Selective muscle hypertrophy, changes in EMG and force, and serum hormones during strength training in older women

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Received 12 January 2001; accepted in final form 5 March 2001

Häkkinen, Keijo, Arto Pakarinen, William J. Kraemer, Arja Häkkinen, Heli Valkeinen, and Markku Alen. Selective muscle hypertrophy, changes in EMG and force, and serum hormones during strength training in older women. J Appl Physiol 91: 569–580, 2001.—Effects of strength training (ST) for 21 wk were examined in 10 older women (64 ± 3 yr). Electromyogram, maximal isometric force, one-repetition maximum strength, and rate of force development of the leg extensors, muscle cross-sectional area (CSA) of the quadriceps femoris (QF) and of vastus lateralis (VL), medialis (VM), intermedius (VI) and rectus femoris (RF) throughout the lengths of 3/12–12/15 (Lf) of the femur, muscle fiber proportion and areas of types I, IIa, and IIb of the VL were evaluated. Serum hormone concentrations of testosterone, growth hormone (GH), cortisol, and IGF-I were analyzed for the resting, preexercise, and postexercise conditions. After the 21-wk ST, maximal force increased by 37% (P < 0.001) and 1-RM by 29% (P < 0.001), accompanied by an increase (P < 0.01) in rate of force development. The integrated electromyograms of the vastus muscles increased (P < 0.05). The CSA of the total QF increased (P < 0.05) throughout the length of the femur by 5–9%. The increases were significant (P < 0.01) at 7/15–12/15 Lf for VL and at 3/15–8/15 Lf for VM, at 5/15–9/15 for VI and at 9/15 (P < 0.05) for RF. The fiber areas of type I (P < 0.05), IIa (P < 0.001), and IIb (P < 0.001) increased by 22–36%. No changes occurred during ST in serum basal concentrations of the hormones examined, but the level of testosterone correlated with the changes in the CSA of the QF (r = 0.64, P < 0.05). An acute increase of GH (P < 0.05), remaining elevated up to 30 min (P < 0.05) postloading, was observed only at posttraining. Both neural adaptations and the capacity of skeletal muscle to undergo training-induced hypertrophy even in older women explain the strength gains. The increases in the CSA of the QF occurred throughout its length but differed selectively between the individual muscles. The serum concentrations of hormones remained unaltered, but a low level of testosterone may be a limiting factor in training-induced muscle hypertrophy. The magnitude and time duration of the acute GH response may be important physiological indicators of anabolic adaptations during strength training even in older women.
area determination by muscle biopsy, or muscle cross-sectional area (CSA) determination by computed tomography or magnetic resonance imaging (MRI) that muscle hypertrophy has accounted for the strength gains not only in young and middle-aged adults but also in older men and women (7, 13, 16–18, 37, 43). The basic requirements for training-induced hypertrophy, not only in older men, but also in older women, who usually show a large degree of muscle atrophy, are that the overall training intensity [the load in relation to the 1-repetition maximum (1 RM) action] as well as the duration of the training period should be sufficient.

Training-induced hypertrophy in older men and women seems to take place in both fast- and slow-twitch muscle fibers. However, much less information is available on training-induced hypertrophy of individual muscle fibers in older women (7, 17, 37), including also data of no training-induced hypertrophy (28). It is also important to point out that it has been shown in younger adults that training-induced muscle hypertrophy (measured by use of MRI) can be nonuniform along the belly of the muscle (33, 34). Until now, only one study, conducted by Tracy et al. (43), has examined the phenomenon of selective hypertrophy in older women during strength training. The data indicated that strength training-induced muscle hypertrophy was greatest in the region of largest CSA (at midthigh) and the increases in CSA became progressively smaller toward the proximal and distal regions of the quadriceps femoris (QF). The authors concluded that the single-slice method may overestimate the true muscle CSA changes in other regions of the QF and may be prone to error. However, the authors reported the data only about the total QF muscle group and not about the training-induced selective hypertrophy taking place possibly in each of the four individual muscles of the QF. Both the longitudinal shape with regard to the CSA and the overall CSA do differ largely between the four individual muscles. Our interest was focused on the examination of the degree of selective strength training-induced muscle hypertrophy not only in the total QF but also in each of its individual muscles in a group of older women.

Heavy-resistance exercise is well known to be a potent stimulus for acute increases in circulating anabolic hormones in younger men. However, the magnitude of hormonal response is lowered in older men (8, 21, 25). In women, the acute response in serum testosterone and GH is lower than in men, whereas no response at all is necessarily observed in older women (21, 22). During strength training, no systematic changes have been reported to take place in basal blood concentrations of circulating anabolic hormones either in older men (8, 22, 35) or in older women (20, 22). Because of the pulsatile nature of GH secretion, the interpretation of single measures must be done cautiously, but the data available indicate that the response of GH to the same relative heavy-resistance workload is greatly lowered in older women at the age of 67 yr, and they remained nonresponsive also after the 6-mo strength-training period (22). However, the acute responsiveness of serum GH to heavy-resistance exercise in older women needs further investigation.

We hypothesized that systematic strength training, even in older women, would lead to significant hypertrophy of the trained muscles, but we were specifically interested to examine the phenomenon of selective hypertrophy over the entire length of the thigh with regard to the total QF and to each of its individual muscles. Second, because blood concentrations of circulating anabolic hormones and growth factors are known to diminish with aging women, we wanted to examine the underlying endocrine mechanisms related to muscle hypertrophy by studying the possible effects of strength training 1) on basal concentrations and 2) acute responses of serum hormones as well as 3) their possible interrelationships with the overall degree of muscle hypertrophy and strength development in this special group of subjects (older women) during a prolonged strength-training period of 21 wk.

METHODS

Subjects

Ten healthy older women (64 ± 3 yr; n = 10) (mean ± SD) volunteered for the study. The subjects were carefully informed about the design of the study with special information as to possible risks and discomfort that might result. Therefore, 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 Jyväskylä, Finland.

The subjects were healthy and habitually physically active. To keep themselves fit, they had taken part in various recreational low-intensity physical activities such as walking, jogging, cross-country skiing, aerobics, or biking, but none of the subjects had any background in regular strength training. Subjects were recruited through advertisements and were medically screened by a medical doctor. None of the subjects had contraindications to perform rigorous resistance exercise. No medication was being taken by the subjects that would have been expected to affect physical performance.

Experimental Design

The experimental period of 25 wk consisted of a 4-wk control period followed by a 21-wk resistance-training period. The subjects were tested on five different occasions using identical protocols. The first month of the study (between the measurements at week −4 and at week 0) served as a control period during which time no strength training was carried out but the subjects maintained their normal low-intensity recreational physical activities. The subjects were tested before and after this control period. Thereafter, the subjects started a supervised experimental strength-training period for 21 wk. The measurements were repeated during the actual experimental training period at 7-wk intervals (i.e., weeks 0, 7, 14, and 21).
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 week before the measurements at week ~4. Second, 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 (14, 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) (14, 16). 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 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.

The force signal was recorded on a computer (486 DX-100) and thereafter digitized and analyzed with an Codas TM computer system (Data Instruments). Maximal peak force was defined as the highest value of the force (N) recorded during the bilateral isometric leg extension. The force-time analysis on the absolute scale included the calculation of average force (N) produced during 100-ms epochs from the start of the contraction up to 500 ms (14, 16). The RFD (N/s) was also analyzed and defined as the greatest increase in force in a given 50-ms time period.

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) of the right and left leg separately. Bipolar (20-mm interelectrode distance) surface EMG recording (Beckman miniature-sized skin electrodes 650437) was employed. The electrodes were placed longitudinally on the motor point areas determined by an electrical stimulator. EMG signals were recorded telemetrically (Glommer, Biomes 2000). The positions of the electrodes were marked on the skin by small ink tattoos (16). These dots ensured the same electrode positioning in each test over the 25-wk experimental period. The EMG signal was amplified (by a multiplication factor of 200; low-pass cutoff frequency of 360 Hz/2 dB) and digitized at the sampling frequency of 1,000 Hz by an on-line computer system. EMG was full-wave rectified, integrated (iEMG, in mV·s), and time normalized for 1 s in the following phases: 1) in the isometric actions for the periods of 100–500 ms to obtain an iEMG-time curve from the start of the contraction, 2) in the maximal peak force phase of the isometric contractions (500–1,500 ms) to calculate maximal iEMG, and 3) in the concentric action of the 1-RM performance for the entire range of motion (14, 16).

Muscle biopsies were obtained before and after the experimental training period. The samples were obtained from the superficial portion of the VL muscle of the right leg (at the lower third portion of the thigh) utilizing the percutaneous needle biopsy technique of Bergrström (4). Special care was taken to extract tissue from the same location (close to the prebiopsy scar) and depth each time. Muscle tissue samples were frozen in isopentane cooled with liquid nitrogen and stored at −80°C until analyzed. Serial cross sections (10 μm thick) were cut on a cryostat at −20°C for histochemical analyses. Histochemical staining for myofibrillar ATPase was used to classify the fibers as I, IIA, IIB, and IIc (on the basis of the stability of their ATPase activity at pH 4.2, 4.6, and 10.3 in the preincubation medium) according to Brooke and Kaiser (5). IIc fibers were, however, so rare that they were not included in the final statistical analyses. Fiber-type percentages were calculated from the mean number of fibers (at pre- and posttraining) of 481 ± 250 and 356 ± 124, respectively. For the calculation of mean fiber areas, an average number of fibers analyzed were 117 ± 41 and 85 ± 29, respectively. A loaded image of stained cross sections was analyzed by a Videocytometric consisting of a microscope (Olympus BX 50) and a color video camera (Sanyo High Resolution CCD) was used to calculate the mean fiber areas of each fiber type.

The muscle CSA of the right QF was assessed before and after the 21-wk strength training by using MRI (Philips Gyroscan ACS-NT Scanner, 1.5 T) at the Keski-Suomen Maagneittikuvav, Jyväskylä, Finland. Once the subject was positioned within the magnet, the thighs of both legs were kept parallel to the MRI table, and the feet were strapped together to prevent rotation. The lengths of the femur (Lf), taken as the distance from the intercondural notch of the femur to the inferior corner of the femoral head, was measured on a coronal plane. Subsequently, 15 axial scans of the thighs interspaced by a distance of 1/15 Lf were obtained from the level of 1/15 Lf to 15/15 Lf as also done in our laboratory’s previous study (17). Great care was taken to reproduce the same, individual Lf each time by using the appropriate anatomical landmarks. In addition, one scan was taken at the site (marked on the skin by the ink tattoo) of the muscle biopsy of the VL muscle. All MRI images were then ported to a Macintosh computer for the calculation of muscle CSA. For each axial scan, CSA computation was carried out on the QF as a whole and, individually, on the VL, VM, vastus intermedius (VI), and rectus femoris (RF). For the final calculation of the CSA, slices 3/15-12/15 were used (slice 3 being closer to the knee joint of the thigh) for all muscles examined except for the RF, which was analyzed only for the slices 5/15-12/15. CSA (measured as cm²) was determined by tracing manually along the border of each muscle of the QF.

The percentage of fat in the body was estimated from the measurements of skinfold thickness from four different sites (9).

Experimental Strength Training

The supervised 21-wk periodized strength-training program of the subjects was a total body (low-volume) program cut into a 2 day/wk format (the typically recommended frequency for recreational training purposes). A minimum of 2 days of rest was required between the two sessions of each week. 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. We chose these exercises because 1) they are probably the most common ones used in strength training for the thigh musculature, 2) they are easy to perform by any subject at all ages, 3) the thigh muscles can be "maximally"
activated throughout the range of motion by using the present knee-extension exercise, and 4) the biomechanical nature of the bilateral leg press exercise is very similar to that of the testing action used in the present strength measurements. In addition, each training session included four to five exercises for the other main muscle groups of the body (the bench press and/or the triceps push-down 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/unilateral elbow and/or knee flexion exercise and/or leg adduction/abduction exercise). All the exercises were performed using concentric muscle actions followed by eccentric actions during the “lowering” phase of the movement. The loads were determined during the training sessions throughout the 21-wk training period according to the maximum-repetition method.

During the first 7 wk of the training, the subjects trained with loads of 40–70% of the 1 RM. The loads of 40–60% were used during the first 4 wk and those of 50–70% during the last 3 wk. The subjects performed 15–20 repetitions per set at loads of 40%, 12–15 repetitions at loads of 50%, 10–12 repetitions at loads of 60%, and 8–10 repetitions at loads of 70%. Three sets were performed in each exercise during weeks 1–4 and three to four sets during weeks 5–7. The loads were 40–50% and 60–70% of the maximum by week 11 and 50%, 60–70%, and 70–80% by week 14. In the two exercises for the leg extensor muscles, the subjects now performed either 10–12 repetitions per set at loads of 40% and 8–10 repetitions at loads of 50% (loads of 40 and 50% for rapid muscle actions) or 10–12 repetitions per set at loads of 60%, 8–10 repetitions at loads of 70%, and 5–8 repetitions at loads of 80%. Three to four sets were performed by week 11, and four to five sets by week 14. In the other four exercises, the subjects performed 10–12 repetitions per set at loads of 60% and performed 3–4 sets by week 11 and 4–5 sets by week 14. During the last 7 wk of training (weeks 14–21), the subjects performed the two exercises for the leg extensor muscles either 8–10 repetitions per set with loads of 70% and 5–8 repetitions per set with loads of 80% of the maximum or 10–12 repetitions per set with loads of 40% and 8–10 repetitions per set with loads of 50% (loads of 40 and 50% for rapid muscle actions). Five to six sets were performed during weeks 14–18 and four to five sets during weeks 19–21. In the other four exercises, 8–12 repetitions per set (10–12 repetitions per set at loads of 60% and 8–10 repetitions per set at loads of 70%) were performed for four to five sets during weeks 14–18 and three to four sets during weeks 19–21.

The strength training utilized was a combination of heavy and explosive resistance-training programs so that a volume of ~20% of the total volume of the leg extensor exercises (leg press and knee extension) with light loads (40% of the maximum for 10–12 repetitions per set and that of 50% for 8–10 repetitions per set) was performed according to the principle of explosive strength training (16). These repetitions were executed as explosively as possible (i.e., rapid muscle actions) throughout the range of motion. The overall amount of training was progressively increased (in terms of number of sets within the range limits described) until the fifth month, at which point it was slightly reduced for the final 3 wk of the 21-wk training period. During the 21-wk experimental training period, the subjects continued taking part in recreational low-intensity physical activities such as walking, jogging, swimming, biking, or gymnastics one to three times per week in a similar manner to what they were accustomed to before this experiment.

**Heavy-Resistance Protocol for the Examination of Acute Hormone Responses**

The heavy-resistance protocol at week 0 before the training period as well as at week 21 after the 21-wk strength-training period included the bilateral leg press exercise on a machine (David 210, David Fitness and Medical). In the exercise, the subject started from the flexed-knee position (70°) and extended the knees concentrically to a full extension (180°) and thereafter lowered the load eccentrically back to the starting position. The actual loads were always the repetition maximums for each subject so that the subjects performed 10 repetitions per set with the maximal load possible for a total of 5 sets (5 × 10 repetition maximums). The recovery time between the sets was 2 min. The loads were adjusted during the course of the session due to fatigue so that each subject would be able to perform 10 repetitions at each set. If the load happened to become too heavy, the subject was assisted slightly during the last one to three repetitions of the set, while she maintained her maximum performance, so that the required number of repetitions could be reached and the subjects would also maintain the same contraction time.

**Blood Samples During the Heavy-Resistance Loading Protocol**

The control samples. To examine acute hormone responses to the heavy-resistance loading, the control blood samples were drawn from the antecubital vein of each subject twice (two control samples within 1 h of each other) during the control day at week 0. The corresponding two control samples were also drawn twice (two control samples within 1 h of each other) during the second control day after the training at week 21.

The loading samples. Blood samples were drawn four times during the two heavy-resistance exercise days (pre- and postloading samples within ~1 h as well as 15 min and 30 min after termination of the training session) at week 0 and at week 21. The heavy-resistance protocol was performed between 8:00 AM and 6:00 PM but always at the same time of day for each subject (at the corresponding time of the day as the blood sampling during the control days) before and after the 21-wk training period. The subjects were instructed to maintain their normal food intake before the heavy-resistance exercise protocol and to have their last light meal during that day no later than 2 h before the session.

**Basal Blood Samples During the 4-wk Control Period and 21-wk Strength Training**

To examine the basal concentrations of serum hormones, blood samples were drawn from the antecubital vein of each subject after 10 h of fasting and ~8 h of sleep in the mornings (between 7:30 AM and 8:30 AM) during the 1-mo control period (at week −4 and week 0) as well as during the 21-wk training period (at weeks 7, 14, and 21).

**Analytical Methods**

Serum samples for the hormonal analyses were kept frozen at ~20°C until assayed. Serum testosterone concentrations were measured by the Chiron Diagnostics ACS:180 automated chemiluminescence system using a ACS:180 analyzer. The sensitivity of the testosterone assay was 0.42 nmol/l, and the intra-assay coefficient of variation was 6.7%. The concentrations of serum free testosterone and dehydroepiandrosterone sulfate (DHEAS) were measured by radioimmunoassays using kits obtained from Diagnostic Products (Los Angeles, CA). The sensitivity of the free testosterone
assay was 0.52 pmol/l, and the intra-assay variation was 3.8%. The respective values were 0.06 μmol/l and 4.5% for the DHEAS assay. The assays of serum cortisol were carried out by radioimmunoassays. The sensitivity of cortisol assay was 0.05 μmol/l, and the coefficient of the intra-assay variation was 4.0%. Serum sex hormone-binding globulin (SHBG) concentrations were measured by two-site fluoroimmunometric methods with kits obtained from Wallac (Turku, Finland) using the 1235 AutoDELFIA automatic immunoassay system. The sensitivity of the SHBG assay was 0.5 nmol/l, and the intra-assay variation was 4.4%. Concentrations of GH were measured by use of radioimmunoassay kits from Pharmacia Diagnostics (Uppsala, Sweden). The sensitivity of the GH assay was 0.2 μg/l, and the intra-assay variation was 2.5–5.1%. Serum IGF-I concentrations were measured by radioimmunoassays using reagent kits from DiaSorin (Stillwater, MN). The method included an octadecylsilica-silica extraction procedure for the serum samples. The sensitivity of the IGF-I assay was below 2.0 nmol/l, and the intra-assay variation was 9.2%. All samples for each test subject were analyzed in the same assay for each hormone.

Statistical Methods

Standard statistical methods were used for the calculation of means, SD, SE, 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 (from 70.5 ± 6.1 to 70.9 ± 5.1 kg) and body height (from 160.1 ± 5.9 to 160.4 ± 6.1 cm) remained statistically unaltered, but the percentage of body fat decreased (from 38.7 ± 1.6 to 38.1 ± 1.7%; P < 0.001) during the 21-wk strength-training period.

Maximal Isometric Leg Extension Force, Force-Time, and iEMGS

Maximal isometric bilateral force remained unaltered during the 4-wk control period (from week 4 to week 0) (Fig. 1). A large increase of 37% took place in maximal force during the 21-wk training period from 1,435 ± 345 to 1,970 ± 410 N (P < 0.001). The average force produced in 500 ms remained unaltered during the control period but increased during the 21-wk training period from 550 ± 319 to 846 ± 402 N (P < 0.01). The RFD values remained unaltered during the control period but increased significantly during the 21-wk training period from 4,450 ± 2,670 to 6,880 ± 3,413 N/s (P < 0.01).

No significant changes occurred during the control period in the maximum iEMGs of the VL and VM muscles of the isometric actions (Fig. 2). During the course of the 21-wk training, significant increases were observed in the iEMGs of the VL and VM muscles of the right (P values between <0.001 and <0.05) and left leg (P values between <0.001 and <0.05). The iEMGs of the VL and VM muscles during the first 500 ms of the isometric action increased (P < 0.05) during the training.

1-RM Leg Extension Values and Maximum iEMGs

The 1-RM bilateral leg extension values remained statistically unaltered during the control period (Fig. 3). During the 21-wk training, the 1-RM values improved by 29% from 106 ± 23 to 137 ± 23 kg (P < 0.001).
No statistically significant changes occurred during the control period in the iEMGs of the VL and VM muscles of the 1-RM actions, but the iEMG values increased during the 21-wk training both in the left \((P\) values between \(0.01\) and \(0.05\)) and right leg \((P\) values between \(0.01\) and \(0.05\)).

**Muscle CSA**

The CSA of the QF increased during the 21-wk training period significantly \((P < 0.05–0.01)\) throughout the length of the quadriceps from 4/15 to 12/15 Lf (Fig. 4). The mean relative increase at different Lf of the QF was 7.5% ranging from 6 to 11% but did not differ significantly from each other. However, for individual muscles, the CSA of the VL increased during the 21-wk training significantly \((P < 0.01 \text{ and } <0.05)\) at 7–12/15 Lf (by 9–14%) but not at 3–6/15 Lf (Fig. 5), whereas the corresponding increases of the VM were significant \((P < 0.05 \text{ and } 0.01)\) at 3–8/15 (by 6–12%) but not at 9–12/15 Lf (Fig. 5). The increases of the CSAs of the VI were significant \((P < 0.05)\) at 5–9/15 and 11–12/15 (by 4–11%) (Fig. 5), and the only significant increase \((P < 0.05)\) in the case of the RF was observed at 9/15 (by 8%) (Fig. 5). The increases of the CSAs of the muscles measured at the length of the muscle biopsy site were significant for the VL \((P < 0.01)\) and VM \((P < 0.05)\) and for the whole QF \((P < 0.05)\) but not for the VI or RF (Fig. 6).

**Muscle Fiber Characteristics**

The percent values for the muscle fiber distribution of the VL muscle did not differ significantly before or after the training period (Table 1). The mean fiber areas of type I as well as those of types IIa and IIb increased after the 21-wk training period \((P < 0.05 \text{ and } P < 0.001)\) (Table 2). The relative increases for type I area and the average area of type II were 22 ± 5% and 36 ± 20%, respectively.

The individual mean fiber areas of type II correlated significantly with the individual CSAs of the VL muscle (at the length of the biopsy site) both before \((r = 0.94; P < 0.001)\) and after the 21-wk training period \((r = 0.81; P < 0.01)\). The correlation coefficients be-

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**Fig. 4.** Mean ± SD cross-sectional areas (CSAs) of the total quadriceps femoris (QF) muscle group at the lengths of the femur (Lf) from 3/15 to 12/15 in older women before and after the 21-wk strength-training period \((**P < 0.05; ***P < 0.01)\).

**Fig. 5.** Mean ± SD CSAs of the individual muscles of the VL (A), VM (B), vastus intermedius (VI) (C), and rectus femoris (RF) (D) of the QF muscle group at Lf from 3/15 to 12/15 in older women before and after the 21-wk strength-training period \((**P < 0.05; ***P < 0.01; ****P < 0.001)\).
pretraining or at posttraining (Figs. 7 and 8). The mean concentration of GH did not increase significantly at pretraining, whereas a significant acute increase took place at posttraining (P < 0.05) and remained significant (P < 0.05) up to 15 min (P < 0.05) and up to 30 min (P < 0.05) postloading (Fig. 9). The relative acute changes in GH at pretraining correlated with the relative changes recorded in maximal force during the latest training period of the 21-wk training (r = 0.68, P < 0.05).

DISCUSSION

The present progressive strength training performed only twice a week but for 21 wk led to large gains in maximal and explosive isometric as well as concentric force production characteristics of the leg extensors in older women. The strength gains were accompanied by significant increases in the voluntary neural activation of the trained agonist muscles accompanied by significant enlargements in muscle fiber areas of types I, IIa, and IIb as well as in the total CSA of the trained extensor muscles. Interestingly, the data further showed that the increases in the CSA of the total QF took place throughout the Lf, but the magnitudes of the CSA increases along the Lf differed specifically between the four individual muscles of the QF. No significant training-induced changes occurred in the basal concentrations of serum anabolic and catabolic hormones, but the mean level of individual serum testosterone correlated significantly with the gains recorded in the CSA of the trained muscles, and a systematic acute exercise-induced increase of GH was observed only after the 21-wk strength-training period.

The 21-wk progressive strength training, although performed only twice a week, led to large gains in maximal strength recorded in both isometric and concentric bilateral actions of the leg extensors in our older women. It is of some importance to point out that the present increases in maximal strength were as large as 29–37%, although the subjects trained only two times a week. These strength gains in our older women were thus well in line with previous observations that maximal muscle strength in previously untrained healthy subjects can be increased “easily” during progressive strength training independently of age, gender, and type of actions, whether isometric or dynamic (7, 12, 13, 15–18, 22, 26, 28, 30, 31). Thus, an important conclusion from the practical standpoint is the fact that the frequency of strength training in

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Table 2. Fiber areas of the vastus lateralis muscle before and after a 21-wk strength-training period in older women

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<tr>
<th>Type</th>
<th>Pre</th>
<th>Post</th>
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<tr>
<td>Type I, μm²</td>
<td>4,131 ± 980</td>
<td>4,878 ± 778*</td>
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<tr>
<td>Type IIa, μm²</td>
<td>3,051 ± 902</td>
<td>3,899 ± 946†</td>
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<tr>
<td>Type IIb, μm²</td>
<td>2,183 ± 820</td>
<td>3,014 ± 839†</td>
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Values are means ± SD; n = 10 subjects. Significant difference pre- to posttraining (*P < 0.05; †P < 0.001).

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Table 1. Fiber distribution of the vastus lateralis muscle before and after a 21-wk strength-training period in older women

<table>
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<th>Type</th>
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<tr>
<td>Type I, %</td>
<td>45 ± 17</td>
<td>40 ± 14</td>
</tr>
<tr>
<td>Type IIa, %</td>
<td>32 ± 11</td>
<td>38 ± 11</td>
</tr>
<tr>
<td>Type IIb, %</td>
<td>23 ± 15</td>
<td>22 ± 14</td>
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Values are means ± SD; n = 10 subjects. Pre, before strength training; Post, after strength training.
Table 3. Serum total and free testosterone, GH, DHEAS, IGF-I, cortisol, and SHBG basal concentrations in older women during the 4-wk control period (week −4 to week 0) and the course of the 21-wk strength-training period (weeks 0, 7, 14, and 21)

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<td>Testosterone, nmol/l</td>
<td>1.8±1.2</td>
<td>1.9±0.9</td>
<td>1.6±0.6</td>
<td>1.1±0.5</td>
<td>1.5±0.7</td>
</tr>
<tr>
<td>Free testosterone, pmol/l</td>
<td>4.9±2.0</td>
<td>4.8±1.9</td>
<td>4.2±2.2</td>
<td>3.4±0.7</td>
<td>4.3±2.6</td>
</tr>
<tr>
<td>GH, µg/l</td>
<td>0.9±0.7</td>
<td>2.4±2.5</td>
<td>1.6±3.3</td>
<td>2.3±3.6</td>
<td>2.2±3.7</td>
</tr>
<tr>
<td>DHEAS, µmol/l</td>
<td>2.4±1.1</td>
<td>2.3±1.3</td>
<td>2.4±1.0</td>
<td>2.1±1.2</td>
<td>2.3±1.0</td>
</tr>
<tr>
<td>IGF-I, nmol/l</td>
<td>18.4±8.8</td>
<td>17.7±8.9</td>
<td>18.8±9.9</td>
<td>17.3±6.3</td>
<td>17.4±5.8</td>
</tr>
<tr>
<td>Cortisol, µmol/l</td>
<td>0.57±0.20</td>
<td>0.49±0.17</td>
<td>0.36±0.10</td>
<td>0.47±0.13</td>
<td>0.47±0.10</td>
</tr>
<tr>
<td>SHBG, nmol/l</td>
<td>51.4±19.9</td>
<td>56.6±20.8</td>
<td>59.4±21.3</td>
<td>58.5±20.8</td>
<td>56.8±17.9</td>
</tr>
</tbody>
</table>

Values are means ± SD; n = 10 subjects. GH, growth hormone; DHEAS, dehydroepiandrosterone sulfate; IGF-I, insulin-like growth factor I; SHBG, sex hormone-binding globulin.

previously untrained older female (or male) subjects can be as low as twice a week, when the loading intensity of training is sufficient and increased progressively (i.e., periodized) throughout the training period. Both muscle strength and the ability of the leg extensor muscles to develop force rapidly are important performance characteristics in older people, contributing to several functional performance tasks of daily life such as climbing stairs, walking actions such as crossing the road, or even prevention of falls and/or trips (3, 12, 17, 39, 42, 44). In the present study, we approached the aspect of explosive strength only so that heavy-resistance training was combined with exercises of explosive nature. Nevertheless, the present observation that explosive force production capacity of the neuromuscular system did remain trainable even in older women should also be of practical value, for example, in primary and secondary prevention of frailty and in physical rehabilitation programs for aging people of both genders (16, 17).

The strength training led to large increases in the maximal voluntary activation of the agonist muscles recorded during both isometric and concentric leg extension actions. The magnitudes and the time courses of the EMG increases (Fig. 2) were rather similar to those changes recorded for the isometric voluntary strength (Fig. 1) of the same muscle group. This finding indicates that the contributing role of the nervous system for strength development during the present heavy-resistance training may have been of great importance. The largest increases in the iEMGs were noted during the first 7 wk of training, supporting the concept that, in previously untrained subjects, not only in younger adults but also in older persons, large initial increases in maximal strength observed during the initial weeks of strength training can be attributed largely to the increased motor unit activation of the trained agonist muscles (16–18, 22, 32, 38). Strength training-induced increases in the magnitude of EMG could result from the increased number of active motor units and/or increase in their firing frequency (38). Increases in net excitation of the motoneurons may result from increased excitatory input, reduced inhibitory input, or both (38). The present EMG data additionally showed that the increases in the maximal iEMGs took place in our older women to some degree also during the later course of the 21-wk training period. This may be explained by the facts that the training loads of the exercises were progressively increased in a periodized manner and that the subjects activated their muscles highly also during the explosive actions throughout the training period. Although the actual nature of the adaptations in the nervous system is difficult to determine, not only can progressive strength training lead to increased activation of the agonists but also training-induced learning effects in terms of reduced coactivation of the antagonists may play a contributive role. The latter phenomenon can also enhance the net strength production of the agonists in younger adults (6) and, maybe even more importantly, especially in older subjects during multi-joint actions (16).

No statistically significant transformation of type II muscle fiber subtypes or changes in the percentage of type I fibers were observed pre- to posttraining in our older women. Type II subtype transformation, going from type IIb to IIab to IIa, has been previously observed in younger (1, 27, 40, 41) and older men (18) but...
not significantly in older women (17). The present subject group also showed a similar trend for this during the training period, although some caution must be exercised with the data because of the low numbers of subjects and muscle fibers included in the analysis. However, skeletal muscles of older people of both genders seem to retain the capacity to undergo training-induced hypertrophy provided that the volume, intensity, and the duration of the training period are sufficient (7, 12, 13, 17, 18, 37). The present resistance training performed only twice a week did lead to significant increases in muscle fiber areas of types I, IIa, and IIb of the VL, in line with some previous findings in older women (7, 17, 37), although no training-induced hypertrophy has also been reported (28). In line with previous studies using older men as subjects (13), the increases in the sizes of individual muscle fibers of both types I and II were in the present study larger than the enlargements observed in the total CSA of the QF. However, some caution must be exercised when interpreting the present muscle fiber area data with a relative low number of fibers analyzed in the present biopsy sample obtained from the VL muscle.

Recently, Tracy et al. (43) examined the phenomenon of selective hypertrophy of the QF in older women during strength training. Their data showed that strength training-induced muscle hypertrophy was greatest in the region of the largest CSA (at midthigh) and that the increases in the CSA became progressively smaller toward the proximal and distal regions of the QF. The authors concluded that the single-slice method may overestimate the true muscle CSA changes in other regions of the QF and may be prone to error. However, the individual muscles of the QF are known to differ, with regard to not only the average CSA of each muscle but also largely the CSAs along the belly of these muscles. Interestingly, the present data showed that the increases in the CSA of the total QF took place throughout the Lf, whereas the magnitudes of the CSA increases along the Lf did differ specifically between the individual muscles of the QF. Thus the CSA of the VL increased during the 21-wk training significantly at 7–12/15 Lf but not at 3–6/15 Lf (Fig. 5), whereas the corresponding increases of the VM were significant at 3–8/15 Lf but not at 9–12/15 Lf (Fig. 5). The increases in both cases were thus greater in the regions of the largest CSAs, at proximal portions for the VL and at distal portions for the VM. However, this was not the case for the increases recorded in the VI or RF muscles. Although the large training-induced increases observed in the maximal global iEMG of the VL and VM muscles did not differ significantly from each other, the differences in the degree of hypertrophy between the two muscles could be explained by specific differences in muscle activation (and tension) and/or differences in contractile proteins synthesis along the belly of the individual muscles (34). It should also be pointed out that we did use a typical training program with two common exercises for the thigh musculature and that the choice of the exercises might contribute to the degree of the selective hypertrophy of the muscles trained. Because the present increase in strength was much greater than the overall degree of muscle hypertrophy, it is also possible that, in addition to increased voluntary muscle activation, architectural changes, e.g., changes in pennation angle of the muscle fibers, may have taken place during strength training (23), contributing to strength development. The present data obtained in older women further showed that the increases of the CSAs of the muscles measured at the length of the muscle biopsy site were significant for the VL and VM and for the whole QF (Fig. 6). Thus the present biopsy site for the VL, as commonly used, to determine the degree of hypertrophy of individual muscle fibers, may actually be a reasonable one. How-

Fig. 7. Mean ± SD values for serum testosterone concentrations before (pre), immediately after the heavy-resistance loading sessions (post), and after a recovery for 15 min (post 15) and 30 min (post 30) both before (pretraining) and after the 21-wk strength training (posttraining) in older women.

Fig. 8. Mean ± SD values for serum free testosterone concentrations at pre, post, post 15, and post 30 time points both pretraining and posttraining in older women.

Fig. 9. Mean ± SD values for serum growth hormone (GH) concentrations pre, post, post 15, and post 30 both pretraining and posttraining in older women (*P < 0.05).
ever, the same site may not be that valid for the VI or RF. To conclude, the present MRI data showed that the enlargements of the muscle CSA seem to differ largely between the individual muscles of the QF muscle group when measured at the same Lf, suggesting the advantages of the multiple-slice method to indicate the accurate growth of the muscle tissue taking place during the strength training.

No systematic changes were observed during the course of the 21-wk strength-training period in the concentrations of serum testosterone, free testosterone, DHEAS, GH, IGF-I, or cortisol, nor in the testosterone-SHBG ratios. In general, these observations are rather similar to those found earlier in both middle-aged and older subjects of both genders, when they have utilized typical heavy-resistance training programs over a period of a few months (20, 22, 26, 35).

The overall loading of the present training program may have thus been within the physiological range normal, because maximal strength increased greatly throughout the 21-wk training period with no systematic changes in the concentrations of anabolic and catabolic hormones. In general, the data indicate that although a basal level of the anabolic hormone testosterone is lowered in older women, they seem to be able to gain in strength to about the same extent as middle-aged or young adult women or men (22) when utilizing the present type of low-volume total-body strength-training protocol over the 5- to 6-mo period. However, it has been shown that, in those older women who have demonstrated very low basal testosterone levels, the individual gains in maximal strength during the strength-training period may be minor compared with those with higher testosterone concentrations (22). The present data further showed that also the individual gains in the CSA of the trained muscles were minor in those older women who demonstrated lower basal testosterone concentrations compared with those with higher testosterone concentrations ($r = 0.64, P < 0.05$). The findings strengthen the suggestion that basal concentrations of blood testosterone may be of great importance; even so, a low level of testosterone may be a limiting factor in older women, for both strength development and overall training-induced muscle hypertrophy, when typical total body heavy-resistance training programs are utilized. In this study, only the serum levels of testosterone were measured. It is possible that, even though the blood testosterone levels would remain unaltered, strength training can induce changes, e.g., at the receptor level. Dehydroepiandrosterone and its conjugated form DHEAS are androgens secreted from adrenal cortex (2). As in the case of testosterone, no systematic training-induced changes were observed in the circulating levels of this androgen in our older women during the present 21-wk strength-training period. No systematic changes occurred in GH for resting concentrations with the present training, either. However, the lack of changes in immunoreactive GH may not present the complete picture of the adaptational responses of GH variants to resistance training (26). The lack of changes in serum IGF-I with the training may suggest that IGF-I in the circulation may not be a good marker of the implicit activity of the GH-IGF-I system. Actually, strength training in older people has been shown to lead to a substantial increase in the presence of IGF-I in skeletal muscle tissue (11).

In addition to the basal levels of the hormones, serum total and free testosterone as well as GH concentrations were measured in the present study during the single heavy-resistance exercise session both before and after the 21-wk strength-training period. Serum testosterone concentration is known to increase during a typical heavy-resistance session in young men, whereas the response in women may be minor (10, 21, 24, 45). The acute exercise-induced testosterone response is usually lower in older than in younger men (8, 21, 25). In the present study, no acute responses were observed at pretraining in serum total and free testosterone in our older women. This is in line with previous observations (21, 22). The same was true also after the 21-wk training period. It is also unclear whether the lack of serum testosterone response in our older women in both loading conditions is a limiting factor in strength development or muscle hypertrophy as seems to be the case for the low basal serum testosterone level (22). It has been shown previously that the acute response of GH to heavy-resistance loading is decreased due to aging both in men and especially in older women at the age of ~70 yr (21, 22). The present results showed that the loading at pretraining did result in some acute increase in GH, but it was not statistically significant because of large interindividual variation in the response (Fig. 9). However, it was physiologically interesting to observe that the individual acute changes noted in GH at pretraining correlated with the individual changes in maximal force during the latest training period of the 21-wk training. Second, after the 21-wk training period the increase in serum GH concentrations in our older women at the age of 64 yr not only was significant immediately at postloading but also remained significant up to 30 min postloading. Because of the pulsatile nature of GH secretion, the interpretation of single measures must be done cautiously. However, the observation can be considered as an indication of the training-induced adaptation of the endocrine system showing that the acute GH hormone response may become more systematic after strength training even in older women. The magnitude and time duration of the response may be important physiological indicators of training-induced anabolic adaptations.

In summary, the present progressive strength training performed twice a week for 21 wk led to large gains in maximal and explosive force production characteristics of the leg extensors in older women. The strength gains were accompanied by significant increases in the voluntary neural activation of the trained agonist muscles accompanied by significant enlargements in muscle fiber areas of types I, Ila, and IIB as well as in the total CSA of the trained extensor muscles. Interestingly, the increases in the CSA of the total QF took
place throughout the Lf, but the magnitudes of the CSA increases along the Lf differed between the four individual muscles of the QF. The increases were greater in the regions of the largest CSAs, at proximal portions for the VL and at distal portions for the VM, whereas this was not the case for the increases recorded in the VI or RF muscles. No systematic changes occurred in the basal concentrations of serum anabolic and catabolic hormones examined during the training period, but a low level of testosterone, especially in older women, may be a limiting factor in overall training-induced muscle hypertrophy. A systematic acute exercise-induced increase of GH not only took place in older women, but may be a limiting factor in overall training-induced muscle hypertrophy. A systematic acute exercise-induced increase of GH not only took place in older women, may be a limiting factor in overall training-

The increases were greater in the regions of the largest CSAs, at proximal portions for the VL and at distal portions for the VM, whereas this was not the case for the increases recorded in the VI or RF muscles. No systematic changes occurred in the basal concentrations of serum anabolic and catabolic hormones examined during the training period, but a low level of testosterone, especially in older women, may be a limiting factor in overall

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