

Skeletal muscle adaptations to endurance training in 60- to 70-yr-old men and women

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COGGAN, ANDREW R., ROBERT J. SPINA, DOUGLAS S. KING, MARC A. ROGERS, MARYBETH BROWN, PATTI M. NEMETH, AND JOHN O. HOLLOSZY. *Skeletal muscle adaptations to endurance training in 60- to 70-yr-old men and women*. *J. Appl. Physiol.* 72(5): 1780-1786, 1992.—Previous studies of endurance exercise training in older men and women generally have found only minimal skeletal muscle adaptations to training. To evaluate the possibility that this may have been due to an inadequate training stimulus, we studied 23 healthy older (64 ± 3 yr) men and women before and after they had trained by walking/jogging at 80% of maximal heart rate for 45 min/day 4 days/wk for 9–12 mo. This training program resulted in a 23% increase in maximal O_2 consumption. Needle biopsy samples of the lateral gastrocnemius muscle were obtained before and after training and analyzed for selected histochemical and enzymatic characteristics. The percentage of type I muscle fibers did not change with training. The percentage of type IIb fibers, however, decreased from 19.1 ± 9.1 to $15.1 \pm 8.1\%$ ($P < 0.001$), whereas the percentage of type IIa fibers increased from 22.1 ± 7.7 to $29.6 \pm 9.1\%$ ($P < 0.05$). Training also induced increases in the cross-sectional area of both type I (12%; $P < 0.001$) and type IIa fibers (10%; $P < 0.05$). Capillary density increased from 257 ± 43 capillaries/mm² before training to 310 ± 48 capillaries/mm² after training ($P < 0.001$) because of increases in the capillary-to-fiber ratio and in the number of capillaries in contact with each fiber. Lactate dehydrogenase activity decreased by 21% ($P < 0.001$), whereas the activities of the mitochondrial enzymes succinate dehydrogenase, citrate synthase, and β -hydroxyacyl-CoA dehydrogenase increased by 24–55% in response to training ($P < 0.001$ – 0.05). We conclude that, given an adequate training stimulus, the skeletal muscles of older men and women undergo adaptations to endurance exercise training similar to those observed in young people.

exercise; aging; muscle fiber type; muscle fiber area; capillarity; glycolytic enzymes; mitochondrial enzymes

ENDURANCE EXERCISE TRAINING of young people or animals induces major adaptations in skeletal muscle (cf. Ref. 19). These include conversion of type IIb muscle fibers into type IIa (3, 7); an increase in capillarization (4, 14); a small decrease in the activity of some glycolytic enzymes, particularly lactate dehydrogenase (6, 29); and a marked increase in mitochondrial respiratory enzyme levels (4, 18). These adaptations to endurance exercise play a major role in the decreased reliance on carbohydrate during submaximal exercise and therefore the increased endurance that results from exercise training (cf. Ref. 19).

It is unclear, however, whether endurance training can elicit similar adaptations in the skeletal muscles of older people. Denis et al. (14), for example, found no changes in fiber type distribution, in capillary-to-fiber ratio, or in the number of capillaries in contact with each muscle fiber after training of 57- to 69-yr-old men (although capillary density did increase because of an apparent decrease in muscle fiber area). Similarly, Aniansson and co-workers (5, 24) were unable to detect any changes in capillary density, capillary-to-fiber ratio, lactate dehydrogenase activity, citrate synthase activity, β -hydroxyacyl-CoA dehydrogenase activity, or mitochondrial volume in elderly men in response to training. Furthermore, Suominen et al. (31), using malate dehydrogenase as a marker for mitochondrial respiratory capacity, observed only minimal increases (5–15%) as a result of training in older men and women. The training programs employed in most of these studies (5, 24, 31), however, were brief and of low intensity and would be unlikely to induce significant adaptations in the muscles of young people. Although the training program used by Denis et al. (14) was more strenuous, many of these subjects had already been training for a number of years, reducing the probability of eliciting further adaptations.

In contrast to the above results, in a subsequent study Souminen et al. (30) found that 8 wk of exercise training, including up to 20 min of running each session, increased malate dehydrogenase and succinate dehydrogenase activities in the vastus lateralis of 56- to 70-yr-old men by 45%. More recently, Meredith et al. (22) demonstrated a 41% increase in skeletal muscle respiratory capacity in older men and women as a result of a strenuous 12-wk-cycle ergometer exercise training program. Therefore these latter two studies (22, 30) suggest that aged human muscle retains the ability to adapt to endurance training, at least in terms of mitochondrial respiratory capacity, and that the failure of previous studies (5, 24, 31) to observe such an adaptation may have been due to an inadequate training stimulus. However, there are few data in the literature to indicate that the skeletal muscles of older people can adapt to endurance training with alterations in fiber subtype distribution, decreases in glycolytic enzyme activity, or increases in capillarization.

Because of the uncertainty regarding the capacity of the muscles of older people to adapt to endurance exercise training, we obtained needle biopsy samples from the lateral gastrocnemius muscles of older men and

women before and after they completed a strenuous 9- to 12-mo endurance training program. These samples were analyzed for fiber type distribution, fiber areas, capillarization, and the activities of selected glycolytic and mitochondrial respiratory enzymes. The results demonstrate that, given an adequate training stimulus, the skeletal muscles of older people undergo adaptations to endurance training similar to those observed in young people.

METHODS

Subjects and experimental design. Thirty initially sedentary men and women, 60–70 yr old, volunteered for this study. Twelve of the men and 11 of the women underwent endurance exercise training. An additional five men and two women also volunteered to exercise but lived too far from the medical center or otherwise did not have sufficient time to participate in the training program. These subjects were therefore studied as nonexercising controls. The present subjects were randomly selected from a larger group of men and women participating in an investigation of the cardiovascular and metabolic effects of endurance exercise training in older adults, the design of which recently has been described in detail (21). The present subjects did not differ significantly from this larger group in terms of either their physical characteristics before training [e.g., weight, percent body fat, maximal $\dot{V}O_{2\max}$] or in terms of their response to training (e.g., decrease in weight and percent body fat, increase in $\dot{V}O_{2\max}$). The study protocol was approved by the Human Studies Committee of the Washington University School of Medicine, and written informed consent was obtained from each individual.

All of the subjects were nonsmokers who were free of detectable cardiovascular, metabolic, or musculoskeletal disease. Before entry into the study, each subject's health status was assessed by means of a medical history, physical examination, hematologic evaluation, SMA-12 blood chemistry, urinalysis, 75-g oral glucose tolerance test, and chest X-ray. In addition, each subject underwent two graded treadmill tests to exhaustion with blood pressure and electrocardiogram monitoring. The first of these tests, using a Bruce exercise protocol, was used to screen for cardiovascular abnormalities. Provided that none were found, a second exercise test was subsequently performed with the use of an individually adjusted walking or running protocol (21) to determine $\dot{V}O_{2\max}$. During this second test, $\dot{V}O_2$ uptake ($\dot{V}O_2$) was measured every 30 s during exercise with an automated open-circuit system that incorporated a dry gas meter (Parkinson-Cowan CD-4), mixing chamber, and electronic O_2 and CO_2 analyzers (Applied Electrochemistry S3-A and Beckman LB-2, respectively). $\dot{V}O_{2\max}$ was defined as the mean of the two highest consecutive 30-s $\dot{V}O_2$ measurements. For assurance that $\dot{V}O_{2\max}$ had indeed been reached, at least two of the following criteria had to be met: a plateau in $\dot{V}O_2$ despite an increase in treadmill speed and/or grade, a respiratory exchange ratio >1.10 , and a heart rate within 10 beats/min of age-predicted maximal heart rate.

Body composition was assessed via hydrostatic weighing (8), with residual lung volume determined by O_2 dilution (33). Calf circumference was measured at the point

of greatest girth with the use of a Gulick tape (Country Technology, Gay Mills, WI). To minimize potential variability, all calf circumference measurements were performed by the same individual.

After this preliminary testing, subjects in the exercise training group participated in a 2- to 3-mo flexibility exercise program, followed by 9–12 mo of endurance exercise training. This training program has been described in detail previously (21). Briefly, flexibility training consisted of various static stretching movements involving all major joints and muscle groups. The flexibility program was intended to reduce the likelihood of injury during the subsequent endurance exercise program and was not intended to induce any increase in muscular or cardiovascular fitness. During the subsequent endurance exercise training program, the subjects exercised primarily by walking and/or jogging on an indoor track or on a treadmill. A few of the participants also performed additional exercise on cycle and/or rowing ergometers. Training was performed for ~ 45 min/day ~ 4 days/wk, and the intensity of exercise was progressively increased from 60–70% of maximal heart rate during the first 3 mo of training to 80–85% of maximal heart rate by the end of training. Individual exercise prescriptions were updated weekly. To monitor improvements due to training and to provide information for adjusting exercise prescriptions, we remeasured $\dot{V}O_{2\max}$ every 3 mo during training. As previously described (21), most of the increase in $\dot{V}O_{2\max}$ occurred in the first 6 mo of training; subjects who failed to demonstrate a further increase in $\dot{V}O_{2\max}$ between 6 and 9 mo of training were therefore given the option of exiting the study after 9 mo of training. In the present group of subjects, 17 trained for 9 mo, whereas the other 6 completed the full 12 mo of training.

To be able to confidently ascribe possible skeletal muscle adaptations as being the result of endurance training, initial muscle biopsies in the exercise group were obtained after completion of flexibility training but before endurance training was begun. Thus, if significant muscular adaptations had been induced by flexibility training, this approach would have resulted in an underestimation of the effects of increased physical activity in older adults. However, no significant differences were observed between the pretraining biopsies from the exercise group (obtained after the flexibility program) and those from the control group, suggesting that the effects of the flexibility program on skeletal muscle characteristics, if any, were minimal.

Muscle biopsy samples and measurements of body composition, calf circumference, and $\dot{V}O_{2\max}$ were obtained from the control subjects on two occasions, ~ 12 mo apart. They were instructed to make no major changes in their lifestyle (e.g., diet, exercise habits) in the interim period. Posttesting interviews indicated that they complied with these instructions.

Muscle sampling and analyses. Biopsy samples were obtained from the lateral head of the right gastrocnemius muscle with a 5-mm Bergström needle (Stille-Werner, Ronkonkoma, NY). One portion of the muscle specimen was oriented longitudinally in embedding medium, frozen in liquid N_2 -cooled isopentane, and stored in liquid N_2 . Transverse sections (10 μm) were subsequently cut

on a cryostat maintained at -20°C . Muscle fiber type distribution (i.e., the percentage of type I, type IIa, type IIb, and type IIc fibers) was determined in sections stained for adenosinetriphosphatase activity at pH 9.4 after preincubation at pH 4.3, 4.6, and 10.3 (25). On average, 436 ± 129 (range 138–1,199) fibers were used in making these determinations. Type IIc fibers constituted $<0.5\%$ of any biopsy sample and were therefore excluded from further analyses. Muscle fiber areas were determined by projecting samples at $\times 150$ magnification onto a digitizer interfaced with an IBM computer, choosing 1 fiber at random, and then measuring the areas of the nearest 25 fibers of each type. Capillarization was determined by staining additional sections with periodic acid-Schiff's reagent after removal of glycogen with a 1% amylase solution (2). Sections were projected at $\times 300$ magnification, and capillary density, capillary-to-fiber ratio, and the number of capillaries in contact with each muscle fiber were determined in four to six randomly selected 0.25-mm^2 regions.

The remainder of the sample was frozen and stored in liquid N_2 . A 5- to 10-mg portion of each sample was subsequently homogenized in 50 vol of sodium phosphate buffer (20 mM, pH 7.4, containing 0.5 mM EDTA, 5 mM β -mercaptoethanol, 0.02% bovine serum albumin, and 50% glycerol) and was assayed as previously described (12, 13) for phosphorylase, phosphofructokinase, lactate dehydrogenase, succinate dehydrogenase, citrate synthase, and β -hydroxyacyl-CoA dehydrogenase activities by use of the methods of Chi et al. (11). All assays were conducted at room temperature ($24 \pm 0.5^{\circ}\text{C}$).

Statistical analyses. Data from the nonexercising control subjects were compared with the use of paired t tests. Data from the exercise group were analyzed by two-way analyses of variance, with gender as a between-subjects factor and training as a within-subjects factor. Significant differences were identified by $P \leq 0.05$. Although these analyses revealed significant main effects for training and gender for a number of variables, no significant interaction effects were observed, indicating that the effects of training were similar in men and women. Therefore the P values reported herein refer to these significant main effects. For comparison purposes, however, data for men and women are presented separately as means \pm SD.

RESULTS

Averaged over the entire training period, the subjects exercised for 44 ± 4 min/day 3.9 ± 0.6 days/wk at $81 \pm 5\%$ of maximal heart rate for 9.9 ± 1.4 mo. Energy expenditure during training (estimated from the average O_2 cost of various activities; cf. Ref. 21) averaged $1,515 \pm 591$ kcal/wk.

Physical characteristics (Table 1). Training resulted in a 4% decrease in body weight in both men and women. This decrease in body weight was entirely due to a reduction in percent body fat, as fat-free mass did not change with training. Despite this decrease in adiposity, calf circumference increased significantly with training, with 18 out of the 23 subjects demonstrating an increase in calf circumference. This $\sim 1\%$ increase in calf circumference corresponds to an $\sim 3\%$ increase in lower leg cross-sectional area.

$\dot{V}\text{O}_{2\text{max}}$ (in l/min) increased by 24% in the men and by 21% in the women as a result of training. The magnitude of this increase was not significantly different between men and women. When expressed relative to body weight, $\dot{V}\text{O}_{2\text{max}}$ increased by 29% in the men and 26% in the women. Again, the magnitude of the relative improvement in $\dot{V}\text{O}_{2\text{max}}$ did not differ significantly between men and women.

Maximal heart rate demonstrated a slight but nonsignificant decrease with training in the men, whereas maximal heart rate did not change with training in the women.

Muscle fiber type distribution and fiber areas (Table 2). The percentages of type I, type IIa, and type IIb fibers in the lateral gastrocnemius muscle did not differ between men and women. The areas of all three fiber types were greater in men than in women, and this difference was greatest for type IIb fibers. Consequently, the type IIb-to-type I area ratio was smaller in women than in men.

The percentage of type I fibers did not change with training. However, training resulted in a significant decrease in the percentage of type IIb fibers and a corresponding increase in the percentage of type IIa fibers. The magnitude of these shifts in the type II fiber subpopulation tended to be greater in men than in women, but this difference was not statistically significant.

Training resulted in 10 and 12% increases in the areas of the type I and the type IIa fibers, respectively. Although type IIb fiber area increased by a similar amount (11%), this latter increase was not statistically significant ($P = 0.09$). Because the increase in fiber area was of similar magnitude in all three fiber types, the type IIa-to-type I and type IIb-to-type I area ratios did not change with training.

Muscle capillarization (Table 3). Capillary-to-fiber ratio and the number of capillaries in contact with each muscle fiber were lower in women than in men both before and after training. However, because of the women's smaller muscle fibers, capillary density did not differ between men and women.

The number of capillaries per square millimeter increased by 21% in response to endurance training. This increase in capillary density was the result of significant increases in the capillary-to-fiber ratio and the number of capillaries in contact with each muscle fiber.

Muscle enzyme activities (Table 4). Phosphofructokinase activity was higher and succinate dehydrogenase and citrate synthase activities were lower in women than in men. The activities of the other three enzymes examined (phosphorylase, lactate dehydrogenase, and β -hydroxyacyl-CoA dehydrogenase) did not differ between men and women.

Phosphorylase and phosphofructokinase activities did not change with training, whereas lactate dehydrogenase activity decreased by 21% as a result of training. In contrast, the activities of the mitochondrial enzymes succinate dehydrogenase, citrate synthase, and β -hydroxyacyl-CoA dehydrogenase increased by 24–55% as a result of the exercise program.

Control subjects. No significant change was observed for any variable in the five older men and two older women who served as nonexercising controls (data not shown).

TABLE 1. *Physical characteristics of the subjects*

	Men		Women		Gender Effect	Training Effect
	Pretraining	Posttraining	Pretraining	Posttraining		
Age, yr	65±3		64±3		NS	
Height, cm	178±7		167±6		<i>P</i> < 0.001	
Weight, kg	81.4±7.9	77.8±6.3	62.6±10.1	60.3±10.2	<i>P</i> < 0.001	<i>P</i> < 0.001
Percent fat	27.9±3.6	24.9±3.9	36.0±5.0	33.0±5.2	<i>P</i> < 0.001	<i>P</i> < 0.001
FFM, kg	58.6±5.3	58.6±5.7	39.8±5.4	40.1±5.2	<i>P</i> < 0.001	NS
Calf circ, cm	37.2±2.4	37.9±2.6	35.2±2.5	35.5±2.4	<i>P</i> < 0.05	<i>P</i> < 0.001
$\dot{V}O_{2\max}$ l/min	2.20±0.33	2.72±0.44	1.39±0.22	1.68±0.21	<i>P</i> < 0.001	<i>P</i> < 0.001
$\dot{V}O_{2\max}$ ml·kg ⁻¹ ·min ⁻¹	27.0±2.7	34.8±4.0	22.3±2.8	28.2±2.7	<i>P</i> < 0.001	<i>P</i> < 0.001
HR _{max} , beats/min	170±12	164±11	161±11	161±9	NS	NS

Values are means ± SD for 12 men and 11 women. FFM, fat-free mass; calf circ, calf circumference; $\dot{V}O_{2\max}$, maximal O₂ uptake; HR_{max}, maximal heart rate.

DISCUSSION

In a number of prior studies, significant skeletal muscle adaptations did not occur in older people in response to endurance exercise training (5, 14, 24, 31). However, both Souminen et al. (30) and Meredith et al. (22) have observed significant increases in muscle mitochondrial respiratory capacity as a result of vigorous endurance training of elderly individuals, and Frontera et al. (16) have demonstrated a similar increase in response to a strenuous strength training program. Additionally, we have found that fiber type distribution, capillary density, and mitochondrial enzyme activities are similar in master endurance athletes and comparably trained young athletes (13). On the basis of these findings, we hypothesized that the muscles of older people would retain the ability to adapt normally to exercise training if the training stimulus were of adequate intensity and duration.

The present results support this hypothesis. Thus, although the percentage of type I fibers did not change with training, the percentage of type IIb fibers decreased, whereas the percentage of type IIa fibers increased. Accompanying this shift in muscle fiber type were significant increases in the cross-sectional area of the type I and type IIa fibers. Calf circumference also increased significantly with training, despite a significant decrease in percent body fat. Similar shifts in the type II fiber population [which are believed to reflect changes in the predominant myosin heavy chain being synthesized (7)] also occur in young people in response to endurance training (3, 7). Likewise, although endurance training is not nor-

mally considered a major stimulus for muscle hypertrophy, moderate increases in muscle size are frequently observed with endurance training of young subjects (4, 18, 26). The present results therefore suggest that aged human muscle retains some plasticity in the type and quantity of myosin that is expressed. Despite the increase in fiber size observed in the present study, however, fat-free mass did not change in response to training, suggesting that this hypertrophy must have been confined to too small a fraction of the total muscle mass to be detectable via hydrostatic weighing. Furthermore, because the magnitude of the increase in fiber size was similar in all three fiber types (although not statistically significant in the type IIb fibers), the type IIa-to-type I and type IIb-to-type I area ratios were unaltered by training and therefore remained significantly below those we have observed in the gastrocnemius muscles of untrained young men and women (12). Thus the exercise program did not reverse the relative type II atrophy associated with aging. Interestingly, studies of strength training of older people have also failed to consistently demonstrate increases in the type II-to-type I area ratio, even when large increases occurred in strength and in muscle fiber areas (10, 17). Similarly, the type II-to-type I area ratio in master weight lifters (20) is not as high as that in young strength-trained men (1, 32), although it is equal to that in young sedentary men and consequently is greater than that in older sedentary men (20). These results suggest that the relative type II atrophy that occurs with aging may be due to factors other than, or in addition to, simple disuse.

TABLE 2. *Skeletal muscle fiber type distribution and fiber areas*

	Men		Women		Gender Effect	Training Effect
	Pretraining	Posttraining	Pretraining	Posttraining		
Type I, %	58.6±14.6	54.5±12.6	59.2±9.9	56.1±11.4	NS	NS
Type IIa, %	22.0±8.9	31.4±10.0	22.2±7.0	27.7±8.4	NS	<i>P</i> < 0.001
Type IIb, %	19.4±10.0	14.1±9.5	18.7±8.4	16.2±6.8	NS	<i>P</i> < 0.05
Area, μm^2						
Type I	5,291±1,004	5,966±846	2,872±656	3,203±729	<i>P</i> < 0.001	<i>P</i> < 0.001
Type IIa	5,918±1,304	6,286±1,416	2,688±412	3,159±873	<i>P</i> < 0.001	<i>P</i> < 0.05
Type IIb	5,538±1,585	6,186±1,358	2,417±466	2,642±768	<i>P</i> < 0.001	NS*
Area ratio						
Type IIa/type I	1.12±0.12	1.06±0.17	0.96±0.14	0.99±0.17	NS	NS
Type IIb/type I	1.06±0.26	1.05±0.22	0.86±0.14	0.84±0.17	<i>P</i> < 0.01	NS

Values are means ± SD for 12 men and 11 women. * *P* = 0.09.

TABLE 3. *Skeletal muscle capillarization*

	Men		Women		Gender Effect	Training Effect
	Pretraining	Posttraining	Pretraining	Posttraining		
Capillaries/mm ²	254±40	295±45	260±49	326±50	NS	<i>P</i> < 0.001
Capillaries/fiber	1.65±0.40	2.08±0.33	0.89±0.22	1.23±0.29	<i>P</i> < 0.001	<i>P</i> < 0.001
Capillaries in contact with each muscle fiber	4.18±0.98	5.19±0.66	2.55±0.53	3.27±0.73	<i>P</i> < 0.001	<i>P</i> < 0.001

Values are means ± SD for 12 men and 11 women.

Despite the increases in muscle fiber size, capillary density increased by 21% in response to training. This increase in capillary density was the result of the formation of new capillaries, as indicated by the 25–30% increases in the capillary-to-fiber ratio and in the number of capillaries around each muscle fiber. These results are again similar to those observed after endurance training of young people (4) but contrast with results of Aniansson and Gustafsson (5) and Denis et al. (14), who found no evidence of capillary proliferation in older men as a result of endurance training. In support of the concept that capillary neof ormation can occur in older adults, Frontera et al. (16, 17) found that intensive strength training of the vastus lateralis muscle of older men, which resulted in a 28–43% increase in muscle fiber size, was associated with a smaller (10%) but still significant increase in capillary-to-fiber ratio.

We have previously reported that the increase in $\dot{V}O_{2\max}$ in the present study population appeared to be mostly the result of an increase in peak cardiac output (15). Nevertheless, the increase in capillary bed volume with training may still have contributed to the increase in $\dot{V}O_{2\max}$ by preventing a decrease in capillary mean transit time and therefore O_2 extraction despite (presumably) a training-induced increase in maximal muscle blood flow. Maintenance or improvement of O_2 extraction during maximal exercise also may have been aided by the significant increase in muscle mitochondrial respiratory capacity (see below).

The exercise program also resulted in changes in muscle enzyme activities similar to those observed after endurance training of young people (4, 6, 18, 19, 29). Thus, although phosphorylase and phosphofructokinase activities did not change with training, lactate dehydrogenase activity decreased and the activities of the mitochondrial enzymes succinate dehydrogenase, citrate synthase, and

β -hydroxyacyl-CoA dehydrogenase increased. Several prior studies have found no changes in lactate dehydrogenase or mitochondrial respiratory enzyme activities in the muscles of older humans in response to endurance training (5, 24, 31), probably due to an inadequate training stimulus. Other reports (16, 22, 30) support the present observation of an adaptive increase in mitochondrial respiratory capacity in response to training in older people. This increase in respiratory capacity is believed to play a major role in the smaller blood lactate accumulation and slower rate of carbohydrate utilization observed during exercise performed at the same absolute intensity after training (15, 19, 22, 27, 30).

Despite these structural and biochemical adaptations to endurance training, muscle capillarization and mitochondrial respiratory enzyme activities after training of the older subjects of the present study were similar to those young untrained men and women (12). Thus, although 9–12 mo of training reversed the decreases in these parameters associated with aging, it did not increase these values above the young untrained range. Along the same lines, although the decrease in type IIB fiber percentage and the increases in type I and type IIA fiber area in the present study were statistically significant, they were relatively small compared with the changes observed with endurance training of young people (3, 4, 7, 18, 26). These results might be construed as indicating that aging results in a diminished ability of skeletal muscle to adapt to endurance training. A more likely explanation for these observations, however, is that the volume and intensity of exercise performed by the subjects were relatively low in absolute terms, even after 9–12 mo of training (e.g., walking/jogging ~20 km/wk at ~125 m/min). Thus it is possible that skeletal muscle adaptations to training would have been greater if the subjects had run faster or farther. In keeping with

TABLE 4. *Skeletal muscle enzyme activities*

	Men		Women		Gender Effect	Training Effect
	Pretraining	Posttraining	Pretraining	Posttraining		
Phosphorylase	8.26±2.07	9.23±1.84	8.93±2.99	8.97±3.43	NS	NS
Phosphofructokinase	6.94±2.45	6.24±1.26	9.57±3.08	10.35±4.27	<i>P</i> < 0.01	NS
Lactate dehydrogenase	56.3±27.9	44.5±21.3	40.1±16.1	31.2±13.0	NS	<i>P</i> < 0.001
Succinate dehydrogenase	1.11±0.29	1.83±0.63	0.76±0.29	1.05±0.39	<i>P</i> < 0.001	<i>P</i> < 0.001
Citrate synthase	2.97±0.71	3.83±1.10	2.21±0.41	2.58±0.55	<i>P</i> < 0.001	<i>P</i> < 0.05
β -Hydroxyacyl-CoA dehydrogenase	5.95±1.03	8.45±2.72	5.29±1.55	7.19±1.54	NS	<i>P</i> < 0.001

Values are means ± SD for 12 men and 11 women. Enzyme activities are expressed as mol · kg protein⁻¹ · h⁻¹ measured at room temperature (24 ± 0.5°C).

this hypothesis, we have found previously that fiber type distribution, capillarization, and mitochondrial respiratory enzyme activities are similar in comparably trained young and master endurance athletes (13). Studies of rats also indicate that the increase in mitochondrial respiratory capacity due to training is similar in young and old animals subjected to the same training program (9, 34).

No statistical interactions between training and gender were found, indicating that the effects of training were similar in older men and women. However, significant differences in skeletal muscle characteristics between genders were observed for a number of variables, both before and after training. For example, the cross-sectional areas of all three fiber types were significantly larger in men than in women. This was especially true of the type IIb fibers, so that the type IIb-to-type I area ratio was also higher in men. Capillary density in men was equal to that of women, despite the men's larger muscle fibers, because the men had higher capillary-to-fiber ratios and more capillaries in contact with each muscle fiber. Enzyme activities also differed between men and women, with phosphofructokinase activity being lower in men than in women, and the opposite being observed for succinate dehydrogenase and citrate synthase activities. These gender differences are similar to previous observations of young people (12, 23, 28). Others, however, have reported that phosphofructokinase activity is higher in young men than in young women (28), whereas we have consistently observed the opposite in both younger (12) and older (present study) people. We have no explanation for this discrepancy.

In summary, 9–12 mo of endurance exercise training of ~65-yr-old men and women resulted in changes in fiber subtype distribution, fiber size, capillarization, and glycolytic and mitochondrial respiratory enzyme activities similar in relative magnitude to those observed in young people. These results add to the increasing body of evidence indicating that, contrary to some prior reports, older men and women retain the ability to adapt to exercise training.

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