Neuromuscular adaptation during prolonged strength training, detraining and re-strength-training in middle-aged and elderly people

Accepted: 2 May 2000

Abstract Effects of a 24-week strength training performed twice weekly (24 ST) (combined with explosive exercises) followed by either a 3-week detraining (3 DT) and a 21-week re-strength-training (21 RST) (experiment A) or by a 24-week detraining (24 DT) (experiment B) on neural activation of the agonist and antagonist leg extensors, muscle cross-sectional area (CSA) of the quadriceps femoris, maximal isometric and one repetition maximum (1-RM) strength and jumping (J) and walking (W) performances were examined. A group of middle-aged (M, 37–44 years, n = 12) and elderly (E, 62–77, n = 10) and another group of M (35–45, n = 7) and E (63–78, n = 7) served as subjects. In experiment A, the 1-RM increased substantially during 24 ST in M (27%, P < 0.001) and E (29%, P < 0.001) and in experiment B in M (29%, P < 0.001) and E (23%, P < 0.01). During 21 RST the 1-RM was increased by 5% at week 48 (P < 0.01) in M and 3% at week 41 in E (n.s., but P < 0.05 at week 34). In experiment A the integrated electromyogram (IEMG) of the vastus muscles in the 1-RM increased during 24 ST in both M (P < 0.05) and E (P < 0.001) and during 21 RST in M for the right (P < 0.05) and in E for both legs (P < 0.05). The biceps femoris co-activation during the 1-RM leg extension decreased during the first 8-week training in M (from 29 ± 5% to 25 ± 3%, n.s.) and especially in E (from 41 ± 11% to 32 ± 9%, P < 0.05). The CSA increased by 7% in M (P < 0.05) and by 7% in E (P < 0.001), and by 7% (n.s.) in M and by 3% in E (n.s.) during 24 ST periods. Increases of 18% (P < 0.001) and 12% (P < 0.05) in M and 22% (P < 0.001) and 26% (P < 0.05) in E occurred in J. W speed increased (P < 0.05) in both age groups. The only decrease during 3 DT was in maximal isometric force in M by 6% (P < 0.05) and by 4% (n.s.) in E. During 24 DT the CSA decreased in both age groups (P < 0.01), the 1-RM decreased by 6% (P < 0.05) in M and by 4% (P < 0.05) in E and isometric force by 12% (P < 0.001) in M and by 9% (P < 0.05) in E, respectively, while J and W remained unaltered. The strength gains were accompanied by increased maximal voluntary neural activation of the agonists in both age groups with reduced antagonist co-activation in the elderly during the initial training phases. Neural adaptation seemed to play a greater role than muscle hypertrophy. Short-term detraining led to only minor changes, while prolonged detraining resulted in muscle atrophy and decreased voluntary strength, but explosive jumping and walking actions in both age groups appeared to remain elevated for quite a long time by compensatory types of physical activities when performed on a regular basis.

Key words Ageing · Strength training · Detraining · Muscle hypertrophy and atrophy · Agonist-antagonist

Introduction

Human muscle strength and the ability to develop explosive force are well known to decrease in both genders with increasing age, especially at the onset of the sixth decade (Larsson 1978; Bosco and Komi 1980; Clarkson et al. 1981; Häkkinen 1994; Porter et al. 1995; Vandervoort 1998). The decrease in strength performance capacity can be explained in part by the decreased maximal voluntary activation of the agonist muscles and/or

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changes in the degree of agonist-antagonist co-activation (Kamen et al. 1995; Håkkinen et al. 1998b) and, to a greater extent, by the reduction in muscle mass associated with age-related changes in hormone balance (Håkkinen and Pakarinin 1993) and the decline in the intensity of daily physical activities (Mäkiä et al. 1994). The decline in muscle mass is thought to be mediated by a reduction in the size and/or number of individual muscle fibres, especially of fast-twitch fibres (Esen-Gustavsson and Borges 1986; Lexell et al. 1988).

However, it has been shown that systematic strength training not only in middle-aged but also in older people can lead to substantial increases in strength performance. This results primarily from the considerable neural adaptation observed especially during the earlier weeks of training (Moritani and DeVries 1980; Håkkinen and Håkkinen 1995; Keen et al. 1994; Håkkinen et al. 1996, 1998a, b). This initial training-induced increase in strength in elderly people may be accounted for primarily by increases in the voluntary activation of the agonist muscles (Moritani and DeVries 1980; Håkkinen et al. 1998a) although changes in co-activation of the antagonists may occur also (Håkkinen et al. 1998a). Muscle hypertrophy of both fibre types may also contribute to further strength development during subsequent months when using typical heavy-resistance training programs with older people (Frontera et al. 1988; Charette et al. 1991; Pyka et al. 1994; Håkkinen et al. 1998b).

Much less information is available on training-induced neuromuscular adaptation in older people during prolonged strength training lasting for several months, a year, or even longer (Lexell et al. 1995; Morganti et al. 1995; McCartney et al. 1996). Furthermore, in addition to maximal strength of various muscle groups, the role of explosive strength characteristics of the leg extensors is also important for various functional physical activities in the elderly (Bassey et al. 1991). As in the case of younger adults, to achieve increases in the explosive strength capacity of older people heavy resistance training should probably be combined with explosive exercises by paying special attention to the higher action/movement velocities of the exercises performed (Håkkinen and Håkkinen 1995; Håkkinen et al. 1998a). The extent to which these resistance training-induced increases in maximal and explosive strength characteristics are related to changes in dynamic functional capacities, such as jumping and walking performances, is of both scientific and practical interest. Finally, although it is known that detraining leads within a few weeks to a decrease in maximal voluntary muscle activation, muscle atrophy and decreased strength in young adults (Håkkinen et al. 1985; Narici et al. 1989), only very limited information is available on effects of short-term and prolonged detraining on neuromuscular performance in older people (Lexell et al. 1995).

This study was conducted to examine both functional and structural adaptation in the neuromuscular system and changes in vertical jumping and normal walking performance in middle-aged and elderly people during prolonged strength training lasting for 24 weeks followed (after 3 weeks) by an additional re-strengthening period of 21 weeks utilizing a program planned not only for maximal strength development but also including exercises of an explosive nature. The second aim of this study was to examine neuromuscular adaptation and changes in the functional capacities of these middle-aged and older people during both short-term and prolonged detraining periods of 3 and 24 weeks after the termination of systematic strength training.

**Methods**

Subjects

A group of middle-aged (M, age range 37–44 years, n = 12, six women and six men) and of elderly (E, 62–77, n = 10, five women and five men) subjects volunteered as subjects for a strength-training-detraining-re-strengthening training study (experiment A). Another group of M (35–45, n = 7, four women and three men) and elderly E (63–78, n = 7, four women and three men) subjects volunteered as subjects for a strength-training-detraining study (experiment B). The actual recruitment took place so that subjects volunteered to enter either group A or B.

The percentage of fat in the body was estimated from the measurements of skinfold thickness (Durnin and Womersley 1967). The subjects were informed carefully about possible risks and discomfort that might result and each gave written consent prior to 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 recruited from the town of Jyväskylä via various fliers delivered all over the town. Only healthy subjects, based on medical screening, were accepted. All were living independently and, according to data collected via questionnaire, were habitually physically active. To keep fit and as recreation they took part in various physical activities such as walking, jogging, swimming, biking and aerobics 1–3 times weekly but none had any background of regular strength training. The subjects were taking no medication that would have been expected to affect physical performance or endocrine profile.

**Experimental design**

The total duration of the present study was 48 weeks. The first 4-week period (between measurements made at weeks 4 and 0) in both experiments A and B was used as a control period, during which no strength training was carried out, although 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, all subjects in both experiments started a supervised experimental strength-training period for 24 weeks utilizing the same program. The measurements were repeated during the 24-week training period in both experiments A and B at 8-week intervals (i.e. at weeks 0, 8, 16 and 24). Thereafter, the subjects in experiment A underwent a 3-week detraining period without any strength training at all (until week 27). This 3-week detraining period was then followed by a re-strength-training period for 21 weeks (weeks 27–48). The measurements were repeated during the re-strength-training period at 7-week intervals (i.e. at weeks 27, 34, 41 and 48). The subjects in experiment B terminated their strength training for the entire detraining period of 24 weeks (weeks 24–48). The present study is the continuation of a previous project (Håkkinen et al. 1998a).

**Testing**

The subjects were familiarized carefully with the testing procedures of voluntary force production of the bilateral leg extension and
unilateral isometric knee extension actions about 1 week before the measurements at week -4. This was done to minimize possible effects of learning on the force production performances measured prior to the start of the training phase. Secondly, during the actual testing occasion several warm-up actions were performed prior to the measurement of maximal performance.

A David 210 dynamometer (David Fitness and Medical, Finland) was used to measure maximal bilateral concentric force production of the leg extensors (hip, knee and ankle extensors) (Häkkinen et al. 1998a). The subject was seated 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 to 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 allowing 1.5 min for recovery between the trials. 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 the 1-RM.

A David 200 dynamometer modified for strength testing (Häkkinen et al. 1996) was used to measure maximal unilateral isometric torque of the right knee extensors. The subject was seated so that the hip and knee angles were 110° and 90° respectively. On verbal command the subject performed a maximum isometric knee extension action of the right leg. A minimum of three maximal actions were recorded and the best maximum was retained for further analysis. The period of rest between the maximal contractions was 1.5 min. The force signal was recorded on a computer (486 DX-100), digitized and analysed with a Codas TM computer system (Data Instruments). Maximal peak torque was defined as the highest value of the torque (in Newton-metres) recorded during the unilateral isometric knee extension.

Electromyogram (EMG) activity during the bilateral concentric leg extension and unilateral isometric knee extension actions was recorded from the agonist muscles vastus lateralis (VL) and vastus medialis (VM) and from the antagonist muscle biceps femoris (BF, long head) of the right and left legs separately. Bipolar (20 mm interelectrode distance) surface EMG recording (miniature-sized skin electrodes No. 650437, Beckman, Ill. USA) was employed. The electrodes were placed longitudinally on the motor point areas determined by an electrical stimulator. EMG signals were recorded telemetrically (Biomes 2000, Gloner). The positions of the electrodes were marked on the skin by small ink tattoos (Häkkinen and Komi 1983) to ensure the same electrode positioning in each test over the 48-week experimental period. The EMG signal was amplified (vibration factor of 100), low-pass cut-off frequency of 360 Hz 3 dB(-1) and digitized at a sampling frequency of 1000 Hz by an on-line computer system. The EMG was full-wave rectified, integrated (IEMG, millivolt-seconds) and time-normalized for 1 s at two phases: the concentric action of the 1-RM for the entire range of motion and the maximal peak torque phase of the unilateral isometric knee extension action (500–1500 ms) to calculate the maximal IEMG. The IEMG values of the right and the left muscles recorded during the maximal 1-RM action were taken for further analysis. The EMG of the BF muscles acting as an agonist was recorded during the maximal unilateral isometric knee flexion of the right leg (with hip and knee angles of 110 and 90° respectively) using the David 200 dynamometer (Häkkinen et al. 1996). The EMG of the BF during the knee flexion was analysed in a similar manner as were those from the VL and VM muscles during the isometric knee extensions. The maximum IEMG values recorded for the right BF was taken for further analysis to calculate the antagonist BF activity recorded during the maximal unilateral isometric knee extension and bilateral concentric leg extension actions (expressed relative to maximum agonist values of the BF).

Dynamic explosive force characteristics of the leg muscles were measured on a force platform 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 centre of gravity in the SJ was calculated from the flight time. Three maximal jumps were recorded and the best maximum in terms of height was taken for further analysis.

Maximal walking speed was measured over a distance of 10 m. The subjects were encouraged to walk as fast as possible along the corridor in the laboratory building. A minimum of three trials were taken and the best time was taken for further analysis.

The cross-sectional area (CSA) of the quadriceps femoris (QF) muscle group (rectus femoris, VL, VM and vastus intermedius) was measured with a compound ultra-sonic scanner (SSD-190, Aloka Famosmaximal) and 5-MHz convex transducer. The CSA was measured at the lower third portion between the greater trochanter and lateral joint line of the knee. During scanning the subjects lay supine with the legs extended and relaxed on the examination table. To avoid tissue compression, a generous amount of gel was used under the probe. The position and orientation of the probe was altered until the best echo was achieved with an assumption that it was then at right-angles to the femur. 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 (Sipilä and Suominen 1991; Häkkinen et al. 1996). The coefficient of variation for CSA measurements repeated on consecutive days is 4% and the correlation coefficient 0.99 (Sipilä and Suominen 1991). The CSA measurements were taken before (at week 0) and after the 24-week strength training period (at week 24) and after the re-strength training (experiment A) and detraining (experiment B) (at week 48).

Experimental strength training program

All subjects in both experiments participated in a supervised 24-week strength-training period using the same program. Three students of the department supervised the training throughout the experiment. The training took place twice weekly. Each training session included two exercises for the knee 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 pull downs 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). The major muscle group under investigation was the leg extensors. However, we wanted to use the so-called whole-body training system to provide balanced gains in strength for the other muscle groups as well and not only the leg extensors. This was crucial, for example, for the motivation of the training program.

During the first 8 weeks of the training the subjects trained with loads of 50–70% of the 1-RM. The subjects performed 10–15 repetitions per set completing three or four sets of each exercise. The loads were 50–60% and 60–70% of the maximum by week 12 and 50–60% and 70–80% by week 16. In the two exercises for the leg extensor muscles the subjects now performed either 8–12 repetitions per set (at lower loads) or five or six repetitions per set (higher loads) and performed between three and five sets. In the other four exercises the subjects performed 10–12 repetitions per set and performed between three and five sets. During the last 8 weeks of training (weeks 16–24) the subjects performed in the two exercises for the leg extensor muscles between three and six repetitions per set with loads of 70–80% of the maximum and 8–12 repetitions per set with loads of 50–60% and completed between four and six sets. In the other four exercises the subjects performed 8–12 repetitions per set and completed between three and five sets altogether. The intensities for the leg extensors were based on the 1-RM recorded at pre-training and repeated at 8-week intervals for adjustment. In addition, the loads in these exercises and in those exercises in which no 1-RM test actions were performed were further adjusted throughout the study according to the maximum repetition method.

The strength training program was a combination of heavy resistance and "explosive" strength training. A major part of the knee extension exercises were performed using the basic principles of heavy-resistance training. In these exercises the instructions for
the subjects were to use the modest velocity (about 2–2.5 s for the concentric action followed by the “lowering” action with a duration of about 1–1.5 s) for each repetition. A portion (20%) of the leg exercises with light loads (50–60% of the maximum) were performed so that each repetition of each set was executed as “explosively” as possible (rapid muscle actions). The average duration for each repetition was 0.5–1.0 s for the concentric action depending on the load. However, the instruction for each subject was the use the maximum velocity he/she was able to produce. The lowering took about the same time as the corresponding lowering during the heavy-resistance actions i.e. about 1–1.5 s.

During the first 24-week experimental training period the subjects continued their recreational physical activities such as walking, jogging, swimming, biking or gymnastics 1–3 times weekly in a similar manner as before the experiment.

In experiment A, the above-mentioned 24-week strength training period was then followed by a 3-week detraining period. Strength training was terminated during this period but the subjects were allowed to continue their usual recreational physical activities as above. This detraining period was then followed by a re-strength-training period for 21 weeks. The training program was similar in terms of frequency, relative volume and intensity to that carried out during the first 24-week training period but the training was performed in 7-week cycles for a total of 21 weeks (weeks 27–48).

In experiment B the initial 24-week strength training period was followed by a 24-week detraining period (weeks 24–48). Strength training was terminated during this period but the subjects were allowed to continue their customary recreational physical activities as above. In the final analyses it was noted from the questionnaire that that two M subjects and one E subject continued some strength training during the detraining period. Since this training was very limited (only once weekly for a total period of 1 or 3 months) the data from these three subjects were still included in the detraining data.

Statistical analyses

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 analysed utilizing multivariate analysis of variance (MANOVA) with repeated measures. Probability-adjusted t-tests were used for pair-wise comparisons where appropriate. \( P \leq 0.05 \) was regarded as significant.

Results

Physical characteristics

Body mass and the percentage of body fat did not change during the first 24-week training period but body fat had decreased during the re-strength training \( (P < 0.05) \) in the E group (experiment A) and increased \( (P < 0.05) \) during detraining in the M group (Table 1).

1-RM leg extension values and maximum IEMGs

The 1-RM bilateral leg extension values remained unaltered during the 4-week control periods (weeks –4 to 0) in experiment A and B in both age groups (Fig. 1A and B). In experiment A large increases took place in the 1-RM in both age groups during the first 24-week training: in M 27\% \( (P < 0.001) \) and in E 29\% \( (P < 0.001) \). In experiment B the 1-RM increased correspondingly during the 24-week strength training in M (29\%, \( P < 0.001) \) and E (23\%, \( P < 0.01) \). In experiment A no change occurred in the 1-RM during the 3-week detraining. During the second training period the increases in the 1-RM were 5% by week 48 \( (P < 0.01) \) and 3% by week 41 (n.s., but \( P < 0.05 \) at week 34) in M and E, respectively. In experiment B the 1-RM decreased during the 24-week detraining by 6\% \( (P < 0.05) \) in M and by 4\% \( (P < 0.05) \) in E. The 1-RM remained elevated in both age groups at week 48 compared to week 0 \( (M P < 0.01; E P < 0.05) \).

In experiment A the IEMG of the VL and VM muscles increased during the first 24-week training period in both M \( (P < 0.05) \) and E \( (P < 0.001) \) (Fig. 2A) and also during the second 21-week period in M for the right VL \( (P < 0.05) \) and in E for the right leg \( (P < 0.05) \) and for the left VL \( (P < 0.05) \). A significant decline \( (P < 0.05) \) occurred during the 3-week detraining for the right leg in E. In experiment B the maximum IEMG increased in M in both right \( (P < 0.05 \) at week 16) and left leg \( (P < 0.05) \) for the VL at week 16) during the 24-week strength training (Fig. 2B) and decreased \( (P < 0.05) \) for the left leg during the 24-week detraining. In E the IEMG increased in both left \( (P < 0.01) \) and right \( (P < 0.05) \) legs during the 24-week training followed by slight decreases (n.s.) during the 24-week detraining. In experiment A there was a significant correlation between the changes in 1-RM and IEMG of both legs in M \( (0–24 \text{ weeks } r = 0.65, P < 0.05 \text{ and } r = 0.62, P < 0.05) \; 0–48 \text{ weeks } r = 0.58, \text{ P } < 0.05 \))

| Table 1 | Physical characteristics (mean ± SD) of middle-aged and elderly subjects before and after the strength training periods at weeks 0–24 (experiments A and B) and after the additional re-strength-training period at week 48 (experiment A) and after the detraining period at week 48 (experiment B) |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | |
| n | Age (years) | Height (cm) | Body mass (kg) | | | | | |
| | Week 0 | Week 24 | Week 48 | Week 0 | Week 24 | Week 48 | |
| Experiment A | Middle-aged | 12 | 41 ± 2 | 173 ± 11 | 76 ± 18 | 77 ± 18 | 76 ± 17 | 24 ± 7 | 23 ± 7 | 24 ± 6 |
| Elderly | 10 | 70 ± 4 | 165 ± 11 | 73 ± 12 | 73 ± 12 | 72 ± 12 | 29 ± 6 | 28 ± 7 | 28 ± 7* |
| Experiment B | Middle-aged | 7 | 41 ± 4 | 168 ± 8 | 65 ± 11 | 65 ± 11 | 65 ± 8 | 21 ± 5 | 20 ± 5 | 22 ± 6* |
| Elderly | 7 | 69 ± 5 | 166 ± 7 | 75 ± 11 | 75 ± 10 | 74 ± 9 | 30 ± 8 | 30 ± 9 | 31 ± 8 |

*\( P < 0.05 \) (between week 0 and week 48)
Fig. 1 Mean (± SE) maximal voluntary bilateral concentric one repetition maximum (1-RM) action of the leg extensor muscles in middle-aged and elderly subjects during a 4-week control period and during a 24-week strength-training period followed either by a 3-week detraining and a 21-week re-strengthening period (A) or by a 24-week detraining period (B).

P < 0.05 and r = 0.54, P < 0.05 for the right and left legs respectively) and in E (0–24 weeks r = 0.65, P < 0.05 for the right leg; 0–48 weeks r = 0.88, P < 0.001 and r = 0.86, P < 0.0001 for the right and left legs respectively).

Maximal unilateral isometric torque
and maximum IEMGs

Maximal unilateral isometric knee extension torque remained unaltered during the 4-week control periods (weeks -4 to 0) in experiment A and B in both age groups (Fig. 3A and B). In experiment A large increases took place in maximal torque in both age groups during the first 24-week training: in M by 22% (P < 0.001) and in E by 23% (P < 0.001). In experiment B the torque increased correspondingly during the 24-week strength training in M (30%, P < 0.001) and E (32%, P < 0.01). In experiment A maximal torque decreased during the 3-week detraining in M (6%, P < 0.05) and by 4% (n.s.) in E. During the second training period maximal torque returned (P < 0.05) within 7 weeks (by week 34) to the same level recorded at week 24 in both groups but no further gains took place in either M or E during the final 14 weeks of training. In experiment B maximal torque decreased during the 24-week detraining by 12% (P < 0.001) in M and by 9% (P < 0.05) in E.
Maximal torque remained elevated in both age groups at week 48 compared to week 0 (M $P < 0.05$ and E $P < 0.05$).

In experiment A the IEMG of the right VL and VM muscles during the maximal isometric knee extension increased during the first 24-week training period in both M ($P < 0.01$) and E ($P < 0.01$) (Fig. 4A). It also increased during the first 7 weeks of training of the second 21-week period for the right VM ($P < 0.05$) and the right VL and VM ($P < 0.01$) in both M and E. No significant changes occurred during the 3-week detraining either in M or E. In experiment B the maximum IEMG of the right leg increased slightly (n.s.) in M during the first 8 weeks of the training of the 24-week strength training period and decreased slightly (n.s.) during the 24-week detraining. In E the IEMG increased in the VL ($P < 0.05$) and VM muscles ($P < 0.01$) during the 24-week training followed by slight decreases (n.s.) during the 24-week detraining.
Antagonist IEMGs

The BF activity of the right leg (relative to maximum agonist values of the BF) during the isometric knee extension decreased slightly, but not significantly, in both age groups during the initial 8 and/or 16 weeks of training in experiment A with no changes in experiment B. M subjects showed lower \((P < 0.05)\) antagonist co-activation values than E subjects at all measurements. The BF co-activation of the right leg during the bilateral leg extension decreased slightly in experiment A during the first 8-week training in M (from 29 ± 5% to 25 ± 3%, n.s.) and significantly in E (from 41 ± 11% to 32 ± 9%, \(P < 0.05\)) with no further changes thereafter (Fig. 5A). In experiment B no significant changes took place either in M or E during the study (Fig. 5B).

Muscle CSA

In experiment A the CSA of the QF increased by 7% in M \((P < 0.05)\) and by 7% in E \((P < 0.001)\) during the first 24-week strength training period and remained stable during the second period in both groups (Fig. 6A). A significant correlation was observed between the changes in 1-RM and in CSA (0–48 weeks \(r = 0.73, P < 0.01\)) in M. In experiment B the CSA increased by 7% (n.s.) in M and by 3% in E (n.s.) during the 24-week strength training period and decreased in both age groups \((P < 0.01)\) during the detraining (Fig. 6B). At week 48 the CSAs in both groups were smaller (M n.s., E \(P < 0.01\)) than at week 0.

Squat jump and walking performances

The vertical height in the SJ remained unaltered during the 4-week control periods (weeks –4 to 0) in experiment A and B in both age groups (Fig. 7A and B). The increase of 18% \((P < 0.001)\) in SJ took place during the first 24-week training period by week 16 in M and of 22% in E \((P < 0.001)\) by week 24. Only slight decreases

![Graph](image1.png)

*Fig. 5* Mean (± SE) IEMG activity relative to agonist values (%) for the biceps femoris muscle during the maximal voluntary bilateral concentric 1-RM leg extension action in the right leg in middle-aged and elderly subjects during a 24-week strength training period followed either by a 3-week detraining and a 21-week re-strength-training period (A) or by a 24-week detraining period (B) (no data are available for the end of the control period).

![Graph](image2.png)

*Fig. 6* Mean (± SE) cross-sectional area (CSA) of the quadriceps femoris muscle in middle-aged and elderly subjects before and after a 24-week strength training period followed either by a 21-week re-strength-training period (A) or by a 24-week detraining period (B)
occurred during the 3-week detraining. During the second 21-week training period the SJ performances regained ($P < 0.05$) the level recorded at week 24 of the first training period in both groups with no further increases. In experiment B the SJ increased in M by 12% ($P < 0.05$) and in E by 26% ($P < 0.05$) by the first 16 weeks of training of the 24-week training period. No significant changes took place during the 24-week detraining.

Walking speed increased during the 4-week control periods in experiment A and B in both age groups ($P < 0.05$) (Fig. 8A and B). In experiment A walking speed increased ($P < 0.05$) in M during both training periods (by 8% by week 48), while in E it increased significantly ($P < 0.05$) by 24 weeks (by 11% by week 48). A significant correlation was observed in experiment A between the changes in the 1-RM and in walking speed during the second 24-week training period in E (weeks 27 and 48 $r = 0.78$, $P < 0.01$). No changes occurred during the 3-week detraining. In experiment B walking speed remained unaltered in M during the 24-week training period while in E it increased by 13% ($P < 0.05$) during the 24-week training and remained elevated in both groups after the detraining at week 48 ($P < 0.05$) compared with week 0.

**Discussion**

The results from both experiments show that both middle-aged and elderly subjects were able to achieve large increases not only in maximal dynamic and isometric strength but also in the explosive jumping and walking performances due to the 24-week resistance training with only two sessions a week. The strength gains were accompanied by considerable increases in the maximal voluntary neural activation of the agonist muscles in both isometric and concentric leg extension actions in both age groups with significant reductions occurring during the initial training phases in the
antagonist co-activation in the elderly in experiment A. During the additional training period some further strength development took place in the dynamic 1-RM action until week 48 in the middle-aged subjects and until week 41 in the elderly. The enlargements during the first 24-week training periods in the CSA of the QF were significant but minor in magnitude and no further enlargements occurred during the additional 21-week training. Only minor changes occurred in maximal strength, explosive jumping and walking performances during the 3-week detraining. During the 24-week detraining, maximal strength and muscle CSA decreased in both age groups while the jumping and walking performances did not change.

Some twenty years ago, Moritani and DeVries (1980) reported that older people could increase their muscle strength during a resistance-training period of a couple of months to about the same extent as younger adults. Although there is a potential limitation in making direct comparisons of the data between the present two subject populations, the results from the experimental periods showed clearly that both middle-aged and elderly subjects achieved large increases in both maximal dynamic and isometric strength of the QF throughout the 24-week resistance training with only two weekly sessions. The rate of strength development thereafter is diminished during more prolonged training periods, depending on the intensity, frequency and type of training (Häkkinen 1994). During the second training period some further development still took place in the 1-RM strength until week 48 in our middle-aged subjects and until week 41 in the elderly, despite the low frequency of the training. The present results are consistent with the findings by Morganti et al. (1995); Lexell et al. (1995) and McCartney et al. (1996) who have shown that older subjects can increase their muscle strength during a prolonged resistance-training lasting for as long as a year or even longer. It is important to note that the explosive jumping and walking performances also improved in both middle-aged and elderly subjects to some extent almost throughout the 48-week training period, probably as the result of the combination of heavy and explosive exercises. These data also suggest that ongoing resistance training in the elderly may be an excellent method of counteracting not only the loss of strength (McCartney et al. 1996) but also that of functional capacity – such as a minimum knee extension strength needed to rise from a chair (Young 1986) – normally associated with ageing. Ongoing resistance training may also serve to delay the threshold for dependency by several years (Young 1986; McCartney et al. 1996).

In previously untrained young men and women the large increases in maximal strength during the first weeks of strength training are attributed predominantly to the increased motor unit activation of the trained muscles, while gradually increasing muscle hypertrophy contributes to strength development primarily during the later phases of training (Komi 1986; Sale 1991; Häkkinen 1994). The present training in experiments A and B also led to great increases throughout the 24-week period in the maximal voluntary activation of the agonist muscles during both concentric and isometric actions in both age groups. The present findings support the concept that increases in maximal strength during the first weeks/months of strength training in previously untrained subjects of both genders and at all ages can be attributed largely to the increased motor unit activation of the trained agonist muscles (Moritani and DeVries 1979, 1980; Häkkinen and Komi 1983; Sale 1991; Keen et al. 1994; Häkkinen et al. 1996, 1998a, b). Strength training-induced increases in the magnitude of the EMG could result from the increased number of active motor units and/or increase in their firing frequency (Enoka 1988; Sale 1991) in both young and older subjects. The present increases of 30–40% in the IEMGs were much larger than the increases noted in the muscle CSA indicating the important role of neural adaptation for strength development. Interestingly, neural adaptation seemed to continue, although to a much lesser extent, even during a more prolonged training period, because the maximal IEMGs increased also during the second 21-week training period in both age groups. This was probably due to the fact that the training loads of the exercises were progressively increased and that the subjects attempted to activate their muscles maximally during the explosive actions throughout the training period.

The resistance training intervention in experiment A also led to some decreases in the co-activation of the antagonists recorded during the maximal isometric knee and dynamic 1-RM leg extension actions in both age groups, although it was significant only in the elderly for the concentric leg extension. In line with our earlier observations (Häkkinen et al. 1998a), the decrease of the antagonist co-activation in the elderly subjects took place primarily during the initial 8–16 weeks of the training although the decrease was rather minor in magnitude. Second, the present data also showed that the amount of antagonist co-activation in the elderly in experiment A remained somewhat higher (although not significantly) than in our middle-aged subjects in both actions throughout the 48-week experimental period. Third, the amount of antagonist co-activation seemed to be rather variable, since in experiment A both age groups showed somewhat higher (although not significant) mean values in both actions than those recorded for the corresponding age groups in experiment B. Fourth, no significant training-induced decreases took place in experiment B. The magnitude and the time course of the changes in the antagonist co-activation may be related to the types of actions used, 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 and/or gender of the subjects (Carolan and Cafarelli 1992; Häkkinen et al. 1998a). Nevertheless, the present results support the concept that strength training can lead not only to the increased activation of the agonist muscles but
training-induced learning effects in terms of reduced co-activation of the antagonist muscle also plays a role enhancing the net force production of the agonists. The extent to which reduced co-activation of the antagonists is mediated by mechanisms in the central nervous system (Carolan and Cafarelli 1992) or associated also with peripheral neural control, especially during various dynamic actions, is difficult to establish.

Several resistance-training studies during the last decade have shown muscle hypertrophy to account for strength gains not only in young adults but also to some extent in the elderly. Skeletal muscles of the elderly people seem to retain the capacity to undergo training-induced hypertrophy when the volume, intensity and the duration of the training period are sufficient (Frontera et al. 1988; Fiatarone et al. 1990; Charette et al. 1991; Hakkinen et al. 1996, 1998b). The present training also led to significant enlargements in the CSA of the QF muscles in both age groups although the magnitude of these changes was minor compared with the changes taking place in the voluntary activation and strength of the same muscles during the same training period. Moreover, no further enlargements occurred in experiment A during the additional 21-week training period. The specific nature of the present training program, comprising both heavy resistance and explosive types of exercises, could in part explain the findings. Although neural activation during the exercises used in power training can be rather high, even in elderly subjects, the duration of this activation during each single muscle action remains much shorter than that of a typical heavy-resistance training program suggested to be crucial for training-induced hypertrophy (MacDougall 1991; Hakkinen et al. 1998a, b). Second, the frequency of training was possibly not high enough to produce further hypertrophy during the second training period independently of age although caution must be exercised when interpreting the present muscle CSA data because of limitations related to the ultrasound imaging method utilized. Nevertheless, CSA data obtained using ultrasonography correlates highly with those measured by computed tomography in the case of the QF (Siipilä and Suominen 1993). An additional reason for some caution in the interpretation is the fact that the muscle CSA data were obtained only at one particular portion of the thigh whereas training-induced muscle hypertrophy can be non-uniform along the belly of the muscle and even between the individual components of the quadriceps group (Narici et al. 1996). Nevertheless, the contribution of the nervous system to strength development during the present training may have been more important in both age groups than that of muscle hypertrophy.

Typical heavy-resistance strength training leads to greater increases in maximal force in both younger and older subjects while the changes in the earlier portions of the isometric force-time, or in the higher velocity portions of the force-velocity curves, remain minor (Frontera et al. 1988). The present strength training program comprised both heavy-resistance and explosive types of exercises for the leg extensor muscles. This type of training regimen has been shown during short term follow-up periods of a few months to lead to increased explosive force production in both isometric and dynamic actions (Hakkinen and Hakkinen 1995; Hakkinen et al. 1998a). In addition to the gains in maximal force, the present training led also to considerable increases in explosive strength of the trained muscles recorded in the jumping action in both age groups primarily during the first 16 to 24 weeks of training while no further increases took place during the additional 21-week training. It is possible that the overall volume of training should have been increased and/or the type of the training modified to produce further increases in explosive force in both age groups. Nevertheless, the increases observed in explosive strength during the initial weeks of training indicate that considerable training-induced changes may have taken place in the voluntary and/or reflex induced rapid neural activation of the motor units in both age groups (Hakkinen et al. 1998a) because the enlargements in the CSA of the trained muscles remained minor in magnitude. Since both muscle strength and the ability of the leg extensor muscles to develop force rapidly are important performance characteristics contributing to tasks of daily life such as climbing stairs, walking or even prevention of falls and/or trips (Bassett et al. 1991), optimal construction of strength training programs is necessary for both middle-aged and elderly men and women. Our middle-aged subjects improved their walking speed throughout the training and the elderly improved their walking speed primarily during the first 24 weeks of the training and also to some degree during the latter 21-week period. The significant correlation observed between the changes in the leg extension 1-RM strength and in the walking speed during the second training period in our older group indicates the importance of muscle strength for walking performance, especially in the elderly. It seems obvious that both middle-aged and elderly people can carry out successful strength training for prolonged periods and attain considerable functional adaptation in the neuromuscular system.

An interesting finding from experiment A was the observation that maximal concentric leg extension strength and jumping and walking performances did not decrease significantly during the 3-week detraining and maximal isometric force decreased only by 6% and 4% in our middle aged and elderly subjects respectively. Moreover, in experiment B maximal concentric strength decreased during the 24-week detraining by only 6% and 4% and isometric strength values by only 12% and 9% in the middle-aged and elderly subjects respectively. These findings are consistent with the decreases of 5% and 8% reported for the unilateral knee extension actions in older people during a 24-week detraining (Lexell et al. 1995). The data suggest that the effects of detraining (including recreational physical activity but no heavy resistance exercises) on strength remain minor in
middle-aged and elderly people compared with the considerable detraining-induced decreases observed in younger adults (Häkkinen et al. 1985; Narici et al. 1989). The present finding is also well in line with previous research results on older subjects showing that when the training frequency was reduced to one session per week, older people could maintain their dynamic strength levels for several months (Lexell et al. 1995). It was also interesting to observe that the improvements obtained during the present training period in the walking speed and squat jump remained elevated for several months after the termination of strength training, in spite of the decreases in the QF CSA. The extent to which these rather minor detraining-induced decreases in the functional performance capacity of the neuromuscular system in the present age groups are related to the low frequency of the preceding training and/or type of training regimen used compared to those used in previous training/detraining experiments is difficult to establish (Häkkinen and Komi 1983; Häkkinen et al. 1985; Narici et al. 1989). Second, the amount and intensity of physical activities carried out during the detraining period contributes to the magnitude of changes observed in strength. Nevertheless, the present data suggest the importance of ongoing resistance training for increasing or maintaining muscle mass and strength but indicate that various functional actions such as jumping and walking in both middle-aged and older people may remain rather elevated for some time by compensatory types of physical activities as performed on a regular basis by our subjects.

In summary, both subject groups achieved large increases not only in maximal dynamic and isometric strength but also in the jumping and walking actions due to the 24-week resistance training with only two sessions per week followed by some further strength development in the 1-RM action until week 48 in the middle-aged subjects and until week 41 in the elderly. The strength gains were accompanied by considerable increases in the maximal voluntary neural activation of the agonists in both age groups with significant reductions occurring during the initial training phases in the antagonist co-activation in the elderly. The enlargements in muscle CSA were significant, although minor in magnitude, indicating that neural adaptation seemed to play a greater role than muscle hypertrophy in explaining strength/explosive performance gains during the present strength training. Short-term detraining led to only minimal changes in the neuromuscular performance but prolonged detraining was associated with significant muscle atrophy and decreased voluntary strength. The data suggest the importance of ongoing resistance training for increasing or maintaining muscle mass, strength and explosive performance but indicate that functional actions such as explosive jumping and walking performances in both middle-aged and older people may still remain elevated for quite a long time when compensatory types of other physical activities are performed on a regular basis.

Acknowledgements This study was supported in part by a grant from the Ministry of Education, Finland.

References