Adaptive responses to muscle lengthening and shortening in humans

TIBOR HORTOBÁGYI, JEFF P. HILL, JOSEPH A. HOUMARD, DAVID D. FRASER, NANCY J. LAMBERT, AND RICHARD G. ISRAEL
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Hortobágyi, Tibor, Jeff P. Hill, Joseph A. Houmard, David D. Fraser, Nancy J. Lambert, and Richard G. Israel. Adaptive responses to muscle lengthening and shortening in humans. *J. Appl. Physiol.* 80(3): 765–772, 1996.—We tested the hypothesis that exercise training with maximal eccentric (lengthening) muscle actions results in greater gains in muscle strength and size than training with concentric (shortening) actions. Changes in muscle strength, muscle fiber size, and surface electromyographic (EMG) activity of the quadriceps muscle were compared after 36 sessions of isokinetic concentric ($n = 8$) or eccentric ($n = 7$) exercise training over 12 wk with use of a one-leg model. Eccentric training increased eccentric strength 3.5 times more (pre/post 46%, $P < 0.05$) than concentric training increased concentric strength (pre/post 13%). Eccentric training increased concentric strength and concentric training increased eccentric strength by about the same magnitude (5 and 10%, respectively, $P > 0.05$). Eccentric training increased EMG activity seven times more during eccentric testing (pre/post 86%, $P < 0.05$) than concentric training increased EMG activity during concentric testing (pre/post 12%). Eccentric training increased the EMG activity measured during concentric tests and concentric training increased the EMG activity measured during eccentric tests by about the same magnitude (8 and 11%, respectively, $P > 0.05$). Type I muscle fiber percentages did not change significantly, but type IIa fibers increased and type IIb fibers decreased significantly ($P < 0.05$) in both training groups. Type I fiber areas did not change significantly ($P > 0.05$), but type II fiber area increased ~10 times more ($P < 0.05$) in the eccentric than in the concentric group. It is concluded that adaptations to training with maximal eccentric contractions are specific to eccentric muscle actions that are associated with greater neural adaptation and muscle hypertrophy than concentric exercise.

eccentric exercise; muscle fibers; electromyography

CLASSICAL VIEWS hold that gains in muscle strength and size are directly proportional to the magnitude of functional overload (1, 28). Overload stimulates protein synthesis and slows degradation (3), resulting in a net increase in the size of individual muscle fibers and the whole muscle. However, the magnitude of mechanical, metabolic, and neural stimuli varys according to the type of muscle contraction, as dictated by the force-velocity relationship (21). When a skeletal muscle actively shortens (i.e., concentric contraction), the force, hence the mechanical stimulus, is less than the forces and mechanical stimuli during lengthening (eccentric contraction).

Several studies have compared the effects of resistive training with concentric and/or eccentric actions, postulating that eccentric training should result in superior gains in muscle strength and size due to the greater overload represented by muscle lengthening. However, no consensus has emerged. Whereas some authors have reported benefits from incorporating eccentric actions into resistive exercise paradigms (8, 22), others have reported no superiority of eccentric training over concentric training to induce greater strength gains (20, 29). These latter studies seem to support the premise of a general strength component (15, 16); i.e., strength gains can be achieved by any method as long as force levels exceed a critical threshold. The published data are also discrepant on hypertrophy; some authors report significantly more hypertrophy with muscle lengthening (13), whereas others report similar changes (20) or no changes (5) after training with the two modes of resistive exercise.

Several recent studies suggest that muscle activation may not be complete during maximal eccentric compared with concentric contractions (12, 31). This lack of complete activation may be due to differences in central drive and/or in the processes involved in the transformation of axonal action potential to sarcolemmal action potential, i.e., neuromuscular propagation (9). Submaximal muscle activation could represent a greater reserve for neural adaptation to repeated eccentric contractions. In addition, at the same activation level, forces are 20–30% greater during eccentric than during isometric contractions in humans (9, 21). This greater loading could provide a greater mechanical stimulus to muscle fibers for hypertrophy (3). Thus the aim of the present study was to test the hypothesis that maximal eccentric exercise training brings about greater neuromuscular adaptations through neural as well as hypertrophic mechanisms than does maximal concentric training.

METHODS

Subjects and design. Table 1 describes the physical characteristics of the 21 sedentary male volunteers who were randomly assigned to one of three groups: eccentric training (Ecc; $n = 7$), concentric training (Con; $n = 8$), and control (Kon; $n = 6$). A subject was included in the study if he did not participate in resistive training for ≥1 yr before the study, was free of lower extremity orthopedic problems, and agreed to sign an informed consent form.

Figure 1 depicts the experimental design. The three groups of subjects were tested twice initially (*week 0*), once at *week 6* during training, and once after 12 wk of training (*week 12*). Two initial testing sessions, 3 days apart, were used to assess the reliability of the strength and electromyographic (EMG) measures. Strength and EMG were measured, and a percutaneous muscle biopsy of the vastus lateralis was performed on each leg. Biweekly blood samples were drawn, and thigh muscle soreness was subjectively evaluated weekly on a

Table 1. *Physical characteristics of the subjects*

	Ecc ($n=7$)	Con ($n=8$)	Kon ($n=6$)
Age, yr	20.1 ± 0.5	21.3 ± 1.6	22.5 ± 1.1
Height, cm	173.1 ± 2.0	176.6 ± 1.9	176.1 ± 1.7
Mass, kg	73.9 ± 1.9	76.5 ± 3.9	75.8 ± 7.0

Values are means ± SE. Ecc, eccentric training; Con, concentric training; Kon, control.

questionnaire. The subjects in the control group were subjected to all testing except muscle biopsy and blood sampling, and they did not train.

Strength testing and EMG. Unilateral maximal voluntary isometric and isokinetic eccentric and concentric strength of the left knee extensors and flexors was measured with a dynamometer (Kin-Com, 500H, Chattecx, Chattanooga, TN). Subjects sat with knees and the hip at a joint angle of 1.57 rad (90°) and arms folded in front of the chest. The anatomic zero was set at a knee angle of 3.14 rad. Extraneous 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. Torque was measured by a strain gauge embedded in the ankle cuff. Gravity-corrected force was computed by the software based on lever arm length and torque data. Familiarization with the dynamometer included two trials of 50, 75, and 90% of perceived maximal isometric and dynamic contractions at each speed separated by 1 min of rest.

Maximal isometric force was measured at a knee angle of 2.36 rad. Two maximal-effort 5-s trials were performed with 1 min of rest between trials. Maximal concentric and eccentric strength of the knee extensors and flexors was measured at 1.05, 2.09, and 3.14 rad/s, but only the data at 1.05 rad/s for the quadriceps muscle are presented. Subjects performed two trials with a 1-s pause at either end of the range of motion to avoid the facilitating effects of the prior 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 concentric and eccentric force-angle curves were digitized at a constant angle of 2.36 rad. The average of two trials was used as the criterion measure. Reliability, as estimated with an intraclass correlation coefficient (R) over 2 days and two trials, was acceptable and ranged from $R = 0.74$ (eccentric 3.14 rad/s) to $R = 0.92$ (concentric 3.14 rad/s). There were no significant trials or days effects for any of the strength variables. The coefficient of variation ranged from 6.9 to 16.7% for strength and from 7.8 to 32.6% for the EMG variables.

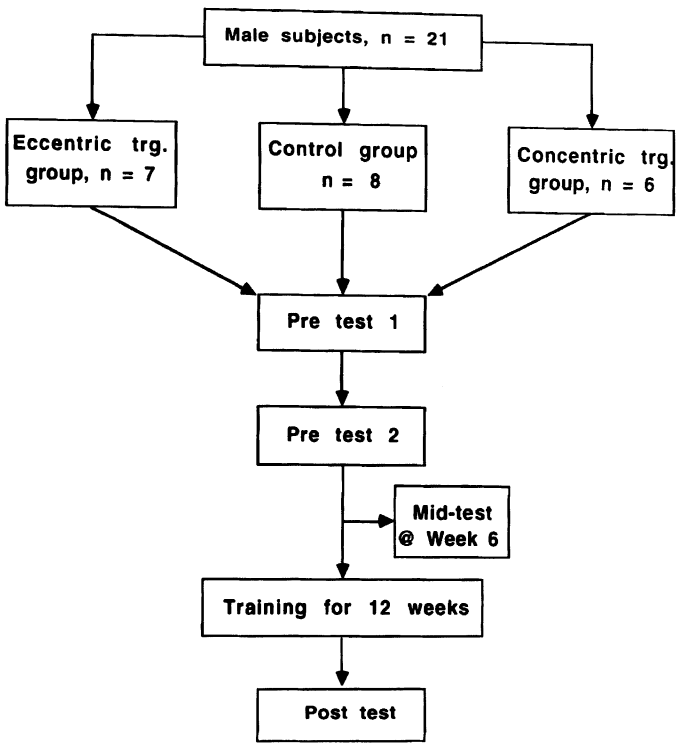

Fig. 1. Experimental design.

According to standard procedures (9), the bellies of the vastus lateralis and biceps femoris and the lateral aspect of the knee joint were shaved and washed with alcohol. We report EMG data only for the qudriceps muscle. Two electrocardiogram electrodes, spaced 2.5 cm apart, were placed on each muscle belly and one ground electrode was placed on the lateral aspect of the uninvolved knee. The electrode sites were marked weekly with an indelible marker for reliable repositioning. The signals were preamplified (model HDX-82, Oxford Medical, Oxford, UK) with a nominal gain of 1,000, input impedance of 0.5 MΩ, bandwidth of 0.4–400 Hz, and common mode rejection ratio ≥100 dB. The signal passed through an isolation amplifier for patient safety, a buffer amplifier, and then a 60-Hz notch filter. The signal was then band-pass filtered between 58 and 490 Hz at 3 dB and passed through a variable-gain amplifier (21–41 dB). The signal from this amplifier was averaged over 10 ms, and the peak root mean square (in μV) values are reported after normalization to the EMG of the isometric tests. Figure 2 depicts a typical force-EMG recording in one subject.

Muscle biopsy and histochemistry. Muscle samples were taken from both thighs before and after training in the exercising groups. Under local anesthesia (3 ml of 1% lidocaine), a 20- to 80-mg sample was removed from the belly of the vastus lateralis by application of suction to a 5-mm Bergström needle. The repeat biopsy was taken 2–3 cm proximal to the first sample at 4- to 5-cm depth. The specimens were dissected of visible fat and connective tissue, mounted in an OCT-trigacanth gum mixture (Miles, Elkhart, IN), frozen in precooled isopentane, and stored in liquid nitrogen. Fiber types I, IIa, and IIb were determined from 10-μm sections by use of myosin adenosinetriphosphatase staining at preincubations of pH 10.3 and 4.54 (4). Additional sections were stained with the α-glycerophosphate technique, and cross-sectional area was calculated from ~25 representative type I and II fibers by computerized digitometry (model 2.0, Autosketch, Sausalito, CA). The total number of fibers counted before and after training averaged 492 ± 37 and 524 ± 54, respectively.

Blood sample. Sampling was done at *pretests 1* and *2* and *weeks 2, 4, 6, 8, 10,* and *12* in the training groups and *pretests 1* and *2* and posttraining in the control subjects. In the morning, a 5-ml blood sample was drawn from an arm vein after a 12-h overnight fast. The samples were centrifuged at 4°C, and the serum was removed and stored at −80°C for further analysis. Serum creatine kinase (CK) was determined with a standard kit (Sigma Diagnostics, St. Louis, MO). All determinations were done in duplicate at biweekly intervals for the duration of the study.

Soreness. Subjects were weekly asked to rate the soreness of the quadriceps muscle on a scale of 1 (no soreness) to 10

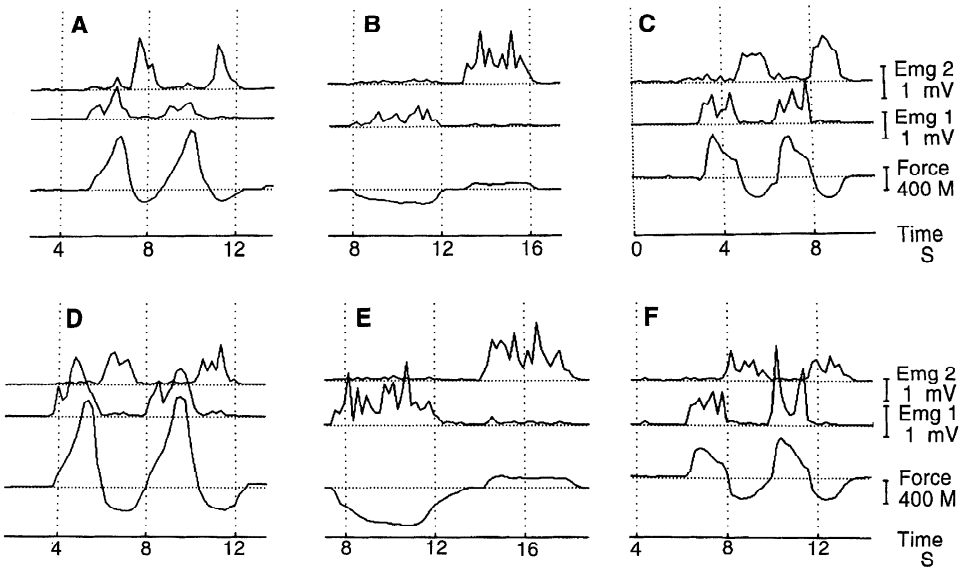

Fig. 2. Typical recording of force and EMG activity in 1 subject who has undergone eccentric training. Eccentric (*A* and *D*; 2 contractions of knee extensors and flexors), isometric (*B* and *E*; 1 contraction of knee extensors and flexors), and concentric (*C* and *F*; 2 contractions of knee extensors and flexors) muscle actions are shown before and after training, respectively. For dynamic actions, speed was 1.047 rad/s and isometric test was done at 2.36-rad inclusive knee angle. Extensor forces are positive deviations, whereas isometric extensor forces are negative deviations. EMG1, vastus lateralis EMG; EMG2, biceps femoris EMG. EMG signals are root mean square. Force calibration bar for isometric test is 800 N. Note substantial gain in eccentric and isometric knee extensor force and virtually unchanged concentric knee extensor and flexor forces.

(extremely sore). This assessment was done at the beginning of the last training session of each week.

Training. The training regimen consisted of 12 wk of isokinetic eccentric (Ecc) or concentric (Con) quadriceps strengthening of the left leg at 1.05 rad/s. Table 2 displays the training protocol. The subjects performed 1,890 maximum-effort repetitions distributed over 36 training sessions fluctuating 4–6 sets of 8–12 repetitions from week to week according to the periodization principle (30). There was a 1-min rest period between sets.

During the last session of each week of training, repetitions of the initial, middle, and final sets were recorded. The initial and final two repetitions of each set were averaged. Percent fatigue was computed in two ways: within a set (initial − final/initial value * 100 within a set) and within a session for a given week (initial value of first set − final value of last set/initial value * 100).

Statistical analysis. The BMDP PC-90 statistical package was used to perform the group (Ecc, Con, Kon)-by-testing mode (eccentric, concentric)-by-time (pre/mid, mid/post, pre/post) repeated-measures analysis of variance for force ratios and EMG ratios, respectively. Instead of the absolute values, the analysis was done on the ratios with use of the isometric value as an internal reference (force and EMG) and to reduce error due to electrode placement (EMG). Fiber type data were analyzed with a group (Ecc, Con)-by-leg (trained, untrained)-by-time (pre, post) repeated-measures analysis of variance.

Table 2. *Training protocol*

Week	Sessions/wk	Sets	Reps/Set	Reps/Session	Reps/wk
1	3	4	8	32	96
2	3	4	10	40	120
3	3	4	12	48	144
4	3	5	8	40	120
5	3	5	10	50	150
6	3	5	12	60	180
7	3	6	8	48	144
8	3	6	10	60	180
9	3	6	12	72	216
10	3	6	8	48	144
11	3	6	10	60	180
12	3	6	12	72	216
Total	36				1,890

Reps, repetitions.

Because of the significant differences in the initial scores between groups, the fiber area data were analyzed with group-by-leg-by-time analysis of covariance with the pretest data as a covariate for type I and II fiber areas, respectively. The percent fatigue data were analyzed by a group (Ecc, Con)-by-set (initial, middle, final)-by-week (initial and final scores for 12 wk) analysis of variance. 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

Strength and EMG. Figure 3 shows the changes in force in absolute values. In the pre-to-post comparison, the eccentric group improved eccentric and isometric force by 116 and 45% and the concentric group improved concentric and isometric force by 53 and 36%. Figure 3 also shows the changes in EMG in absolute values. In the pre-to-post comparison, the eccentric group increased the EMG activity associated with eccentric and isometric contractions by 188 and 58% and the concentric group increased EMG associated with concentric and isometric actions by 28 and 36%. The largest change in the control group was 8%.

Figure 4 shows the percent changes in eccentric-to-isometric and concentric-to-isometric force ratios. There was a significant group (Ecc, Con, Kon)-by-testing mode (eccentric, concentric)-by-time (pre/mid, mid/post, pre/post) three-way interaction ($F_{2,36} = 4.3$; $P = 0.030$). Eccentric training increased eccentric strength 3.5 times more (pre/post 46%, $P < 0.05$) than concentric training increased concentric strength (pre/post 13%). Eccentric training increased concentric strength and concentric training increased eccentric strength by about the same magnitude (5 and 10%, respectively, $P > 0.05$). The largest change in the control group was 4% ($P > 0.05$).

Figure 5 depicts the percent changes in the eccentric-to-isometric and concentric-to-isometric EMG activity ratios in the vastus lateralis. There was a significant group-by-mode-by-time three-way interaction ($F_{2,36} = 4.4$; $P = 0.036$). Eccentric training increased the EMG

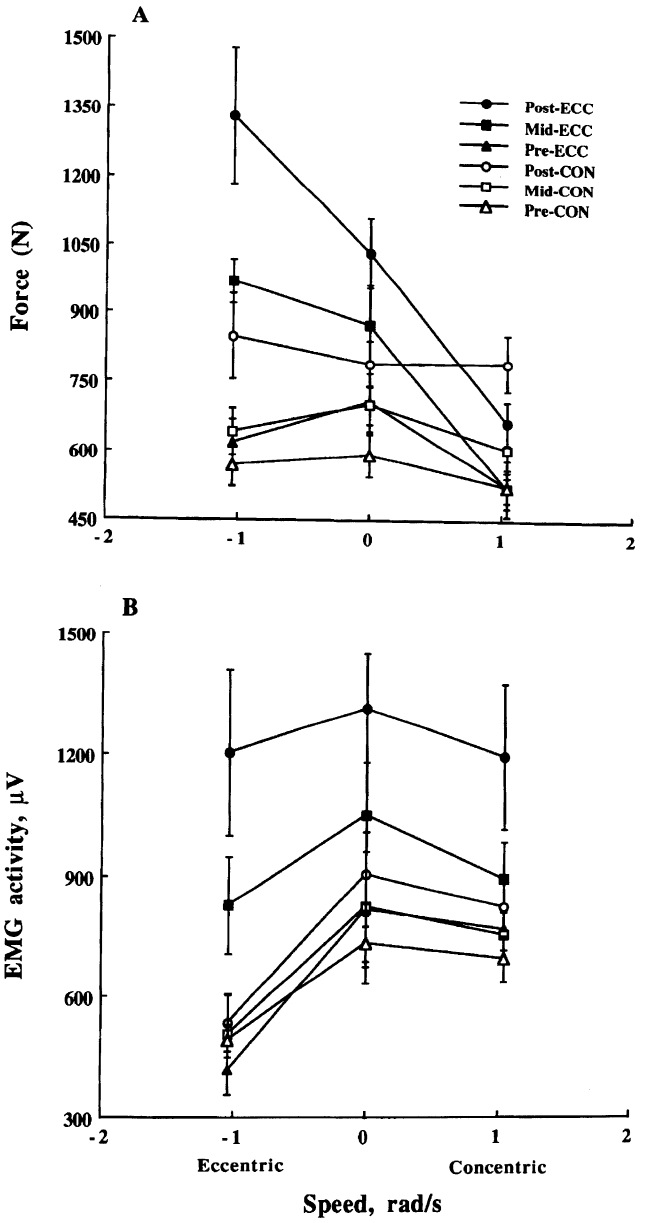

Fig. 3. Changes in knee extensor muscle force (*A*) and vastus lateralis surface peak root-mean-square EMG activity (*B*) in eccentrically (Ecc) and concentrically (Con) trained groups. For clarity, control group's data are not shown. See results of statistical analyses in Figs. 4–6.

activity during eccentric testing seven times more (pre/post 86%, $P < 0.05$) than concentric training increased EMG activity during concentric testing (pre/post 12%). Eccentric training increased EMG activity measured during the concentric test and concentric training increased EMG activity measured during the eccentric test by about the same magnitude (8 and 11%, respectively, $P > 0.05$). EMG activity increased significantly more initially (pre-to-mid) under both training and testing modes, except for the changes in EMG activity measured during eccentric testing after concentric training (Fig. 5*A*, left open bar). The EMG activity of the antagonist biceps femoris muscle did not change significantly ($P > 0.05$) during training or between groups (data not shown). The largest change in the control group was 6% ($P > 0.05$).

Percent fatigue. Figure 6 shows the percent fatigue data during training. No significant two- or three-way group (Ecc vs. Con)-by-set (3 sets)-by-week (12 wk) interactions occurred ($P > 0.05$), but there was a significant group main effect ($P < 0.05$). Over the 12 wk of training, the eccentric group showed an average fatigue rate of 3%, which is actually an increase in force from the beginning to the end during a given session. In contrast, the concentric group demonstrated a −12% fatigue rate, yielding a 15% net between-group difference ($P < 0.05$).

Muscle size. Type I muscle fiber percentage did not change significantly, but type IIa increased and type IIb decreased significantly ($P < 0.05$) in both training groups (Table 3). Analysis of covariance revealed no

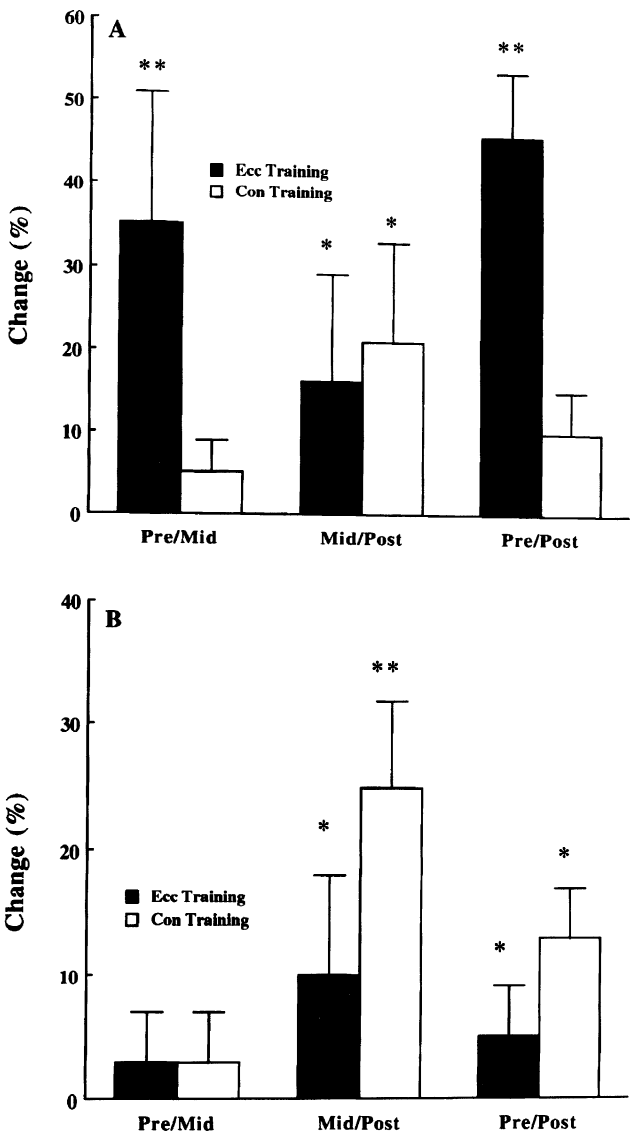

Fig. 4. Percent change in eccentric (1.05 rad/s)-to-isometric (*A*) and concentric (1.05 rad/s)-to-isometric (*B*) force ratios at pre/mid, mid/post, and pre/post in eccentrically trained and trained exercise groups. For clarity, control group's data are omitted. *Significant ($P < 0.05$) change; **significantly ($P < 0.05$) more change than opposite group.

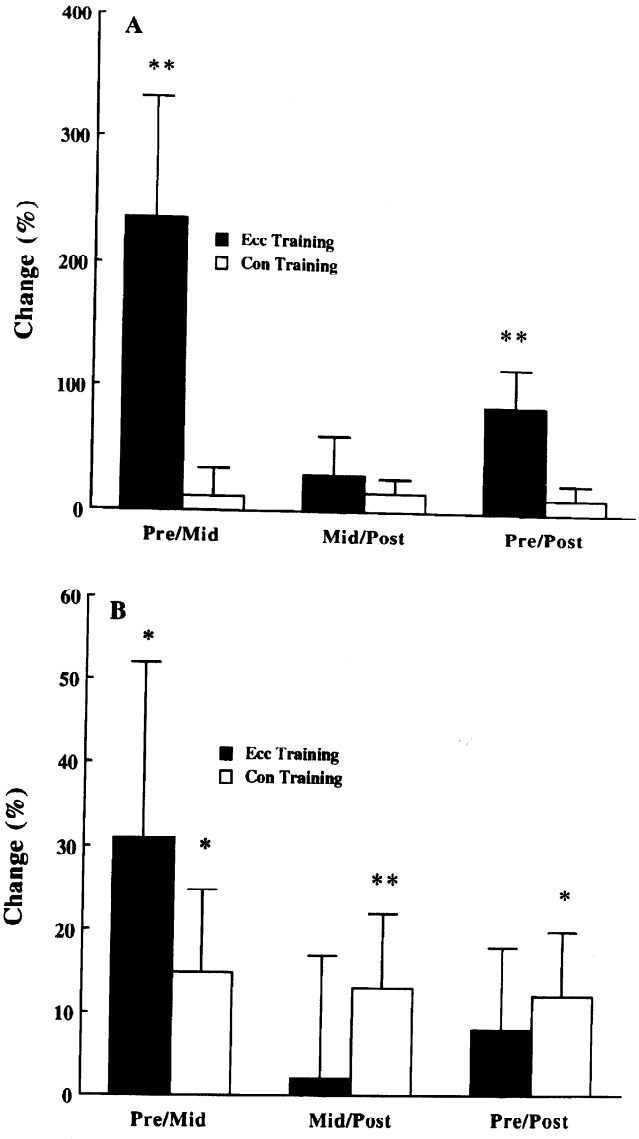

Fig. 5. Percent change in eccentric (1.05 rad/s)-to-isometric (*A*) and concentric (1.05 rad/s)-to-isometric (*B*) EMG ratios of vastus lateralis muscle at pre/mid, mid/post, and pre/post in eccentrically and concentrically trained exercise groups. *Significant ($P < 0.05$) change; ** significantly ($P < 0.05$) more change than opposite group.

significant changes in type I fiber areas ($P > 0.05$; Table 4). After an adjustment for the significant initial differences between groups ($P < 0.05$), type II fiber area increased 10.3 times more ($P < 0.05$), and these fibers were greater after training in the eccentric than in the concentric group ($P < 0.05$). There were no significant changes in fiber type or size of the untrained leg ($P > 0.05$).

CK and soreness. No significant ($P > 0.05$) changes occurred in serum CK level in either group over the 12-wk training period. The highest mean value was 80.4 ± 33.7 and 162.4 ± 69.7 IU/l in the eccentric and concentric groups, respectively.

Muscle soreness of the vastus lateralis, subjectively assessed by the subjects on a scale of 1–10, was not different between groups and did not change significantly over the 12-wk training period. The highest value was 2.9 ± 1.1 at *week 9* in the eccentric group and 1.5 ± 0.9 also at *week 9* in the concentric group.

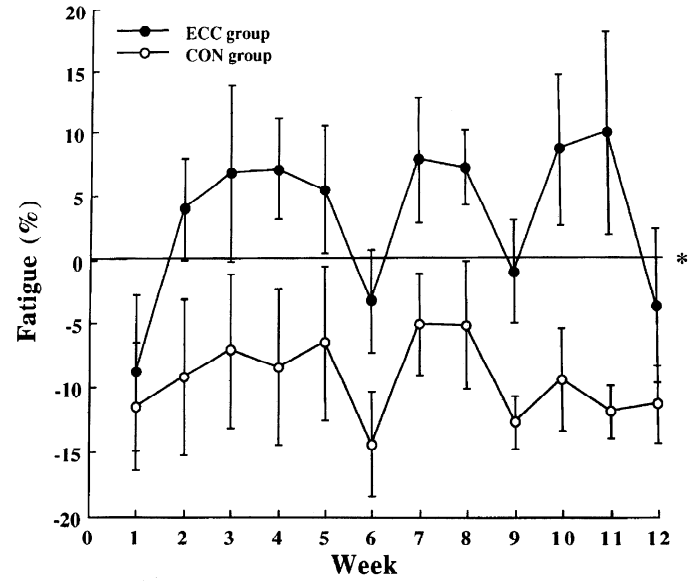

Fig. 6. Percent fatigue during eccentric (●) and concentric training (○). Each symbol corresponds to percent fatigue during last session of each week. Error bars, SE. *Significant between-group difference over 12 wk ($P < 0.05$).

DISCUSSION

Strength and muscle adaptations. There were two important observations concerning muscle strength and size. One was that eccentric training increased eccentric strength 3.5 times more than concentric training increased concentric strength, and strength gains were similar in the mode opposite to which training occurred. The second was that type II muscle fiber area increased ~10 times more after eccentric than concen-

Table 3. *Changes in fiber type composition consequent to eccentric and concentric training*

	Pretraining	Posttraining	Change
	Trained leg		
Type I			
Ecc	47.7 ± 2.7	42.7 ± 2.4	−5.0 ± 2.6
Con	48.9 ± 2.1	47.1 ± 2.1	−1.8 ± 2.1
Type IIa			
Ecc	38.1 ± 3.8	50.0 ± 2.2	11.9 ± 3.0*
Con	39.5 ± 1.9	48.2 ± 2.7	8.7 ± 2.3*
Type IIb			
Ecc	14.1 ± 1.4	7.4 ± 1.9	−6.7 ± 1.7*
Con	11.7 ± 1.8	4.7 ± 1.0	−7.0 ± 1.4*
	Untrained leg		
Type I			
Ecc	47.5 ± 2.1	48.3 ± 1.9	0.8 ± 1.9
Con	52.3 ± 3.0	47.7 ± 3.4	−4.6 ± 3.2
Type IIa			
Ecc	39.1 ± 2.7	42.3 ± 1.3	3.2 ± 2.0
Con	38.0 ± 2.7	42.9 ± 3.5	4.9 ± 3.1
Type IIb			
Ecc	13.4 ± 1.1	16.2 ± 6.2	2.8 ± 3.6
Con	9.7 ± 1.9	9.4 ± 1.0	−0.3 ± 1.4

Values are means ± SE in percent. *Significant change ($P < 0.05$).

Table 4. *Changes in fiber areas consequent to eccentric and concentric training*

	Pretraining	Posttraining	Posttraining (Adjusted)*	Change
		Trained leg		
Type I				
Ecc	3,530 ± 331	3,883 ± 298	4,038 ± 263	14.4 ± 4.2
Con	4,261 ± 257	4,609 ± 222	4,473 ± 244	4.9 ± 3.9
Type II				
Ecc	4,168 ± 283	5,535 ± 208	5,742 ± 201	37.8 ± 5.3†
Con	4,935 ± 289	5,269 ± 239	5,088 ± 187	3.1 ± 4.8
		Untrained leg		
Type I				
Ecc	3,329 ± 316	3,487 ± 286	3,581 ± 254	7.6 ± 4.1
Con	4,425 ± 311	4,375 ± 307	4,213 ± 324	−4.8 ± 5.3
Type II				
Ecc	4,163 ± 284	4,248 ± 293	4,246 ± 276	1.9 ± 4.4
Con	4,898 ± 371	4,928 ± 344	4,767 ± 355	−2.7 ± 3.9

Values are means ± SE in μm^2. *Adjusted for pretraining differences by analysis of covariance. †Significantly more change than opposite group ($P < 0.05$).

tric training. Overall these results are in concert with some findings reported previously (7, 15, 22, 23, 32) but are also in disagreement with several other reports (18–20, 26, 29).

Eccentric and concentric training may differently influence the contribution of mechanical and metabolic stimuli to increases in strength per unit cross section of a muscle. It is possible that concentric strength gains after concentric training were primarily caused by a metabolic stimulus. The greater metabolic demand of concentric than of eccentric exercise training is apparent when one considers that combining eccentric actions with concentric leg press results in a similar net caloric cost: 3.5 ± 0.3 and 3.1 ± 0.2 × 10^{-3} (SE) cal/J, respectively (7). This metabolic demand may have placed the muscle in a hypoxic state that in turn induced capillary proliferation (13), leading to an enhanced (predominantly glycolytic) energy delivery.

Fatigue may be one mechanism that can mediate strength gains through increased metabolic flux. Figure 5 provides some evidence for this reasoning. The concentrically trained subjects revealed a force deficit at the end of every session, implying fatigue. However, the link between the subcellular mechanism of metabolic flux and strength gain is unclear. If such a mechanism is nonetheless in operation, then it is surprising that no significant differences occurred in protein synthesis of the rat gastrocnemius between acute and chronic stimulated concentric training (3). Such data would imply that once a threshold of concentric activity is exceeded, no further benefits would ensue in terms of muscle enlargement. Interestingly, in humans, doubling the number of concentric actions doubled strength gains (15%) compared with training with half the number of concentric actions (8%) (13). In contrast, during our training, eccentric muscle force was ~35% greater than concentric force, providing a greater mechanical stimulus for strength and hypertrophy. Similarly, imposing a greater resistance on the rat tibialis anterior by stimulated eccentric contractions resulted in a higher protein synthesis rate, as did an increase in the number of eccentric contractions from 24 to 192 further increase protein synthesis by 15% (3). The increased specific tension by eccentric training in the rat resulted in no fatigue, as was also the case for the eccentrically trained subjects in the present study (cf. Fig. 5). Thus the increased mechanical load seems to be directly related to increases in protein synthesis rates, muscle size, and strength in humans and animals.

Despite the recent description of a human skeletal muscle fiber-specific gene cluster (33), it is unknown whether protein synthesis is greater in the type II fibers, as the preferential enlargement of these fibers would suggest in the present study (Table 3) and, though not as distinctly, in some prior studies (13). One reason for the 10 times greater hypertrophy of the type II fibers in the present study could be a preferential use of these fibers during eccentric actions. Fridén et al. (11) reported greater glycogen depletion in type II fibers after 8 wk of bicycle exercise training using eccentric contractions. Interestingly, a preferential type II fiber hypertrophy occurred even at an intensity as low as 50–60% of the maximal eccentric force in a combined eccentric-concentric leg press paradigm (8, 13). In contrast, eccentric and concentric training resulted in no significant differences in computerized axial tomographic-scanned quadriceps areas (20) or in muscle fiber areas (5). With type II muscle fiber hypertrophy following eccentric training, one would have also expected increases in concentric strength, but this did not occur. Apparently eccentric training resulted in an activation pattern during concentric actions that failed to recruit hypertrophied larger units, leading to a minimal increases in concentric strength.

In summary, according to the specificity principle of exercise training, eccentric training has brought about greater strength gain in the specific contraction type than has concentric training. This greater strength gain seems to be associated with a significant type II muscle fiber hypertrophy. The modest strength gains in the contraction mode opposite to the one used during training may imply a failure in one or more of the events of transformation of axonal action potential to sarcolemmal action potential (9) and/or a different recruitment pattern of muscle fibers during eccentric and concentric contractions.

Neural mechanisms. Eccentric training increased EMG activity during eccentric test contractions about seven times more than concentric training increased EMG activity during concentric test contractions. Our working hypothesis was that eccentric training may lead to greater strength gains caused, at least in part, by a greater neural adaptation. This hypothesis has emerged from two prior findings. One was that untrained individuals displayed depressed forces, especially on the eccentric segment of the force-velocity curve (14), suggesting incomplete muscle activation. Second, EMG analysis of repeated eccentric contractions revealed an incomplete muscle activation in un-

trained subjects (12, 31). Incomplete muscle activation at the initial stages of exercise training would represent a greater reserve for neural adaptation.

Several mechanisms could mediate such increases in EMG activity. Eccentric actions are associated with higher forces at lower EMG activity than concentric actions, possibly because of passive elements (21). Thus an increased EMG activity must emanate from muscle fibers specially adapted to repeated eccentric actions. Data in Table 3 suggest that type II muscle fibers were probably preferentially recruited during eccentric training, leading to a selective recruitment and hypertrophy of the type II fibers. When more of the available type II fibers are recruited after eccentric training, surface EMG activity may increase.

This mechanism, i.e., recruitment of more of the available type II muscle fibers after training, seems also feasible for the following reason. If one wishes to account for an increase in surface EMG activity through an increase in central neural drive during training (9, 21), such an increase could occur from two sources. First, for surface EMG to increase, an increased neural drive must activate a greater number of motor units after than before training. However, there is no evidence for exercise training to increase the number of motor units in humans (9). Second, if there were no more large motor units activated after training, the only alternative for surface EMG to increase is an increase in the discharge rate of motor units. Although Freund (10) concluded that the "force generation in the upper force range is mainly accomplished by firing-rate modulation" (p. 408), there is no evidence to suggest that exercise training actually increases discharge rate as a means for strength gains. Even if discharge rate were increased by training, in large muscles only the final 15% of maximal force is due to a modulation of discharge rate (27), a narrow margin to account for the doubling of eccentric strength observed in the present study.

The mechanism of recruiting more of the available type II muscle fibers after eccentric training is further strengthened by the recent findings that suggest a preferential recruitment of type II motor units during eccentric actions in the human of the triceps surae (25) and first dorsal interosseus (17). Although these observations were made during submaximal eccentric contractions, they seem to correlate with the selective hypertrophy of the type II muscle fibers observed in the present study after eccentric training (Table 4). In addition, selective glycogen depletion of type II muscle fibers after eccentric contractions in the rabbit tibialis anterior (24) and the human quadriceps (11) also seems to validate the hypothesis that the greater strength gains with eccentric training were probably mediated by learning to recruit more of the available type II fibers within a motoneuron pool after training.

Finally on a practical note, subjects in the eccentric group indicated moderate soreness initially and no soreness later, whereas subjects in the concentric group complained throughout the study of the large motivation required to sustain every contraction at a maximal level. This observation correlates well with the data in Fig. 5 that suggest that concentric actions lead to fatigue. We are not advocating pure maximal eccentric regimens to replace conventional conditioning methods; instead we suggest that the benefits of emphasizing eccentric muscle actions in recreational settings and in the rehabilitation of patients with orthopedic (2) or neuromuscular deficits be explored.

In conclusion, adaptations to training with maximal eccentric contractions are specific to eccentric muscle actions that are associated with greater neural adaptation and muscle hypertrophy than concentric exercise. The lack of hypertrophy and moderate strength gains with concentric training is not unusual (6) and once again underscores the important role of muscle lengthening in these adaptive processes.

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REFERENCES

1. **Atha, J.** Strengthening muscle. In: *Exercise and Sport Sciences Reviews*, edited by D. I. Miller. Philadelphia, PA: Franklin Institute, 1981, p. 1–73.
2. **Bennett, J. G., and W. T. Stauber.** Evaluation and treatment of anterior knee pain using eccentric exercise. *Med. Sci. Sports Exercise* 18: 526–530, 1986.
3. **Booth, F. W., and D. B. Thomason.** Molecular and cellular adaptation of muscle in response to exercise: perspectives of various models. *Physiol. Rev.* 71: 541–585, 1991.
4. **Brooke, M. H., and K. K. Kaiser.** The myosin adenosine triphosphatase systems: the nature of their pH lability and sulfhydryl dependence. *J. Histochem. Cytochem.* 18: 670–672, 1970.
5. **Colliander, E. B., and P. A. Tesch.** Effects of eccentric and concentric muscle actions in resistance training. *Acta Physiol. Scand.* 140: 31–39, 1990.
6. **Côté, C., J. Simoneau, P. Lagassé, M. Boulay, M. Thibault, M. Marcotte, and C. Bouchard.** Isokinetic strength training protocols: do they induce skeletal muscle hypertrophy? *Arch. Phys. Med. Rehabil.* 69: 282–285, 1988.
7. **Dudley, G. A., P. A. Tesch, R. T. Harris, C. L. Golden, and P. Buchanan.** Influence of eccentric actions on the metabolic cost of resistance exercise. *Aviat. Space Environ. Med.* 62: 678–682, 1991.
8. **Dudley, G. A., P. A. Tesch, B. J. Miller, and P. Buchanan.** Importance of eccentric actions in performance adaptations to resistance training. *Aviat. Space Environ. Med.* 62: 543–550, 1991.
9. **Enoka, R. M.** *Neuromechanical Basis of Kinesiology.* Champaign, IL: Human Kinetics, 1994.
10. **Freund, H. J.** Motor unit and muscle activity in voluntary motor control. *Physiol. Rev.* 63: 387–436, 1983.
11. **Fridén, J., J. Seger, M. Sjöström, and B. Ekblom.** Adaptive responses in human skeletal muscle subjected to prolonged eccentric training. *Int. J. Sports Med.* 4: 177–183, 1983.

12. **Gravel, D., A. Y. Belanger, and C. L. Richards.** Study of human muscle contraction using electrically evoked twitch responses during passive shortening and lengthening movements. *Eur. J. Appl. Physiol. Occup. Physiol.* 56: 623–627, 1987.
13. **Hather, B. M., P. A. Tesch, P. Buchanan, and G. A. Dudley.** Influence of eccentric actions on skeletal muscle adaptations to resistance training. *Acta Physiol. Scand.* 143: 177–185, 1991.
14. **Hortobágyi, T., and F. I. Katch.** Eccentric and concentric torque-velocity relationships during arm flexion and extension: influence of strength level. *Eur. J. Appl. Physiol. Occup. Physiol.* 60: 395–401, 1990.
15. **Hortobágyi, T., and F. I. Katch.** Role of concentric force in limiting improvements in muscular strength and hypertrophy. *J. Appl. Physiol.* 68: 650–658, 1990.
16. **Hortobágyi, T., F. I. Katch, and P. F. LaChance.** Interrelationships between various measures of upper body strength assessed by different contraction modes: evidence for a general strength component. *Eur. J. Appl. Physiol. Occup. Physiol.* 58: 749–755, 1989.
17. **Howell, J. N., A. J. Fuglevand, M. L. Walsh, and B. Bigland-Ritchie.** Motor unit firing during shortening and lengthening contractions. *Soc. Neurosci. Abstr.* 20: 1759, 1994.
18. **Johnson, B. L.** Eccentric vs. concentric muscle training for strength development. *Med. Sci. Sports* 4: 111–115, 1972.
19. **Johnson, B. L., J. W. Adamczyk, K. O. Tennøe, and S. B. Strømme.** A comparison of concentric and eccentric muscle training. *Med. Sci. Sports* 8: 35–38, 1976.
20. **Jones, D. A., and O. M. Rutherford.** Human muscle strength training: the effects of three different regimes and the nature of the resultant changes. *J. Physiol. Lond.* 391: 1–11, 1987.
21. **Komi, P. V.** Training of muscle strength and power: interaction of neuromotoric, hypertrophic, and mechanical factors. *Int. J. Sports Med. Suppl.* 7: 10–15, 1986.
22. **Komi, P. V., and E. R. Buskirk.** Effect of eccentric and concentric muscle conditioning on tension and electrical activity of human muscle. *Ergonomics* 15: 417–434, 1972.
23. **Lacerte, M., B. J. deLatour, A. D. Alquist, and K. A. Questad.** Concentric versus combined concentric-eccentric isokinetic training programs: effect of peak torque on human quadriceps femoris. *Arch. Phys. Med. Rehabil.* 73: 1059–1062, 1992.
24. **Lieber, R. L., and J. Fridén.** Selective damage of fast glycolytic muscle fibres with eccentric contraction of the rabbit tibialis anterior. *Acta Physiol. Scand.* 133: 587–588, 1988.
25. **Nardone, A., C. Romàno, and M. Schieppati.** Selective recruitment of high-threshold motor units during voluntary lengthening of active muscles. *J. Physiol. Lond.* 409: 451–471, 1989.
26. **Pavone, E., and M. Moffat.** Isometric torque of the quadriceps femoris after concentric, eccentric, and isometric training. *Arch. Phys. Med. Rehabil.* 66: 168–170, 1985.
27. **Person, R. S., and L. P. Kudina.** Discharge frequency and discharge pattern of human motor units during voluntary contraction of muscle. *Electroencephalogr. Clin. Neurophysiol.* 32: 471–483, 1972.
28. **Saltin, B., and P. D. Gollnick.** Skeletal muscle adaptability: significance for metabolism and performance. In: *Handbook of Physiology. Skeletal Muscle*. Bethesda, MD: Am. Physiol. Soc., 1983, sect. 10, p. 555–631.
29. **Smith, R. C., and O. M. Rutherford.** A comparison of eccentric and concentric contractions in strength training in humans (Abstract). *J. Physiol. Lond.* 475P: 26P, 1994.
30. **Stone, M. H., H. O'Bryant, and J. Garhammer.** A hypothetical model for strength training. *J. Sports Med.* 21: 342–351, 1981.
31. **Tesch, P. A., G. A. Dudley, M. R. Duvoisin, and B. M. Hather.** Force and EMG signal patterns during repeated bouts of concentric or eccentric muscle actions. *Acta Physiol. Scand.* 138: 263–271, 1990.
32. **Tesch, P. A., A. Thorsson, and E. B. Colliander.** Effects of eccentric and concentric resistance training on skeletal muscle substrates, enzyme activities and capillary supply. *Acta Physiol. Scand.* 140: 575–580, 1990.
33. **Yoon, S. J., S. H. Seiler, R. Kucherlapati, and L. Leinwand.** Organization of the human skeletal myosin heavy gene cluster. *Proc. Natl. Acad. Sci. USA* 89: 12078–12082, 1992.