Greater initial adaptations to submaximal muscle lengthening than maximal shortening

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Hortobágyi, Tibor, Jason Barrier, David Beard, John Braspennincx, Peter Koens, Paul Devita, Line Dempsey, and Jean Lambert. Greater initial adaptations to submaximal muscle lengthening than maximal shortening. J. Appl. Physiol. 81(4): 1677–1682, 1996.—The purpose of this study was to compare the short-term strength and neural adaptations to eccentric and concentric training at equal force levels. Forty-two sedentary women (age = 21.5 yr) were ranked based on the initial quadriceps strength score, and trios of subjects were randomly assigned to either an eccentric (n = 14), a concentric (n = 14), or a nonexercising control group (n = 14). Training involved a total of 824 eccentric or concentric quadriceps actions at 1.05 rad·s⁻¹ administered in four sets of 6–10 repetitions, four times per week for 6 wk. Before and after training, all subjects were tested for unilateral maximal isometric and eccentric and concentric actions at 1.05 rad·s⁻¹ and for a 40-repetition eccentric and concentric fatigue series of the left and right quadriceps. Surface electromyographic activity of the vastus lateralis and medialis was monitored during testing. Concentric training increased eccentric (36%, P < 0.05), isometric (18%, P < 0.05), and eccentric strength (13%), and eccentric training increased eccentric (42%, P < 0.05), isometric (30%, P < 0.05), and concentric (13%) strength. Eccentric training improved eccentric and isometric strength more (P < 0.05) than did concentric training. The electromyographic adaptations were greater with eccentric training. Cross‐education was 6%, and neither training mode modified fatigability. The data suggest that training of the quadriceps muscle with submaximal eccentric actions brings about greater strength adaptations faster than does training with maximal‐level concentric actions in women. This greater adaptation is likely to be mediated by both mechanical and neural factors.

Exercise; muscle; electromyography; fatigue; cross-education

MUSCLE STRENGTH AND SIZE increase due to overload (1). To maximize the training effect and minimize the time involvement, researchers (5, 11, 13, 16, 18, 19) have become interested in taking advantage of the greater forces (17) associated with muscle lengthening. Yet the data remain equivocal. While several studies reported greater gains in muscle strength and size after eccentric (11, 18) compared with concentric training, other studies found similar changes (5, 16, 19) or actually greater changes with concentric training (23). One reason for the inconsistency in the findings could be that isometric contractions were used in some studies (6, 13, 23), whereas in other studies isokinetic actions were used (11, 19). Another and perhaps more important reason could be that the eccentric and concentric forces were not equated during the training programs. While the concentric portion of the movement used for training in these studies was maximal (16), the eccentric portion of movement was underloaded as low as ~50% of maximum (6). Thus one aim of the study was to train subjects at the same absolute force level by using either eccentric or concentric contractions. Because neural inhibition of force production in untrained individuals causes a greater deviation from the expected eccentric forces than from the expected concentric forces (14, 27), we hypothesized that a greater neuromuscular adaptation should occur after eccentric compared with concentric training, even if the force levels are equated during training.

Although adaptability of women to resistive exercise is similar to men’s (25), less attention has been devoted to the adaptations to exercise with muscle lengthening in women. Except for one study (19), the initial adaptive responses to exercise with muscle lengthening were studied in men. This is unfortunate, because some researchers suggested that perhaps women, compared with men, tend to plateau earlier in their responses to resistive exercise (9). Recent studies also suggest that, although the rapid initial gains in muscle strength are associated with neural adaptations (21), intramuscular changes also occur specifically in female muscles, perhaps as a precursor for hypertrophy (24). To be able to directly compare the outcome of the present study with the results of prior studies that used a 6- to 12-wk training period, we also adopted a 6-wk training period. Thus the second aim of the present study was to examine the initial adaptations to muscle lengthening and shortening in women.

Finally, prior studies have also paid little attention to the relationship between strength gains with these two contraction modes and fatigue and failed to use fatigue to evaluate the nature of neural adaptation to training. One suggestion was that fatigue is a stimulus for strength gains (20). Paradoxically, several researchers observed that very little fatigue occurs during repeated eccentric compared with concentric actions (8), yet several studies suggest that eccentric actions are crucial for strength gains and hypertrophy (6). Thus the third aim of the study was to examine the role of fatigue in eliciting strength gains with eccentric and concentric actions. The prediction was that fatigue does not need to occur to induce an increase in muscle strength. In total, the purpose of the study was to compare the short-term strength and fatigue adaptations to eccentric and concentric training of the quadriceps muscle at equal force levels in women.

METHODS

Subjects and design. Forty-two female volunteers were recruited from the University community. A subject was
included in the study if she had not participated in resistive or aerobic exercise training for at least 1 yr before the study and had no history of knee pathology or injury based on a physical therapy examination. A written informed consent, approved by the university’s Policy and Review Committee on Human Research, was obtained before testing.

The study was completed in 8 wk and included pre- (week 1) and posttraining testing (week 8) and training of the left quadriceps muscle four times per week for 6 wk (weeks 2-7). A 6-wk period was used to investigate the early phase of adaptations. Muscle strength, electromyogram (EMG), and a 40-repetition fatigue series were measured in both quadriceps in all subjects. Left and right quadriceps in each subject were tested 2–3 days apart, and the limb test order was counterbalanced across subjects.

During week 1, in two sessions separated by 2–3 days, subjects were familiarized with the dynamometer by performing two trials of 50, 75, and 90% of perceived maximal isometric and concentric and eccentric actions at each speed, separated by 1 min of rest. The testing followed this familiarization. After the pretraining testing, all subjects were ranked on the aggregate maximal isometric, concentric, and eccentric score. Of the first three subjects, at random, one subject was assigned to one exercise group; another subject to the other exercise group, and the third subject to the control group. This method was used to assign the remaining subjects to one of three groups, creating strength-matched subject trios in the three groups.

Subjects in the concentric training group (n = 14) exercised by using maximal effort concentric actions of the quadriceps muscle. Each subject in the eccentric group (n = 14) exercised the quadriceps muscle at the same force as did the subject pair in the concentric group. Practically, the eccentric subject pairs exercised after the concentric subject pairs finished their sessions. For the first training session, the eccentric group’s training intensity was determined based on the maximal concentric force produced by the concentric subject pair, measured during the pretraining test. During the subsequent training sessions, the average of all repetitions performed by the concentric trainee in one session was computed and used as a target force by the eccentric subject pair. For the subjects exercising in the eccentric group, two markers were set around the target force value creating a ±5% band on the dynamometer’s computer screen. The concentric subject pairs also had biofeedback: a marker appeared on the monitor at the maximal force recorded during the previous session. These subjects were encouraged to exceed the force level indicated by the marker.

Strength testing and EMG. Unilateral maximal voluntary isometric and isokinetic eccentric and concentric strength of the left and right knee extensors was measured on a dynamometer (Kin-Com, 500H, Chattecx, Chattanooga, TN). Subjects sat on the seat of the dynamometer with a knee and hip joint angle of ~1.57 radians and with arms folded in front of the chest. The anatomic zero was set at a knee angle of 3.14 radians. Extrinsic movement of the upper body and the involved leg was limited by two crossover shoulder harnesses, a lap belt, a thigh strap, and an ankle cuff. The transverse axis of the knee joint was aligned with the transverse axis of the dynamometer’s power shaft. The length of the lever arm was individually determined. Force was measured by a strain gauge embedded in the ankle cuff. The force values were corrected by the software for leg mass that was measured in the horizontal position. Maximal isometric force was measured at a knee angle of 2.36 radians. Two maximal-effort 5-s trials were performed with 1 min of rest between trials. Maximal concentric and eccentric force of the knee extensors was measured at 1.05, 2.09, and 3.14 rad·s⁻¹. Subjects performed two repetitions with a 1-s pause at either end of the range of motion to avoid the facilitating effects of the preceding action. The order of isometric vs. dynamic actions and eccentric vs. concentric actions was counterbalanced across subjects, and the order of speeds was randomized. The higher value of two trials was used as the criterion measure. Note that strength data are reported only at 1.06 rad·s⁻¹.

Surface EMG activity was recorded in the vastus lateralis and vastus medialis. We recorded from these synergistic muscles to increase validity of the EMG measures. The skin surface was cleaned with alcohol. One box electrode with a built-in preamplifier (Motion Control, Salt Lake City, UT), powered by 9-V batteries, was placed axially, taped, and ace-bandaged on each muscle belly. The two electrodes had similar electronics characteristics: a common mode rejection ratio of 370 dB, a bandwidth of 8 Hz to 28 kHz, quiescent current of 0.12 mA, and a direct current input impedance of 1 MΩ.

The force and the goniometer signals from the dynamometer’s analog-to-digital board and the EMG signals were input to a digital adapter (model 4000A, Vetter, Rebersburg, PA) that sampled the signals at 80 MHz. The adapter was connected to a modified videocassette recorder (JVC, HR-D860U, model 500C, Vetter, Rebersburg, PA). Data from the videotape were transferred through a 12-bit analog-to-digital board (Data Translation, model 2801A, Marlboro, MA). The Myosoft software package (Noraxon, Scottsdale, AZ) was used to store and digitize the data.

Before digitization, the direct EMG signals were inspected and, if movement artifacts (6.5% of all tracings) were present, another representative segment of the data was digitized that was artifact free. Each data file was checked and, if needed, adjusted for baseline shift. The root mean square (RMS) of the direct EMG data was obtained by using a 20-ms window. Across all channels, the first marker was placed at peak force, and a second marker was placed 250 ms before the first marker. Within this 250-ms window, the highest RMS value was taken as peak EMG (µV) and the average over the 250-ms window as an average EMG (µV·s). Peak and average EMG data were digitized at 2.36-rad·angle for the eccentric only at 1.06 rad·s⁻¹.

Fatigue testing. Seven of fourteen subjects in each group performed 40 repetitions of quadriceps concentric actions with the trained and untrained leg, and the remaining seven subjects did 40 repetitions of eccentric actions with the trained and untrained leg at 1.05 rad·s⁻¹. Only the quadriceps muscle was exercised, and the operator returned the lever arm to the starting position for the next repetition. The order of eccentric and concentric fatigue bouts was balanced between subjects.

Training. Subjects trained the left quadriceps four times per week for 6 wk, except during week 1 when, for a gradual introduction, there were only three sessions. Each training session consisted of four sets of 6–10 repetitions of either concentric or eccentric actions at 1.05 rad·s⁻¹ on the same isokinetic dynamometer on which the testing was done (Kin-Com, 500H, Chattecx). The number of repetitions fluctuated: week 1, 6; week 2, 8; week 3, 10; week 4, 6; week 5, 8; week 6, 10 (7). The total number of repetitions was 824. Visual feedback was provided to both groups of subjects to encourage maximal effort in the concentric group and to exercise at the preset target force for the eccentric group (as described in Subjects and design).

Statistical analyses. The BMDP PC-90 statistical package was used to perform all analyses. A test of skewness (26) was used to check the force and EMG data for normal distribution.
The data were assumed to be normally distributed if the ratio of skewness value to its standard error (6/N)^1/2, where N is number of observations, was within ±2.58. Reliability of force and EMG data was estimated by computing the intraclass correlation coefficient from the control group's data (n = 14). The force data were analyzed with a group (concentric, eccentric, control) by speed (−1.05, 0, 1.05 rad·s⁻¹) by time (pre- and postraining) analysis of variance with repeated measures on the last two factors. A similar design was used for the EMG data. The EMG data were analyzed by taking the arc sine of the eccentric peak EMG-to-isometric peak EMG and concentric peak EMG-to-isometric peak EMG ratios for each subject. However, Table 3 shows not the arcsine values but the actual ratios. The EMG data were analyzed as a ratio to reduce the error caused by electrode placement before and after training and by changes in skin properties (28). The fatigue data were analyzed with a group (concentric, eccentric, control) by contraction mode (concentric, eccentric) by time (pre- and postraining) analysis of variance, with the group and contraction mode being factors and time being within factor. This analysis was done on the percent change in fatigue (average of repetitions 1–3 (initial score) – average of repetitions 38–40 (final score) ÷ initial score × 100). In case of a significant F-ratio, Tukey’s post hoc contrast was performed to determine the means that were different at the significance level of P < 0.05.

RESULTS

Skewness analysis revealed that the skewness/SE of skewness scores ranged from −1.66 (vastus lateralis peak EMG) to 1.65 (isometric force). Thus the distribution of the force and EMG variables was assumed to be normal. Reliability of the strength measures was acceptable, and the intraclass correlation coefficients ranged from r = 0.82 (peak EMG of the vastus lateralis muscle during concentric action at 3.14 rad·s⁻¹) to r = 0.96 (eccentric force at 1.05 rad·s⁻¹). There were no significant trials or time (pre- and posttest) effects for any of the strength or EMG variables. The coefficient of variation ranged from 3.7 to 13.4% for strength and from 8.7 to 27.5% for the EMG variables.

Table 1 shows that subjects in the three groups were similar in age, mass, height, and body fat. Percent body fat was determined based on triceps, suprailiac, and thigh skinfolds (15).

Figure 1 shows the weekly average forces during training. The group by time interaction was not significant (F = 0.6, P = 0.68), suggesting that the two groups improved at the same rate and exercised at the same force levels. There was a significant time main effect (F = 15.8, P = 0.0001), and the two groups combined improved 25% from 465 to 582 N. The largest difference between the two groups in training intensity was 13 N at week 2. At weeks 1, 2, 3, 4, 5, and 6, the eccentric group exercised at 89, 97, 99, 104, 109, and 111%, respectively, of their maximum pretest eccentric force. At weeks 1, 2, 3, 4, 5, and 6, the eccentric group exercised at 111, 120, 123, 127, 135, and 137%, respectively, of their maximum pretest concentric force. At weeks 1, 2, 3, 4, 5, and 6, the eccentric group exercised at 109, 118, 122, 128, 134, and 138%, respectively, of their maximum pretest concentric force.

Table 2 shows the changes in muscle strength. There was a significant (F = 22.1, P = 0.000) group by speed by time three-way interaction. Concentric training significantly (P < 0.05) improved concentric strength by 152 N or 36% and isometric strength by 87 N or 18%. Concentric training improved eccentric strength by 68 N or 13% (P > 0.05).
Submaximal-effort eccentric training improved maximal eccentric strength by 222 N or 42%. Eccentric training improved isometric strength (140 N) significantly ($P, 0.05$) more than did concentric training (87 N). Eccentric training improved concentric strength by 94 N or 14% ($P, 0.05$). Eccentric training increased eccentric strength (222 N) significantly ($P, 0.05$) more than concentric training increased concentric strength (152 N). The control group did not show significant changes ($P, 0.05$).

Because average and peak EMG values correlated ($r, 0.92; n, 42$), Table 3 shows the changes in the eccentric-to-isometric and concentric-to-isometric peak EMG ratios only. For the vastus lateralis, there was a significant group by speed by time interaction ($F = 8.9$, $P = 0.000$). Concentric training increased ($P < 0.05$) the eccentric-to-isometric EMG ratio in the concentric test, and eccentric training significantly increased ($P < 0.05$) EMG eccentric-to-isometric ratio in the eccentric test. The 92% change was significantly ($P < 0.05$) greater in the eccentric test after eccentric training than the 36% change in the concentric test after concentric training. No significant changes occurred in the control group’s vastus lateralis and vastus medialis activity. In the vastus medialis, the post hoc analysis of the EMG ratios for the significant group by speed by time interaction ($F = 13.7$, $P = 0.000$) revealed a similar pattern of changes to those observed in the vastus lateralis.

Figure 2A shows the percent changes in fatigue. The group by contraction mode by time interaction was not significant, but there was a significant contraction (concentric and eccentric fatigue) main effect ($F = 123.3$, $P = 0.000$, pooled across groups and time): fatigue was significantly greater during the concentric ($48.2 \pm 13.6\%$) than during the eccentric series ($5.8 \pm 18.8\%$).

Figure 2B shows the fatigue data for the contralateral leg. Except for the significant contraction mode main effect ($F = 7.6$, $P = 0.04$), indicating that fatigue was greater with the concentric ($49.2 \pm 24.2\%$) than with the eccentric ($7.7 \pm 12.2\%$) test (pooled across groups and time), there were no other significant three- or two-way interactions or main effects. There were no significant main or interaction effects for the changes in strength (6% for all groups and conditions pooled) and EMG of the contralateral quadriceps.

### DISCUSSION

The key findings of the present study were that 1) submaximal training with eccentric actions improved maximal eccentric and isometric strength significantly more than maximal-effort concentric training improved

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**Table 3. Changes in peak EMG activity ratios in VL and VM muscles**

<table>
<thead>
<tr>
<th>Velocity, rad·s⁻¹</th>
<th>Pre Mean ± SD</th>
<th>Post Mean ± SD</th>
<th>Δ Mean ± SD</th>
<th>%Δ</th>
<th>Pre Mean ± SD</th>
<th>Post Mean ± SD</th>
<th>Δ Mean ± SD</th>
<th>%Δ</th>
<th>Pre Mean ± SD</th>
<th>Post Mean ± SD</th>
<th>Δ Mean ± SD</th>
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<tbody>
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<td>VL</td>
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<tr>
<td>−1.05</td>
<td>1.2 ± 0.15</td>
<td>1.3 ± 0.21</td>
<td>0.1</td>
<td>8</td>
<td>1.3 ± 0.11</td>
<td>2.5 ± 0.33</td>
<td>1.2*†</td>
<td>92</td>
<td>1.2 ± 0.17</td>
<td>1.1 ± 0.26</td>
<td>−0.1</td>
<td>−8</td>
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<tr>
<td>1.05</td>
<td>1.1 ± 0.09</td>
<td>1.5 ± 0.21</td>
<td>0.4*†</td>
<td>36</td>
<td>1.2 ± 0.10</td>
<td>1.3 ± 0.17</td>
<td>0.1</td>
<td>8</td>
<td>1.1 ± 0.06</td>
<td>1.1 ± 0.12</td>
<td>0</td>
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<td>VM</td>
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<td>1.3 ± 0.22</td>
<td>1.5 ± 0.34</td>
<td>0.2</td>
<td>15</td>
<td>1.5 ± 0.20</td>
<td>2.7 ± 0.31</td>
<td>1.2*†</td>
<td>80</td>
<td>1.3 ± 0.19</td>
<td>1.4 ± 0.23</td>
<td>−0.1</td>
<td>−8</td>
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<tr>
<td>1.05</td>
<td>1.2 ± 0.18</td>
<td>1.7 ± 0.42</td>
<td>0.5*†</td>
<td>42</td>
<td>1.2 ± 0.16</td>
<td>1.4 ± 0.20</td>
<td>0.2</td>
<td>17</td>
<td>1.2 ± 0.22</td>
<td>1.3 ± 0.17</td>
<td>0.1</td>
<td>8</td>
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Values are eccentric-to-isometric and concentric-to-isometric ratios. VL, vastus lateralis; VM, vastus medialis. *Significant ($P < 0.05$) change; †significantly more change than concentric group at 1.05 rad·s⁻¹.
maximal concentric and isometric strength; 2) changes in EMG activity of the vastus lateralis and medialis paralleled the strength adaptations; and 3) fatigability was not affected by either training method.

We pursued the hypothesis that muscle lengthening compared with shortening is superior to cause neuromuscular adaptation. Evidence in humans to support this hypothesis is equivocal. At one extreme is the report that only \( \sim 50\% \) of maximal eccentric force during a stretch-shortening activity may be sufficient to cause greater strength (6) and muscle adaptations (10). At the other extreme is the finding that exercise training with 80% of maximal eccentric actions results in less improvement in strength compared with training with maximal concentric actions (23). In between these extremes are other studies that report similar improvements in strength after eccentric and concentric training (16). Training with maximal eccentric actions brings about the greatest neural adaptations in the quadriceps (11) and in the forearm flexors (18).

One reason for the inconsistency in the findings could be that eccentric and concentric forces were not equated during the training programs. Thus one cannot differentiate the effects due to differences in forces and the effects caused by the differences in contraction modes. We addressed this problem by equating the force levels during training. The inconsistency in the findings can also be due to the differences between studies in which isokinetic (11) or isotonic (6) contraction modes were used, but we did not address this problem in the present work.

Even when forces were equated in the two training modalities, eccentric training improved eccentric force 70 N more than concentric training improved concentric force, and eccentric training improved isometric force 53 N more than did concentric training (all \( P < 0.05 \)). During concentric training, the passive elements are less involved in force production (4). Eccentric training may increase the stiffness of the passive elements and could account for the greater increases in eccentric and isometric forces. This mechanism could also account in part for the dampened increases in eccentric force after concentric training and in concentric force after eccentric training.

To isolate intrinsic muscular adaptations from simple effects of practice, we administered an isometric test contraction in addition to eccentric and concentric test contractions. Isometric contraction was used by neither training group, and an increase in isometric force can be taken as adaptation without the confounding effects of learning (21). Although both types of training have brought about strength increases due to some neural adaptations, submaximal, like maximal (11, 18), eccentric training is associated with a greater intrinsic muscular adaptation.

There also was a significantly (\( P < 0.05 \)) greater neural adaptation associated with submaximal eccentric than with maximal concentric training, as suggested by the changes in surface EMG activity (Table 3). Neural inhibition of force production in untrained individuals appears to cause a greater deviation from the expected eccentric forces than from the expected concentric forces (13, 27). One can thus predict a greater neural adaptation after eccentric than after concentric training. The results (Table 3) did confirm this prediction. Most (21) but not all (7) researchers hold the view that initial strength gains are largely due to nonhypertrophic factors such as increased motor unit activation, reflected by an increased EMG activity after training. Perhaps training has also reduced coactivation in the antagonist muscles (7), but we failed to observe such changes after maximal eccentric and concentric training for twice the duration of the present study (11).

We also used fatigue to evaluate the nature of neural adaptation in the trained leg. It is known that motor unit activation increases with fatigue (3). Because eccentric actions require fewer active motor units (2) and a greater involvement of the passive elements (18), less fatigue is expected to occur with repeated eccentric compared with concentric actions, as indeed was the case during training and the fatigue tests. Thus submaximal eccentric training is associated with less fatigue and greater strength adaptations compared with concentric training, which causes more fatigue but less of a strength adaptation. This would suggest that the neural mechanism may be different between the two training modes as far as fatigue being a contributing factor to strength gains (20).

Whether this neural adaptation is peripheral (noncortical) or central (cortical) is unclear. We addressed this issue by administering an eccentric and concentric fatigue bout in the nontrained leg before and after training. The prediction was that if there is central adaptation, then fatigue is less after training in the unexercised muscles because the nervous system would be able to compensate more effectively for the fatigue induced by the contraction series. The data suggest that the magnitude of fatigue was the same before and after training with both contraction modes (Fig. 2), suggesting that the nature of neural adaptation in the trained leg is most likely to be peripheral. Whether such a peripheral adaptation is linked to the greater muscle lengthening-related afferent traffic is to be seen.

After 824 submaximal eccentric and maximal concentric contractions administered over 23 sessions for 6 wk, we observed only \( \sim 6\% \) of cross-education in strength to the unexercised limb. This is somewhat smaller than observed by others for cross-education with maximal isometric actions (22). It is also in contrast to our previous observations that maximal eccentric training resulted in significantly greater cross-education of strength than did concentric training (12). However, in that study, we used 1,890 maximal contractions administered over 12 wk. Thus training intensity (submaximal vs. maximal) as well as duration (6 vs. 12 wk) may both play a role in the magnitude of cross-education associated with eccentric training.

Subjects for this study were women. In agreement with prior data on women’s adaptations to resistive
exercise in general (25), the present study also shows that women are as responsive to training with lengthening as are men (11). Furthermore, the adaptations in these women's quadriceps muscle were faster with eccentric than with concentric training. In studies that used up to 12 (11) or 16 wk of training (6), about one-half or more of the final adaptation occurred at 6–8 wk. Perhaps, during the second half of the training period in these studies, the adaptations were less due to overtraining.

It is unclear whether continued training with submaximal eccentric contractions beyond the 6 wk used in this study would result in similar rates of gains as training with maximal loads. This is important because some researchers contended that strength gains in women may plateau at 3 or 4 mo (9). Nonetheless, the rate of early strength and muscle adaptation seems to be similar between men and women (24), as also confirmed by the present study compared with our previous work in men (11). The submaximal training effects of muscle lengthening are also important because maximal eccentric actions, however effective they are, may not be the choice of training in a fitness or a rehabilitation setting. It is also worth noting the rapid trainability of the subjects in the present and prior studies (16). The rapid initial adaptation is most likely related to the untrained status of these healthy and active subjects. It should also be noted that the conclusions of this study are confined to the quadriceps muscle and the results may be different in muscles of different architecture or fiber composition.

In summary, the results of the present study suggest that training at ~80% of maximal eccentric contractions of the quadriceps brings about greater strength and neural adaptations than does training with maximal concentric contractions in women. This greater adaptation is likely to be mediated by both mechanical and neural factors.

This work was supported in part by an National Institute of Child Health and Human Development Grant 30422 and by a Research/Creative Activity grant from East Carolina University's Faculty Senate (to T. Hortobágyi). J. Braspennincx and P. Koens were on an internship from the Free University of Amsterdam, Faculty of Human Movement Sciences, The Netherlands.

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Received 18 October 1995; accepted in final form 6 May 1996.

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