

Effects of concentric and eccentric training on muscle strength, cross-sectional area, and neural activation

ELIZABETH J. HIGBIE, KIRK J. CURETON,
GORDON L. WARREN III, AND BARRY M. PRIOR

Department of Exercise Science, The University of Georgia, Athens, Georgia 30602-3654

Higbie, Elizabeth J., Kirk J. Cureton, Gordon L. Warren III, and Barry M. Prior. Effects of concentric and eccentric training on muscle strength, cross-sectional area, and neural activation. *J. Appl. Physiol.* 81(5): 2173–2181, 1996.—We compared the effects of concentric (Con) and eccentric (Ecc) isokinetic training on quadriceps muscle strength, cross-sectional area, and neural activation. Women (age 20.0 ± 0.5 yr) randomly assigned to Con training (CTG; $n = 16$), Ecc training (ETG; $n = 19$), and control (CG; $n = 19$) groups were tested before and after 10 wk of unilateral Con or Ecc knee-extension training. Average torque measured during Con and Ecc maximal voluntary knee extensions increased 18.4 and 12.8% for CTG, 6.8 and 36.2% for ETG, and 4.7 and -1.7% for CG, respectively. Increases by CTG and ETG were greater than for CG ($P < 0.05$). For CTG, the increase was greater when measured with Con than with Ecc testing. For ETG, the increase was greater when measured with Ecc than with Con testing. The increase by ETG with Ecc testing was greater than the increase by CTG with Con testing. Corresponding changes in the integrated voltage from an electromyogram measured during strength testing were 21.7 and 20.0% for CTG, 7.1 and 16.7% for ETG, and -8.0 and -9.1% for CG. Quadriceps cross-sectional area measured by magnetic resonance imaging (sum of 7 slices) increased more in ETG (6.6%) than in CTG (5.0%) ($P < 0.05$). We conclude that Ecc is more effective than Con isokinetic training for developing strength in Ecc isokinetic muscle actions and that Con is more effective than Ecc isokinetic training for developing strength in Con isokinetic muscle actions. Gains in strength consequent to Con and Ecc training are highly dependent on the muscle action used for training and testing. Muscle hypertrophy and neural adaptations contribute to strength increases consequent to both Con and Ecc training.

electromyography; isokinetic muscle actions; muscle hypertrophy; training specificity; quadriceps muscle; women

IT IS WELL ESTABLISHED that the primary stimulus for increasing the maximal force that can be exerted in a given movement (strength) is the repeated development of force by skeletal muscles at levels above those encountered in everyday activities (17). The increase in strength is proportional to the amount of overload as measured by the relative force developed and the number of muscle actions performed during conditioning (17). Because greater maximum force can be developed during maximal eccentric (Ecc) muscle actions than during concentric (Con) or isometric muscle actions (6), it has been suggested that heavy-resistance training using Ecc muscle actions may be more effective than training using Con or isometric muscle actions in increasing strength (3, 7, 13).

Studies comparing the effectiveness of Ecc and Con muscle actions in increasing muscular strength have

been equivocal (3, 4, 7–9, 18, 20–22, 24, 26, 40, 43). Different training protocols and methods of assessment have contributed to different outcomes. In studies in which submaximal muscle actions with the same absolute load were used for training, Ecc and Con training produced similar increases in Con (20) or isometric strength (25). In studies in which the training resistance was proportional to strength of the respective muscle actions (greater for Ecc) and weight lifting or an accommodating resistance machine was used for training, Ecc training produced a similar (21, 22) or greater (24) increase in isometric strength; similar (9, 21, 26, 40), greater (8, 24), or no (43) increase in Con strength; and similar (26, 40), greater (8, 24, 43), or no (9) increase in Ecc strength. In other studies, training with coupled Con/Ecc muscle actions of the same submaximal force (7, 18, 34) or different maximal force (3) resulted in a greater (3, 7, 34) or no different (18, 34) gain in strength than training with Con muscle actions when testing was performed with Con, Ecc, or combined Con/Ecc muscle actions. Increases in strength after Con and Ecc training have tended to be greatest when assessed with the same type of muscle action as that employed in training, but this finding is not universal (27).

Increases in strength after heavy-resistance training are due to hypertrophy and/or increased neural activation of muscle (12, 22, 38). However, only one study comparing the relative effectiveness of Con and Ecc training included measurements of both muscle dimensions and neural activation (24). As a result, a comprehensive understanding of the physiological basis underlying differences in the relative effectiveness of the training modes, when observed, is lacking. The greater effectiveness of Ecc or coupled Con/Ecc training has been attributed to greater changes in neural activation (3) and to greater muscle hypertrophy (16, 24, 34). It has been argued that Ecc muscle actions are a necessary stimulus for muscle hypertrophy (5), and some studies have found that muscle hypertrophy is greater after Ecc or coupled Con/Ecc training than after Con training (16, 24, 34). Lack of muscle hypertrophy in studies that used Con isokinetic or accommodating resistance training (5, 8, 16, 18, 24, 35) support this conclusion. On the other hand, other studies have found substantial muscle hypertrophy after Con training on an isokinetic or accommodating resistance device (19, 31, 34) and no difference between Con training and training including Ecc muscle actions when Ecc training involved development of greater (3) or the same (22) force. In theory, because force development is greater (6, 24) but neural activation is the same (24) or less (41) in maximal Ecc compared with Con muscle

actions, greater strength changes after maximal Ecc compared with Con training should be explained by greater muscle hypertrophy or a combination of greater hypertrophy and neural activation. Because muscle dimensions are the same regardless of test mode, test-mode differences in strength changes after Ecc and Con training should be accounted for by differences in neural activation.

The objectives of this study were 1) to compare the effects of Con and Ecc heavy-resistance isokinetic training on strength, cross-sectional area (CSA), and neural activation of the quadriceps muscle and 2) to determine the relationship of changes in strength to changes in muscle CSA and neural activation. First, we hypothesized that increases in muscle CSA are greater after Ecc than Con training but that increases in neural activation and strength are specific to mode of training, i.e., greater after Con training when measured during Con muscle actions and greater after Ecc training when measured during Ecc muscle actions. Second, we hypothesized that increases in strength are related to increases in quadriceps CSA and neural activation when measured during the same test mode as that used in training but are related only to muscle hypertrophy when measured in the test mode not used in training. The unique aspect of the study, compared with previous research, is the attempt to explain changes in strength resulting from Con and Ecc training, and possible test mode specificity, with direct measurements of muscle CSA and electrical activity (neural activation).

METHODS

Subjects. Sixty women, 18–35 yr of age, in good health and free of right knee pathology, were recruited from a large university student population. Women were used because the effects of heavy-resistance training have been studied less in women and because their prior involvement in resistance exercise was likely to be less than that in men. These subjects were unfamiliar with the Kin-Com dynamometer (model 500H, Chattex) and had not participated in a lower extremity heavy-resistance weight-training program for 6 mo before the study. Each subject gave written consent before testing.

Subjects were randomly assigned to a Con-only (CTG) or Ecc-only (ETG) training group or a control group (CG). Six subjects were unable to complete the study due to leaving school (1), time commitments (4), and illness (1). Therefore, a total of 54 subjects completed the study with 19 in CG, 16 in CTG, and 19 in ETG. Physical characteristics of the subjects in each of the three groups are presented in Table 1. A one-way analysis of variance (ANOVA) indicated that there were no significant differences ($P > 0.05$) among the three

groups for age, height, weight, fat-free mass, and percent body fat at the pretest.

Data collection protocol. Pretest data collection involved four test sessions for each subject: an orientation session, two sessions at which muscular strength and electromyographic (EMG) activity measurements were obtained, and a session during which CSA of the quadriceps muscle was assessed by using magnetic resonance imaging (MRI). During the orientation session, subjects were familiarized with the Kin-Com dynamometer by practicing the complete testing protocol. The second pretest session occurred 2 days after the orientation session. Average torque and EMG activity during maximal voluntary Con and Ecc isokinetic knee extensions at 60°/s were measured. The third pretest session occurred 2 days after the second pretest session. Measurements made during the second session were repeated to determine their reliability. At the fourth pretest data-collection session, MRI scans of the right thigh were obtained to assess quadriceps CSA. Ten subjects were measured a second time before the start of the training program to determine reliability of the MRI measurements. Measurements were repeated after 10 wk of training.

Test procedures. Strength of the knee extensors of the right leg was assessed by having subjects perform maximal voluntary Con and Ecc isokinetic knee extensions at 60°/s by using a Kin-Com dynamometer. High turn points on the Kin-Com dynamometer were used to control acceleration and deceleration rates of the leg. Each subject had to generate >40 N of force during testing and training before movement of the lever arm occurred. The Kin-Com dynamometer was externally calibrated with weights before testing and electronically calibrated before each test session. Data were acquired, stored, and retrieved on a 386 IBM-compatible microcomputer, which was interfaced with the Kin-Com dynamometer by using Labtech Notebook software and a sampling frequency of 1,000 Hz per channel. Data from each knee extension were individually stored during all test sessions. From the data collected during isokinetic muscle actions, average torque during 0–70° of the muscle action and integrated voltage from an EMG (iEMG) were obtained. A correction for the mass of the limb and lever arm system was made on all torque curves.

During the strength tests, the subject was seated upright on the Kin-Com dynamometer seat. Two 10-cm-wide Velcro straps were placed in a crossed fashion on the subject's chest. A seat belt was hooked tightly across the subject's hips and lower abdomen. The subject's right knee joint axis was aligned with the axis of the dynamometer head by palpation of the subject's lateral joint space between the lateral femoral condyle and the fibular head. The lower edge of the actuator arm was placed in the center of the tibia ~3 cm above the right lateral malleolus. A manual goniometer was used to measure the right hip joint and knee joint angles. The hip joint angle was set at $85 \pm 1^\circ$ of hip flexion, and the knee joint angle was set at $90 \pm 1^\circ$ ($0^\circ =$ horizontal). The left leg was fully extended on an elongated pad. The subject was instructed to cross her arms across her lap and was not allowed to hold on to the sides of the seat during testing or training. The stated goal during the maximal isokinetic muscle actions was to exert as much force as possible on each trial and to attempt to achieve a higher peak force on each successive trial of a given type.

Three maximal Con and Ecc isokinetic muscle actions were obtained. During isokinetic testing, the Con mode was always tested before the Ecc mode to reduce any potentiation effect of the Ecc movements on the Con movements (33). Three submaximal isokinetic muscle actions, performed for warm-up

Table 1. *Physical characteristics*

Variable	CTG ($n=16$)	ETG ($n=19$)	CG ($n=19$)
Age, yr	20.1 \pm 2.1	20.1 \pm 1.1	21.3 \pm 1.6
Height, cm	163.9 \pm 6.2	166.0 \pm 4.7	164.1 \pm 5.8
Mass, kg	63.7 \pm 9.5	58.6 \pm 7.7	61.5 \pm 10.0
FFM, kg	49.1 \pm 5.4	47.1 \pm 5.0	48.7 \pm 6.1
Body fat, %	22.4 \pm 9.7	19.4 \pm 4.7	20.4 \pm 4.0

Values are means \pm SD; n , no. of subjects. CTG, concentric (CON) training group; ETG, eccentric (ECC) training group; CG, control group; FFM, fat-free mass.

and practice, were followed by three maximal isokinetic muscle actions for each isokinetic test mode. The muscle actions were separated by a rest interval of 25 s. During the 25-s rest period, the Kin-Com dynamometer lever arm moved at 30°/s to slowly return the leg to the initial test position without requiring any muscular activity from the limb. Intraclass reliability coefficients, determined by using a one-way ANOVA for a single trial, were 0.84 for average torque during maximal Con muscle actions and 0.83 during maximal Ecc muscle actions.

While the subject was performing the maximal-effort isokinetic muscle actions, EMG data were obtained from the contracting right vastus lateralis and vastus medialis muscles. The range of motion during which these data were collected was the same as that for average torque. The EMG activity data from the two muscles were summed and used to assess the degree of electrical excitation (neural activation) of the underlying musculature. EMG activity was recorded with a two-channel Coulbourn recorder with a high-gain bioamplifier, band-pass filter with cutoffs of 8 and 1,000 Hz, and a gain of 10,000. Two silver-silver chloride surface electrodes were placed 30 mm apart over each muscle approximately over the motor point. The two ground electrodes were placed 30 mm apart over the right anterior superior iliac spine of the pelvis. Before the electrodes were placed, the skin was thoroughly cleaned with isopropyl alcohol and slightly scratched with a sterile needle to reduce interelectrode impedance below 5,000 Ω . Acetate paper was used to trace the electrode placement to ensure the same electrode placement was made in subsequent tests. The EMG data were rectified and integrated over the same time period as the average force measurements. The iEMG data for three trials for each test mode were averaged. Intraclass reliability coefficients for the maximal iEMG activity during Con and Ecc muscle actions were 0.90 and 0.88, respectively.

The CSA of the quadriceps muscle was measured with MRI by using a General Electric Sigma Advantage unit with software version 4.6.8. T2 proton density images from 5-mm-thick axial scans at 20, 30, 40, 50, 60, 70, and 80% of the femur length were obtained by using a multislice spin-echo pulse sequence (repetition time = 2,000 ms; echo time = 10 ms), 24-cm field-of-view, and 256 \times 192 pixel matrix. Total scan time was 6.8 min. Computer-assisted planimetry analysis was used to determine CSA measurements from the images with a pixel counting routine. Intraclass reliability coefficients for muscle CSA at the different levels ranged from 0.97 to 0.99.

Heavy-resistance training. Each experimental subject trained her right leg on the Kin-Com dynamometer using either Con or Ecc isokinetic muscle actions, depending on the training group to which she was assigned. Training was 3 days/wk for 10 wk for a total of 30 training sessions. During training, subjects performed three sets of 10 repetitions with no rest between repetitions. A 3-min rest was given between sets. Subjects were stabilized for training with the same procedure as for testing. Because speed, not force, is controlled by the Kin-Com dynamometer during isokinetic muscle actions, force of muscle actions varied with individual effort. During the first week of training, a force marker on the Kin-Com screen was set at the pretest peak force measured during Con or Ecc muscle actions. The subject was asked to reach or exceed the force marker with each repetition. The force marker placement was adjusted each week based on isokinetic strength tests.

Subjects in CG were instructed to maintain their previous level of activity and not begin a lower-extremity strength training program until the study was over. None of the

subjects in CG reported altering their level of physical activity.

Statistical analysis. Intraclass correlation coefficients were calculated by using a one-way ANOVA to assess the reliability of torque, CSA, and iEMG activity measurements. The statistical significance of differences in pretest-to-posttest changes among groups was determined by a three- (group \times time \times test mode) or two- (no test mode for quadriceps CSA) factor ANOVA with repeated measurements on the time and test mode factors followed by post hoc tests for simple effects and interaction and simple contrasts as appropriate (23). Differences in the adaptation to training were indicated by significant group \times time or group \times time \times test mode interactions. Simple and multiple correlation and regression analysis were used to determine the relative contributions of changes in quadriceps CSA and neural activation to changes in strength. An alpha level of $P \leq 0.05$ was used for all tests of significance.

RESULTS

The pattern of results for peak and average torque, measured during maximal Con and Ecc muscle actions, was the same. Therefore, only the data for average torque are reported. Changes in average torque of the right quadriceps muscle for the three groups measured during maximal Con and Ecc isokinetic muscle actions are presented in Table 2. When tested in the Ecc mode, the mean and percent changes for ETG, CTG, and CG were 34.0 (36.2%), 12.5 (12.8%), and -1.8 (-1.7%) N·m, respectively. Maximum average torque in ETG and CTG increased significantly more than in CG. The increase in average torque in ETG was significantly greater than the increase in CTG.

When tested in the Con mode, the mean and percent changes in average torque for ETG, CTG, and CG were 5.4 (6.8%), 14.4 (18.4%), and 3.8 (4.7%) N·m, respectively. The change in average torque was significantly greater in CTG than in CG. There was no significant difference in the change in average torque between ETG and CG. The increase in average torque in CTG was significantly greater than that for ETG.

Ecc isokinetic training increased strength more than Con isokinetic training when measurements were made by using the same muscle action as that used during training. The change in average torque measured dur-

Table 2. Average torque at pretest and posttest for CON and ECC test modes

Group	Pretest	Posttest	Mean Change	Mean % Change
<i>ECC Test Mode</i>				
CTG	97.7 \pm 23.5	110.2 \pm 30.2	12.5*	12.8
ETG	93.9 \pm 18.7	127.9 \pm 22.0	34.0*†	36.2
CG	104.6 \pm 24.3	102.8 \pm 26.2	-1.8	-1.7
<i>CON Test Mode</i>				
CTG	78.4 \pm 18.5	92.8 \pm 23.4	14.4*‡	18.4
ETG	79.5 \pm 11.7	84.9 \pm 13.8	5.4	6.8
CG	81.7 \pm 16.2	85.5 \pm 18.8	3.8	4.7

Values are means \pm SD in N·m. Based on group \times time partial interaction from analysis of variance (ANOVA): *significantly different ($P < 0.05$) compared with CG; †significantly greater ($P < 0.05$) compared with CTG and CG; ‡significantly greater ($P < 0.05$) compared with ETG and CG.

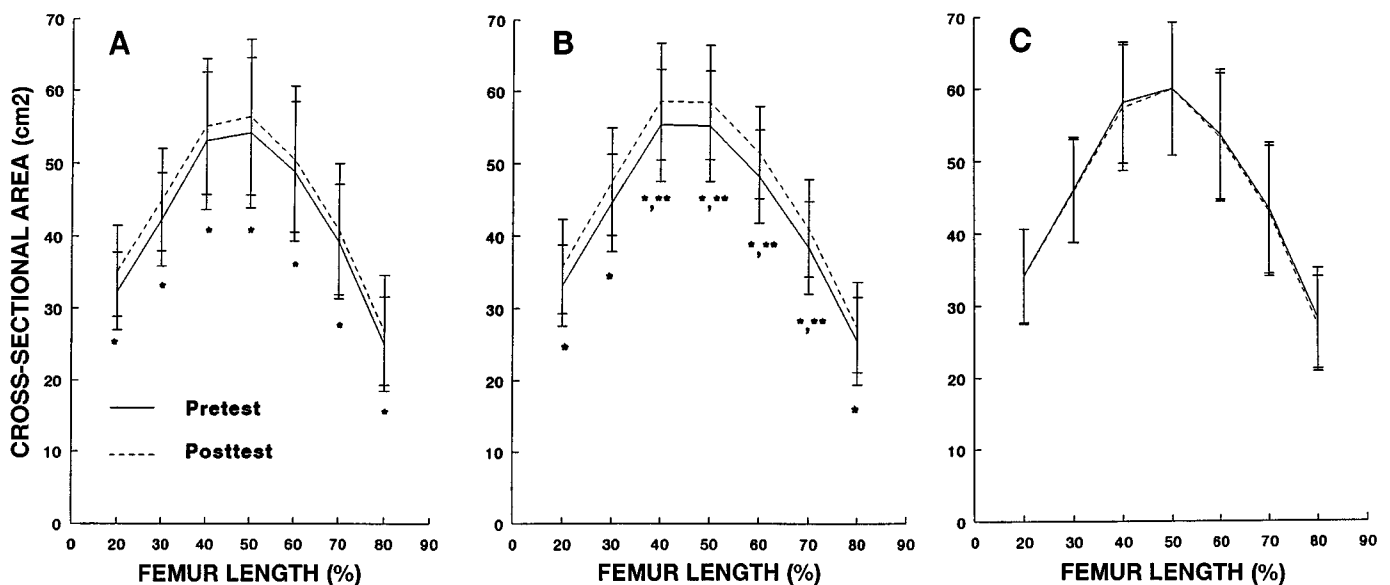


Fig. 1. Values are means \pm SE. Change in cross-sectional area (CSA; cm^2) of quadriceps muscle measured from magnetic resonance imaging scans at 7 levels at pretest and posttest in concentric (Con; A), eccentric (Ecc; B), and control (C) groups. *Significantly greater compared with control group at $P \leq 0.05$. **Significantly different compared with Con group at $P \leq 0.05$.

ing Ecc muscle actions after Ecc training (36.2%) was significantly greater than the corresponding change in average torque measured during Con muscle actions after Con training (18.4%).

Changes in the CSA of the quadriceps muscle determined from MRI scans after training are presented in Fig. 1. For the seven levels (20–80% femur length), the mean and percent increases in CSA of the quadriceps for ETG and CTG ranged from 1.9 to 3.3 cm^2 (6.0–7.8%) and from 1.7 to 2.8 cm^2 (3.5–8.6%), respectively. For the sum of the seven levels, the CSA of the quadriceps increased 19.9 cm^2 (6.6%) in ETG compared with 15.0 cm^2 (5.0%) for CTG (Table 3). No increase in CSA of the quadriceps muscle was found in CG. The increases in CSA of the quadriceps for the two training groups were significantly greater than the increase for CG. The increases for ETG were significantly greater than for CTG at the 40, 50, 60, and 70% levels and for the sum of the seven levels. The significance of the small ETG-to-CTG differences may have been due in part to the greater variability of the changes in CTG (see Fig. 2).

Changes in iEMG of the right quadriceps muscle for the three groups measured during maximal voluntary

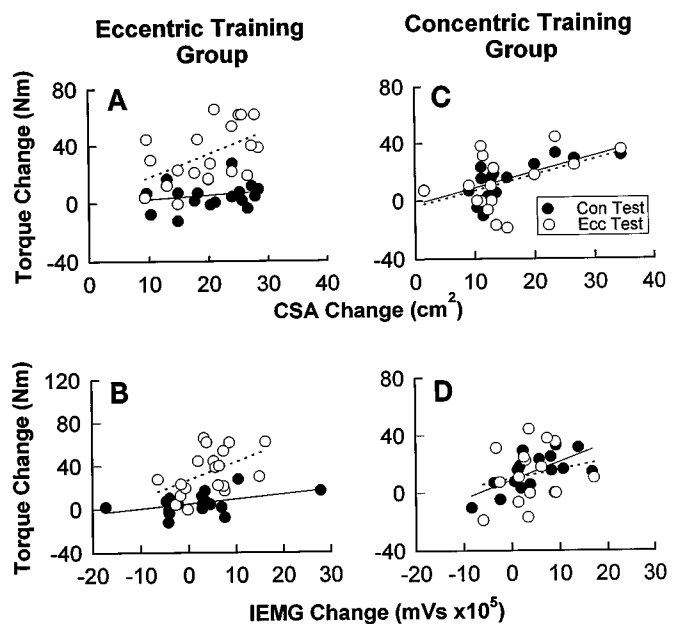


Fig. 2. Scatter plots of change in average torque measured during maximal Con and Ecc knee extensions to changes in quadriceps CSA (sum of 7 slices) and integrated voltage from EMG (iEMG) in Ecc training group (ETG) and Con training group (CTG). Linear regression lines are shown. For ETG tested during Ecc muscle actions (A and B; \circ), change in (Δ) torque = $1.63 \cdot \Delta\text{CSA} + 1.47$; $r = 0.51$; standard error of estimate (SEE) = 18.1 N·m and Δ torque = $1.69 \times 10^4 \cdot \Delta\text{iEMG} + 26.68$; $r = 0.48$; SEE = 18.6 N·m. For ETG tested during Con muscle actions (A and B; \bullet), Δ torque = $0.29 \cdot \Delta\text{CSA} - 0.34$; $r = 0.20$; SEE = 9.1 N·m and Δ torque = $4.39 \times 10^4 \cdot \Delta\text{iEMG} + 4.68$; $r = 0.43$; SEE = 8.4 N·m. For CTG tested during Con muscle actions (C and D; \circ), Δ torque = $1.11 \cdot \Delta\text{CSA} - 3.95$; $r = 0.70$; SEE = 9.3 N·m and Δ torque = $1.29 \times 10^5 \cdot \Delta\text{iEMG} + 8.6$; $r = 0.68$; SEE = 9.5 N·m. For CTG tested during Ecc muscle actions (C and D; \bullet), Δ torque = $1.09 \cdot \Delta\text{CSA} - 3.95$; $r = 0.44$; SEE = 17.8 N·m and Δ torque = $6.6 \times 10^4 \cdot \Delta\text{iEMG} + 9.65$; $r = 0.19$; SEE = 19.5 N·m.

Table 3. Cross-sectional area of quadriceps muscle (sum of 7 levels) at pretest and posttest

Group	Pretest	Posttest	Mean Change	Mean % Change
CTG	295.4 \pm 52.0	310.3 \pm 56.2	15.0*	5.0
ETG	300.8 \pm 41.3	320.7 \pm 43.7	19.9*†	6.6
CG	323.7 \pm 52.8	320.9 \pm 53.0	-2.8	-0.9

Values are means \pm SD in cm^2 of sum of cross-sectional areas from 7 levels (20–80% femur length). Based on group \times time partial interaction from ANOVA: *significantly greater ($P < 0.05$) compared with CG; †significantly greater ($P < 0.05$) compared with CTG and CG.

Con and Ecc muscle actions are presented in Table 4. When tested in the Ecc mode, the mean and percent changes in maximal iEMG for ETG, CTG, and CG were 0.4 (16.7%), 0.4 (20.0%), and -0.2 (-9.1%) $\text{mV}\cdot\text{s}$, respectively. Changes in maximal iEMG for the two training groups were significantly greater than change in CG. However, the increases in maximal iEMG activity for the two training groups were not significantly different. When tested in the Con mode, the mean and percent changes in maximal iEMG for ETG, CTG and CG were 0.2 $\text{mV}\cdot\text{s}$ (7.1%), 0.5 $\text{mV}\cdot\text{s}$ (21.7%), and -0.2 $\text{mV}\cdot\text{s}$ (-8.0%), respectively. The change in maximal iEMG was significantly greater in CTG than in CG. There were no significant differences in the changes in maximal iEMG between the two training groups or between ETG and CG. Means for maximal iEMG were higher across the respective groups in the Con test mode than in the Ecc test mode at the pretest and posttest. There was no significant test-mode training-mode (group \times time \times mode) interaction for changes in maximal iEMG.

Scatter plots of changes in average torque measured during maximal Con and Ecc knee extensions to changes in quadriceps CSA (sum of 7 slices) in ETG and CTG are shown in Fig. 2. In ETG, changes in average torque measured during Ecc muscle actions were moderately related to changes in quadriceps CSA ($r = 0.51$; $P < 0.05$) and iEMG ($r = 0.48$; $P < 0.05$). The linear combination of quadriceps CSA and iEMG accounted for 37% of the variance in average torque change [$R = 0.61$; standard error of estimate (SEE) = 17 $\text{N}\cdot\text{m}$]. Changes in average torque measured during Con muscle actions in ETG were small and, as reported above, were not significantly different from the corresponding change in CG. Therefore, they were not significantly related to changes in quadriceps CSA ($r = 0.20$; $P > 0.05$) or iEMG ($r = 0.43$; $P > 0.05$). The linear combination of quadriceps CSA and iEMG accounted for 24% of the variance ($R = 0.48$; SEE = 8 $\text{N}\cdot\text{m}$) in average torque change. In CTG, changes in average torque measured during Con muscle actions were moderately strongly related to changes in quadriceps CSA ($r = 0.70$; $P < 0.05$) and iEMG ($r = 0.68$; $P < 0.05$). The linear combination of quadriceps CSA and iEMG accounted for 65% of the variance in average torque

change ($R = 0.80$, SEE = 8 $\text{N}\cdot\text{m}$). Changes in average torque measured during Ecc muscle actions were not significantly related to changes in quadriceps CSA ($r = 0.44$; $P > 0.05$) or iEMG ($r = 0.19$; $P > 0.05$). The linear combination of quadriceps CSA and iEMG accounted for 21% of the variance in average torque change ($R = 0.46$, SEE = 18 $\text{N}\cdot\text{m}$).

DISCUSSION

Our objective was to expand on studies that have compared the effects of training with maximal Con-only and Ecc-only isokinetic muscle actions on strength changes measured during Con and Ecc muscle actions (8, 9, 24, 43) by providing additional insight into the mechanisms underlying strength changes. We directly compared the effects of Con and Ecc heavy-resistance isokinetic training on strength, CSA, and neural activation of the quadriceps muscle and determined the relationship of changes in strength to changes in muscle CSA and neural activation in young women. We found that Ecc training increased strength measured with Ecc but not Con muscle actions and that Con training increased strength measured with Con and Ecc muscle actions. Test mode specificity was observed; changes in strength were greatest when measured during the muscle action used in training. However, Ecc training increased strength measured with Ecc muscle actions more than Con training increased strength measured with Con muscle actions. Ecc and Con training caused similar increases in quadriceps CSA and maximal iEMG, except that maximal iEMG did not increase after Ecc training when measured using Con muscle actions. Increases in strength after Ecc and Con training were related almost equally to muscle hypertrophy and increased neural activation.

Our findings that maximal Con-only and Ecc-only muscle actions improve strength measured during the same muscle action as that used in training agree with many other studies (7–9, 18, 21, 22, 24, 26, 34, 36, 40, 43). However, Ecc training increased strength measured during Ecc muscle actions more than Con training increased strength measured during Con muscle actions. This is a consistent finding in similar studies (8, 24, 43). One interpretation of this result is that maximal Ecc muscle actions provide a superior stimulus to increase strength compared with maximal Con muscle actions, if strength is assessed using the same muscle actions as those employed in training. However, if the extent of improvement in strength is linked to properties associated with the type of muscle action used in training, greater generalization to Con muscle actions would have been expected. It is possible that performance of Ecc muscle actions is necessary for the complete neural adaptation to be expressed. An alternate interpretation is that the subjects were less able to activate the quadriceps during Ecc than Con muscle actions before training, and, therefore, there was more potential for improvement of strength measured during Ecc muscle actions through increased neural activation. Although EMG activity during maximal Ecc muscle actions was less than that during maximal Con muscle

Table 4. *Integrated electromyographic activity at pretest and posttest for CON and ECC test modes*

Group	Pretest	Posttest	Mean Change	Mean % Change
<i>ECC Test Mode</i>				
CTG	2.0 ± 0.5	2.4 ± 0.8	0.4*	20.0
ETG	2.4 ± 0.6	2.8 ± 0.7	0.4*	16.7
CG	2.2 ± 0.8	2.0 ± 1.0	-0.2	-9.1
<i>CON Test Mode</i>				
CTG	2.3 ± 0.7	2.8 ± 1.0	0.5*	21.7
ETG	2.8 ± 0.9	3.0 ± 0.8	0.2	7.1
CG	2.5 ± 0.8	2.3 ± 1.1	-0.2	-8.0

Values are means \pm SD in $\text{mV}\cdot\text{s}$. *Significantly greater compared with CG at $P < 0.05$ based on group \times time partial interaction from ANOVA.

actions before training, the similar pretest-to-posttest changes in EMG activity during maximal Con and Ecc muscle actions after training suggest that the neural adaptation was not greater after Ecc training. Therefore, the reason for the greater effectiveness of Ecc training in improving Ecc strength compared with Con training in improving Con strength remains uncertain.

Based on previous reports of mode specificity in muscular strength adaptations to heavy resistance training (27), we hypothesized that increases in muscular strength would be greater when testing employed the same muscle action as that used during training and less when strength was measured using a different muscle action. This hypothesis was supported. The change in strength after Ecc training was greater when measured during Ecc (36.2%) than during Con (6.8%) muscle actions. The nonsignificant increase during Con muscle actions indicates that Ecc training did not generalize to Con muscle actions. A test-mode specificity in the adaptation of strength after maximal Ecc-only training has been reported in some studies (8, 24, 43) but not in others (9, 37). Similarly, the change in strength after Con training was greater when measured during Con (18.4%) compared with during Ecc (12.8%) muscle actions, but the test-mode specificity was not as great. The effects of Con training generalized to a considerable extent to Ecc muscle actions. This finding is consistent with other studies (8, 9, 24, 36, 43).

Increases in strength after heavy-resistance training are due to muscular and/or neural adaptations. Muscular adaptations include an increase in the CSA of the prime movers (muscle hypertrophy) or adaptations that increase specific tension (force per unit CSA). Neural adaptations include increased prime mover motor unit activation, increased activation of synergistic muscles, or decreased activation of antagonistic muscles (38). To our knowledge, this is the first study to directly quantify changes in the CSA and neural activation of the prime movers that underlie changes in Con and Ecc isokinetic strength resulting from Con and Ecc isokinetic training.

Both Ecc and Con isokinetic training caused muscle hypertrophy. The sum of seven CSA measurements of the quadriceps between 20 and 80% of femur length increased by 19.9 cm² (6.6%) in ETG and by 15 cm² (5.0%) in CTG. The increase of ETG was significantly greater than that of CTG, but the difference was small. This finding is consistent with other studies in which Ecc (22, 24) or Con muscle actions only (16, 22, 31, 34, 36) performed on isokinetic or accommodating-resistance machines, or Con muscle actions only performed by weight lifting (16), have increased directly measured muscle CSA, limb girth, or muscle fiber CSA. Other studies have found no significant muscle hypertrophy resulting from training with Ecc-only (8) or Con-only (3–5, 8, 18, 24) muscle actions performed on isokinetic or accommodating-resistance machines. A variety of factors can explain these discrepant findings, including the sensitivity of the measurement used to assess muscle size, the initial state of training, and the intensity and duration of the training.

Based on previous research, we hypothesized that Ecc training would cause greater muscle hypertrophy than Con training. Our statistical findings support this hypothesis. Moreover, this outcome is consistent with studies that have found that training with Ecc (24) or coupled Con/Ecc muscle actions produce greater muscle hypertrophy than training with Con muscle actions (16, 18, 34), although this is not a universal finding (3, 22, 34). However, our data and most comparative studies suggest that the difference in muscle hypertrophy between training modes is relatively small. Although it has been claimed that Ecc muscle action is necessary to obtain muscle hypertrophy (5), it is clear from many studies (19, 22, 31, 34), including ours, that this is not the case. Training with Ecc muscle actions only, in which the force developed is substantially higher than that during Con muscle actions, does not always lead to greater muscle hypertrophy (22). The fact that somewhat greater muscle hypertrophy has often been obtained by weight lifting using coupled Con/Ecc muscle actions (16, 18, 34), in which the weight lifted is limited by the force that can be developed at the point of least mechanical advantage in the Con muscle action, compared with Con muscle actions also suggests that under these conditions it is not the greater force that can be developed during Ecc-only muscle actions that provides the stimulus for greater hypertrophy. This point is underscored by studies in which greater muscle hypertrophy has been found after weight training compared with after training involving the same movement with Con-only muscle actions performed on an accommodating-resistance device, in which the force developed at many points of the range of motion and the overall intensity stimulus were greater during the Con muscle actions (18, 34).

At any given level of submaximal force and during a maximal voluntary muscle action, the ratio of force to iEMG activity is greater, suggesting that fewer motor units are activated during Ecc compared with Con muscle actions (1, 24). A greater proportion of force developed is apparently provided through passive stretch of the series elastic elements or increased force production per cross bridge. Therefore, there is greater force developed per activated muscle fiber and per unit CSA of active muscle during Ecc muscle actions than during Con muscle actions, regardless of whether the force exerted is the same or greater during Ecc muscle actions. The greater force and stretch placed on muscle fibers, sometimes resulting in fiber damage in unconditioned muscle, has been suggested as providing the signal leading to greater muscle hypertrophy (34). In addition, increased recruitment of fast-twitch fibers (28–30) with greater potential for hypertrophy (34) may also contribute to greater hypertrophy during training involving Ecc muscle actions. Animal studies suggest that the greater specific tension imposed through Ecc compared with Con muscle actions may differentially increase protein synthesis (44).

Maximal iEMG was measured to assess one element of the neural adaptation to training. Maximal iEMG changes after training may reflect the degree of electri-

cal excitation of the underlying muscles and is affected by the number and size of motor units recruited, frequency of stimulation, and the synchrony of firing. Changes in iEMG do not reflect other possible neural adaptations such as activation of synergists and antagonists and thus should not be considered a measurement of all neural adaptations (38).

We hypothesized that changes in maximal iEMG activity after Con and Ecc training would be dependent on mode of testing; i.e., iEMG activity would increase to the same extent in CTG and ETG when measured during Con and Ecc muscle actions, respectively, but would increase less when measured during muscle actions not used in training. This hypothesis was confirmed in part. The increase in maximal iEMG in CTG measured during maximal Con muscle actions (21.7%) was not different from the increase in ETG measured during maximal Ecc muscle actions (16.7%). In ETG, the increase in maximal iEMG activity measured during Con muscle actions (7.1%) did not increase significantly more than in CG and was less than the increase measured during Ecc muscle actions, supporting the hypothesis. In CTG, however, the increases in maximal iEMG activity measured during Con and Ecc muscle actions were not different (21.7 and 20.0%), indicating that there was no test mode specificity. The pattern of adaptations was very similar to that obtained for strength changes, except there was not a significant group \times time \times test mode interaction. The increases in maximal iEMG activity after Con and Ecc training are consistent with studies that observed significant increases after dynamic weight or isokinetic heavy-resistance training (12, 14, 31) but different from those that did not (24, 42).

The interpretation of the increases in iEMG during maximal muscle actions after training is uncertain. Increases in iEMG can reflect increases in motor unit recruitment and/or motor unit firing rates. Some studies that used the twitch interpolation technique with isometric muscle actions (38) have suggested that motor unit activation during maximal voluntary contractions before training is maximal. If this were the case, the increase in iEMG after training should reflect increased motor unit firing frequency, which may or may not cause greater force (11). However, recruitment during an interpolated twitch is different from that during a more sustained tetanic stimulation, and recruitment during dynamic isokinetic muscle actions with superimposed tetanic stimulation is not always complete (32). Therefore, increases in motor unit recruitment after training cannot be ruled out. It is also possible that increased surface area of hypertrophied muscle fibers could contribute to increased iEMG after training, but the relatively small muscle hypertrophy that occurred and the fact that muscle hypertrophy is not always accompanied by increased maximal iEMG (11) suggest that this is unlikely. A reduction in subcutaneous fat on the thigh could also contribute to increased maximal iEMG after training. Because surface electrodes sample from a fixed volume, a reduction in the fat layer separating the electrodes from the underlying

muscle could increase the muscle sampled. However, fat CSA measured by MRI (sum 7 slices) on the thigh did not change in ETG or CTG more than in CG, indicating that a change in fatness was probably not responsible for the increased iEMG. Furthermore, if muscle hypertrophy or reduced subcutaneous fat were solely or largely responsible for the EMG increases, the increases would be similar regardless of test mode. This was not the case.

We have no proof that motor unit activation at the pretest was maximal. The lower pretraining Ecc compared with Con EMG activity suggests that motor unit activation was not maximal during Ecc muscle actions. The positive relationships between increased maximal iEMG and increased strength after Ecc and Con training, when strength was measured during the same muscle action as that used in training, suggest that increased recruitment and/or frequency of stimulation of motor units occurred at the posttest after Con and Ecc training. Similar positive relationships between strength changes and maximal iEMG changes after resistance training have been observed by others (12, 15). Tesch et al. (41) have pointed out that indirect evidence suggests that a lower proportion of the available motor units are activated during maximal Ecc compared with Con muscle actions, implying that there may be more potential for increasing motor unit recruitment and iEMG with Ecc than Con training. Although we also found lower iEMG values during maximal Ecc than Con before training, our data do not support this hypothesis, because changes in maximal iEMG after Ecc and Con training were nearly the same, with the exception of maximal iEMG measured during Con muscle actions after Ecc training, which did not change. Maximal iEMG activity during Ecc muscle actions was still lower than during Con muscle actions after training. Whether additional training would increase the maximal EMG activity during Ecc muscle actions up to the level of that during Con muscle actions is unknown. Our data suggest that motor unit activation was not maximal during Con or Ecc testing at the pretest.

The significant changes in strength after Con and Ecc isokinetic training resulted from a combination of muscle hypertrophy and increased neural activation. However, it was not possible to precisely determine the relative importance of the two adaptations. Based on the magnitude of the mean changes, and the correlations between changes in torque and changes in quadriceps CSA and maximal iEMG, muscle hypertrophy and neural adaptations appeared to contribute approximately equally to the changes in strength after both Ecc and Con training. However, a substantial part of the strength change could not be accounted for by these two factors. This finding is interesting but anticipated. Other studies have found that changes in muscle size or maximal iEMG after heavy resistance training are only moderately or poorly correlated with strength changes (12, 22). The iEMG activity measured does not reflect all of the possible neural adaptation to training, and the CSA of the entire quadriceps is not exactly proportional to the CSA of muscle fibers activated during

different muscle actions at different points in the range of motion, nor does it reflect the differences among fiber types in their ability to generate force during muscle contraction at a given velocity. Therefore, percent changes in quadriceps CSA and maximal iEMG should not be expected to sum to the percent change in average muscle torque and strong relationships between changes in measured strength and changes in muscle CSA and maximal iEMG would be surprising.

We hypothesized that increases in strength would be explained by muscle hypertrophy and neural activation when strength was measured with the same muscle action as that used in training and by changes in muscle hypertrophy when strength was measured with muscle actions not used in training. Thus we predicted that the effects of muscle hypertrophy would generalize to different muscle actions but that neural adaptations, because the adaptation would result from a specific pattern of activation, would not. This hypothesis was supported in part. Based on the percent changes and the correlations between the average torque and the muscle CSA and maximal iEMG changes, changes in muscle CSA and neural activation appeared to contribute approximately equally to changes in strength during muscle actions used in training in CTG and ETG. In CTG, changes in muscle CSA and neural activation also appeared to contribute approximately equally to changes in strength during Ecc muscle actions not used in training; i.e., the maximal iEMG and torque changes were almost as large when measured during muscle actions not used in training as those used in training. Thus the effects of Con training generalized to Ecc muscle actions. For ETG, the pattern of changes was different; the strength and iEMG changes measured during Ecc muscle actions were greater compared with during Con muscle actions, and there was little generalization of the effects of Ecc training to Con muscle actions. For both CTG and ETG, the strength of the relationships between torque changes and changes in muscle CSA and iEMG were poorer for muscle actions not used in training, indicating that factors other than the measured changes in quadriceps CSA and maximal iEMG explained more of the change.

An interesting finding was that there was no significant increase in Con strength after Ecc training, despite significant muscle hypertrophy. Muscle hypertrophy without increased strength measured in a type of muscle action not used in training but involving the same muscles has been observed by others. Sale et al. (39) found that leg press weight training increased leg press 1 repetition maximum strength by 29% and CSA of the left and right knee extensors measured by computerized axial tomography scanning by 11%. Isometric knee extension strength, electrically invoked knee extensor peak twitch torque, and knee extensor motor unit activation measured by the interpolated twitch method were not increased. Sale et al. suggested that failure to increase strength despite significant muscle hypertrophy might be the result of a decrease in specific tension or neural adaptations that reduce strength such as inhibition of agonists or increased

cocontraction of antagonists. Data from two other studies on older men (2, 10) followed the same pattern. In our data, mean specific tension, calculated from the average torque and quadriceps CSA during maximal Con muscle actions, remained constant and maximal iEMG did not change significantly in ETG. Strength increases measured during Con muscle actions by CTG and during Ecc muscle actions by ETG were accompanied by increases in specific tension and maximal iEMG. Because we did not have measurements that would rule out changes in motor unit activation as a contributing factor, changes in motor unit activation as well as muscular adaptations could have contributed to the increased torque per unit CSA. Thus failure for strength to increase during Con muscle actions by ETG appears to be explained by the absence of positive neural adaptations that were evident in CTG during testing in both modes and in ETG during testing with Ecc muscle actions.

We conclude that gains in strength after Con and Ecc isokinetic training are highly dependent on the muscle action used for training and testing. Ecc is more effective than Con isokinetic training for developing strength in Ecc isokinetic muscle actions, and Con is more effective than Ecc isokinetic training for developing strength in Con isokinetic muscle actions. Ecc training appears to provide a greater mode-specific stimulus for strength increase because it increases Ecc strength more than Con training increases Con strength. In most activities, Con and Ecc muscle actions are employed consecutively, suggesting that training for most purposes should involve both types of muscle actions. Increases in muscle hypertrophy are slightly greater with Ecc compared with Con training, and neural adaptations are similar but are dependent on training and test mode. Muscle hypertrophy and neural adaptations contribute to strength increases consequent to both Con and Ecc isokinetic training.

The authors thank St. Mary's Hospital, Athens, GA, for providing MRI services.

This study was supported by a grant from the Foundation for Physical Therapy.

Address for reprint requests: E. J. Higbie, Georgia State Univ., Dept. of Physical Therapy, College of Health Sciences, Univ. Plaza, Atlanta, GA 30303-3083.

Received 25 May 1995; accepted in final form 10 June 1996.

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