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Skeletal muscle enzymes and fiber composition in male and female track athletes

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COSTILL, D. L., J. DANIELS, W. EVANS, W. FINK, G. KRAHENBUHL, AND B. SALTIN. *Skeletal muscle enzymes and fiber composition in male and female track athletes.* J. Appl. Physiol. 40(2): 149–154. 1976.—Muscle samples were obtained from the gastrocnemius of 17 female and 23 male track athletes, 10 untrained women, and 11 untrained men. Portions of the specimen were analyzed for total phosphorylase, lactic dehydrogenase (LDH), and succinate dehydrogenase (SDH) activities. Sections of the muscle were stained for myosin adenosine triphosphatase, $NADH_2$ tetrazolium reductase, and alpha-glycerophosphate dehydrogenase. Maximal oxygen uptake ($\dot{V}O_{2\ max}$) was measured on a treadmill for 23 of the volunteers (6 female athletes, 11 male athletes, 10 untrained women, and 6 untrained men). These measurements confirm earlier reports which suggest that the athlete's preference for strength, speed, and/or endurance events is in part a matter of genetic endowment. Aside from differences in fiber composition and enzymes among middle-distance runners, the only distinction between the sexes was the larger fiber areas of the male athletes. SDH activity was found to correlate 0.79 with $\dot{V}O_{2\ max}$, while muscle LDH appeared to be a function of muscle fiber composition. While sprint- and endurance-trained athletes are characterized by distinct fiber compositions and enzyme activities, participants in strength events (e.g., shot-put) have relatively low muscle enzyme activities and a variety of fiber compositions.

maximal oxygen uptake; lactic dehydrogenase; succinic dehydrogenase; phosphorylase

RECENT APPLICATION of histochemical and biochemical techniques to human muscle has provided some insight into the characteristics and function of muscle fibers in trained and untrained men (5, 14, 15). However, little information is available to describe the metabolic characteristics and fiber composition in high-caliber athletes, especially female athletes. The present study afforded an opportunity to examine the muscle fiber composition and selected oxidative and glycolytic enzymes of female and male track athletes. Moreover, direct comparisons between female and male athletes could be performed, as there were participants of both sexes in similar running events as well as in jumping and throwing.

SUBJECTS AND METHODS

The subjects employed in these studies were 17 female and 23 male international-caliber track athletes. In addition, measurements were made on 11 untrained men and 10 untrained women who had not participated in any regular physical activity for at least 2 yr preceding these tests. Selected characteristics of all subjects are presented in Table 1. At the time of these observations, the track athletes had just completed 10 days of intense training. It should be noted, however, that these studies were conducted in early January at a time when most of the athletes were not at a high level of competitive fitness. All subjects were fully informed of the risks and discomfort associated with these studies before giving their written consent to participate. Parental consent was obtained for all participants under the age of 18 yr.

Muscle samples were obtained from the lateral head of the gastrocnemius with the needle biopsy technique (2) as shown in Fig. 1. The specimen was divided into two parts. One portion was mounted in OCT and frozen in isopentane cooled with liquid nitrogen for histochemical analysis. The remaining portion of the sample was quickly frozen in liquid nitrogen and later weighed. These samples were subsequently analyzed for total phosphorylase, lactic dehydrogenase (LDH), and succinate dehydrogenase (SDH) activities.

Enzyme procedures follow the general principles described by Lowry and Passonneau (19). Whole muscle homogenates of 1:100 dilution were made at 0–4°C in an 0.1 M triethanolamine buffer (pH 7.6; 0.05% bovine serum albumin (BSA), 5 mM 2-mercaptoethanol).

Lactic dehydrogenase activity was assayed at 25°C by the direct fluorometric measure of NADH oxidation in a reaction mixture of 0.02 M imidazole (pH 7.0), 0.02% BSA, 0.01 mM NADH, and 1.0 mM sodium pyruvate. The reaction was begun by the addition of the muscle homogenate and followed on a chart recorder for 3 min. Calculations were made on the average ΔF/min.

Total phosphorylase activity was assayed at 25°C by the direct fluorometric measure of NADP reduction in a reaction mixture of 0.05 M imidazole (pH 7.0), 0.5 mM $MgCl_2$, 0.1 mM EDTA, 0.02% BSA, 20 mM P_i, 0.1 mM 5′-AMP, 0.05 mM NADP, 25 mM glycogen (as glucosyl units), 1 mM cysteine, 3 mg/ml phosphoglucomutase, and 1.5 mg/ml glucose-6-phosphate dehydrogenase. The reaction was begun by the addition of glycogen and followed for 8–10 min, with the average ΔF of the last 5 min used for calculations.

Succinate dehydrogenase was assayed by a two-step indirect method (P. D. Gollnick, unpublished): *1*) An aliquot of muscle homogenate was incubated at 37°C for 5 min in an equal volume of incubation medium 600 mM in sodium succinate and 8 mM in potassium ferricya-

TABLE 1. *Characteristics and performance data for all participants*

Subj	Sex	No.	Age, yr	Ht, cm	Wt, kg	Event	Performance
Sprint runners	F	2	19.5 (18–21)	168 (163–174)	55.6 (52.2–59.0)	100 m	11.4 s (11.4–11.4)
	M	2	19.5 (17–22)	181 (178–184)	71.5 (67.6–75.3)	100 m	10.5 s (10.3–10.5)
Middle-distance runners	F	7	19.9 (16–25)	166 (163–168)	52.5 (48.2–55.5)	800	2 min 8.1 s (2:04.7–2:10.3)
	M	7	22.9 (19–32)	179 (173–185)	65.7 (58.2–74.5)	800	1 min 51.5 s (1:48.9–1:54.1)
Distance runners	M	5	24.2 (20–32)	180 (173–185)	70.8 (63.5–83.5)	5,000 m Marathon	14 min 9 s (14:05–14:14) 2 h 44 min (2:19–2:57)
Long-high jumpers	F	3	22.3 (21–23)	177 (173–182)	61.1 (58.2–65.9)	High jump Long jump	1.84 m (1.83–1.87) 5.92 m (5.23–6.60)
	M	2	29 (26–32)	183 (180–185)	77.3 (75–79.5)	Long jump	7.96 m (7.52–8.41)
Javelin throwers	F	3	20.7 (17–26)	169 (159–180)	65.3 (56.7–78.0)	Javelin	51.8 m (49.1–57.0)
	M	3	25.3 (23–30)	176 (170–180)	83.6 (78.2–86.4)	Javelin	78.6 m (76.2–81.1)
Shot-put, discus throwers	F	2	23.5 (21–26)	171 (166–177)	77.0 (74.5–79.5)	Discus	54.8 m (53.0–56.6)
	M	4	26.8 (21–32)	198 (195–200)	129.0 (113.6–145.5)	Discus Shot-put	61.1 m (60.9–61.3) 19.3 m (18.9–19.7)
Untrained	F	10	22.2 (20–30)	163 (154–171)	60.2 (57.5–90.5)		
	M	11	27.3 (17–42)	177 (169–183)	78.2 (68.2–86.6)		

Values are means with ranges in parentheses.

nide. The reaction was stopped with the same volume of 3 M perchloric acid and neutralized with 3 M KOH. Tissue blanks were also run. *2*) An aliquot of the supernatant from *step 1* was added to a reaction mixture of 0.1 M hydrazine (pH 9.2) and 0.36 mM NAD. The initial fluorescence was read and the reaction begun by adding an aliquot of 0.25 mg/ml fumarase and 5 mg/ml malate dehydrogenase. The ΔF was read after a 2-h incubation at room temperature.

Muscle samples frozen for histochemical analysis were sectioned (10 μm thick) in a cryostat at -20°C and stained for myosin adenosine triphosphatase (ATPase), $NADH_2$ tetrazolium reductase, and alpha-glycerophosphate dehydrogenase. The methods employed for these histochemical stains have been previously described by Padykula and Herman (23), Novikoff et al. (22), and Wattenberg and Leong (26), respectively. Microphotographic enlargements (20 x 25 cm) of the slides were used for fiber classification, estimation of the oxidative and glycolytic capacity of the fibers, and for the determination of the cross-sectional area of the fibers. Mean muscle fiber area for each sample was determined by planimetry from 20 fast- (FT) and 20 slow-twitch (ST) fibers. We have chosen to classify the muscle fibers as ST and FT on the basis of their contractile characteristics (12). Although ST fibers generally stain dark for $NADH_2$ tetrazolium reductase, it is difficult to use this as a basis for fiber classification since both ST and FT fibers may appear heavily stained in endurance trained muscles.

The decision to sample muscle from the gastrocnemius of all participants was based on previous research (6), which demonstrated that during endurance running the muscles of the lower leg (gastrocnemius and soleus) are metabolically more active than those of the thigh. Although the thigh and shoulder muscles are used extensively during sprinting, jumping, and throwing, the gastrocnemius plays a major role in the performance of all three skills. For these reasons, it was felt that the gastrocnemius was the muscle group that would best represent the specificity of training and muscular prerequisite for all three events (running, throwing, and jumping) when only one muscle could be biopsied. It should be noted that no complications resulted from the biopsies, and all athletes trained at normal levels on the day following the muscle sampling.

Maximal oxygen uptake was measured on a treadmill for 6 female athletes, 11 male athletes, 10 untrained women, and 6 untrained men (4). Oxygen uptake was determined either by a semiautomated system (27) or by collection of expired air in meteorological balloons (7). In the latter case, O_2 and CO_2 in expired air were determined by Haldane analysis, and the volume of gas was measured with a dry gas meter.

Because of the small number of subjects in some events, no statistical comparisons were performed between events or for males and females within events. However, differences between the characteristics of all male and female athletes were subjected to a t-test for independent observations. Mean differences between ST and FT fiber areas were tested for significance with a paired t-test.

RESULTS

Fiber characteristics. On the average, the fiber distributions of the athletes (males plus females) and untrained subjects were 50.2 and 51.8% ST, respectively. Similar fiber compositions were observed for both male (50.2% ST) and female (50.2% ST) athletes, and for the untrained men and women (Table 2). An examination of the fiber distributions within the various events sug-

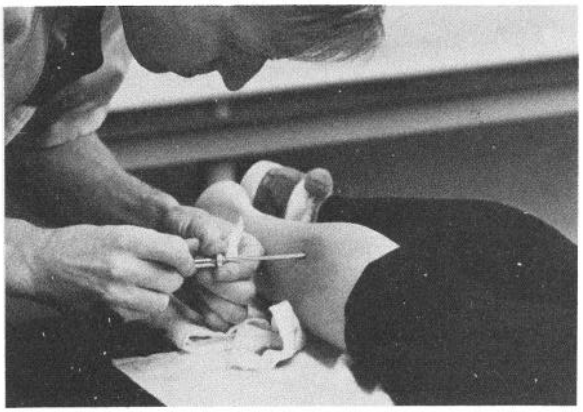

FIG. 1. Biopsy needle inserted into lateral aspect of gastrocnemius.

TABLE 2. *Fiber distribution, size, and relative areas of all groups studied*

Subj	Sex	No.	% ST Fibers	ST Fiber Area, μm^2	FT Fiber Area, μm^2	% Area ST Fibers	ST/FT Area
Sprint runners	F	2	27.4 (26.6–28.2)	3,752 (3,540–3,964)	3,930 (3,366–4,495)	26.8 (23.6–29.9)	0.99 (0.79–1.18)
	M	2	24.0 (21.0–27.0)	5,878 (3,975–7,782)	6,034 (5,877–6,192)	23.5 (15.3–31.8)	0.98 (0.64–1.32)
Middle-distance runners	F	7	60.6 (44.0–73.3)	6,069 (3,076–9,952)	5,642 (4,012–7,500)	60.4 (41.2–78.5)	1.05 (0.68–1.40)
	M	7	51.9 (40.5–69.4)	6,099 (4,551–8,447)	7,117 (4,889–9,212)	46.5 (31.2–62.1)	0.87 (0.67–1.08)
Distance runners	M	5	69.4 (63.4–73.8)	6,613 (3,644–10,111)	7,627 (4,729–11,330)	62.3 (51.0–75.9)	0.90 (0.72–1.24)
Long-high jumpers	F	3	48.7 (38.6–61.2)	4,163 (3,502–5,078)	5,113 (4,354–6,623)	44.0 (33.6–54.7)	0.83 (0.77–0.90)
	M	2	46.7 (44.0–49.3)	4,718 (4,475–4,961)	6,523 (6,301–6,745)	38.8 (35.8–41.7)	0.72 (0.71–0.74)
Javelin throwers	F	3	41.6 (41.2–42.0)	4,864 (4,264–5,464)	4,569 (4,272–4,866)	42.9 (40.9–44.9)	1.06 (1.00–1.12)
	M	3	50.4 (46.5–56.2)	5,585 (2,567–8,254)	5,771 (4,205–7,607)	47.7 (34.6–67.7)	0.92 (0.61–1.08)
Shot-put, discus throwers	F	2	51.2 (48.3–54.0)	5,192 (3,295–7,088)	5,851 (4,766–6,935)	46.9 (39.2–54.5)	0.86 (0.69–1.02)
	M	4	37.7 (13.0–52.0)	7,702 (5,037–10,345)	9,483 (9,131–9,718)	34.0 (7.6–50.0)	0.81 (0.55–1.08)
Untrained	F	10	51.0 (27.4–72.0)	3,875 (2,548–5,043)	4,193 (2,565–6,159)	48.8 (27.7–76.0)	0.98 (0.60–1.82)
	M	11	52.6 (38.0–73.2)	5,699 (3,402–8,721)	4,965 (3,881–6,855)	56.0 (34.9–77.7)	1.15 (0.88–1.27)

Values are means with ranges in parentheses.

gests that distance runners have a larger percentage of ST fibers than do participants in sprint, throwing, and jumping events (Table 2).

Since it is impossible to control the degree of fiber shortening at the time the biopsies are taken, some caution must be used in making comparisons of fiber areas between selected subjects. Nevertheless, some differences were observed and are worthy of notice. On the average, female track athletes have significantly ($P < 0.05$) smaller ST and FT fibers than the male athletes (Table 2). Similar differences were found between the untrained men and women.

Despite individual variations in fiber areas, the athletes' (men plus women) FT fibers were found to be significantly ($P < 0.05$) larger (6,375 μm^2) than the ST (5,661 μm^2). Unlike previous studies (15), it was difficult to relate the ST/FT area ratios to specific forms of training (Table 2). Initially one might be inclined to associate the large FT fibers of the shot-put and discus throwers with strength training. This may well be the case, but it should be mentioned that three of these men disclosed that they had been taking anabolic steroids (Dianabol) for the previous 6 mo to 8 yr, with dosages ranging from 10 to 30 mg/day. It is possible that the large FT and ST fibers of the male shot-put-discus throwers may in part be a combined function of the steroids and strength training.

The relative area of a muscle occupied by slow-twitch muscle fibers (% area ST) was markedly different for the endurance and nonendurance athletes (Table 2). The smallest % area ST, for example, was observed in a male shot-putter (7.6%), while the % area ST for one of the male distance runners was 75.9%. Middle-distance runners seem to possess a wider range of % area ST (31.2–78.5) than participants in the other events. Among the male middle-distance runners there appears to be a trend toward better performance times in the 800 m by those individuals having smaller % area ST. The fastest performance (1 min 48.9 s), for example, was recorded by a runner having 31.2% area ST, while the slowest 800-m runner (1 min 54.1 s) had 62.1% area ST. This relationship was not observed for performances in events longer than 800-m or among the female middle-distance runners.

Enzyme activities. Mean activities for muscle SDH, LDH, and phosphorylase are presented for all groups in Table 3. SDH activities of untrained men (7.4 $\mu mol/g \cdot min^{-1}$) were not significantly different from the mean activities observed for the jumpers (male and female) or female throwers. However, the male throwers appear to have lower SDH activities (4.5 $\mu mol/g \cdot min^{-1}$) than the other trained and untrained men and women. Male middle-distance runners were found to possess 48% more SDH activity than their female counterparts, and 100% more than the untrained men. The highest SDH activity was found in a distance runner (20.9 $\mu mol/g \cdot min^{-1}$), and the lowest in a male javelin thrower (1.5 $\mu mol/g \cdot min^{-1}$).

TABLE 3. *Muscle succinate dehydrogenase, lactic dehydrogenase, and phosphorylase activities for male and female track athletes and a group of untrained men*

Subj	Sex	No.	SDH, $\mu mol/g \cdot min^{-1}$	LDH, $\mu mol/g \cdot min^{-1}$	PHOSP, $\mu mol/g \cdot min^{-1}$
Sprint runners	F	2	10.4 (10.1–10.7)	1,350 (1,340–1,360)	20.0 (16.5–23.5)
	M	2	12.9 (12.4–13.4)	1,287 (1,048–1,525)	15.3 (12.8–17.7)
Middle-distance runners	F	7	10.0 (6.0–13.9)	744 (488–927)	12.6 (9.2–15.1)
	M	7	14.8 (13.2–18.6)	868 (688–1,140)	8.4 (4.8–10.3)
Distance runners	M	5	16.6 (8.2–20.9)	764 (632–847)	8.1 (5.6–9.8)
Long-high jumpers	F	3	8.4 (6.3–9.4)	1,048 (913–1,177)	7.5 (3.9–11.0)
	M	2	9.4 (8.9–9.9)	992 (775–1,208)	10.5 (7.5–13.5)
Javelin throwers	F	3	9.0 (7.7–10.3)	1,100 (1,101–1,099)	9.3 (5.2–16.8)
	M	3	4.8 (1.5–7.7)	1,101 (1,049–1,132)	9.5 (9.4–9.6)
Shot put, discus throwers	F	2	8.1 (6.3–9.9)	822 (813–832)	6.9 (6.1–7.6)
	M	4	4.3 (2.9–5.8)	1,058 (751–1,465)	7.7 (5.3–13.5)
Untrained	F	10	8.2 (5.4–14.9)	764 (630–940)	6.8 (4.1–10.5)
	M	11	7.4 (5.2–10.1)	822 (603–1,192)	7.6 (4.3–12.0)

Values are means with ranges in parentheses. SDH = succinate dehydrogenase; LDH = lactic dehydrogenase; PHOSP = phosphorylase.

Mean LDH activities were lowest in middle-distance and distance runners and untrained men and women (Table 3). The greatest LDH activities were observed in subjects having the greatest % FT fibers. Thus, it appears that skeletal muscle LDH activity is a function of fiber composition, since these LDH data correlate highly ($r = -0.70$) with the % area ST fibers. To demonstrate this relationship it can be noted that one sprinter having only 15.3% area ST had an LDH activity of 1,525 μmol/g·min^{-1}, while a middle-distance runner with 78.5% area ST had an LDH activity of 632 μmol/g·min^{-1}. As might be anticipated, the men and women (trained and untrained) had similar mean LDH activities.

Phosphorylase activities in the male and female athletes averaged 9.14 and 11.32 μmol/g·min^{-1} ($P > 0.05$). The only notable difference between the male and female athletes was observed among the middle-distance runners, the women having 50% more phosphorylase activity than the men. Unlike the LDH activity, phosphorylase showed little relationship to fiber composition ($r = -0.31$). Although details of individual training requirements were not available, the data suggest that elevated phosphorylase activities may be a function of high intensity anaerobic training (13). Sprinters, for example, had a mean phosphorylase activity (17.7 μmol/g·min^{-1}) that was 2.2 times greater than that of the distance runners (8.1 μmol/g·min^{-1}). It is interesting to note that the jumpers, throwers, distance runners, and the male middle-distance runners had phosphorylase activities that were similar to the values observed for untrained men and women. Female middle-distance runners, who were utilizing high-intensity interval training, had phosphorylase activities that averaged 1.66-fold greater than the untrained men.

Maximal oxygen uptake. $\dot{V}O_{2\,max}$ was measured in 6 female and 5 male middle-distance runners, 4 male distance runners, 2 male throwers, 10 untrained women, and 6 untrained men. The $\dot{V}O_2$ values for these groups averaged (range) 59.3 (51.7–66.5), 70.4 (65.9–76.5), 71.2 (62.5–78.6), 45.6 (42.4–48.8), 41.1 (32.1–47.0), and 34.4 (26.1–44.5) ml/kg·min^{-1}, respectively. As demonstrated in Fig. 2, $\dot{V}O_{2\,max}$ shows a strong relationship ($r = 0.79$) to the SDH activity in skeletal muscle. Efforts to correlate $\dot{V}O_{2\,max}$ to the other variables measured (fiber composition or other enzyme activities) revealed no significant relationships. The % ST fibers, for example, correlated 0.13 with $\dot{V}O_{2\,max}$, while the two glycolytic enzymes, LDH and phosphorylase, correlated 0.08 and 0.05 with oxygen uptake capacities, respectively.

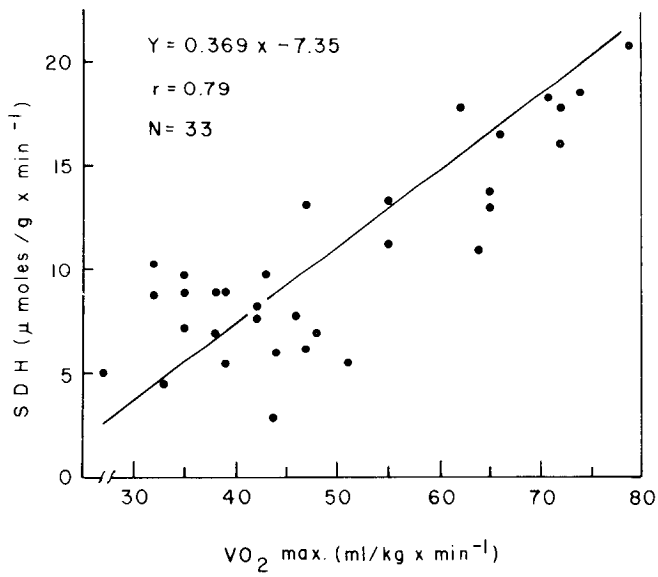

FIG. 2. Relationship between maximal oxygen uptake ($Vo_{2\,max}$) and gastrocnemius muscle succinate dehydrogenase (SHD) activity.

DISCUSSION

Gollnick et al. (15) have previously taken up the question of whether the percentage distribution of a specific fiber type in skeletal muscle can be altered by training. Although some studies have shown that training increases the number of fibers with high oxidative capacities (1, 9, 20), there is no evidence to suggest a change in the contractile properties of ST and FT fibers as measured by the ATPase stain. Recent studies have demonstrated that fiber distribution is unchanged by 4–6 mo of training in young boys (11–13 yr old) and adult men (13, 14). However, the oxidative capacities of both fast- and slow-twitch fibers appear to increase. Such findings may be interpreted as evidence that fiber composition, as measured by its contractile characteristics, is established early in life and that only the metabolic qualities of these fibers adapt to chronic exercise.

In keeping with earlier studies (11, 21), only two fiber types have been identified in the gastrocnemius of subjects in the present study. This is in contrast to the more complex classification established for animal muscle (16, 25). Dubowitz and Brooke (8), however, have shown that FT (type 2) human fibers can be subtyped as 2A (high NADH tetrazolium reductase activity) and 2B (low NADH tetrazolium reductase activity). In the present study, tissue serial sections were preincubated at pH 4.3 and 4.6 in an effort to distinguish 2A from 2B fibers. Brooke and Kaiser (3) have suggested that in the adult human biceps, approximately one-third of the muscle fibers are ST (type 1), one-third type 2A, and one-third type 2B. In most subjects examined in the present study, no separation could be made between the 2A and 2B fibers. The greatest distinction between the FT subtypes (2A and 2B) was noted in a shot-putter whose muscle was composed of 45.7% ST, 39.1% 2A (FT), and 15.2% 2B (FT) fibers. As a result of the random and often nonexistent differentiation between the FT subtypes, comparisons between the groups and sexes have been limited to only the pH 4.3 or 10.3 ATPase stain, thereby combining the 2A and 2B fibers.

The large percentage of ST fibers observed in the muscle of endurance runners confirms previous observations (5, 15). Nevertheless, contrary to our previous report (5), the % ST fibers showed little relationship to endurance capacity as measured by $\dot{V}O_{2\,max}$. These earlier measurements, however, were made on a rather homogenously trained group of runners. Since the endurance training of the men and women in the present study varied markedly, it is not surprising to find a low correlation between physiological endurance measurements and % ST fibers. When one considers athletes by event, it is obvious that endurance athletes possess

substantially more ST fibers than the sprint oriented men and women. These data and previous studies (5, 13, 14) suggest that, while training dictates the ultimate capacity for endurance, success in either sprint or distance running is in part predetermined by muscle fiber composition. Jumpers, throwers, and middle-distance runners, however, are represented by a wide range of fiber compositions.

Although the male and female athletes (all groups) had similar fiber compositions, female middle-distance runners had a higher % ST fibers than male middle-distance runners. Since this event demands both high glycolytic and aerobic capacities, it is not surprising to find a broad range of fiber compositions. Traditionally, however, few distance running events (>10 km) have been provided for women. It is possible, therefore, that the female middle-distance runners have been recruited from among those who had predominately ST fibers. One might speculate that international success at 800 m would be more likely for men and women who have 40–50% ST fibers than for those with 60–70% ST fibers, since these individuals should have both the speed and the capacity for endurance essential at that distance.

Although the degree of shortening of the biopsy specimen cannot be judged from sections, it is generally agreed that FT fibers have larger cross-sectional areas than ST fibers (14, 15). Moreover, it has been suggested that endurance or strength training may result in the selective hypertrophy of the ST or FT fibers, respectively (24). This may in part explain the very large FT fibers of the male shot-putter. It is also conceivable that the anabolic steroids consumed by these men may have influenced the cross-sectional areas of their FT and ST fibers. However, the fiber areas reported for these men are similar to those previously reported for weight lifters (10, 15). In any event, these data do not permit us to evaluate the role of steroids in muscle hypertrophy.

Numerous studies have shown that endurance training increases muscle SDH activity 1.6–2.2 times the level of untrained muscle (13, 14, 17, 18). This compares favorably with the values for untrained and endurance trained men in this study. One point of interest is the difference in SDH activities of the male and female middle-distance runners. Despite a greater % ST fibers, the women had significantly less SDH activity than the men. Although it is possible that endurance training does not produce the same gains in SDH activity in women as in men, we cannot exclude the possibility that the women were either at a different level of training fitness or that their training program entailed less aerobic exercise. As previously mentioned, these measurements were made at a time when many of the subjects were not in top competitive condition. Most of the male distance and middle distance runners had actively engaged in endurance competition (cross-country running) for several months preceding these tests. The female middle-distance runners, on the other hand, were placing relatively greater emphasis on a high-intensity intermittent type of training at the time of these measurements.

The strong relationship between SDH activity and $\dot{V}O_{2\,max}$ is compatible with previous studies which demonstrate that endurance training enhances both the oxidative potential of skeletal muscle and physical working capacity (13, 14). However, these data do not afford us an opportunity to assess the merits of arguments which describe oxygen transport and/or tissue oxygen utilization as factors limiting oxygen consumption during maximal effort.

Another point of interest is the extremely low SDH activity observed in the male throwers (4.51 μmol/g·min^{-1}). Although they do not engage in endurance training it is difficult to understand why they have significantly less SDH activity than the untrained men (7.4 μmol/g·min^{-1}). It might be suggested that these low activities are a function of sarcoplasmic dilution as a result of fiber hypertrophy. One male javelin thrower, for example, was found to have a mean cross-sectional fiber area of 8,254 μm^2 and a muscle SDH activity of 1.5 μmol/g·min^{-1}, roughly 20% of the activity seen in untrained muscle. Similar findings reported for weight lifters (15) suggest that intense strength training in men may result in a reduction in muscle SDH activity.

Conclusion. These observations demonstrate that female and male track athletes are similar in terms of muscle fiber composition and selected enzyme activities. Aside from a few differences in enzymes and % ST within various events, the only distinction between the sexes was the larger fiber areas of the male athletes. These measurements confirm earlier reports which suggest that the athlete's success in strength, speed, and/or endurance events results, in part, from his or her genetic endowment (24). While sprint- and endurance-trained athletes are characterized by distinct fiber compositions and enzyme activities, participants in strength events have relatively low muscle enzyme activities and a variety of fiber compositions. Additional studies are needed to describe the changes in muscle enzyme activities at various stages of training and to relate both glycolytic and oxidative enzyme activities to performance in speed, endurance, and strength events.

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REFERENCES

1. Barnard, R. J., V. R. Edgerton, and J. B. Peter. Effect of exercise on skeletal muscle. I. Biochemical and histochemical properties. *J. Appl. Physiol.* 28: 762–766, 1970.
2. Bergström, J. Muscle electrolytes in man. *Scand. J. Clin. Lab. Invest. Suppl.* 68: 11–13, 1962.
3. Brooke, M. H., and K. K. Kaiser. The use and abuse of muscle histochemistry. *Ann. N.Y. Acad. Sci.* 228: 121–144, 1974.
4. Costill, D. L. Metabolic responses during distance running. *J. Appl. Physiol.* 28: 251–255, 1970.
5. Costill, D. L., P. D. Gollnick, E. D. Jansson, B. Saltin, and

E. M. STEIN. Glycogen depletion patterns in human muscle fibers during distance running. *Acta Physiol. Scand.* 89: 374–383, 1973.

6. COSTILL, D. L., E. JANSSON, P. D. GOLLNICK, AND B. SALTIN. Glycogen utilization in leg muscles of men during level and uphill running. *Acta Physiol. Scand.* 91: 475–481, 1974.
7. DANIELS, J. Portable respiratory gas collection equipment. *J. Appl. Physiol.* 31: 164–167, 1971.
8. DUBOWITZ, V., AND M. H. BROOKE. *Muscle Biopsy: A Modern Approach* Philadelphia, Pa.: Saunders, 1973, p. 50–51.
9. EDGERTON, V. R., L. GERCHMAN, AND R. CARROW. Histochemical changes in rat skeletal muscle after exercise. *Exptl. Neurol.* 24: 110–123, 1969.
10. EDSTRÖM, L., AND B. EKBLOM. Differences in sizes of red and white muscle fibers in vastus lateralis of musculus quadriceps femoris of normal individuals and athletes. Relation to physical performance. *Scand. J. Clin. Lab. Invest.* 30: 175–181, 1972.
11. EDSTRÖM, L., AND B. NYSTROM. Histochemical types and sizes of fibers of normal human muscles. *Acta Neurol. Scand.* 45: 257–269, 1969.
12. ENGEL, W. K., AND M. H. BROOKE. Muscle biopsy as a clinical diagnosis aid. In: *Neurological Diagnostic Techniques,* edited by W. S. Field. Springfield, Ill.: Thomas, 1966, p. 90–146.
13. ERIKSSON, B. O., P. D. GOLLNICK, AND B. SALTIN. Muscle metabolism and enzyme activities after training in boys 11–13 years old. *Acta Physiol. Scand.* 87: 231–239, 1972.
14. GOLLNICK, P. D., R. B. ARMSTRONG, B. SALTIN, C. W. SAUBERT IV, W. L. SEMBROWICH, AND R. E. SHEPHARD. Effect of training on enzyme activity and fiber composition of human skeletal muscle. *J. Appl. Physiol.* 34: 107–111, 1973.
15. GOLLNICK, P. D., R. B. ARMSTRONG, C. W. SAUBERT IV, K. PIEHL, AND B. SALTIN. Enzyme activity and fiber composition in skeletal muscle of untrained and trained men. *J. Appl. Physiol.* 33: 312–319, 1972.
16. GUTH, L., AND H. YELLIN. The dynamic nature of the so-called fiber types of mammalian skeletal muscle. *Exptl. Neurol.* 31: 277–300, 1971.
17. HOLLOSZY, J. O., L. B. OSCAI, I. J. DON, AND P. A. MOLÉ. Mitochondrial citric acid cycle and related enzymes: adaptive responses to exercise. *Biochem. Biophys. Res. Commun.* 40: 1368–1373, 1970.
18. HOLLOSZY, J. O., L. B. OSCAI, P. A. MOLÉ, AND I. J. DON. Biochemical adaptations to endurance exercise in skeletal muscle. In: *Muscle Metabolism During Exercise,* edited by B. Pernow and B. Saltin. New York: Plenum, 1971, p. 51–61.
19. LOWRY, O. H., AND J. V. PASSONNEAU. *A Flexible System of Enzymatic Analysis.* New York: Academic, 1972, p. 93–108.
20. MORGAN, T. E., L. A. COBB, F. A. SHORT, R. ROSS, AND D. R. GUNN. Effects of long-term exercise on human muscle mitochondria. In: *Muscle Metabolism During Exercise,* edited by B. Pernow and B. Saltin. New York: Plenum, 1971, p. 87–95.
21. MORRIS, C. J. Human muscle fiber type grouping and collateral re-innervation. *J. Neurol. Neurosurg. Psychiat.* 32: 440–444, 1968.
22. NOVIKOFF, A. B., W. SHIN, AND J. DRUCKER. Mitochondrial localization of oxidation enzymes: staining results with two tetrazolium salts. *J. Biophys. Biochem. Cytol.* 9: 47–61, 1961.
23. PADYKULA, H. A., AND E. HERMAN. The specificity of the histochemical method of adenosine triphosphatase. *J. Histochem. Cytochem.* 3: 170–195, 1955.
24. SALTIN, B. Metabolic fundamentals in exercise. *Med. Sci. Sports* 5: 137–146, 1973.
25. STEIN, J. M., AND H. A. PADYKULA. Histochemical classification of individual muscle fibers of the rat. *Am. J. Anat.* 110: 103–105, 1962.
26. WATTENBERG, L. W., AND J. L. LEONG. Effects of coenzyme Q_{10} and menadione on succinate dehydrogenase activity as measured by tetrazolium salt reduction. *J. Histochem. Cytochem.* 8: 296–303, 1960.
27. WILMORE, J. H., AND D. L. COSTILL. Semiautomated systems approach to the assessment of oxygen uptake during exercise. *J. Appl. Physiol.*36: 618–620, 1974.