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Eccentric ergometry: increases in locomotor muscle size and strength at low training intensities

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LaStayo, P. C., D. J. Pierotti, J. Pifer, H. Hoppeler, and S. L. Lindstedt. Eccentric ergometry: increases in locomotor muscle size and strength at low training intensities. *Am J Physiol Regulatory Integrative Comp Physiol* 278: R1282–R1288, 2000.—Lengthening (eccentric) muscle contractions are characterized by several unusual properties that may result in unique skeletal muscle adaptations. In particular, high forces are produced with very little energy demand. Eccentrically trained muscles gain strength, but the specific nature of fiber size and composition is poorly known. This study assesses the structural and functional changes that occur to normal locomotor muscle after chronic eccentric ergometry at training intensities, measured as oxygen uptake, that do not influence the muscle when exercised concentrically. Male subjects trained on either eccentric or concentric cycle ergometers for 8 wk at a training intensity starting at 54% and ending at 65% of their peak heart rates. The isometric leg strength increased significantly in the eccentrically trained group by 36%, as did the cross-sectional area of the muscle fiber by 52%, but the muscle ultrastructure remained unchanged. There were no changes in either fiber size, composition, or isometric strength in the concentrically trained group. The responses of muscle to eccentric training appear to be similar to resistance training.

oxygen consumption; strength training

STRENGTH GAINS OCCUR when muscle produces force. If the muscle shortens while producing force, it produces concentric (Con) positive work. If it lengthens while producing force, work is done on muscle, resulting in eccentric (Ecc) negative work.[1] In fact, the magnitude of the strength gains seems to be a function of the magnitude of the force produced, regardless if its Ecc or Con work (21, 23, 26, 27). Because much greater force can be produced eccentrically than concentrically (23–25), Ecc training has the capability of "overloading" the muscle to a greater extent, which can result in greater increases in strength (21, 23, 26, 27) and size (22).

Furthermore, the Ecc mode of contraction has another unique attribute. The metabolic cost required to produce force is greatly reduced; muscles contracting eccentrically get "more for less" as they attain high muscle tensions at low metabolic costs. That is, Ecc contractions cannot only produce the highest forces in muscle (hence greater overload; see Refs. 23–25) vs. Con or isometric contractions but do so at a greatly reduced oxygen requirement ($\dot{V}_{O_2}$; see Refs. 1 and 3). This observation has been well-documented since the pioneering work of Bigland-Ritchie and Woods (3) who reported that the oxygen requirement of submaximal Ecc cycling is only $\frac{1}{6}$-$\frac{1}{7}$ of that for Con cycling at the same workload.

Training primarily with Ecc negative work, however, is not commonly used, as Ecc lengthening contractions have historically been interpreted as a "dangerous" mode of muscle contraction.

This is due in part to the common use of high, acute Ecc work rates to produce profound contraction-induced muscle damage (11, 14) and injury (12).

Typically, single bouts of Ecc exercise at high work rates (200–250 W for 30–45 min) result in muscle soreness, weakness, and damage in untrained subjects (however noting that trained subjects had attenuated or no adverse effects; see Refs. 11 and 14). Nonetheless, Ecc contractions abound in normal activities such as walking, jogging, descending/walking down any incline, or lowering oneself into a chair to name just a few. Obviously, these activities occur in the absence of any muscular damage or injury. Likewise, Ecc resistance exercise regimes have been used to increase both the strength and size of muscle.

The focus of this paper is not to document muscle damage, i.e., histological changes or creatine kinase activity, rather, we set out to document whether the muscle necessarily became injured, specifically defined as the inability of the muscle to produce force equal to preexercise levels (12), during Ecc training. Here we adopt a functional definition. If there is no measurable decrement in the muscle's ability to produce force and if muscle soreness is mild, then no functional injury is apparent (12).

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[1] Because work is force × displacement, it is a product of two vectors. Con "positive" work occurs when the muscle produces force while shortening over a distance. When distance is in the opposite direction of the net force generated, as in an activated muscle that is being lengthened, work is "negative" or is Ecc. In Ecc work, the motor or pedals on the Ecc ergometer are doing work on the muscle while the muscle is activated and lengthening, which differs from Con work, which is done by the activated shortening muscle on the motor/pedals. In this paper, we use the term work independent of the sign to designate the force generated by the muscle times the distance the muscle shortens or lengthens. Likewise, the term power (work rate) is used independent of the sign when describing the work rate.

Because muscles contracting eccentrically produce higher force, and require less energy to do so, Ecc training possesses unique features for producing both beneficial functional (strength increases) and structural (muscle fiber size increases) changes in locomotor muscles. For example, because Ecc work can overload muscle at $\dot{V}O_2$ levels that have little or no impact on muscle when the work is performed concentrically, then strength and muscle size increases might be possible in patients who heretofore have difficulty maintaining muscle mass due to severe cardiac and respiratory limitations.

Previously, we demonstrated the feasibility of Ecc training. After 6 wk of increasing intensity, Ecc cycle ergometry, isometric strength increases occurred without detectable muscle injury when performed at low exercise intensities (27). In that study, we did not investigate any muscle structural adaptations, nor did we equalize training intensity, as measured by $\dot{V}O_2$, comparing Ecc training and Con training. Previous studies comparing both Ecc with Con training and its effects on muscle ultrastructure are equivocal, since greater (22), similar (24), or no change (9) in the size of muscle fibers has been noted. Friden (13), using Ecc leg ergometry for 8 wk, suggested structural adaptations can occur that allow muscle fibers to adapt to and defend against the potentially damaging tensions with Ecc contractions.

The purpose of this study was to address the following question: Is it possible to increase the size and strength of locomotor muscle with Ecc training at a training intensity, measured as $\dot{V}O_2$, insufficient to have any structural or functional impact on locomotor muscles when trained concentrically? To address this question, we compared the structural and functional locomotor muscle responses of Ecc and Con cycle ergometry performed at an identical $\dot{V}O_2$ in healthy male individuals over an 8-wk training period.

METHODS

Subjects. Fourteen healthy male subjects with a mean age of 23.9 yr (range, 19–38 yr) were systematically grouped so as to create two groups of seven subjects, each with an equivalent mean peak oxygen consumption ($\dot{V}O_{2\,peak}$). These two groups were then assigned at random to one of the following two exercise training groups: *1*) an Ecc cycle ergometer group or *2*) traditional Con cycle ergometer. After 2 wk of training, one subject in the Con group dropped out, leaving $n = 7$ for the Ecc group and $n = 6$ in the Con group.

Ecc ergometer. An Ecc ergometer was constructed locally with the power train of a standard Monarch cycle ergometer and has been described in detail previously (27). The Ecc ergometer has an adjustable recumbent seat and is driven by a three-horsepower direct-current (DC) motor. The gear ratio from the flywheel to the pedal crank is 1:3.75. All components are mounted to a steel frame. A DC motor controller, with a 0- to 10-V output for both motor speed and load, controls the motor speed, and a magnetic sensor monitors pedal rpm (which is displayed to the rider during the training session).

$\dot{V}O_{2\,peak}$ and heart rate. Each subject performed a $\dot{V}O_{2\,peak}$ test on a traditional Con ergometer, and the subject's peak heart rate (HR_{peak}) was defined as the heart rate obtained at $\dot{V}O_{2\,peak}$. Subjects rode a cycle ergometer at a constant pedal rate of 60 rpm while the work rate was increased by 60 W every 3 min until exhaustion. $\dot{V}O_2$, respiratory exchange ratio, and heart rate were measured (Consentius Technologies, Provo, UT) continuously during the test and were recorded every 30 s and at $\dot{V}O_{2\,peak}$. The test was discontinued, and $\dot{V}O_{2\,peak}$ was determined when the subject could not maintain the desired pedal rate for 30 s despite verbal encouragement and when no further increases in $\dot{V}O_2$ were noted. HR_{peak} was considered an indirect measure of $\dot{V}O_2$ during training due to the linear relationship between $\dot{V}O_2$ and heart rate (4).

Training exercise intensity, frequency, and training. Training exercise intensity was set to a fixed and identical percentage of HR_{peak} (%HR_{peak}) in both groups of subjects, and heart rate was monitored during every training session over the 8-wk training period. %HR_{peak} was progressively ramped for both groups in an identical fashion during the training period, from an initial 54% to a final 65% HR_{peak} (Fig. 1). The training period extended for 8 wk with a progressively increasing frequency and duration of training. During *week 1*, all subjects rode 2 times/wk for 15 min. Training frequency was 3 times/wk for *weeks 2* and *3* at 25–30 min, 4 times/wk at 30 min for *week 4*, and 5 times/wk for 30 min during *weeks 5* and *6*. The frequency of training was decreased to 3 times/wk, but training duration remained at 30 min for *weeks 7* and *8* due to the Ecc subject's subjective feeling of "fatigue." Pedal rpm was identical for both groups (started at 50 rpm and progressively increased to 70 rpm by the 5th wk).

Ergometry work (Ecc and Con). Total work (joules) on the Ecc ergometer per training session was calculated by integrating the work rate (watts), determined directly from a 0- to 10-V output from the motor, which was calibrated to a known work rate, over the total duration of each training session as described previously (27). The total work per training session was calculated on the Con recumbent ergometer by multiplying the work rate displayed on the calibrated ergometer by the duration of each training session.

Rating of perceived exertion. We asked each subject during the last half of each training session to report a rating of perceived exertion (RPE) for their total body exertion as well

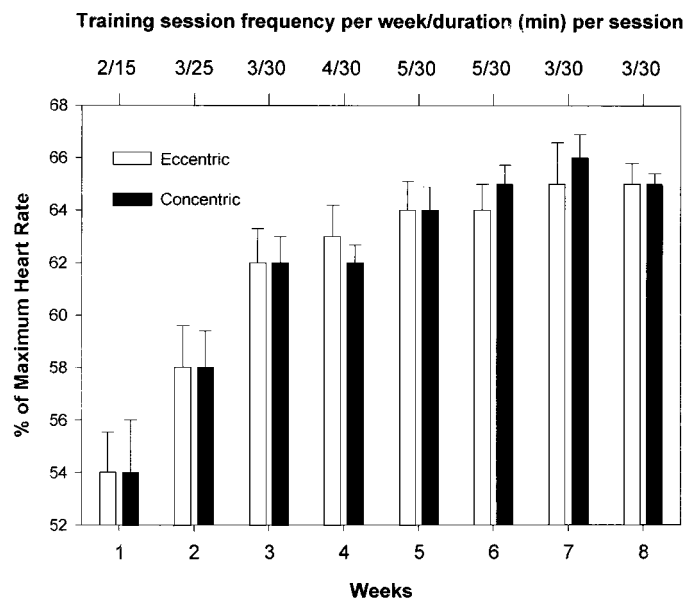**Training session frequency per week/duration (min) per session**

Fig. 1. Eccentric (Ecc; open bars) and concentric (Con; filled bars) training intensities (maximum heart rate) during the 8-wk training period did not differ significantly between groups ($P > 0.05$). Training frequency and duration also remained the same for both groups. Mean values are reported with error bars (1 SE).

as specific leg exertion. A Borg RPE scale (6–20 rating; see Ref. 31) was used as a self-monitoring tool after instructions and training in the use of this scale were provided before the study began.

Leg pain. A visual analog scale (VAS; see Ref. 8) was used to determine the perception of lower extremity muscle soreness after instructions and training in the use of this scale were provided before the study began. Each subject was queried, before and after the 8-wk training period and before each training session, as to their leg pain. They responded by placing a mark on a vertical 14-cm scale anchored by word descriptors (0 = no leg pain, 14 = worst possible leg pain), and the numerical result was determined by measuring where each subject noted leg pain to be along the 14-cm line.

Isometric strength. To assess skeletal muscle strength changes, maximal voluntary isometric knee extension strength was measured (in both the right and left leg) with a Cybex dynamometer (Cybex, Ronkonkoma, NY) before and 10 days after training. The left leg isometric strength was measured weekly during the 8-wk training period. The subject's knee was positioned in 45° of flexion for each of three maximal voluntary isometric trials, the average of which was recorded. All right and left leg measures were referenced to the pretraining left leg value and were recorded as a percent change. This test provided an assessment of both muscle strength and muscle injury (defined here as a loss of muscle force production) that may have occurred (12).

Muscle fiber ultrastructure and fiber area. A single needle biopsy from the vastus lateralis at the midthigh level via the technique of Bergstrom (2) was taken 2 days before the beginning of the study and 1–2 days after the 8-wk study ended. The subjects did not perform any physical exercise for 24 h before the biopsy and did not change their diet significantly with regard to carbohydrate and fat intake. A portion of the muscle tissue sample was immediately frozen in isopentane, cooled in liquid nitrogen, and processed for fiber area measurements. The remainder of the tissue sample was processed for electron microscopy by fixation in 6.25% glutar-aldehyde buffered in sodium cacodylate as described (19). Stereological analysis was performed via the technique described by Weibel (37). Myofibril, mitochondria, and sarcoplasmic reticulum volume densities were determined by point counting using an Aus Jena projector and Morphometrics software (Bern, Switzerland) for data acquisition and analysis.

To calculate muscle fiber cross-sectional area, a 10-µm-thick frozen cross-section from each muscle biopsy was incubated with a primary antibody for the membrane protein laminin (Sigma), which defines each muscle fiber boundary following the protocol of Pierotti et al. (32). A Zeiss microscope interfaced to a video imaging system (Scion, Frederick, Maryland) was used to store a digital image for analysis. The cross-sectional area of each fiber was determined at an objective magnification of ×10 and was calculated as the total number of pixels within the outlined boundary.

Capillary-to-fiber ratio and density. The capillary-to-fiber ratio was determined by counting the number of capillaries and fibers via capillary and fiber profiles from the electron micrographs (37). The capillary density, capillaries per muscle fiber area, was calculated using the capillary profiles divided by the mean cross-sectional area of the muscle fiber assessed from the frozen cross sections of each subject's muscle biopsy (37).

Statistical analysis. Model I fixed-effects ANOVAs (2-way ANOVA, 1-way repeated-measures ANOVA, and a 2-way repeated-measure ANOVA) were used to evaluate the data (34). In all cases, the alpha level of significance was set at 0.05. A Student-Newman-Keul's method (10) for all pairwise multiple comparisons was performed when indicated.

When differences in an individual's performance across treatment levels were of interest, a repeated-measures design was used. In the repeated-measures design, all subjects were tested under all treatment conditions. When independent groups (each group's data pooled independently) were compared, a traditional ANOVA was used. Two-way ANOVAs were used when two independent variables were assessed and when their main effects were of importance. Two-way designs were used for both ANOVAs and repeated-measure ANOVAs. One-factor designs were used only for repeated measures.

RESULTS

$\dot{V}_{O_{2peak}}$ *and heart rate.* There was no significant $\dot{V}_{O_{2peak}}$ difference within or between the two groups before [Ecc group mean $\dot{V}_{O_{2peak}}$ = 51.4 ± 43 (SE) ml·kg^{-1}·min^{-1}; Con group mean $\dot{V}_{O_{2peak}}$ = 52.2 ± 4.8 ml·kg^{-1}·min^{-1}] or after training (Ecc group mean $\dot{V}_{O_{2peak}}$ = 45.5 ± 3.5 ml·kg^{-1}·min^{-1}; Con group mean $\dot{V}_{O_{2peak}}$ = 46.9 ± 6.3 ml·kg^{-1}·min^{-1}), nor was there a difference in the HR$_{peak}$ (Ecc group: mean pretraining = 206 ± 1.9, mean posttraining = 203 ± 2.3; Con group: mean pretraining = 202 ± 4.2, mean posttraining = 201 ± 3.9).

Training exercise intensity and ergometry work (Ecc and Con). Ecc and Con cycle ergometry training workloads increased progressively as the training exercise intensity increased over the weeks of training. Both groups exercised at the same %HR$_{peak}$, and there was no significant difference between groups at any time point during the training (Fig. 1). This increase in work (as assessed with a between-group analysis), however, for the Ecc group was significantly greater ($P < 0.0001$) than the Con group. A significant group times week interaction ($P < 0.0001$) was also evident (Fig. 2). By the 8th wk of training, when both groups were exercis-
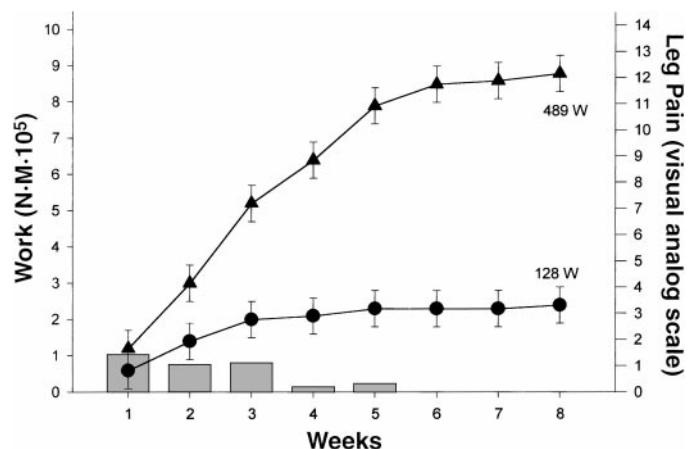

Fig. 2. Amount of Ecc (▲) and Con (●) work [here we use the term "work" independent of the sign (+ or −) to designate the force generated by the muscle × the distance the muscle shortens or lengthens] performed during the 8 wk of training. Ecc and Con workloads were significantly different between groups ($P < 0.0001$). Mean values are reported with error bars (1 SE). Leg pain, as measured by the visual analog scale, was present only in the Ecc group (bars) during *weeks 1–5* and was absent thereafter. No leg pain was noted in the Con group at any time.

ing at an intensity of 65% of HR_{peak}, the Ecc work rate (power) was nearly four times greater (489 W) than the Con group (128 W).

RPE. The perceived exertion of the legs by the Ecc group, as measured by the RPE, was significantly greater ($P = 0.001$) than the Con group over all weeks of training, but no differences between groups were noted in the perceived exertion of the body between the two groups (Fig. 3).

Leg pain. During the first 4–5 wk of cycle ergometry, statistically significant differences ($P = 0.001$) in leg pain were noted between the Ecc and Con groups on the 14-cm VAS (Fig. 2). However, it should be noted that there was no leg pain reported in the Con group and very little in the Ecc group. There was no evidence of muscle injury, as there was no decline in leg strength (Fig. 4).

Isometric strength. Overall significant isometric strength increases were noted in the Ecc group over 7 of the 8 wk of training ($P < 0.0001$), whereas no significant strength changes occurred in the Con group at any time period (Fig. 4). The Ecc improvements (as compared with the pretraining left leg strength) 10 days after the 8-wk training period were significant, as there was a leg times pretraining/posttraining interaction ($P = 0.01$) with a 46% increase in the left leg and a 26% increase in the right leg. The right leg was not tested on the Cybex dynamometer, except for pretraining and posttraining, to control for any potential learning effect that might have occurred during the weekly strength testing session. Therefore, one should conservatively consider the posttraining right leg isometric strength value (26% increase for the Ecc group) as the unbiased minimum estimate of the strength increase, as the apparent left leg strength was higher in both groups.

The Con group showed no significant improvement in isometric leg strength in either leg comparing the pre- and posttraining measurements. No loss in strength was noted at any time in the Ecc group, which is

Fig. 4. Isometric knee extension strength changes pretraining (pre) and posttraining (post) and over the 8-wk training period. All percentage values are referenced to the pretraining left leg value, and different letters denote statistical significance ($P < 0.05$). Isometric strength improvements for the left leg were significantly greater ($P < 0.0001$) every week (except *week 2*) for the Ecc (▲) group. No changes in strength were noted in the Con (●) group at any time. There was a significant right leg (△)/left leg × pre/posttraining interaction for the Ecc group ($P = 0.012$), but no interaction [right leg (○)] occurred for the Con group. Mean values are reported with error bars (1 SE).

consistent with no evidence of muscle injury. Rather, significant strength improvements were noted every week for the Ecc group, with the exception of *week 2*, whereas the Con group's isometric strength never changed from the pretraining strength level (Fig. 4).

Muscle fiber ultrastructure and fiber area. There was no difference ($P > 0.05$) in the pretraining to posttraining volume densities of either myofibers, mitochondria, or sarcoplasmic reticulum in the Ecc or Con group (Table 1). The cross-sectional area (μm^2) of the fibers in the Ecc group significantly increased by 52% ($P = 0.003$) from pre- to posttraining. In contrast, there was no significant change in fiber area of the Con group (Fig. 5).

Capillary-to-fiber ratio and density. The capillary density, defined as capillary number per unit area of muscle fiber, was unchanged by training in both the Ecc and Con groups (Fig. 6). The capillary-to-fiber ratio, however, in the Ecc group did increase significantly ($P = 0.001$) from 0.93 to 1.37 (47% increase) after 8 wk
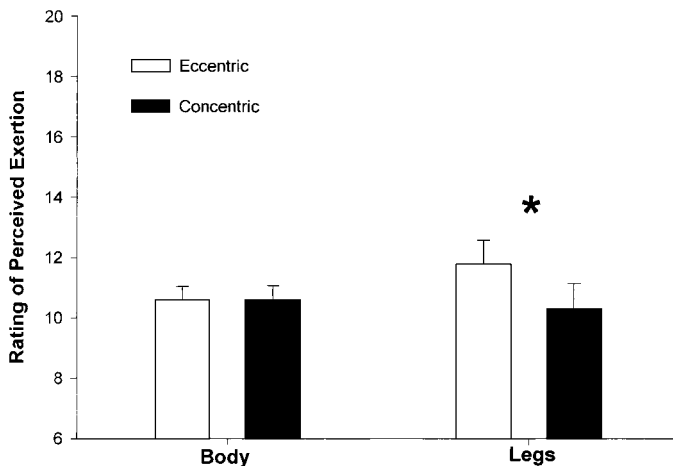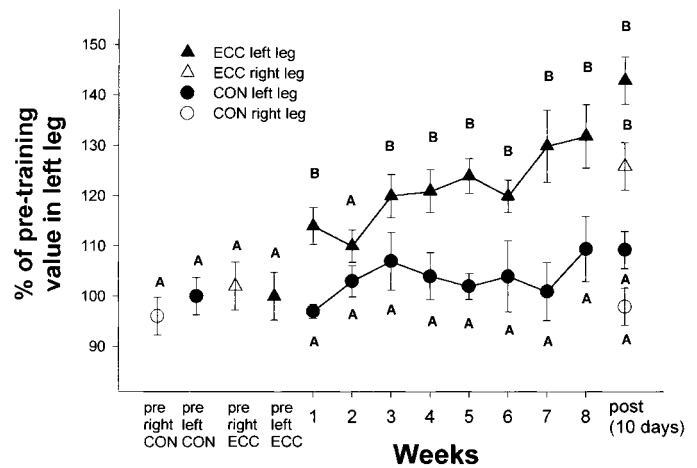

Fig. 3. Rating of perceived exertion for the body and legs during the exercise training period using the Borg scale. Perceived exertion for the body was not significantly different between the Ecc (open bars) and Con (filled bars) groups. *Perceived exertion of the legs, however, was significantly greater ($P = 0.001$) in the Ecc group over the 8-wk training period. Mean values are reported with error bars (1 SE).

Table 1. *Pre- and posttraining volume densities of myofiber, mitochondria, and sarcoplasmic reticulum in the muscle fiber of the Ecc and Con groups*

	Eccentric		Concentric	
	Pre	Post	Pre	Post
Myofiber	90.7 ± 1.0	90.8 ± 0.8	87.6 ± 1.0	91.1 ± 0.8
Mitochondria	5.1 ± 0.4	5.0 ± 0.5	6.3 ± 0.8	4.0 ± 0.3
Sarcoplasmic reticulum	2.5 ± 0.3	3.3 ± 0.2	4.7 ± 0.7	3.8 ± 0.7

Values are means ± SE. Ecc, eccentric; Con, concentric; Pre, pretraining; Post, posttraining. There were no significant pretraining/posttraining differences.
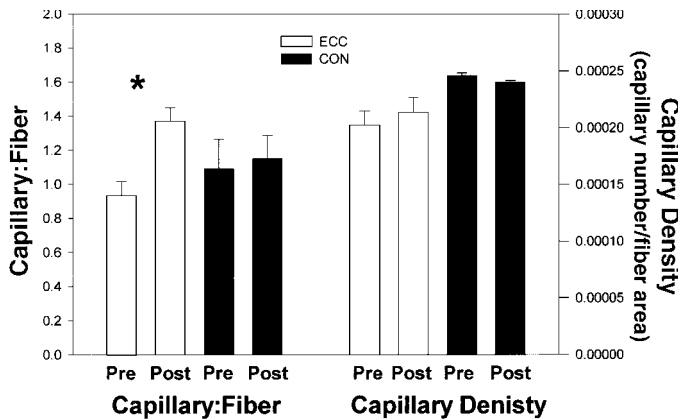
Fig. 5. Fiber cross-sectional area: pretraining and posttraining for the Ecc (open bars) and Con (filled bars) groups. *Ecc fiber area significantly larger ($P = 0.003$) posttraining. No fiber area change was noted for the Con group. No between-group pretraining values were significantly different. Mean values are reported with error bars (1 SE).

of training, whereas no change occurred in the Con group (Fig. 6).

DISCUSSION

Chronic Ecc training is a novel exercise approach that can increase the size and strength of muscle at very low energy demand, hence $\dot{V}O_2$. This study was designed to determine if the locomotor muscles undergo structural and functional changes after 8 wk of Ecc resistance training on a cycle ergometer with healthy subjects. In particular, we examined the following question related to Ecc training. If both the Ecc and Con groups train at a low intensity, i.e., a $\dot{V}O_2$ level unlikely to result in strength or muscle size changes in the Con group, could isometric strength improvements and/or muscle fiber hypertrophy occur in the Ecc group? To probe this question, we progressively ramped the
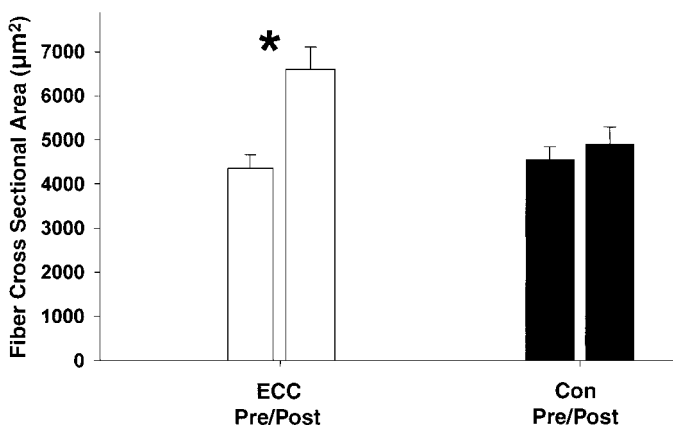

Fig. 6. Capillary-to-fiber ratio and capillary density before and after training. Ecc (open bars) capillary-to-fiber ratio significantly (*$P = 0.001$) increased posttraining (47%), paralleling the increase noted in fiber cross-sectional area, whereas the Con (filled bars) group did not increase. Because the capillary density is a measure of capillary number per area of muscle fiber, there was no change in the Ecc group, nor was there any change in the Con group. No between-group pretraining values were significantly different. Mean values are reported with error bars (1 SE).

Ecc and Con training exercise intensity, %HR$_{peak}$, yet kept it equal in both groups over an 8-wk training period to avoid muscle injury yet still provide "overload" to the Ecc-trained group.

The results of this study demonstrate that, if the training exercise intensity is ramped up and equalized for both groups over the first 5 wk and then maintained for three additional weeks, large differences in muscle force production, measured as total work, result comparing the Ecc and Con groups. This increased force production in the Ecc group apparently stimulated significant increases in isometric strength and fiber size, neither of which occurred in the Con group.

There have been relatively few studies documenting the effectiveness of specific Ecc exercises for increasing muscular strength (21, 23, 26, 27) due largely to the prevailing perception that the high muscle tensions produced with Ecc work produce pain, weakness, and significant muscle damage (11, 14). However, when the Ecc workload starts low and is progressively ramped over a few weeks and then maintained at high levels for several more weeks, the pain associated with Ecc work is nearly eliminated, and muscular strength can be greatly improved without muscle injury (27). Because the production of muscular force above the levels used in normal everyday activities (overloading) is a major stimulus for strength and size increases (35), strength increases follow from the high forces developed with Ecc activity. Furthermore, these high Ecc forces and strength gains are made at $\dot{V}O_2$ levels that result in neither strength nor structural changes when similar exercise is performed concentrically (27).

In this study, we used the left leg pretraining isometric strength value as the reference point for all subsequent left or right leg strength values. The left leg isometric strength increased weekly (with the exception of *week 2*), and the greatest increase occurred 10 days after the training stopped. We speculate that the 10-day posttraining period may have allowed the subjects to rest their legs, as all the Ecc subjects subjectively reported that their legs felt "tired." By *week 7*, all Ecc subjects complained of leg fatigue (which we ascribe to the extremely high work rates, which approached 500 W), thereby prompting the decrease in training frequency from 5 days/wk to 3 days/wk.

Previous studies comparing both Ecc and Con training and the effects on muscle cross-sectional area are equivocal, since greater (22), similar (24), or no change (9) in the size of muscle fibers has been reported. Our finding of increased fiber cross-sectional area in the Ecc-trained group and no change in the fiber area in the Con group is not surprising, since the force production during training was four times greater than the Con workload. The roughly 50% increase in the fiber area of the Ecc group may largely explain the mean isometric strength increase of 36% in both legs. One should not, however, interpret these findings of increases in fiber cross-sectional area as being equivalent to and causally related to increases in isometric strength, since *1*) no measures of whole muscle cross-sectional area, i.e., magnetic resonance imaging or computed tomography

scans, were made, and *2*) the variability in human muscle biopsy samples is high, and the number of fibers sampled with such biopsies is a minute fraction of the number of fibers in whole muscle. Although it remains unclear whether increases in strength can be attributed to fiber hypertrophy (15, 36), hyperplasia (16, 17), or both, in this study both fiber cross-sectional area and isometric strength increased significantly. Despite using leg cycle ergometry, a typical mode of endurance exercise, Ecc ergometry in this study was a strength-training mode of exercise, as evidenced by the strength and fiber size adaptations. Conversely, there was no evidence at the level of the muscle ultrastructure, or with $\dot{V}O_{2peak}$, of an aerobic adaptation typical of an endurance-type response. For example, there was no statistically significant change in the $\dot{V}O_{2peak}$ between or within groups despite a trend toward a decreased $\dot{V}O_{2peak}$ after training. The magnitude of the decrease in $\dot{V}O_{2peak}$, however, was the same in both groups and hence cannot be attributed to Ecc training. It is possible that both groups of college-aged subjects actually experienced a detraining effect, as the change in $\dot{V}O_{2peak}$ was within the range reported in detraining studies (30, 33). All subjects in this study were physically active before the study (and this activity was curtailed during the study), and the 8-wk exercise training intensity ($<65\%$ HR_{peak}) was likely below their regular exercise intensities.

Unlike endurance exercise, resistance training does not promote structural changes associated with aerobic adaptations, such as increased mitochondrial and capillary density (20). In this study, Ecc training mimicked heavy resistance exercise, as there was no change in the volume density of mitochondria or number density of capillaries (although both increased in direct proportion to the apparent increase in fiber size). Although the capillary-to-fiber ratio did increase with Ecc training in this study, the apparent capillary proliferation (47% increase) seemed to be directly related to the muscle cell hypertrophy (52% increase in fiber area). The net result was no change in capillary number density after 8 wk of training. The lack of any change in myofibril and sarcoplasmic reticulum volume density in this study is also consistent with previous strength training findings (7, 28). All structural findings, however, should be interpreted cautiously, as the needle biopsy is only sampling a fraction of the muscle used during exercise, and fiber area measures may be affected by the contracted nature of the samples. As well, this biopsy technique cannot address any potential effects of hyperplasia (16, 17) or neural adaptations (29) that may have occurred with the Ecc training to influence strength changes.

Perspectives

Many elderly individuals with cardiovascular disease cannot exercise at intensities sufficient to provoke improvement in skeletal muscle mass and function (5, 6, 18). The ability of Ecc training to increase locomotor muscle strength and size, with very minimal cardiac demand, may be suited to this population and may

serve as a novel adjunctive rehabilitative countermeasure. As well, the potential for overloading muscle to a greater extent can only be achieved with Ecc work, since the muscle can produce its greatest force eccentrically. Therefore, larger increases in strength and size are possible with Ecc training.

Our long-term goal is to develop an Ecc skeletal muscle training paradigm that could be used in clinical settings to deliver greater stress to locomotor muscles (workloads exceeding 100 W), without severely stressing the oxygen delivery capacity of the cardiovascular system. Patients with, e.g., chronic heart failure and/or obstructive pulmonary disease, etc., could at the very least maintain their muscle mass and perhaps even experience an increase in muscle size and strength using an Ecc biased exercise rehabilitation. In this manner, one problem (cardiovascular limitation) need not escalate into two (cardiovascular limitation and skeletal muscle deterioration) for this population.

Ecc ergometry for 8 wk, in normal healthy subjects, produced isometric leg strength improvements and fiber area increases while training at exercise intensities ($\dot{V}O_2$) that did not promote strength or size increases concentrically. The isometric strength improvements in the Ecc group occurred at identical energy, hence $\dot{V}O_2$, requirements of the Con group. Likewise, the progressive Ecc training did not produce any detectable muscle injury and only very little muscle soreness.

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