DISSERTATIONES KINESIOLOGIAE UNIVERSITATIS TARTUENSIS
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AGE-RELATED CONTRACTILE CHANGES IN PLANTARFLEXOR MUSCLES IN WOMEN: ASSOCIATIONS WITH POSTACTIVATION POTENTIATION AND RECREATIONAL PHYSICAL ACTIVITY

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The thesis is based on the following original papers, which will be referred to in the text by the Roman numerals (I–III):

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

II. Kuu S., Ereline J., Gapeyeva H., Kolts I., Pääsuke M. Age-related changes in contractile properties of plantarflexor muscles in physically active women. Kinesiology, 2005, 37: 133–140.

III. Kuu S., Gapeyeva H., Ereline J., Pääsuke M. Twitch contractile properties of plantarflexor muscles in young and middle-aged recreationally physically active and nonactive women. Aging: Clinical and Experimental Research (accepted for publication 2006).

ABBREVIATIONS

BM	Body mass
BMI	Body mass index
CNS	Central nervous system
CSA	Cross-sectional area
CT	Contraction time
EMG	Electromyography, electromyogram
HRT	Half-relaxation time
mATPase	Myosin adenosine triphosphatase
MHC	Myosin heavy chain
mRNA	Messenger ribonucleic acid
MT	Musculotendinous
MVC	Maximal voluntary contraction
PAP	Postactivation potentiation
PF	Plantarflexor
pH	Activity of hydrogen ions in the solution
PT	Peak force
RFD	Rate of force development
R-LC	Regulatory light chain
RPA	Recreationally physically active
RPN	Recreationally physically nonactive
RR	Rate of relaxation
SR	Sarcoplasmic reticulum
VO_{2max}	Maximal oxygen uptake
yr(s)	Year(s)

1. INTRODUCTION

Reduced isometric MVC force or isokinetic peak torque of the skeletal muscles is a major well-known functional impairment in neuromuscular system associated with ageing. It has been established that the change in electrically evoked twitch contractile properties of the human skeletal muscles, which can be used as a direct measure of the force-generation and force-potentiation capacity, speed of contraction and relaxation of the muscle fibres, is also a typical feature of ageing (McDonagh et al., 1984; Vandervoort & McComas, 1986; Vandervoort, 2002). Age-related reductions in muscle force-generation capacity and speed of contraction have been attributed to the reduced number of both type I (slow-twitch) and type II (fast-twitch) muscle fibres, and type II fibres atrophy (Larsson et al., 1979; Doherty et al., 1993; Thompson & Brown, 1999, Vandervoort, 2002). The other factor that may be responsible for the slowing of muscle contraction with age could be related to alterations in the excitation-contraction coupling process (Klitgaard et al., 1989). However, it is not clear at which age this impairment begins.

The force of an electrically evoked twitch is greater after a brief MVC compared with the corresponding value at rest and this enhancement has been termed PAP (Vandervoort et al., 1986; Hamada et al., 2000). The mechanism responsible for PAP is considered to be phosphorylation of myosin R-LC during the MVC, which renders actin-myosin more sensitive to Ca^{2+} in a subsequent twitch (Grange et al., 1993; Sweeney et al., 1993). A decrease in PAP with increased age has been reported (Vandervoort & McComas, 1986; Petrella et al., 1989; Hamada et al., 2000). Thus, the impairment of the mechanism responsible for PAP is conditioned by ageing; however, it is not clear at which age this impairment in muscle function begins and how it is related with habitual physical activity.

Age-related decrease in muscle function is often combined with a sedentary lifestyle in middle and older ages (Vandervoort, 2002). Regular physical activity has been commonly advocated as an approach to reduce the impact of ageing on human neuromuscular function (Booth et al., 1994; Rantanen et al., 1997; Roubenoff & Hughes, 2000). Most previous ageing studies assessing the effect of physical activity on contractile properties of skeletal muscles have involved a comparison of two separated age groups: young versus older, and usually measurements of strength (resistance) training (Rice et al., 1993; Hicks & McCartney, 1996; Welsh & Rutherford, 1996; Morse et al., 2005). However, the effect of long-term recreational gymnastics practised often by women (aerobics, flexibility and stretching exercises) on age-related changes in contractile properties of skeletal muscles is not well understood. The specific aim of the present study was to examine the influence of the recreational type gymnastics, a suitable leisure-time physical activity for young and middle-aged active women, on contractile characteristics of the skeletal muscles.

The main purpose of this study was to measure age-related differences in twitch contractile properties of skeletal muscles in women with association of PAP and recreational physical activity. Female subjects were recruited because of the relative paucity of the information about their age and physical activity-related differences in contractile properties of skeletal muscles. Recordings were made from the PF muscles that are important in posture and movement and are involved in many everyday, working and sport activities.

The reduced function of the PF muscle group may play a significant role in both decreased postural stability and the decreased locomotion performance of the subjects with increasing age. It has been suggested that PF muscles are an important muscle group in gait speed regulation in healthy subjects because they generate a large part of the energy required to move the limbs forward during the push-off phase (Winter, 1983).

2. REVIEW OF LITERATURE

2.1. Morpho-functional changes in human neuromuscular system with ageing

Ageing results in a gradual loss of muscle function, and there are predictable age-related alterations in skeletal muscle function. The typical adult will lose muscle mass with age, the loss varies according to sex and the level of physical activity. Some authors suggest that the decrease of physical activity induces age-related changes in muscle function (Rode & Shephard, 1971; Kasch et al., 1990; Mälkiä et al., 1994). However, the causes of age-related changes in muscle function can be endogenous, like to denervation resembling neurotropic disturbances (Grimby & Saltin, 1983; Essen-Gustavsson & Borges, 1986; Lexell et al., 1988). Figure 1 illustrates the multifactorial origin of loss of muscle mass with aging. From the age of 24–80 yrs, one loses approximately 40% of total skeletal muscle mass, total muscle cross-sectional area peaks at the age of 24 yrs (Lexell et al., 1988). Muscle cross-sectional area is connected to skeletal muscle mass and has constant relation with static and dynamic strength of muscle irrespective to age (Young, 1986).

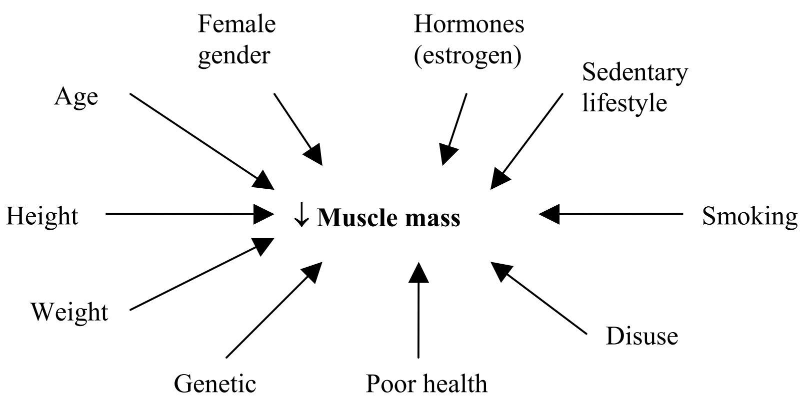

Figure 1. Hypothesized multifactorial influences on the level of muscle mass in old age (Harris, 1997).

Quantitative loss of muscle mass, referred to as sarcopenia, is the most important factor underlying the decline in muscle strength and power with ageing (Roubenoff, 2001; Lynch, 2002). Explosive strength and power output decrease with increasing age even more than maximal isometric strength of the same muscle groups (Izquierdo et al., 1999). Based on limited data, it has been suggested that muscle power, which is an integrated index of force and velocity, is probably the most important muscular predictor of physical function in humans (Bassey et al., 1992). The decrease in muscle mass with ageing has been observed with approximately the same extent as decrease in isometric or dynamic muscle strength (Aniansson et al., 1981; Borkan et al., 1983; Fleg & Lakatta, 1988; Vandervoort, 2002). Distinct changes in muscles with ageing include a decreased number of type II muscle fibres with increased age (Larsson et al., 1979; Karakelides & Nair, 2005) and a decrease in MHC IIa and IIx mRNA levels (Andersen, 2002). Different tissues display different responses to ageing, with more oxidative tissue generally having more age-related changes (Karakelides & Nair, 2005). Some studies have shown positive correlation between VO_{2max} and muscle mass in older subjects (Fleg & Lakatta, 1988; Rodgers et al., 1990).

A decreased number of type I (slow-twitch) and type II (fast-twitch) muscle fibres has been observed with increasing age (Grimby et al., 1982; Lexell et al., 1983, 1988; Vandervoort, 2002). It has been found that between 24^{th} and 52^{th} yr of age the decrease of the number of muscle fibres is not very notable (approximately 5%), however, the humans lose approximately 35% of muscle fibres between 52 and 77 yrs of age (Lexell et al., 1988). Reduced number of type I and type II muscle fibres with ageing seem to be related to loss of α-motoneurons and incomplete reinnervation of denervated muscle cells (Doherty et al., 1993).

Furthermore, the relative area occupied by type II muscle fibres decreases with increased age, resulting from fast-twitch muscle fibre atrophy and fibre type shift towards slow-twitch fibres (Lexell & Downham, 1992). Lexell et al. (1988) demonstrated that atrophy of vastus lateralis muscle begins around 25 years of age and thereafter accelerates. The muscle force depends on number of active muscle fibres, and on the type of muscle fibres, whereas fast-twitch muscle fibres develop greater tension than slow-twitch muscle fibres (Larsson, 1978; Young et al., 1982, 1984). This is one possible explanation for the great decline of muscle force with ageing.

A total of seven muscle fibre types can be identified in human limb and trunk musculature based on the pH stability/lability of mATPase (Staron, 1997). There occurs not so much a change in the ratio between type I and type II muscle fibres in the classic sense but an obfuscation of the border between type I and type II muscle fibres, so that close to one third of the fibres in the muscle fibre pool at very old age are neither strictly type I nor strictly type II muscle fibres but fibres co-expressing both MHC I and IIA (Andersen et al., 1999). The changes in muscle fibres appear to relate to alteration in activity and/or hormonal levels, and perhaps later in life, total fibre number (Staron, 1997).

With ageing the decrease in number of muscle fibres is also accompanied by the decrease in number of motor units and motoneurons in spinal cord (Doherty et al., 1993; Lexell, 1995; Galea, 1996; Roos et al., 1997), whereas this degeneration begins averagely between 50 and 60 yrs of age (Lexell, 1993; Rodgers &

Evans, 1993). Tomlinson and Irving (1977) have suggested that significant decline in the number of motoneurons in spinal cord does not appear before the age of 60 yrs. Cannon et al. (2001) has suggested that in men between 20 and 50 yr of age, no significant changes occur in neurotransmitter release, muscle stimulation sensitivity, or in the ability of the central and/or peripheral nervous system to adequately stimulate muscle tissue. Chung et al. (2005) have also shown that the age-related changes are mainly associated with weaker and slower muscle force generation, but not with significant decrease in motoneuron excitability when compared elderly (mean age of 69.4 yr) with young (mean age of 29.9 yr) healthy subjects.

Ageing is also associated with decreased functional activity of motor units, exactly after the age of 60 yrs (Campbell et al., 1973b; Sica et al., 1974; Roos et al., 1997) and decreased possibility for recruitment of motor units during MVC (Secher et al., 1978; Erim et al., 1999; Rice, 2000), which can be caused by decreased physical activity in older ages (Secher et al., 1978). Harris et al. (1994) have found that with ageing in humans dysgenic denervation is accelerated and neural coordination weakened. Different studies have explained that the changes in neural drive in muscles are with increasing age less expressed than peripheral changes, and these changes can vary between different muscle groups (Enoka, 1988; Häkkinen et al., 1995). In humans after 60 yrs of age clearly expressed changes in CNS, decelerated speed of direction of excitation in peripheral nervous-system and transmission of excitation in neuromuscular synapse have been observed (Sabbahi & Sedgwick, 1982; Vandervoort & Hayes, 1989).

One possible explanation for muscle atrophy associated with ageing, and to accompanying proportional diminishing of different type muscle fibres, are dysgenic changes in terminal sprouting, in the structure of motor end-plate and in performance, as a result of this the transmission of excitation in neuromuscular synapse is disturbed (Pestronk et al., 1980; Cardasis, 1983). The dimension of dysgenic changes of neuromuscular transmission depends on the level of muscle activity in ageing (Appell, 1984; Rosenheimer, 1985; Stebbins et al., 1985). Stebbins et al. (1985) have observed that in type II muscle fibres the transmission of excitation in neuromuscular synapse is disturbed with ageing to a greater extent than in type I muscle fibres.

2.2. Age-related changes in contractile properties of skeletal muscles

It is known that in humans the peak of muscle strength is between the 2nd and 3rd decades, showing thereafter a slow or imperceptible decrease until about 50 yrs of age and then rapid loss of muscle strength begins, especially after the age of 65 yr (Larsson et al., 1979; Grimby & Saltin, 1983; Vandervoort & McComas, 1986; Lindle et al., 1997; Pääsuke et al., 2000). Some observational studies have shown that muscle mass and force reach their peak value between the 2nd and 4th decade of life and then decline steadily with ageing (Clement, 1974; Aniansson et al., 1981; Borges, 1989; Stalberg et al., 1989; Cavanagh & Shephard, 1990; Laforest et al., 1990; Frontera et al., 1991). Most authors are consentient that decrease in muscle strength has been induced by selective decrease in the number and atrophy level of muscle fibres (especially type II) and some authors have suggested that ageing leads this process (Larsson, 1978; Davies & White, 1983; Froese & Houston, 1985).

Strength alterations with age differ between muscle groups (Rantanen et al., 1997). There is a large extent of variation, dependent of muscle location (upper vs. lower extremities) and function (extensors vs. flexors) (Frontera et al., 1991). Significant reduction in voluntary strength of the PF muscles begins from the 6th decade (Fugl-Meyer et al., 1980; Belanger et al., 1983; Vandervoort & McComas, 1986). Vandervoort and Hayes (1989) have compared the young (mean age of 26 yrs) with the elderly (mean age of 82 yrs) and observed a large reduction – until 71% – in MVC force of the PF muscles in women. A major contributor to the decrease in muscle strength is a quantitative loss in muscle CSA with increasing age (Frontera et al., 2000) and this effect is conditioned by decrease in number and size of muscle fibres (MacLennan et al., 1980). Vandervoort and McComas (1986) have found that the decline in the CSA of the gastrocnemius and soleus muscles with age is less than the reduction in voluntary strength of the PF muscles.

In addition to the decline of static and dynamic muscle force also a decrease in the speed of movements appears after 40 yrs of age (Larsson, 1978; Aniansson et al., 1981; Borges, 1989; Stalberg et al., 1989; Cavanagh & Shephard, 1990; Laforest et al., 1990; Kent-Braun & Ng, 1999).

In electrically evoked isometric twitch contractile properties of the skeletal muscles also appear changes with ageing. The twitch PT in older subjects is smaller than in young adults (Vandervoort & Hayes, 1989; Pääsuke et al., 1999a, 2000, 2002a; Rice, 2000). Vandervoort and Hayes (1989) have demonstrated that in PF muscles the PT of the evoked twitch from the elderly (mean age of 81.7 yrs) subjects is 82% of the mean value of the younger (mean age of 25.7 yrs) subjects, i.e. the extent of decrease of PT is 18%. Pääsuke et al. (2000) have shown in the 3rd decade group 43% greater ($p<0.001$) twitch PT of the PF muscles than that of the 8th decade group.

The force of an electrically evoked twitch is greater after a brief MVC compared with the corresponding value at rest and this enhancement has been termed PAP (Vandervoort et al., 1983; Petrella et al., 1989; Hamada et al., 2000; Pääsuke et al., 2002a, b). The PAP decreases with increasing age (Davies et al., 1983; Vandervoort et al., 1983; Petrella et al., 1989; Hicks et al., 1991; Pääsuke et al., 2002b; Baudry et al., 2005). In PAP the most important role is played by intramuscular factors, because the influence of central nervous system is turned off in case of electrically evoked twitch. PAP in fast-twitch muscle fibres is greater than in slow-twitch muscle fibres (Heyters et al., 1994). Therefore, the decline of PAP in muscles with ageing can be explained by relatively greater decrease in the number of fast-twitch muscle fibres rather than decrease in number of slow-twitch muscle fibres (Tomonoga, 1977; Larsson, 1978; Aniansson et al., 1986; Lexell et al., 1988). This change could be related to a greater reliance on habitually slower movements (walking) in the elderly population (Cunningham et al., 1982).

Muscle contractile process is typically slowed in older humans; they have prolonged twitch CT and HRT compared to young subjects (McDonagh et al., 1984; Vandervoort & McComas, 1986; Klein et al., 1988; Vandervoort & Hayes, 1989; Pääsuke et al., 1999a; Rice, 2000). A significantly prolonged CT has been observed in PF muscles in elderly compared to young subjects: 31.6% – (Vandervoort & Hayes, 1989) and 16% (Pääsuke et al., 2000). The time course of isometric twitches has been found to depend on the kinetics of the excitation-contraction coupling mechanisms, including intracellular Ca^{2+} movements (Klug et al., 1982; Kugelberg & Thornell, 1983). Prolongation of muscle contraction in elderly subjects can produce disturbances of muscle fibre membrane depolarization and of the excitation-contraction coupling mechanisms (Payton & Poland, 1983). The prolonged twitch CT in older individuals suggests decreased efficiency in the function of the SR to release Ca^{2+} during contraction (Klitgaard et al., 1989; Petrella et al., 1989). Ageing also weakens the binding of Ca^{2+}-ion with troponin in contraction process (Carlsen & Walsh, 1987), slowing the progress of contraction. Several investigators have reported a prolonged twitch HRT in elderly muscles (Davies & White, 1983; Vandervoort & McComas, 1986; Hicks & McCartney, 1996). Controversially, other authors have not found significant age-related differences in twitch HRT (Klein et al., 1988; Pääsuke et al., 1999a, 2000).

In addition to changes of twitch PT and CT with ageing also appears decrease in twitch maximal RFD and in RR (McDonagh et al., 1984; Vandervoort & McComas, 1986; Pääsuke et al., 2000; Karamanidis & Arampatzis, 2005). The twitch maximal RFD has rarely been used as an indicator of contraction speed. Studies have shown that decline of muscle contraction speed does not associate with diminishing of muscle fibres (Brooks & Faulkner, 1988; Pääsuke et al., 1999a, 2000). Indeed, the twitch maximal RFD depends largely on the effectiveness of the excitation-contraction coupling mechanisms and on the rate of formation of cross-bridges between myosin and actin (Klug et al., 1982;

Kugelberg & Thornell, 1983; Lewis et al., 1986). The decreased twitch maximal RFD has been called early depression and the kinetics of Ca^{2+}-release and binding to troponin have been accounted for by this phenomenon (Stein & Parmiggiani, 1981). Thereby in potentiated state appeared greater speed of twitch contraction than in resting state (Pääsuke et al., 2002b). Houston et al. (1985) has shown that myosin becomes phosphorylated during repetitive contractions and in this state is more receptive to Ca^{2+} activation. The enhanced efficiency is reflected by an increased rate of tension development in the potentiated twitch (MacIntosh & Gardiner, 1987).

Similarly to twitch maximal RFD, the twitch maximal RR decreases with advancing age (Pääsuke et al., 2000, 2002b). Two main factors are responsible for the rate of muscle relaxation: sarcoplasmic reticulum Ca^{2+} uptake and the rate of cross-bridge kinetics (Westerblad et al., 1997). It has been shown that the reduced speed of relaxation of twitch in elderly muscles is an indicator of reduced efficiency of the SR for re-uptake Ca^{2+} (Klitgaard et al., 1989; Petrella et al., 1989).

2.3. Physical activity and ageing

The conception that physical activity diminishes age-related changes in the mechanical and morphological properties of human skeletal muscles is widespread. Most investigators, who have measured age-related changes in contractile properties of skeletal muscles with association of physical activity, assessed the influence of strength or resistance training (Frontera et al., 1988; Häkkinen et al., 1998; Suetta et al., 2004; Morse et al., 2005). The effect of endurance training on contractile characteristics of skeletal muscles with ageing has been measured (Karamanidis & Arampatzis, 2005). Resistance and endurance training has been found to induced different adaptations in neuromuscular system (MacDougall, 1986; Booth & Thomason, 1991; Green et al., 1999). It has been stated that exercise training increases muscle strength, aerobic capacity, and muscle protein synthesis, and also increases muscle mitochondrial enzyme activity in both young and eldery people; however, exercise training does not reverse all age-related changes (Karakelides & Nair, 2005). Endurance training can improve the aerobic capacity of muscle, and resistance training can improve capability of CNS for recruitment of motor units and increase muscle mass (Kirkendall & Garrett, 1998). With resistance training changes in muscle strength and in the structure of muscle in young and in older women take place (Charette et al., 1991; Knight & Kamen, 2001). These changes take place due to increase in recruitment capacity of motor units (Enoka, 1988) and due to hypertrophy of muscle fibres (Lüthi et al., 1986; Akima et al., 1999). In case of resistance training, the neural adaptation seems to play a greater role compared with muscle hypertrophy in elderly subjects (Häkkinen et al., 2000; Barry et al., 2005).

Numerous studies have shown that resistance-type exercise training can improve the ability to perform the tasks of daily living, even in nonagenarians (Fiatrone et al., 1990; Cannon et al., 2001; Evans, 2002; Fielding et al., 2002; Singh, 2002; Seguin & Nelson, 2003). Whereas the same effect could be induced by everyday physical activities: such as household work, walking, and gardening. These are also the most common physically demanding activities for older people and may play an important role in maintaining muscle strength at an adequate level for independent living (Rantanen et al., 1997).

Physical training can reverse ageing atrophy and maintain fibre type distributions in elderly individuals similar to those found in young subjects (Coggan et al., 1990; Frontera et al., 1988, 1990; Fiatrone et al., 1990; Pyka et al., 1994). Hasten et al. (2000) have observed that in response to short-term resistance exercise the vastus lateralis muscle in 78–84-yr-old persons retains the capacity to increase MHC and mixed protein synthesis rates, similarly to 23–32-yr-old subjects.

There persists the significant gender difference in preferred physical activities even into the old age (Dallosso et al., 1988). Women report spending more hours per day on physically active tasks indoors and/or domestic-related activities (Dallosso et al., 1988; Osler et al., 1991; Schuit et al., 1997; Klumb & Baltes, 1999) including walking while shopping (Dallosso et al., 1988). Men have reported more outdoors and leisure activities (Dallosso et al., 1988; Yusuf et al., 1996). Older, physically impaired community-living men have less active lifestyles (as assessed by pedometer) than do similarly impaired women (Hachisuka et al., 1998).

Although improvements in muscle strength and power can be demonstrated in the elderly following therapeutic interventions, the greatest benefits are likely to be seen if this form of exercise is incorporated early in life (well before the age of 50 yrs) and maintained for as long as possible in order to produce the desired preventive benefit (Tseng et al., 1995; Kirkendall & Garrett, 1998).

In old age regular physical activity must be preserved, this guarantees greater physiological influence compared to temporary short-term effort (Rantanen et al., 1992). In this case it is possible to prevent diseases and disabilities caused by illness (like cardiovascular diseases and osteoporosis) (Bouchvard et al., 1990; Pentimone & Del Corso, 1998).

The PF muscles that make up the triceps surae complex are considered to have different functions. The soleus has an important postural role, serving to maintain a standing position, whereas the gastrocnemius is more active in phasic activity (Campbell et al., 1973a). This muscle group is active both at indoors and outdoors activities, training the PF muscles in every way.

2.4. Age-related changes in women

Ageing is a complex of extreme processes containing changes in molecular and cellular level (Menrad, 1996). Several investigators have shown that there is a linear decline in the functional reserves of most body systems after the third decade of life (Strauss, 1984; Siegel et al., 1986). One important milestone for women connected with ageing is menopause. Menopause is typically defined as the point after the loss of ovarian activity, when permanent cessation of menstruation occurs (Speroff et al., 1999). The average age at which this occurs is 51 years (ranging from 44 to 56 yrs). The symptoms that are related to midlife hormonal changes include abnormal bleeding, vasomotor flushes (hot flashes), and urogenital discomfort with decreased libido. With age the skin loses collagen content and thickness, and estrogen deprivation sets in, leading to tissue sagging and wrinkles (Morrissey & Kirchner, 2000).

Menopause is not associated with an increased risk of depression. On the contrary, depression is less common among middle-aged women (Speroff et al., 1999). However Bosworth et al. (2001) have suggested that climacteric symptoms (hot flashes, night sweats, trouble sleeping, mood swings and memory problems) are related to depressive symptoms.

In midlife, women tend to gain weight whether they are menopausal or not. However, after menopause, this weight is distributed more in the abdomen than in the thighs and hips. Insomnia is also a common complaint of postmenopausal women (Morrissey & Kirchner, 2000).

Several common problems of the climacteric age do not seem to be due to estrogen deficiency. Fatigue, nervousness, headaches, irritability, joint and muscle pain, dizziness, and palpitations are common in both men and women in midlife and are probably not attributable to hormonal changes (Speroff et al., 1999).

The greatest threat to the skeletal integrity of the ageing adult after menopause is osteoporosis. Until recently, it was believed that the rate of bone loss in osteoporosis was gender specific, with women experiencing losses two to three times more rapidly than men. It now appears that there are two different types of osteoporosis. Type I osteoporosis affects women only and occurs with the loss of estrogen production that accompanies menopause. Type II osteoporosis affects both sexes and occurs as a direct result of the ageing process (Stillman et al., 1986).

3. OBJECTIVES OF THE STUDY

The general aim of the present study was to examine age-related changes in contractile properties of the skeletal muscles in women with association of PAP and recreational physical activity.

The specific aims were:

1. To measure age-related changes in isometric MVC force and twitch contraction characteristics of the PF muscles (Paper I).

2. To measure age-related differences in PAP of isometric twitch of the PF muscles after short-term MVC (Paper II).

3. To measure the effect of recreational physical activity on twitch contraction characteristics of the PF muscles in young and middle-aged women (Paper III).

4. MATERIALS AND METHODS

4.1. Subjects

The subjects were healthy women aged 20–77 yrs. Table 1 demonstrates the division of the subjects and their anthropometric characteristics in different studies.

Table 1. Anthropometric characteristics of the subjects (mean±SE).

Papers	Age (yrs)	Body height (cm)	Body mass (kg)	BMI ($kg \cdot m^{-2}$)
Paper I				
3rd decade (n=14)	20.6±0.2	169.9±1.4	60.1±1.3	
4th decade (n=13)	33.5±0.7	167.6±1.6	65.5±2.7#	
5th decade (n=11)	44.4±0.9	163.7±1.4*	64.6±3.3	
6th decade (n=12)	54.5±0.9	163.6±1.8*	67.9±1.8#	
8th decade (n=13)	71.0±0.9	160.3±1.7*	64.6±1.8#	
* p<0.05 compared with the 3rd and 4th decade groups; # p<0.05 compared with the 3rd decade group.				
Paper II				
3rd decade (n=13)	20.4±0.2	170.0±1.4	60.2±1.4	20.8±0.4
5th decade (n=12)	44.3±0.9	163.0±1.3*	64.7±3.2	24.0±1.0*
6th decade (n=11)	54.7±0.9	163.7±1.7*	67.8±1.7*	25.5±0.8*
8th decade (n=13)	72.4±0.6	160.4±1.8*	64.7±1.7*	25.1±0.6*
* p<0.05 compared with the 3rd decade group.				
Paper III				
Young RPA (n=19)	24.4±0.6	167.2±1.5	64.4±2.1	23.0±0.6
Young RPN (n=21)	24.0±0.6	167.6±1.5	67.3±2.5	24.0±1.0
Middle-aged RPA (n=23)	47.5±0.6	163.4±1.2	68.5±2.6	25.6±0.8*
Middle-aged RPN (n=11)	49.2±1.0	162.8±2.3	67.4±1.8	25.5±0.7*
* p<0.05 compared with the young RPA women.				

BMI – body mass index;
RPA– recreationally physically active;
RPN – recreationally physically nonactive.

The subjects were screened by a questionnaire to exclude those with diagnosed musculoskeletal and cardiovascular disorders. All subjects completed a questionnaire (Appendix 1) to assess their occupational and leisure-time physical activity.

In papers I and II, the subjects were habitually physically active. Many of them performed recreational physical activities such as walking, jogging, swimming or exercised in groups of volleyball or aerobic gymnastics, on the average 2 times per week. None of the subjects had any background in competitive sports of any kind. The elderly people all lived at home and performed activities of daily life independently and exercised in groups of aerobic gymnastics 1–2 times per week.

In paper III, the purpose of the questionnaire was to discriminate RPA from RPN subjects. The subjects who performed > 3 h of recreational physical activity per week for longer than 12 months were classified as RPA. All RPA women exercised regulary in groups of recreational gymnastics (aerobics, flexibility and stretching exercises) 2–3 times per week. None of them had any backround in competitive sports of any kind. The RPN women had no recreational physical activity in leisure-time. On the basis of the questionnaire, the number of hours, spent on feet (walking + standing) during home- and work-related physical activity did not differ significantly between RPA and RPN women (Table 2).

Table 2. Home- and work-related physical activity of the subjects (mean±SD).

Groups	n	standing + walking (total hours per day)	walking (hours per day)
Young RPA women	19	4.2±1.1	2.1±0.8
Middle-aged RPA women	23	4.5±3.4	2.3±1.5
Young RPN women	21	3.9±1.8	1.9±1.0
Middle-aged RPN women	11	4.1±2.3	2.3±1.6

RPA – recreationally physically active
RPN – recreationally physically nonactive

All the subjects were informed about the purpose of the study and the procedures to be utilized and their written consent for participation was obtained. The study was approval by the University Ethics Committee for Human Studies.

4.2. Study design

The present study was carried out from 1998 to 2005. All measurements were performed at the Laboratory of Kinesiology and Biomechanics, University of Tartu.

Recordings were made from the PF muscles that are important in posture and movement and are involved in many everyday, working and sport activities.

Twenty-four to 48 hours before collecting data the subjects were given instructions and the testing of isometric MVC force 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. All subjects were evaluated at the same time of day and at an experimental room temperature of 23ºC. On reporting to the laboratory, each subject sat resting for approximately 30 minutes before commencing the experiment for minimizing any potentiation effect from walking to the laboratory.

In Paper I, the differences in twitch contractile properties of PF muscles in women with increased age were investigated. The MVC force and twitch characteristics in resting state were compared among the groups of female subjects of the 3^{rd}, 4^{th}, 5^{th}, 6^{th} and 8^{th} decade.

In paper II, the differences in twitch potentiation capacity of PF muscles in women with increasing age were measured. The isometric MVC force and twitch characteristics in resting state and PAP were compared among the groups of female subjects of the 3^{rd}, 5^{th}, 6^{th} and 8^{th} decade.

In paper III, the effects of recreational physical activity on twitch contractile properties of PF muscles were analysed in young and middle-aged women. The isometric MVC force and isometric twitch characteristics in resting and potentiated state were compared among the groups of RPA and RPN young and middle-aged women.

4.3. Methods

Apparatus

During the measurement, the subjects were seated in a custom-made dynamometric chair with the dominant leg flexed to 90° at the knee and mounted inside a metal frame (Pääsuke et al., 2000) (Fig. 2). The foot was connected to an aluminium footplate by inelastic Velcro straps at the location. 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 20º to ensure maximal voluntary and stimulated forces, the situation presumably corresponding to the "optimal" muscle length (Sale et al., 1982). An adjustable pad held down the kneecap and the front side of the thigh. A strain-gauge transducer (0.5% accuracy) connected on the footplate by a rigid bar sensed 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.

Measurement of twitch contractile properties

To determine the contractile properties of the 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 (5x5 cm) was placed over the tibial nerve in popliteal fossa and the anode (5x10 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).

The stimulation intensity was controlled by evoked compound action potential (M-wave) peak-to-peak amplitude of the soleus muscle recorded using bipolar (20 mm interelectrode distance) EMG electrodes (Beckman miniature skin electrodes). The electrodes were placed longitudinally on the motor point area of the soleus muscle determined by electrical stimulation after the skin had been cleaned using alcohol swabs and abraded lightly with fine sand paper. As a reference electrode, a large carbon rubber plate (Nemectron, 7x12.5 cm) was placed over the proximal part of the triceps surae muscle between the stimulating and recording electrodes. The EMG signals were amplified and displayed using a Medicor MG-440 (Budapest, Hungary) preamplifier with a frequency band ranging from 1 Hz to 1 kHz. These signals were sampled at 1 kHz. During 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-s intervals and the voltage was increased in increments of 20–25 V until maximal twitches were reached. The maximal amplitude of the M-wave was used as a criterion for determining the supramaximal intensity of the stimulus. Maximal isometric twitches of the PF muscles were elicited after the subject had rested for 15 min.

After the resting twitch had been recorded, the subject was instructed to hold a MVC for 5 s and then to relax (Papers II and III). A second (potentiated) twitch took place within 2 s after the onset of relaxation.

Skin temperature of the muscle group tested was continously controlled and maintained at 35ºC using an infrared lamp.

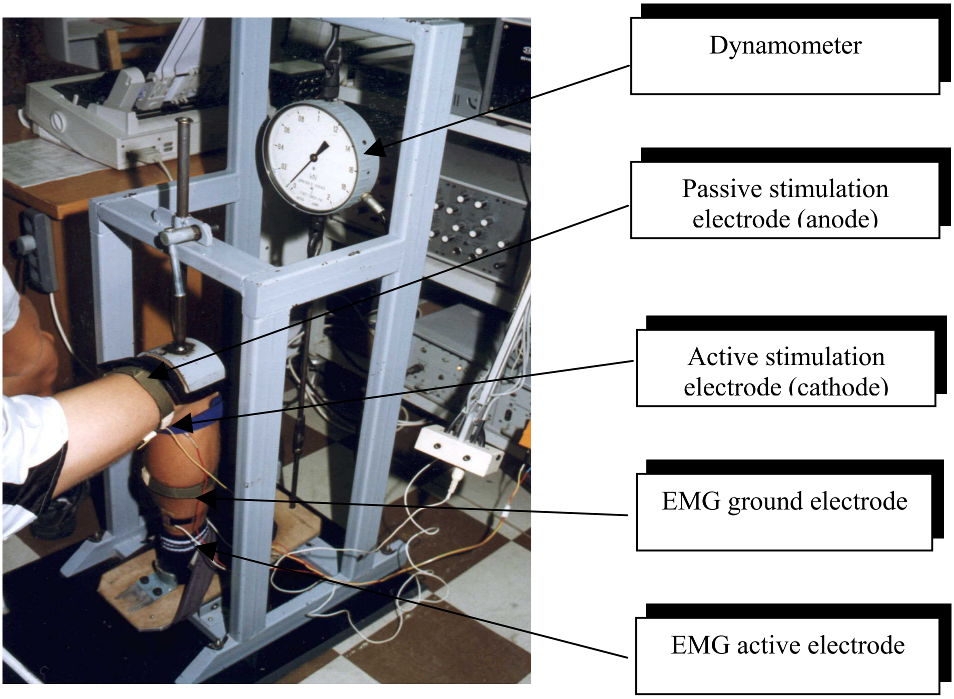

Figure 2. Experimental set-up. The position of the leg of the subject on dynamometric chair during measurement and placement of the electrical stimulation and EMG electrodes.

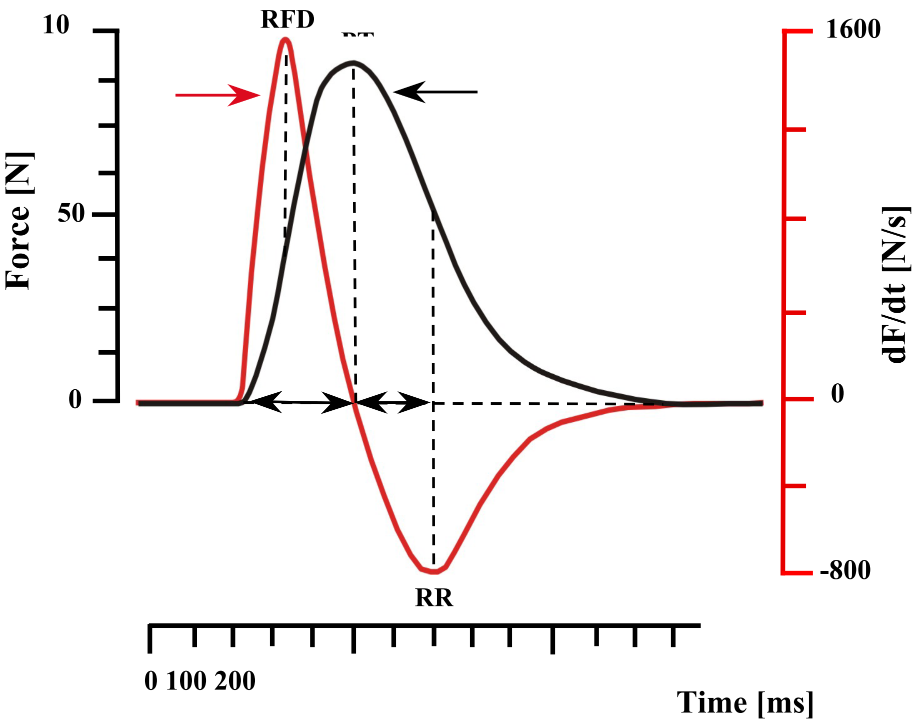

Figure 3. Isometric twitch force-time curve (A) and first derivate (B). PT – peak force; CT – contraction time; HRT – half-relaxation time; RFD – maximal rate of force development (dF/dt); RR – maximal rate of relaxation (-dF/dt).

The following characteristics of the isometric twitch were calculated (Fig. 3): twitch PT – the highest value of isometric force production, CT – the time to twitch peak force, HRT – the time of half of the decline in twitch peak force, maximal RFD – the first derivation of the development of force (dF/dt) and maximal RR as the first derivation of the decline of force (–dF/dt). The percentage increase in potentiated twitch PT in relation to that at rest was taken as an indicator of PAP (Papers II and III). The resting twitch PT were expressed as ratio to the MVC force (Paper I).

Measurement of MVC force
To measure isometric MVC force of the PF muscles, the subjects were instructed to push the footplate as forcefully as possible for 2–3 s. Strong verbal encouragement and visual feedback were provided during contractions to motivate the subjects. The greatest force of the three maximal efforts was taken as the isometric MVC force. A rest of 2 min was allowed between each of three attempts. MVC force/BM ratio was calculated in Paper III.

4.4. Statistical evaluation of the data

Standard statistical methods were used for calculation of means, and standard errors (±SE) and standard deviations (±SD). In Paper I was used one-way analysis of variance (ANOVA) followed by Scheffe post hoc comparisons to test the differences between groups. In Papers II and III was used one-factor ANOVA with Tukey post hoc test to compare the anthropometric parameters, isometric MVC force and twitch contractile characteristics between the groups. A level of $p<0.05$ was selected to indicate statistical significance.

5. RESULTS

5.1. Age-related differences in contractile properties of the plantarflexor muscles

The isometric MVC force in the 6th and 8th decade women was smaller ($p<0.05$) than in the 3rd, 4th and 5th decade women and in the 8th decade was smaller ($p<0.05$) than in the 6th decade women (Fig. 4, see Paper I). The differences in isometric MVC force between three younger groups were not significant ($p>0.05$). The decline in MVC from the 3rd decade to the 6th decade was 27.8% and from the 3rd decade to the 8th decade 41.9%, respectively.

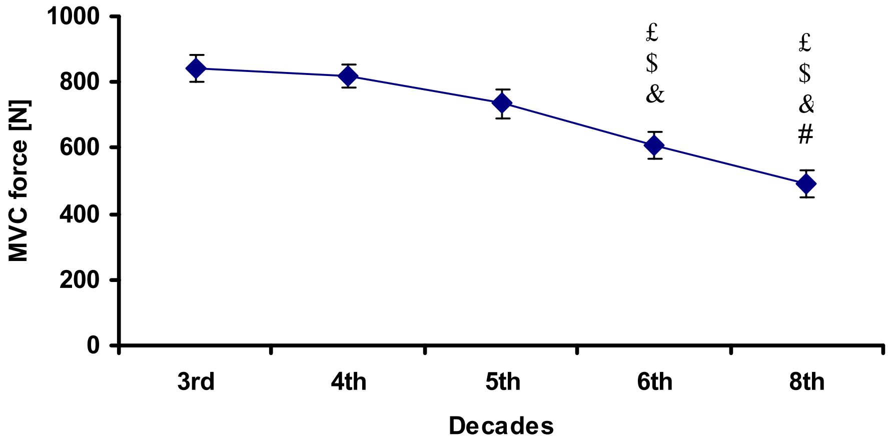

Figure 4. Mean (±SE) values of isometric maximal voluntary contraction (MVC) force in women with different age. £ $p<0.05$ compared with the 3rd decade; $ $p<0.05$ compared with the 4th decade; & $p<0.05$ compared with the 5th decade; # $p<0.05$ compared with the 6th decade.

Similarly to MVC force, the resting twitch PT in the 6th and 8th decade women was smaller ($p<0.05$) than in the 3rd, 4th and 5th decade women, but there were no significant differences ($p>0.05$) between two older groups (Fig. 5a), whereas the differences in MVC force between three younger groups were not significant ($p>0.05$). The decline in PT from the 3rd decade to the 6th decade was 22.5% and from the 3rd decade to the 8th decade 30.0%, respectively.

The PT/MVC force ratio in 8th decade women was greater ($p<0.05$) than in the 3rd decade group, whereas there were no significant differences ($p>0.05$) between the other measured groups (Fig. 5b). The increase of PT/MVC ratio from the 3rd decade to the 8th decade was 26.7%.

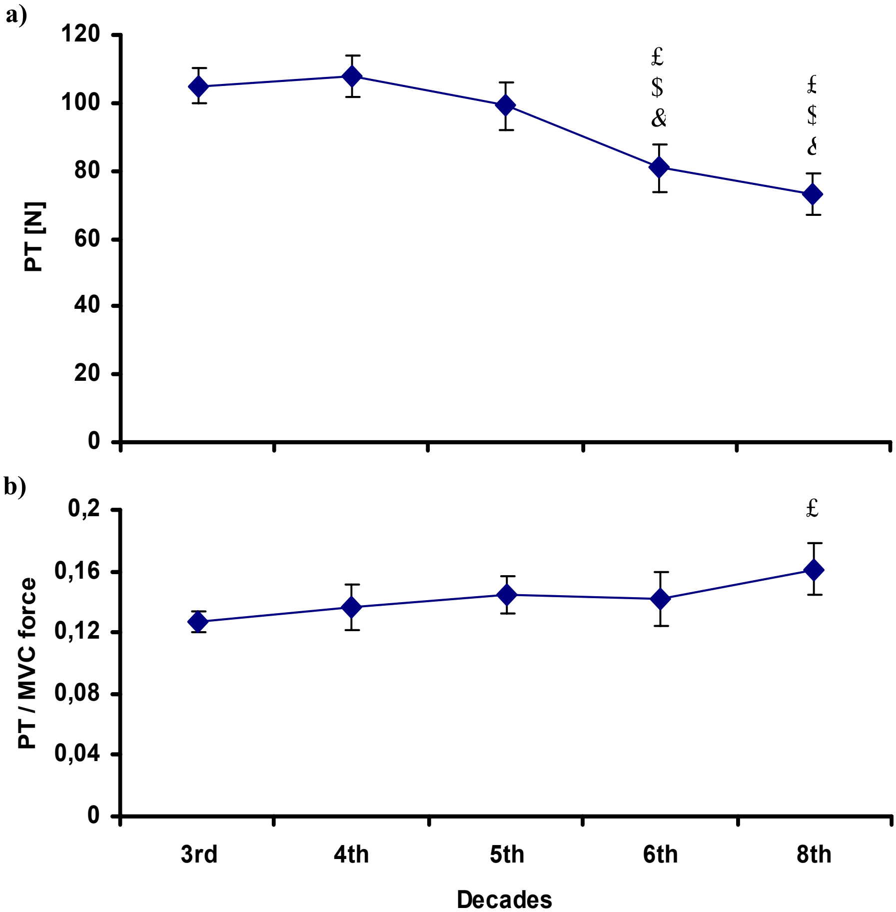

Figure 5. Mean (±SE) values of twitch peak force (PT) (a) and PT relative to isometric maximal voluntary contraction force (PT/MVC) (b) in women with different age. £ $p<0.05$ compared with the 3rd decade; $ $p<0.05$ compared with the 4th decade; & $p<0.05$ compared with the 5th decade.

The resting twitch CT in the 5th, 6th and 8th decade women was longer ($p<0.05$) than in the 3rd and 4th decade women (Fig. 6a). There were no significant differences ($p>0.05$) in twitch CT between two younger and three older women groups. The prolongation of CT from the 3rd decade to the 5th decade was 23.7%.

The resting twitch HRT did not differ significantly ($p>0.05$) between the measured age groups of women (Fig. 6b).

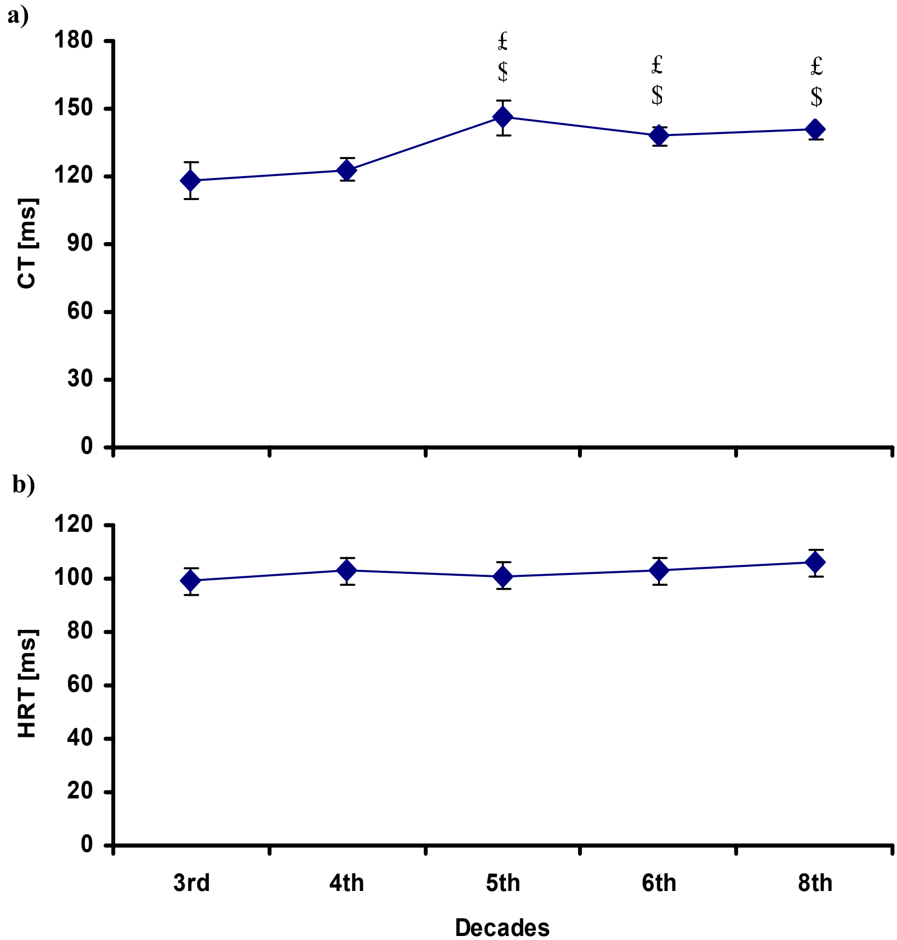

Figure 6. Mean (±SE) values of twitch contraction time (CT) (a) and half-relaxation time (HRT) (b) in women with different age. £ $p<0.05$ compared with the 3rd decade; $ $p<0.05$ compared with the 4th decade.

The resting twitch maximal RFD in the 5th, 6th and 8th decade women was smaller ($p<0.05$) than in the 3rd and 4th decade women, whereas in the 8th decade group was smaller ($p<0.05$) than in the 5th decade group (Fig. 7a). There were no significant differences ($p>0.05$) in RFD between two younger and two older groups. The decline of RFD from the 3rd decade to the 5th decade was 19.2%, from the 3rd decade to the 6th decade 30.8% and from the 3rd decade to the 8th decade 38.6%, respectively.

The resting twitch maximal RR in the 8th decade women was smaller ($p<0.05$) than in the 3rd, 4th, 5th and 6th decade group, whereas in the 6th decade group it was smaller ($p<0.05$) than in the 3rd and 4th decade women (Fig. 7b).

There were no significant differences ($p>0.05$) in RR between the 5th and 6th decade women and three younger groups. The decline of RR from 3rd decade to the 6th decade was 24.1% and from the 3rd decade to the 8th decade 39.6%, respectively.

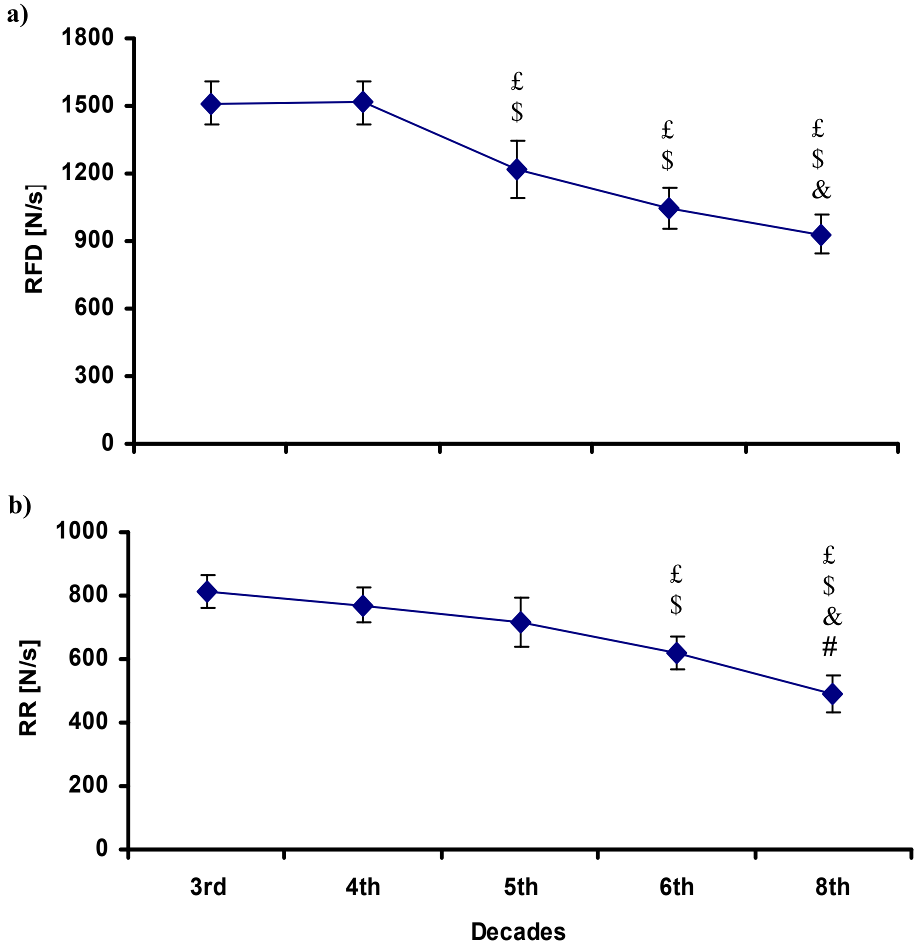

Figure 7. Mean (±SE) values of twitch maximal rate of force development (RFD) and maximal rate of relaxation (RR) in women with different age. £ $p<0.05$ compared with the 3rd decade; $ $p<0.05$ compared with the 4th decade; & $p<0.05$ compared with the 5th decade; # $p<0.05$ compared with the 6th decade.

5.2. Age-related differences in postactivation potentiation of the plantarflexor muscles

The PAP in the 8th decade women was smaller ($p<0.05$) than in the 3rd decade women (Fig. 8), whereas there were no significant differences ($p>0.05$) between three younger groups (see Paper II). The decline of PAP from 3rd decade to 8th decade was 9.7%.

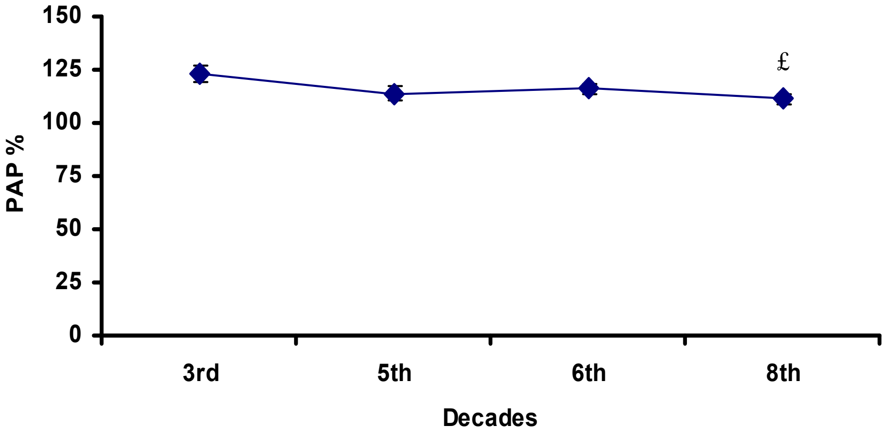

Figure 8. Mean (±SE) values of twitch post-activation potentiation (PAP) in women with different age. £ $p<0.05$ compared with the 3rd decade.

5.3. The effect of recreational physical activity on contractile properties of the plantarflexor muscles

The isometric MVC force in middle-aged RPN women was smaller ($p<0.05$) than in young RPA women (Fig. 9a, see Paper III). There were no significant differences ($p>0.05$) in MVC force between two measured young women's groups and middle-aged RPA women, and between RPA and RPN women of similar age.

The isometric MVC force/BM ratio was smaller in middle-age RPA and RPN, and in young RPN women ($p<0.05$) than in young RPA women (Fig. 9b). There were no significant differences ($p>0.05$) in MVC force/BM ratio between young RPN and two middle-aged women groups and between middle-aged women in RPA and RPN groups.

The twitch PT in resting state did not differ significantly between the measured groups (Fig. 10a). The potentiated twitch PT was smaller ($p<0.05$) in two middle-aged women's groups than in young RPA women, and in middle-aged RPN it was smaller ($p<0.05$) than in young RPN women. There were no significant differences ($p>0.05$) in potentiated twitch PT between young RPN and middle-aged RPA women and between RPA and RPN women of similar age. The potentiated twitch PT was significantly greater ($p<0.05$) compared with resting twitch for all measured groups.

The PAP in two middle-aged women's groups was smaller ($p<0.05$) than in young RPA women (Fig. 10b). There were no significant differences ($p>0.05$) in PAP between young RPN and two middle-aged women's groups and between RPA and RPN women of similar age.

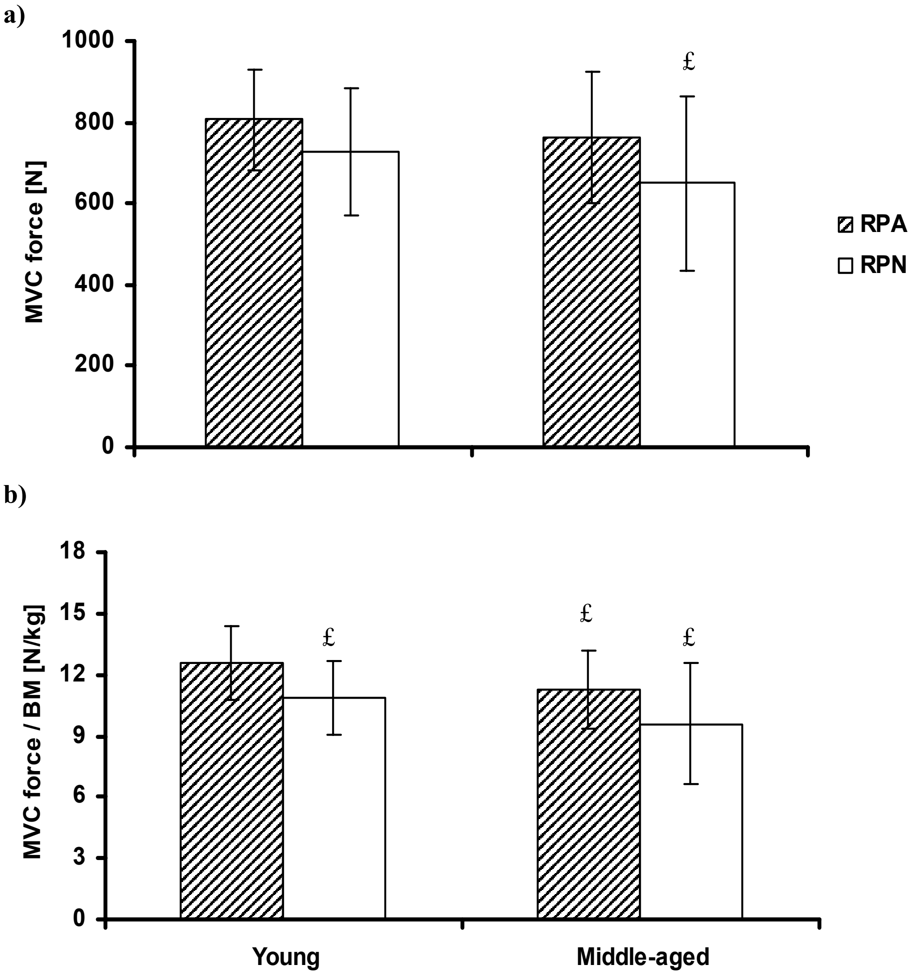

Figure 9. Mean (±SD) values of maximal voluntary isometric contraction (MVC) force (a) and MVC force / body mass (BM) ratio (b) in young and middle-aged recreationally physically active (RPA) and nonactive (RPN) women. £ $p<0.05$ compared with young RPA.

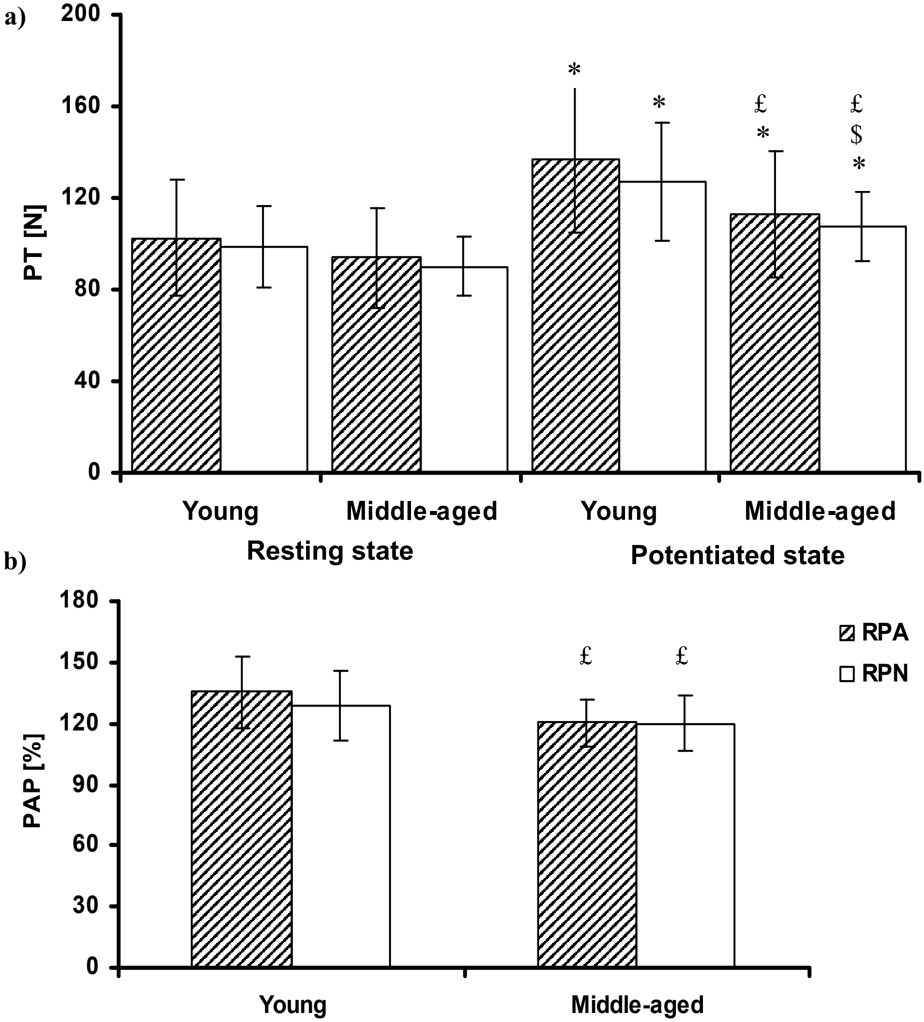

Figure 10. Mean (±SD) values of twitch peak force (PT) in resting and potentiated state (a) and post-activation potentiation (PAP) (b) in young and middle-aged recreationally physically active (RPA) and nonactive (RPN) women. £ $p<0.05$ compared with young RPA; \$ $p<0.05$ compared with young RPN; * $p<0.05$ compared with the same group in resting state.

The resting and potentiated twitch CT in two middle-aged women's groups was longer ($p<0.05$) than in two young women's groups (Fig. 11a). There were no significant differences ($p>0.05$) in resting twitch CT between RPA and RPN women of similar age. The potentiated twitch CT was longer ($p<0.05$) in young RPN than in young RPA women, whereas there were no significant differences ($p>0.05$) in potentiated twitch CT between middle-aged women in RPA and RPN groups. The potentiated twitch CT was shorter ($p<0.05$) compared with resting twitch for young RPA and middle-aged RPN women's groups.

The resting and potentiated twitch HRT did not differ significantly ($p>0.05$) between the measured groups (Fig. 11b).

The resting twitch maximal RFD in two middle-aged women's groups was smaller ($p<0.05$) than in young RPA women (Fig. 12a), and in middle-aged RPN women was smaller ($p<0.05$) than in young RPN women. There were no significant differences ($p>0.05$) in resting twitch maximal RFD between young RPN and middle-aged RPA women, and between RPA and RPN women of similar age. The potentiated twitch maximal RFD in two middle-aged women's groups was smaller ($p<0.05$) than in two young women's groups. There were no significant differences ($p>0.05$) in potentiated twitch maximal RFD between RPA and RPN women of similar age. The potentiated RFD was significantly greater ($p<0.05$) compared with resting twitch for all measured groups.

The resting twitch maximal RR did not differ significantly between the measured groups (Fig. 12b). The potentiated twitch maximal RR was in two middle-aged women's groups smaller ($p<0.05$) than in young RPA women, and in middle-aged RPN smaller ($p<0.05$) than in young RPN women. There were no significant differences ($p<0.05$) in potentiated twitch maximal RR between young RPN and middle-aged RPA women and between RPA and RPN women of similar age. The potentiated RR was significantly greater ($p<0.05$) compared with resting twitch for two young women and middle-aged RPA women's groups.

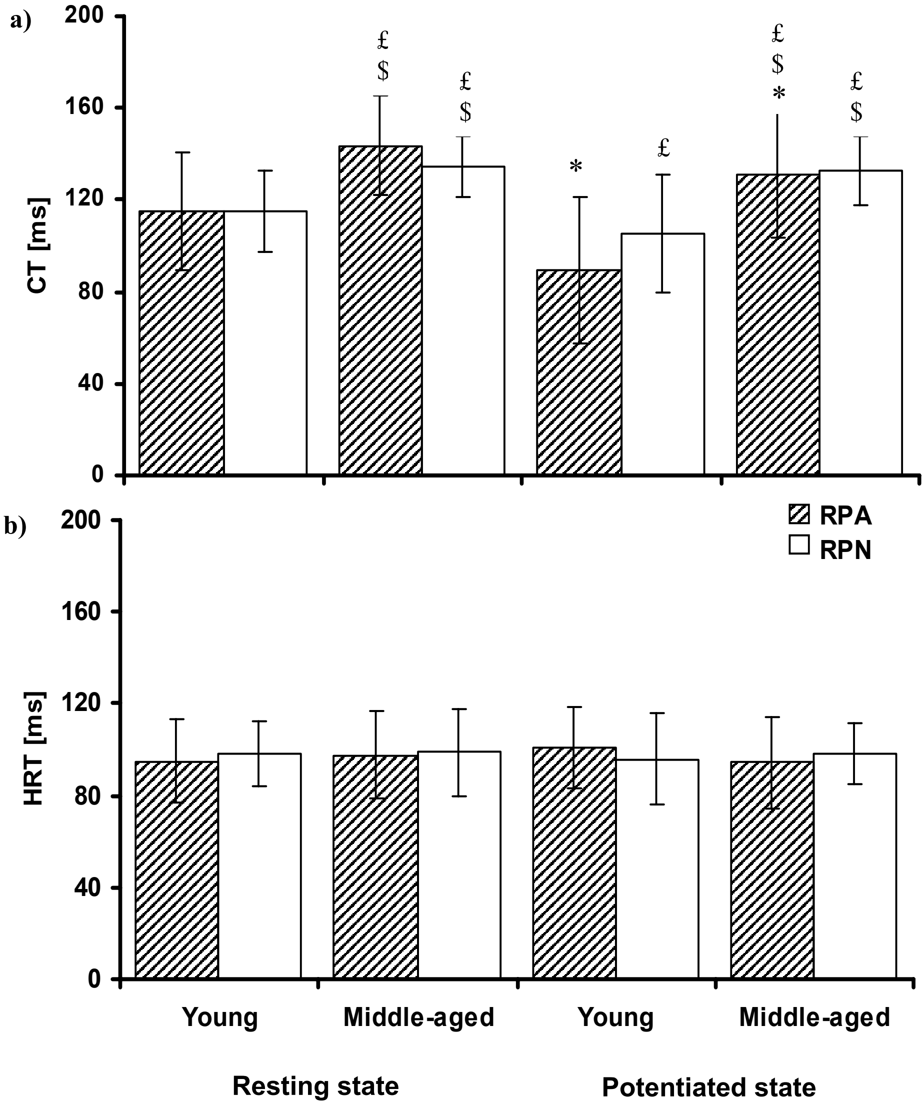

Figure 11. Mean (±SD) values of twitch contraction time (CT) (a) and in half-relaxation time (HRT) (b) in resting and potentiated state in young and middle-aged recreationally physically active (RPA) and nonactive (RPN) women. £ p<0.05 compared with young RPA; $ p<0.05 compared with young RPN; * p<0.05 compared with the same group in resting state.

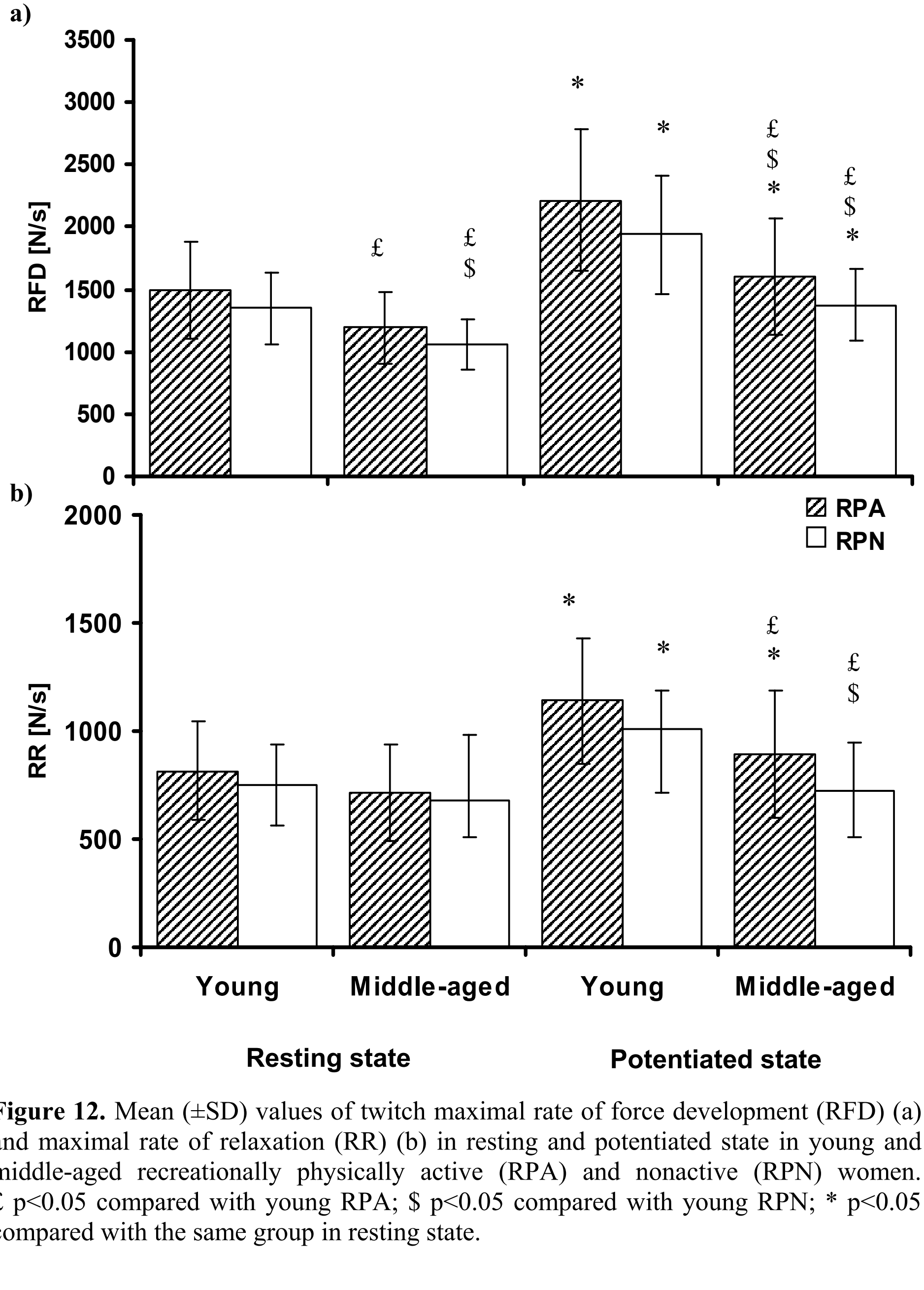

Figure 12. Mean (±SD) values of twitch maximal rate of force development (RFD) (a) and maximal rate of relaxation (RR) (b) in resting and potentiated state in young and middle-aged recreationally physically active (RPA) and nonactive (RPN) women. £ $p<0.05$ compared with young RPA; \$ $p<0.05$ compared with young RPN; * $p<0.05$ compared with the same group in resting state.

6. DISCUSSION

6.1. Age-related differences in contractile properties

Loss of isometric MVC force and electrically evoked twitch PT of the PF muscles (Davies & White, 1983; Vandervoort & McComas, 1986; Petrella et al., 1989; Pääsuke et al., 1999a) is a well-known feature of ageing. The aim of this study was to explain at which age this impairment in women begins. The results of the present study indicated that a significant decline in isometric MVC force of the PF muscle in women begins from the 6^{th} decade, descends evenly from the 3^{rd} decade to the 6^{th} decade 27.8% and from the 3^{rd} to 8^{th} decade 41.9%, respectively. The decrease in voluntary muscle force-generating capacity with increasing age has been attributed in part to the impairment of neural control and in part to changes in muscle fibre composition and muscle mass (Frontera et al., 1991; Kent-Braun & Ng, 1999) which is possibly related to alterations in hormonal balance (Häkkinen & Pakarinen, 1993) and the decline in quantity and intensity of habitual physical activity (Mälkiä et al., 1994). Some other investigators have demonstrated similar age-related decrease of MVC force in PF muscles. Ochala et al. (2004) have presented significantly lower MVC in old men (61–74 yrs) compared with young men (19–24 yrs), leading to a mean difference of 37%. Vandervoort and McComas (1986) have observed that MVC force of the PF muscle began to decline from the 6^{th} decade. In addition to changes in muscle morphology, a decline in maximal voluntary muscle strength with ageing may be accompanied in part by a decrease in neural drive to muscles (Häkkinen et al., 1996, 1998).

The present study indicated that similarly to MVC force, a marked loss of electrically evoked isometric twitch PT of the PF muscles in women takes place from the 6^{th} decade, whereas the decrease of twitch PT with increasing age was smaller than decrease in isometric MVC force. The age-related decrease in twitch PT can be caused by loss of muscle area and a decrease in the number of muscle fibres, whereas decrease in force-generating capacity with ageing is more pronounced in type II muscle fibres than in type I muscle fibres (Lexell et al., 1988; Booth et al., 1994).

One indicator of muscle contractile properties is the twitch/tetanus ratio. It has been reported that MVC force is similar to the maximal force of electrically evoked tetanic contractions in human muscles (Bigland-Ritchie et al., 1983). This led to the calculation of the PT/MVC force ratio (Pääsuke et al., 1999a). In this study, PT/MVC force ratio increased from the 3rd decade to the 8th decade 26.7%. This fact indicates that decrease in voluntary isometric strength of the PF muscles in women during ageing associated with marked reduction of motor unit activation under maximal contraction after the age of 70 yrs.

The present study indicated that significant prolongation of electrically evoked isometric twitch CT of the PF muscles in women takes place after the 4^{th}

decade of age (CT prolongated from the 3rd decade to the 5th decade 23.7%), and from there on stayed on a plateau. With increasing age a prolongation of twitch CT has been reported by other investigators (McDonagh et al., 1984; Vandervoort & McComas, 1986; Petrella et al., 1989; Vandervoort & Hayes, 1989). The time course of isometric twitches has been found to depend on excitation-contraction coupling mechanisms, including intracellular Ca^{2+} movements (Klug et al., 1982, Kugelberg & Thornell, 1983). The prolonged twitch CT of the elderly suggests decreased efficiency in the function of the SR to release Ca^{2+} (Klitgaard et al., 1989; Delbono et al., 1997).

The results of this study indicated no significant age-related differences in twitch HRT of the PF muscles. This does not associate with results given in many earlier reports (Davies & White, 1983; McDonagh et al., 1984, Vandervoort & McComas, 1986; Vandervoort and Hayes, 1989), where remarkable prolongation in HRT in elderly muscles has been observed compared to young subjects. Similarly to the results of present study, Petrella et al. (1989) have also not shown significant differences between young and elderly subjects in twitch HRT before and after a brief MVC. At the cellular level, the relaxation process is regulated by enzymes controlling the rate of Ca^{2+} reuptake in the SR and, possibly, also by the rate of cross-bridge detachment (Edwards et al., 1975; Fitts, 1994).

It is known that the electrically evoked twitch maximal RFD decreases with ageing (McDonagh et al., 1984; Petrella et al., 1989). In this study the twitch maximal RFD of the PF muscles was significantly decreased in women after the 4th decade. The twitch maximal RFD has been used as an indicator of contraction speed that depends largely on the rate of formation of cross-bridges between myosin and actin (Lewis et al., 1986). The decreased twitch maximal RFD has been associated with early depression and the kinetics of Ca^{2+}-release and binding to troponin has been accounted for this phenomen. It has been shown that slower contraction speed in the elderly muscles is caused by the selective atrophy of fast-twitch muscle fibres (Larsson et al., 1979). Denervation of type II fibres and reinnervation by axonal sprouting from type I motor units (Grimby et al., 1982; Kanda & Hashizume, 1989; Stalberg et al., 1989) could also contribute to slower contractile properties of the skeletal muscles.

This study indicated that the significant changes in twitch maximal RR of the PF muscles appeared after the 5th decade of age. The twitch maximal RR is an important factor in determining the contractile response of muscle fibres during isometric contraction (Vøllestad et al., 1997). Two main factors are responsible for the rate of muscle relaxation: sarcoplasmic reticulum Ca^{2+} uptake and the rate of cross-bridge kinetics (Westerblad et al., 1997). It has been shown that the decreased rate of relaxation in elderly muscles is an indicator of reduced efficiency of the SR to re-uptake Ca^{2+} (Klitgaard et al., 1989).

6.2. Age-related differences in postactivation potentiation

The force of an electrically evoked twitch is greater after a brief MVC compared with the corresponding value at rest and this enhancement has been termed PAP (Vandervoort et al., 1986; Hamada et al., 2000). The PAP decreases with ageing. The present study indicated that the age-related decrease in PAP of the PF muscles in women begins after the 6th decade. However, Pääsuke et al. (2002b) have shown that in the 5th decade is PAP significantly greater than in the 3rd decade. The most accepted mechanism of PAP is phosphorylation of myosin R-LC during the conditioning MVC, which renders actin-myosin more sensitive to Ca^{2+} in subsequent contraction (Grange et al., 1993; Sweeney et al., 1993). Twitch potentiation is related to the force development for any given submaximal intracellular Ca^{2+} level (Klug et al., 1982; Houston et al., 1985) and myosin R-LC phosphorylation. It has been proposed that phosphorylation of myosin R-LC increases the possibility that cross-bridges will enter the force-producing state, resulting in a higher proportion of active cross-bridges at any given time during twitch (Persechini et al., 1985; MacIntosh & Gardiner, 1987). The rise reflecting the degree of PAP occurs predominantly in type II muscle fibres (Duchateau & Hainaut, 1986). One cause of this decrease in PAP with ageing can be that fast-twitch muscle fibres have a greater potentiation than have slow-twitch muscle fibres (Heyters et al., 1994) and that in the elderly, the atrophy of the fast-twitch muscle fibres is greater than atrophy of slow-twitch muscle fibres (Lexell & Downham, 1992).

6.3. The effect of recreational physical activity on contractile properties

One of the objectives of this study was to examine the impact of recreational gymnastics type physical activity on contractile properties of the PF muscles in young and middle-aged women. The results indicated that long-term recreational gymnastics increase significantly the relative voluntary strength (MVC force/BM ratio) in young women. This phenomenon has not been observed in middle-aged subjects. It was indicated that MVC force did not differ significantly in young and middle-aged RPA women. This shows the positive influence of recreational gymnastic type physical activity to maintain the voluntary force-generating capacity of the PF muscles in middle age. Kent-Braun & Ng (1999) have suggested that healthy women with similar physical activity level have similar MVC (also similar CSA) of the dorsiflexor muscles both in young (mean age of 32 yrs) and in old (mean age of 72 yrs) age. The level of physical activity is related to the isometric MVC force (Seghers et al., 2003). The decrease in number of muscle fibres (both slow-twitch and fast-twitch fibres) with increasing age has been demonstrated (Grimby et al., 1982; Lexell et al., 1983, Vandervoort, 2002). The maximal muscle force is related with muscle composition, whereas it has been observed that until to the 6^{th} decade of age the decrease in muscle fibre number in not significant (Lexell et al., 1988). The training leads to an increase in area of type I and type II muscle fibres in the elderly (Frontera et al., 1988; Kirkendall & Garret, 1998).

Previous studies have suggested that the twitch force-generating capacity of PF muscles decreases with increasing age (Petrella et al., 1989; Vandervoort & Hayes, 1989). In this study, the resting twitch PT did not differ significantly between young and middle-aged groups as in RPA as in RPN women. The potentiated twitch PT was greater in two measured young women groups compared with the middle-aged RPN women, whereas it did not differ significantly in young RPN and middle-aged RPA women. These findings suggest that potentiated twitch PT is more sensitive to ageing than resting PT, whereas recreational physical activity in middle-age reduces age-related decrease in muscle force-generation in the potentiated state. A small effect of recreational physical activity is caused by training which leads to an increase in area of type I and type II muscle fibres in the elderly (Kirkendall & Garret, 1998). However, recreational physical activity does not influence muscle strength to a great extent, and owing to the relative paucity of fast-twitch muscle fibres, which develop greater strength than slow-twitch muscle fibres in older subjects (Grimby et al., 1982; Saltin & Gollnick, 1983; Aniansson et al., 1986; Aoyagi and Shepard, 1992).

The influence of recreational physical activity on PAP is not considerable. Although, there were no significant differences in PAP between RPA and RPN women of similar age, it is important to mark that there were no significant difference between young RPN and middle-aged RPA women either. This means that recreational gymnastic type physical activity in middle-age could retain PAP.

Based of twitch CT, it is possible to conclude that the age had a more noticable effect on time course of isometric twitch than leisure-time physical activity, because the resting twitch and potentiated twitch CT were prolonged in the middle-aged compared with the young women's groups. The twitch CT is the most sensitive contractile characteristic to ageing. In Paper I it was indicated that age-related changes in twitch CT began since the 5^{th} decade and stayed from there on an even plateau. This type of physical activity (recreational gymnastics) like endurance training can advance similar changes to ageing, because it is known that endurance-trained group had lower resting Ca^{2+} release, Ca^{2+} uptake, and Ca^{2+}-ATPase than untrained group (Li et al., 2002), probably because of their lower type II muscle fibre proportion.

In this study, significant activity-related differences in twitch HRT of the PF muscles were not indicated.

This study showed significant age-related differences in potentiated twitch maximal RFD in middle-aged and young women. It is known that twitch potentiation process is sensitive to ageing (Vandervoort & McComas, 1986; Petrella et al., 1989). However, when young women are compared with middle-aged women, it is not possible to explain the decrease in twitch PT with selective atrophy of muscle fibres, because this appears after the age of 50 yr (Lexell et al., 1988). After 40 yrs of age the reduction of muscle contraction speed could be caused in addition to the prior reason, by the relative paucity of fast twitch fibres in PF muscles which make up gastrocnemius and soleus muscles, the gastrocnemius being a mixed muscle with approximately equal proportions of type I and type II muscle fibres while the soleus has primarily slow twitch (type I) fibres (Saltin & Gollnick, 1983).

Age and physical activity-related changes in twitch contractile properties of the skeletal muscles can be also associated with MT compliance, often referred to as series elastic component (SEC) of muscles, which consists of passive (tendon) and active (cross-bridges) elements (Fukashiro et al., 1995). In humans, changes in SEC stiffness were observed as a result of hyperactivity (Pousson et al., 1990), microgravity (Lambertz et al., 2001) and disease (Cornu et al., 2001). It has been shown that ageing is associated with changed stiffness of connective tissue (Shadwich, 1990). Changes in MT stiffness of the PF muscles in ageing can be principally caused by changes of the active fraction of the MT system, i.e. alterations in muscle fibre type (Ochala et al., 2004). It can therefore be hypothesized that SEC stiffness is modified by age and physical activity. Karamanidis and Arampatzis (2005) have suggested that chronic endurance (running) exercise does not counteract the age-related degeneration of the muscle-tendon units. Runners have a higher mechanical advantage for the quadriceps femoris muscle-tendon unit while running (lower gear ratio), compared to non-active subjects, indicating a task-specific adaptation even at old age. It has been suggested that MT stiffness decreases following strength training in elderly individuals, counterbalancing the effect of ageing (Ochala et al., 2005, 2006).

In the present study the influence of recreational physical activity to twitch contracile properties of the PF muscles in women was not considerable. One explanation for this could be the type of physical activity. In this study, the recreational gymnastic type physical activity included aerobics, flexibility and stretching exercises, and was not predominantly resistance type, i.e. would not necessarily have strong influence on muscle contractile characteristics. Physical activity is a major determinant of muscle strength and muscle quality, several studies have reported greater relative increases in strength than in muscle mass after strength training in older subjects (Madsen et al., 1997; Häkkinen et al., 1998; Malbut et al., 2002; Rolland et al., 2004), although physical activity is an important predictor of muscle mass in the elderly (Baumgartner et al., 1999; Suetta et al., 2004). In contrast, endurance training in the elderly has little or no effect on muscle strength (Welle et al., 1996). Analogous to this, Pääsuke et al.

(1998, 1999b) have shown that power training induces a more pronounced increase in muscle force-generation and force-potentiation capacity compared to endurance training.

The present study has some limitations. Despite the self-reported leisure-time physical activity level utilized in the present study, nothing could be inferred about the frequency, duration and intensity of the recreational physical activity performed by the young and middle-aged RPA women.

It can be concluded that recreational gymnastic type physical activity did not have a marked effect on the maximal voluntary force-generation capacity and evoked twitch contractile properties of the PF muscles in young and middle-aged women. However, the middle-aged RPA women did not have a significant decrease in twitch force-generation and post-activation potentiation capacity in PF muscles compared with the young RPN women, whereas the middle-aged RPN women did. Therefore, further studies on the effects of ageing process and recreational physical activity regarding the contractile properties of skeletal muscles are needed.

CONCLUSIONS

1. A significant age-related reduction in isometric maximal voluntary and electrically evoked twitch force-generating capacity, and in speed of relaxation of the plantarflexor muscles takes place in women after 50 years of age.

2. In women, a significant prolongation in contraction time and reduction in speed of contraction of the electrically evoked isometric twitch of the plantarflexor muscles takes place after 40 years of age.

3. A significant decrease in postactivation potentiation of isometric twitch force of the plantarflexor muscles induced by a brief maximal voluntary isometric contraction takes place in women after 70 years of age.

4. Recreational gymnastic type physical activity does not have a significant effect on the maximal voluntary force-generation capacity and evoked twitch contractile properties of the plantarflexor muscles in young and middle-aged women.

5. The middle-aged recreationally physically active women did not have a significant decrease in twitch force-generation and postactivation potentiation capacity in plantarflexor muscles compared with the young recreationally physically nonactive women, whereas the middle-aged recreationally physically nonactive women did. This is indicator of the positive effect of gymnastic type physical activity on muscle contractile properties in middle age.

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APPENDIX

Appendix 1

Questionnaire   Date:

Name…………………………………………………………………………...
Age……..……..… Height……………..... Weight………………………………..
How many hours per day are you on feet (walking + standing)? ………………..
include training for …..…….hours,
include walking (to shop/to work/with dog/ etc.) for ………… hours.
How many times per week do you train? ………………………………………..
For how long have you been regularly training? ………………………………...
Which kind of sport do you practise? …………………………..……………..
What else have you practised and for how long? …………………………….
………………………………………………………………………………
………………………………………………………………………………
………………………………………………………………………………
Do you have any health problems?
What kind? ……………………………………………………………………
………………………..……………………………………...………………
Have you had any problems (if yes, then which)?
with the nervous system…………………………………………………
with the musculoskeletal system......…………………………...…..
with the cardiovascular system………………………………………..
with other internal organs …....……………………………….………
How often are you down with cold? ……………………………………………..
Have you given birth? (for how many times?) …………………………………..
What is your purpose for training? ……………………………………………
………………………………………………………………………………
………………………………………………………………………………

SUMMARY IN ESTONIAN

EALISED MUUTUSED SKELETILIHASTE KONTRAKTIILSETES OMADUSTES NAISTEL: AKTIIVSUSJÄRGSE POTENTSEERUMISE JA KEHALISE AKTIIVSUSEGA SEOTUD ASPEKTID

Sissejuhatus

Organismi vananemisel ilmnevad funktsionaalsed muutused skeletilihastes, mis väljenduvad eelkõige lihaste jõugenereerimise võime ja kontraktsiooni kiiruse languses. Neid muutusi seostatakse sageli lihasmassi, sh lihaskiudude arvu vähenemisega (sarkopeeniaga) vanuse kasvades. Lihasmassi vähenemist võivad põhjustada hormonaalsed muutused ja kehalise aktiivsuse langus seoses vananemisega. Inimese skeletilihaste kontraktiilseid omadusi määratakse tavaliselt elektrostimulatsiooniga esile kutsutud isomeetrilise üksikkontraktsiooni parameetrite alusel, mis võimaldavad hinnata lihaste funktsionaalset seisundit sõltumatult lihaste juhtimisest motoorsete närvikeskuste poolt. Uuringud on näidanud nii üksikkontraktsiooni maksimaaljõu vähenemist kui ka kontraktsiooni- ja lõõgastusaja pikenemist seoses vananemisega. Praegu puudub kindel teadmine, millisest vanusest alates toimub lihaste jõudu ja kontraktsiooni ning lõõgastumise kiirust iseloomustavate parameetrite oluline langus, ja millised faktorid neid muutusi põhjustavad. Samuti on vähe uuritud nimetatud muutuste soolisi iseärasusi.

Elektrostimulatsiooniga esile kutsutud lihase üksikkontraktsiooni jõud suureneb pärast lühiajalist (5–10 s) tahtelist maksimaalset pingutust ja seda nähtust nimetatakse aktiivsusjärgseks potentseerumiseks. Nimetatud fenomeni seostatakse eelkõige müosiini kergete ahelate fosforüülumisega kontraktsiooni käigus, mis suurendab regulaatorvalk troponiini tundlikkust Ca^{2+}-ioonide suhtes ning mille tulemusena suureneb ristisillakeste arv ja nende formeerumise kiirus lihaskontraktsioonil. Uuringud on näidanud aktiivsusjärgse potentseerumise vähenemist erinevates lihastes vananemisel. Pole teada millisest vanusest need muutused muutuvad oluliseks ja kas ning kuidas erineva iseloomuga kehaline aktiivsus neid muutusi mõjutab.

On selgitatud, et süstemaatiline jõutreening parandab skeletilihaste kontraktiilseid omadusi nii naistel kui ka meestel ning aitab vähendada vananemisega seotud funktsionaalseid muutusi lihastes. Samuti on uuritud vastupidavustreeningu mõju inimese skeletilihaste kontraktiilsetele omadustele. Seejuures puuduvad andmed naiste seas populaarse harrastusvõimlemise (tavaliselt venitus-, jõu- ja vastupidavusharjutuste kombinatsioon) mõju kohta skeletilihaste kontraktiilsetele omadustele seoses vanusega.

Uurimistöö eesmärk ja ülesanded

Eelpool toodud probleemist lähtuvalt oli käesoleva töö peaeesmärgiks selgitada ealisi muutusi skeletilihaste kontraktiilsetes omadustes naistel seoses aktiivsusjärgse potentseerumise ja kehalise aktiivsusega. Uuringu objektiks oli sääre kolmpealihas, mis on aktiivne nii liigutustegevusel kui ka kehaasendite säilitamisel. Töös püstitati järgmised ülesanded:

1. Uurida sääre kolmpealihase tahtelist isomeetrilist maksimaaljõudu ja elektrostimulatsiooniga esile kutsutud isomeetrilise üksikkontraktsiooni parameetreid 20–70-aastastel naistel.
2. Selgitada sääre kolmpealihase üksikkontraktsiooni aktiivsusjärgse potentseerumise iseärasused erinevas vanuses naistel.
3. Selgitada harrastusvõimlemise mõju sääre kolmpealihase kontraktiilsetele omadustele noortel ja keskealistel naistel.

Vaatlusalused ja metoodika

Vaatlusalused. Vaatlusaluste (vanuses 20–77 eluaastat, n=186) kehaline aktiivsus ja tervislik seisund selgitati välja ankeetküsitluse põhjal. Uuring viidi läbi Tartu Ülikooli kinesioloogia ja biomehaanika laboris. Uuring oli kooskõlastatud Tartu Ülikooli Inimuuringute Eetika Komiteega.

Elektrostimulatsioon. Sääre kolmpealihaste kontraktiilsete omaduste määramiseks kasutati elektrostimulatsiooni meetodit. Vaatlusalune fikseeriti spetsiaalselt konstrueeritud dünamomeetrilisele seadmele. Labajalg asetati dünamomeetriga ühendatud pedaalile, kusjuures nurk hüppeliigeses moodustas 85°. Elektriärritust andev elektrood asetati sääre kolmpealihast innerveeriva sääreluunärvi (*n. tibialis*) projektsioonile põlveõndlas ja maanduselektrood reie distaalsele osale. Sääre kolmpealihase supramaksimaalne isomeetriline üksikkontraktsioon kutsuti esile ristkülikukujulise ärritusimpulsiga, mille kestus oli 1 ms. Sealjuures kasutati alalisvoolu, mille pinge oli 150 V. Labajala surve (vastu pedaali) muutuse tulemusena saadud dünamogrammilt registreeriti järgmised sääre kolmpealihase isomeetrilise üksikkontraktsiooni näitajad nii puhkeolekus kui ka vahetult peale tahtelist 5 s kestnud maksimaalset pingutust (potentseerunud seisundis): maksimaaljõud, kontraktsioonifaasi kestus, poole lõõgastuse aeg, maksimaalne jõugradient kontraktsiooni- ja lõõgastusfaasis. Arvutati üksikkontraktsiooni maksimaaljõu aktiivsusjärgne potentseerumine ning määrati tahteline isomeetriline maksimaaljõud.

Uurimistöö põhitulemused

Töö tulemused näitavad, et naistel vähenevad sääre kolmpealihase tahteline isomeetriline maksimaaljõud, samuti elektrostimulatsiooniga esile kutsutud üksikkontraktsiooni maksimaaljõud ning lihase lõõgastumise kiirust iseloomustavad näitajad oluliselt pärast 50. eluaastast. Pärast 40. eluaastat hakkab naistel sääre kolmpealihase elektrostimulatsiooniga esile kutsutud üksikkontraktsiooni kontraktsioonifaasi kestus oluliselt pikenema ja kontraktsiooni kiirus vähenema. Alates 70. eluaastast hakkab neil sääre kolmpealihase üksikkontraktsiooni jõu aktiivsusjärgne potentseerumine oluliselt vähenema. Harrastusvõimlemine ei mõjuta märkimisväärselt sääre kolmpealihase tahtelist maksimaaljõudu ja elektrostimulatsiooniga esile kutsutud üksikkontraktsiooni näitajaid noortel ja keskealistel naistel. Seejuures keskealistel harrastusvõimlemisega tegelevatel naistel ei esinenud sääre kolmpealihase tahtelise maksimaaljõu ja elektrostimulatsiooniga esile kutsutud üksikkontraktsiooni näitajates olulist erinevust võrreldes noorte kehaliselt inaktiivsete naistega. Keskealistel kehaliselt inaktiivstel naistel olid lihaste kontraktiilsed omadused võrreldes noorte inaktiivsete naistega oluliselt alanenud. Seega regulaarne harrastusvõimlemisega tegelemine vähendab naistel lihaste kontraktiilsete omaduste langust keskeas.

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PUBLICATIONS

Paper I

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Paper II

Kuu S., Ereline J., Gapeyeva H., Kolts I., Pääsuke M.
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Paper III

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TWITCH CONTRACTILE PROPERTIES OF PLANTARFLEXOR MUSCLES IN YOUNG AND MIDDLE-AGED RECREATIONALLY PHYSICALLY ACTIVE AND NONACTIVE WOMEN

Running head: Twitch contractile properties in women

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

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ABSTRACT

Background and aims: This study examined the effect of recreational physical activity on the contractile properties of skeletal muscles in middle-aged vs. young women. **Methods:** A total 74 young (20–29-year-old) and middle-aged (45–54-year-old) women participated. The subjects were distributed into four groups: (1) young recreationally physically active (RPA) (N=19), (2) young recreationally physically nonactive (RPN) (N=21), (3) middle-aged RPA (N=23) and (4) middle-aged RPN (N=16). RPA women exercised regularly in groups of recreational gymnastics 2–3 times per week. Isometric twitch of the plantarflexor muscles was evoked by supramaximal electrical stimulation of tibial nerve in resting and post-activation potentiation state. **Results:** A greater resting twitch maximal rate of force development (RFD), and potentiated twitch peak force (PF) and maximal rate of relaxation (RR) were observed in the young RPA women compared with two middle-aged women groups. In young RPN women, these characteristics were greater compared to the middle-aged RPN women, whereas they did not differ significantly when compared to the middle-aged RPA women. A shorter resting and potentiated twitch contraction time, and a greater potentiated twitch maximal RFD were found in the young compared with the middle-aged women groups. There were no significant differences in twitch characteristics between RPA and RPN women of similar age. **Conclusions:** The recreational gymnastic type physical activity did not have a marked effect on twitch contractile properties in young and middle-aged women. A reduced speed of isometric twitch contraction was found in middle-aged women, which was more pronounced in post-activation potentiation state.

INTRODUCTION

The human neuromuscular system is known to undergo significant structural and functional changes with increasing age. Reduced isometric maximal voluntary contraction (MVC) force and isokinetic peak torque are major well-known functional impairments in neuromuscular system associated with ageing. It has been established that the change in electrically evoked twitch contractile properties of the human skeletal muscles, which can be used as a direct measure of the force-generation and force-potentiation capacity, speed of contraction and relaxation of the muscle fibres, is also a typical feature of ageing (1–5). Age-related reductions in muscle force-generation capacity and speed of contraction has been attributed to the reduced number of both type I (slow-twitch) and type II (fast-twitch) fibres, and type II fibres atrophy (5–7). The other factor that may be responsible for the slowing of muscle contraction with age could be related to alterations in the excitation-contraction coupling process (8). Contractile changes in human skeletal muscles in older age (after 60 years of age) have been well documented. However, in a smaller number of studies have been assessed twitch contractile characteristics of skeletal muscles in middle-aged subjects (2, 3).

Age-related decrease in muscle function is often combined with a sedentary lifestyle in middle and older ages (5). Regular physical activity has been commonly advocated as an approach to reduce the impact of ageing on human neuromuscular function (9–11). Most previous ageing studies assessing the effect of physical activity on contractile properties of skeletal muscles have involved a comparison of two separated age groups: young versus older, and usually measurements of strength (resistance) training (12–16). However, the effect of long-term recreational gymnastics practised often by women (aerobics, flexibility and stretching exercises) on age-related changes in contractile properties of skeletal muscles in middle age is not well understood.

The force of an electrically evoked twitch is greater after a brief MVC compared with the corresponding value at rest and this enhancement has been termed post-activation potentiation (PAP) (17, 18). The mechanism responsible for PAP is considered to be phosphorylation of myosin regulatory light chain (R-LC) during the MVC, which renders actin-myosin more sensitive to Ca^{2+} in a subsequent twitch (19, 20). The most important muscle characteristic affecting the magnitude of PAP is fibre type (18). The greater PAP in fast-twitch fibres is probably related to their greater capacity of myosin regulatory light chain phosphorylation in response to conditioning contraction (19). A decrease in PAP with increased age has been reported (2, 4, 18, 21). Thus, the impairment of the mechanism of PAP is conditioned by ageing, yet it is not clear at which age this impairment in muscle function begins and how it is related with habitual physical activity. Less attention has been paid to the influence of recreational physical activity on PAP in middle-aged subjects.

The aim of this study was to measure the effect of recreational physical activity on twitch contractile properties of skeletal muscles in middle-aged vs. young women. The isometric MVC force and supramaximal isometric twitch characteristics in resting and post-activation potentiation state were compared among the groups of recreationally physically active (RPA) and recreationally physically nonactive (RPN) young and middle-aged women. Recordings were performed from the plantarflexor muscles which are important in posture and movement and are involved in many everyday, working and sport activities.

METHODS

Subjects

A total 167 women aged 20 to 54 years were initially screened via telephone regarding physical activity habits and general health status. The initial screening determined the subjects who participated more than 3 hours per week in recreational gymnastic exercise and those who did not participate in recreational physical activity (control subjects), at the time they were invited to the laboratory. The total of 74 women agreed o participate in the present study. Depending on their age and leisure-time physical activity, the subjects were distributed into four groups: (1) young RPA (aged 20–29 years, N=19), (2) young RPN (aged 20–29 years, N=21), (3) middle-aged RPA (aged 45–54 years, N=23) and (4) middle-aged RPN (aged 45–54 years, N=11). All subjects were screened by a questionnaire to exclude those with diagnosed musculoskeletal and cardiovascular disorders. Only pre-menopausal middle-aged women were recruited. All women were tested during the follicular phase of menstrual cycle (days 3–10 after the onset of menstrual cycle). All subjects completed a structured questionnaire to assess their leisure-time, home and work-related physical activity. Women were considered RPA if they performed > 3 h of recreational physical activity per week for longer than 12 months. All RPA women exercised regulary in groups of recreational gymnastics (aerobics, flexibility and stretching exercises) 2–3 times per week. None of them had any background in competitive sports of any kind. The RPN women were not involved in recreational physical activity in leisure-time. According to the questionnaire, the home- and work-related physical activity, assessed by time spent on feet, i.e. walking and standing (hours per day) did not differ significantly between RPA and RPN women of similar age. The physical characteristics, indicator of home- and work-related physical activity (time spent on feet, i.e. walking + standing) and MVC force of the plantarflexor muscles of the subjects are presented in Table 1. 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 for Human Studies.

Experimental design

During the measurement, the subjects were seated in a specially designed chair with the dominant leg flexed to 90° at the knee and mounted inside a metal frame (3). The foot was connected to an aluminium footplate by inelastic Velcro straps at the location. 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 20º to ensure maximal voluntary and stimulated forces, the situation presumably corresponding to the "optimal" muscle length (22). An adjustable pad held down the kneecap and the front side of the thigh. A strain-gauge transducer (0.5% accuracy) connected on the footplate by a rigid bar sensed 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 collecting data the subjects were given instructions and the testing of isometric MVC force of plantarflexor 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. All subjects were evaluated at the same time of day in the experimental room with the temperature of 23°C. On reporting to the laboratory, each subject sat resting for approximately 30 minutes before commencing the experiment to minimize any potentiation effect from walking to the laboratory.

To measure isometric MVC force of the plantarflexor muscles, the subjects were instructed to push the footplate as forcefully as possible for 2–3 s. Strong verbal encouragement and visual feedback were provided during contractions to motivate the subjects. The greatest force of the three maximal efforts was taken as the isometric MVC force. A rest of 2 min was allowed between each of three attempts. MVC force relative to body mass was calculated.

To determine the contractile properties of the plantarflexor 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 (5x5 cm) was placed over the tibial nerve in popliteal fossa and the anode (5x10 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).

The stimulation intensity was controlled by evoked compound action potential (M-wave) peak-to-peak amplitude of the soleus muscle recorded using bipolar (20 mm interelectrode distance) electromyogram (EMG) electrodes (Beckman miniature skin electrodes). The electrodes were placed longitudinally on the motor point area of the soleus muscle determined by electrical stimulation after the skin had been cleaned using alcohol swabs and abraded lightly with fine sand paper. As a reference electrode a large carbon rubber plate (Nemectron, 7 x 12.5 cm) was placed over the proximal part of the triceps surae muscle between the stimulating and recording electrodes. The EMG signals were amplified and displayed using a Medicor MG-440 (Budapest, Hungary) preamplifier with a frequency band ranging from 1 Hz to 1 kHz. These signals were sampled at 1 kHz. During 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-s intervals and the voltage was increased in increments of 20–25 V until maximal twitches were reached. The maximal amplitude of the M-wave was used as a criterion for determining the supramaximal intensity of the stimulus.

Isometric twitches of the plantarflexor muscles were elicited after the subject had rested for 15 min. After the resting twitch had been recorded, the subject was instructed to hold a MVC for 5 s and then to relax. A second (potentiated) twitch took place within 2 s after the onset of relaxation. Skin temperature of the muscle group tested was continuously controlled and maintained at 35ºC using an infrared lamp. The following characteristics of the isometric twitch were calculated: twitch peak force (PF) – 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 derivation of the development of force (dF/dt) and maximal rate of relaxation (RR) as the first derivation of the decline of force (–dF/dt). The percentage increase in potentiated twitch PF in relation to that at rest was taken as an indicator of PAP. The test was conducted in the following sequence: twitch at rest, MVC and potentiated twitch.

Statistical analysis

The results are expressed as means and standard deviations (±SD). An one-factor ANOVA with Tukey post hoc test was used to compare the anthropometric parameters, isometric MVC force and twitch contractile characteristics between the groups. A level of $p<0.05$ was selected to indicate statistical significance.

RESULTS

Anthropometric characteristics and isometric MVC force

Anthropometric characteristics and isometric MVC force of the plantarflexor muscles for the all groups studied are presented in Table 1. There were no significant differences in body height and body mass between the measured groups. In the young RPA women, body mass index was smaller ($p<0.05$) compared with the two middle-aged women groups, whereas it did not differ significantly when compared with the young RPN women. Isometric MVC force of the plantarflexor muscles was greater ($p<0.05$) in the young RPA compared with the middle-aged RPN women, whereas did not differ significantly in two young women groups and middle-aged RPN women. There were no significant differences in isometric MVC force between RPA and RPN women of similar age. The isometric MVC force relative to body mass was greater ($p<0.05$) in the young RPA women compared with the other measured groups. The differences in isometric MVC force relative to body mass between the young RPN and two middle-aged women groups were not significant.

Twitch contractile characteristics
No significant differences in isometric resting twitch PF were observed between the measured groups. The potentiated twitch PF was greater ($p<0.05$) in the young RPA women than in two middle-aged women groups. In the young RPN women, potentiated twitch PF was greater ($p<0.05$) compared with the middle-aged RPN women, whereas it did not differ significantly when compared with the middle-aged RPA women. The differences in potentiated twitch PF between RPA and RPN women of similar age were not significant. Potentiated witch PF was greater ($p<0.05$) compared with the resting twitch in all measured groups (Fig. 1a).

PAP was greater ($p<0.05$) in the young RPA women compared with two middle-aged women groups (Fig. 1b). There were no significant differences in PAP between the young RPN women and two middle-aged women groups. PAP did not differ significantly in RPA and RPN women of similar age.

Resting and potentiated twitch CT was shorter ($p<0.05$) in the young compared with the middle-aged women's groups (Fig. 2a). No significant differences in resting twitch CT were observed between RPA and RPN women of similar age. In the young RPA women, potentiated twitch CT was shorter ($p<0.05$) than in the young RPN women. This characteristic did not differ significantly in the middle-aged RPA and RPN women. Potentiated twitch CT was significantly shorter compared with resting twitch in the young and middle-aged RPA women, whereas it did not differ significantly in two young women's groups and middle-aged RPN women. There were no significant differences in resting and potentiated twitch HRT between the measured groups (Fig. 2b). Resting and potentiated twitch HRT did not differ significantly in measured groups.

Resting and potentiated twitch maximal RFD was greater ($p<0.05$) in the young RPA women compared with two middle-aged women groups (Fig. 3a). In the young RPN women, resting twitch maximal RFD was greater ($p<0.05$) compared with the middle-aged RPN women, and potentiated twitch maximal RFD greater ($p<0.05$) compared with two middle-aged women groups. The differences in resting and potentiated twitch maximal RFD between RPA and RPN women of similar age were not significant. Potentiated twitch RFD was greater ($p<0.05$) compared with resting twitch in all measured groups. There were no significant differences in resting twitch maximal RR between the measured groups (Fig. 3b). The potentiated twitch maximal RR was greater ($p<0.05$) in the young RPA women compared with the two middle-aged women groups. In the young RPN women, potentiated twitch maximal RR was greater ($p<0.05$) than in the middle-aged RPN women, whereas it did not differ significantly when compared with the middle-aged RPA women. The differences in potentiated twitch maximal RR between RPA and RPN women of similar age were not significant. Potentiated twitch RR was greater ($p<0.05$) compared with resting twitch in the two young women groups and middle-aged

RPA women. Resting and potentiated twitch maximal RR did not differ significantly in the middle-aged RPN women.

DISCUSSION

The objective of this study was to examine the impact of recreational gymnastics type physical activity on contractile properties of the plantarflexor muscles in the young and middle-aged women. Our data indicated that long-term recreational gymnastics did not have a remarkable effect on isometric MVC force of the plantarflexor muscles. No significant differences in MVC force were observed between the RPA and RPN women of similar age. The young RPA women produced greater isometric MVC force compared with the middle-aged RPN women, whereas differences between other measured groups were not significant. The decrease in muscle maximal voluntary strength with increasing age has been attributed in part to the impairment of neural control and in part to changes in muscle fibre composition and muscle mass (23, 24) which is related, possibly, to alterations in hormonal balance (25) and the decline in quantity and intensity of habitual physical activity (26). In the present study, the middle-aged pre-menopausal women were measured and therefore, hormonal changes did not have a marked influence. It has been indicated that between 20 and 55 years, isometric MVC force of different muscle groups decreased by 8–10% in healthy women (27), whereas legs lost isometric strength at a faster rate than arms (28). Our previous results indicated that in habitually women a significant reduction in isometric MVC force of the plantarflexor muscles takes place after 50 years of age (3).

In this study, resting twitch PF did not differ significantly in measured groups. The differences in potentiated twitch PF between RPA and RPN women of similar age were not significant. The potentiated twitch PF was greater in two young women's groups compared with the middle-aged RPN women, whereas it did not differ significantly in the young RPN and middle-aged RPA women. These findings suggest that potentiated twitch PF is sensitive to ageing, whereas recreational physical activity in middle-age reduces age-related decrease in muscle force-generation in potentiated state.

PAP is enhancement of twitch force after MVC. The most accepted mechanism of PAP is phosphorylation of myosin regulatory light chains (R-LC) during the conditioning MVC, which renders actin-myosin more sensitive to Ca^{2+} in subsequent contraction (19, 20). The phosphorylation of myosin R-LC in human skeletal muscle has been observed in response to brief maximal contraction (20). Myosin R-LC phosphorylation has been thought to produce twitch potentiation by measuring the force development for any given submaximal intracellular Ca^{2+} level (29, 30). It has been proposed that phosphorylation of myosin R-LC increases the possibility that cross-bridges will enter the force-producing state, resulting in a higher proportion of active cross-bridges at any given time during twitch (31, 32). Previous investigators indicated a reduction in twitch PAP in plantarflexor muscles with ageing (4, 18, 21). In the present study, PAP was greater in the young RPA women compared with two middle-aged women groups, whereas it did not differ significantly in the young RPN women when compared to two middle-aged women's groups. There were no significant differences in PAP between RPA and RPN women of similar age. Thus, these results suggest that mechanism of PAP is not significantly influenced by recreational physical activity.

The present study is in good agreement with previous studies that reported prolongation of electrically evoked isometric twitch CT in human muscles with increasing age (1, 33). Resting twitch and potentiated twitch CT was prolonged in the middle-aged compared with the young women's groups. The present study suggests that age had a more marked effect on time course of isometric twitch than leisure-time physical activity. The time course of isometric twitches has been found to depend on the kinetics of the excitation-contraction coupling mechanisms, including intracellular Ca^{2+} movements (29). The prolonged twitch CT of middle-aged individuals suggests decreased efficiency in the function of the sarcoplasmatic reticulum to release Ca^{2+} (8).

This study demonstrated that resting twitch maximal RFD was greater in the young RPA women compared with two middle-aged women's groups, while it did not differ significantly in the young RPN and middle-aged RPA women. A marked age-related decrease in potentiated twitch maximal RFD was observed in middle-aged women in the present study. 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 (34). 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 (6).

No significant differences in resting and potentiated twitch HRT were observed in measured groups in the present study. This is in contrast to the previous findings indicating a marked prolongation of twitch HRT in plantarflexor muscles in the middle-aged compared with the young women (2). There were no significant differences in resting twitch maximal RR between the measured groups. However, the potentiated twitch maximal RR was greater in the young RPA women compared with two middle-aged women's groups. In the young RPN women, potentiated twitch RR was greater compared with the middle-aged RPN women, while it did not differ significantly when compared with the middle-aged RPA women. Two main factors are responsible for the rate of muscle relaxation: sarcoplasmatic reticulum Ca^{2+} uptake and the rate of cross-bridge kinetics (37). The decreased rate of relaxation in muscles is an indicator of reduced efficiency of the sarcoplasmatic reticulum to re-uptake Ca^{2+} (8). The differences in potentiated twitch RR between RPA and RPN women of similar age were not significant in the present study. These findings suggest that mechanisms responsible for the rate of muscle relaxation are not significantly influenced by recreational physical activity.

Several studies reported significant changes in electrically evoked contractile characteristics in older age following long-term resistance (strength) type exercise (12, 13, 15, 16). In this study, recreational gymnastics type physical activity (aerobics, flexibility and stretching exercises) in young and middle-aged women was not predominantly resistance type and would not necessarily have strong influence on muscle contractile characteristics.

The present study has some limitations. Despite the self-reported leisure-time physical activity level utilized in the present study, nothing can be inferred about the frequency, duration and intensity of the recreational physical activity performed by the young and middle-aged RPN women.

CONCLUSIONS

It can be concluded that recreational gymnastic type physical activity did not have a marked effect on the maximal voluntary force-generation capacity and evoked twitch contractile properties of the plantarflexor muscles in young and middle-aged women. However, the middle-aged recreationally physically active women did not have a significant decrease in twitch force-generation and post-activation potentiation capacity in plantarflexor muscles compared with the young recreationally physically nonactive women, whereas the middle-aged recreationally physically nonactive women did. A reduced speed of isometric twitch contraction was found in middle-aged women, which was more pronounced in post-activation potentiation state. Thus, these findings suggest that in women, middle-ages is characterised by decreased efficiency in the function of sarcoplasmic reticulum to release Ca^{2+} and by reduced rate of formation cross-bridges between myosin and actin during isometric twitch contraction.

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Table 1. Mean (±SD) anthropometric characteristics, indicator of home- and work-related physical activity, and isometric MVC force of the plantarflexor muscles in subjects.

Variables	Groups			
	Young RPA (N = 19)	Young RPN (N = 21)	Middle-aged RPA (N = 23)	Middle-aged RPN (N = 11)
Age (years)	24.4 ± 2.5	24.0 ± 2.8	48.5 ± 2.9	49.2 ± 3.3
Height (cm)	167.2 ± 6.6	167.6 ± 6.9	163.4 ± 5.8	162.8 ± 7.6
BM (kg)	64.4 ± 9.3	67.3 ± 11.6	68.5 ± 12.6	67.4 ± 6.0
BMI (kg·m–2)	23.0 ± 2.7	24.0 ± 4.5	25.6 ± 3.9*	25.5 ± 2.5*
Time spent on feet				
(hours per day)	4,2±1,1	3,9±1,8	4,5±3,4	4,1±2,3
MVC force (N)	807 ± 123	728 ± 155	762 ± 163	651 ± 215*
MVC force: BM ($N \cdot kg^{-1}$)	12.6 ± 1.8	10.9 ± 1.8*	11.3 ± 1.9*	9.6 ± 3.0*

MVC: maximal voluntary contraction; RPA: recreationally physically active; RPN: recreationally physically nonactive; BM: body mass; BMI: body mass index.
* $p < 0.05$ compared to the young RPA women.

FIGURES

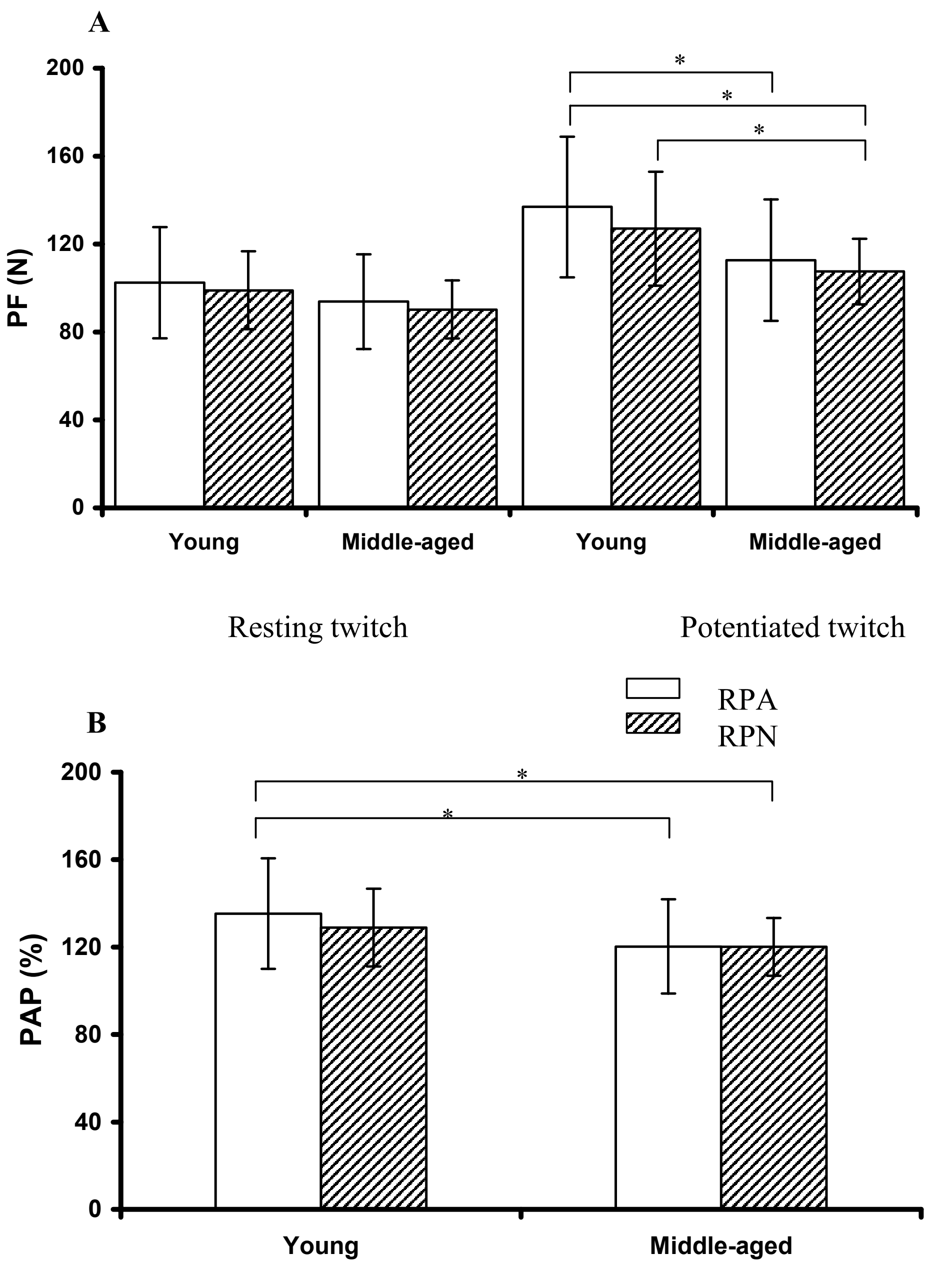

Figure 1. Mean (±SD) resting and potentiated twitch peak force (PF) (A) and post-activation potentiation (PAP) (B) in recreationally physically active (RPA) and nonactive (RPN) young and middle-aged women.
* $p < 0.05$; # $p < 0.05$ compared with resting twitch.

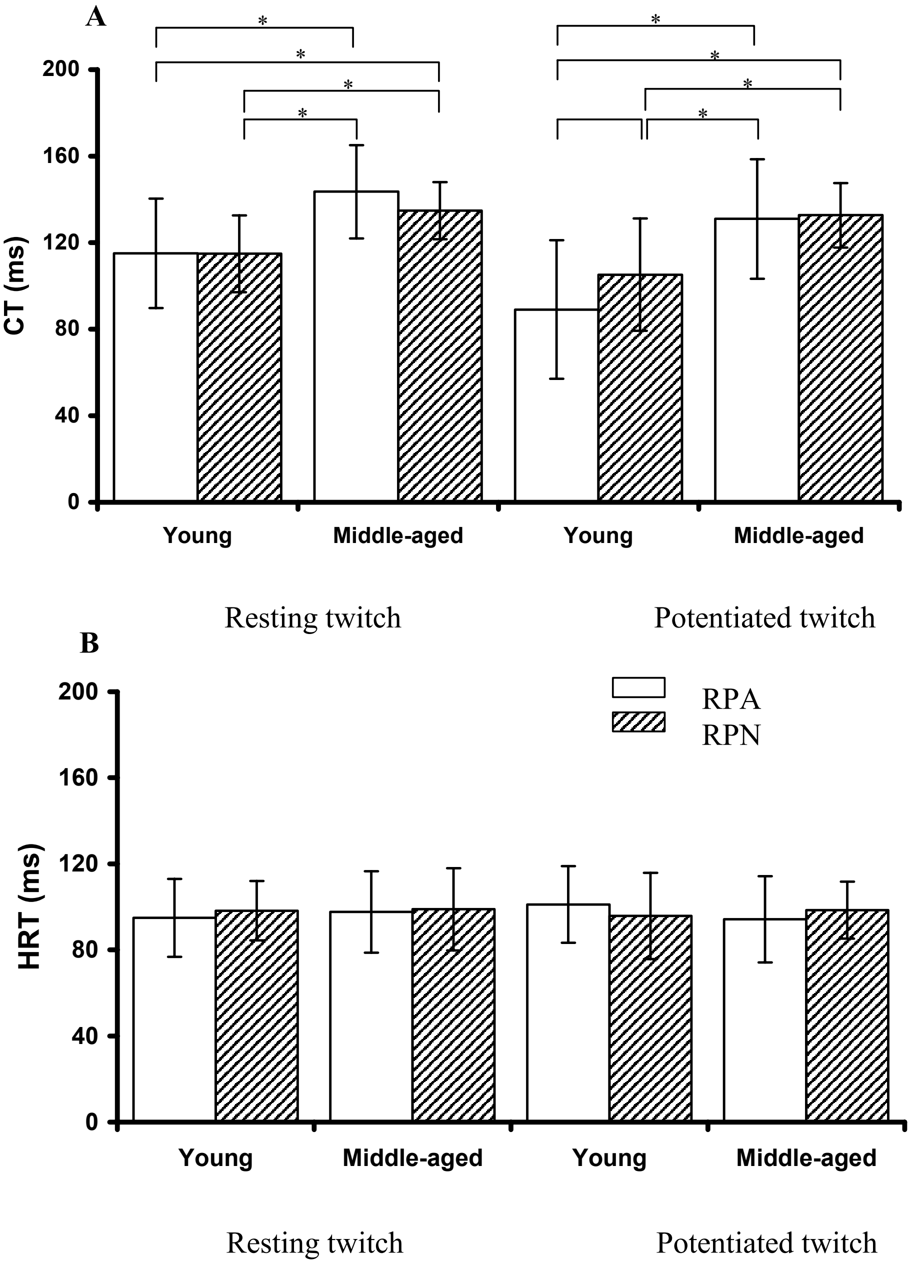

Figure 2. Mean (±SD) resting and potentiated twitch contraction time (CT) (A) and half-relaxation time (HRT) (B) in recreationally physically active (RPA) and nonactive (RPN) young and middle-aged women.
* $p < 0.05$; # $p < 0.05$ compared with resting twitch.

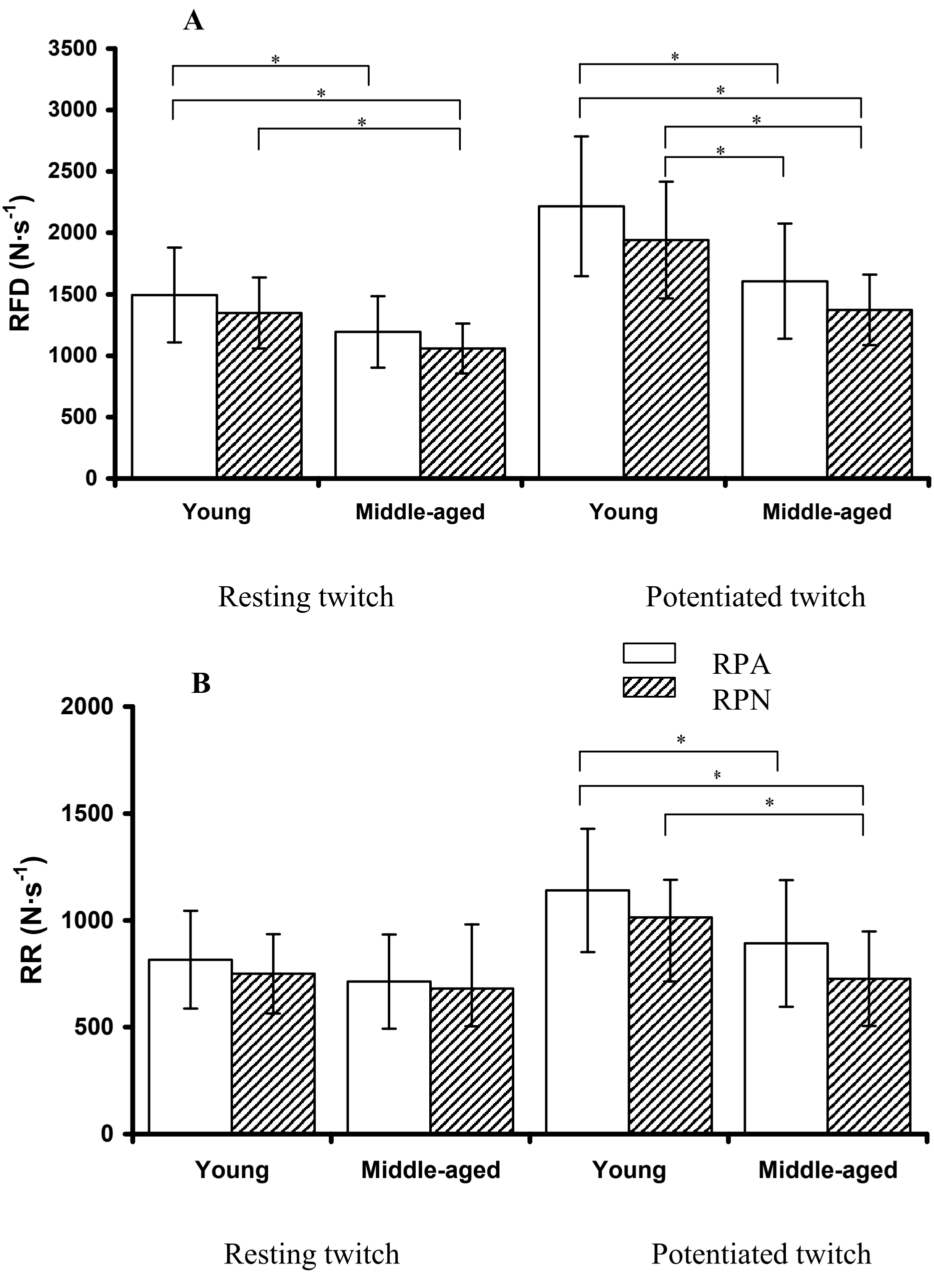

Figure 3. Mean (±SD) resting and potentiated twitch maximal rates of force development (RFD) (A) and relaxation (RR) (B) in recreationally physically active (RPA) and nonactive (RPN) young and middle-aged women.
* $p < 0.05$; # $p < 0.05$ compared with resting twitch.

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Alates 2003 M.I.Massaažikool, direktori asetäitja õppe- ja kasvatustöö alal, kutsepedagoog.

Erialaorganisatsioonid

- Eesti Füsioterapeutide Liit, tegevliige;
- Eesti Massööride Liit, juhatuse esimees alates 2003 a.

Teadustegevus

Peamised uurimisvaldkonnad:

- Motoorne võimekus võimlemisega tegelevatel naistel;
- Vananemisega seotud muutused skeletilihaste kontraktiilsetes omadustes naistel;
- Harrastusliku kehalise aktiivsuse mõju närvi-lihassüsteemi funktsioonidele erinevas eas naistel.

Publikatsioonid:

- Teaduslikud artiklid rahvusvahelise levikuga väljaannetes – 4;
- Muud teadusliku artiklid – 6;
- Konverentside teesid – 6.