Contrasts in muscle and myofibers of elite male and female bodybuilders

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ALWAY, S. E., W. H. GRUMBT, W. J. GONYEA, AND J. STRAY-GUNDERSEN. *Contrast in muscle and myofibers of elite male and female bodybuilders.* J. Appl. Physiol. 67(1): 24–31, 1989.—Muscle cross-sectional area (CSA), fiber area, and fiber number were determined from the biceps brachii of eight elite male bodybuilders (MB) and five elite female bodybuilders (FB) who had similar training characteristics. Biceps CSA was obtained from computer tomographic scanning and corrected for non-contractile tissue. Biceps CSA was twofold greater in MB relative to FB and strongly correlated to lean body mass ($R = 0.93$). Biceps CSA expressed per kilogram lean body mass (LBM) or per centimeter body height (BH) was 35% greater in MB compared with FB. Most of the gender difference in muscle CSA was because of greater absolute mean fiber areas in MB (9,607 μm^2) relative to FB (5,386 μm^2); however, MB also had a significantly greater population of small type II fibers (<2,000 μm^2) compared with FB. Type II fiber area/LBM averaged 1.6-fold greater in MB compared with FB; however, type I fiber area/LBM was similar between groups. Biceps CSA was positively correlated to fiber CSA ($R = 0.75$) and fiber number ($R = 0.55$). This suggests that adaptations to resistance training may be complex and involve fiber hypertrophy and fiber number (e.g., proliferation). Alternatively, since the muscle characteristics before training are not known, these apparent adaptations might be genetically determined attributes.

muscle cross-sectional area; fiber cross-sectional area; fiber number; type I and type II fibers; computerized tomographic scans

ADAPTATIONS OF MUSCLE to heavy resistance training have been studied in men (see 21 for references), but little is known of adaptations in female muscle. The most comprehensive studies in males have been limited by subject number or training status (16, 19, 22). In addition, studies that have used a mixed subject pool of male bodybuilders (MB) and powerlifters (17, 18) may confound the interpretation of the results because these athletes do not train in similar fashion.

The literature on resistance-trained females has methodological weaknesses such as limited training duration and intensity. Furthermore, investigators have used indirect methods to predict changes at the cellular level (i.e., percent body fat, limb girth). However, these studies suggest that females are capable of significant strength gains with minimal or no increase in muscle mass (7, 25). Empirical observations of bodybuilders suggest that females may be capable of substantial increases in muscle mass. This is supported from a published abstract of a study that incorporated needle biopsies and short-term resistance training of the quadriceps muscles in females and found hypertrophy of a fast-twitch fiber subtype (3). These investigators concluded that skeletal muscle hypertrophy in women is possible (3). Nevertheless, it should be noted that these studies (3, 7, 25) involved short-term training programs and do not necessarily reflect adaptations to many years of heavy resistance training in women. Thus the potential for muscular hypertrophy in women may be severely underestimated.

It is not known whether gender differences in muscle mass are the result of greater total number of fibers in males relative to females. In fact, the contribution of muscle fiber number to muscle enlargement in the human is not clear. Fiber number is thought to remain constant after birth, so that any increase in muscle mass in adults occurs exclusively through hypertrophy of the existing fibers (9). It has been clearly shown that in models that induce hypertrophy by ablation of synergists the increases in fiber cross-sectional area (CSA) totally account for the increases in muscle mass (9, 23). There have been, however, several recent reports from animal models that have indicated that total fiber number increased in response to either a stretch overload (2, 14) or resistance exercise (11, 12). In contrast, estimated fiber number in the biceps brachii of MB was not different from untrained controls (16, 19), but males had a greater total number of fibers than females (19). This suggests that females might have a reduced ability to increase muscle mass by virtue of having fewer fibers than males. Nonetheless it is not known whether resistance training that results in muscle enlargement will increase fiber number in females. Thus further study of gender-specific adaptation of fiber number to resistance training is warranted.

Although some studies have shown a preferential increase in area of type II fibers relative to type I fibers with resistance training (1, 15, 16, 19), it is not known whether females will show similar adaptations of fiber area. Although mean fiber CSAs clearly increase in males with heavy resistance training (15), the variance among fiber areas also increases (1). We do not know whether this increased variance is the result of only an increase in fiber size or whether there may be smaller as well as

larger fibers contributing to the variance. Fiber area-frequency distribution curves have not been completed for hypertrophied human muscles of resistance-trained subjects of either gender; however, these curves would demonstrate such variances in fiber area.

It was our supposition that the potential adaptations of fiber area and fiber number could be determined in muscles of elite bodybuilders. Male and female bodybuilders (FB) possess extreme degrees of muscle mass in the biceps and train intensely for many years before competing in bodybuilding events to obtain this mass. Although total muscle mass would likely be less in women than in men, it was not clear whether women could develop muscle CSAs per unit body mass or per unit height similar to their male counterparts. Thus the purpose of this study was to determine whether FB had relative muscle CSA, fiber area, or fiber number [i.e., per unit lean body mass (LBM) or per unit body height (BH)] similar to MB. A second purpose was to describe the variance in fiber areas and to determine whether the relative variance in fiber area was fiber or gender specific. A final purpose was to determine the relationship between fiber number and muscle CSA in MB and FB.

METHODS

Subjects. Subjects consisted of eight elite MB and five elite FB. These athletes had won state-level bodybuilding championships or had placed in the top five in national-level bodybuilding championships. The training status (i.e., caliber) of athlete may be important to determine the adaptations to resistance training. Their physical characteristics are given in Table 1. These athletes trained with resistance exercise for 4 ± 1.1 h/day, 6 days/ wk, and no difference was found between subject groups. The relative intensity of training was assessed from sample exercise programs over 14 days and found to be similar in both groups (Table 2). Likewise, the total length of training did not differ between subject groups. Informed consent was obtained from all subjects. This study was approved by the Institutional Review Board of Human Subjects at the University of Texas Southwestern Medical Center at Dallas.

TABLE 1. *Subject characteristics*

Subj	n	BM, kg	LBM, kg	Age, yr	BH, cm	LBM/BH, kg/cm
MB	8	94.6±6.4*	87.1±5.9*	33.1±2.7	173.3±1.7	0.48±0.03*
FB	5	62.2±2.7	51.0±3.3	36.6±2.5	166.7±3.2	0.31±0.02

Values are means ± SE; n, no. of subjs. MB, male bodybuilders; FB, female bodybuilders; BM, body mass; LBM, lean BM; BH, body height. * $P < 0.05$, MB vs. FB.

LBM. It has been demonstrated that determination of the percent body fat and lean body weights of subjects are equally accurate when standard hydrostatic weighing or body-volume displacement techniques are used (8). Recent designs of the body volume meter allow body composition to be determined with greater accuracy than with hydrostatic weighing and without difficulties of stabilization of measures that are common in hydrostatic weighing (13). The total body volume of subjects was determined by water displacement in a body volume tank (Whitmore Enterprises). Residual lung volume was determined by the method of Wilmore et al. (26). Body volume was calculated as follows: body volume = total body volume displacement from volume meter − residual lung volume − abdominal gas volume. Abdominal gas volume was assumed to be 0.11 liters (4). Mass was determined on land, and density was determined according to the equation: density = mass ÷ volume. Percent body fat was determined from the equation of Siri (20). LBM was calculated as total body mass − (total body mass × percent fat).

Percent fiber distribution. Two needle biopsies were obtained from the same site from the long head of the biceps brachii according to the technique of Bergstrom (5). The tissue was frozen in isopentane cooled to the temperature of liquid N_2 and stored at $-70°C$ before it was processed for histochemistry. Cryostat sections were cut at 10 μm, mounted on coverslips, and stained for myofibrillar ATPase (m-ATPase) activity (6). Fibers were classified as type I or type II from the m-ATPase histochemical reactions. Photographic montages were assembled, and all the fibers in the biopsy sample were counted (667 ± 73) and percent fiber distribution was determined.

Fiber CSA. Fiber areas were determined by planimetry of all fibers in the biopsy sample in two subjects. It was determined that 200 fibers were necessary before the standard deviations within a subject achieved a plateau (Fig. 1). For this reason fiber areas were determined for only the major fiber types, i.e., type I and type II fibers. In the remaining subjects, fiber areas were determined by planimetry on 200 type I fibers and 200 type II fibers from each biopsy. Light micrographs (×100) were taken of cross sections of fibers after an alkaline mATPase reaction (pH 10.25) and printed to a final magnification of approximately ×15,000. Fiber perimeters were manually traced on a Summagraphics digitizing tablet. A minicomputer software computer program was used to store individual fiber areas and also to calculate type I and type II fiber area for each subject. Fiber areas were combined by subject group to determine the type I and

TABLE 2. *Training characteristics of MB and FB*

Subj	n	Duration of Training, yr	Training Sessions for Elbow Flexors, no./wk	Duration of Training for Elbow Flexors, h/day	Repetitions for Elbow Flexors no./set	Repetitions for Elbow Flexors no./workout	LBM Lifted in Elbow Flexors, %/repetition	(Wt Lifted × Repetitions)/LBM, per workout
MB	8	9.3±1.6	2.2±0.2	1.2±0.3	8.0±0.1	96.9±1.6	28.4±1.7	111.6±2.4
FB	5	7.8±0.7	2.4±0.2	1.1±0.4	8.0±0.2	98.1±1.9	25.1±1.3	105.1±6.1

Values are means ± SE of average of 4 training sessions in each subj for elbow flexors of 1 arm. See Table 1 footnote for definition of abbreviations.
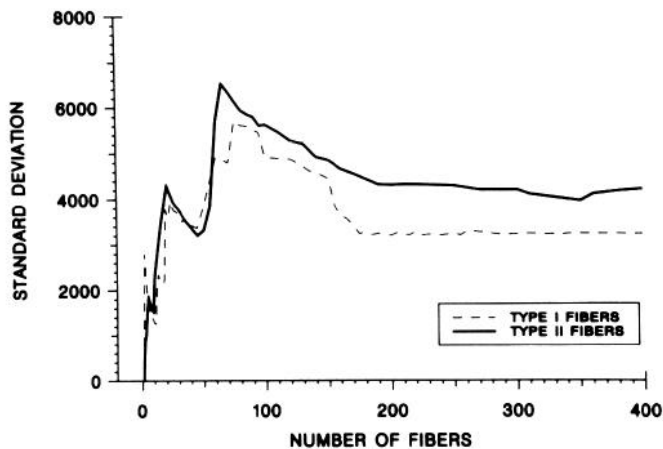
FIG. 1. No. of fibers traced by planimetry for fiber area determination vs. SD of fiber area for representative male who had mean type I and type II areas of 8,001.6 and 12,150.5 μm^2, respectively.

type II fiber area for MB and FB subject groups.

In addition to the areas for type I and type II fibers, mean fiber area (F_a) was calculated to account for fiber distribution in the biceps brachii as follows: F_a = (area of type I fibers × percent of type I fibers) + (area of type II fibers × percent of type II fibers)/100.

Muscle noncontractile tissue. Muscle samples were cut at 10 μm and stained for Gomoris trichrome (10). The volume density of collagen and other noncontractile tissue was determined from a 121-point grid lattice according to standard stereological techniques (24).

Muscle area. CSA of the biceps brachii was determined from computerized tomographic (CT) scans of the upper arm before the muscle biopsy. The hand was supinated and the arm was in the extended position. Six scans were taken at 3-mm intervals from the midbelly region of the upper arm containing the greatest area of the biceps. CT scans were taken with a soft-tissue algorithm. This computer algorithm was part of the software package produced by the manufacturers of the CT scan unit that optimizes the visualization of muscle and other soft tissue (Picker International). Window and level settings were 160 and 64, respectively. The CSA of the biceps brachii was determined by planimetry from five traces of each scan. The scan that had the greatest CSA was selected to represent the biceps CSA. In a similar manner, the entire flexor muscle complex was identified from the CT scans and the greatest area from the six scans was selected to represent the flexor CSA (Fig. 2). Both flexor and biceps CSAs were corrected for the percent of collagen and noncontractile tissue that was determined from biopsies of the biceps.

Fiber number. Biceps fiber number was estimated as follows: number of fibers = biceps CSA (corrected for noncontractile tissue) ÷ F_a. Muscle obtained by the needle biopsy technique undergoes almost complete contracture after excision (16); therefore fiber areas were measured with sarcomeres in a contracted state. Since muscle CSA was measured by CT scanning with the sarcomeres at resting length, the net result is that F_a has been overestimated and, therefore, fiber number has been underestimated. MacDougall et al. (16) corrected fiber number by 36% to account for sarcomere shortening. We
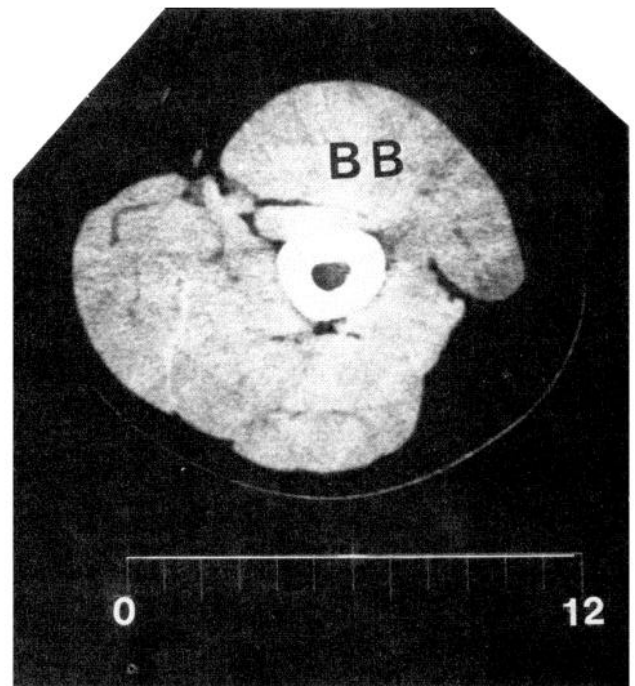

FIG. 2. Computer tomographic scan of elbow flexors. BB, biceps brachii. Scale is in cm.

have provided data uncorrected and have also corrected the estimates of fiber number by 36%. We have assumed that if the degree of sarcomere shortening is the same in both subject groups, valid intergroup comparisons can still be made on fiber numbers uncorrected for sarcomere shortening. Thus all statistical analyses and correlations have been completed with fiber number uncorrected for shortening.

Statistics. Descriptive statistics include means ± SE. Gender differences among morphological characteristics of the biceps and elbow flexors were determined by a one-way analysis of variance. Pearson product correlations (R) were conducted between morphological and structural variables. One-way χ^2 analysis was performed between subject groups on frequency-area data. $P < 0.05$ was selected to indicate statistical significance.

RESULTS

Fiber type distribution. The percent of type I and type II fibers did not differ among subject groups. Type II fibers averaged 59.9 ± 3.3% in MB and 50.1 ± 2.2% in FB.

Noncontractile tissue. The volume density of collagen and other noncontractile tissue was similar in males and females and averaged 9.7 ± 0.7 and 10.7 ± 0.2%, respectively (Table 3).

Relationship among biceps CSA, BH, and LBM. LBM was 71% greater in MB than in FB (Table 1). Biceps CSA was not significantly correlated to BH ($R = 0.50$, $P > 0.05$), and the data showed that subjects of similar height could have large differences in muscle CSA. Conversely, biceps CSA was strongly correlated to LBM ($R = 0.93$, $P < 0.001$), and furthermore the two subject groups were distinctive and did not display any overlap in the data (Fig. 3). This indicates that to achieve a large

TABLE 3. *Morphological characteristics of the biceps brachii*

Subj	n	Noncontractile Tissue, %	Type II Fibers, %	Estimated Fiber No. × 10³		Type I Fiber Area, μm²	Type II Fiber Area, μm²	Type I-to-Type II Area Ratio	Flexor-to-Biceps Area Ratio
				Uncorrected	Corrected*				
MB	8	9.7±0.7	59.9±3.3	301.6±52.6	410.2±70.9	75,259±582†	11,398±1,027†	1.6±0.1†	1.4±0.1
FB	5	10.7±0.2	50.1±2.2	234.3±20.8	318.6±28.3	4,760±602	5,010±769	1.1±0.1	1.3±0.1

Values are means ± SE. See Table 1 footnote for definitions of abbreviations. * Fiber no. was corrected for sarcomere shortening of 36%; † $P < 0.05$, MB vs. FB.
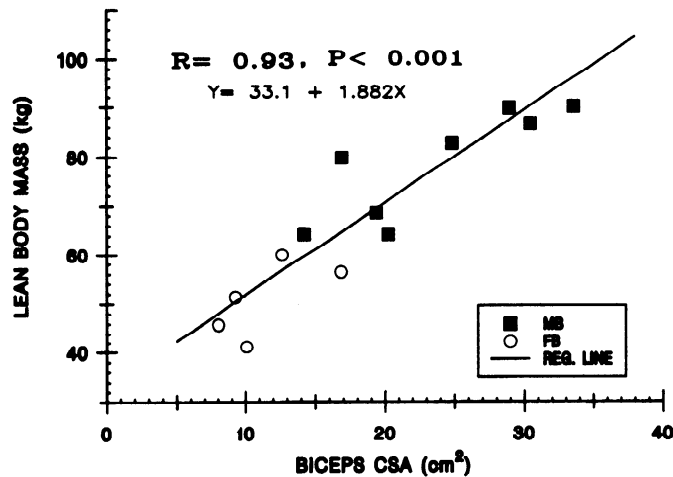

FIG. 3. Relationship between biceps cross-sectional area (CSA) and lean body mass in male (MB) and female bodybuilders (FB). Reg line, regression line.
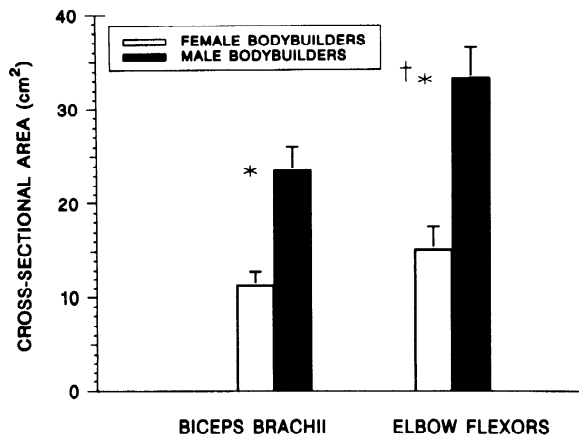

FIG. 4. Biceps brachii and total elbow flexor cross-sectional area (means ± SE) in female and male bodybuilders. *$P < 0.05$, males vs. females; †$P < 0.05$, male biceps vs. elbow flexors.

muscle CSA the subject must also have a high LBM. BH and LBM were not related to each other.

Biceps CSA. MB had biceps and flexor CSA (corrected for noncontractile tissue) 2.07 and 2.17 times greater, respectively, than FB (Fig. 4). The ratio of flexor to biceps CSA was not different between subject groups (Table 3). The ratio of biceps CSA to LBM was significantly greater in MB (0.30 ± 0.02 cm²/kg) than in FB (0.22 ± 0.04 cm²/kg). Biceps CSA normalized for BH was significantly greater in MB (0.13 ± 0.2 cm²/cm) than in FB (0.07 ± 0.01 cm²/cm).

Relationships of LBM and BH to fiber area. LBM was strongly correlated to areas in type I ($R = 0.73, P < 0.01$) and type II fibers ($R = 0.80, P < 0.001$). Conversely, BH

was not significantly correlated to either type I ($R = 0.18, P > 0.05$) or type II fiber area ($R = 0.22, P > 0.05$).

F_a. F_a (corrected for fiber type distribution) averaged 9,607 ± 785 μm² in MB and 5,386 ± 772 μm² in FB. This significantly greater F_a in MB was the result of increased areas in both type I and type II fibers (Fig. 5).

Type I and type II fiber area in MB averaged 1.52- and 2.27-fold greater, respectively, than the corresponding fiber areas of FB. Type II-to-type I fiber area ratios were were 1.57 and 1.05 in MB and FB, respectively ($P < 0.05$). Ratios of type I fiber area to LBM (MB = 92 ± 6 μm²/kg, FB = 93 ± 9 μm²/kg) and type I fiber area to BH (MB = 3,889 ± 427 μm²/cm, FB = 2,789 ± 784 μm²/cm) were similar in both subject groups. Conversely, MB had greater ratios of type II fiber area to LBM (136 ± 11 μm²/kg vs. 97 ± 11 μm²/kg) and type II fiber area to BH (5,960 ± 805 μm²/cm vs. 2,996 ± 406 μm²/cm) than their female counterparts.

Absolute fiber area data plotted as a frequency-distribution curve indicated that average type II fiber area did not simply reflect a shift to larger fibers but reflected a wider distribution of type II fiber areas in MB (Fig. 6, B). One-way χ^2 analysis of the type II fiber data indicated that MB and FB had a similar frequency of fibers <500 μm² in area; however, MB had a significantly greater frequency of fibers between 500 and 2,000 μm² relative to FB (4.73 vs. 2.39%; $P < 0.01$).

Chi-square analysis of frequency-distribution curves indicated that average type I fiber area reflected a shift to larger fibers in MB relative to FB (Fig. 6A). The frequency of type I fibers between 500 and 2,000 μm² was similar in MB relative to FB (4.76 vs. 4.41%).
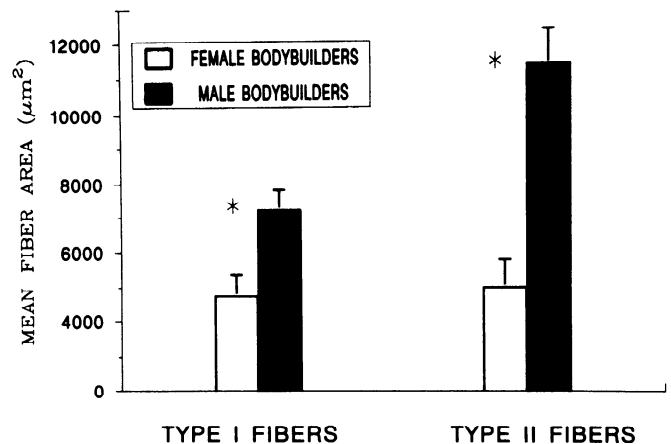
The cumulative frequency distributions of fiber area

FIG. 5. Type I and type II fiber area (means ± SE) in biceps brachii of male and female bodybuilders. Areas are determined from a minimum of 200 fibers of each type. *$P < 0.05$, males vs. females.

(Fig. 6, C and D) further illustrate that type II fibers are not only larger but have considerably more variation than type I fibers in MB, whereas the average fiber area and ranges in fiber area are similar for type I and type II fibers in FB.

Fiber number. Estimated fiber number was similar in MB and FB. Whereas the effect of sarcomere shortening does not influence the comparisons of fiber number between subject groups, it is likely that fiber number will be underestimated. Fiber number was therefore corrected for sarcomere shortening of 36% (16). The relationship between fiber number-to-LBM ratio and fiber number-to-ratio BH was similar for MB and FB (Fig. 7).

Relationship among F_a, fiber number, and biceps CSA. Correlational statistics indicated that F_a was negatively related to biceps fiber number ($R = -0.57$, $P < 0.05$; Fig. 8). However, this correlation appeared to be strongly influenced by *subject JA*, who had an estimated fiber number of 450,252. If this subject was deleted from the correlational calculations, the relationship between F_a and fiber number was not significant ($R = 0.07$, $P > 0.05$).

Biceps CSA was positively correlated to both fiber number ($R = 0.55$, $P < 0.05$) and F_a ($R = 0.75$, $P < 0.01$) (Fig. 9). If *subject JA* was deleted from the data set, the correlation between biceps CSA and fiber number increased to $R = 0.61$ ($P < 0.05$).

DISCUSSION

It is possible that the importance of fiber CSA and fiber number in muscle CSA increases with the degree of hypertrophy and, therefore, the training status of the subject examined. This is suggested from the data of Sale et al. (19) and also in the present data (Fig. 9). Training-induced adaptations in fibers will most likely be seen in muscles of elite athletes who had trained for many years. The present study has examined the greatest number of elite-caliber MB and the only population of elite FB to date. Male subjects used in this study had 5.1% greater biceps CSA and 7.7% greater muscle CSA-to-BH ratios than other bodybuilders labeled as elite (16, 19), and although their BH were similar to subjects of one study (19), body mass was greater in the present subjects. Furthermore, upper arm girth averaged 47.0 ± 0.7 cm in MB, which is greater than girths reported for bodybuilders or powerlifters in two previous studies (17, 18). Thus the importance of fiber CSA and especially fiber number may be more fully realized in subjects from the present study. These data demonstrate that adaptations of fibers to resistance training are more complex than previously believed.

The data from the present study demonstrate several important findings. First, female muscle appears capable of substantial increases in muscle mass, because muscle CSA and F_a were 31% and 1.2-fold greater, respectively, than untrained females as reported by Sale et al. (19). Despite these apparent training-induced differences, we are not able to determine whether FB of this study had similar muscle characteristics before training as seen in untrained female controls.

The second important finding is that, despite similar training intensities and years of training between subject groups, female muscle did not achieve the same level of training effect as male muscle. The present data demonstrate that increases in LBM accompany muscle CSA. Thus, although we expected males to have greater absolute muscle CSA because of greater LBM than females, MB also had greater relative muscle CSA (per kg LBM or per cm BH) than FB. Although we do not know whether males and females of this study had similar biceps CSA-to-LBM ratio before training, unpublished observations from a group of untrained control subjects have demonstrated similar CSA-to-LBM ratios for males (0.18 ± 0.03 $\mu m^2/kg$) and females (0.15 ± 0.03 $\mu m^2/kg$).
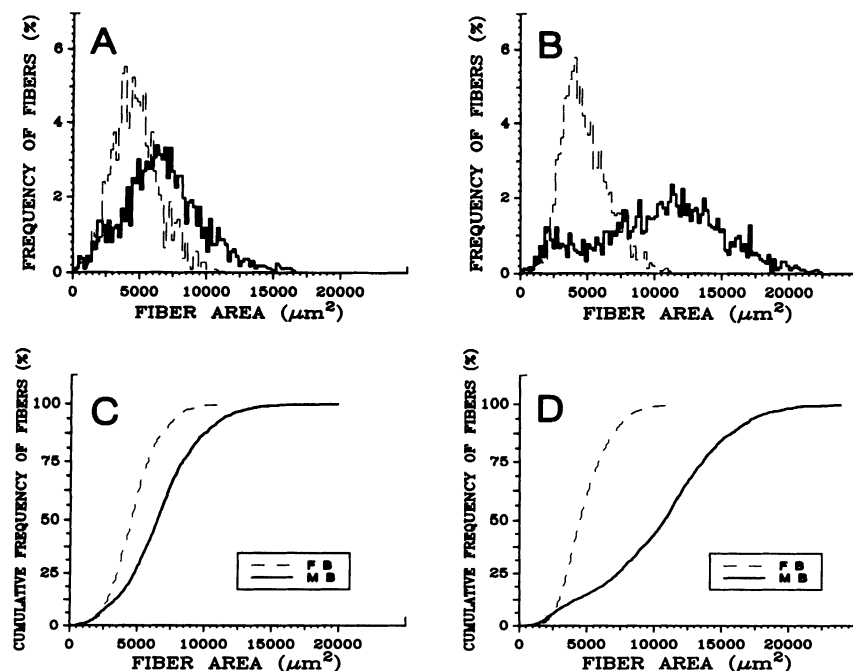

FIG. 6. Fiber area-frequency distribution curves for type I (*A*) and type II fibers (*B*) and cumulative-frequency distribution curves for type I (*C*) and type II fibers (*D*) in male (MB) and female bodybuilders (FB).
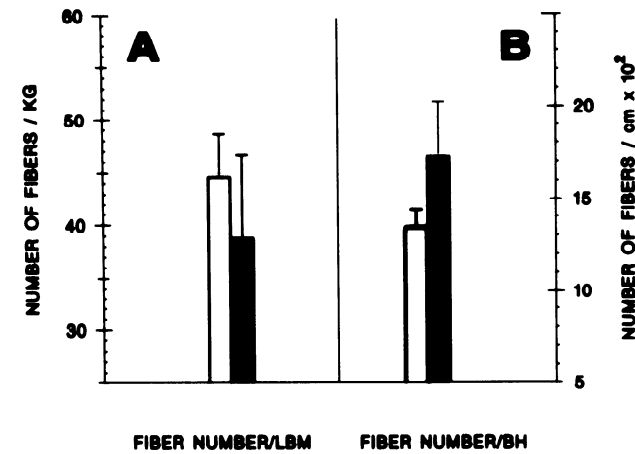
FIG. 7. Relative fiber number in biceps brachii expressed as ratio of fiber number to lean body mass (LBM, A) and fiber number to body height (BH, B) in male (closed bars) and female (open bars) bodybuilders.
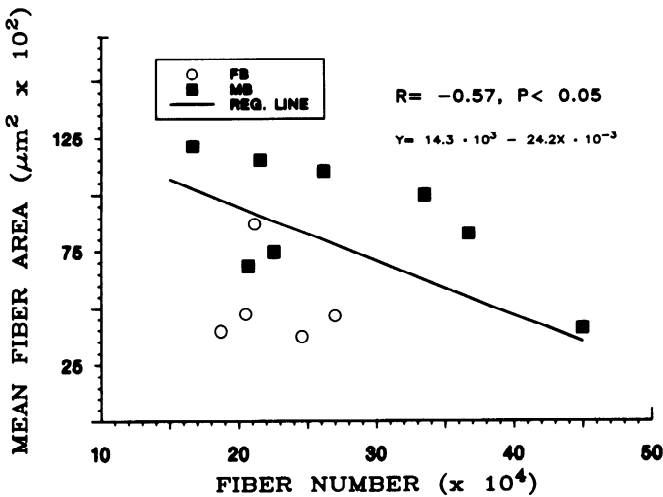

FIG. 8. Mean fiber cross-sectional area (F_a) vs. fiber number in biceps brachii of male (MB) and female bodybuilders (FB). F_a has been calculated to account for fiber-type distribution in biceps brachii. Reg line; regression line.

FIG. 9. Relationships of biceps cross-sectional area (CSA) vs. mean fiber area (*top*) and estimated fiber number (*bottom*). Mean fiber area has been calculated to account for fiber-type distribution in biceps brachii. Reg line, regression line; FB, female bodybuilders; MB, male bodybuilders.

It is clear that the larger biceps CSA in MB was primarily the result of adaptations in type II fibers, because MB had greater type II-to-type I fiber area ratios and relative type II but not type I fiber areas (per cm BH or per kg LBM) compared with FB. This suggests that type II fibers have achieved a preferential relative hypertrophy in MB, whereas adaptations were similar between fiber types in FB. This could limit muscle enlargement in females compared with males. It is possible that type II fibers responded to relative training loads that were different between subject groups, although analysis of sample current training programs of both groups suggests that this is not the case (Table 2). However, it is recognized that the preceding history of training in MB and FB may have been different, although they were training in a similar fashion during the study. Thus differences in prior training might also have accounted for specialized fiber-type adaptations between subject groups.

Although muscle CSA and F_a were greater in MB than in FB, this does not indicate that all type II fibers in MB
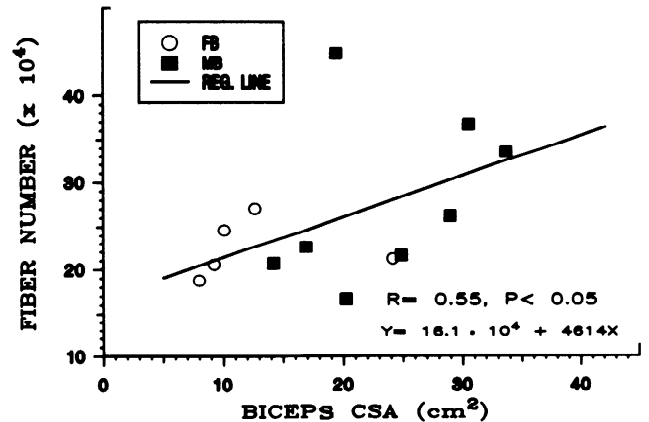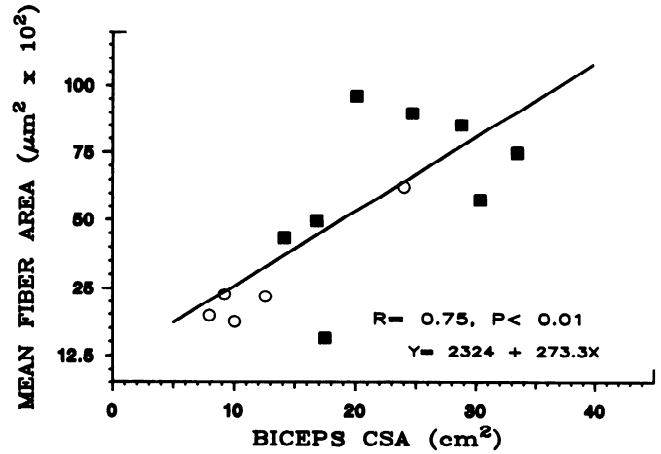
hypertrophied, because there is a significantly greater population of fibers with areas $<2,000$ μm^2 in MB relative to FB. It is clear from these data that expression of fiber area solely in terms of mean $\pm$ SE in the absence of appropriate analysis of fiber area-frequency distributions may miss valuable information. These data confirm the speculation of a previous study (1) in which it was suggested that increased variance in the standard deviation of fiber areas may indicate that there are small as well as large fibers in muscles from resistance-trained subjects. The origin of these small type II fibers is not known. Whereas electron-microscopic examination of these small fibers has not been completed, light-microscopic examination has not provided any evidence to suggest that they are injured, atrophied, or denervated fibers. It is very unlikely that these are atrophied fibers, because this is clearly not a model of disuse and, furthermore, many fibers have achieved marked hypertrophy. Thus the possibility of fiber proliferation must be considered. Although stretch overload does not duplicate resistance exercise, it is important to recognize that fiber proliferation occurs in adult avian slow tonic skeletal muscle in response to stretch (2, 14). Furthermore, an increase in fiber number has been shown after weight-lifting exercise in cats (12), and this type of overload

closely approximates training in bodybuilders.

Data from the present study indicate that fiber number and fiber CSA were significantly correlated to biceps CSA, and these two variables combined to explain 86.5% of the variation in muscle mass. This is the first study to demonstrate a significant relationship between fiber number and muscle CSA among resistance-trained athletes. Nevertheless, the relationship between fiber number and either F_a or muscle CSA needs to be interpreted with caution, because fiber number is derived from both F_a and biceps CSA. Whereas we have obtained a significant correlation between fiber number and biceps CSA (Fig. 9), it is too early to determine whether this is a statistical artifact or whether this has true physiological significance. Data from the weight-lifting cat, however, would suggest the latter is true (11, 12). Although resistance-trained and untrained males have been reported to have similar fiber numbers (16, 19), both groups had greater number of fibers than untrained females (19). Furthermore, since the data from this study indicate that FB have more fibers than untrained females (19), an exercise-induced increase in fiber number in females cannot be eliminated from consideration. This raises the possibility that adaptations to muscle overload by resistance exercise may be more complex than simple increases in fiber size but, rather, may involve interactions of fiber hypertrophy and fiber number. However, the possibility that the female athletes of the present study were all born with more fibers than untrained females (19) cannot be rejected.

The gender-specific adaptations cannot likely be attributed to the current use of anabolic steroids. Four males and two females had previously taken anabolic steroids; however, there were large overlaps in the data of steroid vs. nonsteroid user in fiber number, fiber CSA, muscle CSA, and volume density of noncontractile tissue (i.e., steroid users did not consistently have the largest or smallest data points). Nevertheless, these athletes had used anabolic steroids for 6.2 ± 1.1 yr, and therefore we acknowledge the possibility that muscle adaptation might also exhibit the effect of anabolic steroid used in addition to hypertrophy training.

In summary, this study indicates that females are capable of substantial increases in muscle CSA, fiber number, and hypertrophy of both fiber types compared with data from untrained females (19). Limitations in the magnitude of LBM and muscle CSA in females may be the inability to achieve the same degree of hypertrophy in type II fibers per kilogram body mass or per centimeter BH as their male counterparts, despite achieving apparent similar duration and intensity of resistance training (Table 2). However, these data suggest that muscle adaptation is not a simple process because despite the greater F_a in males, there is a significant population of small type II fibers in biceps of elite MB compared with elite FB. Furthermore, to explain all the variation in biceps CSA, contributions of fiber number must also be considered along with fiber size. Nevertheless these differences in the muscle characteristics of MB and FB or bodybuilders and controls could also be the result of genetically determined muscle endowment in bodybuilders that is determined before training. Alternatively these differences might be explained if training before this study had differed between subject groups.

REFERENCES

1. ALWAY, S. E., J. D. MacDOUGALL, D. G. SALE, J. R. SUTTON, AND A. J. McCOMAS. Functional and structural adaptations in skeletal muscle of trained athletes. *J. Appl. Physiol.* 64: 1114–1120, 1988.
2. ALWAY, S. E., P. K. WINCHESTER, M. E. DAVIS, AND W. J. GONYEA. Regionalized adaptations and muscle fiber proliferation in stretch-induced enlargement. *J. Appl. Physiol.* 66: 771–781, 1989.
3. BAILEY, L. L., W. C. BYRNES, A. L. DICKERSON, AND V. L. FOSTER. Muscular hypertrophy in women following a concentrated resistance training program (Abstract). *Med. Sci. Sports Exercise* 19: S16, 1987.
4. BEDELL, G. N., R. MARSHALL, A. B. DUBOIS, AND J. H. HARRIS. Measurement of the volume of gas in the gastrointestinal tract. Values in normal subjects and ambulatory patients. *J. Clin. Invest.* 35: 336–345, 1956.
5. BERGSTROM, J. Muscle electrolytes in man. *Scand. J. Clin. Lab. Invest. Suppl.* 17: 68–110, 1962.
6. BROOKE, M. H., AND K. K. KAISER. Muscle fibre types: how many and what kind? *Arch. Neurol.* 23: 369–379, 1970.
7. BROWN, C. H., AND J. H. WILMORE. The effects of maximal resistance training on the strength and body composition of women athletes. *Med. Sci. Sports Exercise* 8: 174–177, 1974.
8. BUSKIRK, E. R. Underwater weighing and body density, a review of procedures. In: *Techniques for Measuring Body Composition,* edited by J. Brozek and A. Henschel. Washington, DC: Natl. Acad. Sci., 1961, p. 90–106.
9. GOLLNICK, P. D., B. F. TIMSON, R. L. MOORE, AND M. REIDY. Muscular enlargement and number of fibers in skeletal muscles of rats. *J. Appl. Physiol.* 54: 1292–1297, 1981.
10. GOMORI, G. A rapid one-step trichrome stain. *Am. J. Clin. Pathol.* 20: 661–664, 1950.
11. GONYEA, W. J. Role of exercise in inducing increases in skeletal muscle fiber number. *J. Appl. Physiol.* 48: 421–426, 1980.
12. GONYEA, W. J., D. G. SALE, F. B. GONYEA, AND A. MIKESKY. Exercise induced increases in muscle fiber number. *Eur. J. Appl. Physiol. Occup. Physiol.* 55: 137–141, 1987.
13. HOLLAND, G. J. A review of in vivo quantitative analysis of body composition. In: *AAHPERD Research Consortium Symposium Papers.* Washington, DC: AAHPERD, 1980, p. 46–75.
14. KENNEDY, J. M., B. R. EISENBERG, S. K. REID, L. J. SWEENY, AND R. ZAK. Nascent muscle fiber appearance in overloaded chicken slow-tonic muscle. *Am. J. Anat.* 18: 203–215, 1988.
15. MacDOUGALL, J. D., G. C. B. ELDER, D. G. SALE, J. R. MOROZ, AND J. R. SUTTON. Effects of strength training and immobilization on human muscle fibres. *Eur. J. Appl. Physiol. Occup. Physiol.* 43: 25–34, 1980.
16. MacDOUGALL, J. D., D. G. SALE, S. E. ALWAY, AND J. R. SUTTON. Muscle fiber number in biceps brachii in bodybuilders and control subjects. *J. Appl. Physiol.* 57: 1399–1403, 1984.
17. MacDOUGALL, J. D., D. G. SALE, G. C. B. ELDER, AND J. R. SUTTON. Muscle and ultrastructural characteristics of elite powerlifters and bodybuilders. *Eur. J. Appl. Physiol. Occup. Physiol.* 48: 117–126, 1982.
18. PRINCE, F. P., R. S. HIKIDA, AND F. C. HAGGERMAN. Human muscle fibre types in powerlifters, distance runners and untrained subjects. *Pfluegers Arch.* 363: 19–26, 1976.
19. SALE, D. G., J. D. MacDOUGALL, S. E. ALWAY, AND J. R. SUTTON. Voluntary strength and muscle characteristics in untrained men and women and male bodybuilders. *J. Appl. Physiol.* 62: 1786–1793, 1987.
20. SIRI, W. E. Body composition for fluid spaces and density: analysis

of methods. In: *Techniques for Measuring Body Composition*, edited by J. Brozek and A. Henschel. Washington, DC: Natl. Acad. Sci., 1961, p. 223–244.

21. TESCH, P. A. Skeletal muscle adaptations consequent to long-term heavy resistance exercise. *Med. Sci. Sports Exercise Suppl.* 20: S132–S134, 1988.

22. TESCH, P. A., AND L. LARSSON. Muscle hypertrophy in bodybuilders. *Eur. J. Appl. Physiol. Occup. Physiol.* 49: 301–306, 1982.

23. TIMSON, B. F., B. K. BOWLIN, G. A. DUDENHOEFFER, AND J. B. GEORGE. Fiber number, area, and composition of mouse soleus muscle following enlargement. *J. Appl. Physiol.* 58: 619–624, 1985.

24. WEIBLE, E. R. *Stereological Methods.* London: Academic, 1979, vol. 1.

25. WILMORE, J. H. Alterations in strength, body composition and anthropometric measures consequent to a ten-week weight training program. *Med. Sci. Sports Exercise* 6: 133–138, 1974.

26. WILMORE, J. H., P. A. VODAK, R. B. PARR, R. N. GIRANDOLA, AND J. E. BILLING. Further simplification of a method for determination of residual lung volume. *Med. Sci. Sports Exercise* 12: 216–218, 1980.