Changes in agonist-antagonist EMG, muscle CSA, and force during strength training in middle-aged and older people

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Häkkinen, K., M. Kallinen, M. Izquierdo, K. Jokelainen, H. Lassila, E. Mälkiä, W. J. Kraemer, R. U. Newton, and M. Alen. Changes in agonist-antagonist EMG, muscle CSA, and force during strength training in middleaged and older people. J. Appl. Physiol. 84(4): 1341-1349, 1998.—Effects of 6 mo of heavy-resistance training combined with explosive exercises on neural activation of the agonist and antagonist leg extensors, muscle cross-sectional area (CSA) of the quadriceps femoris, as well as maximal and explosive strength were examined in 10 middle-aged men (M40; 42 \pm 2 yr), 11 middle-aged women (W40; 39 \pm 3 yr), 11 elderly men (M70; 72 \pm 3 yr) and 10 elderly women (W70; 67 ± 3 yr). Maximal and explosive strength remained unaltered during a 1-mo control period with no strength training. After the 6 mo of training, maximal isometric and dynamic leg-extension strength increased by 36 \pm 4 and 22 \pm 2% (P< 0.001) in M40, by 36 \pm 3 and 21 \pm 3% (P< 0.001) in M70, by 66 \pm 9 and 34 \pm 4% (P < 0.001) in W40, and by 57 \pm 10 and 30 \pm 3% (P < 0.001) in W70, respectively. All groups showed large increases (P < 0.05 - 0.001) in the maximum integrated EMGs (iEMGs) of the agonist vastus lateralis and medialis. Significant (P < 0.05-0.001) increases occurred in the maximal rate of isometric force production and in a squat jump that were accompanied with increased (P < 0.05 - 0.01) iEMGs of the leg extensors. The iEMG of the antagonist biceps femoris muscle during the maximal isometric leg extension decreased in both M70 (from 24 \pm 6 to 21 \pm 6%; P < 0.05) and in W70 (from 31 \pm 9 to 24 \pm 4%; *P* < 0.05) to the same level as recorded for M40 and W40. The CSA of the quadriceps femoris increased in M40 by 5% (P < 0.05), in W40 by 9% (P < 0.01), in W70 by 6% (P < 0.05), and in M70 by 2% (not significant). Great training-induced gains in maximal and explosive strength in both middle-aged and elderly subjects were accompanied by large increases in the voluntary activation of the agonists, with significant reductions in the antagonist coactivation in the elderly subjects. Because the enlargements in the muscle CSAs in both middle-aged and elderly subjects were much smaller in magnitude, neural adaptations seem to play a greater role in explaining strength and power gains during the present strength-training protocol

neural control; agonist and antagonist muscles; aging; hypertrophy; electromyogram; cross-sectional area

IT HAS BEEN WELL DEMONSTRATED that human muscular strength decreases during the aging process, especially from the sixth decade on in both men and women (e.g., Refs. 27, 36). The decrease in strength seems to be

explained to a great extent by the reduction in muscle mass, perhaps related to changes in hormone balance (e.g., Ref. 16) and decline in the intensity of daily physical activities (e.g., Ref. 24). The decline in muscle mass is thought to be mediated by a reduction in the size and/or number of individual muscle fibers, especially of fast-twitch fibers (8, 22, 30). Therefore, aging also leads to a considerable decrease in explosivestrength characteristics, whether determined by using dynamic actions (1, 2, 34) or as a slowing in the rate of rise of force during isometric contraction (5, 12, 34, 36).

However, it is difficult to interpret to what extent decreases in maximal and/or explosive strength may be explained solely by structural changes (18, 30). Agerelated decline in strength may also be due to decreased maximal voluntary activation of the agonist muscle or changes in degree of agonist-antagonist coactivation (12, 18, 38). It is likely that age-related changes in maximal neural activation and strength may vary among the different muscles in relation to their decreased use in daily physical activities (7, 11, 18, 38).

On the other hand, it has been shown that systematic strength training not only in middle-aged but also in elderly people can lead to substantial increases in strength performance. This might primarily result from considerable neural adaptations observed, especially during the earlier weeks of training (13, 14, 19, 26). Thereafter, strength development in older people may also take place because of an increasing contribution of muscle hypertrophy. The basic requirements for training-induced hypertrophy and strength development in both older men and women are that the overall training intensity should be high enough and the duration of the training period long enough (4, 9, 10, 13, 14, 19, 31, 35). To what extent the increase in strength in elderly people may be accounted for by changes in the quantity or quality of activation has not been examined as yet. It is likely that the voluntary activation of the agonist muscles is increased during strength training, but changes in coactivation of the antagonists may take place as well. This has been shown to occur in isolated isometric actions in younger subjects (3). In addition to maximal strength of various muscles, the role of explosive-strength characteristics of the leg extensors is also important for various functional physical activities in the elderly (1). It is likely that to induce

increases in their explosive-strength capacity, heavyresistance training should be combined with explosive exercises by paying special attention to the higher action/movement velocities of the exercises performed (13), although such a training program may not always be applicable to older people (29). It should, therefore, be within both scientific and practical interests to examine to what extent increases in strength and power in elderly people actually can take place during this type of strength training and whether the increases might be explained by specific functional adaptations in the neuromuscular system and how much is due to training-induced muscle hypertrophy.

The purpose of the present study was to examine neuromuscular adaptations in middle-aged and elderly men and women during a strength-training period of 6 mo by utilizing a program that not only was planned for maximal strength development but also included exercises of an explosive nature. In addition to the recording of the degree of hypertrophic adaptations of the trained muscles, there was a special interest in the examination of possible training-induced adaptations in the voluntary neural activation of the agonist muscles as well as in coactivation of the antagonist muscles recorded during both isometric and dynamic actions.

METHODS

Subjects. Forty-two healthy men (M) and women (W) volunteered for the study. The subjects were divided into two age groups, i.e., M40 [42 ± 2 (SD) yr; n = 10] and M70 (72 ± 3 ; n = 11) and W40 (39 ± 3 ; n = 11) and W70 (67 ± 3 ; n = 10). The physical characteristics of the four subject groups are presented in Table 1. The subjects were carefully informed about the design of the study, with special information provided on possible risks and discomfort that might result. Thereafter, the subjects signed a written consent form before participation in the project. The study was conducted according to the Declaration of Helsinki and was approved by the Ethics Committee of the University of Jyväskyla, Finland.

Medical control and quantification of the physical activity (by using a questionnaire) revealed that all subjects were healthy and habitually physically active. To keep themselves fit, they had taken part in various recreational physical activities such as walking, jogging, cross-country skiing, aerobics, or biking, but none of the subjects had any background in regular strength training or competitive sports of any kind. No medication was being taken by the subjects that would have been expected to affect physical performance.

This work is a part of a larger research project. Some of the results obtained with these subjects from the first measurements of the follow-up design have been used earlier for various cross-sectional comparative purposes between the two different age groups of both genders (16).

Experimental design. The total duration of the present study was 7 mo. The subjects were tested on five different occasions by using identical protocols. The first month of the study (between the measurements at *month* – 1 and at *month* O) was used as a control period during which time no strength training was carried out but the subjects maintained their normal recreational physical activities (e.g., walking, jogging, biking, swimming, and aerobics). The subjects were tested before and after this control period. Thereafter, the subjects started a supervised experimental strength-training period for 6 mo. The measurements were repeated during the actual experimental training period at 2-mo intervals (i.e., *months 0, 2, 4,* and 6).

Testing. The subjects were carefully familiarized with the testing procedures of voluntary force production of the leg muscles during several submaximal and maximal performances ~ 1 wk before the measurements (at *month* -1). Then, during the actual testing occasion, several warm-up contractions were performed before the maximal test actions.

Isometric force-time curves, maximal isometric force, and maximal rate of isometric force development (RFD) of the bilateral leg extensor muscles (hip, knee, and ankle extensors) were measured on an electromechanical dynamometer (13, 16). In this test, the subjects were in a sitting position so that the knee and hip angles were 107 and 110°, respectively. The subjects were instructed to exert their maximal force as fast as possible during a period of 2.5–4.0 s. A minimum of three trials was completed for each subject, and the best performance trial with regard to maximal peak force was used for the subsequent statistical analysis.

A David 210 dynamometer (David Fitness and Medical) was used to measure maximal bilateral concentric force production of the leg extensors (hip, knee, and ankle extensors) (12). The subject was in a seated position so that the hip angle was 110°. On verbal command, the subject performed a concentric leg extension starting from a flexed position of 70°, trying to reach a full extension of 180° against the resistance determined by the loads chosen on the weight stack. In the testing of the maximal load, separate one-repetition-maximum (1-RM) contractions were performed. After each repetition, the load was increased until the subject was unable to extend the legs to the required position. The last acceptable extension with the highest possible load was determined as 1 RM.

A David 200 dynamometer modified for strength testing (12) was used to measure maximal isometric knee torque of the knee flexors. The subject was in a seated position so that the hip and knee angles were 110 and 90°, respectively. On verbal command, the subject performed a maximum isometric knee flexion separately for the right and left legs. A

Table 1. Physical characteristics of middle-aged and elderly men and women during the control period (month -1 to month 0) and after 6-mo strength-training period (month 0 to month 6)

					Body Mass, kg			Body Fat, %		
	п	Age, yr	Height, cm	Month – 1	Month 0	Month 6	Month – 1	Month 0	Month 6	
M40 M70 W40 W70	10 11 11 10	$\begin{array}{c} 42\pm 2 \\ 72\pm 3 \\ 39\pm 3 \\ 67\pm 3 \end{array}$	$\begin{array}{c} 178 \pm 7 \\ 172 \pm 7 \\ 163 \pm 5 \\ 159 \pm 6 \end{array}$	$\begin{array}{c} 83 \pm 15 \\ 80 \pm 9 \\ 62 \pm 8 \\ 66 \pm 7 \end{array}$	$\begin{array}{c} 83\pm14\\ 80\pm10\\ 62\pm8\\ 66\pm7\end{array}$	$\begin{array}{c} 84\pm15\\ 80\pm10\\ 62\pm8\\ 66\pm7\end{array}$	$19 \pm 4 \\ 24 \pm 4 \\ 26 \pm 6 \\ 34 \pm 4$	$19 \pm 4 \\ 24 \pm 4 \\ 26 \pm 6 \\ 34 \pm 3$	$\begin{array}{c} 19\pm 5\\ 23\pm 5\\ 26\pm 6\\ 34\pm 5\end{array}$	

Values are means \pm SD; *n*, no. of subjects. M40 and M70, middle-aged and elderly men, respectively; W40 and W70, middle-aged and elderly women, respectively.

minimum of two maximal actions was recorded for each leg, and the best maximum was taken for further analysis.

Dynamic explosive force characteristics of the leg muscles were measured on a force platform by using a maximal vertical squat jump (SJ) (from a starting position of 90° for the knee angle). The hands were kept on the hips during the jump. The height of rise of the center of gravity in the SJ was calculated from the flight time, and power was analyzed from the vertical force-time curve. Three maximal jumps were recorded in both cases, and the best maximum in terms of height was taken for further analysis. In all test conditions, the time period of rest between the maximal contractions was always 1.5 min. In all tests, external verbal encouragement was given for each subject.

The force signal was recorded on a computer (486 DX-100) and thereafter was digitized and analyzed with a Codas computer system (Data Instruments). Maximal peak force was defined as the highest value of the force (N) recorded during the bilateral isometric leg extension and unilateral (right and left) isometric knee flexion actions (N·m). The force-time analysis on the absolute scale included the calculation of average force (N) or torque (N·m) produced during 100-ms epochs from the start of the contraction up to 500 ms (13). The maximal RFD (N/s) was also analyzed and was defined as the greatest increase in force in a given 50-ms time period (37).

Electromyographic (EMG) activity during the bilateral extension actions of the leg muscles was recorded from the agonist muscles of the vastus lateralis (VL) and vastus medialis (VM) and from the antagonist muscle of biceps femoris (BF; long head) of the right and left leg separately. Bipolar (20-mm interelectrode distance) surface EMG recording (miniature-sized skin electrodes 650437, Beckman) was employed. The electrodes were placed longitudinally on the motor point areas determined by an electrical stimulator. EMG signals were recorded telemetrically (2000 Glonner, Biomes). The positions of the electrodes were marked on the skin by small ink tattoos (15). These dots ensured the same electrode positioning in each test over the 7-mo experimental period. The EMG signal was amplified (by a multiplication factor of 200; low-pass cutoff frequency of 360 Hz/3 dB) and digitized at the sampling frequency of 1,000 Hz by an on-line computer system. The EMG was full-wave rectified, integrated (iEMG in μ V/s), and time normalized for 1 s in the following phases: 1) in the isometric actions for the periods of 100 ms up to 500 ms to obtain an iEMG-time curve from the start of the contraction, 2) for the maximal peak force phase of the isometric contractions (500-1.500 ms) to calculate maximal iEMG (13), and 3) in the concentric action of the 1 RM and in the SJ performances for the entire range of motion. The EMG of the BF muscles, acting as an agonist recorded during the maximal unilateral isometric knee flexions, was analyzed in a similar way as were the EMGs of the VL and VM muscles of the isometric leg extensions. The highest iEMG value recorded for the right and the left biceps femoris muscle was taken for further analysis.

The cross-sectional area (CSA) of the quadriceps femoris (QF) muscle group (rectus femoris, VL, VM, and vastus intermedialis) was measured with a compound ultrasonic scanner (model SSD-190, Aloka Fansonic) and a 5-MHz convex transducer. The CSA was measured at the lower one-third portion between the greater trochanter and lateral joint line of the knee. Two consecutive measurements were taken from the right thigh and then averaged for further analyses. The CSA of the QF was then calculated from the image by the computerized system of the apparatus (14). The CSA measurements were taken before (at *month 0*) and after

the strength training period (at *month* 6). The percentage of fat in the body was estimated from the measurements of skinfold thickness (6).

Experimental strength training. The subjects participated in a supervised 6-mo period of strength training. Each training session included two exercises for the leg extensor muscles (the bilateral leg press exercise and the bilateral and/or unilateral knee extension exercise on the David 200 machine) and four to five other exercises for the other main muscle groups of the body (the bench press and/or the seated press and/or lateral pull-down exercise for the upper body; the sit-up exercise for the trunk flexors and/or another exercise for the trunk extensors; and the bilateral elbow and/or knee flexion exercise). Only machine exercises were used throughout the training period. All the exercises were performed by using concentric muscle actions followed by eccentric actions during the "lowering" phase of the movement. The loads were determined throughout the study during the training sessions every second month for the 6-mo training period according to the maximum-repetition method.

During the first 2 mo of the training, the subjects trained twice a week with loads of 50-70% of the 1 RM. The subjects performed 10–15 repetitions per set and performed 3–4 sets of each exercise. During the third and fourth months of training, the subjects still trained two times a week. The loads were 50–60 and 60–70% of the maximum by month 3 and 50-60 and 70-80% by month 4. In the two exercises for the leg extensor muscles, the subjects now performed either 8–12 repetitions per set (at lower loads) or 5-6 repetitions per set (higher loads) and performed 3-5 sets. In the other four exercises, the subjects performed 10-12 repetitions per set and performed 3-5 sets. During the last 2 mo of training (months 5-6), the subjects performed in the two exercises for the leg extensor muscles 3-6 repetitions per set with loads of 70–80% of the maximum and 8–12 repetitions per set with loads of 50–60% of maximum and performed 4–6 sets. In the other four exercises, the subjects performed 8-12 repetitions per set and performed 3-5 sets altogether.

The strength-training program utilized in the present study was a combination of heavy-resistance and "explosive"-strength training. Therefore, in addition to the normal principles of heavy-resistance training, the basic requirements for the development of explosive strength were taken into consideration by having the subjects perform a part (20%) of the leg extensor exercises with light loads (50–60% of the maximum) but executing all of these repetitions as "explosively" as possible (rapid muscle actions). The overall amount of training was progressively increased until the fifth month, at which point it was slightly reduced for the final month of the 6-mo training period.

During the 6-mo experimental training period, the subjects continued taking part in physical activities such as walking, jogging, swimming, biking, or gymnastics one to two times per week in a manner similar to what they were accustomed to before this experiment.

Statistical methods. Standard statistical methods were used for the calculation of means, SDs, SEs, and Pearson product-moment correlation coefficients. The data were then analyzed by utilizing multivariate analysis of variance with repeated measures. Probability-adjusted *t*-tests were used for pairwise comparisons when appropriate. The P < 0.05 criterion was used for establishing statistical significance.

RESULTS

Physical characteristics. Body mass and the percentage of body fat remained statistically unaltered during

the entire experimental period in all subject groups (Table 1).

Muscle CSA. The CSA of the leg extensors increased during the 6-mo training in M40 by $4.9 \pm 2.5\%$ (from 53.3 ± 1.5 to 56.2 ± 2.5 cm²; P < 0.05), in W40 by $9.7 \pm 2.5\%$ (from 39.7 ± 1.8 to 43.4 ± 1.8 cm²; P < 0.01), and in W70 by $5.8 \pm 2.0\%$ (from 33.8 ± 1.0 to 35.7 ± 1.2 cm²; P < 0.05), whereas the change of $2.1 \pm 1.9\%$ in M70 (from 43.7 ± 1.9 to 44.6 ± 1.9 cm²) was not significant (Fig. 1).

Maximal isometric leg-extension force, RFD and iEMGs. Maximal isometric bilateral forces remained unaltered during the 1-mo control period (from month - 1 to month 0) in all groups except for an increase (P <0.01) in W70 (Fig. 2). Large increases took place in maximal force during the 6-mo training period in M40 by 36 \pm 4% (from 2,296 \pm 92 to 3,102 \pm 133 N; P <0.001), in M70 by 36 \pm 3% (from 1,799 \pm 155 to 2,468 \pm 239 N; P < 0.001), in W40 by 66 ± 9% from 1,335 ± 113 to 2,186 \pm 221 N (*P* < 0.001), and in W70 by 57 \pm 10% (from 1.104 \pm 139 to 1.682 \pm 204 N; P < 0.001). The increases in both female groups were larger (P < 0.05) than those recorded for the men of the same age group. The RFD values remained unaltered during the 1-mo control period but increased significantly during the 6-mo training period in M40 by $41 \pm 14\%$ (P < 0.01), in M70 by 40 \pm 10% (P < 0.05), in W40 by 31 \pm 18% (P < 0.05) and in W70 by $28 \pm 10\%$ (*P* < 0.05) (Fig. 3).

None of the groups showed statistically significant changes during the control period in the maximum iEMGs of the VL and VM muscles of the isometric actions (Fig. 4). During the 6 mo of training, significant increases were observed in the iEMGs of the VL and VM muscles of the right and left leg in M40 (P < 0.05), in M70 (P < 0.05-0.001), in W40 (P < 0.05-0.01), and in W70 (P < 0.05-0.001). The iEMGs of the VL and VM muscles during the first 500 ms of the isometric action increased (P < 0.05) during the training in all groups.

1-RM leg-extension values and maximum iEMGs. The 1-RM bilateral leg-extension values remained statistically unaltered in all groups during the control period (Fig. 5). During the 6 mo of training, the 1-RM



Fig. 1. Cross-sectional area of quadriceps femoris muscle in middleaged (40 yr) and elderly (70 yr) men (M40 and M70, respectively) and women (W40 and W70, respectively) before and after a 6-mo strengthtraining period. Values are means \pm SE.



Fig. 2. Maximal voluntary bilateral isometric force of leg extensor muscles in M40 and M70 (*A*) and in W40 and W70 (*B*) during 1-mo control period and during 6-mo strength-training period. Values are means \pm SE.

values improved in M40 by $22 \pm 2\%$ (P < 0.001), in M70 by $21 \pm 3\%$ (P < 0.001), in W40 by $34 \pm 4\%$ (P < 0.001), and in W70 by $30 \pm 3\%$ (P < 0.001). The increases in both female groups were larger (P < 0.05) than those recorded for the men of the same age group.

During the 6 mo of training, the maximum iEMGs of the VL and VM muscles of the right and left leg of the 1-RM action increased in M40 (P < 0.05), in M70 (P < 0.05-0.01), in W40 (P < 0.05), and in W70 (P < 0.05-0.001).

SJs and average iEMGs. The maximal vertical heights and power values in the SJs remained statistically unaltered during the 1-mo control period in all groups (Fig. 6). During the 6 mo of training, the SJ height increased in M40 by $11 \pm 8\%$ [P < 0.05 and showing a greater increase of $19 \pm 4\%$ (P < 0.01) after the first 4 mo of the training], in M70 by $24 \pm 8\%$ (P < 0.001), in W40 by $14 \pm 4\%$ (P < 0.01), and in W70 by $18 \pm 6\%$ (P < 0.01). The increases achieved by the elderly groups peaked at 2 mo compared with 4 mo for the middle-aged groups. The power values also increased (P < 0.05-0.01) during the training period.

The average iEMGs of the VL and VM muscles of the right and left leg in the SJ remained statistically unaltered in all groups during the 1-mo control period. During the 6 mo of training, the iEMG values increased in M40 (P < 0.05), in M70 (P < 0.05), in W40 (P < 0.05-0.01), and in W70 (P < 0.05-0.01).



Fig. 3. Maximal rate of force development (RFD) in rapidly produced voluntary bilateral isometric leg-extension action in M40 and M70 (*A*) and in W40 and W70 (*B*) during 1-mo control period and during 6-mo strength-training period. Values are means \pm SE.

Maximal isometric knee-flexion force and maximum iEMGs. Knee-flexion forces remained statistically unaltered during the control period (Fig. 7) but increased during the 6-mo training in M40 by $14 \pm 5\%$ (P < 0.05), in M70 by $14 \pm 7\%$ (P < 0.05), in W40 by $22 \pm 4\%$ (P < 0.001) and in W70 by $17 \pm 6\%$ (P < 0.001).

The iEMGs of the BF muscles during the knee flexion remained statistically unaltered in all groups during the control period. During the 6 mo of training, significant (P < 0.05) increases took place in the iEMG of the BF muscle in all groups.

Antagonist *iEMGs*. The BF activities (relative to maximum agonist values of the BF) during the isometric leg extension remained unaltered during the 1-mo control period in all groups (Fig. 8). During the 6 mo of training, it remained statistically unaltered in M40 and W40 but decreased in both M70 (from 24 ± 6 to $21 \pm 6\%$; P < 0.05 for the left leg; Fig. 8A) and W70 (from 31 ± 9 to $24 \pm 4\%$; P < 0.05 for the right leg; Fig. 8B). The BF activities during the 1-RM leg extension remained unaltered in M40, W40, and M70 but decreased

Fig. 4. Maximal integrated EMG activity [iEMG; averaged for vastus lateralis (VL) and vastus medialis (VM) muscles] of right leg (*A*) and left leg (*B*) in voluntary maximal bilateral isometric leg-extension action in M40 and M70 as well as in right leg (*C*) and left leg (*D*) in W40 and W70 during 1-mo control period and during 6-mo strength-training period. Values are means \pm SE.





Fig. 5. Maximal voluntary bilateral concentric one-repetition maximum (1 RM) of leg extensor muscles in M40 and 70M (*A*) and in W40 and W70 (*B*) during 1-mo control period and during 6-mo strength-training period. Values are means \pm SE.

during the training in W70 (P < 0.05). No significant changes occurred during the study period in the BF activities during the first 500 ms of the isometric leg-extension action. The BF activities during the SJ decreased during the training slightly in all groups, but the change was statistically significant only in W70 (P < 0.05).

DISCUSSION

The present progressive heavy-resistance training program combined with explosive types of exercises led to great gains not only in maximal isometric and dynamic strength but also in explosive force production characteristics of the leg extensor muscles in both middle-aged and elderly men and women. The strength gains were accompanied by considerable increases in the voluntary neural activation of the agonist muscles in both middle-aged and elderly subjects of both genders, with significant reductions taking place in the antagonist coactivation of the maximal extension action in both elderly groups. The training also led to significant enlargements in the CSAs of the leg extensor muscles in both middle-aged and elderly subjects, but these changes were minor in magnitude in all groups in comparison to those changes taking place in the voluntary activation of the same muscles during the same training period.

It is rather well known that in previously untrained young men and women great 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 muscles, whereas gradually increasing muscle hypertrophy contributes to strength development primarily during the later phases of training (11, 15, 20, 25, 28, 33). It has been suggested that strength gains in older subjects would be primarily due to improved neural recruitment pattern rather that hypertrophy of the muscle fibers (e.g., Ref. 26). However, when sensitive techniques such as fiber area determination by muscle biopsy (4, 10, 21)or muscle CSA determination by computed tomography, magnetic resonance imaging, or ultrasound scan (9, 10, 14) have been utilized, muscle hypertrophy has also been shown to account for, to some extent, the strength gains in the elderly. Skeletal muscles of elderly people can retain the capacity to undergo traininginduced hypertrophy when the volume, intensity, and duration of the training period are sufficient (4, 9, 10, 13, 14, 19). However, the nature of the present training program, which was composed of both heavy-resistance and explosive types of exercises, could in part explain the finding that the enlargements of 2-9% in the CSAs of the trained muscles remained much smaller in magnitude than those of neural adaptations in both age groups. Although neural activation during the exer-



Fig. 6. Maximal vertical jumping height in squat jump (SJ) in M40 and M70 (*A*) and W40 and W70 (*B*) during 1-mo control period and during 6-mo strength-training period. Values are means \pm SE.

cises used in power training can be rather high even in elderly subjects (12), the duration of this activation during each single muscle action remains usually much shorter than that of a typical heavy-resistance training program suggested to be crucial for training-induced hypertrophy (11, 23). On the other hand, some caution must be exercised when interpreting the present muscle CSA data obtained only at one particular portion of the thigh because training-induced muscle hypertrophy can also be nonuniform along the belly of the muscle and even between the individual components of the quadriceps group (28). Because no muscle biopsy samples were taken in the present study, it was not possible to compare the enlargement recorded in the total CSA of the muscles with the degree of hypertrophy of individual muscle fibers (10). Second, to what extent the degree of training-induced hypertrophy might be limited in magnitude because of hormonal factors, such as serum levels of anabolic hormones and growth factors, during strength training in elderly and/or middle-aged subjects needs to be examined in more detail in the future (16, 35).

Nevertheless, the present findings showed that the enlargements in the CSA of the trained muscles over the 6-mo training period were minor compared with increases recorded in maximal strength of the subject



Fig. 7. Maximal voluntary isometric force of knee flexor muscles (right plus left leg) in M40 and M70 (*A*) and in W40 and W70 (*B*) during 1-mo control period and during 6-mo strength training period. Values are means \pm SE.



Fig. 8. iEMG activity in relative to agonist values for biceps femoris muscle during maximal voluntary isometric bilateral action of leg extensors in left leg (*A*) in M40 and M70 and in right leg (*B*) in W40 and W70 during 1-mo control period and during a 6-mo strength training period. Values are means \pm SE.

groups. This suggests that the contributing role of the nervous system for strength development during the present training may have been more important than that of muscle hypertrophy. Second, the present training actually led to great increases in the maximal voluntary activation of the agonist muscles during the leg-extension actions in both men and women in both age groups. The maximal iEMGs of the biceps femoris muscles during the maximal knee flexion action increased in all subject groups as well. These findings support the concept that, in previously untrained subjects of both genders and at all ages, great 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 (11, 13, 14, 15, 17, 19, 20, 26, 33). Strength training-induced increases in the magnitude of EMG could result from the increased number of active motor units and/or the increase in their firing frequency (7, 33) in both young and older subjects. The EMG data in Fig. 4 additionally show that the increases in the maximal iEMGs in men and women of both age groups took place not only during the initial phases of the training but also during the entire course of the 6-mo training period. This was probably due to the fact that the training loads of the exercises were

progressively increased and also that the subjects activated their muscles during the explosive actions as highly as possible throughout the training.

The progressive strength training of the present study also led to significant decreases in the coactivation of the antagonists recorded during the maximal isometric and 1-RM dynamic extension actions in both elderly groups. The change of the antagonist coactivation in the elderly subjects took place primarily during the initial phases of the training. The coactivation was at the end of the training period at about the same level in comparison to that recorded for the middle-aged subjects, who demonstrated no further changes in the antagonist coactivation. The present results obtained in our elderly subjects of both genders support the concept that strength training can lead to not only increased activation of the agonist muscles but also to training-induced learning effects in terms of reduced coactivation of the antagonist muscles, which may also play an important role in enhancing the net force production of the agonist muscles. The traininginduced reduction in the antagonist coactivation has been reported to take place in previously untrained young subjects, especially during the initial phases of training (3, 32) and has been speculated to occur in elderly subjects (e.g., Ref. 19). To what extent reduced coactivation of the antagonists is mediated by mechanisms in the central nervous system (3) or is associated also with peripheral neural control, especially during various dynamic actions, is difficult to interpret. Moreover, none of the subject groups of the present study showed significant changes in antagonist coactivation during the rapid-force phase of the isometric action, whereas all groups showed some tendency to traininginduced decreases in the BF activity in the SJs, with W70 even demonstrating a significant decrease. It is possible that the magnitude and the time course of the changes in the antagonist coactivation may be related to the action used in the measurements, to the exercises utilized in the training, and to the initial physical status of the subjects in terms of experience and skill in strength training as well as to the age of the subjects, as suggested by the present findings.

It is well documented that typical heavy-resistance strength-training programs in young men and women lead to greater increases in maximal force, whereas the changes in the earlier portions of the isometric forcetime or in the higher velocity portions of the forcevelocity curves usually remain considerably minor (e.g., Ref. 11). This principle of the specificity of the training seems to be true also during heavy-resistance training in older people (10). Explosive training, which utilizes exercises performed with slightly lower loads but with much higher movement velocities, leads usually in younger men and women to improvements primarily in the earlier portions of the force-time or higher velocity portions of the force-velocity curves (e.g., Refs. 11, 20). The strength-training program of the present study was composed of both heavy-resistance and explosive types of exercises for the leg extensor muscles. The present results demonstrate clearly that in addition to

great increases obtained in maximal force, the training utilized led also to considerable increases in explosivestrength characteristics of the trained muscles recorded in both isometric and dynamic actions in both age groups and genders. It is possible that, to induce increases in explosive strength, older subjects are more sensitive to the duration (Fig. 6.) and/or overall volume and/or specific type of the training utilized than are younger subjects (13, 29). The present increases in the explosive force characteristics of the trained muscles were accompanied by significant increases in the iEMGs of the agonist muscles recorded during the early phase of the isometric action as well as during the initial movement phase of the SJs in all groups. These results indicate that considerable training-induced increases may have taken place in the rapid neural activation of the motor units and/or selective hypertrophy of fasttwitch muscle fibers may have also occurred to some degree not only in middle-aged but also in elderly subjects of both genders (13). Because the enlargements in the CSAs of the trained muscles remained smaller in magnitude, it is likely that training-induced adaptations in voluntary neural control and/or in inhibitory and/or facilitatory reflexes may have played an important role in explosive-strength development during the present training in all subjects independently of age and gender. The fact that muscle strength and the ability of the leg extensor muscles to develop force rapidly are important performance characteristics contributing to several tasks of daily life such as climbing stairs, walking, or even prevention of falls and/or trips (1), should be taken into consideration when strengthtraining programs for both middle-aged and elderly men and women are constructed.

In summary, the present results show that progressive heavy-resistance training combined with explosive types of exercises leads to great increases in both maximal isometric and dynamic strength, which are accompanied also by considerable improvements in explosive force characteristics of the trained muscles not only in middle-aged but also in elderly men and women. The increase in muscle strength could be explained only in part by the enlargements in the muscle CSA while the maximal voluntary activation of the agonist muscles increased to a much greater extent in both men and women of both age groups with a significant reduction in the coactivation of the antagonists in the elderly. These findings suggest that neural adaptations seem to play a much greater role than does training-induced muscle hypertrophy in explaining large strength and power gains in middle-aged and older people during the type of strength training used in the present study.

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