AGE-RELATED CHANGES IN CONTRACTILE PROPERTIES OF PLANTAR FLEXOR MUSCLES IN PHYSICALLY ACTIVE WOMEN

Saima Kuu[1], Jaan Ereline[1], Helena Gapeyeva[1], Ivo Kolts[2] and Mati Pääsuke[1]

[1]Institute of Exercise Biology and Physiotherapy, University of Tartu, Estonia
[2]Institute of Anatomy, University of Tartu, Estonia

Original scientific paper
UDC 611.7:796.15:369-055.2

Abstract:

Twitch contractile properties of the plantar flexor muscles were compared between the groups of women of the 3rd, 5th, 6th and 8th decade participating in regular recreational physical activity. An isometric twitch was evoked by supramaximal electrical stimulation of the tibial nerve in the popliteal fossa by a rectangular pulse of 1 millisecond duration. A significant decrease was found in the twitch peak force, the maximal rates of force development and relaxation from the 6th decade onwards. A significant prolongation in twitch contraction time was observed from the 5th decade onwards. The 3rd decade group showed a significant post-activation potentiation, while the three older groups did not. No significant age-related changes were observed in the isometric twitch peak force and voluntary strength ratio, and the twitch half-relaxation time in women participating in regular recreational physical activity. It was concluded that the marked decrease in twitch force-potentiation and prolongation of the contraction time of the plantar flexor muscles in physically active women seem to begin after 40 years of age, while a reduction in the maximal voluntary and twitch force-generating capacity, and twitch contraction kinetics occurs after 50 years of age.

Key words: *ageing, human skeletal muscles, isometric twitch, physical activity*

ALTERSBEDINGTE ÄNDERUNGEN IN KONTRAKTILEN EIGENSCHAFTEN DER PLANTARFLEXOR MUSKELN BEI PHYSISCH AKTIVEN FRAUEN

Zusammenfassung:

Einzelkontraktile Eigenschaften von M. triceps surae wurden zwischen den Frauengruppen der 3., 5., 6. und 8. Lebensdekade, die regelmäßig physisch aktiv waren, verglichen. Die isometrische Einzelkontraktion wurde mit supramaximaler elektrischer Stimulation des N. tibialis in der Fossa Poplitea bei Rechteckimpulse von 1 ms Dauerhaftigkeit erreicht. Der wesentliche Fall der Einzelkontraktion bei Maximalkraft im maximalen Kraftgradient und im Relaxiongradient wurde ab 6. Dekade und die Erscheinung der Kontraktionszeitverlängerung ab 5. Dekade gefunden. Bei der Gruppe der 3. Dekade erschien die wesentliche postaktive Potensierung, bei den 3 älteren Gruppen wurde diese Erscheinung nicht gefunden. Bei körperlich aktiven Frauen wurden keine wesentlichen Alterserscheinungen sowohl bei maximaler Kraft der Einzelkontraktionen und bei willkürlicher Kraft als auch bei Einzelkontraktion in der Halbentspannungszeit gefunden. Zusammengefasst ergibt sich daraus, dass der wesentliche Fall bei der Fähigkeit des Kraftgenerierens und die Verlängerung der Kontraktionszeit bei physisch aktiven Frauen nach dem 40. Lebensjahr erschienen, wobei der Fall der willkürlichen maximalen Kraft und bei der postaktiven Potensierung der Einzelkontraktion erst nach dem 50. Lebensjahr erscheint.

Schlüsselwörter: *Alterung, Skelettmuskeln, isometrische Einzelkontraktion*

Introduction

A reduced force-generating capacity and speed of contraction of the skeletal muscles has been observed with ageing (Davies & White, 1983; Vandervoort & Hayes, 1989; Häkkinen et al., 1998). There have been numerous studies indicating the age-related decrease in voluntary isometric strength or isokinetic peak torque of the human muscles. The decrease in muscle force-generating capacity with increasing age has been attributed to the reduction in muscle mass (sarcopenia) which is related, possibly, to alterations in hormonal

balance (Häkkinen & Pakarinen, 1993) and the decline in physical activity (Mälkiä, Impivaara, Heliövaara, & Maatela, 1994). A marked change in electrically evoked twitch contractile properties of the human skeletal muscles, which can be used as a direct measure of the force-generating and force-potentiation capacity, speed of contraction and relaxation of the muscle fibers, is also a typical feature of ageing (McDonagh, White, & Davies, 1984; Vandervoort & McComas, 1986; Pääsuke, Ereline, Gapeyeva, Sander, & Sirkel, 2002).

The force of an electrically evoked twitch is greater after a brief maximal voluntary contraction (MVC) compared with the corresponding value at rest and this enhancement has been termed the post-activation potentiation (PAP) (Vandervoort, Hayes, & Belanger, 1986; Hamada, Sale, MacDougall, & Tarnopolsky, 2000). PAP of human skeletal muscles has been measured in respect to childhood and adolescence (Belanger & McComas, 1989; Pääsuke, Ereline, & Gapeyeva, 2000). A decrease in PAP with ageing has been reported (Vandervoort & McComas, 1986; Petrella, Cunningham, Vandervoort, & Paterson, 1989; Pääsuke, Ereline, Gapeyeva, & Maamägi, 2001; Pääsuke et al., 2002), yet it is not clear at which age this impairment begins and how it is related with habitual physical activity.

There is explicit evidence that physical inactivity leads to faster and greater sarcopenia and loss of muscle strength than occurs in physically active elders (Roubenoff, 2001). However, the extent to which the age-related decline in the different characteristics of muscle function (activation, contractile properties, metabolic capacity) is due to a decrease in habitual physical activity level, rather than ageing *per se*, has not been sufficiently explained. Less information is available in age-related differences in the twitch contractile properties of skeletal muscles, including PAP in subjects with regular physical activity.

The aim of this study was to measure the effect of ageing on the twitch contractile properties of the skeletal muscles in women with regular recreational physical activity. The isometric voluntary strength and supramaximal twitch characteristics were compared among groups of physically active female subjects of the 3rd, 5th, 6th and 8th decade. Recordings were taken from the plantar flexor (PF) muscles which are important in posture and movement and are involved in many work-related and sporting activities.

Methods

Subjects

A total of 49 women agreed to participate in the present study. The subjects were divided into 4 age groups: the 3rd decade group (aged 20-25 years, n=13), 5th decade group (aged 40-49 years, n=12), 6th decade group (aged 50-59 years, n=11) and 8th decade group (aged 70-77 years, n=13). The physical characteristics of the subjects are presented in Table 1. The subjects were screened by a questionnaire to exclude those with diagnosed musculoskeletal and cardiovascular disorders. They were interviewed about their occupational and leisure time physical activity. All subjects were recreationally physically active. The young (the 3rd decade) subjects were all physically fit university students and they exercised regularly in groups for volleyball, basketball or aerobic gymnastics two to three times per week. The middle-aged (the 5th and 6th decade) subjects exercised in groups for volleyball or aerobic gymnastics two times per week, and older (the 8th decade) subjects exercised in groups of aerobic gymnastics two times per week. However, none of them had any background in competitive sports of any kind. The older people all lived at home and performed their activities of daily life independently. All the subjects were informed of the procedures to be utilized as well as the purpose of the study and their written informed consent for participation was obtained. The study carried the approval of the University Ethics Committee.

Experimental protocol

The subjects sat on a specially designed chair with the dominant leg flexed to 90° at the knee and mounted inside a metal frame (Pääsuke et al., 2000). The foot was connected to an aluminium footplate by nonelastic Velcro straps at three locations. The inclination of the foot could be altered by rotating the footplate about an axis that corresponded to that of the ankle joint, i.e. the medial malleolus. The ankle was dorsiflexed to 20° to ensure maximal voluntary and stimulated forces, the situation presumably corresponding to the "optimal" muscle length (Sale, Quinlan, Marsh, McComas, & Belanger, 1982). An adjustable pad held down the kneecap and the front side of the thigh. A strain-gauge transducer (0.5% accuracy) was connected to the footplate by a rigid bar which sensed the forces acting on the footplate. Signals from the strain-gauge transducers were linear from 10 to 1600 N. The point of application of force to the footplate was located on articulation regions between the metatarsus and ossa digitorum pedis. The force signals were sampled at the frequency of 1 kHz and stored on a computer hard disk. The reproducibility of the force measurements was calculated with repeated static loads on the footplate.

Twenty-four to 48 hours before data collecting the subjects were given instructions and the testing of the isometric voluntary strength of PF muscles and electrical stimulation procedures were demonstrated. This was followed by a practice session to familiarize the subjects with the procedures. The

determination of the subject's dominant leg was based on a kicking preference.

To measure the isometric voluntary strength of PF muscles, the subjects were instructed to push the footplate as forcefully as possible for 2-3 seconds. Verbal encouragement and visual feedback were used to motivate the subjects. The greatest force of the three maximal efforts was taken as the isometric voluntary strength. A rest of 2 minutes was allowed between each of the three attempts.

To determine the contractile properties of PF muscles during an isometric twitch, the posterior tibial nerve was stimulated through a pair of 2 mm thick, self-adhesive electrodes (Medicompex SA, Ecublens, Switzerland). The cathode (5 x 5 cm) was placed over the tibial nerve in the popliteal fossa and the anode (5 x 10 cm) was placed under the posterior-medial side of the thigh. Supramaximal rectangular pulses of 1 ms duration were delivered from an isolated voltage stimulator Medicor MG-440 (Budapest, Hungary).

During the isometric twitch recording the stimulus intensity varied from approximately 25 V to supramaximal (130-150 V) in increments of 30%--50%. Single stimuli were given at 30-second intervals and the voltage was increased in increments of 20-25 V until supramaximal twitches were reached. To determine the supramaximal stimulation intensity, the voltage of the rectangular electrical pulse was progressively increased to obtain a plateau in the twitch force, i.e. when the twitch force failed to increase despite any additional increases in the stimulation intensity. The supramaximal isometric twitches of PF muscles were elicited after the subject had rested for 15 minutes. After the resting twitch had been recorded, the subject was instructed to hold a MVC for 5 seconds and then to relax. A second (potentiated) twitch took place within 1 second after the onset of relaxation. The skin temperature of the muscle group tested was continously controlled and maintained at 35°C using an infrared lamp. The following characteristics of the isometric twitch were calculated: twitch peak force (PT) - the highest value of isometric force production, contraction time (CT) - the time to twitch peak force, half-relaxation time (HRT) - the time of half of the decline in twitch peak force, maximal rate of force development (RFD) – the first derivate of the development of force (dF/dt) and maximal rate of relaxation (RR) as the first derivate of the decline of force (-dF/dt). The percentage increase in the potentiated twitch PT in relation to that at rest was taken as an indicator of PAP. The order of the test was as follows: twitch at rest, MVC and the potentiated twitch. The resting twitch PT was expressed as a ratio to the voluntary strength.

Statistical analysis

The data used were the means and standard errors (±SE). A one-factor ANOVA with a Tukey's *post hoc* test was used to compare the anthropometric parameters, isometric voluntary strength and twitch contractile characteristics between the groups. A level of $p<0.05$ was selected to indicate statistical significance.

Results

Anthropometric characteristics and isometric voluntary strength

The youngest (the 3rd decade) female group had greater ($p<0.05$) body height than each of the three older (the 5th, 6th and 8th decade) groups, while no significant differences between these older groups were observed (Table 1). The youngest (the 3rd decade) group had a smaller ($p<0.05$) body mass than either of the 6th and 8th decade groups. Body mass in the 3rd and 5th decade groups did not differ significantly. The body mass index was smaller ($p<0.05$) in the 3rd decade group compared to the other groups. There were no significant differences in body mass and body mass index between the 5th, 6th and 8th decade groups. The isometric voluntary strength of PF muscles in the 3rd decade female group was greater ($p<0.05$) than in the 6th and 8th decade group. The 5th decade group had greater ($p<0.05$) isometric voluntary strength than the 8th decade group. There were no significant differences in the isometric voluntary strength between the two younger and two older groups.

Twitch characteristics

Isometric twitch contractile characteristics of PF muscles in women with increasing age are presented in Table 2. Explicit decrements of the iso-

Table 1. Age and physical characteristics of the subjects (mean ± SE)

Groups	n	Age (yr)	Height (cm)	Body mass (kg)	BMI ($kg \cdot m^{-2}$)
3rd decade	13	20.4 ± 0.2	170.0 ± 1.4	60.2 ± 1.4	20.8 ± 0.4
5th decade	12	44.3 ± 0.9	163.9 ± 1.3*	64.7 ± 3.2	24.0 ± 1.0*
6th decade	11	54.7 ± 0.9	163.7 ± 1.7*	67.8 ± 1.7*	25.5 ± 0.8*
8th decade	13	72.4 ± 0.6	160.4 ± 1.8*	64.7 ± 1.7*	25.1 ± 0.6*

Legend: BMI = body mass index; * significant difference ($p<0.05$) compared with the 3rd decade group; n = number of subjects

Table 2. Twitch contractile characteristics and isometric voluntary strength of the plantar flexor muscles in physically active women at different ages (mean ± SE)

Variables	Groups			
	3rd decade n = 13	5th decade n = 12	6th decade n = 11	8th decade n = 13
PT (N)	104.5 ± 5.0	98.7 ± 7.4	81.0 ± 6.8 *	73.2 ± 5.7#
Strength (N)	842 ± 42	734 ± 45	608 ± 43*	489 ± 41#
PT/strength (%)	12.4 ± 0.8	13.4 ± 1.0	13.3 ± 1.7	15.1 ± 1.6
CT (ms)	111.5 ± 5.2	140.4 ± 5.0*	137.9 ± 4.3 *	140.5 ± 4.6*
HRT (ms)	98.7 ± 4.7	100.4 ± 5.2	103.3 ± 5.9	105.8 ± 5.2
RFD (N • s^{-1})	1512 ± 97	1221 ± 127	1046 ± 90 *	929 ± 86 *
RR (N • s^{-1})	813 ± 52	716 ± 76	617 ± 51 *	491 ± 56 #
PAP (%)	123.2 ± 3.9 +	113.9 ± 3.1	116.0 ± 2.7	111.2 ± 2.2 *

Legend: PT = twitch peak force, CT = twitch contraction time, HRT = twitch half-relaxation time, RFD = twitch maximal rate of force development, RR = twitch maximal rate of relaxation; * denotes significant difference ($p<0.05$) compared with the 3rd decade group; # denotes significant difference ($p<0.05$) compared with the 3rd and 5th decade groups; + denotes significant difference ($p<0.05$) compared with resting twitch value.

metric twitch PT were found in relation to increasing age. The mean value of the twitch PT in the 3rd decade group was greater ($p<0.05$) than in the 6th and 8th decade group. The 5th decade group had a greater ($p<0.05$) twitch PT than the 8th decade group. The differences in the twitch PT between the two younger and two older groups were not significant. There were no significant differences in the twitch PT/voluntary strength ratio between the groups.

A prolongation in the isometric twitch CT with increasing age was observed. The mean values of the twitch CT in the youngest group was shorter ($p<0.05$) than those of the three older groups. The differences in the twitch CT between the 5th, 6th and 8th decade groups were not significant. There were no significant differences in the mean values of the twitch HRT between the measured age groups. The isometric twitch maximal RFD and RR decreased with age. The mean value of the twitch maximal RFD in the 3rd decade group was greater ($p<0.05$) than in the 6th and 8th decade groups. The differences in the twitch maximal RFD between the two younger and two older groups were not significant. The mean value of the twitch maximal RR in the 8th decade group was less ($p<0.05$) than that of the two younger groups. Twitch maximal RR in the 3rd decade group was greater ($p<0.05$) compared with the 6th decade group. The differences in the twitch maximal RR between two younger groups and two older groups were not significant. There were no significant differences in the twitch RR in the 6th decade group compared with the 5th decade group. PAP was significant ($p<0.05$) only for the youngest group, whereas for the three older groups PAP was not significant. The 3rd decade group had greater ($p<0.05$) PAP than the 8th decade group, whereas the differences in PAP between the 3rd, 5th and 6th decade groups were not significant. PAP in the 8th decade group did not differ significantly compared with the 5th and 6th decade groups.

Discussion and conclusions

The present study demonstrated that a marked age-related reduction in isometric voluntary and electrically evoked twitch force-generating capacity of PF muscles in physically active women begins after the age of 50 years. The results indicated that women from the 6th and 8th decade groups produced significantly less isometric voluntary strength and evoked twitch PT than the youngest groups of women. The decrease in the muscle force-generating capacity with increasing age has been attributed to the reduction in muscle mass. It has been shown that a reduced muscle mass in older subjects is associated with a decreased number and a selective atrophy of fast-twitch muscle fibres (Aoyagi & Shephard, 1992; Lexell & Downham, 1992). In the present study the 6th and 8th decade groups had significantly higher body mass than did the 3rd decade group. Rice and assosiates (1989) found markedly more non-muscle tissue in the PF muscles of older people. Because of this age-related infiltration of fat and connective tissue, the reduction in muscle contractile tissue is greater than the actual reduction in muscle volume and muscle cross-sectional area. Thus, the age-related changes in the muscle force-generating capacity can be partly explained by differences in body composition.

It has been observed that a decline in isometric voluntary strength with ageing may be accompanied by a decrease in the capacity for the neural activation of the muscles (Doherty, Vandervoort, & Brown, 1993; Stevens, Binder-Macleod, & Snyder-Mackler, 2001). However, the present study indicated no significant differences in twitch PT/voluntary strength ratio in physically active women with increasing age. It was observed that healthy older

adults exhibit no loss of muscle activation as compared to young subjects of similar physical activity level (Kent-Braun & Ng, 1999). Thus, the regular physical activity can prevent a marked decrease in neural activation of the muscles in older subjects. Loss of isometric voluntary strength in highly motivated older subjects is a clear indicator of reduced muscle mass (Vandervoort & McComas, 1986).

In the present study, the youngest (the 3rd decade) women showed a significant PAP of PF muscles after 5-s MVC, while the middle-aged and elderly women did not. These results are in agreement with our previous study which indicated that PAP of PF muscles for the young (the 3rd decade) men was significant, whereas no significant PAP has been observed for men aged 52-63 years (Pääsuke et al., 2001). The present results demonstrated that PAP in recreationally physically active older (the 8th decade) women was markedly reduced, while in middle-aged women (the 5th and 6th decade) PAP did not decrease compared to young women. Our previous results suggest a significant reduction in PAP of PF muscles in habitually physically active middle-aged (40-49-year-old) and older (70-77-year-old) women as compared to young women (Pääsuke et al., 2002). The PF muscle group is composed of the soleus and the two heads of gastrocnemius muscle. The histochemical analyses of human skeletal muscles obtained by biopsy or at autopsy have shown that the gastrocnemius is a mixed muscle with approximately equal proportions of slow-twitch (type I) and fast-twitch (type II) fibres while the soleus has primarily slow-twitch fibres (Edgerton, Smith, & Simpson, 1975; Shorey & Cleland, 1988). Petrella and associates (1989) have shown that the older (the 8th decade) men had similar PAP in the gastrocnemius muscle, but reduced and prolonged twitch in comparison to young adults. However, the contractile characteristics of the PF muscle group, studied as a whole, show changes with ageing toward a reduced capacity for twitch PAP (Vandervoort & McComas, 1986), possibly reflecting a selective atrophy of the fast-twitch muscle fibres with ageing (Larsson, Grimby, & Karlsson, 1979; Lexell & Downham, 1992).

The mechanism responsible for PAP is considered to be phosphorylation of myosin regulatory light chains (R-LC) during the MVC, which renders actin-myosin more sensitive to Ca^{2+} in a subsequent twitch (Grange, Vandenboom, & Houston, 1993; Sweeney, Bowman, & Stull, 1993). The phosphorylation of myosin R-LC in human skeletal muscle has been observed in response to brief maximal contractions (Houston, Green, & Stull, 1985). Myosin R-LC phosphorylation has been thought to produce a twitch potentiation by measuring the force development for any given submaximal intracellular Ca^{2+} level (Klug, Botterman, & Stull, 1982; MacIntosh & Gardiner, 1987). It has been proposed that the phosphorylation of myosin R-LC increases the possibility that cross-bridges will enter the force-producting state, resulting in a higher proportion of active cross-bridges at any given time during a twitch (Persechini, Stull, & Cooke, 1985; Levine, Kensler, Yang, Stull, & Sweeney, 1996). The present study demonstrated that a decrease of isometric twitch force-potentiation capacity of PF muscles in physically active women begins after the age of 40.

This study agreed with the previously mentioned studies that reported a prolonged electrically evoked isometric twitch CT of ageing muscles (McDonagh, White, & Davies, 1984; Vandervoort & Hayes, 1989). The twitch CT for the youngest female group was significantly shorter than that of the three older female groups. The time course of the isometric twitches has been found to depend on the kinetics of the excitation-contraction coupling mechanisms, including intracellular Ca^{2+} movements (Klug, Botterman, & Stull, 1982). The prolonged twitch CT of the older individuals suggests a decreased efficiency in the function of the sarcoplasmic reticulum to release Ca^{2+} (Klitgaard, Ausoni, & Damiani, 1989).

In the present study, subjects from the two older female groups produced significantly less isometric twitch maximal RFD than the youngest group of subjects. The twitch RFD has rarely been used as an indicator of contraction speed which depends largely on the rate of formation of cross-bridges between myosin and actin (Lewis, Al-Amood, & Rosendorff, 1986). The decreased RFD has been called early depression and the kinetics of Ca^{2+}-release and binding to troponin have been accounted for by this phenomenon. It has been shown that slower contraction speed in the elderly muscles is caused by the selective atrophy of fast twitch muscle fibres (Larsson, Grimby, & Karlsson, 1979).

Contrary to many earlier reports (McDonagh, White, & Davies, 1984; Petrella et al., 1989; Vandervoort & Hayes, 1989), the results of this study indicated no significant age-related differences in the twitch HRT of the PF muscles in physically active women. However, a marked decrease in twitch RR (-dF/dt) in the 6th and 8th decade female groups compared with the 3rd decade female group was observed. Twitch RR for the 5th decade group was also greater than that of the 8th decade group. A similar finding has also been reported for the quadriceps femoris muscle (Hunter et al., 1999). Two main factors are responsible for the rate of muscle relaxation: sarcoplasmic reticulum Ca^{2+} uptake and the rate of cross-bridge kinetics (Westerblad, Lännegren, & Allen, 1997). It has been shown that the decreased rate of relaxation in elderly muscles is an indicator of reduced efficiency of the sarcoplasmic reticulum to re-uptake Ca^{2+} (Klitgaard, Ausoni, & Damiani, 1989).

Age-related changes in twitch contractile characteristics can also be related with the series elastic component (SEC) of muscles, which consists of passive (tendon) and active (cross-bridges) elements (Fukashiro, Itoh, Ichinose, Kawakami, & Fukunaga, 1995). Ageing is associated with the changed stiffness of connective tissue (Shadwich, 1990). A more compliant SEC in the muscles tends to decrease the twitch force because the relatively brief active state associated with a twitch is not long enough for their more compliant SEC to be fully stretched so as to effectively transit force through the tendon to the bone (O'Hagan, Tsunoda, Sale, & MacDougall, 1993). Rice, Cunningham, Paterson, & Lefcoe, (1993) demonstrated that increased musculo-tendinous compliance can partly cause a slowing of the twitch contraction.

A significant age-related reduction in isometric maximal voluntary and electrically evoked twitch force-generating capacity, and twitch contraction kinetics, evaluated by rates of force development and relaxation in PF muscles in physically active women begins after the age of 50 years. Contrary to previous reports, no significant age-related changes were observed in the twitch PT/voluntary strength ratio and the twitch half-relaxation time in women with regular recreational physical activity. The mechanisms responsible for twitch potentiation after a brief MVC are markedly influenced by ageing. A decrease of twitch potentiation capacity and a prolongation of the contraction time of the PF muscles in physically active women begins after the age of 40.

References

Aoyagi, Y., & Shephard, R.J. (1992). Aging and muscle function. *Sports Medicine*, *14*, 376-396.

Belanger, A.Y., & McComas, A.J. (1989). Contractile properties of human skeletal muscle in childhood and adolescence. *European Journal of Applied Physiology*, *58*, 563-567.

Davies, C.T.M., & White, M.J. (1983). Contractile properties of elderly human triceps surae. *Gerontology*, *29*, 19-25.

Doherty, T.J., Vandervoort, A.A., & Brown, W.F. (1993). Effects of ageing on the motor unit: a brief review. *Canadian Journal of Applied Physiology*, *18*, 331-358.

Edgerton, V.R., Smith, J.L., & Simpson, D.R. (1975). Muscle fibre populations of human leg muscles. *Histochemical Journal*, *7*, 259-266.

Fukashiro, S., Itoh, M., Ichinose, Y., Kawakami, Y., & Fukunaga, T. (1995). Ultrasonography gives directly but noninvasively elastic characteristic of human tendon in vivo. *European Journal of Applied Physiology*, *71*, 555-557.

Grange, R.W., Vandenboom, R., & Houston, M.E. (1993). Physiological significance of myosin phosphorylation in skeletal muscle. *Canadian Journal of Applied Physiology*, *18*, 229-242.

Häkkinen, K., & Pakarinen, A. (1993). Muscle strength and serum testosterone, cortisol and SHBG concentrations in middle-aged and elderly men and women. *Acta Physiologica Scandinavica*, *148*, 199-207.

Häkkinen, K., Alen, M., Kallinen, M., Izquierdo, M., Jokelainen, K., Lassila, H., Mälkiä, E., Kraemer, W., & Newton, R.U. (1998). Muscle cross-sectional area, force production, and neural activation of leg extensor muscles during isometric and dynamic actions in middle-aged and elderly men and women. *Journal of Ageing and Physical Activity*, *6*, 232-247.

Hamada, T., Sale, D.G., MacDougall, J.D., & Tarnopolsky, M.A. (2000). Postactivation potentiation, fiber type, and twitch contraction time in human knee muscles. *Journal of Applied Physiology*, *88*, 3131-2137.

Houston, M.E., Green, H.-J., & Stull, J.T. (1985). Myosin light chain phosphorylation and isometric twitch potentiation in intact human muscle. *Pflügers Archiv*, *403*, 348-352.

Hunter, S.K., Thompson, M.W., Ruell, P.A., Harmer, A.R., Thom, J.M., Gwinn, T.H., & Adams, R.D. (1999). Human skeletal muscle sarcoplasmic reticulum Ca^{2+}-uptake and muscle function with aging and strength training. *Journal of Applied Physiology*, *86*, 1858-1865.

Kent-Braun, J.A., & Ng, A.V. (1999) Specific strength and voluntary muscle activation in young and elderly women and men. *Journal of Applied Physiology*, *87*, 22-29.

Klitgaard, H., Ausoni, S., & Damiani, E. (1989). Sarcoplasmic reticulum of human skeletal muscle: age-related changes and effect of training. *Acta Physiologica Scandinavica*, *137*, 23-31.

Klug, G.A, Botterman, B.R., & Stull, J.T. (1982). The effect of low frequency stimulation on myosin light chain phosphorylation in skeletal muscle. *Journal of Biological Chemistry*, *257*, 4688-4690.

Larsson, L., Grimby, G., & Karlsson J. (1979). Muscle strength and speed of movement in relation to age and muscle morphology. *Journal of Applied Physiology*, *46*, 451–456.

Levine, R.J.C., Kensler, R.W., Yang, Z., Stull, J.T., & Sweeney, H.L. (1996). Myosin light chain phosphorylation affects the structure of rabbit skeletal muscle thick filaments. *Biophysical Journal*, *71*, 898-907.

Acknowledgments

This study was partly supported by the Estonian Science Foundation, grant No. 5278

Lewis, D.M., Al-Amood, W.S., & Rosendorff, C. (1986). Stimulation of denervated muscle: what do isometric and isotonic recordings tell us? In W.A. Nix & G. Vrbova (Eds.), *Electrical Stimulation and Neuromuscular Disorders* (pp. 101-113). Berlin: Springer-Verlag.

Lexell, J., & Downham, D.Y. (1992). What is the effect of ageing on type 2 muscle fibers? *Journal of Neurological Sciences*, *107*, 250-251.

MacIntosh, B.R., & Gardiner, P.F. (1987). Posttetanic potentiation and skeletal muscle fatigue: interactions with caffeine. *Canadian Journal of Physiology and Pharmacology*, *65*, 260-268.

Mälkiä, E., Impivaara, O., Heliövaara, M., & Maatela J. (1994). The physical activity of healthy and chronically ill adults in Finland at work, at leisure and during commuting. *Scandinavian Journal of Medicine and Science in Sports*, *4*, 82-87.

McDonagh, M.J.N., White, M.J., & Davies, C.T.M. (1984). Different effects of aging on the mechanical properties of human arm and leg muscles. *Gerontology*, *30*, 49-54.

O'Hagan, F., Tsunoda, N., Sale, D.G., & MacDougall, J.D. (1993). Elbow flexor evoked twitch contractile properties in untrained men and women and bodybuilders. *European Journal of Applied Physiology*, *66*, 240-245.

Pääsuke, M., Ereline, J., Gapeyeva, H., Sirkel, S., & Sander P. (2000). Age-related differences in twitch contractile properties of plantarflexor muscles in women. *Acta Physiologica Scandinavica*, *170*, 51-57.

Pääsuke, M., Ereline, J., & Gapeyeva, H. (2000). Twitch contraction properties of plantar flexor muscles in pre- and post-pubertal boys and men. *European Journal of Applied Physiology*, *82*, 459-464.

Pääsuke, M., Ereline, J., Gapeyeva, H., & Maamägi, H. (2001). Comparison of twitch-contractile properties of plantar-flexor muscles in young and 52- to 63-year-old men. *Journal of Aging and Physical Activity*, *10*, 160-168.

Pääsuke, M., Ereline, J., Gapeyeva, H., Sander P., & Sirkel, S. (2002). Twitch potentiation capacity of plantarflexor muscles in women with increased age. *Biology of Sport*, *19*, 213-223.

Persechini, A., Stull, J.T., & Cooke, R. (1985). The effect of myosin phosphorylation on the contractile properties of skinned rabbit skeletal muscle fibers. *Journal of Biological Chemistry*, *260*, 7951-7954.

Petrella, R.J., Cunningham, D.A., Vandervoort, A.A., & Paterson, D.H. (1989). Comparison of twitch potentiation in the gastrocnemius of young and elderly men. *European Journal of Applied Physiology*, *58*, 395-399.

Rice, C.L., Cunningham, D.A., Paterson, D.H., & Lefcoe, M.S. (1989). Arm and leg composition determined by computed tomography in young and elderly men. *Clinical Physiology*, *9*, 207-220.

Rice, C.L., Cunningham, D.A., Paterson, D.H., & Dickinson, J.R. (1993). Strength training alters contractile properties of the triceps brachii in men aged 65-78 years. *European Journal of Applied Physiology*, *66*, 275-280.

Roubenoff, R. (2001). Origin and clinical relevance of sarcopenia. *Canadian Journal of Applied Physiology*, *26*, 78-89.

Sale, D.G., Quinlan, J., Marsh, E., McComas, A.J., & Belanger, A.Y. (1982). Influence of joint position on ankle plantarflexion in humans. *Journal of Applied Physiology*, *52*, 1632-1642.

Shadwich, R.E. (1990). Elastic energy storage in tendons: mechanical difference related to function and age. *Journal of Applied Physiology*, *68*, 1033-1040.

Shorey, C.D., & Cleland, K.W. (1988). Morphometric analysis of frozen transverse sections of human skeletal muscle taken postmortem. *Acta Anatomica*, *131*, 30-34.

Stevens, J.E., Binder-Macleod, S., & Snyder-Mackler, L. (2001). Characterization of the human quadriceps muscle in active elders. *Archives of Physical Medicine and Rehabilitation*, *82*, 973-978.

Sweeney, H.L., Bowman, B.F., & Stull, J.T. (1993). Myosin light chain phosphorylation in vertebrate striated muscle: regulation and function. *American Journal of Cell Physiology*, *264*, C1085-C1095.

Vandervoort, A.A., & McComas, A.J. (1986). Contractile changes in opposing muscles of the human ankle joint with aging. *Journal of Applied Physiology*, *61*, 361-367.

Vandervoort, A.A., & Hayes, K.C. (1989). Plantarflexor muscle function in young and elderly women. *European Journal of Applied Physiology*, *58*, 389-394.

Vandervoort, A.A., Hayes, K.C., & Belanger, A.Y. (1986). Strength and endurance of skeletal muscle in the elderly. *Physiotherapy Canada*, *38*, 167-173.

Westerblad, H., Lännegren, J., & Allen, D.G. (1997). Slowed relaxation in fatigued skeletal muscle fiber of Xenopus and mouse: contribution [Ca^{2+}] and cross-bridges. *Journal of General Physiology*, *109*, 385-399.

Submitted: January 22, 2004
Accepted: September 1, 2005

Correspondence to:
Prof. Mati Pääsuke, PhD
Institute of Exercise Biology and Physiotherapy
University of Tartu
5 Jakobi Str., 51014 Tartu, Estonia
Phone/Fax: +37 27 376 286
E-mail: mati.paasuke@ut.ee

PROMJENE KONTRAKTILNIH SVOJSTAVA MIŠIĆA PLANTARNIH FLEKSORA POVEZANE S DOBI TJELESNO AKTIVNIH ŽENA

Sažetak

Uvod

Cilj ovog istraživanja bio je izmjeriti učinak starenja na trzajna kontraktilna svojstva skeletnih mišića kod žena uključenih u redovitu rekreacijsku tjelesnu aktivnost. Mjereni su mišići potkoljenice, plantarni fleksori stopala, koji su važni za držanje tijela i kretanje, a aktivni su u mnogobrojnim radnim i sportskim aktivnostima.

Metode

Ukupno je 49 žena pristalo sudjelovati u ovom istraživanju. Raspoređene su u 4 dobne skupine: skupina u 3. desetljeću života (u dobi od 20 do 25 godina, n=13), skupina u 5. desetljeću života (u dobi od 40 do 49 godina, n=12), skupina u 6. desetljeću života (u dobi od 50 do 59 godina, n=11) i skupina u 8. desetljeću života (u dobi od 70 do 77 godina, n=13). Sve su mlađe ispitanice bile fizički zdrave studentice uključene u redovitu tjelovježbu dva do tri puta tjedno u skupinama odbojke, košarke ili aerobike. Ispitanice srednje dobi vježbale su u skupinama odbojke ili aerobike dva puta tjedno, a starije ispitanice također su vježbale u skupinama aerobike dva puta tjedno. Tijekom mjerenja, ispitanice su sjedile na posebno dizajniranoj stolici, s dominantnom nogom savijenom u koljenom zglobu pod kutom od 90° i smještenom unutar metalnog okvira. Da bi se utvrdila kontraktilna svojstva mišića plantarnih fleksora tijekom izometričkog trzaja, parom samoljepljivih elektroda podraživali smo stražnji tibijalni živac. Katoda je postavljena iznad tibijalnog živca u poplitealnoj jami, a anoda je postavljena ispod stražnje medijalne strane natkoljenice. Izolirani voltažni stimulator bio je izvor supramaksimalnih pravokutnih podražaja od 1 ms.

Nakon bilježenja mišićne kontrakcije u mirovanju, ispitanice su dobile uputu da 5 sekundi zadrže mišić u maksimalnoj voljnoj kontrakciji (MVC), a zatim da ga opuste. Drugi (potencirani) trzajni podražaj nastupio je unutar 1 s nakon početka relaksacije. Izračunate su sljedeće karakteristike izometričkog trzaja: vršna sila trzaja (PT) – najveća vrijednost izometričke sile, vrijeme kontrakcije (CT) – vrijeme do vršne sile trzaja, poluvrijeme relaksacije (HRT) – vrijeme polovičnog opadanja vršne sile trzaja, maksimalna brzina razvoja sile (RFD) – prva derivacija razvoja sile (dF/dt) i maksimalna brzina relaksacije (RR) kao prva derivacija opadanja sile (-dF/dt). Postotak porasta potencirane vršne sile trzaja (PT) u odnosu na vrijednost u mirovanju uzet je kao pokazatelj postaktivacijske potencijacije (PAP). Vršna sila trzaja u mirovanju izražena je kao omjer s izometričkom voljnom jakosti.

Rezultati

Prosječna vrijednost vršne sile trzaja u skupini žena u 3. desetljeću života bila je veća ($p<0.05$) od prosječnih vrijednosti u skupinama žena u 6. i 8. desetljeću. Skupina u 5. desetljeću pokazala je veću ($p<0.05$) vršnu silu trzaja od skupine u 8. desetljeću. Razlike u vršnoj sili trzaja između dvije mlađe i dvije starije skupine nisu bile značajne. Među skupinama nisu uočene značajne razlike u omjeru između vršne sile trzaja i voljne jakosti. Uočeno je produljenje vremena kontrakcije (CT) izometričkog trzaja s porastom dobi. Prosječna vrijednost vremena kontrakcije (CT) trzaja u najmlađoj skupini bila je manja ($p<0.05$) od vrijednosti triju starijih skupina. Razlike u CT trzaja između skupina u 5., 6. i 8. desetljeću nisu bile značajne. Nije bilo značajnih razlika među izmjerenim dobnim skupinama u prosječnim vrijednostima poluvremena relaksacije (HRT) trzaja. Vrijednosti maksimalne RFD i RR izometričkog trzaja smanjile su se s dobi. Vrijednost aritmetičke sredine maksimalne brzine razvoja sile trzaja (RFD) u skupini u 3. desetljeću bila je veća ($p<0.05$) od vrijednosti u skupinama žena u 6. i 8. desetljeću. Razlike u maksimalnoj RFD trzaja između dviju mlađih i dviju starijih skupina nisu bile značajne. Prosječna vrijednost maksimalne brzine relaksacije (RR) trzaja u skupini u 8. desetljeću bila je manja ($p<0.05$) od vrijednosti u dvije mlađe skupine. Maksimalna RR trzaja u skupini u 3. desetljeću bila je veća ($p<0.05$) u usporedbi s vrijednosti skupine u 6. desetljeću. Razlike u maksimalnoj RR trzaja između dvije mlađe skupine i dvije starije skupine nisu bile značajne. Nisu uočene značajne razlike u RR trzaja u usporedbi skupina u 6. i 5. desetljeću. Postaktivacijska potencijacija (PAP) bila je značajno izražena ($p<0.05$) samo u najmlađoj skupini, dok za tri starije skupine postaktivacijska potencijacija nije bila značajna. Skupina u 3. desetljeću imala je veće vrijednosti ($p<0.05$) PAP od skupine u 8. desetljeću, dok razlike u PAP između skupina u 3., 5. i 6. desetljeću nisu bile značajne. Vrijednost PAP u skupini u 8. desetljeću nije se značajno razlikovala od vrijednosti PAP u skupinama u 5. i 6. desetljeću.

Rasprava i zaključak

Ovo je istraživanje pokazalo da je značajno, s dobi povezano opadanje izometričkog maksimalnog voljnog i električno izazvanog kapaciteta stvaranja sile trzaja, kao i opadanje kinetike trzajne kontrakcije, ocijenjeno brzinama razvoja sile i relaksacije mišića plantarnih fleksora stopala, kod žena uključenih u redovitu tjelesnu aktivnost započelo nakon 50. godine. Suprotno prijašnjim istraživanjima, nisu uočene značajne promjene povezane s dobi u omjeru između vršne sile trzaja i voljne jakosti ni u poluvremenu relaksacije trzaja kod žena uključenih u redovitu rekreacijsku tjelesnu aktivnost. Mehanizmi odgovorni za trzajnu potencijaciju nakon kratke izometričke maksimalne voljne kontrakcije značajno su pod utjecajem starenja. Opadanje kapaciteta trzajne potencijacije i produljenje vremena kontrakcije mišića plantarnih fleksora stopala kod tjelesno aktivnih žena započelo je nakon 40. godine.