficient was derived using the mean of the last 5 reps divided by the mean of the first 5 reps. Subjects were then rank ordered and matched to each group (Figure 1).

Initial and RBs of Eccentric Exercise

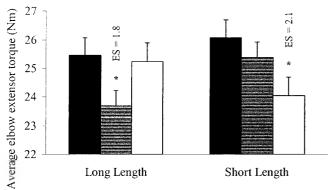
Investigators have previously determined that 75 maximal-effort, eccentric reps through 80° of joint ROM at either short or long length was sufficient to evoke DOMS (5). From a preliminary investigation (unpublished data on different subjects), we determined that 3×25 reps at $60^{\circ} \cdot s^{-1}$, separated by 2–3 minutes of recovery, resulted in decreased torque and DOMS at 2 days after eccentric exercise. Our assumption was that maximal effort with standardized dynamometer speed and standardized ROM (i.e., 80°) would standardize the total volume of work performed by each group. Therefore, we used 3 × 25 maximal reps with 2-3 minutes of recovery between sets for each bout.

To determine whether each group experienced an RBE, subjects performed an RB through full ROM 1 week after the initial bout. All exercise and extensor torque testing was performed on the same isokinetic dynamometer. Stabilizing restraints were placed around the torso and upper arm to prevent accessory movements. A wrist brace was worn to prevent excessive contraction of muscles distal to the elbow.

Estimates of DOMS and Muscle Inflammation

DOMS was quantified by depressing a calibrated mechanical transducer over the triceps brachii (Figure 2; spring displacement-force calibration: r = 0.99; sensitivity = 0.001 N). Two days after each bout (Figure 1), the musculotendinous region of the triceps brachii was palpated and subjects were asked to indicate the area where tenderness was most severe. Two days was selected because this is when DOMS is typically highest during the day-to-day time course after eccentric exercise (4–6, 9, 13, 25, 30). The indicated area of the triceps was depressed 3 times using the mechanical transducer. Each time, the force required to evoke tenderness was recorded.

Delayed, contraction-induced muscle inflammation is associated with increased muscle volume (36). Therefore, upper arm volume was estimated using circumference measures (14) at 3, 5, 7, 9, and 11 cm proximal from the lateral epicondyle (33). These circumferences were col-



■ Baseline ■ 2-d subsequent to initial bout □ 2-d subsequent to RB

FIGURE 3. Average elbow extensor torque $(\pm SE)$ at baseline, 2 days after initial bout, and 2 days after repeated bout *Significantly lower average elbow extensor torque (group × time, p < 0.05) effect size (ES) change from baseline.

lected before each bout and 2 days after each bout (Figure

Concentric Extensor Torque Testing

Before each eccentric exercise bout, immediately after exercise, and 2 days after each bout, subjects performed 3 maximal concentric elbow extensions at 60°·s⁻¹ through full ROM (3-rep test; Figure 1). Average extensor torque and optimum angle were calculated from the rep with the highest torque value.

Statistical Analyses

Descriptive statistics on all outcome measures are reported as mean \pm SE. Normality was assessed with Kolmogorov-Smirnov tests and homogeneity of variance was assessed using Levene's test. Two-way analyses of variance (ANOVA) with repeated measures were used to test for group differences in response to the 2 eccentric exercise bouts. One factor was group, short vs. long; whereas the second factor was the day of testing. A 2×2 configuration was used for DOMS, a 2×3 configuration was used for average extensor torque and optimum angle, and a 2×4 configuration was used for estimated upper arm volume. The main effect for the day of testing was examined using univariate ANOVA with repeated measures and Tukev's post hoc test. Interaction was examined using multiple t-tests with Holm's sequential Bonferonni approach. Effect sizes were calculated using Cohen's d. Significance was accepted at $p \leq 0.05$.

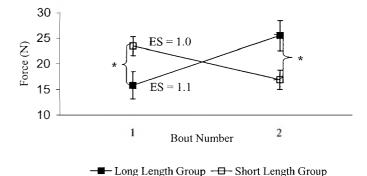


FIGURE 4. Depressive transducer force (mean $\pm SE$) required to elicit perceived muscle soreness. A lower force measure is synonymous with greater delayed onset muscle soreness. *Significantly different (group \times time, p < 0.05) effect size (ES) change between the 2 testing days.

RESULTS

Repeated Bout Effect

Data for each group were normally distributed and homogenous. Cronbach's coefficient for test-retest reliability of the transducer force for quantifying DOMS was 0.99. Analysis of deficits in average extensor torque (Figure 2) and DOMS (Figure 3) indicated that the long-length group experienced an RBE, whereas the short-length group exhibited the opposite effect, comparable in effect size. Torque decrements were greater 2 days after the initial bout for the long-length group, and were greater 2 days after the RB for subjects exercising initially at short length for the initial bout (Table 1 and Figure 3). Subjects exercising at long length had greater DOMS after the initial bout (Figure 4). Conversely, greater DOMS occurred for the short-length group after their RB. Despite the interaction for extensor torque decrements and DOMS across the 2 eccentric exercise bouts, no differences were observed in the estimated upper arm volumes between the groups or across bouts (data not shown).

Angle-Torque Relations

Analysis of angle-torque relations revealed that shifting of optimum angle to longer lengths occurred after the initial bout for the long-length but not the short-length group (Table 1). Shifting of optimum angle to longer lengths did occur for the short-length group after their RB. Further, optimum angle remained shifted to a longer length after the RB for the long-length group (main effect, p < 0.05).

Table 1. Average extensor torque, optimum angle, and transducer force required to elicit delayed onset muscle soreness (DOMS) for the short (S) and long (L) length groups at baseline, 2 days after initial bout (IB), and 2 days after repeated bout (RB).*

	Baseline		2 days after IB		2 days after RB	
	S	L	s	L	S	L
Extensor torque (N·m)	$26.1 \pm 1^{\rm b}$	$25.5 \pm 1^{\rm b}$	$25.4\pm1^{ ext{b}}$	$23.7 \pm 1^{\rm a}$	24.0 ± 1^{a}	$25.2 \pm 1^{\text{b}}$
Optimum angle (°) DOMS (N)	$88.7 \pm 4^{ m a} \ 25.5 \pm 3^{ m b}$	$86.8 \pm 4^{\rm a} \ 15.8 \pm 3^{\rm a}$	$89.0 \pm 3^{\rm a} \ 16.9 \pm 2^{\rm a}$	$97.2 \pm 4^{ m b} \ 23.6 \pm 2^{ m b}$	$103.8\pm4^{\rm b}$	$98.9 \pm 3^{\mathrm{b}}$

^{*} Data are reported as mean \pm SE. Letters in rows indicate significant differences (p < 0.05) where values for a relower than values for b.

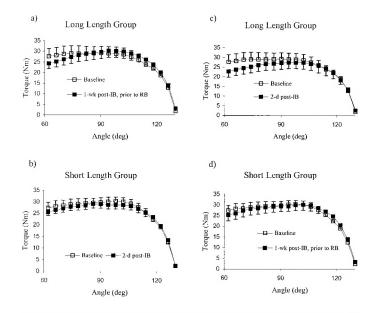
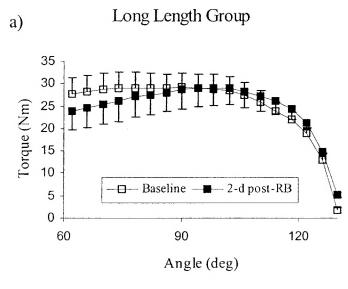


FIGURE 5. Angle-torque relations (mean $\pm SE$) at baseline, 2 days after the initial bout (2-d post-IB), and 1 week after the initial bout, before the repeated bout (1-wk post-IB, prior to RB). In response to the initial bout, lower torque values were observed on the ascending limb of the angle-torque curves after exercise at long but not short muscle length.

Differences in the ascending limb of extensor angletorque curves were observed between the short- and longlength groups across the number of days of testing. Specifically, decreased torque production at joint angles on the ascending limb (i.e., corresponding to shorter muscle lengths) occurred after the initial bout for the long-length group (Figure 5a) but not for the short-length group (Figure 5b). Similar patterns between each group occurred 1 week after the initial bout (Figure 5c and 5d), before performing the RB. Decreased torque on the ascending limb occurred after the RB for the short-length group (Figure 6b) and presented as a sustained shift for the long-length group (Figure 6a). To quantify this phenomenon, differences in torque at angles below 100° (i.e., mean optimum angle for both groups) were calculated at 2 days after the initial bout and RB. There was a $10.5 \pm 1.4\%$ decrease in torque on the ascending limb for the long-length group and a $4.1 \pm 0.5\%$ decrease for the short-length group after the initial bout (group \times bout, p < 0.05). Two days after the RB, the short-length group experienced an 11.6 \pm 0.9% decrease on the ascending limb, whereas the longlength group experienced an 3.4 ± 1.4% decrease (same main effect and interaction for optimum angle appearing in Table 1). Coefficient of determination indicated that a strong, shared variance $(r^2 = 0.71)$ existed between the concentric extensor torque deficit after the RB and the average percent change of torque of the ascending limb of the angle-torque curve after the initial bout.

Angle-torque relations from baseline were also compared with angle-torque relations immediately after each eccentric exercise bout. As illustrated in Figure 7, a decrease in the ascending limb of the angle-torque curve was observed immediately after the initial bout for the long-length but not the short-length group. This immediate shift, however, was observed for the short-length group after the RB, a bout performed through full ROM



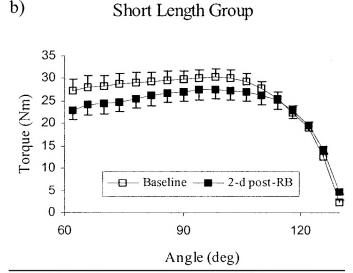
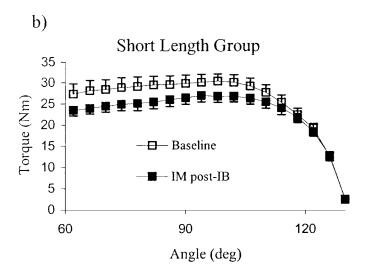


FIGURE 6. Angle-torque relations (mean $\pm SE$) at baseline and 2 days after the repeated bout (2-d post-RB). A decrease in torque on the ascending limb of the angle-torque curve was now observed for subjects who completed their initial bout at short length.

(i.e., a longer length of eccentric exercise compared with the length for the initial bout).

DISCUSSION

Consistent with our hypothesis, an initial bout of eccentric exercise at short muscle length caused decrements in average extensor torque production (Figure 3) and DOMS (Figure 4), yet failed to evoke an RBE, whereas eccentric exercise at long muscle length did evoke an RBE. Subjects who initially exercised at short length experienced greater torque decrements and DOMS after the RB (Table 1). Previous investigators (5, 30, 33) have reported that an isolated bout of eccentric exercise performed at long vs. short muscle length causes greater torque decrements and DOMS.



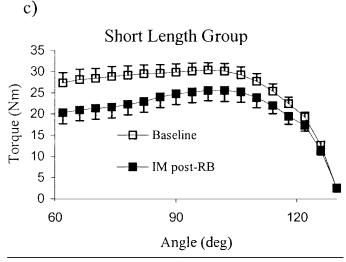


FIGURE 7. Angle-torque relations (mean \pm SE) at baseline and immediately after (IM) eccentric exercise for the initial bout (IB) and repeated bout (RB). Note that the long-length group experienced a decrease in torque on the ascending limb of the angle-torque curve after the IB and RB, whereas the short-length group only experienced this after the RB, a bout performed through full range of motion.

Our results indicate that eccentric exercise at short muscle length fails to evoke shifting of angle-torque relations immediately after (Figure 7b), 2 days after (Figure 5b), or 1 week after (Figure 5d) exercise, a result consistent with previous research (5). Only in response to the RB, did subjects in the short-length group experience immediate (Figure 7c) and sustained (Figure 6b) shifts of angle-torque relations to longer lengths, presumably because this bout was performed at longer muscle length. Despite exercising through limited ROM (50-130°), subjects exercising at long length during the initial bout experienced an RBE (Table 1 and Figures 3 and 4) along with immediate (Figure 7a) and sustained (Figure 5a,c) shifts of angle-torque relations to longer lengths. Indeed, the effect size or magnitude of torque deficit and DOMS experienced by the short-length group 2 days after their RB were similar to those observed for the long-length group after their initial bout (Table 1). These findings suggest that muscle strain (i.e., length of muscle during exercise), as opposed to ROM, per se, is responsible for the shifting of angle-torque relations in previously untrained individuals, and that shifting of angle-torque relations to longer lengths mediates the RBE.

Data from in situ muscle preparations have indicated that rightward shifting of L_{\circ} occurs only from repetitive eccentric strain performed at lengths beyond L_{\circ} (16, 28). Based on a computer model, Morgan (27) originally hypothesized that nonuniform sarcomere lengthening occurred after "popping" of actin-myosin units of weaker sarcomeres. This observation is consistent with more recent analyses of electron micrographs (37) and laser diffraction analysis techniques (22). The immediate postexercise change in angle-torque relations observed in the present study (Figure 7) indicated that shifting of angletorque relations to longer lengths required repetitive eccentric strain through angles beyond optimum (i.e., >100° for the elbow extensors). This observation parallels animal experiments (16, 28), and is consistent with Morgan's popped sarcomere hypothesis (27).

Our findings support a second aspect of Morgan's popped sarcomere hypothesis, which states that weaker sarcomeres, stretched beyond filament overlap, "pop" and are replaced by a greater number of sarcomeres in series. This would explain the sustained shifts of angle-torque relations we observed 2 days and 1 week after the initial bout for the long-length group. For example, earlier work by Lynn and Morgan (21) showed that the mean sarcomere count in series was greater for animals completing a short-term eccentric vs. concentric running protocol. In the present study, both short- and long-length groups had full recovery of extensor torque 1 week after the initial bout, however, the long-length group had sustained shifting of angle-torque relations. After the RB, the longlength group experienced an RBE, whereas the shortlength group experienced the opposite effect. Serialized addition of sarcomeres could explain why the elbow extensors of the subjects in the long-length group were more resilient to decrements in torque production and experienced less DOMS after the RB.

PRACTICAL APPLICATIONS

DOMS often discourages individuals from continuing a progressive resistance exercise program. Therefore, it is important to understand the mechanisms contributing to the RBE so that measures can be implemented to prevent

and/or lessen soreness, and/or hasten recovery from soreness. The results of this study provide insight into factors evoking the RBE and, by extension, are useful to those designing and monitoring resistance exercise programs for previously untrained individuals.

Our results combined with previous research allow us to advance the following explanation for the RBE in previously untrained individuals. To evoke an RBE for a particular joint, exercise should be performed through a ROM exceeding optimum angle to promote strain at long muscle length, although full ROM, per se, is not required. Eccentric exercise at long length causes greater DOMS and decrements in muscle force production (5, 30, 33); however, this seems to be necessary to cause immediate shifting of angle-torque relations (Figure 7) synonymous with underlying nonuniform sarcomere lengthening (22, 27). In the days that follow an initial bout performed at longer lengths, angle-torque relations remain shifted to longer lengths, presumably because of the serialized addition of sarcomeres (21). Exercise of limited motion that does not exceed optimum angle (i.e., shorter lengths) does not evoke shifting of angle-torque relations to longer lengths, a change that seems to mediate $(r^2 = 0.71)$ the RBE.

A recent experiment by Nosaka and colleagues (34) determined that the protective effect of an initial bout of eccentric exercise may last up to 6 months. Our results illustrate that relying solely on a client's reporting of DOMS may not guarantee attainment of this protective effect from eccentric exercise. Indeed, subjects in our short-length group experienced DOMS and torque decrements, albeit in less magnitude than those in the long-length group.

Strength and conditioning professionals starting a sedentary individual on a training program may consider initially prescribing a larger variety of single-joint exercises, with the movement of the joint ending at full ROM, before advancing to a program with a smaller number of multi-joint exercises. The rationale for this recommendation is that a larger number of single-joint exercises would expose a larger number of muscles to strain at longer lengths. The result of this beginning program would be better global protection from future eccentric-induced muscle damage.

REFERENCES

- BROCKETT, C.L., D.L. MORGAN, J.E. GREGORY, AND U. PROSKE. Damage to different motor units from active lengthening of the medial gastrocnemius muscles of the cat. J. Appl. Physiol. 92: 1104–1110. 2002.
- BROCKETT, C.L., D.L. MORGAN, AND U. PROSKE. Human hamstring muscles adapt to eccentric exercise by changing optimum length. Med. Sci. Sports Exerc. 33:783-790, 2001.
- BROOKS, S.V., AND J.A. FAULKNER. Severity of contraction-induced injury is affected by velocity only during stretches of large strain. J. Appl. Physiol. 91:661–666. 2001.
- Brown, S.J., R.B. Child, S.H. Day, and A.E. Donnelly. Exercise-induced skeletal muscle damage and adaptation following repeated bouts of eccentric muscle contractions. *J. Sports Sci.* 15:215–222. 1997.
- CHILD, R.B., J.M. SAXTON, AND A.E. DONNELLY. Comparison of eccentric knee extensor muscle actions at two muscle lengths on indices of damage and angle-specific force production in humans. J. Sports Sci. 16:301–308, 1998.
- CLARKSON, P.M., K. NOSAKA, AND B. BRAUN. Muscle function after exercise-induced muscle damage and rapid adaptation. Med. Sci. Sports Exerc. 24:512–520. 1992.

- 7. Clarkson, P.M., and I. Tremblay. Exercise-induced muscle damage, repair, and adaptations in humans. *J. Appl. Physiol.* 65:1–6. 1988.
- 8. Connolly, D.A.J., S.P. Sayers, and M.P. McHugh. Treatment and prevention of delayed onset muscle soreness. *J. Strength Cond. Res.* 17:197–208. 2003.
- DOLEZAL, B.A., J.A. POTTEIGER, D.J. JACOBSEN, AND S.H. BENEDICT. Muscle damage and resting metabolic rate after acute resistance exercise with an eccentric overload. *Med. Sci. Sports Exerc.* 32:1202–1207. 2000.
- GOLDEN, C.L., AND G.A. DUDLEY. Strength after bouts of eccentric or concentric actions. *Med. Sci. Sports Exerc.* 24:926– 933. 1992.
- HIGBIE, E.J., K.J. CURETON, G.L. WARREN III, AND B.M. PRIOR. Effects of concentric and eccentric training on muscle strength, cross-sectional area, and neural activation. J. Appl. Physiol. 81: 2173–2185. 1996.
- HORTOBAGYI, T., J. BARRIER, D. BEARD, J. BRASPENNINCX, P. KOENS, P. DEVITA, L. DEMPSEY, AND J. LAMBERT. Greater initial adaptations to submaximal muscle lengthening than maximal shortening. J. Appl. Physiol. 81:1677–1682. 1996.
- HORTOBAGYI, T., J. HOUMARD, D. FRASER, R. DUDEK, J. LAM-BERT, AND J. TRACY. Normal forces and myofibrillar disruption after repeated eccentric exercise. J. Appl. Physiol. 84:492–498. 1998
- 14. Jones, P.R., and J. Pearson. Anthropometric determination of leg fat and muscle plus bone volumes in young male and female adults. *J. Physiol. (Lond.)* 204:63P–66P. 1969.
- KANNUS, P., L. COOK, AND D. ALOSA. Absolute and relative endurance parameters in isokinetic tests of muscular endurance. J. Sports Rehabil. 1:2–12. 1992.
- Katz, B. The relation between force and speed in muscular contraction. J. Physiol. (Lond.) 96:45-64. 1939.
- LIEBER, R.L., AND J. FRIDEN. Selective damage of fast glycolytic muscle fibers with eccentric contraction of the rabbit tibialis anterior. Acta Physiol. Scand. 133:587–588. 1988.
- LIEBER, R.L., AND J. FRIDEN. Muscle damage is not a function of muscle force but active strain. J. Appl. Physiol. 74:520–526. 1993.
- LIEBER, R.L., T.M. WOODBURN, AND J. FRIDEN. Muscle damage induced by eccentric contractions of 25% strain. J. Appl. Physiol. 70:2498–2507. 1991.
- LYNCH, G.S., AND J.A. FAULKNER. Contraction-induced injury to single muscle fibers: Velocity of stretch does not influence the force deficit. Am. J. Physiol. 275:C1548-C1554. 1998.
- LYNN, R., AND D.L. MORGAN. Decline running produces more sarcomeres in rat vastus intermedius muscle fibers than does incline running. J. Appl. Physiol. 77:1439–1444. 1994.
- MACPHERSON, P.C.D., R.G. DENNIS, AND J.A. FAULKNER. Sarcomere dynamics and contraction-induced injury to maximally activated single muscle fibres from soleus muscles of rats. *J. Physiol.* 500:523–533. 1997.
- McCully, K.K., and J.A. Faulkner. Injury to skeletal muscle fibers of mice following lengthening contractions. *J. Appl. Physiol.* 59:119–126. 1985.
- McHugh, M.P. Recent advances in the understanding of the repeated bout effect: The protective effect against muscle damage from a single bout eccentric exercise. Scand. J. Med. Sci. Sports 13:88–97. 2003.
- McHugh, M.P., D.A.J. Connolly, R.G. Eston, E.J. Gartman, AND G.W. Gleim. Electromyographic analysis of repeated bouts of eccentric exercise. *J. Sports Sci.* 19:169–170. 2001.
- McHugh, M.P., and D.T. Tetro. Changes in the relationship between joint angle and torque production associated with the repeated bout effect. J. Sports Sci. 21:927–932. 2003.
- MORGAN, D.L. New insights into the behavior of muscle during active lengthening. *Biophys. J.* 57:209–221. 1990.
- MORGAN, D.L., D.R. CLAFLIN, AND F.J. JULIAN. The effects of repeated active stretches on tension generation and myoplasmic calcium in frog single muscle fibres. J. Physiol. (Lond.) 497: 665–674. 1996.

- NEWHAM, D.J., D.A. JONES, AND P.M. CLARKSON. Repeated high-force eccentric exercise: Effects on muscle pain and damage. J. Appl. Physiol. 63:1381–1386. 1987.
- Newham, D.J., D.A. Jones, G. Ghosh, and P. Aurora. Muscle fatigue and pain after eccentric contractions at long and short length. Clin. Sci. 74:553-557. 1988.
- 31. Newham, D.J., K.R. Mills, B.M. Quigley, and R.H.T. Edwards. Pain and fatigue after concentric and eccentric muscle contractions. *Clin. Sci.* 64:55–62. 1983.
- NOSAKA, K., AND P.M. CLARKSON. Muscle damage following repeated bouts of high force eccentric exercise. Med. Sci. Sports Exerc. 27:1263–1269. 1995.
- 33. Nosaka, K., and K. Sakamoto. Effect of elbow joint angle on the magnitude of muscle damage to the elbow flexors. *Med. Sci. Sports Exerc.* 33:22–29. 2001.
- Nosaka, K., K. Sakamoto, M. Newton, and P. Sacco. How long does the protective effect on eccentric exercise-induced muscle damage last? *Med. Sci. Sport Exerc.* 33:1490–1495. 2001.
- SAXTON, J.M., AND A.E. DONNELLY. Length-specific impairment of skeletal muscle contractile function after eccentric muscle actions in man. Clin. Sci. 90:119–125. 1996.
- SMITH, L.L. Acute inflammation: The underlying mechanism in delayed onset muscle soreness? *Med. Sci. Sports Exerc.* 23: 542–551. 1991.

- Talbot, J.A., and D.L. Morgan. Quantitative analysis of sarcomere non-uniformities in active muscle following a stretch. J. Mus. Res. Cell Motil. 17:261–268. 1996.
- THORSTENSSON, A., AND J. KARLSSON. Fatiguability and fibre composition of human skeletal muscle. Acta Physiol. Scand. 98: 318–322. 1976.
- WARREN, G.J., K.M. HERMANN, C.P. INGALLS, M.R. MASSELLI, AND R.B. ARMSTRONG. Decreased EMG median frequency during a second bout of eccentric contractions. *Med. Sci. Sports Exerc.* 32:820–829. 2000.
- WOOD, S.A., D.L. MORGAN, AND U. PROSKE. Effects of repeated eccentric contractions of structure and mechanical properties of toad sartorius muscle. Am. J. Physiol. 265:C792–C800. 1993.

Acknowledgments

We thank Tom Maddock for designing the mechanical transducer used for this study, and Kim Howard, John Poteet, and Michael Weldy for assisting with preliminary investigations. We also thank Dr. David L. Morgan for his review of this manuscript. Funding provided by the 2003 NSCA Graduate Student Research Award.

Address correspondence to Robert W. Pettitt, bpettitt@mesastate.edu.