

Julien Ochala · Daniel Lambertz
Jacques Van Hoecke · Michel Pousson

Effect of strength training on musculotendinous stiffness in elderly individuals

Received: 5 July 2004 / Accepted: 25 November 2004 / Published online: 9 February 2005
© Springer-Verlag 2005

Abstract The present study deals with the question whether 24-week strength training alters neuromechanical properties of plantar flexors in elderly people (73–83 years). The first purpose of the present study was to evaluate the effect of strength training on musculotendinous (MT) stiffness of the triceps surae (TS). The training was performed twice per week and mainly consisted of three series of ten repetitions of calf-rise and leg-press exercises at 75% of the three-repetition maximum. Using quick-release movements at different levels of submaximal torques performed measurements of MT stiffness. Surface electromyograms (EMG) of each part of the TS and the tibialis anterior were also recorded. A stiffness index (SI), defined as the slope of the angular stiffness–torque relationship ($SI_{MT-Torque}$), was used to quantify changes in MT stiffness. Results showed a significant decrease in $SI_{MT-Torque}$ by 25.2% following training ($P < 0.05$). The second purpose of the study was to evaluate whether neural mechanism has influences on this decrease. Therefore, an activation SI, defined as the slope of the angular stiffness–EMG relationship (SI_{MT-EMG}) was used to overcome the influence of changes in agonist activity, and thus to quantify changes in MT intrinsic elastic properties. SI_{MT-EMG} only decreased by 11.2% following training ($P < 0.05$). The present results underlined that MT stiffness decreases following training in elderly individuals, counterbalancing the effect of ageing. These changes seem not only to be due to peripheral but also to neural adaptations.

Keywords Triceps surae · Musculotendinous stiffness · Myoelectrical activity · Exercise · Ageing

Introduction

During the ageing process, impairments of skeletal muscle contractile and elastic properties in humans have been reported (Ochala et al. 2004). Using a classical model of the musculotendinous (MT) system mechanics (Hill 1950), elastic properties are generally described by the series elastic component (SEC), which is composed of an active fraction (i.e. muscle fibres) and a passive fraction (i.e. extramuscular tendon, aponeurosis and intramuscular connective tissue) (Huxley and Simmons 1971). SEC behaviour is generally obtained by means of a quick-release technique (Goubel and Pertuzon 1973). The stiffness of the SEC, i.e. the ratio between changes in force and changes in length is classically linearly related to force. In ageing, the stiffness of the SEC, i.e. MT stiffness, has been found to increase in various muscle groups such as plantar flexors (Blanpied and Smidt 1993; Ochala et al. 2004), and elbow flexors (Valour and Pousson 2003). This increase in MT stiffness may compensate the reduction in force in the elderly (Valour and Pousson 2003; Ochala et al. 2004). In fact, this may induce a better transmission of the force via tendon directly to bone and shorten the coupling time between eccentric and concentric phases during the stretch-shortening cycle when walking, for instance.

Strength training in old age has been effective for improving muscle contractile properties such as force (Frontera et al. 1988) and shortening velocity (e.g. Ferri et al. 2003). Despite numerous reports on the adaptations of contractile properties to strength training, data in the literature concerning changes in elastic properties of the MT system with regimens of increased loading in old age, remain scarce. Only the study of Blanpied and Smidt (1993) reported that strength training led to a decrease in stiffness of the plantar flexors in elderly

J. Ochala (✉) · J. V. Hoecke · M. Pousson
Equipe INSERM ERM 207
Motricité-Plasticité, Faculté des Sciences du Sport,
Université de Bourgogne,
BP 27 877, 21 078 Dijon Cedex, France
E-mail: Julien.Ochala@u-bourgogne.fr
Tel.: +33-3-80396761
Fax: +33-3-80396702

D. Lambertz
Département de Génie Biologique, CNRS UMR-6600,
Université de Technologie,
60205 Compiègne Cedex, France

women, whereas Kubo et al. (2003) reported no significant changes in tendon stiffness in elderly people after low-load resistance training. In young subjects, the use of eccentric exercises led to an increase in MT stiffness (Pousson et al. 1990), whereas concentric training showed a decrease in MT stiffness (Poulain and Pertuzon 1988). These opposite changes in MT stiffness were discussed in terms of opposite adaptation of the active and passive fraction of the SEC. As reported by Kubo et al. (2001a, 2002), dynamic resistance training (eccentric-concentric) and static resistance training (isometric) increased the elastic properties of tendinous structures in humans, although the latter depends on the duration of the exercise (Kubo et al. 2001b). Moreover, isometric training led to higher increases in tendinous elastic properties (Kubo et al. 2001a) than resistance training (Kubo et al. 2002).

Thus, the first aim of the present study was to quantify changes in MT stiffness of plantar flexor muscles following a strength-training program, in the elderly, thanks to the quick-release technique. Regarding neurophysiological alterations occurring during strength training periods in the elderly, it can be hypothesized that MT stiffness decreases.

As seen above, according to the literature, following training, changes in MT stiffness have been commonly interpreted in terms of adaptation of the properties of the muscles and tendons involved. Nevertheless, Lambertz et al. (2001, 2003) reported recently that MT stiffness could also be influenced by neural adaptations such as changes in muscle activation capacities. Therefore, the second purpose of the present study was to evaluate whether neural adaptations have influences on possible changes in MT stiffness. For that, myoelectrical activities of triceps surae (TS) muscles were assessed by using surface electromyography (EMGs), and differences were quantified by using EMG-torque relationships. Changes in tibialis anterior (TA) muscle myoelectrical activities were also quantified. Regarding adaptations within the nervous system during the first few weeks of training (Sale 1988; Häkkinen et al. 1998) and muscle hypertrophy later in the process (Frontera et al. 2003), it can be hypothesized that if MT stiffness changes occur following the present training, it could be influenced by neural alterations.

Methods

The experiment described here is part of a comprehensive physical conditioning programme study designed to provide an overall conditioning stimulus, involving both the upper and lower limbs. However, this particular paper deals with the MT stiffness adaptations during plantar flexion to strength training in ageing. It should be noticed that the measurements were carried out on plantar flexors because these muscles are involved during the daily most important motor task, i.e. walking.

Subjects

The experiment was performed on 21 healthy elderly subjects (age range 73–83 years). Fourteen individuals (six women and eight men) were assigned (by randomization) to the training group; the remaining subjects (three females and four males) were assigned to the control group. Physical characteristics of the subjects are shown in Table 1. All subjects received medical clearance from a general practitioner prior to the training program. All of them were voluntary, sedentary and free from any neurological deficit and/or orthopaedic disability. All procedures were explained to the subjects verbally and a written consent form was completed, before the experimental procedures. A local ethics committee approved the protocol and the experiment was carried out according to the guidelines of the Declaration of Helsinki.

Strength training program

The subjects participated in a 24-week physical conditioning training (48 sessions). Each training session consisted of a warm-up and strength exercises. The programme frequency was twice per week. The warm-up was in line with international recommendations and a position statement from the American College of Sports Medicine for safe exercise with elderly people. It lasted 20 min and consisted of walking, marching, sidestepping, isolated mobility and supported stretches (held statically for 8–10 s). The strength exercises were carried out on commercially available strengthening machines. During the first six sessions, before the beginning of the study, subjects were familiarized with the equipment and with the exercise technique. The training of the lower limb muscles involved bilateral movements, performed (1) on a sitting calf-rise machine and (2) on a leg-press machine. For the calf-rise exercise, subjects plantar flexed from a position of ~ 0.34 rad of dorsi flexion to maximum plantar flexion (~ 0.52 rad). In the leg press, leg extension was performed from a knee angle of 1.57 rad to ~ 0.08 rad from full extension, to prevent knee-joint damage (leg extension contributes to the training of the plantar flexor muscles by stretching medial and GL). The subjects were instructed to perform the lifting of the weight (concentric action) in ~ 2 s and, immediately after, lowering of the weight (eccentric action) in ~ 3 s.

Table 1 Physical characteristics of subjects

	Training group	Control group
<i>n</i>	14	7
Age (years)	75.4 ± 2.2	77.2 ± 1.9
Height (cm)	162 ± 2.8	163 ± 2.1
Weight (kg)	69.3 ± 2.6	71.4 ± 2.8

Values are means ± SE

The training protocol consisted, for the first 4 weeks, of three sets of ten repetitions with an initial load of ~ 50 – 55% of the three-repetition maximum (3-RM: the maximum load that can be lifted three times only) and was then increased to 75% of the 3-RM. The training load was updated every 2 week to match it, as close as possible, to 75% of the 3-RM. It should be noticed that the three sets were interspaced by 2 mn rest during which subjects carried out 20 s length stretches of the trained muscle groups. Subjects were individually supervised during programme sessions at all times.

Testing machine

An ankle ergometer was used for the experiment. It was especially designed to test the stiffness properties of plantar flexor muscles and ankle joint (Tognella et al. 1997). Briefly, the ergometer consisted of two main units: (1) a power unit that contained the actuator, its power supply unit, position, velocity and torque transducers, and its associated electronics; and (2) a driving unit controlled by a 486 PC-type computer equipped with a specific 12-bit A/D timer board. Angular displacement was measured with an optical digital sensor, and angular velocity was captured from a resolver bound to the rotor, except for velocities $> 15.70 \text{ rad s}^{-1}$ that required a tachometer. Torque was obtained by using a strain-gauge torque transducer. Specific menu-driven software controlled all procedures and recorded mechanical variables and electromyograms (EMG) (2 kHz sampling frequency) for later analysis. Instructions were presented to the subject on an oscilloscope.

Study design

All subjects were tested at baseline. Subjects were tested again after 24 weeks of training. The control group continued their usual activities and were then tested after 24 weeks of normal activity.

During an experimental session, the subject laid comfortably, in a supine position, on an adjustable table with the left ankle placed at the anatomical position, i.e. 0 rad (with 0 rad being the perpendicularity of the ergometer footplate to the long axis of the tibia), attached rigidly to the actuator of the ankle ergometer. The horizontal bi-malleolar axis coincided with the axis of rotation of the actuator. The knee was flexed to 2.08 rad to minimize the contribution of the gastrocnemii muscles (Cresswell et al. 1995). Special shoulder holders maintained the shoulders.

Surface EMG were detected on each part of the TS and on the TA. Pairs of silver-chloride surface electrodes (recording diameter 10 mm) were pasted over the soleus (Sol), medial (GM) and lateral (GL) gastrocnemii with an interelectrode (centre-to-centre) distance of 2 cm. The low resistance ($< 5 \text{ k}\Omega$) was obtained by abrading the skin with emery paper and cleaning with alcohol.

For the Sol, recording electrodes were placed along the mid-dorsal line of the leg, about 5 cm distal from where the two heads of the gastrocnemii join the Achilles tendon. ML and GL electrodes were fixed lengthwise over the middle of the muscle belly. The ground electrode was attached to the contra lateral patella. EMGs were recorded differentially, amplified, and bandpass filtered (1–1,000 Hz).

The experimental session started with the acquisition of five maximal motor direct responses (M_{\max}) by applying a supramaximal electrical stimulus to the posterior tibial nerve with the cathode located in the poplitea fossa and the anode placed on the thigh, proximal to the patella. The stimulus intensity was adjusted so as to obtain the maximal M wave on each part of the TS. The M_{\max} was used to normalize the EMG signals and thus to account for different conditions of skin and surface electrodes impedance.

Second, three maximal voluntary contractions (MVC) in plantar flexion under isometric conditions were asked. The trial with the highest value was considered to be the effective MVC.

Finally, the elastic properties of the MT complex were assessed by means of a quick-release technique adapted for in vivo experiments (Goubel and Pertuzon 1973). Quick-release movements were performed from the neutral position, by a sudden releasing of the moving parts of the device, while the subject maintained a sub-maximal plantar flexion torque equal to 25%, 50% and 75% of MVC. Four measurements were recorded per torque level. For each trial, torque, angular displacement and angular velocity further differentiated to obtain angular acceleration, were stored for further analysis (see Fig. 1).

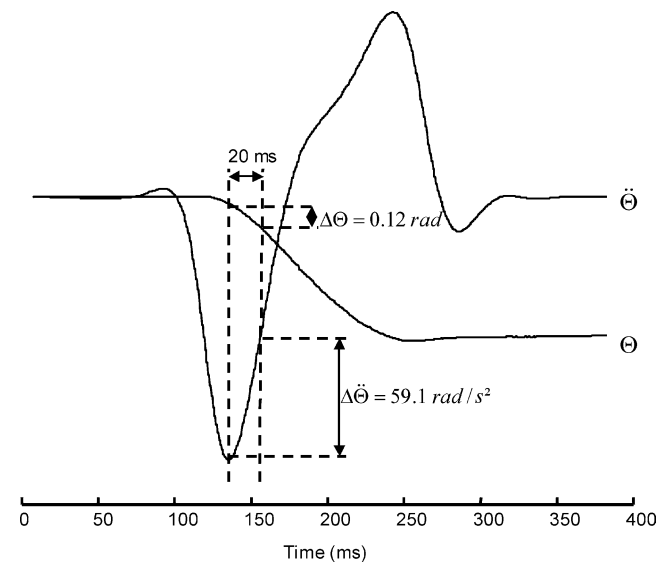


Fig. 1 Typical data for quick-release movement. Changes in acceleration ($\Delta\ddot{\theta}$) and position ($\Delta\theta$) were calculated during the first 20 ms of the movement

Data processing

The M_{\max} response was obtained by averaging five M wave records. Then, Sol, GL and GM EMG signals were rectified and summed up to get TS M_{\max} . Mean amplitude of the TS M_{\max} response ($M_{\max \text{ ampl}}$) was calculated as the ratio between TS M_{\max} area and TS M_{\max} duration (Sale et al. 1982). According to Lambertz et al. (2003), this method takes into account the polyphasic response in some of the recorded M waves of GL and GM muscles.

To construct EMG-torque relationships for the TS, the EMG signals of Sol, GL and GM were rectified and summed up to get TS activity; TS activity was expressed as mean amplitude, calculated as the ratio between the TS EMG area and duration over 200 ms isometric torque just before the quick-release movement. For subject-to-subject comparisons, TS EMG was normalized with respect to TS $M_{\max \text{ ampl}}$ and expressed in percentage ($\text{EMG}/M_{\max \text{ ampl}}$). Similar to the method proposed by Moritani and deVries (1979), TS $\text{EMG}/M_{\max \text{ ampl}}$ -torque relationships were constructed to attest possible changes in muscle activation capacities following strength training. Then, as proposed in the study of Lambertz et al. (2003), to express force output per electrical input, the inverse of the slope of these relationships gave an index of neuromuscular efficiency (NME). This NME index can be viewed as the responsiveness of muscle to neural excitation.

In the same way, TA EMG was quantified over the same duration. An index of co-activation capacities was calculated for the dorsi flexors during plantar flexion as one ratio between TA $\text{EMG}_{25\% \text{ MVC}}/\text{TS EMG}_{25\% \text{ MVC}}$ and TA $\text{EMG}_{75\% \text{ MVC}}/\text{TS EMG}_{75\% \text{ MVC}}$ (Lambertz et al. 2003).

For each level of torque, MT stiffness (S) was calculated as the ratio between variations in angular acceleration ($\ddot{\Theta}$) and angular displacement (Θ) multiplied by the corresponding inertia value (I) as expressed by the formula:

$$S = (\Delta\ddot{\Theta}/\Delta\Theta) \cdot I \quad (1)$$

In this equation, inertia (I) is calculated and assumed to be constant. This can be verified easily by considering the transition between the static phase and the dynamic phase. At this moment, static torque (T) equals dynamic torque and acceleration is maximal ($\ddot{\Theta}_{\max}$). Then:

$$T = I \cdot \ddot{\Theta}_{\max} \quad (2)$$

Series elastic component characteristics were measured at the beginning of the movement, when the elastic elements are supposed to recoil. Stiffness calculation was carried out within the first 20 ms of the movement. During this time lapse, no reflex changes in muscle activation (e.g. unloading reflex) are possible. A possible source of measurement error may be the influence of the shortening of the contractile component during the release. Nevertheless, maximal angular velocity of the release at lowest torque (25% of MVC) was higher than the maximal

shortening velocity of the adult plantar flexors found in the literature (6–7 rad s^{-1}) (Wickiewicz et al. 1984). Consequently, this high-release was higher than the maximal shortening velocity of elderly humans known to be smaller than those of young individuals (Ochala et al. 2004). This high-release should minimize the influence of a shortening of the contractile component, which could lead to an underestimation of the MT stiffness.

Then, MT stiffness was related to the corresponding isometric torque initially exerted by the subject. As in other studies (de Zee and Voigt 2001; Lambertz et al. 2001), MT stiffness was expressed in angular terms which should simplify the comparison between the groups before and following training, since no assumption about the geometry of the MT system is required. The slope of the linear angular stiffness–torque relationship so obtained was defined as the stiffness index (SI) of the SEC, i.e. the MT complex ($\text{SI}_{\text{MT-Torque}}$). Using a SI should avoid the influences of anatomical and physiological data (i.e. tendon moment arm, pennation angle, maximal voluntary contraction, cross-sectional area) for normalizing MT stiffness, making the SI as a reliable parameter to quantify changes in MT stiffness (Lambertz et al. 2003).

Musculotendinous stiffness was also related to TS myoelectrical activity to give an activation stiffness index ($\text{SI}_{\text{MT-EMG}}$), defined by the slope of the angular stiffness—TS $\text{EMG}/M_{\max \text{ ampl}}$ relationships.

Statistics

Baseline differences between the training and the control groups for the reported variables were tested using independent-samples Student's t -tests. Paired-samples Student's t -tests were used to test for differences in the 3-RM following training. Statistical analyses also included linear regression analyses to test angular stiffness–torque, TS $\text{EMG}/M_{\max \text{ ampl}}$ -torque and angular stiffness—TS $\text{EMG}/M_{\max \text{ ampl}}$. Two-factor (group \times time) ANOVA with repeated measures on time were used to compare the variables. When significant treatment effects occurred, *Tukey* post hoc tests were used to evaluate differences among means. A level of $P < 0.05$ was selected to indicate statistical significance. Values are represented as means \pm SE.

Results

No differences were found between the training group and the control group at baseline on any of the measured and calculated parameters.

Maximal force production and weight-lifting capacities

Following training, the 3-RM increased by 47% for the calf-rise exercise ($P = 0.003$) whereas maximal isometric

Table 2 Measured and estimated variables before and following the strength training and the control period

	Training group		Control group	
	Before	Following	Before	Following
Calf-rise 3-RM (kg)	34.6 ± 3.9	51.2 ± 4.4*	–	–
MVC (N m)	40.3 ± 2.1	52.4 ± 2.5*, **	39.1 ± 2.5	38.2 ± 2.8
NME Index (N m% ⁻¹)	4.48 ± 0.4	5.32 ± 0.4*, **	4.28 ± 0.4	4.44 ± 0.4
Index of co-activation	1.21 ± 0.11	1.08 ± 0.1	1.3 ± 0.13	1.24 ± 0.12
SI _{MT-Torque} (rad ⁻¹)	5.12 ± 0.31	3.83 ± 0.26*, **	5.33 ± 0.33	5.35 ± 0.31
SI _{MT-EMG} (N.m.rad ⁻¹ .% ⁻¹)	22.59 ± 0.92	20.05 ± 0.8*, **	22.12 ± 1.1	21.99 ± 1.2

Values are means ± SE

MVC maximal voluntary contraction; NME Index neuromuscular efficiency, SI_{MT-Torque} musculotendinous stiffness index; SI_{MT-EMG} activation SI. *n* training group = 14, *n* control group = 7

*Significantly different from values before training ($P < 0.05$);

**Significantly different from values of the control group at the same time ($P < 0.05$)

plantar flexion torque (MVC) only increased by 30% ($P = 0.006$). In the control group, no significant differences were found (Table 2).

EMG–torque relationships

Figure 2 illustrates typical normalized EMG–torque relationships for an individual before and following training, in which best fit was a linear regression. For each individual relationship, the correlation coefficient (r^2) was found to be significant ($0.834 < r^2 < 0.969$, $P < 0.05$). In the same way, for the population, the global normalized EMG–torque relationships gave a global coefficient of correlation equal to $r^2 = 0.583$ ($P < 0.05$) before training and equal to $r^2 = 0.608$ ($P < 0.05$) following training.

The inverse of the slope of the relationships was defined as NME index. A significant 18.6% increase in NME index was found following training ($P = 0.04$). In the control group, no significant difference was found (Table 2).

Concerning the index of co-activation, following training, no significant differences were found neither in the training group nor in the control group (Table 2).

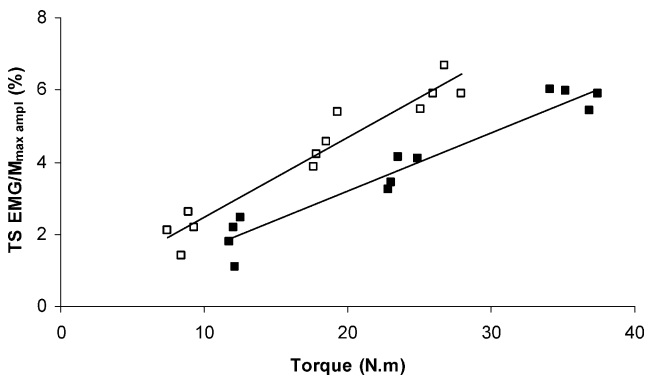


Fig. 2 Typical relationships between normalized EMG of TS and torque for a subject (S1) before (*open square*) and following training (*filled square*); the slopes are $0.22\% \text{ N}^{-1} \text{ m}^{-1}$ and $0.16\% \text{ N}^{-1} \text{ m}^{-1}$, respectively. Therefore, the inverse of the slopes, defined as NME indexes are 4.54 N m^{-1} and 6.25 N m^{-1} , respectively

Stiffness–torque relationships

Figure 3 illustrates typical angular stiffness–torque relationships for an individual before and following training. For each subject, MT stiffness increased gradually when increasing the target torque and best fit was always a linear regression ($0.814 < r^2 < 0.971$, $P < 0.05$). In the same way, for the population, the global angular stiffness–torque relationships gave a global coefficient of correlation equal to $r^2 = 0.652$ ($P < 0.05$) before training and equal to $r^2 = 0.699$ ($P < 0.05$) following training.

The slope of the angular stiffness–torque relationship, defined as SI_{MT-Torque} decreased by 25.2% following training ($P = 0.03$). In the control group, no significant difference was found (Table 2).

Stiffness–EMG relationships

Typical angular stiffness–EMG relationships are shown in Fig. 4 for an individual before and following training, in which best fit was a linear regression. For each individual relationship, the correlation coefficient (r^2) was found to be significant ($0.799 < r^2 < 0.954$, $P < 0.05$). In the same way, for the population, the global angular stiffness–EMG relationships gave a global r^2 equal to

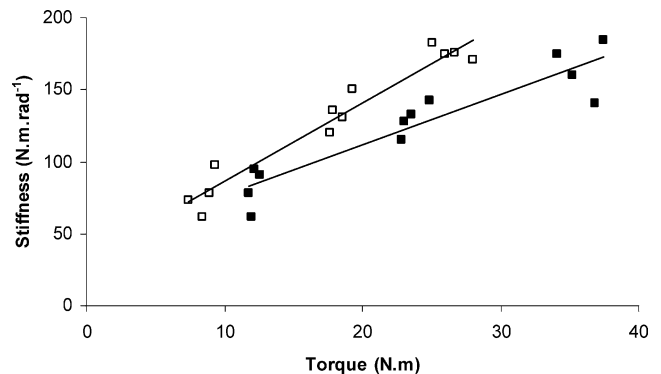


Fig. 3 Typical relationships between MT stiffness and torque for S1 before (*open square*) and following training (*filled square*); the slopes (SI_{MT-Torque}) are 5.46 rad^{-1} and 3.5 rad^{-1} , respectively

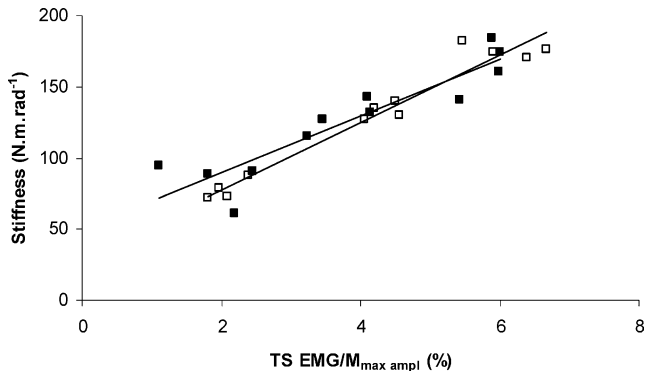


Fig. 4 Typical relationships between MT stiffness and normalized EMG of TS thanks to $M_{\max \text{ ampli}}$, for S1 before (*open square*) and following training (*filled square*); the slopes ($SI_{\text{MT-EMG}}$) are $23.43 \text{ N m rad}^{-1} \%^{-1}$ and $19.77 \text{ N m rad}^{-1} \%^{-1}$, respectively

0.574 ($P < 0.05$) before training and equal to 0.605 ($P < 0.05$) following training.

The slope of the angular stiffness–EMG relationship, defined as $SI_{\text{MT-EMG}}$ decreased by 11.2% following training ($P = 0.04$). In the control group, no significant difference was observed (Table 2).

Discussion

The first purpose of the present study was to examine the effect of 24 weeks (48 sessions) of strength training on MT stiffness of the plantar flexors in a group of elderly individuals. The second aim was to evaluate whether neural alterations have influences on MT stiffness changes following training.

Weight-lifting and maximal force production capacities

The present study confirmed that elderly adults, aged between 73 years and 83 years, positively respond to a strength-training program in terms of increments in weight-lifting capacity (average improvement per training session of 0.97% for the calf-rise exercise). This result is in agreement with the literature. In fact, for training protocol on the plantar flexors and knee extensors involving a concentric and eccentric component, the rates of dynamic force gain per training session, reported in the literature in elderly subjects (36–52 sessions) ranged from 0.37 to 1.48% (Lexell et al. 1995; Häkkinen et al. 1998; Scaglioni et al. 2002; Ferri et al. 2003; Frontera et al. 2003). Otherwise, in the present experiment, MVC gains (30%) were lower than the gains in force measured by the 3-RM on the calf-rise exercise (47%). It appears to be common that the gain in the 3-RM load is greater than that for MVC after participation in a strength-training program, which is usually interpreted to indicate a significant role for coordination in the improvement in performance (Jones and Rutherford 1987).

Maximal voluntary contractions gains following strength training in elderly individuals have been widely observed on numerous muscle groups such as elbow flexors (Lexell et al. 1995; Valour et al. 2003) and knee extensors (Häkkinen et al. 1998; Frontera et al. 2003). For instance, Häkkinen et al. (1998) found a 30% knee extension MVC increase following 52 strength training sessions. To the best of our knowledge, few studies have examined the effect of strength training on plantar flexor muscles in elderly individuals (Scaglioni et al. 2002; Ferri et al. 2003). After 48 sessions of strength training, Scaglioni et al. (2002) found a significant increase of 18% in plantar flexors MVC, while Ferri et al. (2003) observed gains of about 12.4%.

In the present study, the high gain in strength of about 30% after 24 weeks of strength training (48 sessions) can be due to muscular hypertrophy and changes in the activation capacities. As reported by, Narici et al. (1996), differences in muscle size account for only about the half of the differences in strength between young individuals. According to the literature, adaptations within the nervous system, such as activation capacities, may occur during the first few weeks of training in elderly individuals (Häkkinen et al. 1998) and muscle hypertrophy may appear later in the process (Frontera et al. 2003).

MT stiffness and training

The present study reported for the first time, changes in the MT SI of the plantar flexors of elderly individuals, by means of a quick-release technique. Such an index has already allowed for detecting changes in MT stiffness in ageing. In fact, elderly individuals appear to have higher MT SIs than young subjects on plantar flexors (Ochala et al. 2004) as well as on elbow flexors (Valour and Pousson 2003).

In the present experiment, $SI_{\text{MT-Torque}}$ values decreased following 24 weeks of strength training. This result is in accordance with the results obtained by using a free-oscillation method (Blanpied and Smidt 1993). Figure 5 summarizes the behaviour of $SI_{\text{MT-Torque}}$ values for several groups of different ages. Figure 5 refers to data from the present experiment and from another study of our laboratory (Ochala et al. 2004). Ochala et al. (2004) used the same device and experimental conditions but only tested two groups of men: one termed “young group” ($n = 12$, 21.7 ± 1.5 years) and another termed “older group” ($n = 11$, 67.9 ± 3.6 years). Nevertheless, it seems that following training, $SI_{\text{MT-Torque}}$ values become closer to values of younger individuals. The smaller $SI_{\text{MT-Torque}}$ values observed following training in the present study might counterbalance the effect of ageing known to induce an increase in $SI_{\text{MT-Torque}}$ values.

Such a decrease in $SI_{\text{MT-Torque}}$ may suggest differences in MT tissues stiffness following training. Since MT stiffness characterizes the stiffness properties of the active and the passive fraction of the SEC, changes may

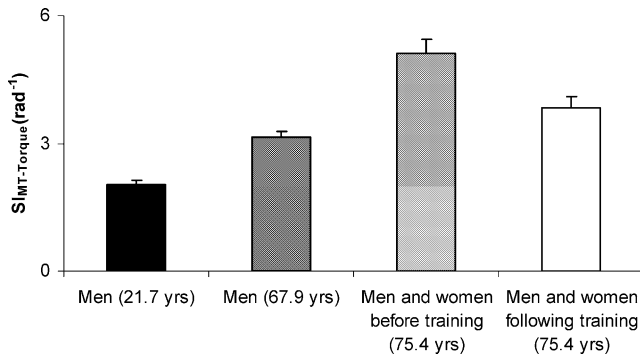


Fig. 5 Comparison of $SI_{MT-Torque}$ values between several groups of different ages. Data from the present experiment and from another study of our laboratory using the same device and experimental conditions (Ochala et al. 2004) are presented. Nevertheless, Ochala et al. (2004) only tested two groups of men

exist in the stiffness properties of both fractions. Indeed, Pousson et al. (1990) reported an increase in MT stiffness after a period of eccentric strength training in young adults, whereas Poulain and Pertuzon (1988) reported the opposite evolution after a period of concentric training, i.e. a decrease in MT stiffness. These opposite changes in MT stiffness were discussed in terms of opposite adaptation of the active and the passive fraction of the SEC.

Concerning the SEC active fraction, some experiments have examined the effect of strength training on muscles in elderly people at the single fibre level and observed some differences in the contractile properties (Trappe et al. 2000, 2001; Frontera et al. 2003). For instance, after 36 sessions of high-intensity resistance training in men, Trappe et al. (2000) observed large increases in single cell specific force, maximal unloaded shortening velocity and peak power of slow- and fast-twitch fibres, expressing MHC I and IIa isoforms, respectively. Unfortunately, no one has raised the question of investigating changes in the stiffness properties of muscle fibres following high-intensity resistance training in elderly individuals. Nevertheless, it is well known that muscle fibres, which have different contractile properties such as unloaded shortening velocity, may well also have different stiffness properties (Toursel et al. 1999). In fact, according to Toursel et al. (1999), fast-twitch fibres may have a bigger unloaded shortening velocity and may be less stiff than slow-twitch fibres.

With regard to the passive SEC properties, which are composed of tendon, aponeurosis and intramuscular connective tissue, controversial results have been found. A study in humans showed that patella tendons became stiffer following a strength training of 42 sessions in elderly individuals by using ultrasonography technique (Reeves et al. 2003). However, as reported by Kubo et al. (2003), low-load resistance training in elderly people showed no significant changes in tendinous elastic properties of the vastus lateralis. These differences in tendinous stiffness might be due to the duration and intensity of training. In fact, it is well known that in

animals changes in tendinous structures can be only obtained after a long-term training (e.g. Woo et al. 1980). In young subjects, long-duration isometric training seems to have the strongest effect on changes on tendon stiffness of the gastrocnemius medialis (Kubo et al. 2001a) when compared to resistance training (Kubo et al. 2002). Whatever the case, it seems to be obvious that hyper-solicitation led to increases in tendon stiffness.

Taking these results into consideration, it appears that the active and the passive fraction of the SEC might be affected differently by strength training. Furthermore, the decrease in $SI_{MT-Torque}$ values observed in the present experiment may be due to modifications of intrinsic properties of muscle fibres, induced by the predominately concentric action of the present training period.

Influence of neural alterations on MT stiffness

In the present study, the increase in NME index supports the hypothesis of changes in the recruitment patterns of voluntary activated muscles. It should reflect an improvement in muscle control to maintain the target torque in post-training conditions, leading to a lower co-activation. Controversial results have already been observed in the literature in co-activation values during maximal contractions as an effect of strength training in elderly people (Häkkinen et al. 1998; Reeves et al. 2003). After 52 sessions of strength training, Häkkinen et al. (1998) found a significant decrease of 22% in knee flexors co-activation, while Reeves et al. (2003) observed no significant difference after 42 sessions. It is possible that differences in the training protocol, i.e. number of sessions, weight-lifting loads, could account for the variability in co-activation results in the literature. In the present experiment, no statistically significant differences in co-activation index values were found during sub-maximal maintained torques following training. However, the co-activation index is the ratio between antagonist EMG and agonist EMG and it can be supposed that subjects co-activated less the antagonist muscles in post-training conditions, since the NME index increased (see above). Consequently, since MT release occurs against the resistance of the agonist and antagonist muscles (de Zee and Voigt 2002), these changes in the agonist and antagonist EMG may explain in part the observed decrease in $SI_{MT-Torque}$ values following training in elderly subjects.

Therefore, in this study, MT stiffness has been related to normalized TS EMG, in order to overcome the influence of the muscle activation capacities (Lambertz et al. 2003). By using such an approach, SI_{MT-EMG} only decreased by 11.2% following training, compared to the 25.2% $SI_{MT-Torque}$ decrease. This smaller decrease in SI_{MT-EMG} compared to $SI_{MT-Torque}$ may confirm that the changes in $SI_{MT-Torque}$ may not only be due to peripheral adaptations but also to neural alterations.

In conclusion, the present study has demonstrated that the 24-week strength-training program may be an effective stimulus to counterbalance some effects of the neuromuscular system ageing, i.e. modifications of contractile and elastic properties of the MT system. It has improved the force of the plantar flexor muscles and induced a decrease in MT SI. MT stiffness changes occurring following the present training would not only be due to peripheral alterations but also to neural modifications.

Acknowledgements The authors thank Yves Ballay for technical assistance and the participants in the Better Ageing program. This work was supported by grants from the European Commission (Framework Program V, QLRT-2001-00323).

References

- Blanpied P, Smidt GL (1993) The difference in stiffness of the active plantar flexors between young and elderly human females. *J Gerontol* 48:58–63
- Cresswell AG, Loscher WN, Thorstensson A (1995) Influence of gastrocnemius muscle length on triceps surae torque development and electromyographic activity in man. *Exp Brain Res* 105:283–290
- Ferri A, Scaglioni G, Pousson M, Capodaglio P, Van Hoecke J, Narici MV (2003) Strength and power changes of the human plantar flexors and knee extensors in response to resistance training in old age. *Acta Physiol Scand* 177:69–78
- Frontera WR, Hughes VA, Krivickas LS, Kim SK, Foldvari M, Roubenoff R (2003) Strength training in older women: early and late changes in whole muscle and single cells. *Muscle Nerve* 28:601–608
- Goubel F, Pertuzon E (1973) Evaluation de l'élasticité du muscle in situ par une méthode de quick-release. *Arch Int Physiol Biochim Biophys* 81:697–707
- Häkkinen K, Kallinen M, Izquierdo M, Jokelainen K, Lassila H, Malkia E, Kraemer WJ, Newton RU, Allen M (1998) Changes in agonist-antagonist EMG, muscle CSA, and force during strength training in middle-aged and older people. *J Appl Physiol* 84:1341–1349
- Hill AV. (1950) The series elastic component of muscle. *Proc R Soc Lond B Biol Sci* 137:273–280
- Huxley AF, Simmons RM. (1971) Mechanical properties of the cross-bridges of frog striated muscle. *J Physiol (Lond)* 218:59–60
- Jones DA, Rutherford OM. (1987) Human muscle strength training: the effects of three different regimens and the nature of the resultant changes. *J Physiol (Lond)* 391:1–11
- Kubo K, Kanehisa H, Ito M, Fukunaga T (2001a) Effects of isometric training on the elasticity of human tendon structures in vivo. *J Appl Physiol* 91:26–32
- Kubo K, Kanehisa H, Fukunaga T (2001b) Effects of different duration isometric contractions on tendon elasticity in human quadriceps muscles. *J Physiol* 536:649–655
- Kubo K, Kanehisa H, Fukunaga T (2002) Effects of resistance and stretching training programmes on the viscoelastic properties of human tendon structures in vivo. *J Physiol* 538:219–226
- Kubo K, Kanehisa H, Miyatani M, Tachi M, Fukunaga T (2003) Effect of low-load resistance training on the tendon properties in middle-aged and elderly women. *Acta Physiol Scand* 178:25–32
- Lambertz D, Perot C, Kaspranski R, Goubel F (2001) Effects of long-term spaceflight on mechanical properties of muscles in humans. *J Appl Physiol* 90:179–188
- Lambertz D, Mora I, Grosset JF, Perot C (2003) An evaluation of musculo-tendinous stiffness in prepubertal children and adults, taking into account muscle activity. *J Appl Physiol* 95:64–72
- Lexell J, Downham DY, Larsson Y, Bruhn E, Morsing B (1995) Heavy-resistance training in older Scandinavian men and women: short- and long-term effects on arm and leg muscles. *Scand J Med Sci Sports* 5:329–341
- Moritani T, deVries HA. (1979) Neural factors versus hypertrophy in the time course of muscle strength gain. *Am J Phys Med* 58:115–130
- Narici MV, Hoppeler H, Kayser B, Landoni L, Claassen H, Gavaardi C, Conti M, Cerretelli P (1996) Human quadriceps cross-sectional area, torque and neural activation during 6 months strength training. *Acta Physiol Scand* 157:175–186
- Ochala J, Lambertz D, Pousson M, Goubel F, Van Hoecke J (2004) Changes in mechanical properties of human plantar flexor muscles in ageing. *Exp Gerontol* 39:349–358
- Poullain P, Pertuzon E (1988) Etude comparative des effets de trois méthodes de musculation sur les propriétés contractiles et élastiques du muscle. *Ann Kinesi ther* 15:167–177
- Pousson M, Van Hoecke J, Goubel F (1990) Changes in elastic characteristics of human muscle induced by eccentric exercise. *J Biomech* 23:343–348
- Reeves ND, Narici MV, Maganaris CN (2003) Strength training alters the viscoelastic properties of tendons in elderly humans. *Muscle Nerve* 28:74–81
- Sale DG (1988) Neural adaptation to resistance training. *Med Sci Sports Exerc* 20:135–145
- Sale D, Quinlan J, Marsh E, McComas AJ, Belanger AY (1982) Influence of joint position on ankle plantar flexion in humans. *J Appl Physiol* 52:1636–1642
- Scaglioni G, Ferri A, Minetti AE, Martin A, Van Hoecke J, Capodaglio P, Sartorio A, Narici MV. (2002) Plantar flexor activation capacity and H reflex in older adults: adaptations to strength training. *J Appl Physiol* 92:2292–2302
- Tognella F, Mainar A, Vanhoutte C, Goubel F (1997) A mechanical device for studying mechanical properties of human muscles in vivo. *J Biomech* 30:1077–1080
- Toursel T, Stevens L, Mounier Y (1999) Evolution of contractile and elastic properties of rat soleus muscle fibres under unloading conditions. *Exp Physiol* 84:93–107
- Trappe S, Williamson D, Godard M, Porter D, Rowden G, Costill D (2000) Effect of resistance training on single muscle fiber contractile function in older men. *J Appl Physiol* 89:143–152
- Trappe S, Godard M, Gallagher P, Carroll C, Rowden G, Porter D (2001) Resistance training improves single muscle fiber contractile function in older women. *Am J Physiol Cell Physiol* 28:398–406
- Valour D, Pousson M (2003) Compliance changes of the series elastic component of elbow flexor muscles with age in humans. *Pflugers Arch* 445:721–727
- Wickiewicz TL, Roy RR, Powell PL, Perrine JJ, Edgerton VR (1984) Muscle architecture and force-velocity relationships in humans. *J Appl Physiol* 57:435–443
- Woo SL, Ritter MA, Amiel D, Sanders TM, Gomez MA, Kuei SC, Garfin SR, Akeson WH (1980) The biomechanical and biochemical properties of swine tendons—long term effects of exercise on the digital extensors. *Connect Tissue Res* 7:177–183
- de Zee M, Voigt M (2001) Moment dependency of the series elastic stiffness in the human plantar flexors measured in vivo. *J Biomech* 34:1399–1406
- de Zee M, Voigt M (2002) Assessment of functional series elastic stiffness of human dorsiflexors with fast controlled releases. *J Appl Physiol* 93:324–329