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Changes in the relationship between joint angle and torque production associated with the repeated bout effect

MALACHY P. McHUGH* and DANIELLE T. TETRO

Nicholas Institute of Sports Medicine and Athletic Trauma (NISMAT), Lenox Hill Hospital, 130 East 77th Street, New York, NY 10021, USA

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A single bout of eccentric exercise induces a protective adaptation against damage from a repeated bout. The aim of this study was to determine whether this repeated bout effect is due to a change in the length–tension relationship. Twelve individuals performed an initial bout of six sets of 10 eccentric quadriceps contractions and then performed a repeated bout 2 weeks later. Eccentric contractions were performed on an isokinetic dynamometer at 1.04 $rad \cdot s^{-1}$ with a target intensity of 90% of isometric strength at 70° of knee flexion. Isometric strength and pain were recorded before and after both eccentric bouts and on each of the next 3 days. Isometric strength was tested at 30°, 50°, 70°, 90° and 110° of knee flexion. On the days following the initial bout, there was a significant loss of isometric strength at all knee flexion angles except 110° (bout × angle: $P < 0.01$). On day 2, strength averaged 86% of baseline for 30–90° and 102% of baseline for 110°. Strength loss and pain after the initial bout was contrasted by minimal changes after the repeated bout (pain: $P < 0.001$; strength: $P < 0.01$). The repeated bout effect was associated with a rightward shift in the length–tension curve; before the repeated bout, isometric strength was 6.8% lower at 30° and 13.6% higher at 110° compared with values before the initial bout (bout × angle: $P < 0.05$). Assuming that torque production at 110° occurs on the descending limb of the length–tension curve, the increase in torque at 110° may be explained by a longitudinal addition of sarcomeres. The addition of sarcomeres would limit sarcomere strain for subsequent eccentric contractions and may explain the repeated bout effect observed here.

Keywords: eccentric exercise, length–tension relationship, muscle damage, quadriceps.

Introduction

The repeated bout effect refers to the protective effect provided by a single bout of eccentric exercise against muscle damage from a subsequent eccentric bout (McHugh *et al*., 1999). This protective effect of previous exercise was first indicated by Highman and Altland (1963) and specifically attributed to eccentric contractions in later work (Schwane and Armstrong, 1983). The repeated bout effect has subsequently been demonstrated in humans and in animal models, with various types of activities using different muscle groups (see McHugh *et al*., 1999, for a review). Many theories have been proposed to explain the repeated bout effect, but a specific mechanism has yet to be identified.

One theory to explain the repeated bout effect is the sarcomere strain theory of muscle damage proposed by Morgan (1990). According to this theory, muscle damage is the result of irreversible sarcomere strain during eccentric contractions. Evidence to support this theory was provided by Wood *et al*. (1993), who demonstrated that strength loss in the frog sartorius muscle immediately after a series of eccentric contractions was associated with a shift to the right in the length–tension relationship. These findings are consistent with the intact sarcomeres adopting a shorter length subsequent to strain of disrupted sarcomeres. Electron micrographs of damaged sarcomeres provided additional support. Saxton and Donnelly (1996) and Child *et al*. (1998) demonstrated greater strength loss at short muscle lengths in humans after bouts of eccentric exercise of the elbow flexors and knee extensors, respectively. The disproportionate strength loss at short muscle lengths was also attributed to intact sarcomeres

* Author to whom all correspondence should be addressed.
e-mail: mchugh@nismat.org

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adopting a shorter length subsequent to strain of disrupted sarcomeres.

Based on the theory that muscle damage is due to irreversible sarcomere strain, Morgan (1990) proposed that an increase in the number of sarcomeres connected in series would reduce sarcomere strain during a repeated bout and limit the subsequent damage. Data from animal studies have provided evidence of the addition of sarcomeres with eccentric exercise (Lynn and Morgan, 1994; Lynn *et al.*, 1998). Indirect evidence of the longitudinal addition of sarcomeres in humans was recently demonstrated after a damaging bout of eccentric hamstring contractions (Brockett *et al.*, 2001). A rightward shift in the length–tension relationship following recovery from the initial bout was attributed to the longitudinal addition of sarcomeres. To date this is the only study (Brockett *et al.*, 2001) to show a sustained shift in the length–tension relationship. It is not known if the rightward shift in the length–tension relationship is specific to the hamstring muscle group. Furthermore, the length–tension relationship has been shown to return to normal within 5 h in toad sartorius muscles (Wood *et al.*, 1993) and within 2 days in the human triceps surae muscles (Jones *et al.*, 1997; Whitehead *et al.*, 2001). The aim of this study was to compare changes in the length–tension relationship between repeated bouts of eccentric quadriceps exercise of sufficient intensity to demonstrate a repeated bout effect. We hypothesized that the repeated bout effect would be associated with a rightward shift in the length–tension relationship.

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Methods

Experimental procedures

Twelve individuals (7 males, 5 females; age 28 ± 6 years, height 1.72 ± 0.09 m, mass 76.6 ± 15.3 kg: mean $\pm s$) volunteered to participate in the study. All participants provided written informed consent and the protocol was approved by the institutional review board. None of the participants had an orthopaedic injury and none had been involved in any weight training in the preceding months. All participants were asked to refrain from other exercise and not to take any pain medication during the course of the study. The participants performed an initial bout of six sets of 10 eccentric quadriceps contractions at 90% isometric maximal voluntary contraction (MVC) and then performed a repeated bout 2 weeks later. Isometric strength and pain were recorded before and immediately after both eccentric bouts and on each of the next 3 days. Isometric MVCs were performed at 30°, 50°, 70°, 90° and 110° of knee flexion.

Eccentric contractions were performed on an isokinetic dynamometer (Biodex System 2, Shirley, NY) from full extension to 115° of knee flexion. The participants were seated in an upright position with the trunk at approximately 90° of flexion. The knee joint was aligned with the axis of rotation of the dynamometer and the leg was secured to the dynamometer arm at the ankle. The dynamometer arm was set to move through the selected range of motion at 1.04 $rad \cdot s^{-1}$; the participants resisted with sufficient intensity to reach a visually displayed target equal to 90% of isometric MVC at the optimal angle. This target torque was the same for the initial and repeated bouts. On each occasion, six sets of 10 contractions were performed with 1 min rest between sets.

Isometric strength testing was performed on the same dynamometer as eccentric testing, in the same seated position. At each of the test angles, the participants were asked to perform a maximal contraction for 3 s. Three contractions were performed at each angle with 5 s between contractions and 2 min between tests at the different angles. Peak torque was identified for each contraction and the average of the three peak torques was recorded for each test angle.

Before eccentric exercise and on each of the subsequent 3 days, the participants were asked to report their perception of pain. They were asked specifically to report a single score for quadriceps pain elicited with activities of daily living such as walking, stepping and squatting. Pain ratings were recorded on a scale of 0 = 'no discomfort' to 10 = 'walking with a limp' (it was assumed that if the pain was sufficient to cause a limp, the participants would also have pain with stepping or squatting).

Sample size estimate

The sample size for this study was based on the ability to detect a change in isometric strength at the different angles between bouts of eccentric exercise (i.e. a shift in the length–tension relationship). An error estimate of 10% for normal within-individual variability in repeated isometric strength tests was used – that is, the standard deviation of the between-test differences would equal 10% of the mean strength. This estimate for within-individual variability was based on values reported for repeated isometric strength tests of the hamstrings (McHugh *et al.*, 2001) and elbow flexors (Komi and Buskirk, 1978). With 12 participants, an alpha of 0.05 and a beta of 0.2 (80% power), a minimum effect size of 8% was estimated (Kirkwood, 1988). Given the hypothesis that torque would be decreased at short muscle lengths and increased at long muscle lengths (rightward shift), the estimated minimum effect size represents a net difference of at least 8% (e.g. 4%

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decrease *vs* a 4% increase) between effects at short and long muscle lengths.

Statistical analysis

Strength after the initial bout of exercise was expressed as a percentage of strength before the eccentric bout (baseline). Strength loss was assessed using a time (pre, post, day 1, 2, 3) × angle (30°, 50°, 70°, 90°, 110°) repeated-measures analysis of variance (ANOVA). Evidence of a repeated bout effect was tested with a bout (initial *vs* repeated) × time (post, day 1, 2, 3) repeated-measures ANOVA for isometric strength and pain. Evidence of a shift in the length–tension curve was assessed with a bout × angle repeated-measures ANOVA for isometric strength before the initial and repeated bouts. Greenhouse-Geisser corrections were applied to significant analyses of variance that did not meet Mauchly's sphericity assumption. The Greenhouse-Geisser correction reduces the likelihood of a type I error. Probability values that have been corrected are denoted by the subscript $_{GG}$.

Results

Repeated bout effect

There was significant loss of strength ($P < 0.05$) and pain ($P < 0.001$) after the initial bout. Strength loss was significantly affected by test angle ($P < 0.01$), with less strength loss at 110° than at the other angles (Fig. 1). Strength (averaged across all angles) had returned to baseline before the repeated bout (159 ± 40.2 *vs* 157 ± 45.4 N · m; $P = 0.71$). The participants also reported resolution of all pain before the repeated bout. After the repeated bout, there was minimal strength loss (Fig. 2) and pain (Fig. 3), providing clear evidence of a repeated bout effect (bout effect: strength loss, $P < 0.01$; pain, $P < 0.001$).

Length–tension relationship

Comparison of the angle–torque curves before the initial and repeated bouts of eccentric exercise provided an indication of whether the repeated bout affect was associated with a change in the length–tension relationship. This bout × angle interaction ($P = 0.022_{GG}$) demonstrated a decrease in torque at knee flexion angles below the optimal angle and an increase in torque above the optimal angle (Fig. 4). Specifically, torque was 6.8% lower at 30°, 7.4% lower at 50° and 3.5% lower at 70° before the repeated bout, compared with values before the initial bout. By contrast, torque was 13.6% higher at 110° before the repeated bout.

Discussion

In this study, there was clear evidence of a repeated bout effect, with strength loss and pain after the

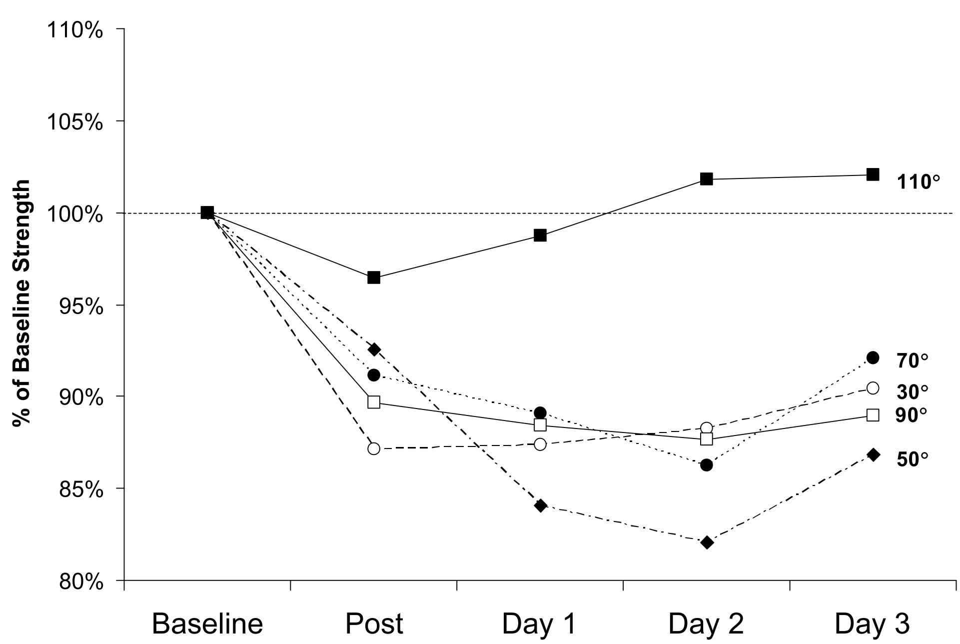

Fig. 1. Isometric strength loss after the initial bout of eccentric exercise. Strength values are percent of isometric strength immediately before the eccentric bout (baseline strength). Strength loss (main effect: $P < 0.05$) was significantly affected by test angle (time × angle: $P < 0.01$).

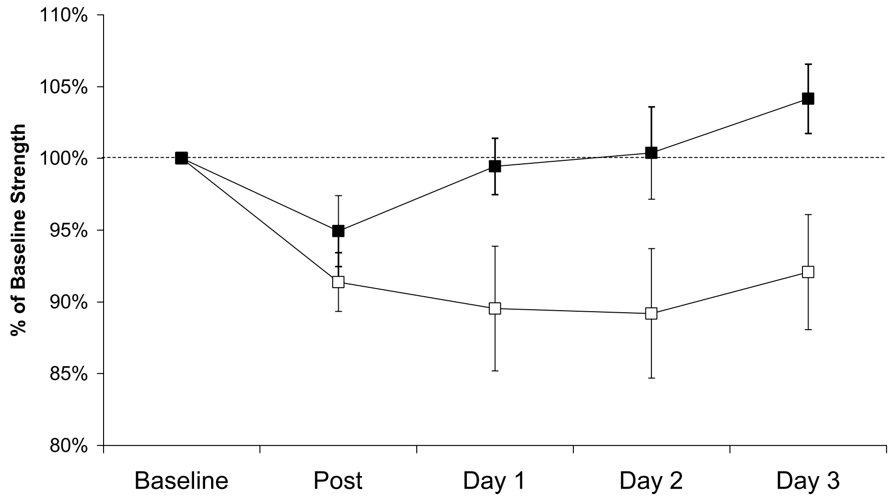

Fig. 2. Isometric strength loss (averaged across all five test angles) after the initial (□) and repeated (■) eccentric bouts. Strength loss was significantly greater after the initial than after the repeated bout (bout × time: $P < 0.01$).

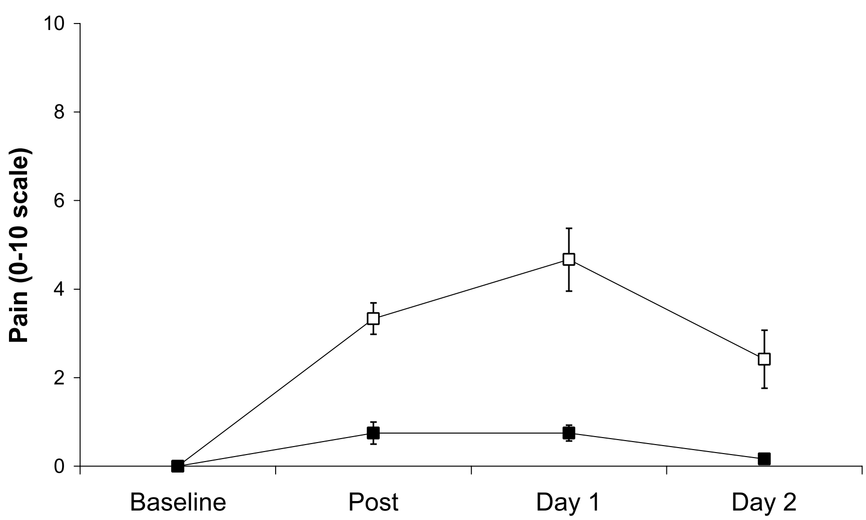

Fig. 3. Subjective reports of pain on a 0–10 scale (0 = no discomfort, 10 = walking with a limp) after the initial (□) and repeated (■) eccentric bouts. Pain was significantly higher after the initial than after the repeated bout (bout × time: $P < 0.001$).

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initial bout contrasting with no strength loss or pain after the repeated bout. The main findings were that strength loss after the initial bout was less apparent at the longest muscle length tested and that the repeated bout effect was associated with a rightward shift in the length–tension curve. These results are consistent with the sarcomere strain theory of muscle damage and the longitudinal addition of sarcomeres as the adaptation explaining the repeated bout effect.

Greater strength loss on the ascending limb (30°, 50°, 70°) than on the descending limb (110°) of the length–tension curve can be explained by excessive strain in disrupted sarcomeres, such that at any given muscle length the intact force-producing sarcomeres are at a shorter length. This effectively shifts the length–tension curve to the right and is consistent with previous studies (Wood *et al.*, 1993; Jones *et al.*, 1997; Whitehead *et al.*, 2001) showing a rightward shift in the length–tension curve following the induction of muscle damage. Furthermore, knee extension strength loss after 75 maximal eccentric contractions was shown to be greater at 20° (short length) than at 100° (Child *et al.*, 1998) of knee flexion. This effect was most apparent immediately after exercise. A similar effect was evident in the present study; however, it was more apparent on the days following the eccentric exercise (Fig. 1).

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A rightward shift in the length–tension curve is in line with the findings of Brockett *et al.* (2001), who demonstrated a similar effect in the hamstring muscle group. Peak isokinetic knee flexion torque occurred at approximately 6° less knee flexion (greater muscle length) after recovery from an initial eccentric bout. Torque production at shorter muscle lengths was less than values before the initial bout and torque production at longer muscle lengths was greater than values before the initial bout (Brockett *et al.*, 2001). In the present study, there was no obvious change in the optimal angle for peak torque (Fig. 4), while force was decreased at short muscle length ($<70°$) and increased at 110°. These changes demonstrate a rightward shift in the length–tension curve with no change in maximal torque production. Since loss of force production on the descending limb of the length–tension curve is a function of myofilament overlap, an increase in torque production at 110° can be interpreted as an increase in myofilament overlap. Such an effect would occur with a longitudinal addition of sarcomeres as proposed by Morgan (1990).

An alternative explanation for increased torque production at 110° would be a decrease in tendon–aponeurosis stiffness, thereby allowing greater muscle fibre shortening during eccentric contractions. The ability of the tendon–aponeurosis complex to absorb muscle–tendon unit lengthening during eccentric contractions has been demonstrated in cats (Griffiths, 1991). Decreased tendon–aponeurosis stiffness would decrease the series elastic stiffness of the contracted muscle–tendon unit. However, eccentric training is associated with an increase in series elastic stiffness (Pousson *et al.*, 1990; Reich *et al.*, 2000).

In the present study, angle–torque relationships were taken to represent the length–tension relationship. In the quadriceps muscle group, the patellar tendon moment arm changes with knee flexion angle and the true length–tension curve is shaped differently from the torque–angle curve. The patellar tendon moment arm is maximal at around 30–60° of knee flexion and is reduced at 90° and 120° (Nisell, 1985). The optimal knee flexion angle for peak torque production before the initial bout was 50° in one participant, 70° in seven participants and 90° in four participants. Therefore, it is likely that peak muscle force occurred at 70° or 90° in all participants. Since there is minimal difference in the patellar tendon moment arm between 90° and 120° (Nisell, 1985), it can be concluded that torque production at 110° occurred on the descending limb of the length–tension curve.

If a rightward shift in the length–tension curve serves a protective mechanism, it follows that the shape of the length–tension curve may affect an individual's susceptibility to damage. To examine this possibility in the present study, the participants were ranked according to the severity of their symptoms (pain and strength loss) after the initial bout. The participants were then ranked according to the decline in torque from 70° to 110° as an indication of the decline in torque on the descending limb of the length–tension curve. There was a positive correlation (Spearman rho) between these rankings ($r = 0.59$, $P < 0.05$), indicating that participants with a greater decline in force on the descending limb of the length–tension curve experienced more symptoms of damage. In a related study, Marginson and Eston (2001) recently demonstrated that the length–tension curve is shifted to the right in children compared with

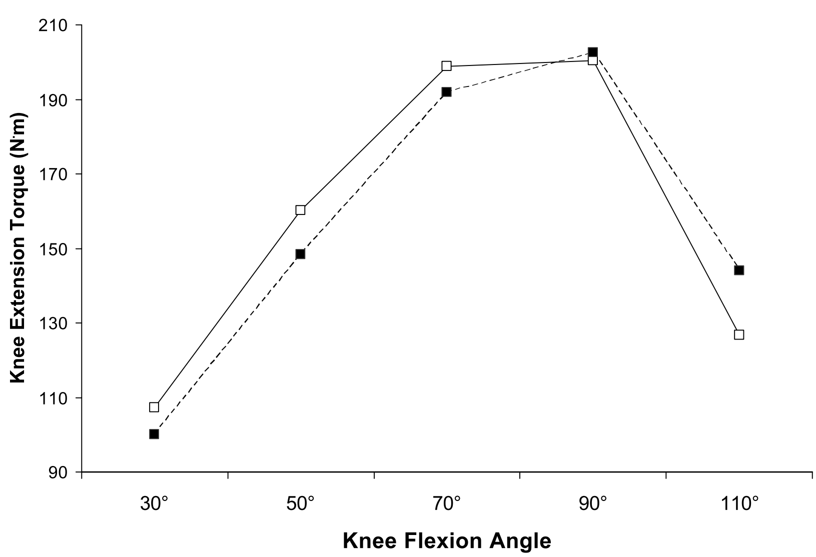

Fig. 4. Isometric torque at 30°, 50°, 70°, 90° and 110° for contractions performed before the initial (□) and repeated (■) bouts (bout × angle: $P < 0.05_{GG}$).

adults and concluded that this may explain the apparent decreased susceptibility of children to muscle damage (Duarte *et al.*, 1999). In another study (Gleeson *et al.*, 2003), concentric strength training was shown to increase the susceptibility to muscle damage and this effect was thought to reflect a leftward shift in the length–tension curve. Together these findings point to the need for further examination of the relationship of the shape of the length–tension curve to the susceptibility to damage from eccentric exercise.

In conclusion, the protective adaptation to a single bout of eccentric exercise (repeated bout effect) was associated with a rightward shift in the length–tension relationship. This effect is consistent with the theory that the repeated bout effect is due to a longitudinal addition of sarcomeres, thereby limiting sarcomere strain during the subsequent eccentric exercise. However, it is unlikely that longitudinal addition of sarcomeres is the exclusive mechanism for the repeated bout effect. Other inflammatory (Pizza *et al.*, 2002) and neural (Warren *et al.*, 2000) adaptations may be occurring concurrently and the repeated bout effect may be due to the interaction of various protective adaptations dependent on the particulars of the initial exercise bout and the muscle groups involved (McHugh *et al.*, 1999).

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