

Changes in Muscle Morphology, Electromyographic Activity, and Force Production Characteristics During Progressive Strength Training in Young and Older Men

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*Effects of a 10-week progressive strength training program composed of a mixture of exercises for increasing muscle mass, maximal peak force, and explosive strength (rapid force production) were examined in 8 young (YM) (29 ± 5 yrs) and 10 old (OM) (61 ± 4 yrs) men. Electromyographic activity, maximal bilateral isometric peak force, and maximal rate of force development (RFD) of the knee extensors, muscle cross-sectional area (CSA) of the quadriceps femoris (QF), muscle fiber proportion, and fiber areas of types I, IIa, IIb, and IIab of the vastus lateralis were evaluated. Maximal and explosive strength values remained unaltered in both groups during a 3-week control period with no training preceding the strength training. After the 10-week training period, maximal isometric peak force increased from 1311 ± 123 N by 15.6% (p < .05) in YM and from 976 ± 168 N by 16.5% (p < .01) in OM. The pretraining RFD values of 4049 ± 791 N*s⁻¹ in YM and 2526 ± 1197 N*s⁻¹ in OM remained unaltered. Both groups showed significant increases (p < .05) in the averaged maximum IEMGs of the vastus muscles. The CSA of the QF increased from 90.3 ± 7.9 cm² in YM by 12.2% (p < .05) and from 74.7 ± 7.8 cm² in OM by 8.5% (p < .001). No changes occurred in the muscle fiber distribution of type I during the training, whereas the proportion of subtype IIab increased from 2% to 6% (p < .05) in YM and that of type IIb decreased in both YM from 25% to 16% (p < .01) and in OM from 15% to 6% (p < .05). The mean fiber area of type I increased after the 10-week training in YM (p < .001) and OM (p < .05) as well as that of type IIa in both YM (p < .01) and OM (p < .01). The individual percentage values for type I fibers were inversely correlated with the individual changes recorded during the training in the muscle CSA of the QF (r = -.56, p < .05). The present results suggest that both neural adaptations and the capacity of the skeletal muscle to undergo training-induced hypertrophy even in older people explain the gains observed in maximal force in older men, while rapid force production capacity recorded during the isometric knee extension action remained unaltered during the present mixed strength training program.*

HUMAN muscle strength decreases during the aging process, especially from the sixth decade on in both men and women (1–5). The decrease in strength can be explained to a great extent by the reduction in muscle mass thought to be mediated by a reduction in the size and/or a loss of individual fibers, especially of type II fibers (6–11). Aging is also associated with a remarkable decrease in explosive strength characteristics of the neuromuscular system whether determined using dynamic actions (12–14) or as a maximal rate of rapid isometric force production (3,5,13,15). However, it is difficult to interpret to what extent decreases in maximal and explosive strength may be explained solely by structural changes or by age-related decline in the maximal voluntary activation and/or the maximal rate of activation of the muscles and/or changes in the agonist–antagonist activation pattern (5,11,14,16).

Conversely, systematic strength training in both young and older people can lead to substantial increases in strength performance resulting from considerable neural adaptations, especially during the earlier weeks of training

(17–19). Strength training in older men and women can lead to increased activation of the agonist muscles (17,20). Training-induced learning effects (21) in terms of reduced coactivation of the antagonist muscles (22) and/or an optimized activation of the synergists may also be important in enhancing the net force production of the agonists. Recent data (19,23,24) show that strength development during strength training even in older people may include a considerable contribution of muscle hypertrophy, when both the overall training intensity and the duration of the training period are sufficient (19,23–27). To what extent the muscle fiber distribution would be related to the degree of training-induced hypertrophy and/or strength development is not known conclusively. Although conversion of the fast twitch-type subunits in human skeletal muscle following strength training may take place in young subjects (28–32), it is unlikely that such training would alter the proportions of type I and II fibers (33). In addition to maximal strength of the muscles, the role of explosive strength characteristics, especially the leg extensor muscles, is also important

for various functional physical activities in elders such as climbing stairs, walking, and preventing falls and/or trips (34). Typical heavy resistance training utilizing high loads performed with slow movement velocities tends to lead (also in older persons) to improved maximal strength with only minor changes in explosive characteristics of the trained muscles (23). It is likely that in order to induce increases in explosive strength capacity, heavy resistance training should be combined with explosive types of exercises by emphasizing the higher action velocities of the exercises performed (20). Actually, this type of resistance training, combining exercises for maximal and explosive strength, has been shown to lead in older people to improvements in both maximal force and in the earlier force portions of the isometric-force time curve (20) or in rapid explosive force production during concentric muscle actions (22).

Because optimization of training-induced muscle hypertrophy and maximal peak strength development require slightly different training protocols, not to mention a great specificity required for explosive strength development, this study examined the effects of a 10-week progressive resistance training program whose program variables were manipulated to train simultaneously for three dimensions of muscle characteristics: hypertrophy, maximal force, and explosive strength. We hypothesized that such a program would therefore lead not only to increased neural activation and hypertrophy of the trained muscles contributing to strength development but also to increased rapid force production capacity of the neuromuscular system in both younger and older men.

METHODS

Subjects.—Eighteen healthy men were drawn from two age groups: 8 young men (YM; 29 ± 5 yrs) and 10 old men (OM; 61 ± 4 yrs) volunteered as subjects for the study. The subjects were carefully informed about the design of the study and possible risks and discomfort that might result. Thereafter, the subjects signed a written consent form prior to participation in the project. The study was conducted according to the declaration of Helsinki and was approved by the Institutional Review Board for Use of Human Subjects, The Pennsylvania State University. Medical control and quantification of the physical activity (via a questionnaire created for this study) revealed that all subjects were healthy and habitually physically active. To keep themselves fit they had taken part over the years (1–3 times a week) in various recreational activities such as walking, jogging, aerobics, or biking, but none of the subjects had any background in regular strength training or competitive sports of any kind, nor were they on any medications during the study. The physical characteristics of young and old men before and after the strength training are presented in Table 1.

Experimental design.—The total duration of the experimental period was 13 weeks. The subjects were tested on five different occasions using identical protocols. The first 3 weeks of the study period were used as a control period during which time no strength training was carried out, but

the subjects maintained their normal physical activities. Thereafter, the subjects started a supervised experimental strength training period for 10 weeks. The measurements were taken during control and actual experimental training period at weeks $-3, 0, 3, 6,$ and 10 .

Testing.—The subjects were carefully familiarized with the testing procedures of voluntary force production of the leg muscles at week -3 during several submaximal and maximal performances prior to the maximal tests. This was done to ensure that all subjects would be able to fully activate their muscles under the present maximal and rapid isometric force production test actions. Maximal isometric force, and maximal rate of isometric force development (RFD; used as a measure of explosive strength in rapid isometric action) in the force-time curve of the bilateral knee extensor muscles were measured on a chair (a slightly modified version from Cybex, Ronkonkoma, NY). In this test the subjects were in a sitting position so that the knee and hip angles were 90 and 110 degrees, respectively. The force output was recorded using resistive force transducers in series (Entran, NJ) with a chain securing the subject's leg. The subjects were instructed to exert their maximal force as fast as possible during a period of 2.5 – 5.0 sec. Three to four maximal trials were completed (allowing a recovery of 2 min between the trials) for each subject until no further increases in peak force were produced. Maximal peak force was defined as the highest value of the force (N) recorded during the bilateral isometric knee extension. The force-time analysis included the calculation of the maximal rate of force development (RFD; $N \cdot s^{-1}$) (35) from the same three to four maximal actions recorded for maximal peak force. The RFD was defined as the greatest increase in force over a given 50 msec period calculated at any portion of the curve.

Electromyographic (EMG) activity during the bilateral isometric knee extension actions was recorded from the vastus lateralis (VL) and vastus medialis (VM) of the right and left leg. Two active silver/silver chloride surface EMG electrodes (pregelled, disposable) separated by 2 cm were attached to the belly of each muscle on the approximate position of the motor point area (determined using an anatomical picture for this purpose), and a third ground electrode was attached to the lateral malleolus. The active electrodes were aligned parallel with the fibers of the muscle under investigation. Before electrode application each site was shaved, cleansed with alcohol, and gently abraded. The positions of the electrodes were marked by an ink pen. As marks washed off they were followed carefully and re-

Table 1. Physical Characteristics (Mean \pm SD) of Young and Old Men Before and After a 10-Week Strength Training Period

	Young ($n = 8$)		Old ($n = 10$)	
	Pretraining	Post-training	Pretraining	Post-training
Age (yrs)	29.2 ± 5.0	—	60.8 ± 4.0	—
Body height (cm)	179.8 ± 7.7	—	176.7 ± 6.9	—
Body mass (kg)	87.4 ± 12.5	90.4 ± 13.8	85.2 ± 12.7	86.0 ± 14.0
Body fat (%)	15.7 ± 6.7	17.7 ± 5.3	19.9 ± 4.6	21.4 ± 3.7

marked to keep them visible throughout the entire 13-week experimental period. This ensured the same electrode positioning at each test. The signals were amplified using a Noraxon EMG amplifier (Noraxon, Phoenix, AZ), and the amplified myoelectric signals and force transducer output were collected at 500 Hz per channel using a 80486DX computer running Windows 3.11 and a DT21-EZ analog-to-digital card (Data Translation, Marlboro, MA). The digitized EMG data were stored together with the isometric force recordings on a computer disk for later analysis. The average EMG was calculated by full wave rectification followed by integration (IEMG) over the peak force phase (500–1500 msec) of the maximal isometric action (to calculate maximum IEMG) for each muscle separately and then averaged for further analyses.

Thigh bone-free muscle cross-sectional area (TMCSA) of the dominant leg was assessed before and after the 10-week strength training using an MRI 0.5-Tesla super conduction magnet (Picker International, Highland Heights, OH) with MR6B software. Images were obtained by alteration of the spin-lattice or longitudinal relaxation time (T1). Weighting of T1 was with repeat time (TR) of 500 msec, and echo time (TE) of 13 msec; radio frequency (RF, at 90 degrees) power absorption was .028 watts/kg. Analysis of the TMCSA was determined from the MRI scans using a gradient echo technique that allows the greatest delineation and distinction between muscles and has been shown to be more sensitive than CT scan for determining muscle size change (36). Once the subject was positioned within the magnet, the thigh of the dominant leg was supported under the knee so as to be parallel to the MRI table, and the feet were strapped together to prevent rotation. Sagittal images of the thigh were obtained, and a 15-slice grid was placed over the sagittal images; the transaxial images were then obtained. Fifteen transaxial images of 1 cm slices were obtained equidistantly between the base of the femoral head and mid-knee joint of the thigh.

All MR images were then ported to a Macintosh computer for calculation of muscle CSA using the NIH (ikosian 1-55.20A) image program (36). For the TMCSA, slice 8 was used (slice 1 being the base of the femoral head). Cross-sectional area (measured as cm²) was determined by tracing along the border of each muscle of the the quadriceps femoris. Two hundred initial tracings with the dominant hand were used to establish tracing validity of the investigator according to methods of Blomstrand et al. (37). The same investigator did all measurements for a single subject with a reliability of intraclass $R = .99$. Inter-investigator validity for absolute magnitude of size measures was evaluated, and an intraclass $R = .98$ was observed. Thus, the time to time and magnitude of each measure was considered well within the accuracy for these established methods for the technology (37). The MRI was performed before the biopsy sampling and with no exercise for 48 hours prior to the scan to limit muscle damage prior to scanning. The same conditions were held constant for the pre- and post-training tests.

Muscle biopsies were obtained before the start of training and about 72 hours after the last training session. The samples were obtained from the superficial portion of the

vastus lateralis muscle of the dominant leg utilizing the percutaneous needle biopsy technique of Bergström (38) with suction (about 100 mls) as modified by Evans et al. (39). Due to possible variation in fiber type distribution from superficial to deep and proximal to distal sites, special care was taken to extract tissue from approximately the same location each time using the prebiopsy scar (approximately 0.5 cm from scar going from medial to lateral) and marked needle depth (usually 2 cm). In addition, care was taken to address concerns for biopsy samples (40–42) and to utilize a procedure similar to one previously published (30,42). Muscle tissue samples were oriented in embedding medium (i.e., tragacanth gum), frozen in isopentane cooled to -159°C with liquid N₂ and stored at -85°C until analyzed. Serial cross-sections (12 μm thick) were cut on a cryostat (American Optical, Buffalo, NY) at -20°C for histochemical analyses.

Pre- and post-training samples were histochemically analyzed in the same staining run to avoid interassay variances. In our laboratory, data from repeat biopsies (randomly performed) demonstrated nonsignificant intrabiopsy variations in fiber type distributions. Histochemical staining for myofibrillar adenosinetriphosphatase (ATPase) was used to classify the fibers as a type I and type II as well as for subtypes of Iia, Iiab, and Iib according to Staron (43). Histochemical analyses used for fiber typing consisted of assaying for myofibrillar ATPase activity at pH 4.3, 4.6, and 10.3. Muscle fiber types were divided into four groups (types I, Iia, Iiab, Iib) based on the stability of their ATPase activity in the preincubation medium (43,44). Fiber type percentages were calculated from the number of fibers (900 ± 100) in the muscle tissue sections, and areas were calculated from 150 fibers and minimum of 50 for type Iib fibers post-training when low numbers of these fibers existed. Fiber analyses were analyzed with a National Institutes of Health (NIH) program (NIH Image 1.55b 20) and a Macintosh Quadra 800 computer interfaced to an Olympus BH-2 microscope. The perimeters of all fibers of each muscle fiber type were individually measured.

All anthropometric measurements were obtained by the same investigator on the right side of the subject's body. Skinfold thicknesses were obtained with a Harpenden skinfold caliper (H.E. Morse Co., 10 g/mm constant pressure) at the chest, midaxillary, abdomen, suprailiac, subscapula, triceps, and thigh following the procedures described by Lohman et al. (45). Repeated trials were performed until two measures within 1 mm were obtained, with the mean of these two measures being utilized. The Jackson and Pollock (46) seven-site equation was used to estimate body density, and percent body fat was subsequently calculated using the Siri (47) equation.

Experimental strength training.—The subjects participated 3 times a week in a supervised strength training period for 10 weeks. Each training session included a typical squat exercise (using a squat rack), typical knee extension (in a sitting position) and flexion (lying on a bench) exercises, trunk extension and trunk flexion exercises using free weights, and/or a typical bench press (using a bench press machine) or a calf raise exercise (in a standing posi-

tion with the load on the shoulders). The exercises used for the thigh and calf muscles were always performed first, followed by the upper extremity and trunk muscle exercises. During each week, the days were broken into a "hypertrophy day," a "strength day," and a "power day." Specifically, one session of the week the subjects performed 8–10 RM (repetition maximum) sets, another session they did 3–5 RM sets, and for the third session the subjects performed the squat and the knee extension exercises with lower loads (representing the load of 15 RM); however, the movement velocities of each repetition were kept as high as possible (explosive strength training) for 6–8 reps per set. The weights were increased during the course of training at any time a subject was able to perform a given set with more than 10 repetitions (hypertrophy day) or more than 5 repetitions (strength day). All exercises were performed using concentric muscle actions followed by eccentric actions during the "lowering" phase of the movement. The number of sets increased progressively during the course of training from 3 (during the initial weeks) to 6 (during the last weeks) depending on the exercise and the day of training. Therefore, the overall volume of training increased progressively throughout the 10-week training period.

During the 10-week experimental training period the subjects continued taking part in physical activities such as walking, jogging, or biking 1–2 times per week in a similar manner to what they were accustomed to before this experiment.

Statistical methods.—Standard statistical methods were used for the calculation of means, standard deviations (*SD*), standard errors (*SE*), and Pearson product moment correlation coefficients. The data were then analyzed utilizing multivariate analysis of variance (MANOVA) with repeated measures. Probability adjusted *t* tests were used for pairwise comparisons when appropriate. The $p < .05$ criterion was used for establishing statistical significance.

RESULTS

Body mass and the percentage of body fat remained statistically unaltered during the experimental period in both subject groups (Table 1).

Maximal isometric knee extension force, RFD and IEMGs.—Maximal isometric bilateral force of 1368 ± 151 (mean and *SD*) N at week -3 in YM was significantly greater ($p < .01$) than that of 1013 ± 185 N recorded for OM. The maximal forces remained statistically unaltered during the 3-week control period in both groups (Figure 1). Significant increases from 1311 ± 123 N to 1504 ± 105 N (by 15.6%) ($p < .05$) in YM and from 976 ± 168 N to 1132 ± 218 N (by 16.5%) ($p < .01$) in OM took place in maximal force during the 10-week training. The changes did not differ significantly between the groups. The initial RFD values of 4440 ± 743 (*SE*) $N \cdot s^{-1}$ in YM and of 2819 ± 398 $N \cdot s^{-1}$ in OM (YM vs OM; $p < .001$) remained statistically unaltered during both the control and strength training periods in both groups. Neither group showed statistically significant changes during the control period in the averaged maximum IEMGs of the VL and VM muscles of the isometric actions (Figure 2). The 10-week training led to significant

increases in the averaged IEMGs of the muscles in both YM ($p < .05$) and OM ($p < .05$). The changes did not differ significantly between the groups. Also, the increase during the last 4 weeks of training was significant ($p < .05$) for a total group of subjects (YM and OM combined).

Muscle CSA.—The pretraining value of 90.3 ± 7.9 (*SD*) cm^2 in the cross-sectional area of the quadriceps femoris in YM was significantly larger ($p < .001$) than that of 74.7 ± 7.8 cm^2 recorded for OM. The individual values of the mus-

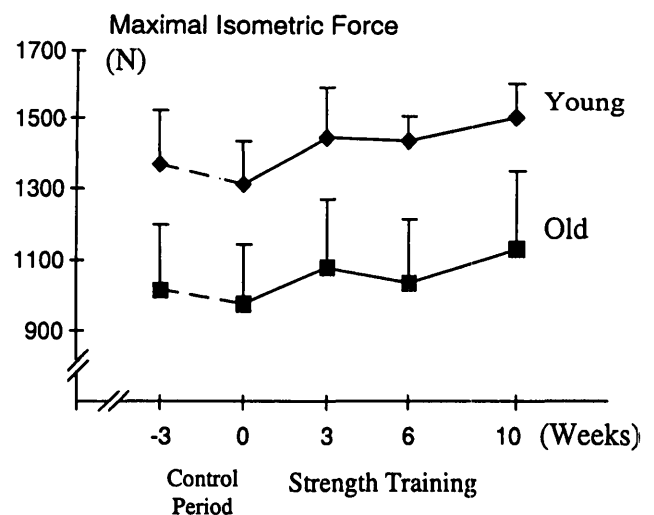


Figure 1. Mean (\pm *SD*) maximal voluntary isometric force of the bilateral knee extension in young ($n = 8$) and old ($n = 10$) men during the 3-week control period and the 10-week strength training period ($p < .05$ in YM between weeks 0 and 10 and $p < .01$ in OM between weeks 0 and 10).

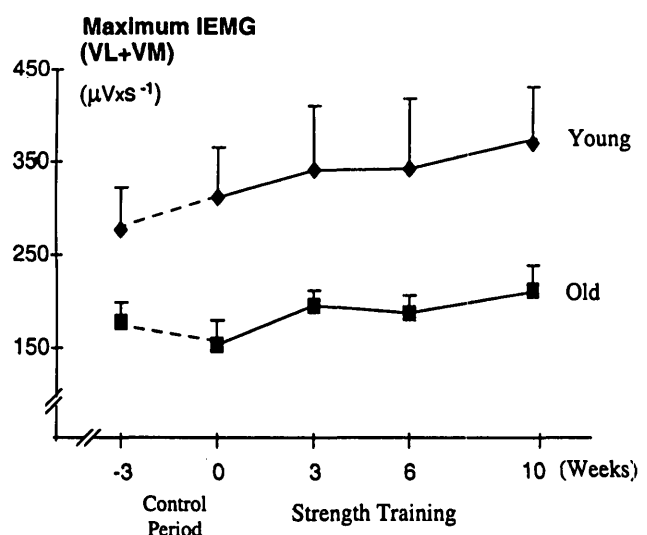


Figure 2. Mean (\pm *SD*) maximum integrated electromyographic activity (IEMG averaged for the vastus lateralis and medialis muscles of both legs) in the voluntary maximal bilateral isometric knee extension action in young ($n = 8$) and old ($n = 10$) men during the 3-week control period and the 10-week strength training period ($p < .05$ in YM between weeks 0 and 10 and $p < .05$ in OM between weeks 0 and 10).

cle CSA correlated significantly with the individual pre-training values of maximal isometric force in OM ($r = .64$, $p < .05$) and in the total group of subjects (YM and OM) ($r = .59$, $p < .01$) but not in YM ($r = -.07$, n.s.). For individual muscles, the cross-sectional areas of the vastus lateralis, medialis, and intermedius and rectus femoris increased significantly during the 10-week training in both YM (p values between .001 and .05) and OM (p values between .001 and .05) (Figure 3). The changes did not differ significantly between the groups. The average relative increase in the cross-sectional area of the total QF was 12.2% ($p < .01$) for YM and 8.5% ($p < .001$) for OM, but the changes did not differ significantly between the groups. The pre- and post-training mean values for maximal force per CSA of the total QF muscle were $13.9 \pm 2.9 \text{ N}\cdot\text{cm}^{-2}$ and $15.1 \pm 1.5 \text{ N}\cdot\text{cm}^{-2}$ (n.s.) in YM, and 13.1 ± 1.6 and $14.1 \pm 2.6 \text{ N}\cdot\text{cm}^{-2}$ (n.s.) in OM. In the total group of subjects (YM and OM), the respective value increased during the training from 13.4 ± 2.2 to $14.5 \pm 2.3 \text{ N}\cdot\text{cm}^{-2}$ ($p < .05$).

Muscle fiber characteristics.—The percentage values for the muscle fiber distribution of the vastus lateralis muscle did not differ significantly between YM and OM either before or after the training period except for type IIb, with YM showing greater values ($p < .05$) than OM at both times (Table 2). No statistically significant changes took place in the fiber distribution of type I during the training period either in YM or OM. The relative proportion of type IIab increased from 2% to 6% ($p < .05$) in YM, and those of type IIb decreased in both YM from 25% to 16% ($p < .01$) and in OM from 15% to 6% ($p < .05$).

The individual percentage values for type I fibers correlated significantly with the individual changes recorded during the training in the muscle cross-sectional area of the quadriceps femoris muscle ($r = -.56$, $p < .05$) (Figure 4). The respective correlation coefficient with regard to the changes in the cross-sectional area of the vastus lateralis muscle was also significant ($r = -.50$, $p < .05$). The individual percentage values for type I fibers did not correlate sig-

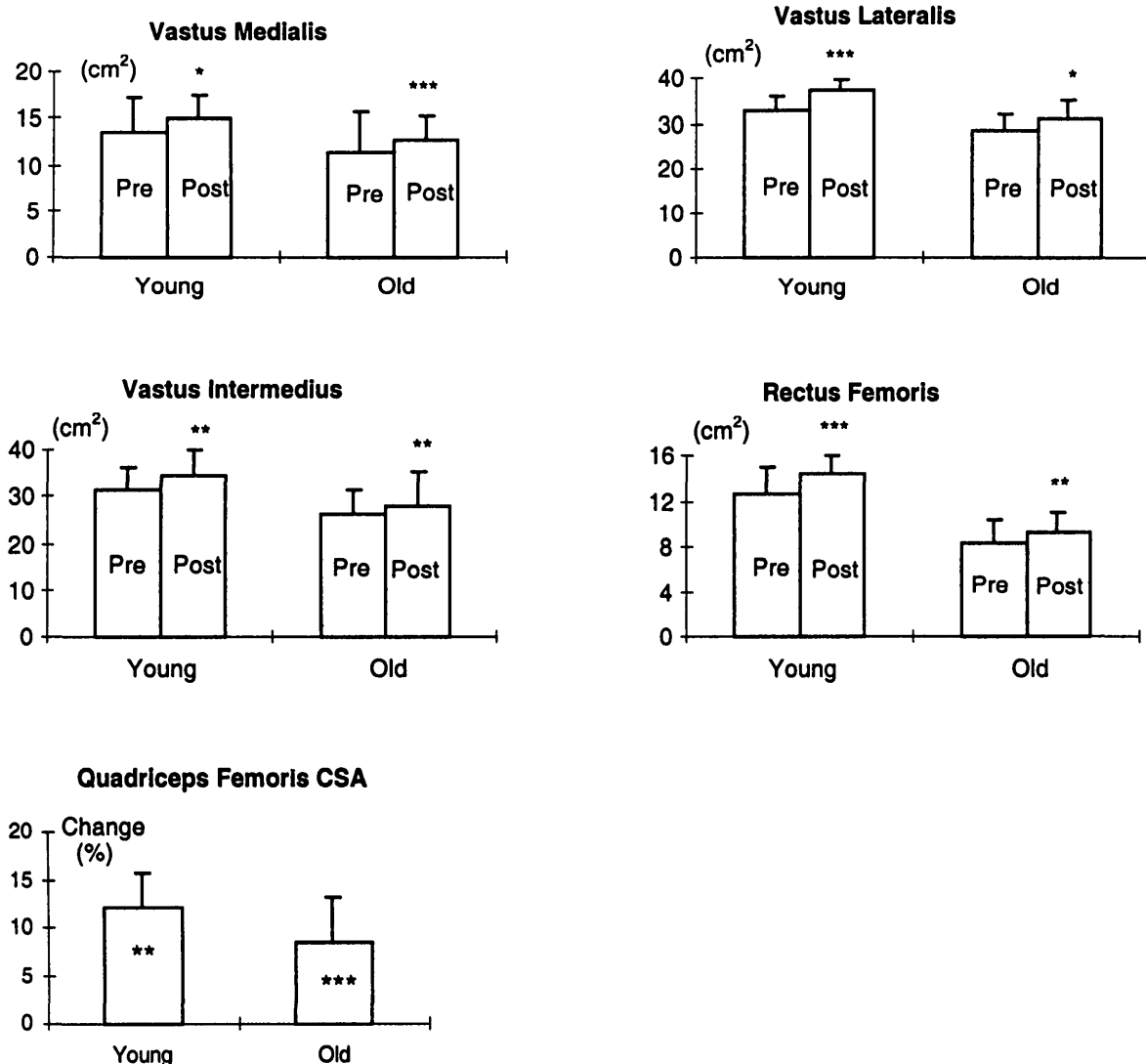


Figure 3. Mean (\pm SD) cross-sectional areas of the individual muscles of the quadriceps femoris muscle group and the relative change in the total area of quadriceps femoris before (pre) and after (post) the 10-week strength training period in young ($n = 8$) and old ($n = 10$) men (* $p < .05$, ** $p < .01$, *** $p < .001$).

Table 2. Mean \pm SD Fiber Distribution of the Vastus Lateralis Muscle Before and After a 10-Week Strength Training Period in Young and Older Men

	Young (n = 8)		Old (n = 7)	
	Pretraining	Post-training	Pretraining	Post-training
Type I (%)	41 \pm 15	41 \pm 9	48 \pm 9	46 \pm 13
Type IIa (%)	32 \pm 12	37 \pm 15	35 \pm 13	44 \pm 13
Type IIab (%) (young n = 7, old n = 4)	2 \pm 1	6 \pm 7*	2 \pm 1	4 \pm 3
Type IIb (%)	25 \pm 7†	16 \pm 8**,†	15 \pm 12	6 \pm 6*

* $p < .05$; ** $p < .01$, significant difference pre-post training.

† $p < .05$, significant difference from old group at that time point.

Table 3. Mean \pm SD Fiber Areas of the Vastus Lateralis Muscle Before and After a 10-Week Strength Training Period in Young and Older Men

	Young (n = 8)		Old (n = 6)	
	Pretraining	Post-training	Pretraining	Post-training
Type I (μm^2)	3757 \pm 704	4618 \pm 831***	4091 \pm 1354	5044 \pm 862*
Type IIa (μm^2)	4594 \pm 518†	5775 \pm 1087**	3879 \pm 323	5337 \pm 851**
Type IIab (μm^2) (young n = 7, old n = 4)	4883 \pm 1526	4027 \pm 962	4209 \pm 889	5200 \pm 918
Type IIb (μm^2)	4146 \pm 849	4713 \pm 1047	4220 \pm 1566	5027 \pm 774

* $p < .05$; ** $p < .01$; *** $p < .001$, significant difference pre-post training.

† $p < .05$, significant difference from old group at that time point.

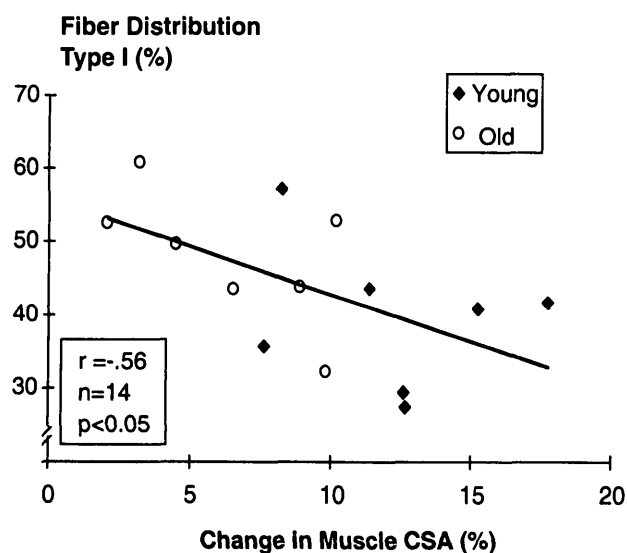


Figure 4. The relationship between the muscle fiber distribution (type I %) and the relative change in the cross-sectional area of the quadriceps femoris muscle after the 10-week strength training period in young and old men.

nificantly with the changes in maximal isometric force ($r = .21$, n.s.), or in explosive strength ($r = .19$, n.s.).

At pretraining, YM demonstrated larger ($p < .05$) mean fiber area of type IIa than OM with no significant differences observed in the mean areas of the other fiber types (Table 3). The mean fiber area of type I increased after the 10-week training in YM ($p < .001$) and OM ($p < .05$) as did that of type IIa in both YM ($p < .01$) and OM ($p < .01$).

DISCUSSION

The present progressive strength training program composed of a mixture of exercises for the development of three qualities—muscle mass, maximal peak force, and explosive strength—led to significant gains in maximal isometric force in both young and older men. However, the training did not lead to significant gains in rapid force production recorded during the isometric knee extension action. The maximal strength gains were accompanied by significant increases in the voluntary neural activation of

the trained muscles accompanied by significant enlargements in muscle fiber areas of types I and IIa as well as in the total CSA of the knee extensors in both young and older men. The present training also led to significant decreases in the muscle fiber proportion of type IIb in both young and old men and an increase of type IIab in young men, while the relative proportion of the two main fiber types remained statistically unaltered.

The increased IEMGs during the first 3 weeks of training (Figure 2) support the concept that in previously untrained subjects, both young and old, initial increases in maximal strength observed during the first few weeks of strength training can be attributed largely to the increased motor unit activation of the trained agonist muscles (17,19,48–53). Strength training-induced increases in the magnitude of EMG (IEMG) could result from the increased number of active motor units and/or increase in their firing frequency (51,54) in both young and older subjects. The EMG data in Figure 2 additionally show that the increases in the maximal averaged IEMGs in men of both age groups took place also during the last 4 weeks of the 10-week training period, further suggesting the important contributing role of the nervous system for strength development. This was probably due to the fact that the training loads in all exercises for both maximal peak force development and hypertrophic purposes were progressively increased throughout the training period. Because the EMG data were recorded only for the agonists, it could not be evaluated to what extent the present training may also have led to decreases in the coactivation of the antagonist muscles as reported to occur in younger (55) and older subjects (22).

Muscle hypertrophy has also been shown to account for a considerable portion of the strength gains in elders (19,23,25,26,56,57). Accordingly, the present training program led to similar enlargements of 12% and 9% in the total CSAs of the trained knee extensor muscles in young and old men, respectively. The enlargements were also very similar in magnitude in all of the individual muscles of the quadriceps group in both age groups (Figure 3). Skeletal muscles of older people seem to retain the capacity to undergo training-induced hypertrophy when the volume, intensity, and duration of the training period are sufficient (18,19,23,26). However, some caution must be exercised when interpreting the present muscle CSA data obtained

only at one particular portion of the thigh, as training-induced muscle hypertrophy can also be a nonuniform process along the belly of the muscle (58).

The possible role of muscle fiber distribution (percent type II fibers) on increased strength or the magnitude of muscle hypertrophy during strength training in young men has not been conclusively determined. In fact, some conflicting results were reported already in the 1970s (59,60) or there exists data (52) that improvement/enlargements would not be dependent upon muscle fiber distribution. The present findings indicated that the subjects (total group of young and older men) with a higher relative proportion of type II fibers demonstrated greater increases in the CSA of the trained muscle than those subjects possessing a lower proportion of type II in their muscles (Figure 4). Because aging is known to be associated with not only muscle atrophy but also a loss of muscle fibers, especially of type II fibers (8), this may be of importance in older subjects. Whether the ultimate degree of muscle hypertrophy and/or strength development would be conclusively dependent upon the muscle fiber distribution of the main type cannot be answered until further research work has been performed using experimental designs with longer durations of training, a larger number of subjects, and a larger variability in the age of subjects under investigation.

A transformation of type II muscle fiber subtypes and no changes in the percent of type I fibers were observed pre- to post-training for both the younger and old men. This type II subtype transformation going from type IIb to IIab to IIa has been previously observed only in younger men (29–32). Such muscle fiber transformations indicate that a large amount of the muscle tissue mass was recruited using this study's training protocol with alterations in myosin ATPase isoforms and myosin heavy chains (28,29,31,32,61–63). The remaining IIb muscle fibers were either not recruited by the heavy resistance exercise program or, if recruited, have higher oxidative enzyme levels and had not yet made the protein changes needed for isoform transformation (29,62). Prior studies in younger men with longer training periods (i.e., > 3 months) have typically demonstrated the absence or very low percentages (< 2%) of type IIb muscle fibers after a heavy resistance training program (29–32). Our data are similar to those of Staron et al. (30), which indicate that with shorter training periods, muscle fibers make only partial transformation in the type IIb fiber population.

Both younger and older subjects demonstrated muscle hypertrophy (e.g., 23,64) with significant increases in their type I and IIa muscle fiber areas with the present resistance training. The concomitant hypertrophy of both the type I and IIa subtypes with the use of only a heavy resistance training program is consistent with prior studies in younger men (31,32). The wider range of resistance loads used in the present program may have encompassed recruitment of both slow and fast motor units. Interestingly, the relative magnitudes of muscle fiber hypertrophy in Type I and IIa fibers were similar in both the younger and older subjects. This finding is well in line with the similar enlargements observed in the total CSA of the QF muscle in our young and older subjects. The lack of differences at the cellular level may indicate that protein metabolism for men approx-

imately 60 years old in response to a progressive resistance training program is not compromised despite a smaller absolute amount of muscle mass. This might be due to an adequate intake of protein and total calories to support the anabolic changes at the cellular level (61,65–67). Thus, the use of a progressive resistance training program at the threshold of dramatic age in active 60-year-olds may be effective in offsetting continued declines as demonstrated in the age-related differences in absolute muscle mass (see MRI data).

Muscle strength and the ability of the leg extensor muscles to develop force rapidly, especially during dynamic actions, are important performance characteristics, especially in older people, contributing to several tasks of daily life such as climbing stairs, walking, or even preventing falls and/or trips (34). It has been shown that a very low level of maximal strength in older people may be associated with a lower ability to produce force rapidly in both dynamic and isometric actions (14). The present strength training program was expected to produce significant increases in both maximal strength and rapid force production in the earlier portions of the isometric force-time curve. It has been demonstrated earlier that strength training two times a week using a combination of exercises for maximal and explosive strength in both middle-aged and older subjects of both genders led to significant increases in maximal peak force and rapid force production recorded in both isometric and dynamic actions of the leg extensors [hip, knee, and ankle extensors; (20,22)]. However, the present results showed that increases obtained in maximal force were not accompanied by the increases in explosive strength characteristic of the trained muscles recorded during the isometric knee extension action. It is possible that the large overall volume of the training with three sessions a week and/or too "large" a mixture of three different qualities leaving only one third for explosive muscle actions may have in part explained the finding that the maximal rate of force development in the force-time curve remained unaltered in both our young and older subjects. Third, it is also possible that while the training was conducted using dynamic actions, a possible improvement caused by the training could not be transferred into or verified in the rapid isometric force production of the knee extension action. Therefore, further research is needed to examine various training protocols in order to optimize muscle hypertrophy, maximal peak force, and explosive strength development in various isometric and dynamic force production conditions of the knee and/or leg extension actions in young and older subjects.

In summary, the present results show that progressive strength training composed of a mixture of three types of exercises—for muscle mass, maximal peak force, and explosive strength—led to significant increases in maximal isometric strength in both young and older men. However, no changes took place in the shape of the force-time curve recorded during the isometric knee extension action. The strength increases were accompanied by significant improvements in the maximal voluntary activation of the agonist muscles as well as by the increases in the individual muscle fiber areas of types I and IIa and in the total CSA of

the QF muscle group in both age groups. No significant changes took place in the relative proportion of the two main fiber types, but a significant decrease took place in IIb in both young and older subjects and an increase in IIab in young men. The magnitude of the enlargement in the CSA was similar in both groups, but the individual changes were larger in those subjects who demonstrated a greater relative proportion of the main type II muscle fibers. The present results suggest that both neural adaptations and the capacity of the skeletal muscle to undergo training-induced hypertrophy in elders explain strength gains in older men, whereas the area of explosive strength development during this type of a mixed strength training protocol in various isometric and dynamic force production conditions of the knee and/or leg extension actions requires further research.

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