Human hamstring muscles adapt to eccentric exercise by changing optimum length

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ABSTRACT

BROCKETT, C. L., D. L. MORGAN, and U. PROSKE. Human hamstring muscles adapt to eccentric exercise by changing optimum length. *Med. Sci. Sports Exerc.*, Vol. 33, No. 5, 2001, pp. 783–790. **Purpose:** It is now established that unaccustomed eccentric exercise leads to muscle fiber damage and to delayed-onset muscle soreness (DOMS) in the days after exercise. However, a second bout of eccentric exercise, a week after the first, produces much less damage and soreness. The purpose of this study was to provide evidence from muscle mechanical properties of a proposed mechanism for this training effect in human hamstring muscles. **Methods:** The eccentric exercise involved 12 sets of 6 repetition "hamstring lowers," performed on specially designed equipment. Hamstring angle-torque curves were constructed for each of 10 subjects (8 male and 2 female) while they performed maximum voluntary knee extension and flexion movements on an isokinetic dynamometer. Testing sessions were performed over the week before eccentric exercise, immediately post exercise, and daily, up to 8 d post exercise. Subject soreness ratings and leg girth measurements were also made post exercise. Six subjects performed a second bout of eccentric exercise, 8 d after the first, and measurements were continued up to 10 d beyond that. **Results:** There was a significant shift in the optimum angle for torque generation (L_o), to longer muscle lengths immediately post exercise (7.7° $\pm$ 2.1°, $P < 0.01$), indicating an increase in series compliance within some muscle fibers. Subsequent measurements showed increases in leg girth and some muscle soreness, suggesting muscle damage. The shift in L_o persisted, even after other injury parameters had returned to normal, consistent with a training effect. Subjects also showed fewer signs of muscle damage after the second exercise bout. **Conclusion:** This is the first study to show a sustained shift in optimum angle of human muscle as a protective strategy against injury from eccentric exercise. Implications of this work for athletes, particularly those prone to hamstring strains are discussed. **Key Words:** LENGTHENING CONTRACTIONS, ISOKINETIC, MUSCLE SORENESS, MUSCLE DAMAGE, ADAPTATION

Hamstring muscle strains have been one of the most frequent sporting injuries over the last 8–10 yr, particularly in sports such as football and athletics (20,23,24). In addition, the fact that hamstring strains have one of the largest recurrence rates suggests that current protective training programs and rehabilitation strategies are not very effective.

One factor that makes hamstring muscle so susceptible to injury is their anatomical arrangement (12). Being a biarticular muscle group means that they may be subjected to large length changes. During everyday movements, such as walking, squatting, and sitting, flexion of the hip and knee occur together, with opposing effects on hamstring length. However, in running and kicking, in particular, the knee is extended and the hip flexed, bringing hamstrings to long lengths where risk of muscle tears become significant (9,14).

Antagonists to prime movers, muscles that are used to control or resist motion, are also at a greater risk of injury than the prime movers themselves. While decelerating the body, these muscles will contract while being rapidly lengthened. Therefore, they are performing "eccentric contractions" (9,24). It is well established that repeated eccentric contractions have the potential to damage muscle fibers (2,8,15,29). In the days after sports such as skiing, horse riding, or bushwalking, for example, we often have sore and tender muscles. This delayed onset muscle soreness (DOMS) is one of the indicators of fiber damage induced by eccentric exercise (5–7). The damage process involves an initial mechanical event, leading to microscopic disruptions within fibers, which are thought to lead to cell membrane damage and then the loss of intracellular calcium homeostasis (1). That, in turn, leads to fiber damage and death. The

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breakdown products of the damaged tissue sensitize nociceptors to produce DOMS.

Work in this laboratory, over the last 10 years, has investigated the mechanical changes that take place after eccentric exercise (13,17,19,29). The experiments are based on a hypothesis that attributes to a mechanical event the initial step in the process leading to muscle fiber damage (18). Briefly, during the eccentric contraction, some sarcomeres are stretched beyond myofilament overlap to become disrupted when the muscle relaxes. With repeated contractions, areas of disruption grow, until a point is reached where there is membrane damage ("micro-tears") and a loss of calcium homeostasis (1,2). That may, in due course, lead some muscle fibers to die. The intermediate stage of nonfunctioning sarcomeres in series with sarcomeres generating active force means that the effective series compliance of the fiber increases, leading to a shift of the whole muscle's length-tension relation in the direction of longer muscle lengths.

A measure commonly used to quantify the damage from eccentric exercise is the drop in force (for review, see 1). There are a number of reasons why a shift in length-tension relation is preferable as a measure of muscle damage. It is not confounded by fatigue effects, avoids the problem of uncertainty over the optimum length for a contraction, and, in our experience, is more reliable (25). Similar shifts in optimum length have been recorded from whole toad muscle (29), single frog fibers (19), rat vastus intermedius muscles (17), and in human triceps surae muscles (13).

Hamstring strains are one of the commonest injuries encountered by the sports physician. We hypothesize that the "micro-tears" (8,29) associated with fiber damage from eccentric exercise may be the starting point for more major tears. These micro-tears can be reduced by a program of training biased toward eccentric exercise (28). The aim of the experiments reported here was to provide, for hamstring muscles, a measure of a training effect after an acute bout of eccentric exercise. If our hypothesis is correct, such a measure would also be an indicator of the muscle's susceptibility to more major tears and would therefore be a useful guide for the design of training programs.

MATERIALS AND METHODS

Healthy human subjects gave their written informed consent for these experiments, which had been approved by the Monash University Committee for Ethics in Human experimentation. A total of 10 subjects (8 male and 2 female) aged (18–29 yr) took part in this study. None of the subjects were involved in regular weight training for their leg muscles.

Isokinetic Dynamometry

The same experiments were performed on two dynamometry units. First, a Cybex® 2000 Extremity System (Ronkonkoma, NY) was used to test the angle-torque relationship of the knee flexors for four subjects. A Biodex® System 3 Quick Set (Shirley, NY) then became available, and the last six subjects were tested on this equipment. For the purposes of this study, an angle-torque curve is defined by the torque, as a function of joint angle, produced when the muscle is maximally activated during isovelocity shortening. The optimum angle is the joint angle that maximizes muscle torque. Zero angle, where the lower leg was in the vertical position, was checked each day with a spirit level.

Based on a preliminary study (3), it was decided that angle-torque curves for the hamstrings could be reliably generated when performed at a velocity of $60°\cdot s^{-1}$; hence, the testing protocol used an average of seven isokinetic concentric contractions at $60°\cdot s^{-1}$. During the test, subjects were seated with their hips at approximately 90° flexion and their upper bodies secured with dual crossover straps. Each contraction was carried out over approximately a 110° knee angle range. Only the right leg was tested; the left was stabilized with the knee braced at 90° to minimize other body movements, particularly movement at the hip. Subjects also gripped handles to assist in maintaining stable body posture. Direct access was arranged for analog torque, angle, and direction signals from the Cybex. The data were then digitized using an A-D converting card (National Instruments, DAQ Card^{TM}-1200) in a Macintosh computer. For the Biodex®, digital signals were directly available through the systems software. All digital data was stored and analyzed using the program Igor Pro® (Wavemetrics, Lake Oswego, OR).

Eccentric Exercise

A custom-made piece of equipment was used to enable human subjects to perform eccentric exercises with their hamstring muscles. The equipment consisted of a 2-m long wooden board with upholstered areas for the knees and chest (Fig. 1). The subjects kneeled on the padded board and had their lower legs stabilized with Velcro® ankle straps. Subjects were asked to slowly lower their body against the force of gravity toward the prone position, while maintaining an open and constant hip angle. It was important that as the body was lowered, the hamstring muscles bore the weight of the upper body for as long as possible to ensure that they contracted eccentrically at as long a length as possible. Most subjects were unable to control body motion much beyond 30° from the vertical, in the process carrying out hamstring contractions of near-maximal strength.

An exercise bout typically consisted of 12 sets of six repetitions. Generally subjects had about 10-s rest between repetitions and 2- to 3-min rest periods between sets. Subjects were encouraged to complete all repetitions; however, some subjects were unable to do so. All subjects completed a minimum of 66 repetitions.

Experimental Measures

Optimum angle. A continuous recording was made over a period of about 23-s during flexion and extension movements about the knee (Fig. 2). Torque values during flexion were then extracted and ordered according to knee

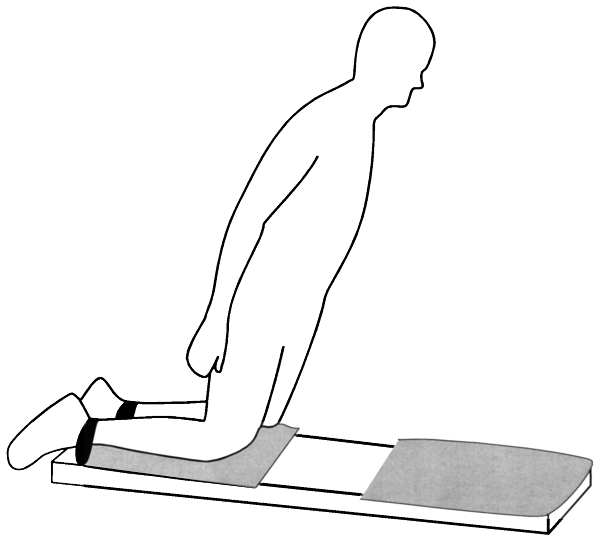

FIGURE 1—Eccentric exercise equipment. The subject kneeled on a padded board and with their ankles restrained by straps slowly lowered their body to the prone position while maintaining a rigid body posture to restrict the exercise to the hamstring muscles.

angle, and the data were compressed using a decimation function which averaged every 20 successive data points. The resulting plot of torque against angle allowed determination of optimum angle (Fig. 3).

The knee angle for which the average torque in hamstring muscles reached its peak was calculated by fitting a Gaussian curve to the decimated data points that were above 90% of the maximum torque (Fig. 3). This curve fit was chosen because it gave an appropriate, smooth fit to the data, and provided a convenient means of locating the optimum angle. Shifts in the optimum angle for peak torque were obtained by subtracting the optimum angle before the exercise from that measured after the exercise.

Peak active torque. For each session, the maximum torque produced (N-m) was determined as the peak of the fitted curve. During the control measurements, subjects were required to produce maximum contractions with $<$10% variability between peak torques from day to day. All subjects fulfilled this criterion.

Muscle soreness rating. Over the days after the eccentric exercise bout, subjects were required to rate the amount of soreness in their hamstrings in response to locally applied pressure and when standing up and walking. They were asked to give a numerical value out of 10, where "0" equated with "absolutely no soreness," and "10," "the most muscle soreness that they could possibly bear" (22). A rating of "5" meant that the hamstrings "were tender to touch," but subjects experienced no soreness during walking.

Muscle swelling. The exercise-induced muscle damage triggers an inflammatory response in the muscle which produces local swelling. In this study, muscle swelling was documented by taking girth measurements at three locations, on the upper, middle, and lower thigh. Changes in hamstrings volume were expected to show up as small changes in girth, keeping in mind that girth measurements included both quadriceps and hamstrings.

Experimental protocol. Control measurements were made on the dynamometer on three separate occasions during the week before the exercise, including two measurements of leg girth. The last control measurement was made just before the exercise. The period of exercise took typically about 40–45 min to complete. Immediately after the exercise, subjects were remeasured on the dynamometer, more girth measurements were made, and soreness ratings were recorded. Further testing sessions were then carried out on days 1–5, 7, 8, and 10. Not all subjects were available on each of these days. It meant that on day 5 measurements were obtained for only eight subjects; for day 8, seven subjects; and for day 10, four subjects. For the six subjects who were tested on the Biodex®, as well as making measurements immediately after the exercise, an additional "2 h post exercise" measurement was made. These subjects went on to perform a second set of exercises 8 d after the first. Once again, there was an immediately post exercise session, one at 2 h and further measurements on days 1–3, 5, and 10.

Statistical analysis. For each measured parameter, means and standard errors were calculated across subjects. Analysis of variance, Bonferroni *post hoc* tests, were performed on the data to test for significant shifts in optimum angle, changes in peak torque, soreness ratings, and muscle swelling by using the statistical program Data Desk (Data Description, Ithaca, NY).

RESULTS

Single Exercise Bout

Complete data sets were obtained from a total of 10 subjects. Examples of torque and angle signals from the dynamometer, recorded for one individual during a testing session are shown in Figure 2. This subject worked over a knee angle range of $-10°$ to 90°, where 0° represented the shin perpendicular to the thigh, that is, the lower leg hanging vertically. An increased angle represented an extended knee. Figure 2 shows the knee flexion torque during seven repetitions of knee extension and flexion. A positive torque represents hamstring contraction, a negative torque, quadriceps contraction. The sequence begins with a knee extension, producing a torque of about 150 N-m, presumably largely activity in quadriceps. This is followed by knee flexion with a peak torque of 100 N-m, due to contracting hamstrings. Average maximum hamstring torque is about half of that of quadriceps, which is what would be expected from an untrained individual.

Data such as that of Figure 2 was used to construct angle-torque curves (see Methods). A typical example is shown in Figure 3. Here each of the seven torque records was sorted according to angle (Fig. 3, upper panel) and averaged to calculate means and standard errors (Fig. 3, lower panel). To locate the angle for peak torque a Gaussian fit was applied to the top 10% of the decimated values

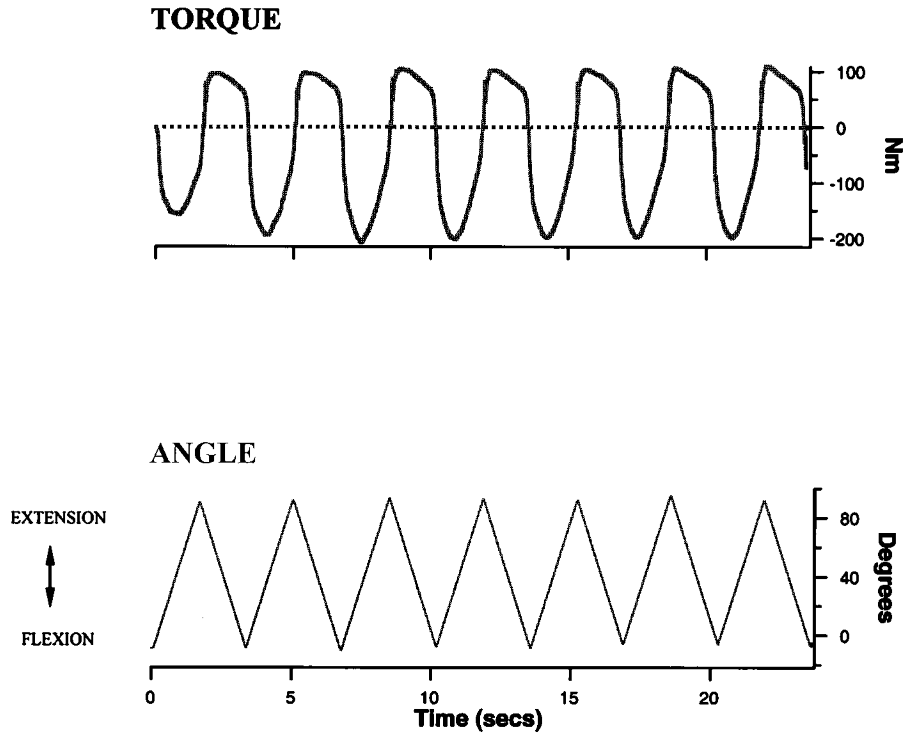

FIGURE 2—Torque (upper panel) and angle (lower panel) records from one subject. A series of seven successive maximal voluntary, isokinetic knee flexions and extensions were carried out at an angular velocity of 60°·s^{-1}. A positive torque indicates hamstrings contraction, a negative torque, quadriceps contraction. The movements began with a knee extension, from an initial angle of −10° to an angle of 90°. An angle of 0° represented the lower leg hanging vertically. A torque of 0 N-m (*dashed line*) represented the end of extension and beginning of flexion.

(continuous line in Fig. 3, lower panel). In this record, optimum angle was 54.2° and peak torque 161 N-m.

After the exercise, there was a change in the angle-torque relationship (Fig. 4, upper panel). Optimum angle for torque generation shifted in the direction of longer muscle lengths, that is, a greater knee angle (from 52.2° to 59.4° in this case). Values from each subject were collated and averaged. For the 10 subjects, immediately after the exercise there was an average shift of 7.7° ± 2.1° SEM (Fig. 5). There was a further small shift during the following days, reaching a mean peak on day 4 at 8.5° (±1.9° SEM). Using the parameters "day" and "subject," a two-way analysis of variance (ANOVA) showed that there were significant shifts in optimum angle over the whole postexercise period ($P < 0.05$). Bonferroni *post hoc* tests showed the mean shifts in optimum to longer muscle lengths that were recorded immediately post exercise, on days 1–4 and on day 7 post exercise, were all significantly different from the control values ($P < 0.01$). For the subject shown in Figure 4, peak torque fell from 140.4 to 127.8 N-m. The average torque for the 10 subjects, immediately postexercise was down to 80.4% ± 3.7% SEM of control values (Fig. 5). This was significant ($P < 0.5$, two-way ANOVA). However, unlike optimum angle, torque had recovered back to control values by day 3 postexercise. A Bonferroni *post hoc* test showed that there was no significant difference between preexercise torque and that over the period, day 3 to day 10 postexercise. The most important result of these experiments was that the shift in optimum angle persisted right out to day 10, by which time torque levels had long since returned to control values (Fig. 4, lower panel; Fig. 5).

Subjects did not report any muscle soreness immediately after the exercise; however, all subjects experienced delayed onset muscle soreness (DOMS) that commonly accompanies eccentric exercise. Soreness peaked by the first day postexercise (Fig. 5) with a mean rating of 5.55 (±0.77 SEM) indicating that, subjects' hamstring muscles were tender to touch and only mildly sore when they moved about. During the following day muscle soreness declined, and subjects reported no pain at all from day 4 onward (Fig. 5).

Increases in leg girth suggested that some small, but not significant, amount of swelling was present immediately postexercise and on day 1 and 2 postexercise (Fig. 5). On day 3, a significant increase in leg girth was recorded. This peaked on day 4. Over the following days, swelling gradually abated and leg dimensions were back close to normal by day 8 postexercise.

Two Bouts of Exercise

The six subjects performing a second bout of eccentric exercise 8 d after the first, showed, in response to the second exercise, very much smaller changes in all measured parameters, compared with the changes after the first exercise (Fig. 6). So, for these subjects, after the first exercise, mean optimum angle showed an immediate shift to longer muscle lengths (7.29° ± 3.59° SEM), peaking by day 3 (10.85° ± 2.23° SEM). This was largely maintained, dropping only to 6.47° (± 4.08° SEM) by day 8. Subjects then undertook their second exercise, and immediately afterward, the mean optimum angle shifted by a further 1.19°. This was followed at 2 h by a small return back toward control values but which reversed again by 24 h. Mean shift in optimum angle peaked on day 2. Here the shift (8.60° ± 3.94° SEM) was only 2.13° above the value immediately before the second bout. Values stayed at approximately this level throughout

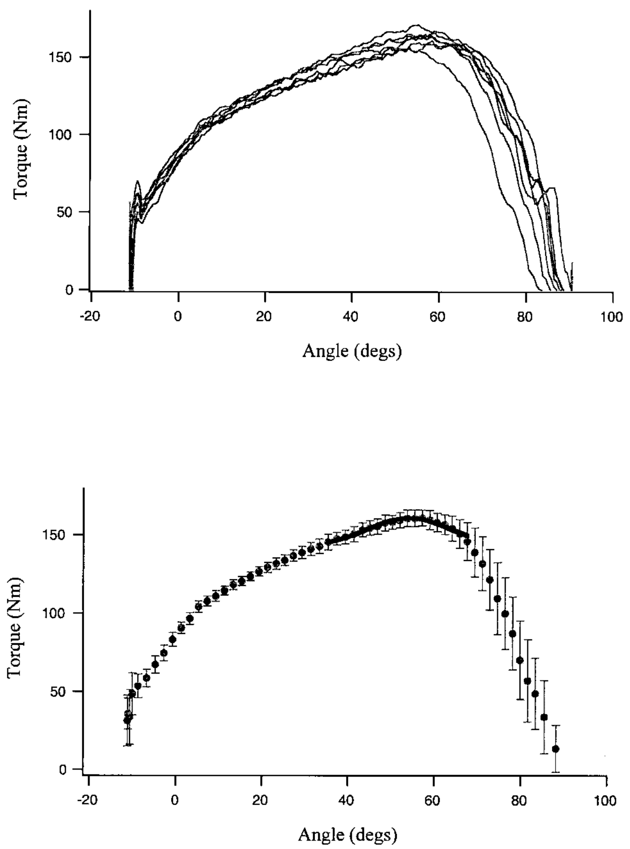

FIGURE 3—Upper panel: Superimposed torque records from seven knee flexions, plotted against knee angle. Lower panel: Data have been decimated (average of every 20 continuous points) to show typical values (means ± SEM) for hamstrings angle-torque relation for one subject. A Gaussian curve was fitted to the top 10% of the curve to determine the angle for peak torque.

the remaining period of testing, with a shift on day 10 of 6.53° (± 3.49° SEM). This was now 18 d after the first exercise.

A significant drop in mean force to 75.61% (± 4.18% SEM) of control values was recorded immediately after the first exercise, dropping a further 3.3% in the next 2 h, to 72.31% (± 10.61% SEM). By day 1, and continuing to day 8 postexercise, peak torque gradually returned to preexercise values (Fig. 6). Immediately after the second bout, torque dropped to 90.85% (± 9.2% SEM), which was a 15.17% drop from the value recorded just before the exercise (106.02% ± 6.02% SEM). This was considerably less than the 24.39% torque drop after the first exercise. Two hours after bout 2, torque had recovered to 99.52% ± 12.78 SEM and by 1 d postexercise had returned to preexercise levels. Peak torque then remained constant with no further significant changes between days. However, the average torque for these days was elevated above the original control values (112.28% ± 10.07% SEM), perhaps representing some mild strength gains by the muscles from the exercise (Fig. 6).

Soreness after the first exercise peaked on day 3 for these subjects, slightly later than for the whole group (Fig. 6). However, there was almost no soreness after the second bout of eccentric exercise 8 d later. Small, insignificant, increases in muscle swelling were observed after the second exercise (Fig. 6).

DISCUSSION

This is the first report of a long-lasting change in length-tension property of human limb muscle brought about by a period of eccentric exercise. The exercise produced some muscle fiber damage, as indicated by delayed onset muscle soreness, and this was accompanied by transient changes in the length-tension relation. A second period of exercise, 1 wk after the first, produced much less soreness and a smaller transient change. This is the well-known training effect, where the first exercise provides protection against further damage from subsequent exercise. This training effect was indicated by a long-lasting shift in the muscle's optimum length for a contraction.

In the response of muscle to eccentric exercise there are two shifts in length-tension relation. According to our hypothesis, the first is a direct result of disruption of sarcomeres in muscle fibers and therefore is present immediately after the exercise. Here, the disrupted sarcomeres, because

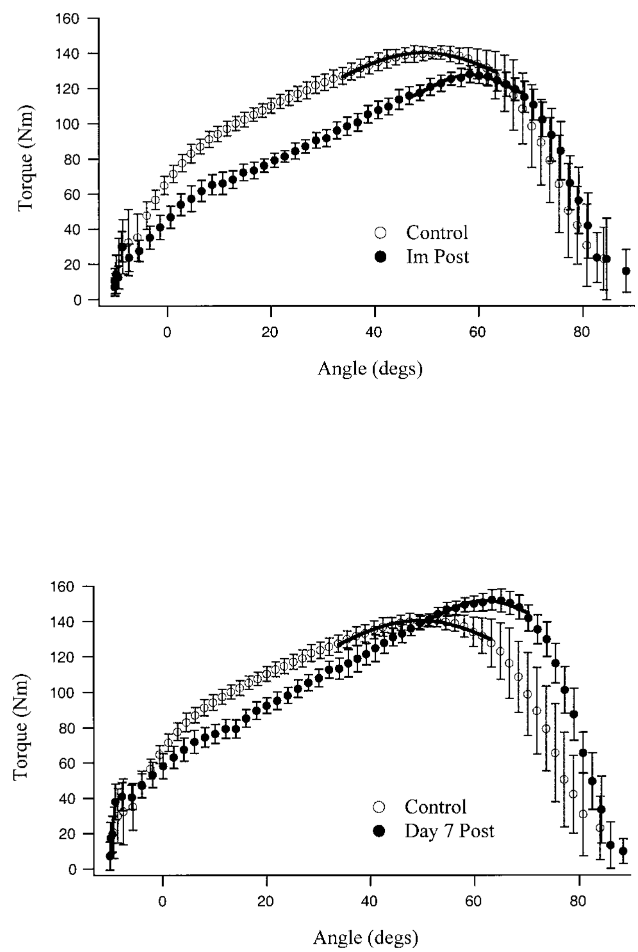

FIGURE 4—Upper panel: Hamstrings angle-torque curves from one subject before eccentric exercise (Control) and immediately post exercise (Im Post). Lower panel: Angle-torque curves from before, and 7 d post exercise (Day 7 Post). Data are means ± SEM. Gaussian curves have been fitted to the top 10% of each curve.

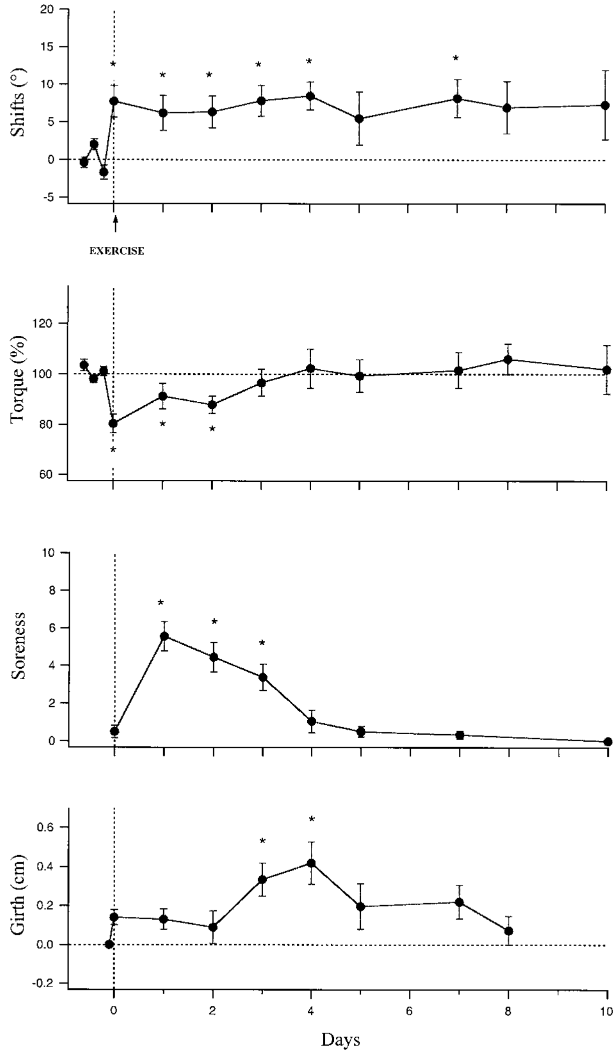

FIGURE 5—Shifts in optimum knee angle, changes in peak torque, muscle soreness and muscle swelling (girth) for 10 subjects after one eccentric exercise bout. Data are means ± SEM. * Significantly different to the average of preexercised values. *Vertical dashed line* indicates the day of the exercise, *horizontal dashed line*, the level of the average control value.

they lie in series with still-contracting parts of the fibers, increase the muscle's series compliance, leading to a shift of the length-tension relation in the direction of longer muscle lengths. Subsequently, some fibers die and therefore no longer contribute to the length-tension relation, whereas in others the regions of disruption are able to recover their normal arrangement. As a result, this shift reverses back toward control levels within 2 d of the exercise (13). The fact that the reversal is so rapid make unlikely explanations based on proprioceptive reflexes or changes in elastic filament properties. At the same time, there is development of a second, more sustained shift in length-tension relation, representing a training effect in the muscle. In this study the first shift was small (Fig. 6) or absent (Fig. 5), presumably because of the larger shift from the training effect.

Although these are the first observations of such a sustained shift for human muscle, the result was predicted by observations from animal studies (13,29). These support the view expressed by Morgan (18), that the training effect is the result of an increase in sarcomere number in muscle fibers. It was postulated that the addition of sarcomeres in series allows muscle fibers to operate at longer lengths while avoiding the descending limb of the length-tension curve, which is the region of instability for sarcomere length distributions. Evidence of the addition of sarcomeres after eccentric exercise has been reported for hind-limb muscle of rats by using laser light diffraction to measure sarcomere numbers (16). In a second study, it was shown that angle-torque curves became wider and the optimum length for contraction occurred at longer lengths, consistent with the presence of a greater number of sarcomeres in series (17). This meant that the muscle had increased its working range and less of the working range was likely to be on the descending limb of the length-tension curve.

Changes similar to those reported in animals have now been shown here in human hamstring muscles, the major

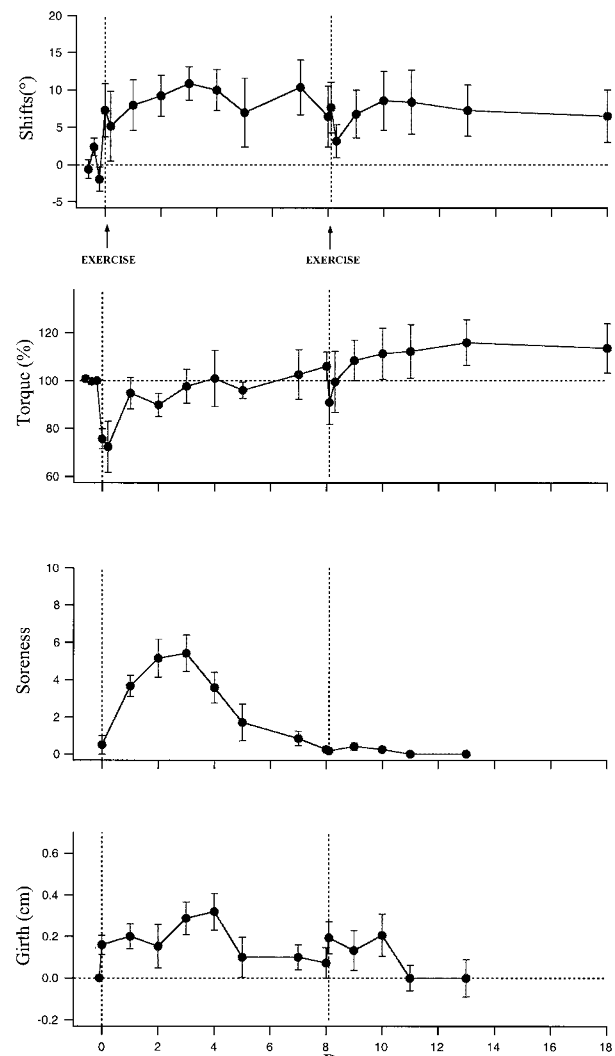

FIGURE 6—Shifts in optimum knee angle, changes in peak torque, muscle soreness, and swelling (girth) shown for six subjects after two eccentric exercise bouts, which were performed 8 d apart. Data are means ± SEM. *Vertical dashed lines* indicate times of occurrence of the two exercise bouts, *horizontal dashed lines,* control values.

result being the sustained shift in optimum length after a single bout of eccentric exercise. The shift to longer lengths was sustained over the full 10-d test period. This is in contrast to previous studies on human subjects by our group, where only a transient shift was seen. For triceps surae, after eccentric exercise, the shift in optimum length had reversed by 2 d post exercise (13). There are several possible explanations for this difference. Triceps surae generally performs more eccentric contractions during normal everyday movements than do the hamstring muscles. Whenever we step down a set of stairs, we land on our toes and so perform an eccentric contraction of ankle extensors until heel contact is made. It means that the "control" condition for triceps already incorporates a certain degree of adaptation to eccentric exercise. There do not appear to be many occasions in everyday life where we carry out regular eccentric contractions of hamstrings. Consequently, these muscles are more susceptible to injury from eccentric exercise and are therefore more likely to show a large training effect. Second, the exercise regimes to which the muscles were subjected were quite different for the two groups. For hamstrings, subjects lowered their upper bodies from a kneeling position, generating hamstring muscle torques at close to maximum levels. Triceps surae muscles were eccentrically exercised by walking subjects backwards down an inclined treadmill (for 2 h), where muscle torque would have been well below maximum. The results appear to reflect this point, the immediate post exercise shift in triceps optimum length was 3.9 $\pm$ (1.50)°, compared with the much bigger shift of 7.7 $\pm$ (2.1)° in hamstrings.

This may, however, not be the whole explanation. The gastrocnemii are biarticulate and carrying out the exercise with an open knee angle, as was done (13), is likely to have damaged them. Soleus, on the other hand, is monoarticulate and may therefore have been less damaged. Jones et al. (13) measured torque-angle curves with a flexed knee, where the gastrocnemii might be expected to be rather short. So the curve was likely to be dominated by tension in soleus, the least damaged of the three muscles. Consequently, any training effect that developed in the gastrocnemii, may have gone undetected.

If our hypothesis (18) is correct and protection against muscle damage and DOMS from eccentric exercise is achieved by the addition of sarcomeres to muscle fibers, the opposite might be expected from a reduction in sarcomere number. Here, there might be an increased susceptibility to damage. In support of this view, it has been found that rats trained on an inclined treadmill (concentric contractions) had fewer sarcomeres in series in their muscle fibers, compared with declined trained (eccentric contractions) and sedentary animals. The incline-trained rats showed more signs of muscle damage than the other two groups after a subsequent test series of eccentric contractions (16,17). Now it has been shown for human subjects that training biased toward concentric exercise led subjects to show more signs of muscle damage after an acute period of eccentric exercise compared with those who undertook training biased toward eccentric exercise before the test bout or whose muscles remained unexercised (28).

The obvious question that this work raises is whether protection against DOMS and its associated micro-tears also means that subjects will be protected against gross muscle tears, such as the common hamstring strain. The sequence of events that gives rise to a hamstring tear are not well defined. From clinical reports, the common conclusion is that hamstring injury most often occurs as a result of eccentric contractions (9,14,21,24). Magnetic resonance imaging shows damage and inflammation near the muscle-tendon junction (4,11). This has led to the proposal that the injury is the result of failure at the tendon junction, a view supported by findings from experiments in which passive or contracting muscles are stretched to long lengths (10,26,27). Our working hypothesis is that the initial microscopic damage grows and leads to a muscle tear. A tear originating in the belly of a highly pennate muscle is likely to spread to the aponeurosis and then follow the tendon. The high incidence of repeat-injury, we believe, is likely to be due to rehabilitation programs which are insufficiently biased toward eccentric exercise.

In summary, this research provides the first evidence in human subjects of a sustained shift in a muscle's torque-angle curve after a single bout of eccentric exercise. The shift indicated a training effect, providing the muscle with protection against further damage from eccentric exercise. If our hypothesis is correct, that DOMS and gross muscle tears have a common origin, the findings presented here point to a new training strategy for athletes who are at risk from muscle strains, particularly the common hamstring strain.

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