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Muscle hypertrophy and fast fiber type conversions in heavy resistance-trained women

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Summary. Twenty-four women completed a 20-week heavy-resistance weight training program for the lower extremity. Workouts were twice a week and consisted of warm-up exercises followed by three sets each of full squats, vertical leg presses, leg extensions, and leg curls. All exercises were performed to failure using 6–8 RM (repetition maximum). Weight training caused a significant increase in maximal isotonic strength (1 RM) for each exercise. After training, there was a decrease in body fat percentage ($p < 0.05$), and an increase in lean body mass ($p < 0.05$) with no overall change in thigh girth. Biopsies were obtained before and after training from the superficial portion of the vastus lateralis muscle. Sections were prepared for histological and histochemical examination. Six fiber types (I, IC, IIC, IIA, IIAB, and IIB) were distinguished following routine myofibrillar adenosine triphosphatase histochemistry. Areas were determined for fiber types I, IIA, and IIAB + IIB. The heavy-resistance training resulted in significant hypertrophy of all three groups: I (15%), IIA (45%), and IIAB + IIB (57%). These data are similar to those in men and suggest considerable hypertrophy of all major fiber types is also possible in women if exercise intensity and duration are sufficient. In addition, the training resulted in a significant decrease in the percentage of IIB with a concomitant increase in IIA fibers, suggesting that strength training may lead to fiber conversions.

Key words: Fiber type conversions — Hypertrophy — Resistance training — Skeletal muscle

Introduction

The biochemical, physiological, and morphological responses of skeletal muscle to endurance training programs have been extensively studied (Saltin et al. 1977; Holloszy and Booth 1980; Howald 1982; Hoppeler 1986). Low-resistance, repeated contractions cause alterations within and around the muscle, increasing its capacity for aerobic metabolism and resistance to fatigue. Conversely, adjustments to training emphazing strength and the anaerobic energy systems are not well defined or understood (Howald 1982; Saltin and Gollnick 1983; Hoppeler 1986; Enoka 1988; Jones et al. 1989). Compared with endurance training, very little is known about the effects of heavy-resistance strength training on skeletal muscle, especially for women.

Strength training uses brief, maximal contractions and requires a very high rate of anaerobic energy production (Tesch et al. 1986). Consequently, increased activities of key enzymes involved in the phosphagen system, anaerobic glycolysis, and glycogenolysis (Thorstensson et al. 1976; Costill et al. 1979), as well as increases in the resting concentrations of muscle creatine and adenosine energy pools (MacDougall et al. 1977; Costill et al. 1979) have been observed following high-intensity strength training programs. In addition, heavy-resistance training produces an increase in muscle strength and size (Costill et al. 1979; MacDougall et al. 1980, 1982). This hypertrophy may be selective for fast-twitch fibers (Thorstensson 1977; Houston et al. 1983; Tesch et al. 1987) and appears to be the result of an absolute increase in the amount of contractile elements within the fibers (MacDougall et al. 1979, 1982; Lüthi et al. 1986).

Despite the large number of women participating in weight training, few studies have thoroughly examined its effect on the development of strength, muscle mass, and fiber composition in women. In addition, previous investigations have used indirect measurements (i.e. girth and percent

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body fat) to predict changes occurring at the cellular level (Brown and Wilmore 1974; Wilmore 1974; Mayhew and Gross 1974; Moritani and DeVries 1979). As a result, most research to date suggests that, unlike men, heavy resistance-trained women gain strength primarily as a result of neuromuscular adaptations with minimal hypertrophy.

Surprisingly, very few studies have been done addressing this issue. To our knowledge, only one investigation (a recently published abstract) has combined muscle biopsies and strength training in women (Bailey et al. 1987). They found a significant increase (21%) in the cross-sectional area of a fast-twitch subtype (type IIB) after resistance training and suggested that women's muscle may indeed be capable of substantial hypertrophy. These data have been supported by increases in whole muscle cross-sectional area (determined from computed tomography scans of the upper arm) of heavy resistance-trained women (Sale et al. 1987; Cureton et al. 1988). Therefore, the potential for muscular hypertrophy in females consequent to resistance training may be severely underestimated. Moreover, intracellular alterations of contractile proteins and possible fiber type conversions, which could affect the ability of the muscle to produce greater force, have not been examined. The purpose of the present study was to investigate the extent of muscular adaptations (hypertrophy and alterations in fiber type composition) in women following a high-intensity strength training program of long duration.

Methods

Subjects. Twenty-nine women volunteered to participate. Of these, 24 completed the program (22.8 ± 3.8 years, 1.63 ± 0.06 m, 60.9 ± 9.0 km). The 5 who did not complete the study had either scheduling conflicts or recurrence of previous injuries. All subjects were informed of the procedures, risks, and potential benefits prior to providing written consent. Ten were involved in regular exercise programs: aerobics (5), field hockey (2), swimming (1), and weight lifting for the upper body (2). These activities ceased 2 months before and throughout the study. Fourteen were inactive and considered sedentary. Throughout the entire period of this investigation, the subjects maintained a detailed training diary containing date, body mass, menstrual phase, weights lifted, repetitions, sets, degree of lifting difficulty, and general impressions of each workout. The subjects were closely supervised at all times and used the proper lifting techniques.

Training protocol. The 20-week training period was divided into a 2-week orientation/preconditioning phase and an 18-week training phase. Practice of the proper lifting techniques and adaptation to the exercises occurred during the first 2 weeks. This was followed by 8 weeks of heavy-resistance training, 1 week of rest, and 10 more weeks of heavy-resistance training.

Training consisted of four basic lower limb exercises to induce increases in the strength of the thigh musculature. These exercises included full squats (knee bends), vertical leg presses, leg extensions, and leg curls. Each repetition was performed slowly (4–6 s) and the subjects rested approximately 3–6 min between sets. The resistance used for each exercise was based upon the subjects' 1 RM (repetition maximum). The 1 RM value is equal to the maximal amount of weight the subject can lift successfully for one repetition. Therefore, 6 RM is equal to the maximal amount of weight the subject can lift successfully for six repetitions. Training sessions were designed to duplicate competitive power training and took place twice a week (Monday and Friday). These workouts consisted of two warm-up sets (10 repetitions/set using approximately 40% and 60% of the 1 RM value) and three sets to failure of 6–8 RM for each exercise (using approximately 80–85% of their 1 RM value). A progressive resistance training principle was employed. Therefore, the weights were increased as necessary to maintain the range of 6–8 repetitions/set with the subjects going until failure in each of these training sets. Every workout began and ended with 10–15 min of flexibility exercises combined with calisthenics.

Strength testing was performed at the beginning and end of the study. In addition, Wednesdays were used once a month as a testing day consisting of a 1 RM for each exercise and anthropometric measurements. For the 1 RM measurements, the subjects performed warm-up sets (10 repetitions/set at 40% and 60%, three repetitions at 75% and one repetition at approximately 90% of the 1 RM weight) followed by an attempt at the target 1 RM determined for each exercise (O'Shea and Wegner 1981). The weight was increased for each subsequent set until failure.

Anthropometric measurements. Body composition and thigh girth were determined at the beginning, every 4 weeks, and at the end of the study. Percent body fat was calculated using skinfold measurements from three sites (anterior thigh, posterior triceps, and suprailiac) (Jackson et al. 1980). Circumferential measurements (using a cloth measuring tape) were taken from the relaxed right lower limb to assess thigh girth at three sites: (1) 5 cm above the superior aspect of the patella, (2) immediately inferior to the gluteal fold, and (3) midway between these two sites.

Muscle biopsies. Muscle biopsies (80–160 mg) were taken 160 mm proximal to the superior border of the patella from the superficial portion (25–30 mm deep to the fascia lata) of the right vastus lateralis muscle using the percutaneous needle biopsy technique of Bergström (1962) as modified by Evans et al. (1982). Depth was gauged by interval markings engraved in the biopsy needles (Mahon et al. 1984). Biopsies were taken immediately prior to the orientation period and at the conclusion of the heavy-resistance training program. Because of minor knee inflammation, some women were biopsied after either 14 weeks (2), 15 weeks (2), or 16 weeks (3) of high-individual variations in muscle fiber type composition (Blom-pre-biopsy site of each subject (using the pre-biopsy scar and depth markings). Repeated pre- and post-biopsies were obtained from most subjects by the use of a double-chop method to ensure adequate sample sizes and to reduce possible intra-individual variations in muscle-fiber type composition (Blomstrand and Ekblom 1982). As such, a mean of more than 2,000 fibers (Table 1) for both the pre- and post-training samples was obtained for analyses. The vastus lateralis muscle was chosen because of its accessibility, fiber composition, and

Table 1. Distribution of fibre types (mean %±SD) before and after training

	I	IC	IIC	IIA	IIAB	IIB	*n*
Before	45.0 ±14.9	1.0 ±1.9	0.5 ±0.8	32.5 ±11.1	4.8 ±2.6	16.2 ±10.7	2537 ±1336
After	48.7 ± 9.9	1.4 ±1.8	1.4 ±1.7	39.3 ± 7.2*	6.5 ±4.9	2.7 ± 4.3*	2149 ± 968

* Significantly different from values before training

training potential. The muscle samples were removed from the needle, oriented in tragacanth gum, immediately frozen in isopentane cooled by liquid nitrogen to −159° C and stored at −70° C. Care was taken to ensure that the interval between removal of the muscle sample and freezing was between 2 and 4 min (Larsson and Skogsberg 1988). Pre- and post-biopsies were identically treated.

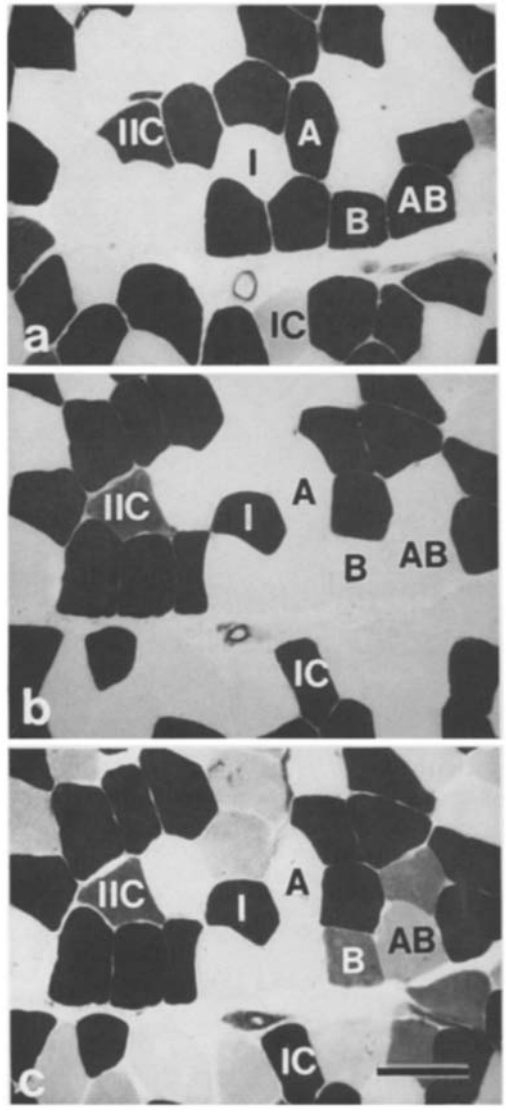

Fig. 1. Serial cross-sections assayed for myofibrillar ATPase activity after preincubation pH values of **a** 10.4, **b** 4.3, and **c** 4.6. Six skeletal muscle fiber types have been delineated. *I*, type I; *IC*, type IC; *IIC*, type IIC; *A*, type IIA; *AB*, type IIAB; *B*, type IIB. *Bar* = 100 μm

Histochemistry. The muscle biopsy samples were thawed to −20° C and serially sectioned (12 μm thick) for histological [toluidine blue and hematoxylin and eosin (H & E)] and histochemical [nicotinamide adenine dinucleotide (NADH) and myofibrillar adenosine triphosphatase (mATPase) activities] analyses. Routine mATPase analysis was performed following preincubation pH values of 4.3, 4.6, and 10.4 (Brooke and Kaiser 1970) with previously used modifications (Staron et al. 1983a). Cross-sections of pre- and post-biopsies from the same individual were placed on the same glass coverslip and assayed simultaneously for mATPase activity.

A total of six fiber types were distinguished (I, IC, IIC, IIA, IIAB, IIB) based upon their staining intensities (Staron and Pette 1987a, b) (Fig. 1). The type I fibers were stable in the acid ranges, but labile at pH 10.4. Type IIA fibers displayed a reverse pattern. All fibers that were stable at pH 10.4 and 4.6 but labile at pH 4.3 were classified as either type IIB or IIAB depending upon their staining intensity (type IIAB stained intermediate between fiber types IIA and IIB after preincubation pH 4.6). Fibers classified as type IC or IIC remained stable, to varying degrees, throughout the entire pH range (Fig. 1). The IC fibers were indistinguishable from the type I fibers following the acid preincubation, and the IIC fibers were indistinguishable from type II fibers following alkaline preincubation (Staron and Pette 1986).

A composite picture of each mATPase preparation (preincubation pH 4.6) was made using Polaroid micrographs (×56). These photomontages and the histochemical preparations were used to determine the total fiber number and fiber type percentages in each biopsy. Determination of the cross-sectional area of at least 100 fibers per type was made from direct tracings (×200) by the use of a digitizing tablet. Due to the scarcity of particular fiber types, some of the subtypes were collapsed (IIAB + IIB) to ensure adequate numbers. Therefore, a total of three groups were used for area determinations (I, IIA, and IIAB + IIB).

Statistical analysis. Standard statistical analyses (mean±SD) were performed on all variables. A two-way analysis of variance with repeated measures was used to determine whether a significant difference between groups existed. In the presence of a significant F-ratio, post hoc comparisons of means were provided by Tukey's *w*-procedure. Where applicable, Student *t*-tests were used to determine differences between pre- and post-values. Statistical significance was accepted at $p<0.05$.

Results

Percent body fat was significantly lower after training (22.7±5.3% to 20.3±4.3%) while lean body mass increased (46.2±6.2 kg to 51.3±9.3 kg). Pre- and post-training total body masses were similar (60.9±9.0 kg vs 61.9±8.6 kg, respectively); leg girth (measured at three sites) did not change as a result of the training. However, anterior thigh skinfold measurements decreased ($p<0.05$) after training (from 23.7±6.3 mm to 20.0±5.4 mm).

As expected, isotonic strength increased significantly throughout the duration of the training

for each exercise. By week 8 of the study (6th week of high-intensity training) the 1 RM values were significantly greater than the respective pre-training values for all four lower limb exercises. This trend continued through week 16. Maximal isotonic strength measurements determined at the end of training revealed a "leveling off" with no significant difference between week 16 and week

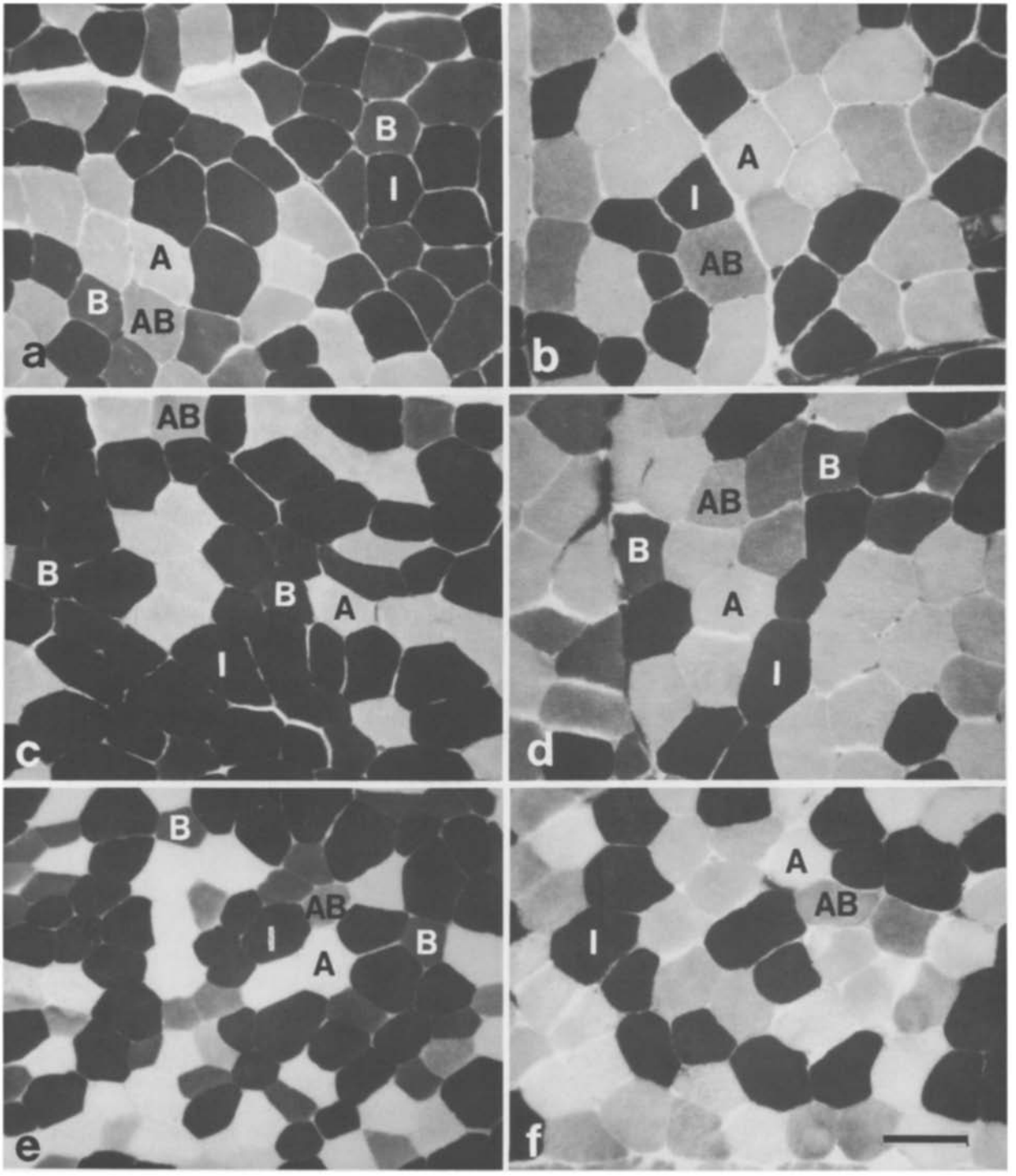

Fig. 2. Cross sections of pre- (**a, c, e**) and post-biopsies (**b, d, f**) assayed simultaneously for myofibrillar ATPase activity after preincubation at pH 4.6 from three different women: a/b, c/d, and e/f. Note the disappearance of the numerous dark staining type IIB fibers in the post-biopsy micrographs. *I*, type I; *A*, type IIA; *AB*, type IIAB; *B*, type IIB. *Bar* = 100 μm

20, with the exception of the vertical leg press exercise.

The cross-sectional areas of all fiber types were significantly different from each other in the pre-training samples, the type I fibers having the largest cross-sectional area ($4253 \pm 949\ \mu m^2$), the type IIA fibers intermediate ($3370 \pm 1048\ \mu m^2$), and the type IIAB + IIB fibers the smallest area ($2697 \pm 931\ \mu m^2$). Following the training regimen, the cross-sectional areas of all three major fiber types significantly increased: type I = $4893 \pm 770\ \mu m^2$, type IIA = $4888 \pm 967\ \mu m^2$, and type IIAB + IIB = $4233 \pm 1433\ \mu m^2$. In addition, the hierarchy of fiber sizes was altered in the post-training biopsies such that type I and IIA fiber areas were not significantly different from each other. The area for group IIAB + IIB was still significantly smaller than the areas of both type I and IIA.

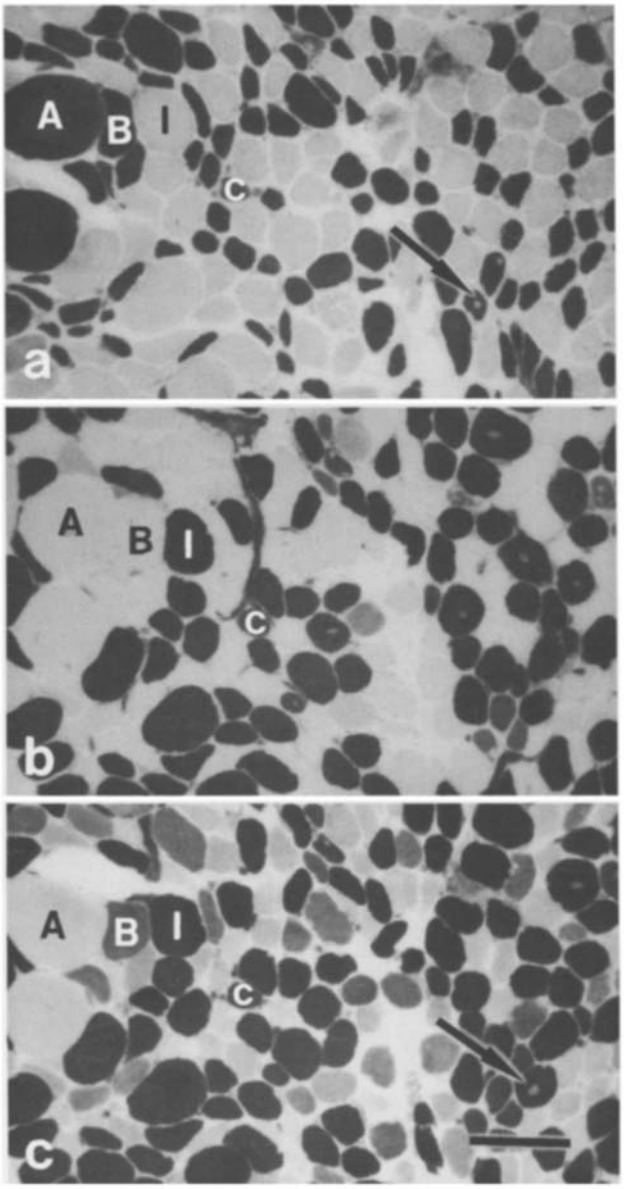

Fig. 3. Serial cross-sections of a post-biopsy specimen from a region undergoing degeneration/regeneration and assayed for mATPase activity after preincubation pH values of **a** 10.4, **b** 4.3, and **c** 4.6. *Arrows* indicate possible internalized nuclei. *I*, type I; *C*, type IIC; *A*, type IIA; *B*, type IIB. *Bar* = 100 μm

Fiber type distributions differed between pre- and post-biopsies. The mean percentage of type IIB fibers significantly decreased with a concomitant increase in the mean percentage of fiber type IIA after heavy-resistance weight training (Table 1). This alteration in fiber composition was further supported by comparing pre- and post-training muscle samples assayed simultaneously for mATPase activity (Fig. 2). No significant differences were found between the pre- and post-training mean percentages of fiber types I, IC, IIC, or IIAB.

The normal mosaic fiber type appearance was disrupted in one biopsy sample (micrograph not shown). This pre-training biopsy contained extensive type grouping, an indication of previous denervation/reinnervation (Karpati and Engel 1968). In addition, seven of the post-biopsy samples, two from women who had given "early" biopsies, contained either large group (three) or small group (four) atrophy. Some of the affected areas were quite extensive, involving more than 3,500 fibers. Although the atrophic regions were not specific for any particular fiber type, the fast fibers appeared to be affected to a greater extent than the slow fibers (Fig. 3). Close inspection of these regions revealed evidence of degeneration (necrosis, phagocytosis, monocyte infiltration, liquefied appearance, target fibers, etc.) and regeneration (internal nuclei, basophilia, small normal fibers, etc.) (Fig. 4).

Discussion

Similar to the adaptations found in strength-trained men (Houston et al. 1983; MacDougall et al. 1979, 1980), skeletal muscle fibers from strength-trained women in the present study underwent considerable hypertrophy. This increase in the cross-sectional area of the muscle fibers was not detectable from thigh girth measurements. However, anterior thigh skinfold measurements significantly decreased suggesting a decrease in subcutaneous fat and an increase in whole muscle cross-sectional area. The present results support and extend recent findings (Bailey et

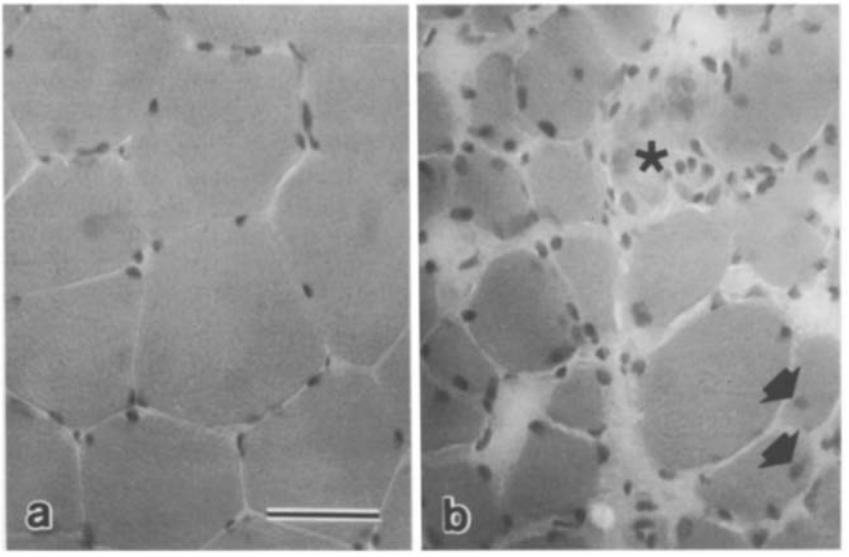

Fig. 4a, b. Cross-sections of different regions within a post-biopsy obtained from one subject. Sections were stained with hematoxylin and eosin. * Region of cellular infiltration/degeneration. *Arrows* indicate internalized nuclei. *Bar* = 50 μm

al. 1987; Sale et al. 1987; Cureton et al. 1988) that, like men, women are capable of responding to heavy resistance training with significant increases in the cross-sectional area of their muscle.

Previous strength-training investigations have indicated possible selective hypertrophy of fast-twitch (type IIA and IIB) fibers in men (Thorstensson et al. 1976; Houston et al. 1983; Tesch et al. 1987) and the fast type IIB fibers in women (Bailey et al. 1987). If the intensity and duration are sufficient, involvement and adaptation of all fibers would be expected (Vøllestad et al. 1984; Vøllestad and Blom 1985). Therefore, it is not surprising that hypertrophy of both fast- and slow-twitch fibers have been reported in men following a heavy-resistance training program (MacDougall et al. 1979, 1980). Likewise, in the present investigation, the cross-sectional area of all major fiber types increased after training. The fast-twitch fibers (being the smallest in cross-sectional area) underwent the greatest amount of hypertrophy (type IIA 45%, IIAB and IIB 57%) and the largest pre-training fiber type (type I) underwent the least amount of change (15%).

To our knowledge, no previous study has demonstrated alterations in fiber type composition as a result of strength training. Fiber type conversions reflect the dynamic nature of skeletal muscle and its adaptability to various workloads. Until now, this adaptive response in human muscle has been reported only as a result of endurance training and detraining. Alterations in the percentage of type I fibers in human muscle have been suggested following aerobic training (Howald et al. 1985), high-intensity intermittent training (Jansson et al. 1978; Simoneau et al. 1985), and after detraining of elite endurance athletes (Larsson and Ansved 1985). In addition, endurance training causes a decrease in the percentage of type IIB fibers with a concomitant increase in the percentage of type IIA fibers (Jansson and Kaijser 1977; Andersen and Henriksson 1977; Ingjer 1979; Green et al. 1979; Baumann et al. 1987), and may cause an increase in the percentage of type IIC (hybrid type I and IIA) fibers (Jansson and Kaijser 1977; Jansson et al. 1978; Schantz et al. 1982, 1983).

It is not surprising that various types of endurance training result in an increase in type IIA fibers with a concomitant decrease in fibers classified as type IIB. Although the oxidative capacities of the type IIA and type IIB fibers vary, both between and within individuals (Reichmann and Pette 1982; Staron et al. 1983b; Hintz et al. 1984), generally (as a group), the type IIA fibers are more oxidative than the type IIB fibers (Staron et al. 1983b). Therefore, an increase in type IIA fibers should help increase the oxidative capacity of the muscle. Indeed, the percentage of type IIB fibers is negatively correlated with maximal oxygen consumption (Staron et al. 1984) and immobilization causes a conversion in the opposite direction: type IIA to type IIB (Häggmark and Eriksson 1979; Häggmark et al. 1981).

A necessary requirement for IIB $\rightleftharpoons$ IIA fiber conversions may be related to the total recruitment time. Glycogen depletion experiments in humans have demonstrated that the recruitment of type IIB fibers depends upon the intensity and

duration of exercise (Essén 1978; Green 1978; Thomson et al. 1979; Vøllestad et al. 1984; Vøllestad and Blom 1985). The dramatic hypertrophy found in the present investigation suggests that the high-intensity strength training involved all major fiber types. This increased usage of the rarely recruited IIB fibers apparently caused their conversion to type IIA fibers.

This suggests that the strength-trained muscle in the present investigation may have increased its oxidative capacity. This may not be the case if there is a "dilution effect" and the volume percentage of mitochondria (MacDougall et al. 1979; Lüthi et al. 1986) and capillary density (Tesch et al. 1984) decrease as muscle fiber cross-sectional area increases during resistance training. However, Staron et al. (1984) found a significantly higher volume percentage of mitochondria in the muscles of weight lifters compared with untrained controls. In addition, the conversion of IIB fibers to IIA may explain previously observed increases in short-term endurance after heavy-resistance training (Hickson et al. 1980). Variable results have been obtained depending upon the type of resistance training (body building versus power or Olympic lifting) (Tesch 1987). We are currently quantifying various enzymes of oxidative metabolism in these muscles to address this question.

The observance of fiber damage in strength-trained muscle is interesting. Fiber damage can occur during aerobic (Fridén et al. 1983; Hikida et al. 1983; Apple et al. 1987) or anaerobic (Fridén et al. 1981, 1988) exercise and appears to be most related to the eccentric component (Newham et al. 1983; Clarkson et al. 1986). Recent evidence suggests that weight lifting exercise may also induce skeletal muscle damage in humans (Paul et al. 1989; Pivarnik et al. 1989). However, the extent of damage found in the present investigation suggests that a combination of the pre-biopsy procedure (insertion of the biopsy needle and extraction of muscle tissue) and the high-intensity training may be responsible. Perhaps the area traumatized by the pre-biopsy procedure was prevented from entirely recovering due to the training.

In conclusion, women are capable of significant muscular hypertrophy if sufficiently stressed at a high enough intensity for a long enough period of time. Large increases in the cross-sectional areas of all major muscle fiber types (types I, IIA, and IIAB+IIB) are possible. Also, heavy-resistance training causes significant alterations in the percentages of specific fast fiber types, suggesting a conversion of type IIB fibers to IIA.

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