

**CONTRACTILE PROPERTIES OF HUMAN
SKELETAL MUSCLES: ASSOCIATION
WITH SPORTS TRAINING, FATIGUE
AND POSTTETANIC POTENTIATION**

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS	7
ABBREVIATIONS	8
1. INTRODUCTION	9
2. REVIEW OF LITERATURE	11
2.1. Morpho-functional organization of human neuromuscular system.....	11
2.2. Contractile properties of skeletal muscles	13
2.2.1. Measurement of contractile properties of human skeletal muscles	13
2.2.2. Twitch potentiation	16
2.3. Adaptive changes in neuromuscular system during strength, power and endurance training.....	17
2.3.1. Strength and power training	17
2.3.2. Endurance training	20
2.4. Muscle fatigue.....	21
2.4.1. Physiological characterization of muscle fatigue.....	21
2.4.2. Muscle fatigue during maximal dynamic contractions	22
3. OBJECTIVES OF THE STUDY	25
4. MATERIALS AND METHODS	26
4.1. Subjects.....	26
4.2. Study design	26
4.3. Methods	28
4.3.1. Isometric dynamometry and electrical stimulation	28
4.3.2. Isokinetic dynamometry	32
4.4. Statistical evaluation of the data.....	33
5. RESULTS.....	35
5.1. Isometric maximal voluntary and evoked twitch contraction characteristics of plantarflexor muscles in power and endurance-trained athletes and sedentary subjects.....	35
5.1.1. Maximal voluntary contraction force.....	35
5.1.2. Twitch peak force	36
5.1.3. Postactivation potentiation.....	36
5.1.4. Time-course characteristics of isometric twitch	37
5.1.5. Twitch maximal rates of force development and relaxation....	38
5.1.6. Correlation analysis	39
5.2. Changes in contractile properties of knee extensor muscles after fatiguing maximal isokinetic contractions in power-lifters and sedentary subjects.....	40

5.2.1. Contractile changes in knee extensor muscles after 30 maximal isokinetic contractions	40
5.2.2. Results of correlation analysis.....	44
5.3. Changes in contractile properties of knee extensor muscles after high-frequency submaximal percutaneous electrical stimulation.....	45
5.3.1. Changes in conditioning tetanic contraction force	45
5.3.2. Changes in twitch, doublet and 10 Hz tetanic contraction characteristics.....	45
6. DISCUSSION	48
6.1. Maximal voluntary and evoked twitch contraction characteristics of plantarflexor muscles in power and endurance-trained athletes and sedentary subjects	48
6.2. Contractile changes in knee extensor muscles after fatiguing maximal isokinetic contractions.....	51
6.3. Posttetanic potentiation in knee extensor muscles after high-frequency submaximal percutaneous electrical stimulation.....	54
CONCLUSIONS.....	57
REFERENCES	58
SUMMARY IN ESTONIAN	71
ACKNOWLEDGEMENTS	74
PUBLICATIONS	75

LIST OF ORIGINAL PUBLICATIONS

The work is based on the following publications:

- I. **Pääsuke M., Ereline J., Gapeyeva H.** Twitch potentiation capacity of plantarflexor muscles in endurance and power athletes. *Biology of Sport*, 1998, 15 (3): 171–178.
- II. **Pääsuke M., Ereline J., Gapeyeva H.** Twitch contractile properties of plantar flexor muscles in power and endurance trained athletes. *European Journal of Applied Physiology and Occupational Physiology*, 1999, 80 (5): 448–451.
- III. **Pääsuke M., Ereline J., Gapeyeva H., Torop T.** Twitch contractile properties of plantarflexor muscles in female power-trained athletes. *Medicina dello Sport*, 2002, 55 (4): 279–286.
- IV. **Ereline J., Gapeyeva H., Pääsuke M.** Contractile changes in knee extensor muscles after repetitive maximal isokinetic contractions in male power-lifters and untrained subjects. *Medicina dello Sport*, 2004, 57 (1): 29–39.
- V. **Requena B., Ereline J., Gapeyeva H., Pääsuke M.** Posttetanic potentiation in knee extensors after high-frequency submaximal percutaneous electrical stimulation. *Journal of Sport Rehabilitation*, 2005, 14 (3): 258–267.

ABBREVIATIONS

ATP	—	adenosine triphosphate
ATPase	—	adenosine triphosphatase
BM	—	body mass
BMI	—	body mass index
CT	—	contraction time
EMG	—	electromyography, electromyogram
FI	—	fatigue index
FF	—	fast fatiguable
FG	—	fast-twitch glycolytic
FOG	—	fast-twitch oxidative-glycolytic
FR	—	fatigue resistant
FT	—	fast-twitch
HRT	—	half-relaxation time
LAT	—	latency time
MU	—	motor unit
MVC	—	maximal voluntary contraction
PAP	—	postactivation potentiation
PES	—	percutaneous electrical stimulation
PF	—	peak force
pH	—	activity of hydrogen ions in solution
PT	—	peak torque
PTP	—	posttetanic potentiation
RFD (dF/dt)	—	rate of force development
RR (-dF/dt)	—	rate of relaxation
SO	—	slow-twitch oxidative
ST	—	slow-twitch
TWO	—	total mechanical work output
VO ₂ max	—	maximal oxygen uptake

1. INTRODUCTION

Exercise training induces an adaptation in the human neuromuscular system through changes in the neural control as well in the structure and function of the skeletal muscles. It is well known that strength and power-trained athletes demonstrate greater isometric MVC force as well as power output than endurance-trained athletes. However, the extent to which neural and/or muscular factors explain these differences has not been well documented.

The measurement of electrically evoked twitch or tetanic contraction characteristics has been used for the evaluation of the nature of muscular adaptation during exercise training independent from neural factors, i.e. from the influence of the skill or motivation of the subject. The measurement of the changes in electrically evoked twitch contractile properties of the human skeletal muscles has been used to study the adaptation of peripheral neuromuscular system mainly to heavy-resistance strength training (Davies & Young, 1982; Sale *et al.*, 1983; Davies *et al.*, 1985; Alway *et al.*, 1989; Ishida *et al.*, 1990; Aagaard, 2003). However, the results of these studies have been controversially reported. It has been shown that isometric MVC force may increase without a corresponding increase in evoked twitch PF (McDonagh *et al.*, 1983; MacIntosh & Gardiner, 1987; Ishida *et al.*, 1990), suggesting that increase in voluntary strength was largely the result of neural adaptation. Schmidtbleicher *et al.* (1981 & 1988) found a significant shortening in twitch CT after 8-week strength training period, whereas changes in the opposite direction (prolongation) of twitch HRT were established. On the other hand, the prolongation of twitch CT has been reported in cross-sectional studies comparing weightlifters to untrained subjects (Sale *et al.*, 1982a; Sleivert *et al.*, 1995). However, longitudinal studies have reported no changes (Duchateau & Hainaut, 1984; Davies *et al.*, 1985; Kyröläinen & Komi, 1994), or shortening in twitch CT (Davies & Young, 1982; Alway *et al.*, 1988) after strength training. Alway *et al.* (1988) found that twitch CT in plantarflexor muscles was 20% longer in strength-trained athletes compared to endurance-trained athletes. An increase in twitch PF and prolongation of CT was recorded in weight trainers compared to controls (Sale *et al.*, 1983). However, less is known about the changes in twitch contractile properties of skeletal muscles during prolonged power and/or endurance training.

Intensive muscular work leads to muscle fatigue, which is defined as any exercise-induced reduction in force-generation capacity (Edwards, 1981). Fatigue can be central and peripheral in origin. It has been found that in case of central fatigue, the recruitment of new MUs and/or firing frequency of the active MUs is lowered, while peripheral fatigue is primarily due to the failure of contractile process in active muscles (Bigland-Ritchie *et al.*, 1983). It has been suggested that continuous and/or intermittent heavy-resistance exercise results

in acute neuromuscular fatigue which is caused by a decrease in the force-generation capacity and/or decreased neural activation of the active muscles (Newham *et al.*, 1991). Neuromuscular fatigue following heavy-resistance exercise has been investigated mostly during repeated maximal isometric contractions (Kroll *et al.*, 1980), high-force eccentric contractions (Tiidus & Shoemaker, 1995), squat exercises (Raastad & Hallen, 2000) and explosive strength loading (Linnamo *et al.*, 1998). Less information is available in regard of fatigue-induced changes in twitch contraction characteristics of skeletal muscles during maximal isokinetic contractions. However, an examination of changes in twitch contractile properties during fatiguing maximal isokinetic contractions in well-trained strength athletes may provide additional information about the adaptation of the human neuromuscular system to the heavy-resistant strength training.

Neuromuscular electrical stimulation has been often used for the prevention and/or restoration of muscle function after injuries, and as a modality of strengthening in healthy subjects and highly trained athletes (Hainaut & Duchateau, 1992). It is commonly known that indirect or direct PES affects the contractile properties of skeletal muscles (Houston & Grange, 1991). This induced activation may evoke muscle fatigue but may also result in increased muscle force potentiation. Potentiation induced by electrical stimulation may be defined as staircase or the PTP. The phenomenon of PTP in different human skeletal muscles after submaximal high-frequency or low-frequency direct PES has been previously investigated. However, it is difficult to compare these studies with each other, as different muscle groups and electrical stimulation protocols have been used in them. The development of PTP in human muscles after brief high-frequency submaximal direct PES is not fully understood.

The first part of the present study was designed to compare the electrically evoked twitch contraction characteristics of the plantarflexor muscles, including PAP in male and female power-trained and male endurance-trained athletes, and male and female sedentary subjects. The second part of the study measured changes in isometric MVC and electrically evoked submaximal tetanic contraction characteristics of knee extensor muscles after repetitive maximal isokinetic knee extensions in male heavy-strength trained athletes (power-lifters) and sedentary men. In the third part of the study the effect of PTP induced by direct PES in knee extensor muscles on electrically evoked twitch, doublet and unfused tetanic contraction characteristics in healthy sedentary men was investigated.

2. REVIEW OF LITERATURE

2.1. Morpho-functional organization of human neuromuscular system

The human neuromuscular system consists of skeletal muscles innervated by α -motoneurons. The neural and muscular parts cannot be separated and it is appropriate to consider muscle fibres and α -motoneurons as one whole. A single α -motoneuron and the multiple branches of its axon, and muscle fibres that it innervates have been defined by Sherrington (1929) as MU. Most skeletal muscles comprise a few hundred MUs (McComas, 1996). The average number of muscle fibres innervated by a single α -motoneuron in human muscle ranges from about 5 for the lateral *rectus* (an eye muscle) up to about 2000 for the medial *gastrocnemius muscle* in the leg (Feinstein *et al.*, 1955). Since each α -motoneuron innervates several muscle fibres, a few hundred α -motoneurons are able to activate the thousands of muscle fibres that compose each muscle. The variation in the innervating number is the most significant factor that contributes to differences in MU force production (Kanda & Hashizume, 1989). The size of a α -motoneuron can be indicated by the diameter of the soma, the surface area of the cell body, the number of dendrites arising from the soma and the diameter of the axon (Tesch, 1988). Motoneurons innervating FT muscle fibres appear to be larger than those innervating ST muscle fibres (Enoka, 1997).

Each human muscle consists of small and large MUs. However, this classification of MUs is relative and can be used for describing MUs within a single muscle (Sjøgaard *et al.*, 1978; Sjöholm *et al.*, 1983). The functional characteristics of MUs (force-generation capacity and contraction speed of muscle fibres) are in direct correlation with size: larger MUs produce greater force and contract faster than smaller ones (Sjøgaard *et al.*, 1978; Burke, 1981, Brown & Loeb, 1999). On the basis of contractile properties (speed of contraction, force-generation capacity) and fatigability, the MUs in mammalian muscles have been classified into three main types (Burke, 1981): slow (type S), fast fatigue resistant (type FR) and fast fatigable (type FF).

The three types of MUs differ in certain physiological, histochemical and biochemical properties of their muscle fibres. Type S motor unit develops relatively small tension and resistance to fatigue. The muscle fibres which have high contents of mitochondrial enzymes, are low in glycogen, stain weakly for alkalistable myosin ATPase, and have rich capillary networks. These fibres appear to be well equipped for aerobic metabolism and hence for prolonged activity and have been classified as ST oxidative (type SO) (Peter *et al.*, 1972) or Type I (Engel, 1962). Type FR motor unit has intermediate properties. It has a fast twitch, develops moderate tension, and is resistant to fatigue. The muscle

fibres have high contents of glycogen and mitochondrial enzymes, and have considerable myosin ATPase activity; they are well supplied with capillaries. These fibres would be expected to work under both aerobic and anaerobic conditions and are therefore likely to be involved in prolonged sustained contraction as well as intense effort. These muscle fibres correspond to FT oxidative-glycolytic (type FOG) (Peter *et al.*, 1972) or type IIa (Brooke & Engel, 1969). Type FF motor unit has a fast twitch, commonly develops large tension, and is susceptible to fatigue. The muscle fibres have low contents of mitochondrial enzymes, are rich in glycogen, stain strongly for capillary network. They are suited for anaerobic metabolism and can engage in brief and strong contractions. These muscle fibres correspond to FT glycolytic fibres (type FG) (Peter *et al.*, 1972) or type IIb (Brooke & Engel, 1969). All muscle fibres in a single MU are of the same type (Emerson, 1987).

MUs are the smallest elements of neuromuscular control, and the activation of MUs is the final common path for all neural control strategies. Muscle force production in humans is controlled by the central nervous system through MU recruitment and modulation of firing rate (rate coding) of recruited MUs (Henneman *et al.*, 1965; Milner-Brown *et al.*, 1975; Burke, 1981; Gregorevic *et al.*, 2004). In addition, force production depends on the pattern and number of impulses when the impulse trains are brief, as in ballistic movements (Desmedt & Godaux, 1977). In most motor functions, there seems to be an orderly recruitment of MUs. According to Henneman's "size principle" (Henneman *et al.*, 1965), the motoneurons with slow-conducting axons innervating ST and fatigue-resistant muscle fibres appear to be recruited during voluntary and reflexory induced contractions before the motoneurons with fast-conducting axons innervating FT fatigable muscle fibres. It appears that some morphological (e.g. number of dendrites, axon diameter, innervation ratio), biophysical (e.g. input resistance, rheobase, after hypolarization) and input (e.g. Renshaw cell pool, group Ia afferent) characteristics correlate to the α -motoneuron size so that the smallest α -motoneurons can be excited more easily (Kugelberg & Thornell, 1983; Enoka, 1997). Type-specific differences in synaptic organization, the sensitivity of the neurotransmitter receptors and the average amount of neurotransmitter liberated at each synapse may also affect the recruitment pattern (Burke, 1981). As the force level increases, larger and faster MUs are recruited up to 40–80% MVC, depending on the muscle (Milner-Brown *et al.*, 1975; Edwards, 1981) after which the additional increase in force is accomplished with increased firing rate of the active MUs (Milner-Brown *et al.*, 1975; Gydikov *et al.*, 1982; Thomas *et al.*, 2002). At higher force levels this increase is mainly due to increased firing rate of the fast MUs, which may increase almost linearly up to 100% MVC, while slow MUs reach a saturation frequency of discharge at lower force levels of approximately 60%–80% MVC (Gydikov *et al.*, 1982; Alway *et al.*, 1988; Hamada *et al.*, 2003). Average MU

firing rates during MVC in humans range from 10 Hz in *soleus* muscle to approximately 30 Hz in *adductor pollicis* and *biceps brachii* muscles (Bellemare *et al.*, 1983). Typical submaximal MU firing rates in *biceps brachii* muscle range from 10 to 25 Hz with a target force of 10–65% MVC (Garland *et al.*, 1994).

Submaximal direct PES has often been used for the prevention of injuries and/or restoration of neuromuscular function after injuries, and as a modality of strengthening in healthy subjects (Hainaut & Duchateau, 1992) and elite athletes (Malatesta *et al.*, 2003; Brocherie *et al.*, 2005). The recruitment pattern of MUs during direct PES is different from that reported during voluntary contractions. Unlike the orderly recruitment of MUs during low intensity voluntary contractions in which slow MUs with small ST muscle fibres are activated first during direct PES, both the large fast MUs with FT muscle fibres as well as small slow MUs appear to be recruited at relatively low contraction intensities (Feiereisen *et al.*, 1997). It has been indicated that during direct PES FT muscle fibres with greater force-generation and force-potential capacity can be activated at relatively low stimulation intensities because of their large axons, which have lower electrical resistance for the given externally applied electrical current (Knaflitz *et al.*, 1990; Sinacore *et al.*, 1990).

2.2. Contractile properties of skeletal muscles

2.2.1. Measurement of contractile properties of human skeletal muscles

The contractile properties of skeletal muscles are investigated using electrical stimulation techniques. The analysis of the recorded force signal provides information about the mechanical features of a muscle. Electrical stimulation techniques, when used to induce involuntary twitches or tetanic contractions, can be used to measure the force-generation capacity of muscles and time-course of muscular contraction independent of volition and are not influenced by the skill or motivation of the subjects (Vandervoort *et al.*, 1983).

The contractile properties of human skeletal muscles are often studied by analysing the isometric force-time characteristics of a single twitch evoked by supramaximal electrical stimulation of motor nerve (indirect stimulation) or muscle belly (direct stimulation) by rectangular pulses of 0.2–1 ms (Vandervoort *et al.*, 1983; Vandervoort & Hayes, 1989; Pääsuke *et al.*, 2000b). The following characteristics of isometric twitch are calculated (Fig. 1): twitch PF – highest value of isometric force production, CT – the time to twitch PF, HRT – the time of half of decline in twitch PF, maximal RFD – the first derivate of the development of force during contraction (dF/dt) and maximal RR – the first derivate of decrease of force during relaxation ($-dF/dt$).

Twitch PF is direct indicator of evoked force-generation capacity of muscles, which is more expressed in FT (type II) than in ST (type I) muscle fibres (Gydikov & Kosarov, 1974; Alway *et al.*, 1989; Asmussen *et al.*, 2003). The time-course of isometric twitches has been thought to be highly dependent on the kinetics of excitation-contraction coupling, including intracellular Ca^{2+} movements (Klug *et al.*, 1988; Li *et al.*, 2002). Twitch CT has been found to be closely connected with the degree of sarcoplasmic reticulum development (Josephson, 1975), Ca^{2+} release and sequestration rate, and with Ca^{2+} concentration in the interfibrillar area (Salviati *et al.*, 1982). On the other hand, the rising phase on the development of an isometric contraction has been shown to be determined by net rate of cross-bridge attachment that is proportional to myosin ATPase activity (Drachman & Johnston, 1973). The twitch RFD has rarely been used as an indicator of contraction speed, which depends largely on the rate of formation of cross-bridges between myosin and actin (Lewis *et al.*, 1986). Two main factors have been described as responsible for the duration and rate of muscle relaxation: sarcoplasmic reticulum Ca^{2+} uptake and rate of cross-bridge kinetics (Westerblad *et al.*, 1997).

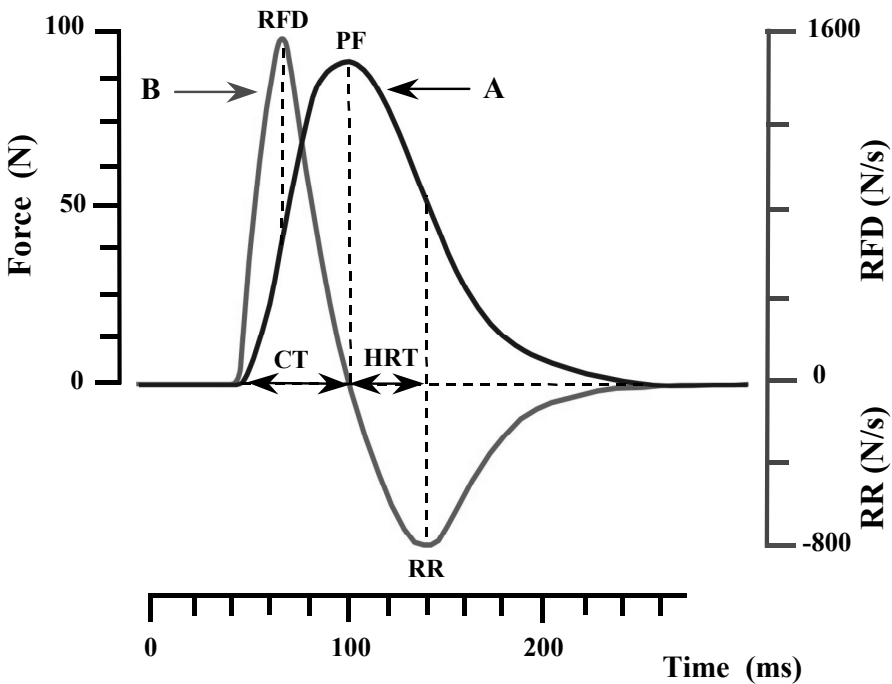


Figure 1. Isometric twitch force-time curve (A) and first derivate (B). PF – twitch peak force; CT – contraction time; HRT – half-relaxation time; RFD – maximal rate of force development; RR – maximal rate of relaxation.

FT (type II) muscle fibres show greater contraction force, rates of force development and relaxation, and shorter contraction and relaxation times compared to ST (type I) muscle fibres (McComas & Thomas, 1968). It has been found that myosin ATPase activity is a strong factor in the contraction force and rate of force development, which is more expressed in FT fibres (Barany, 1967; Larsson & Moss, 1993). Muscles with a higher percentage of FT fibres have a greater force-generation capacity during electrically evoked supramaximal isometric twitch (McComas & Thomas, 1968). It has been suggested that FG fibres have the greatest and SO fibres have the least (ca 35% from FG fibres level) twitch PF (McComas & Thomas, 1968; Chan *et al.*, 2001). Schematic illustration of isometric twitch force-time curves of the three main types of muscle fibres is presented in Fig. 2. A reduction of twitch PF, maximal RFD and maximal RR and a prolongation of twitch CT in elderly muscles compared with those of young adults has been demonstrated (Davies & White, 1983; Vandervoort & Hayes, 1989; Pääsuke *et al.*, 2000b), whereas twitch HRT has been found to be prolonged (Davies & White, 1983) or unchanged (Pääsuke *et al.*, 2000a, 2002).

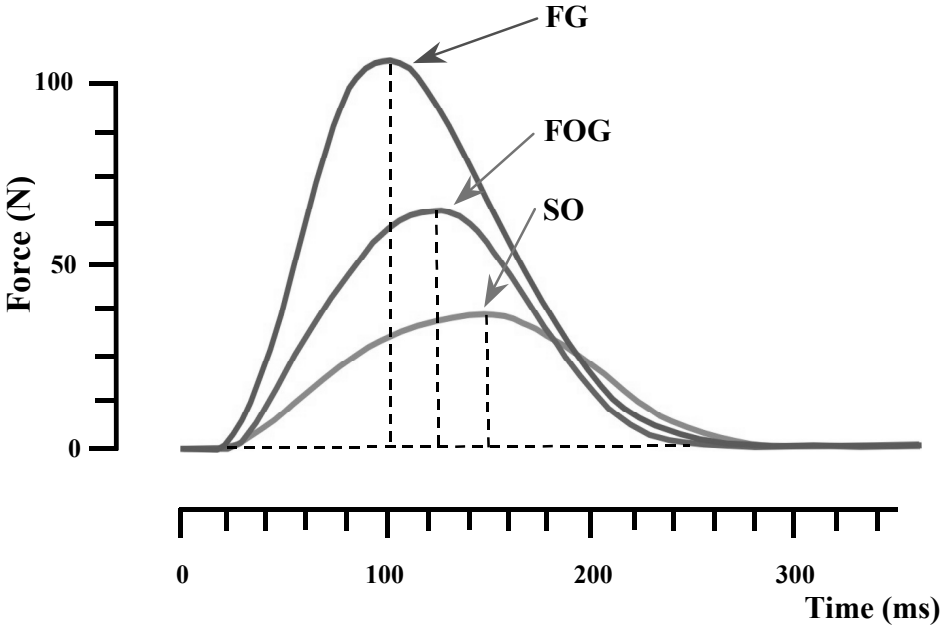


Figure 2. Schematic illustration of isometric twitch force-time curves of the three main types of muscle fibres. SO – slow-twitch oxidative; FOG – fast-twitch oxidative-glycolytic; FG – fast-twitch glycolytic.

2.2.2. Twitch potentiation

It is commonly known that the force of isometric twitch contractions is increased after repeated low-frequency electrical stimulation (staircase) (Moore & Stull, 1984), a conditioning high-frequency tetanic stimulation (PTP) (O'Leary *et al.*, 1997; Abbate *et al.*, 2001) or a brief isometric MVC (PAP) (Hamada *et al.*, 2000; Pääsuke *et al.*, 2000b; Sale, 2002). For simplicity, these increases in twitch force, which result from prior activity, can be referred to as twitch potentiation. Twitch potentiation has been shown in a variety of human muscles, including small hand muscles (Takamori *et al.*, 1971), elbow flexors (Krarup & Horowitz, 1979; Klein *et al.*, 2001), knee extensors (Stuart *et al.*, 1988; Green & Jones, 1989; Hamada *et al.*, 2000), ankle dorsiflexors (Vandervoort & McComas, 1986; O'Leary *et al.*, 1997) and plantarflexors (Vandervoort and McComas, 1983; Petrella *et al.*, 1989; Hamada *et al.*, 2000; Pääsuke *et al.*, 2000b). Twitch potentiation is the greatest immediately after a brief supra-maximal high-frequency tetanic stimulation (Green & Jones, 1989; O'Leary *et al.*, 1997) or isometric MVC (Hamada *et al.*, 2000) and then decreases rapidly but is still evident for approximately 10 min (O'Leary *et al.*, 1997; Hamada *et al.*, 2000). Twitch potentiation is often associated with a shortened twitch CT (Green & Jones, 1989; Petrella *et al.*, 1989; O'Leary *et al.*, 1997; Pääsuke *et al.*, 2000b) and increased twitch maximal RFD and maximal RR (Green & Jones, 1989; Grange *et al.*, 1993; O'Leary *et al.*, 1997; Pääsuke *et al.*, 2000b), and with shortened (O'Leary *et al.*, 1997) or unchanged (Baudry & Duchateau, 2004; Pääsuke *et al.*, 2002) twitch HRT.

The most accepted mechanism of twitch potentiation is phosphorylation of myosin regulatory light chains during a conditioning contraction, which renders actin-myosin more sensitive to Ca^{2+} in subsequent twitch contraction (Moore & Stull, 1984; Persechini *et al.*, 1985; Palmer & Moore, 1989; Grange *et al.*, 1993; Vandenboom *et al.*, 1993). The most important muscle characteristic affecting the magnitude of twitch potentiation is the fibre type. Muscles with the shortest twitch CT and HRT and highest proportion of FT (type II) muscle fibres show the greatest twitch potentiation (O'Leary *et al.*, 1997; Hamada *et al.*, 2000). The greater twitch potentiation in FT fibres is probably related to their greater capacity of myosin regulatory light chains phosphorylation in response to high frequency activation (Grange *et al.*, 1993).

The extent of twitch potentiation can vary. For example, it increases with the intensity and duration of the conditioning contraction (Vandervoort *et al.*, 1983) and is maximal after a conditioning MVC of 5 to 10 s but declines with longer-duration contraction, due to the counteracting effects of fatigue (Vandervoort *et al.*, 1983; Garner *et al.*, 1989).

PAP induced by short MVCs has been found to increase knee extension isokinetic peak torque (French *et al.*, 2003), vertical jumping height (Güllich & Schmidtbleicher, 1996; French *et al.*, 2003) and bench press performance (Güllich & Schmidtbleicher, 1996).

2.3. Adaptive changes in neuromuscular system during strength, power and endurance training

2.3.1. Strength and power training

The development of muscle strength in sport is defined by several factors, including age, anthropometric indicators (height, body mass), psychological (attitude, motivation) and environmental factors (temperature, humidity, altitude) (Agbonjinmi *et al.*, 2001). In addition to the factors mentioned above, the development of muscle strength also depends on the muscle structure, the type and structure of muscle fibres, on the MUs, on the adaption of the neuromuscular system and on the characteristics of training (Ishida *et al.*, 1990; Häkkinen *et al.*, 2001). It has been found that BM is also an important factor in affecting muscle strength (Jaric, 2002).

The voluntary maximal force-generation capacity of skeletal muscles is associated with three groups of physiological factors (Enoka, 1988): central (central nervous), peripheral (muscular) and energetic. The central factors ensure the regulation between the excitation of spinal motoneurons and muscular activity, and their input to the muscle force production is apparent in the so-called intramuscular coordination: 1) in recruitment of MUs; 2) in synchronizing the impulses of motoneurons, and 3) in regulation of the firing frequency of impulses of MUs (Enoka, 1988). The peripheral factors define the contractile properties and functional state of the muscles and affect the force-generation capacity (Häkkinen & Komi, 1984) which is defined by two main factors (Enoka, 1988) – the ratio of FT and ST fibres and the quantitative level of ensuring muscular energy and the metabolic processes in muscles.

The extent and speed of a muscle contraction depend largely on the functional capacity of the contractile mechanisms of skeletal muscles (Eloranta & Komi, 1980; Knapik *et al.*, 1983; Häkkinen *et al.*, 2001). The mechanisms are defined by the duration of the active state of muscles, i.e. by the excitation-induced chemical-mechanical changes which result in a mechanical tension which is transferred to the lever arms of bones. During the isometric MVC, all types of muscle fibres are recruited (Komi, 1979; Häkkinen *et al.*, 1984; Enoka, 1988; Narici *et al.*, 1996). Studies of muscle biopsy have shown that highly qualified endurance-trained athletes (cross-country skiers, long-distance runners) have ST muscle fibres dominating in the *vastus lateralis* muscle, whereas in the

case of power-trained athletes the FT muscle fibres prevail (Froese & Houston, 1985).

Depending on the type on muscle contraction and characteristics of muscle force-generation, the muscle strength is divided into 1) maximal strength; 2) explosive strength; 3) speed strength, and 4) strength endurance (Bosco, 1982; Enoka, 1988; Scott, 2000). The maximal strength of the muscles is characterized by isometric MVC force (Enoka, 1988; Alway *et al.*, 1989). Isometric MVC force decreases when the duration of activity is prolonged (Edwards, 1981; Davies & Young, 1982; Häkkinen, 1993; Gandevia *et al.*, 1996; Gandevia, 2001). Both FT and ST muscle fibres are recruited during isometric MVC. The isometric MVC force is defined by the amount of muscle fibres being activated (Elder *et al.*, 1982; Klitgaard *et al.*, 1989). Speed strength appears in the case of fast movements carried out under low or medium external resistance (Enoka, 1988). It is known that the speed of movements decreases during slow activity (Davies & Young, 1982). In developing speed strength, the frequency of movements has to increase continuously, often even exceeding the frequency of activity during competitions (Madsen, 1996). The explosive strength means overcoming the external resistance with maximal speed (Enoka, 1988) and is crucial in jumping, throwing, weightlifting, etc. One of the forms of explosive strength is the jumping capacity (Bosco, 1988). Strength endurance is the capacity to maintain optimal parameters of movement during a longer period of time (Bosco, 1988). Strength endurance is more important in cyclic activities, either in aerobic, anaerobic or mixed mode, depending on the distance (Enoka, 1988). Strength endurance occurs in two forms – dynamic and static. Dynamic strength endurance is specific to cyclic activities during which the muscle contraction is repeated in every cycle (running, swimming, etc.) and to acyclic exercises which are performed after pauses (jumps, throws, etc.). Static strength endurance is specific to sports activities during which the movements are performed with the need to maintain muscle contraction with certain heaviness and duration (wrestling, etc.) or a certain position (shooting sports, speed skating) (Enoka, 1988).

The speed of a movement is always the result of the acceleration impulse, therefore speed strength activities are mainly described by the RFD and the maximal power output. In this context, muscle mass and the percentage of FT muscle fibres in muscles seem to be the main factors (Tesch & Karlsson, 1985; Van Cutsem *et al.*, 1998; Putman *et al.*, 2004). The RFD is the capacity to activate maximal amount of MUs with maximal speed during voluntary contractions (Freund *et al.*, 1975). The RFD depends on the following factors: the previous state of the muscle, the reflectory activity, the range of the effect of inhibitory neurons and the elastic properties (compliance) of muscles and tendons (Dietz *et al.*, 1981). Among the morphological changes occurring as a result of power training, the most characteristic one is the increase in muscle

mass. This applies to athletes trained in both power (speed strength) and maximal strength (Caiozzo *et al.*, 1981; Coyle *et al.*, 1981). The increase in the amount of contractile proteins improves chances to overcome external resistance during muscle contraction (Gollnick *et al.*, 1974; Carolan & Cafarelli, 1992; Brown *et al.*, 1997). This explains why the physiological cross-sectional area of muscle is in proportion with the muscle strength. As a result of heavy-resistance strength training, the amount and size of myofibrils and their nuclei increase inside the muscle fibres, as does their placement (MacDougall *et al.*, 1980; Lexell, 1995; Liu *et al.*, 2003). The muscle area used for attaching to the skeleton increases. In heavy strength-trained athletes, the hypertrophy of muscles occurs to a larger extent than it does in power-trained athletes (Schmidtbleicher & Haralambie, 1981; Häkkinen & Keskinen, 1989; Izquierdo *et al.*, 2002;). The amount of MUs which can voluntarily be activated in MVC increases during both heavy-resistance strength and power training (Caiozzo *et al.*, 1981; Schmidtbleicher *et al.*, 1988).

Strength training with heavy resistance and a small number of repetitions mobilizes a large part of FT muscle fibres, whereas training with medium resistance and a large number of repetitions mobilizes both FT and ST muscle fibres (Thorstensson & Karlsson, 1976; Jenkins *et al.*, 1984; Johansson *et al.*, 1987; Häkkinen & Keskinen, 1989). It has been found that prolonged heavy-resistance strength training and power training do not affect the ratio of FT and ST fibres in muscles (Izquierdo *et al.*, 2002; Lattier *et al.*, 2003), whereas both types of muscle fibres become hypertrophied in the process (Tesch & Karelsson, 1985; Suter *et al.*, 1993; Paavolainen *et al.*, 1994). The cross-sectional area of FT muscle fibres increases more than that of ST muscle fibres, referring to the hypertrophy of the FT muscle fibres. In general, the hypertrophy of muscle fibres is apparent in the increased cross-sectional area due to the increase in myofibrils (Thorstensson *et al.*, 1976; Jenkins *et al.*, 1984; Johansson *et al.*, 1987; Häkkinen & Keskinen, 1989). In case of high-power short-duration strain the muscles are supplied with energy mainly via anaerobic alactatic processes. The ATP re-synthesis can only take place by using the intramuscular creatine phosphate. When repetitive movements become more frequent, anaerobic lactatic processes (glycogenolysis) will also take part in supplying the muscles with energy (Cavagna *et al.*, 1968; Ivy *et al.*, 1981; Häkkinen & Komi, 1984). Studies have shown that power-trained athletes have higher percentage of FT (Type II) muscle fibres than the untrained (Tesch & Karlsson, 1985; Sleivert *et al.*, 1995). It has also been found that power training increases isometric MVC force via neural adaptation mechanisms which increase the capacity to recruit MUs (Moritani & Vries, 1979; Thepaut-Mathieu *et al.*, 1988; Izquierdo *et al.*, 2002), also increasing the synchronization of MUs during contractions (Milner-Brown *et al.*, 1975) and the reflectory activity (Sale *et al.*, 1982a; Sale *et al.*, 1982b; Milner-Brown *et al.*, 1975). It has been shown that long-duration power

training causes changes in excitation-contraction coupling of muscular cells and in the contractile apparatus of muscle fibres, affecting their force-generation capacity. The structure and function of sarcoplasmic reticulum may change due to power training, affecting therefore the kinetics of the Ca^{2+} ions in muscular cells during contraction process (Vandervoort *et al.*, 1983; Zhong *et al.*, 2004).

2.3.2. Endurance training

The development of endurance is connected with the economization of energetic potential in organism – the increase in the use of fat and the proportional decrease in the use of carbohydrates (Hoh, 1992; Behm, 1995; Gerdle *et al.*, 1998). In response to endurance training, adaptation occurs on several levels of the nervous system, e.g. in supraspinal centres, descending pathways, spinal centres and in motor end-plate, which are connected to motoneurons and muscle fibres. It has been shown that endurance training causes adaptation in several parts of the muscular system which are connected to motor functions and which also affect the efficiency and economy of movements (Behm, 1995; Carroll *et al.*, 2001). It has been found that strength-oriented endurance training which is over 50% MVC, depends largely on maximal strength. This shows that heavy-resistance strength training simultaneously improves strength endurance (Pampus *et al.*, 1989). At the same time, to maintain the oxidative properties of muscles to ensure good aerobic capacity, the strength increase of endurance-trained athletes should be small (1.5% per week) (Rusko, 1987). It has been noted that isometric MVC does not differ significantly in endurance-trained athletes and untrained individuals (Rusko, 1987; Lattier *et al.*, 2003). It has been shown that endurance training significantly increases VO_2max and the anaerobic threshold in athletes having a large percentage of ST muscle fibres (Rusko & Rahkila, 1983; Sale, 1988; Gerdle *et al.*, 1998). It has also been found that aerobic and anaerobic threshold and VO_2max correlate positively with the percentage of ST muscle fibres (Rusko & Rahkila, 1983). Thus, the higher percentage of SO muscle fibres, the more explicit the effect of endurance training (Leveritt *et al.*, 1999). It has been noted that in endurance-trained athletes the share of ST muscle fibres dominating in their leg muscles, and in long-distance runners the proportion of ST muscle fibres may reach 80% (in plantarflexor muscle 61–80%) (Tesch, 1988; Saltin, 1997).

2.4. Muscle fatigue

2.4.1. Physiological characterization of muscle fatigue

Muscle fatigue has been often defined as a reduction in the force-generation capacity of a muscle due to previous activity (Edwards, 1981; Bruton *et al.*, 1998). Fatigue during voluntary muscular contraction may be caused by central nervous factor as well as changes in the peripheral site of the neuromuscular system (Green, 1987; Cady *et al.*, 1989). There are several opinions about the physiological nature and localization of fatigue, but it is a shared belief that fatigue is a defence reaction of an organism prior to exhaustion (Edwards, 1981; Vollestad *et al.*, 1988; Hultman *et al.*, 1991). Several studies in this field have claimed that fatigue develops simultaneously in the central nervous system and in periphery (Bigland-Ritchie & Woods, 1984; Mc Kay *et al.*, 1995; Kent-Brown, 1997). Moreover, the particular site or combination of sites that fails first may appear to be task dependent (Kirkendall, 1990; Gandevia, 2001). Depending on the type of exercise performed, fatigue may develop owing to failure at one or several sites along the pathway of force production. Some possible sites of fatigue are: excitatory input to motor cortex, excitatory drive to lower motoneuron, motoneuron excitability, neuromuscular transmission, sarcolemma excitability, excitation-contraction coupling, contractile mechanism, metabolic energy supply (Bigland-Ritchie *et al.*, 1983a; Edwards, 1981; Kent-Braun, 1997). As a result, the working performance decreases. The working performance may also be significantly affected by hormonal changes. The extent of the latter is especially large during prolonged activation (Linnamo *et al.*, 1998). Changes in these systems may lead to disruptions in vegetative functions and in energy supplies (Sahlin, 1986; Pasquet *et al.*, 2000). In any type of physical activation, the leading systems can be distinguished. The functional capacity of a leading system not only defines, but also limits the intensity, extent and quality of activation. Reasons for fatigue are different for activations with different levels of intensity (Sacco *et al.*, 1997; Strojnik & Komi, 1998).

Studies have shown that muscles in which the ST oxidative muscle fibres are dominating, are more resistant to fatigue than muscles in which FT glycolytic muscle fibres prevail. It has also been found that subjects with a larger percentage of FT muscle fibres in *quadriceps femoris* muscle are more sensitive to fatigue than those with ST muscle fibres dominating (Gregor *et al.*, 1981). In addition, it has been found that a large amount of lactic acid accumulates first and foremost into glycolytic muscle fibres already after 25 maximal contractions (Thorstensson & Karlsson, 1976; Toniolo *et al.*, 2004). Decrease in muscle contractions may result from the accumulation of lactic acid and subsequent changes in pH in muscle fibres. Decrease in isometric MVC

force of active muscles is connected to both central and peripheral changes. In case of fatigue, MVC force can decrease because of cortical impairment in motor areas in brain or in the spinal cord (Brasil-Neto *et al.*, 1994; Mc Kay *et al.*, 1995; Sacco *et al.*, 1997). On the other hand, it may result from intramuscular processes (Hultman & Sjöholm, 1983; Brody *et al.*, 1991; Pavlat *et al.*, 1995). For example, prolongation of evoked twitch HRT refers to disruption in the functions of the Ca^{2+} pumping mechanism in sarcoplasmic reticulum of muscle fibres and to reduced capacity of reaccumulating Ca^{2+} during relaxation process (Hultman & Sjöholm, 1983; Vandervoort *et al.*, 1983; Alway *et al.*, 1987). Reduction in force-generation capacity and speed of contraction of electrically evoked isometric twitch after fatiguing exercise is an informative indicator of the decreased contractile capacity of muscular cells (Vandervoort *et al.*, 1983; Petrella *et al.*, 1989; Westerblad *et al.*, 1997, 1998).

2.4.2. Muscle fatigue during maximal dynamic contractions

The nature, intensity and duration of exercise are important factors affecting muscle fatigue as well as the post-fatigue recovery (Bigland-Ritchie & Woods, 1984). Fatigue during maximal dynamic muscle contractions may occur as a result of 1) reduction or lack of glycogen in active muscles; 2) the inability of the central nervous system to innervate muscles; 3) reduced transportation of ions into muscular cells; 4) reduced pH and increased levels of lactic acid in muscles, or 5) changes in the function of excitation-contraction coupling and contractile apparatus of the muscle fibres (Schwendner *et al.*, 1995; Allman & Rice, 2002).

In different forms of exercise different forms of energy sources are used. During short-term maximal anaerobic alactatic muscle activity is used the energy created from creatine phosphate system and muscular ATP, whereas during short-term maximal anaerobic lactic muscle activity, energy from glycolysis together with the formation of lactic acid is used (Enoka, 1988; Paavolainen *et al.*, 1994). During glycolysis, ATP is formed 2–3 times faster than during oxidative phosphorylation. This enables to reduce ATP 2–3 times faster, resulting in 2–3 times greater mechanical work output than in the case of solely aerobic endurance activity. That is why a sprinter can achieve almost twice the speed of a long-distance runner (Sahlin *et al.*, 1998). Naturally, fast formation of ATP and subsequent extensive mechanical power output can last for a short period of time (approximately 30 s), because anaerobically used energy supplies are limited and during glycolysis, lactic acid cumulates in cell fluid and blood, finally resulting in metabolic acidosis and fatigue, which limit the working performance (Thorstensson & Karlsson, 1976). Changes in intracellular pH and the accumulation of metabolites have been detected via nucleus magnetic resonance (NMR) spectroscopy method both in cardiac and skeletal muscles (Dawson *et al.*, 1978). Studies have shown that the highest

concentration of lactic acid in blood occurs at the end of a 400 m run, it can even exceed 26 mmol/l; at the end of a 200 m run the concentration of lactic acid in blood is about 18–20 mmol/l (Lacour, 1996). Processes supplying the body with anaerobic energy are necessary in the short run not only for top physical achievements, but often even at the beginning of a muscle activity with a smaller intensity than the marginal force of an endurance activity, because oxidative metabolism (and glycolysis) needs some initiation time for adapting to the metabolism of increased activity (Wilkie, 1979). For this reason a stationary state, where during oxidative phosphorylation only as much ATP is formed as it can be reduced in ATPase in a time unit, is achieved not earlier than after 1/2–2 minutes (Konstantinov *et al.*, 1980; Moore *et al.*, 1984; Paavolainen *et al.*, 1994).

Post-fatigue recovery is defined as recovery of the capacity of the muscles to generate force after an exhausting exercise. Recovery takes place during different stages after the exercise and depends largely on the nature of the exercise and on the muscle groups involved. Several researchers demonstrated that recovery after maximal dynamic exercise takes place within 4 minutes after the end of exercise (Paavolainen *et al.*, 1994; Strojnik & Komi, 1998). Recovery is considered to have taken place when levels of MVC force have reached 80% of the pre-fatigue value (Schwendner *et al.*, 1995). It has been suggested that in the subjects with greater post-fatigue, the MVC force is decreased and they needed more time for recovery (Newham *et al.*, 1991).

Numerous studies have examined the fatigue after dynamic heavy-resistance exercise. It has been suggested that continuous and/or intermittent heavy-resistance exercise results in acute neuromuscular fatigue which is caused by a decrease in the force-generation capacity and/or decreased neural activation of the active muscles (Newham *et al.*, 1991; Häkkinen, 1994). The most documented changes in contractile properties of the skeletal muscles following heavy-resistance exercise seem to be reduced maximal voluntary force production (Bigland-Ritchie *et al.*, 1983; Newham *et al.*, 1991; Häkkinen, 1993), reduced force production during electrically evoked twitch or tetanic contraction (Bigland-Ritchie *et al.*, 1983; Newham *et al.*, 1991; Raastad & Hallen, 2000), and slowing of the RFD and RR of voluntary or electrically evoked contractions (Bigland-Ritchie *et al.*, 1983; Häkkinen, 1993). Most studies in which neuromuscular fatigue following heavy-resistance exercise has been investigated, were repeated maximal isometric MVCs (Kroll *et al.*, 1980; Bigland-Ritchie *et al.*, 1983), high-force eccentric contractions (Newham *et al.*, 1987; Tiidus & Shoemaker, 1995; Brown *et al.*, 1997), squat exercises (Raastad & Hallen, 2000) and explosive strength loading (Linna *et al.*, 1998).

During the last decades, isokinetic dynamometer has been widely used for assessing muscle fatigability. Isokinetic exercise allows major muscle groups to exert maximal force throughout the full range of motion (Perrin, 1993).

Numerous studies have demonstrated that TWO and average power during isokinetic exercise are reliable measures (Gross *et al.*, 1991; Madsen, 1996; Pincivero *et al.*, 1997). During repetitive maximal isokinetic contractions the peak torque and mechanical work or power output decreases during the initial 40–60 contractions followed by a stable level with no further decrease (Gerdle *et al.*, 1998). Thorstensson and Karlsson (1976) originally recommended the use of a FI as an indicator of isokinetic endurance capacity for a muscle group, which has been modified later by several investigators (Gross *et al.*, 1991; Pincivero *et al.*, 2001; Pincivero *et al.*, 2003). Less attention has been paid to the measurement of the electrically evoked contractile properties of skeletal muscles during high-intensity isokinetic exercise. However, examination of the changes in electrically evoked contraction characteristics of muscles during short-term fatiguing maximal contractions in well-trained strength athletes may provide additional information about the adaptation of the human neuromuscular system to heavy-resistant strength training.

3. OBJECTIVES OF THE STUDY

The general objective of the present study was to measure contractile properties of human skeletal muscles in association with long-term adaptation to power and endurance training, muscle fatigue and PTP.

More specifically, the present study had the following aims:

- (1) to compare the isometric MVC force and electrically evoked isometric twitch characteristics of plantarflexor muscles in power and endurance-trained athletes, and sedentary subjects (Study I, II and III);
- (2) to measure PAP in plantarflexor muscles after a brief isometric MVC by electrically evoked isometric twitch characteristics in power and endurance-trained athletes, and sedentary subjects (Study I and III);
- (3) to measure changes in isometric MVC force and electrically evoked submaximal tetanic contraction characteristics of knee extensor muscles after fatiguing high-intensity isokinetic exercise in heavy-resistance strength-trained athletes and sedentary subjects (Study IV);
- (4) to measure PTP in knee extensor muscles after a brief high-frequency submaximal direct PES by changes in electrically evoked twitch, doublet and unfused tetanic contraction characteristics (Study V).

4. MATERIALS AND METHODS

4.1. Subjects

In total 97 male and 25 female subjects aged 19–28 years participated in this study. The subjects were male power-trained (sprinters and jumpers), heavy-strength trained (power-lifters), endurance-trained (long-distance runners) athletes and sedentary men. Power-trained female athletes (sprinters and jumpers) and sedentary women were also measured. The training experience in athletes was 6–12 years, whereas the majority of athletes competed at national and some athletes at international level. Sedentary subjects were university students with no history of regular participation in recreational physical activity. The subjects had no history of neuromuscular disorders. After routine medical examination all subjects were informed of the procedures and the purpose of the study and their written informed consent was obtained. The studies carried the approval of the Ethics Committee for Human Studies of the University of Tartu.

The anthropometric characteristics of the measured subject groups are presented in Table 1.

4.2. Study design

Five studies with different subjects' groups were performed during the period of 1998–2003 in the Laboratory of Kinesiology and Biomechanics, University of Tartu. All measurements were performed at the same time of day. Subjects were given instructions 2–14 days before collecting data, and the testing of isometric and isokinetic voluntary contractions and electrical stimulation procedures were demonstrated. During practice sessions the subjects were familiarized with the related procedures. The determination of leg dominance was based on a kicking preference.

In Study I, II, III and V, on reporting to the laboratory, each subject sat resting for 25–30 min before commencing the experiment to minimize any potentiation effect from walking to the laboratory. In Study IV, prior to testing, each subject underwent a 10-min warming-up period that consisted of submaximal leg ergometry followed by stretching exercises.

In Study I and III, isometric MVC force and electrically evoked twitch contraction characteristics of plantarflexor muscles in resting state and after MVC of 5 s duration (PAP) were compared in athletes of different sports and in sedentary subjects. The measured athletes were male (Study I) and female (Study III) sprinters and jumpers, and male long-distance runners (Study I).

Table 1. Anthropometric characteristics and age of the subjects (mean \pm SE).

Papers	n	Age (yr)	Height (cm)	Body mass (kg)	BMI (kg·m ⁻²)
Study I (Paper I)					
Male sprinters and jumpers	12	22.4 \pm 1.0	187.7 \pm 1.8	79.4 \pm 1.5	22.3 \pm 0.9
Male long-distance runners	11	20.8 \pm 1.1	180.8 \pm 1.6	67.7 \pm 1.7	20.2 \pm 0.7
Study II (Paper II)					
Male sprinters and jumpers	12	23.6 \pm 1.0	187.4 \pm 1.7	79.6 \pm 1.5	22.7 \pm 0.8
Male long-distance runners	12	21.4 \pm 1.4	180.2 \pm 1.6	67.9 \pm 1.7	20.4 \pm 0.5
Sedentary men	12	20.4 \pm 0.4	182.0 \pm 1.5	76.9 \pm 1.5	22.4 \pm 0.7
Study III (Paper III)					
Female sprinters and jumpers	11	20.6 \pm 0.7	172.3 \pm 1.6	52.9 \pm 1.6	18.9 \pm 0.8
Sedentary women	14	20.7 \pm 0.2	169.9 \pm 1.3	61.0 \pm 1.7	20.6 \pm 0.7
Study IV (Paper IV)					
Male power-lifters	11	25.5 \pm 1.6	176.2 \pm 1.9	85.8 \pm 5.0	27.7 \pm 2.6
Sedentary men	14	23.3 \pm 1.6	180.4 \pm 2.2	75.7 \pm 3.7	23.4 \pm 2.9
Study V (Paper V)					
Sedentary men	13	21.6 \pm 0.8	180.7 \pm 2.1	73.9 \pm 2.5	22.7 \pm 2.1

In Study II, isometric MVC force and electrically evoked supramaximal twitch contraction characteristics of plantarflexor muscles in resting state were compared in male sprinters, long-distance runners and sedentary men.

In Study IV, isometric MVC and electrically evoked submaximal tetanic contraction characteristics of knee extensor muscles after high-intensity fatiguing isokinetic exercise were compared in male power-lifters and sedentary men. Fatigue test consisted of 30 repetitive maximal isokinetic knee extensions at angular velocity of 1.57 rad·s⁻¹ and 0.5 Hz frequency on Cybex II isokinetic dynamometer. The measured characteristics were assessed before the exercise, and 1 and 10 min after the end of exercise.

In Study V, to measure PTP in knee extensor muscles, the electrically evoked twitch, doublet and 10-Hz tetanic contraction characteristics were assessed before and after a brief (7-s) high-frequency (100 Hz) submaximal (25% MVC) direct PES in sedentary men. The posttetanic testing contractions were evoked after 2 s and 1, 3, 5 and 10 min. The decrease in force during conditioning 7-s tetanic contraction was also determined.

4.3. Methods

4.3.1. Isometric dynamometry and electrical stimulation

Measurement of plantarflexor muscles. During the experiment, the subjects were seated in a custom-made dynamometric chair, the dominant leg flexed at 90° at the knee and mounted inside a metal frame (Pääsuke *et al.*, 2000b) (Fig. 3). The foot was strapped on aluminium footplate. The inclination of the foot could be altered by rotating the footplate about an axis corresponding to that of the ankle joint, i.e. the medial *malleolus*. The ankle was dorsiflexed to 20° to ensure maximal voluntary and stimulated torques and presumably corresponded to the “optimal” muscle length (Sale *et al.*, 1982b). The knee cap and front side of the thigh were held down by an adjustable pad. Torques acting on the footplate were sensed by standard strain gauge transducer connected with the footplate by a rigid bar. The electrical signals from the strain gauge transducer 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 original force signals were digitized on-line (sampling frequency 1 kHz) using a personal computer. The digitized signals were stored on a hard disk for further analysis.

To determine the contractile properties of plantarflexor muscles during isometric twitch, the posterior tibial nerve was stimulated through a pair of surface carbon-rubber electrodes (Nemectron, Germany). The cathode (2x4 cm) was placed over the tibial nerve in the *popliteal fossa* and the anode (7x12.5 cm) under the posterior-medial side of the thigh (Fig. 3 B). Supramaximal square wave pulses of 1-ms duration were delivered from an isolated voltage stimulator (Medicor MG-440, Hungary). The compound action potential (M-wave) of the *soleus* muscle was recorded using bipolar (20 mm interelectrode distance) EMG electrodes, placed longitudinally on the motor point area of the *soleus* muscle determined by electrical stimulation. As a reference electrode a large carbon-rubber plate (Nemectron, Germany), was placed over the proximal part of the *triceps surae* muscle between the stimulating and recording electrodes. The EMG signals were amplified using standard preamplifiers (Medicor MG-440, Hungary) with the frequency band ranging from 1 Hz to 1 kHz. These signals were sampled at 1 kHz. The stimulus intensity during isometric twitch recording varied from about 25 V to a supramaximal in increments of 30–50% (130 – 150 V) (Zhou *et al.*, 1995). Single stimuli were given at 30-s intervals and the voltage was increased in increments of 20–25 V. The maximal amplitude of the M-wave was used as a criterion for determining the supramaximal stimulus intensity.

After the resting twitch had been recorded, the subjects were instructed to make an isometric MVC for 5 s and then to relax (Study I and III). A second

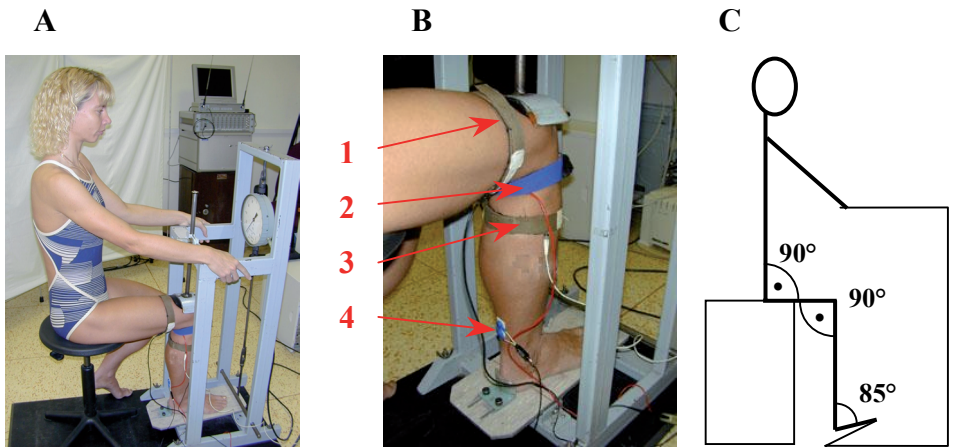


Figure 3. Experimental setup for the measurement of isometric MVC force and electrically evoked twitch contraction characteristics of plantarflexor muscles. A – position of the subject in dynamometric chair; B – location of the electrical stimulation and EMG electrodes on the leg; C – illustration of hip, knee and ankle joint angles during measurement; 1 – stimulation ground electrode (anode); 2 – active stimulation electrode (cathode); 3 – EMG ground electrode; 4 – EMG recording electrode.

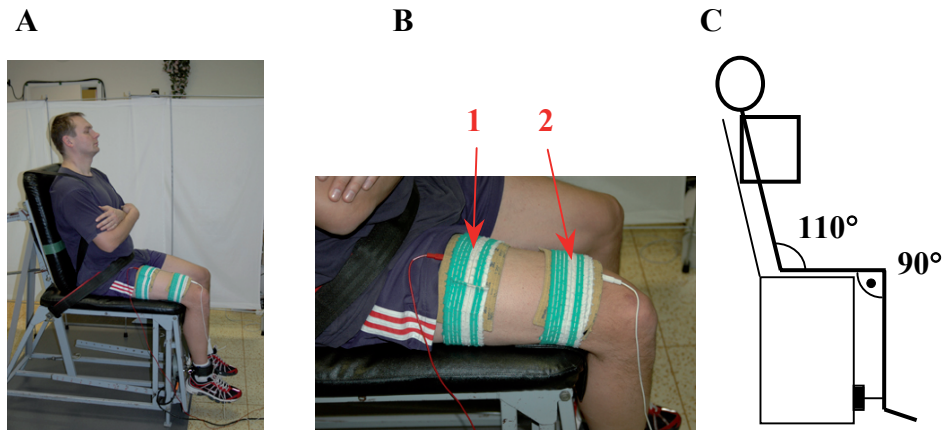


Figure 4. Experimental setup for the measurement of isometric MVC force and electrically evoked contraction characteristics of knee extensor muscles. The position of the subject in dynamometric chair; B – location of the electrical stimulation electrodes on the quadriceps femoris muscle; C – illustration of hip and knee joint angles during measurement; 1 – stimulation electrode (cathode); 2 – ground electrode (anode).

(potentiated) twitch took place within 1 s after the onset of relaxation. The following characteristics in resting and potentiated twitch condition were computed (Fig. 1): twitch PF – the highest value of isometric force production; CT – the time from the onset of contraction to the twitch PF; HRT – time of decline of the twitch PF to half of the maximum; maximal RFD – the first derivate of the development of the twitch force (dF/dt) and maximal RR – the first derivate of the decline of the twitch force (–dF/dt). Twitch PF was expressed as a ratio to the MVC force (PF:MVC force) (Study II). The percentage increase in the potentiated twitch PF in relation to the resting one was taken as an indicator of the PAP (1):

$$\text{PAP} = \frac{\text{PF}_p}{\text{PF}_r} \cdot 100 \quad (\%) \quad (1)$$

where PF_p is potentiated twitch and PF_r resting twitch peak force, respectively.

During the recording of isometric MVC force of plantarflexor muscles, the subjects were instructed to push the footplate as forcefully as possible for 2–3 s. Verbal encouragement and visual on-line feedback were used to motivate the subjects. The greatest force of the three maximal efforts was taken as the isometric MVC force. A rest period of 2 min was allowed between the attempts (Studies I, II and III). MVC force relative to body mass (MVC force:BM) was calculated (Study III).

Measurement of knee extensor muscles. During the measurement of isometric MVC and electrically evoked twitch, doublet and tetanic contraction characteristics of knee extensor muscles, the subjects were seated on a custom-made dynamometric chair with the knee and hip angles equal to 90 and 110°, respectively (Pääsuke *et al.*, 1999) (Fig. 4).

The body position of the subjects was secured by three Velcro belts placed over the chest, hip and thigh. The unilateral knee extension isometric force production was recorded by standard strain-gauge transducer mounted inside a metal frame that was placed around the distal part of the ankle of the dominant leg above the *malleoli* using Velcro belt. Inside the metal frame the strain-gauge transducer could be moved vertically and horizontally. The strain gauge transducer proved to be linear within the measurement range of 10–1600 N. The electrical signals from the strain-gauge transducer were digitized on-line (sampling frequency 1 kHz) using a personal computer. The digitized signals were stored on a hard disk for further analysis. The output from the strain-gauge amplifier was also displayed on an analogue voltmeter, which the subjects could observe during their efforts in order to obtain immediate feedback.

In Study IV, during the isometric MVC testing the subjects were instructed to react to the light signal (ignition on the lamp, placed 1.5 m from the subject)

as quickly and as forcefully as possible by extending the dominant leg against a cuff fixed to a strain-gauge system, to maintain the maximal effort as long as the signal was on (2 s) and to relax the muscles after the disappearance of the signal. The isometric force-time curve was analyzed on a personal computer. The following characteristics were calculated: MVC force – the highest value of force production recorded during isometric contraction; RFD – the slope of the isometric force-time curve (dF/dt) over time interval of 0.2 s relative to the onset of contraction and HRT – the amount of time to half of the decline in isometric MVC force. Three trials were performed with rest period of 2 min between the attempts.

In Study IV, the position of the subjects during the recording of isometric force-time and relaxation-time characteristics of the electrically evoked submaximal tetanic contraction of knee extensor muscles was the same as during isometric MVC measurements. Two large (23x7 cm) carbon rubber electrodes (Nemectron, Germany) were used. The skin over the *quadriceps* muscle was washed with liquid soap and water to reduce electrical impedance. The anode was placed distally and the cathode was placed proximally on the anterolateral thigh (Fig. 4B). Elastic bandages were used to keep the electrodes in place and to ensure good electrode contact. The electrical stimuli were rectangular voltage pulses of 1-ms duration delivered from an isolated voltage stimulator (Medicor MG-440, Hungary). The duration of stimulation train was 1 s and stimulation voltage was adjusted to provide the initial force of about 25% of the isometric MVC force of knee extensor muscles (Fig. 5).

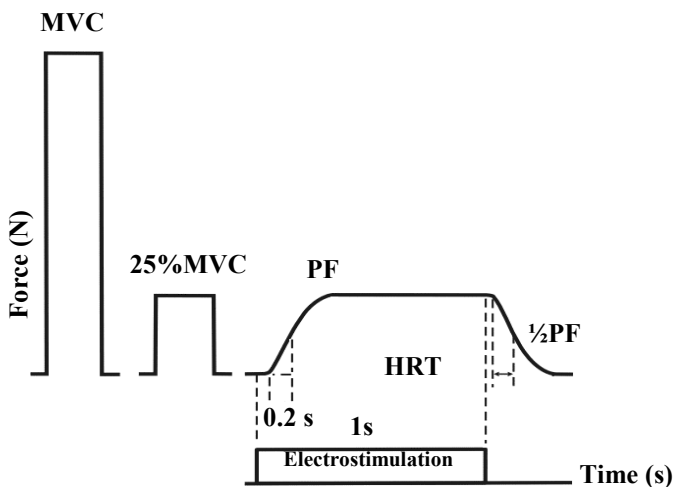


Figure 5. Schematic presentation of the isometric force-time curve of electrically evoked submaximal tetanic contraction of knee extensor muscles. MVC – maximal voluntary contraction; PF – tetanic contraction peak force; HRT – half-relaxation time.

In Study IV, the time interval between the final isometric MVC trial and start of the electrical stimulation trials in pre-exercise condition was 5 min in order to minimize the effects of muscle fatigue. Prior to stimulation subjects had been instructed to relax their musculature. The isometric force-time curves of the electrically elicited submaximal tetanic contraction were analyzed on-line. The following characteristics were calculated: PF – the highest value of isometric force production recorded during evoked tetanic contraction, RFD – the slope of the isometric force-time curve (dF/dt) over time interval of 0.2 s relative to the onset of contraction and HRT – the time to half of the decline in isometric tetanic peak force.

Immediately after the end of fatiguing isokinetic exercise, the subject was re-transferred on the isometric dynamometric chair. Post-exercise testing of isometric MVC and electrically evoked submaximal tetanic contraction characteristics of knee extensor muscles was performed 1 and 10 min after the end of exercise. The same electrical stimulation protocol was used during pre- and post-exercise testing.

In Study V, to assess the contractile characteristics of knee extensor muscles, electrically evoked isometric twitch, doublet and 10-Hz tetanic contractions were elicited by supramaximal percutaneous nerve stimulation. Before the stimulating electrodes were applied, electrode gel was applied to the contact surface, and the underlying skin was prepared by shaving, sanding, and rubbing with isopropyl alcohol. Two 2-mm-thick, self-adhesive stimulating electrodes (Medicompex SA, Switzerland) were used – the cathode (5x5 cm) placed on the skin over the femoral nerve in the inguinal crease and the anode (5x10 cm) placed over the mid-portion of the thigh (Fig. 6). The electrical stimuli were rectangular voltage pulses of 1-ms duration applied at supramaximal intensity (130–150 V) delivered from an isolated voltage stimulator (Medicor MG-440, Hungary). To determine the supramaximal stimulation intensity, the voltage of electrical pulse was progressively increased to obtain a plateau in the twitch force, that is, when twitch force failed to increase despite additional increases in stimulation intensity. The same stimulation intensity (~20% greater than that needed for maximal twitch response) was further used for twitches, doublets (with interstimulus interval of 10 ms), and 10-Hz tetanic contractions (with duration of 1 s) evoked before the conditioning tetanic stimulation and during the recovery period.

The following characteristics of isometric twitch were calculated: PF – the highest value of isometric force production, maximal RFD – the first derivative of the development of force ($+dF/dt$) and maximal RR – the first derivative of the decline of force ($-dF/dt$). PF for supramaximal doublet and 10-Hz tetanic contractions were calculated as the highest value of isometric force production during doublet and unfused tetanus, respectively. Two supramaximal single twitches, doublets and 10-Hz tetanic contractions were given to relaxed knee

extensor muscles with 5 s interval between stimulations before and after a conditioning 7-s submaximal high-frequency direct PES.

Two min after MVC force testing, direct tetanic PES voltage for target level of force at 25% MVC of knee extensor muscles was determined and controlled by two separated stimulations with 2 s duration. A portable stimulator Compex Sport 400 (Medicompex SA, Switzerland) was used. Three 2 mm-thick, self-adhesive electrodes were placed over the thigh (Fig. 6). The stimulating electrodes (5x5 cm), which had membrane depolarizing properties, were placed to the motor point area of *vastus lateralis* and *vastus medialis* muscle and near the proximal insertion of each muscle. The ground electrode (5x10 cm) was placed over the proximal portion of the thigh between stimulating electrodes for the measurement of muscle contractile properties. Rectangular voltage pulses of 0.4-ms duration at the frequency of 100 Hz were used. The stimulation voltage was calculated for each subject prior to the testing, according to the individual force response. After 15 minutes resting the submaximal tetanic contraction (approximately 25% MVC) of knee extensor muscles of 7-s duration was evoked by direct PES. After the end of direct tetanic PES, the subject remained seated without moving his/her legs for a recovery period of 10 min. The posttetanic isometric twitch, doublet and 10-Hz tetanic contractions were evoked at 2 s and 1, 3, 5 and 10 min. The decrease in force during 7-s conditioning tetanic contraction was also determined as compared with initial level.

4.3.2. Isokinetic dynamometry

After 10 min of recovery, the subject was transferred on the isokinetic dynamometer Cybex II (Lumex Inc., USA) for knee extensor muscles fatigue testing (Study IV). After calibration of the dynamometer, the subjects were seated on the adjustable chair and their thigh, hip and chest stabilized using straps. The axis of rotation of the knee joint was aligned with axis of the dynamometer lever arm. The force pad was placed 3–4 cm superior to the medial *malleolus* with the foot in plantigrade position. The knee and hip of the dominant leg was positioned at 90 and 110° of flexion, respectively. The range of motion during testing was set using the goniometer through an arc from 90° of knee angle to full extension. Torque measured by the dynamometer was recorded using a personal computer. Subjects were instructed to hold their arms across the chest to isolate extension movements in knee joint. During the fatigue test the subjects were asked to perform 30 repetitive maximal concentric isokinetic knee extensions through a complete range of motion at angular velocity $1.57 \text{ rad}\cdot\text{s}^{-1}$ and at 0.5 Hz frequency with intervening passive knee flexion as modified from Thorstensson and Karlsson (1976). Fig. 7 illustrates the fatigue curve during 30 maximal isokinetic concentric knee extensions. A TWO during exercise was

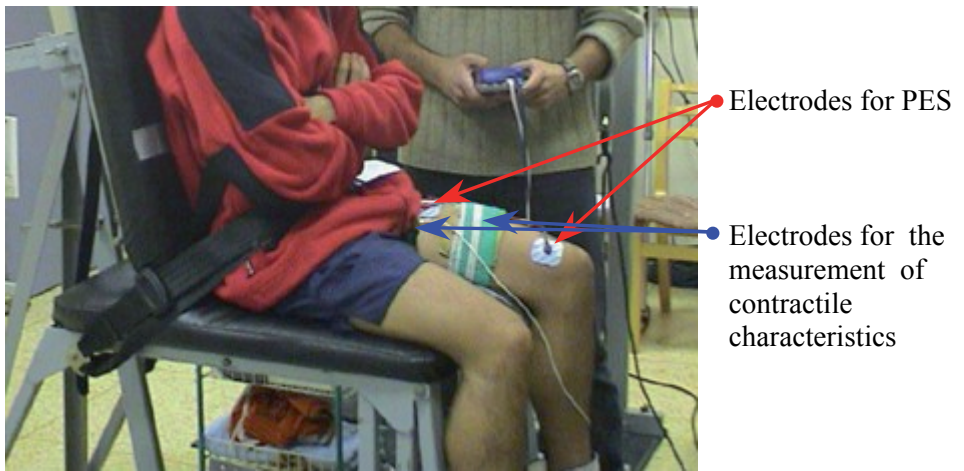


Figure 6. Placement of stimulation electrodes to assess the contractile characteristics of knee extensor muscles before and after a conditioning 7-s submaximal high-frequency direct PES.

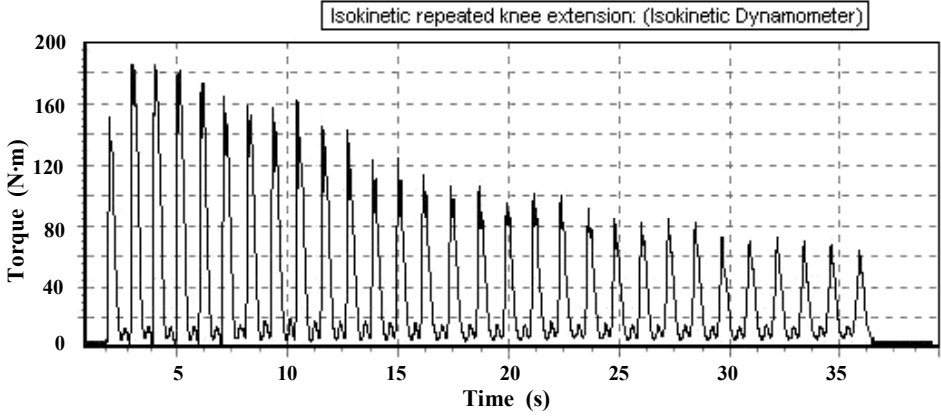


Figure 7. A representative fatigue curve from knee extensor muscles. Thirty maximal isokinetic concentric contractions were performed at $1.57 \text{ rad}\cdot\text{s}^{-1}$.

defined as the sum of areas under each isokinetic torque curve throughout a given range of motion (Ivy *et al.*, 1981; Perrin, 1993; Tis & Maxwell, 1996). The initial (prefatigue) peak torque PT_S was calculated as the mean of the 2nd to 6th contractions (PT_2 , PT_3 , PT_4 , PT_5 , PT_6) during the test. The final peak torque PT_E during the test was calculated as the mean of the 25th to 29th contraction (PT_{25} , PT_{26} , PT_{27} , PT_{28} , PT_{29}). The FI (decline of peak torque in percent) was calculated by formula (Li *et al.*, 2002).

$$FI = \frac{PT_S - PT_E}{PT_S} \cdot 100 \quad (\%) \quad (2)$$

where $PT_S = (PT_2 + PT_3 + PT_4 + PT_5 + PT_6)/5$ and $PT_E = (PT_{25} + PT_{26} + PT_{27} + PT_{28} + PT_{29})/5$.

4.4. Statistical evaluation of the data

Standard statistical methods were used to calculate the means and standard errors of mean ($\pm SE$). The between-group differences in mean values were evaluated by using Student's t-test for unpaired data (Study I). One-way analysis of variance (ANOVA) followed by Tukey (Studies III, IV and V) and Scheffe (Study II) *post hoc* comparisons were used to test for differences between groups. Repeatedly measured variables were analyzed using a two-way analysis of variance (ANOVA) for repeated measures with time as the within-

subject factor and a group (male power-lifters vs. untrained vs. untrained) as the between-subject factor (Study IV).

Pearson's linear correlations were calculated on the basis of the relations between the PAP and other contraction characteristics of plantarflexor muscles (Studies I, II and III).

The Pearson's correlations were calculated to observe the relationship between the pre-exercise values of contractile characteristics of knee extensor muscles, TWO during exercise and FI (Study IV).

For normally distributed variables the level of $p < 0.05$ was selected to indicate statistical significance.

5. RESULTS

5.1. Isometric maximal voluntary and evoked twitch contraction characteristics of plantarflexor muscles in power and endurance-trained athletes and sedentary subjects

5.1.1. Maximal voluntary contraction force

Male power-trained athletes (sprinters and jumpers) had a significantly greater isometric MVC force of plantarflexors muscles than endurance-trained athletes (long-distance runners) and sedentary men (Table 2). No significant differences in MVC force were found in male long-distance runners and sedentary men.

Isometric MVC force of plantarflexor muscles in female power-trained athletes (sprinters and jumpers) was significantly greater compared to sedentary women.

Table 2. Isometric maximal voluntary contraction (MVC) force and MVC force relative to body mass (MVC:BM) of plantarflexor muscles in athletes and sedentary subjects (mean \pm SE).

Study	Subject group	n	MVC force (N)	MVC:BM (N·kg ⁻¹)
II	Male sprinters and jumpers	12	1280 \pm 52	16.9 \pm 0.7
	Male long-distance runners	12	1009 \pm 59 \$\$\$	15.4 \pm 0.6
	Sedentary men	12	966 \pm 57 \$\$\$	12.2 \pm 0.8 \$\$ \diamond
III	Female sprinters and jumpers	11	1052 \pm 36	17.8 \pm 0.6
	Sedentary women	14	821 \pm 37 ###	13.5 \pm 0.5 ###

Note:

\$\$ $p < 0.01$, \$\$\$ $p < 0.001$ compared to male sprinters and jumpers;
 ### $p < 0.001$ compared to female sprinters and jumpers;
 \diamond $p < 0.05$ compared to male long-distance runners.

Sedentary men had a significantly lower MVC:BM than that of the measured groups of male athletes, whereas this parameter did not differ significantly in athletes' groups (Table 2). In sedentary women, MVC:BM was significantly lower compared to female power-trained athletes (sprinters and jumpers).

5.1.2. Twitch peak force

Male power-trained athletes (sprinters and jumpers) had a significantly greater resting twitch PF of plantarflexor muscles compared to endurance-trained athletes (long-distance runners) and sedentary men (Table 3). No significant differences were observed in twitch PF between male long-distance runners and sedentary men. Twitch PF did not differ significantly in female power-trained athletes (sprinters and jumpers) and sedentary women.

Twitch PF:BM ratio was significantly greater in male power-trained athletes (sprinters and jumpers) compared to long-distance runners and sedentary men (Table 3). This parameter did not differ significantly in long-distance runners and sedentary men. Female power-trained athletes (sprinters and jumpers) had significantly greater twitch PF:BM compared to sedentary women.

Table 3. Twitch peak force (PF) and PF relative to body mass (PF:BM) of plantarflexor muscles in athletes and sedentary subjects (mean \pm SE).

Study	Subject group	n	PF (N)	PF:BM (N·kg ⁻¹)
I	Male sprinters and jumpers	12	147 \pm 5.8	1.8 \pm 0.04
	Male long-distance runners	11	116 \pm 5.7 \$\$\$	1.6 \pm 0.06 \$\$
III	Female sprinters and jumpers	11	113 \pm 5.1	1.9 \pm 0.05
	Sedentary women	14	105 \pm 6.5	1.7 \pm 0.07 #

Note:

\$\$ $p < 0.01$, \$\$\$ $p < 0.001$ compared to male sprinters and jumpers in resting state;

$p < 0.05$ compared to female sprinters and jumpers in resting state.

5.1.3. Postactivation potentiation

Male power-trained athletes (sprinters and jumpers) had a significantly greater twitch PAP compared to the other measured groups (Fig. 8). No significant differences in PAP were observed between the groups of male long-distance runners and sedentary men. Female power-trained athletes (sprinters and jumpers) had a significantly greater twitch PAP compared to sedentary women (Fig. 8).

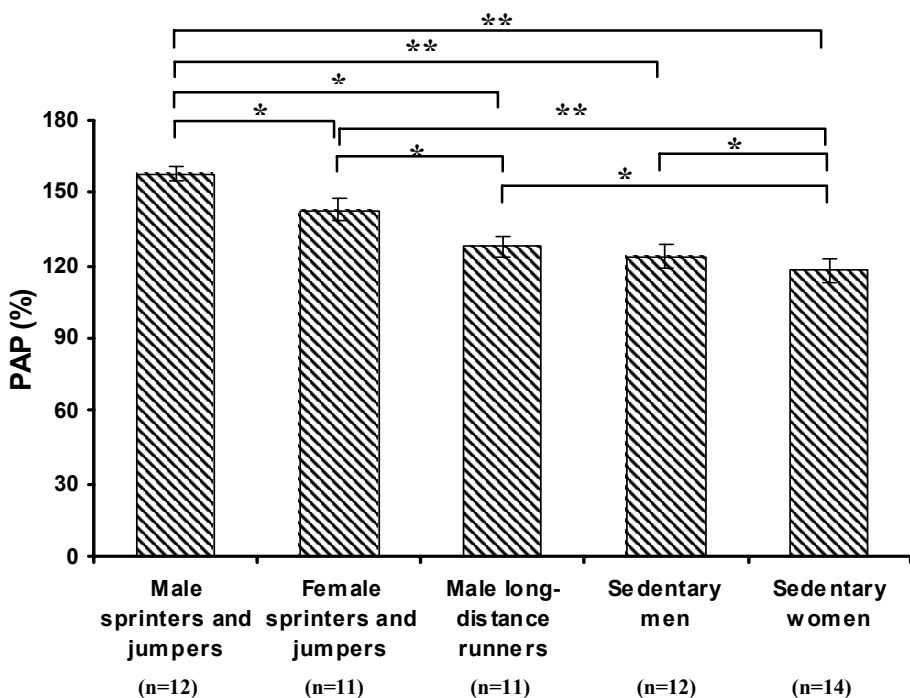


Figure 8. Postactivation potentiation (PAP) of plantarflexor muscles (mean \pm SE).
 * $p<0.05$; ** $p<0.01$.

5.1.4. Time-course characteristics of isometric twitch

In sedentary men, resting twitch CT was significantly longer than in male sprinters and jumpers and long-distance runners (Table 4). No significant differences in twitch CT were observed between the measured groups of male athletes. Female power-trained athletes (sprinters and jumpers) had a significantly shorter twitch CT compared to sedentary women.

Twitch HRT in sedentary men was significantly longer compared to the measured groups of male athletes, whereas it did not differ significantly in the measured athletes' groups (Table 4). No significant differences in twitch HRT were observed between female power-trained athletes (sprinters and jumpers) and sedentary women.

Table 4. Twitch contraction (CT) and half-relaxation (HRT) time of plantarflexor muscles in athletes and sedentary subjects (mean ± SE).

Study	Subject group	n	CT (ms)	HRT (ms)
I	Male sprinters and jumpers	12	92 ± 3.5	97 ± 4.1
	Male long-distance runners	11	84 ± 4.9	100 ± 3.6
III	Female sprinters and jumpers	11	89 ± 4.6	99 ± 5.3
	Sedentary women	14	110 ± 6.9 ###	90 ± 6.5

Note:
$p<0.001$ compared to female sprinters and jumpers in resting state.

5.1.5. Twitch maximal rates of force development and relaxation

Twitch maximal RFD in resting state was significantly greater in male power-trained athletes (sprinters and jumpers) compared to male endurance-trained athletes (long-distance runners) and sedentary men (Table 5). No significant differences in twitch maximal RFD were found between the groups of male long-distance runners and sedentary men.

Twitch maximal RFD in female power-trained athletes (sprinters and jumpers) did not differ significantly when compared to sedentary women (Table 5).

Table 5. Twitch maximal rates of force development (RFD) and maximal relaxation (RR) of plantarflexor muscles in athletes and sedentary subjects (mean ± SE).

Study	Subject group	n	RFD (N·s ⁻¹)	RR (N·s ⁻¹)
I	Male sprinters and jumpers	12	2215 ± 92	1225 ± 65
	Male long-distance runners	11	1256 ± 93 \$\$\$	882 ± 76 \$\$
III	Female sprinters and jumpers	11	1560 ± 77	810 ± 51
	Sedentary women	14	1462 ± 62	805 ± 59

Note:
\$ $p<0.05$, \$\$ $p<0.01$, \$\$\$ $p<0.001$ compared to male sprinters and jumpers in resting state.

Twitch maximal RR in resting state was significantly greater in male power-trained athletes (sprinters and jumpers) compared to long-distance runners and sedentary men (Table 5). No significant differences in twitch maximal RR were observed between the groups of male long-distance runners and sedentary men. Twitch maximal RR did not differ significantly in female power-trained athletes (sprinters and jumpers) and sedentary women.

5.1.6. Correlation analysis

The Pearson correlation coefficients were calculated on the basis of the determined indicators in Studies I, II and III, whereas the respective groups were joined together (Table 6).

Table 6. Correlation coefficients between twitch postactivation potentiation (PAP) and twitch contraction (CT) and half-relaxation (HRT) time, maximal rates of force development (RFD) and relaxation (RR), and maximal voluntary contraction force (MVC) of plantarflexor muscles and body mass (BM) in athletes and untrained subjects.

Subject group	CT	HRT	RFD	RR	MVC	BM
Male sprinters and jumpers (n=12)	0.11	0.12	0.56*	0.31	0.45	0.70**
Female sprinters and jumpers (n=11)	0.39	−0.35	0.53	0.28	0.26	0.49
Male long-distance runners (n=11)	−0.58*	0.19	0.50	0.52	0.27	0.39
Sedentary men (n=12)	−0.16	−0.56*	0.65*	0.26	0.39	0.49
Sedentary women (n=14)	0.24	−0.31	0.46	0.37	−0.24	0.31

Note:
 * $p<0.05$; ** $p<0.01$.

In male long-distance runners, twitch PAP correlated negatively ($p<0.05$) with resting twitch CT ($r = -0.58$), whereas in sedentary men PAP correlated negatively with resting twitch HRT ($r = -0.56$). No significant correlations were found between twitch PAP and time-course characteristics of resting twitch in male and female sprinters and jumpers, and sedentary women. In male sprinters and jumpers, PAP correlated positively ($p<0.01$) with the BM ($r = 0.70$). PAP correlated positively ($p<0.05$) with resting twitch RFD in male power-trained athletes (sprinters and jumpers) and sedentary men ($r = 0.56$ and $r = 0.65$, respectively).

5.2. Changes in contractile properties of knee extensor muscles after fatiguing maximal isokinetic contractions in power-lifters and sedentary subjects

5.2.1. Contractile changes in knee extensor muscles after 30 maximal isokinetic contractions

Study IV described the changes in isometric MVC and electrically evoked submaximal tetanic contraction characteristics of knee extensor muscles after a short-term high-intensity fatiguing isokinetic exercise in male power-lifters and sedentary men as controls (Table 1). The fatigue test consisted of 30 repetitive maximal isokinetic knee extensions at angular velocity of $1.57 \text{ rad}\cdot\text{s}^{-1}$.

TWO during repetitive maximal isokinetic knee extensions was significantly greater in power-lifters than in controls (Fig. 9A). Power-lifters had a significantly greater FI as compared to sedentary men (Fig. 9B).

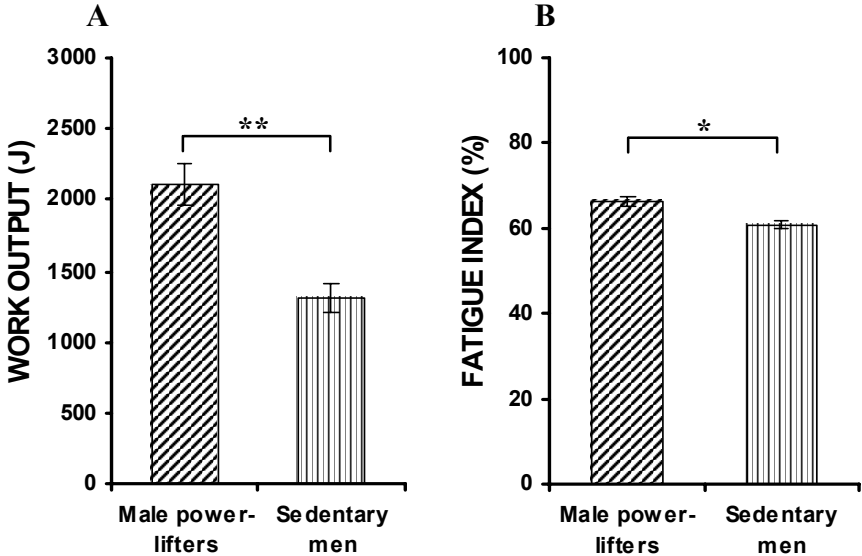


Figure 9. Total mechanical work output during repetitive maximal isokinetic knee extensions (A) and fatigue index (B) in male power-lifters and sedentary men (mean \pm SE). * $p < 0.05$; ** $p < 0.01$.

Isometric MVC force was significantly decreased 1 min after exercise for both measured groups compared to the pre-exercise level (Fig. 10). This parameter was recovered to the pre-exercise level for sedentary men within 10 min after the exercise, while it did not recover for power-lifters.

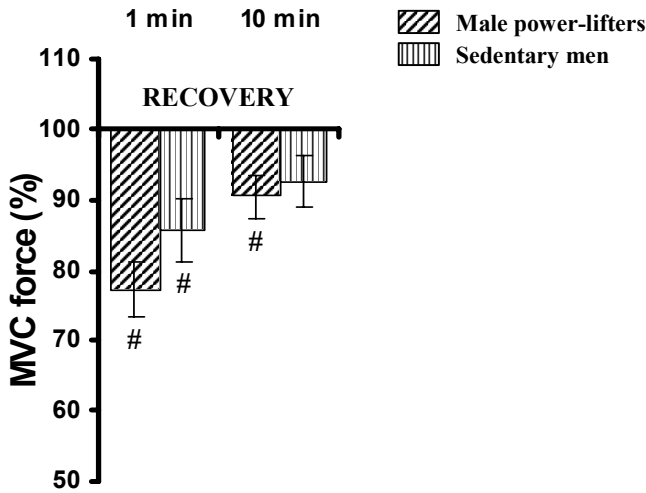


Figure 10. Changes in isometric maximal voluntary contraction (MVC) force in power-lifters and sedentary men. Values, expressed as percentage of the pre-exercise value, are means \pm SE. # significant difference from the pre-exercise value.

Power-lifters had a significantly greater decrease in electrically evoked tetanic contraction PF 1 min after exercise than the corresponding decrease in sedentary controls (Fig. 11). A decrease in power-lifters in tetanic contraction PF within 10 min of recovery period was significant as compared to controls.

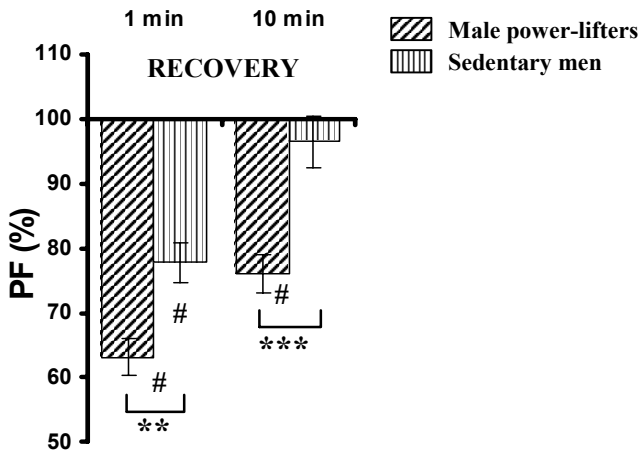


Figure 11. Changes in isometric submaximal tetanic contraction peak force (PF) in male power-lifters and sedentary men. Values, expressed as a percentage of the pre-exercise value, are means \pm SE. # significant difference from the pre-exercise value. ** $p < 0.01$; *** $p < 0.001$.

In power-lifters, HRT during MVC and during evoked tetanic contraction were significantly prolonged 1 min after exercise compared to the pre-exercise level, whereas this parameter was recovered to the pre-exercise level within 10 min after exercise (Table 7). No significant changes in HRT during MVC and during tetanic contraction were observed after 30 repetitive maximal isokinetic knee extensions in sedentary men.

Table 7. Half-relaxation time (HRT) during isometric maximal voluntary contraction (MVC) and during electrically evoked submaximal tetanic contraction before and 1 and 10 min after fatiguing exercise (mean ± SE).

Study	Subject group	Time	HRT during MVC (ms)	HRT during tetanic contraction (ms)
IV	Male power-lifters (n=11)	INITIAL	83 ± 4.2	74 ± 4.1
		1 min	112 ± 3.8 ###	97 ± 3.9 ##
		10 min	92 ± 4.5	82 ± 4.4
	Sedentary men (n=14)	INITIAL	107 ± 3.7	97 ± 3.7
		1 min	103 ± 4.3	102 ± 2.9
		10 min	102 ± 3.1	95 ± 2.6

Note:
 ## *p*<0.01; ### *p*<0.001 compared to the pre-exercise (initial) value.

Isometric RFD during MVC and during tetanic contraction was significantly decreased 1 min after exercise for the both measured groups as compared to the pre-exercise level (Fig. 12). Power-lifters had a significantly greater decrease in RFD during MVC 1 min after exercise as the corresponding decrease in sedentary men. Isometric RFD during MVC and during tetanic contraction was recovered to the pre-exercise level for sedentary men within 10 min after the cessation of exercise, while it did not recover for power-lifters. A decrease in power-lifters’ RFD during tetanic contraction after 10 min of recovery period was significant as compared to sedentary men.

RR during MVC and during evoked tetanic contraction was significantly decreased 1 min after exercise for the both measured groups as compared to the pre-exercise level (Table 8). Maximal RR during MVC was recovered to the pre-exercise level within 10 min after exercise for both groups, whereas maximal RR during tetanic contraction recovered only for sedentary men.

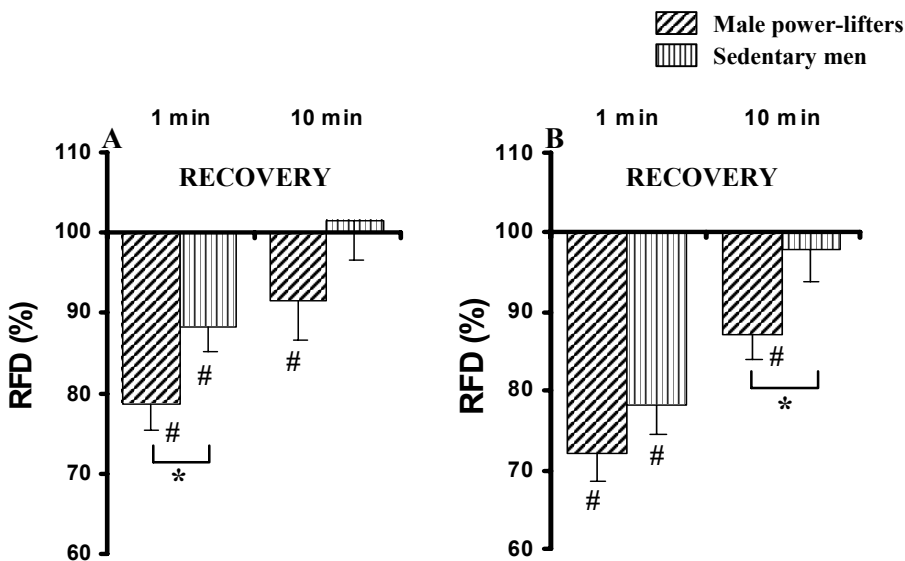


Figure 12. Changes in rate of force development (RFD) during maximal voluntary contraction (A) and during electrically evoked isometric submaximal tetanic contraction (RFD) (B) in male power-lifters and sedentary men (Study IV). Values, expressed as percentage of the pre-exercise value, are means \pm SE.
 * $p < 0.05$; # significant difference from the pre-exercise (initial) value.

Table 8. The maximal rate of relaxation (RR) during maximal voluntary contraction (MVC) and during electrically evoked submaximal isometric tetanic contraction of knee extensor muscles. Values, expressed as percentage of the pre-exercise value, are means \pm SE.

Study	Subject group	Time	RR during MVC (%)	RR during tetanic contraction (%)
IV	Male power-lifters (n=11)	1 st min	81.6 \pm 5.2 #	72.8 \pm 4.8 #
		10 th min	90.4 \pm 5.8	88.7 \pm 5.0 #
	Sedentary men (n=14)	1 st min	82.6 \pm 6.7 #	75.3 \pm 5.9 #
		10 th min	92.2 \pm 6.9	91.1 \pm 5.7

Note:

significant difference from the pre-exercise (initial) value.

5.2.2. Results of correlation analysis

In Study IV, the correlation coefficients between the pre-exercise values of contractile characteristics of knee extensor muscles, TWO and FI during fatiguing isokinetic exercise were calculated in male power-lifters and sedentary men (Table 9).

Table 9. Correlations between the pre-exercise values of contractile characteristics of knee extensor muscles, total mechanical work output (TWO) and fatigue index (FI) during exercise in male power-lifters and sedentary men.

Para- meters	MVC	RFD during MVC	PF during tetanic contraction	Maximal RFD during tetanic contraction	HRT during tetanic contraction	FI
Male power-lifters (n=11)						
TWO	0.18	0.12	0.37	-0.08	0.17	0.82***
FI	0.24	0.41	0.11	-0.51	0.18	-
Sedentary men (n=14)						
TWO	0.62*	0.40	0.51	0.65*	0.47	0.36
FI	0.22	0.04	-0.39	-0.46	-0.07	-

Note:

MVC – isometric maximal voluntary contraction; RFD – rate of force development 0.2 s after the onset of voluntary force production; PF – peak force; HRT – half-relaxation time. * $p < 0.05$; *** $p < 0.001$.

The pre-exercise contractile characteristics of knee extensor muscles, TWO and FI did not correlate significantly in male power-lifters. However, in power-lifters TWO during isokinetic exercise correlated positively with FI ($r = 0.82$, $p < 0.001$). In sedentary controls, TWO during isokinetic exercise correlated significantly positively with the pre-exercise value of MVC force ($r = 0.62$, $p < 0.05$) and RFD during tetanic contraction ($r = 0.65$, $p < 0.05$). No significant correlations were observed between the pre-exercise contractile characteristics of knee extensor muscles and FI, and between TWO and FI during isokinetic exercise in sedentary controls.

5.3. Changes in contractile properties of knee extensor muscles after high-frequency submaximal percutaneous electrical stimulation

5.3.1. Changes in conditioning tetanic contraction force

Figure 13 shows the changes in conditioning submaximal tetanic contraction force of knee extensor muscles of 7-second duration, which was evoked by direct PES (Study 5). The mean value of tetanic force in the beginning of conditioning contraction was significantly greater than at the end of conditioning contraction (116.4 ± 9.7 N and 91.7 ± 7.8 N, respectively). The force decreased approximately by 21% during a 7-second tetanic contraction.

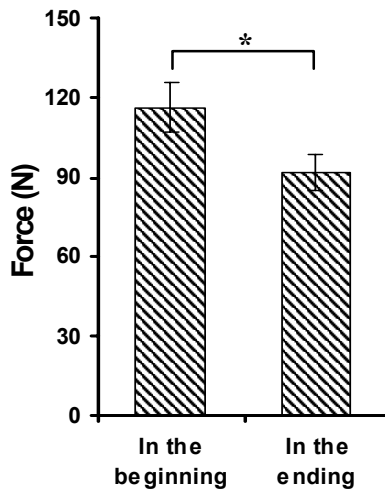


Figure 13. Changes in conditioning submaximal tetanic contraction force of knee extensor muscles, evoked by direct PES (mean \pm SE). * $p < 0.05$.

5.3.2. Changes in twitch, doublet and 10 Hz tetanic contraction characteristics

The mean pre-tetanic values of twitch, doublet and 10-Hz tetanic contraction PF were 63.8 ± 3.5 N, 113.8 ± 22.4 N and 96.9 ± 6.9 N, respectively (Study V). The mean pre-tetanic values of twitch maximal RFD and maximal RR were 526.1 ± 2.7 N/s and 265.5 ± 18.7 N/s, respectively.

Figure 14A shows the mean relative potentiation of isometric twitch, doublet and 10-Hz tetanic contraction PF after direct submaximal tetanic PES.

Immediately after the end of applied direct tetanic PES, the 10-Hz tetanic contraction PF was significantly potentiated (16% from the pre-tetanic value), whereas twitch and doublet contraction PF did not potentiate significantly (12% and 7% from the pre-tetanic value, respectively). The potentiation of 10-Hz tetanic contraction PF significantly exceeded potentiaion of the doublet contraction PF. A significant potentiation of twitch, doublet and 10-Hz tetanic contraction PF has been observed at 1, 3, 5 min post-tetanic. The greatest potentiation of the 10-Hz tetanic contraction PF has been observed at 1 min, and potentiation of twitch and doublet contraction PF at 3 min post-tetanic (20%, 17% and 13%, from the pre-tetanic value, respectively).

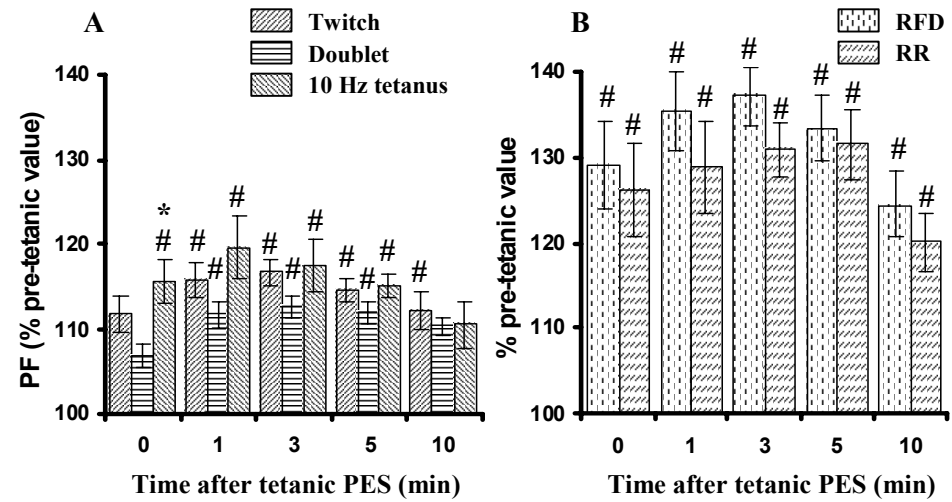


Figure 14. Changes in isometric twitch, doublet and 10-Hz tetanic contraction peak force (A), and in isometric twitch maximal rates of force development (RFD) and maximal relaxation (RR) of knee extensor muscles after a brief direct submaximal PES (B). Values, expressed as percentage of the pre-tetanic value, are means±SE.
 * $p < 0.05$ significantly different from doublet contraction value at designated time point; # significantly different from the pre-tetanic value.

Twitch PF was significantly potentiated at 10 min post-tetanic, while doublet and 10-Hz tetanic contraction peak force did not potentiate significantly. There were no significant differences in the potentiation of twitch, doublet and 10-Hz tetanic contraction PF at 1, 3, 5 and 10 min post-tetanic.

Figure 14B shows the mean relative potentiation of isometric twitch maximal RFD and RR after direct submaximal tetanic PES. Twitch maximal RFD and maximal RR were significantly potentiated immediately after direct tetanic PES (29% and 26% from the pre-tetanic value, respectively). The potentiation was significant throughout the 10-min post-tetanic period, while the greatest potentiation of twitch maximal RFD and maximal RR (38% and 32% from the pre-tetanic value, respectively) was observed at 3 and 5 min post-tetanic, respectively. There were no significant differences between the relative potentiation of twitch maximal RFD and maximal RR throughout the 10-min post-tetanic period.

6. DISCUSSION

6.1. Maximal voluntary and evoked twitch contraction characteristics of plantarflexor muscles in power and endurance-trained athletes and sedentary subjects

This study demonstrated differences in maximal voluntary and electrically evoked twitch contraction characteristics of plantarflexor muscles between male power-trained athletes (sprinters and jumpers), endurance-trained athletes (long-distance runners), and sedentary men. Besides, differences in contractile characteristics of plantarflexor muscles between female power-trained athletes (sprinters and jumpers) and sedentary women were observed. It emerged that male power-trained athletes had a greater isometric MVC force and twitch PF, PAP, and maximal RFD and RR compared to other measured athletes' groups and sedentary men. The similar tendency was observed when female power-trained athletes and sedentary women were compared.

Several factors could contribute to the increase of force-generating capacity in power-trained muscles. Power-trained athletes have a larger muscle cross-sectional area than endurance-trained athletes (Sale *et al.*, 1982b; Häkkinen & Keskinen, 1989; Sleivert *et al.*, 1995). The increasing maximal voluntary force-generating capacity of muscles has been connected both with the hypertrophy of FT muscle fibres and increasing activity of myosin ATPase in these muscle fibres that accompanies the power and/or strength training (Moritani & Vries, 1979; Häkkinen & Komi, 1984; McDougall, 1986), as well as with the improvement of intramuscular coordination mechanisms as a result of which it is possible to recruit more MUs at the motoneuron pool level during forceful voluntary contraction (Schmidtbleicher *et al.*, 1988; Häkkinen & Keskinen, 1989). It has been demonstrated that during isometric MVC all types of muscle fibres are active (Thortensson *et al.*, 1976; Eloranta & Komi, 1980; Mero *et al.*, 1981). The isometric tension is not determined so much by the ratio of ST and FT muscle fibres, as by the number of fibres activated during the contraction (Davies *et al.*, 1985; Gregorevic *et al.*, 2004). Long-term strength and power training does not influence the percentage ratio of FT and ST muscle fibres but changes the size of the muscle fibres of both types (Komi, 1984; Narici *et al.*, 1996). At that the cross-section area of FT fibres is increased more than that of ST fibres that causes hypertrophy of FT muscle fibres. Muscle hypertrophy is expressed in the increase of physiological cross-section area of muscles due to the increased volume of myofibrils (Alway *et al.* 1988; Häkkinen & Keskinen, 1989). Power-trained athletes have also larger FT/ST fibre area ratios than sedentary subjects and endurance-trained athletes (Johnson *et al.*, 1973; Green *et al.*, 1981; Tesch & Karlsson, 1985; Sleivert *et al.* 1995). Power and strength

training induce an improvement in voluntary muscle strength through neural adaptation, perhaps in respect of the increased MU activity (Komi & Tesch, 1979; Moritani & Vries, 1979), improved MU unit synchronization (Milner-Brown *et al.* 1975) and potentiation of reflex activity (Milner-Brown *et al.* 1975; Sale *et al.* 1982b).

One indicator of muscle contractile properties is the twitch:tetanus ratio. Isometric MVC force is similar to maximal force of tetanically evoked contractions in human muscles (Bigland-Ritchie *et al.*, 1983) and therefore we calculated twitch PF:MVC force ratio (Study II). Power-trained athletes had a smaller twitch PF:MVC force ratio compared to sedentary subjects. Similar data are available for body builders (O'Hagan *et al.*, 1993). The smaller twitch:tetanus ratio in power-trained athletes can be related to the greater muscle and myofibril size (MacDougall *et al.*, 1982). In fast muscles, the twitch:tetanus ratio is smaller compared with slow muscles (Hainaut & Duchateau, 1992).

Power-trained athletes (sprinters and jumpers) and endurance-trained athletes (long-distance runners) had a significantly shorter isometric twitch CT compared to sedentary subjects. Male power-trained athletes had also a shorter twitch HRT compared to sedentary men, this was demonstrated in the changes occurring in time-course characteristics of the evoked twitch during strength training. Schmidtbleicher and Haralambie (1981) found a 20% shortening of twitch CT after 8-week strength training in the *deltoideus* muscle and 22% in the *triceps brachii* muscle, and established a prolongation of HRT. However, Sale *et al.* (1983) showed a prolongation of twitch CT in weight trainers compared with sedentary controls. Mc Donagh *et al.* (1983) and Davies *et al.* (1985) noted no changes in time-course characteristics of twitch following strength training. Rice *et al.* (1993) noted a prolongation of twitch CT and Brown *et al.* (1990) found a prolongation of twitch HRT after strength training period in men aged 60–78 years.

The time-course of isometric twitches is probably highly dependent on the kinetics of excitation-contraction coupling mechanisms, including intracellular calcium movements (Kugelberg & Thornell, 1983; Klug *et al.* 1988; Blanc *et al.*, 2003). The shortened twitch CT of the athletes' muscles noted in the present study indicates increased efficiency in sarcoplasmic reticulum function (Krenács *et al.*, 1989). Another possibility of a change evoked at the cellular level with systematic training could be caused by the binding of Ca^{2+} to myosin (Metzger & Moss, 1990; Liu *et al.*, 2003; Zhong *et al.*, 2004). In the present study, twitch maximal RFD and RR were significantly greater in male sprinters and jumpers compared to male long-distance runners and sedentary men (Table 5). The twitch RFD depends largely on the rate of formation of cross-bridges between myosin and actin (Lewis *et al.*, 1986), whereas the duration and rate of muscle relaxation depend on sarcoplasmic reticulum Ca^{2+} uptake and rate of cross-bridge kinetics (Westerblad *et al.*, 1997). Thus, our data indicated a higher

speed of contraction and relaxation of isometric twitch in plantarflexor muscles in power-trained athletes compared to endurance-trained athletes and sedentary subjects. Skeletal muscle is a two-component system consisting of a contractile component connected in series with one passive elastic component (Dyer & Enna, 1976; Fukashiro *et al.*, 1995). The time-course and RFD and RR of isometric twitches depend on the properties of both the contractile and the series elastic component. These data suggest a different functional organisation of the neuromuscular system in athletes engaged in sports requiring very rapid and intense contractions compared to endurance-trained athletes and untrained subjects.

In the present study, mean values of twitch PAP in plantarflexor muscles varied from 120% to 161% for female sedentary subjects and male power-trained athletes (sprinters and jumpers), respectively (Fig. 8). In female power-trained athletes (sprinters and jumpers), the mean value of twitch PAP of plantarflexor muscles was 148%. These data are in agreement with the values of twitch PAP published by other authors in plantarflexor muscles (Alway *et al.*, 1989; Belanger & McComas, 1989; Petrella *et al.*, 1989). In the present study, male sprinters and jumpers had a significantly greater twitch PAP compared to long-distance runners and sedentary men, and female sprinters and jumpers had a significantly greater twitch PAP compared to sedentary women (Fig. 8). There were no significant differences in PAP between male long-distance runners and sedentary men. Thus, power training induces a more evident increase in twitch PAP than endurance training.

The mechanism responsible for PAP is considered to be phosphorylation of myosin regulatory light chains (R-LC) during muscle contraction, which renders actin-myosin more sensitive to Ca^{2+} in a subsequent twitch (Grange *et al.*, 1993; Sweeney *et al.*, 1993; Yang *et al.*, 1998). It was proposed that phosphorylation of R-LC increases the probability that cross-bridges will enter the force-producing state, resulting in higher proportion of active cross-bridges at any given time during the twitch (Sweeney *et al.*, 1990). The measurement of R-LC phosphorylation during a brief period of repetitive stimulation confirms that there is a strong relationship between potentiation and R-LC phosphorylation (Klug *et al.*, 1982; MacIntosh *et al.*, 1993). It was noted that similarly to the muscles of small mammals, human muscles with a high percentage of type II fibres exhibit greater PAP (Hamada *et al.*, 2000). In humans, the two muscles which make up the plantarflexor (*triceps surae*) complex are considered to have different functions. The *soleus* muscle has an important postural role, whereas the *gastrocnemius* muscle is more active in phasic activity (Campbell *et al.*, 1973). The differences in potentiating ability between these muscles have been attributed to their distinctive fibre type proportions, the *soleus* muscle is composed mainly of type I fibres (70% to 90%) and the *gastrocnemius* being a mixed muscle with

approximately equal proportion of type I and type II fibres (Johnson *et al.*, 1973; Elder *et al.*, 1982).

Several factors can contribute to the increase of twitch PAP in power-trained athletes compared to endurance-trained athletes and untrained subjects. A possible reason in respect of differences in force potentiation in athletes' skeletal muscles could be variations in their muscle fibre composition and training status. It is well known that high-level power-trained athletes have a greater number of type II (FT) fibres in their muscles than endurance-trained athletes or untrained subjects (Costill *et al.*, 1976; Maffiuletti *et al.*, 2001), although some studies have shown selective hypertrophy of type II fibres after systematic strength training (MacDougall *et al.*, 1980; MacDougall *et al.*, 1984; Alway *et al.*, 1988). On the other hand, longitudinal power training causes changes in excitation-contraction coupling and contractile apparatus of the muscle fibres which can affect their force potentiating ability. The structure and function of the sarcoplasmic reticulum may change with power-training, thus influencing the amount of Ca^{2+} available to the contractile apparatus for potentiation (MacDougall *et al.*, 1979).

An additional factor which may influence the contractile properties of human skeletal muscles is stiffness of series elastic component. It is possible that twitch potentiation is related to increased stiffness of series elastic component and this persists after MVC (Vandervoort & McComas, 1983).

6.2. Contractile changes in knee extensor muscles after fatiguing maximal isokinetic contractions

The results of the present study (Study IV) indicated that the initial pre-fatigue values of isometric MVC force and RFD during MVC were significantly greater in male power-lifters than in sedentary control subjects (32.3 and 25.2%, respectively). Increased muscle voluntary force-generating capacity following long-term heavy-resistance strength training is mainly due to hypertrophic changes in muscles and neural adaptation (Tesch, 1988; Newham *et al.*, 1991; Behm, 1995; Westerblad *et al.*, 1998; Pääsuke *et al.*, 1999). The greater isometric MVC force in power-lifters than in controls observed in the present study may be partly explained by athletes' greater BM.

It has been suggested that heavy-resistance strength training is associated with increased BM, lean body mass, and muscle cross-sectional area (Tesch, 1988; Kitai & Sale, 1989; Komi, 2000). The increased muscle cross-sectional area is mainly due to hypertrophy of individual muscle fibres, whereas there is a greater increase in the area of FT (type II) fibres compared to ST (type I) fibres (MacDougall, 1986; Putman *et al.*, 2004). Heavy-resistance strength training induces muscle fibre hypertrophy primarily by disproportionate increases in contractile protein relative to sarcoplasmic constituents

(MacDougall *et al.*, 1979; MacDougall *et al.*, 1982). It has been suggested that the most important functional contribution to power lifting is the fibre type distribution and size within the type II fibre population (Fry *et al.*, 2003). These morphological and functional adaptations to long-term heavy-resistance strength training might affect both maximal voluntary and electrically evoked contraction response.

This study (Study IV) demonstrated significantly greater (14.9%) pre-exercise value of RFD during electrically evoked submaximal tetanic contraction of knee extensor muscles in power-lifters as compared to control subjects, which is an indicator of increased speed of muscle contraction due to systematic strength training. The RFD depends largely on the rate of formation of cross-bridges between myosin and actin (Lewis *et al.*, 1986). The greater value of the RFD during electrically evoked submaximal tetanic contraction of knee extensor muscles in power-lifters compared to controls could be a result of increased activity of the myosin ATPase, which is well-known adaptation reaction to long-lasting strength training. The present study indicated that the pre-exercise value of the HRT of electrically evoked submaximal tetanic contraction was significantly shorter (12.9%) in power-lifters than in controls. It has been reported that the shortened muscle relaxation time could suggest increased efficiency in the function of sarcoplasmic reticulum to re-uptake Ca^{2+} (Klitgaard *et al.*, 1989).

Power-lifters produced greater TWO during 30 repetitive maximal isokinetic knee extensions ($1.57 \text{ rad}\cdot\text{s}^{-1}$) than control subjects (Fig. 9A). An increase in the concentration of muscle creatine, creatine phosphate (CrP), adenosine energy pools and lactic acid buffering capacity has been observed following high-intensity resistance training (MacDougall, 1986; Graig *et al.*, 1991). All these changes are advantageous to the activity that calls for maximal work and power output during a short time period. In untrained controls, TWO correlated significantly positively with the pre-exercise values of isometric MVC force and RFD during MVC (Table 9), i.e. subjects with greater voluntary isometric force-generating capacity of knee extensor muscles produced greater work output during isokinetic knee extension exercise. No significant ($p>0.05$) correlations between these characteristics have been found in power-lifters (Table 9).

This study indicated a greater FI in power-lifters during repetitive maximal isokinetic knee extensions than in sedentary controls (Fig. 9B). The acute decrease in force production during high-intensity exercise may be resulted from decreased central drive of impaired neuromuscular propagation (Green, 1987). The great increase in intramuscular lactate concentration may have impaired the function of the contractile elements of the active muscle fibres contributing to the great decrease observed in muscle isokinetic torque production. Accumulation of lactic acid with the resulting lowered pH has been

found to inhibit the rate of cross-bridge binding (Metzger & Moss, 1990; Raastad & Hallen, 2000; Komi, 2000), leading to increased requirement for Ca^{2+} , decreased maximal muscle torque, decreased myosin ATPase activity and increased protein binding of Ca^{2+} in the sarcoplasmic reticulum (Sahlin, 1986). However, it has to be emphasized that the primary cause of the great decline in isokinetic torque during high-intensity exercise is difficult to interpret due to limitations of the present methods. A significant positive correlation ($r=0.82$, $p<0.001$) (Table 9) has been found between TWO during isokinetic exercise and FI in power-lifters, i.e athletes with greater work output during exercise fatigued faster. However, no significant correlations between TWO during exercise and FI have been observed in sedentary controls. The models used for short-time local exercises performed against high resistances (weight lifting and strength-training programmes) are generally related to strength instead of muscle anaerobic capacity.

The fatiguing exercise resulted in a significant decrease in isometric MVC and electrically evoked submaximal tetanic contraction characteristics of knee extensor muscles in power-lifters and controls, while this decrease was greater and recovery was slower in power-lifters (Study IV). The causes of fatigue after this type of repetitive maximal contractions may be both central (reduced motor drive) and peripheral (within the working muscles) in origin. A greater decrease in force production characteristics of electrically evoked submaximal tetanic contraction compared with MVC after exercise in both groups observed in the present study indicates that the reduction in the voluntary isokinetic performance is, at least partly, of peripheral origin. This peripheral muscle fatigue seems to be more expressed in power-lifters than controls. However, the applied electrical stimulation was submaximal, i.e the force produced by 50-Hz stimulation was approximately 25% of MVC. Therefore, in case of these results central fatigue cannot be excluded. Superimposed brief electrical shocks during isometric MVC have indicated reduced neural activation of knee extensor muscles after high-intensity isokinetic exercise (Duchateau & Hainaut, 1984; Newham *et al.*, 1991; Gandevia *et al.*, 1996). However, reduced neural activation seems to recover within 5 min after exercise (Behm, 1995). Isometric MVC force and electrically evoked submaximal tetanic contraction characteristics of knee extensor muscles were recovered to the pre-exercise level within 10 min after exercise in control subjects, while they did not recover in power-lifters (Fig. 10). A worsening in force-generating characteristics of electrically evoked tetanic contraction in power-lifters 10 min after exercise was significant as compared to controls. We conclude that some extent the fatigue observed in this study 10 min after the cessation of exercise in power-lifters is located within the muscles.

The mechanisms underlying fatigue can be of metabolic and structural origin. Accumulation of lactic acid, reduced pH and creatine phosphate (CrP)

concentration and increased inorganic phosphate (P_i) and hydrogen ion (H^+) concentrations in muscle fibres are possible causes of fatigue (Sahlin, 1986; Brody *et al.*, 1991; Sahlin *et al.*, 1998; Westerblad *et al.*, 1998). The CrP, P_i and H^+ concentrations seem to recover to nearly pre-exercise values within 5 min after repeated maximal contractions (Saugen *et al.*, 1997). It was suggested that metabolic changes are not the major causes of fatigue observed 5–20 min after exercise (Raastad & Hallen, 2000). One mechanism that reduces force-generation capacity of muscle is a change in the excitation-contraction coupling depressing the release of Ca^{2+} from the sarcoplasmic reticulum (Bruton *et al.*, 1998). It has been reported that reduced Ca^{2+} release due to changes in the excitation-contraction coupling, and disruptions of contractile proteins, are the most likely explanations for the peripheral fatigue observed 5–20 min after exercise (Raastad & Hallen, 2000).

After the end of isokinetic exercise, HRT of the evoked tetanic contraction of knee extensor muscles was significantly prolonged in both groups, while this prolongation was greater in power-lifters than controls (Table 7). It was also observed that within 10 min after exercise this parameter was recovered to the initial pre-exercise level in controls, while it did not recover in power-lifters. Several previous investigations noted the slowing of muscle relaxation during fatigue (Sjöholm *et al.*, 1983; Westerblad *et al.*, 1997). The significant prolongation of relaxation phase of evoked tetanic contraction of knee extensor muscles after repetitive maximal isokinetic contractions indicates the failure of Ca^{2+} -pumping mechanism of active muscle fibres during fatigue. The rate and duration of muscle relaxation depends on Ca^{2+} handling and altered cross-bridge kinetics (Cady *et al.*, 1989; Westerblad *et al.*, 1997). It has been suggested that fatigue reduces Ca^{2+} release, Ca^{2+} uptake and Ca^{2+} -ATPase activity in human skeletal muscles, and those decreases are correlated with fast twitch muscle fibre proportion (Li *et al.*, 2002; Liu *et al.*, 2003).

Thus, Study IV indicated that fatigue-induced slowing of muscle relaxation after repetitive maximal isokinetic exercise is more expressed in male power-lifters than sedentary subjects.

6.3. Posttetanic potentiation in knee extensor muscles after high-frequency submaximal percutaneous electrical stimulation

The present study (Study V) indicated that PTP in knee extensor muscles after a 7-s submaximal tetanic PES at 100 Hz was associated with a significant increase in twitch, doublet and 10-Hz tetanic contraction PF at 1, 3 and 5 min (Fig. 14A), whereas immediately after tetanic PES twitch and doublet contraction PF did not potentiate significantly. The potentiation of the twitch maximal RFD and RR was significant throughout the 10-min posttetanic period

with a small increase at 3 and 5 min. Thus this study indicated that PTP in knee extensor muscles had a small increase at 1–5 min followed by small decrease at 10 min. However, the twitch potentiation we observed in knee extensor muscles with submaximal direct PES, was less than the potentiation induced by MVC in knee extensor muscles (Stuart *et al.*, 1988; Hamada *et al.*, 2000; Rassier & Herzog, 2001) and by supramaximal indirect PES in dorsiflexor muscles (O’Leary *et al.*, 1997). The present results indicated that the decay in PTP from the immediate posttetanic value was not a simple exponent function, as sometimes observed (Kraup, 1977; Kraurup & Horowitz, 1979; Houston & Grange, 1991). In this study, PTP showed after direct submaximal PES a small increase at 1, 3, and 5 min followed by a small decrease at 10 min. In dorsiflexor muscles, PTP after 7-s indirect supramaximal tetanic stimulation at the frequency of 100 Hz declined over the 1st min but then showed a small increase at 2 min before it decreased again. The potentiation of twitch PF, and maximal RFD and RR was maximal immediately after supramaximal tetanic stimulation. This triphasic pattern of decay has been shown after MVC by several investigators (Vandervoort *et al.*, 1983; Green & Jones, 1989;).

It has been suggested that an increase in twitch potentiation is caused particularly by fatigue; as fatigue wanes, the level of potentiation increases before falling away (Vandervoort *et al.*, 1983). Fatigue may have been a factor in the present study, since PF of conditioning tetanic contraction decreased by 21% ($p < 0.05$) during the 7-s direct submaximal PES (Fig. 17). Direct PES evokes action potentials in intramuscular nerve branches generating force directly by the activation of motor axons. It is well known that during direct PES the current is applied extracellularly to the nerve endings with preferential activation of the larger FT (type II) muscle fibres. These FT fibres have larger axons with much lower electrical resistance for a given externally applied electrical current. FT muscle fibres show greater potentiation (Hamada *et al.*, 2000) but are more susceptible to fatigue. The fatigability of preferentially activated FT fibres is one possible explanation of marked decline in submaximal tetanic force during a 7-s direct PES observed in the present study (Fig. 13). The asynchronous and orderly (slow to fast) recruitment of MUs that occurs during voluntary activation is absent during direct PES. This lack of asynchrony and orderly recruitment contributes to the increased fatigability observed with electrical stimulation when compared to voluntary contraction. The tetanic force failure during electrostimulation at the frequency of 100 Hz results in an impaired propagation of muscle action potentials with no metabolic changes (Darques *et al.*, 2003). However, no significant changes in M-wave amplitude during a 7-s supramaximal indirect PES at 100 Hz in dorsiflexors have been shown (O’Leary *et al.*, 1997).

Our results indicated that immediately after the end of direct PES, the potentiation of 10-Hz tetanic contraction PF exceeded markedly the potentiation

of doublet contraction peak force, whereas no significant differences were observed in relative potentiation of these characteristics at 1, 3, 5 and 10 min posttetanic (Fig. 14A). Doublets were evoked with interstimulus interval of 10 ms, i.e. with the stimulation frequency of 100 Hz (O'Leary *et al.*, 1997; Hamada *et al.*, 2000). These facts suggest that the PTP assessed by low-frequency supra-maximal indirect activation immediately after direct submaximal tetanic PES is less affected by fatigue than PTP assessed by high-frequency activation.

The mechanism of PTP involves excitation-contraction coupling and/or myosin-actin interaction, rather than amplified excitation of muscle, i.e. enlarged muscle action potential (Houston & Grange, 1991; Grange *et al.*, 1993). Potentiation is caused by phosphorylation of the regulatory light chains of myosin, a Ca^{2+} -dependent process (Persecini *et al.*, 1985; Sweeney & Stull, 1990). However, it has been shown that the muscle M-wave amplitude increased sharply at 2 min after high-frequency tetanic stimulation and then subsided (O'Leary *et al.*, 1997). The M-wave amplitude may also grow after low-frequency tetanic stimulation or brief MVC-s (Hicks *et al.*, 1989; McComas *et al.*, 1994; Hamada *et al.*, 2000). The mechanism of M-wave potentiation is due to the stimulation of the sarcolemma's Na^+ - K^+ -pumping mechanism (McComas *et al.*, 1994). An increase of action potential might increase Ca^{2+} release from the sarcoplasmic reticulum, thereby increasing force (Moore & Stull, 1984).

Study V indicated that after tetanic stimulation a relative potentiation of twitch maximal RFD and RR was greater than the potentiation of twitch PF (with peak values of 38%, 32% and 17%, respectively) (Fig. 14B). Thus, these results indicated that twitch maximal RFD and RR seem to be more sensitive indicators of PTP than twitch PF. This is in agreement with O'Leary *et al.* (1997) who suggested a greater potentiation of twitch maximal RFD and RR (approximately 75 and 71%) in dorsiflexor muscles after a 7-s supramaximal indirect PES at 100 Hz as compared to potentiation of twitch PF (50%). The RFD has rarely been used as an indicator of muscle contraction speed and probably depends largely on the rate of formation of cross-bridges between myosin and actin during contraction (Lewis *et al.*, 1986). The RR is an indicator of muscle relaxation speed and depends on the rate of re-attachment of cross-bridges during the relaxation process (Klug *et al.*, 1982; Vandervoort *et al.*, 1983).

Neuromuscular electrical stimulation is often used by physical therapists to improve muscle performance. The present results may have important clinical relevance when using brief trains of electric stimulation to strengthening muscles and to aid patients in performing functional movements in rehabilitation. These results contribute to our understanding of relationship between the activation pattern of muscles and the force output produced.

CONCLUSIONS

1. Power-trained athletes had a greater maximal voluntary and electrically evoked twitch force-generating capacity and speed of contraction and relaxation of plantarflexor muscles compared to endurance-trained athletes. Both power and endurance training induced a shortening of evoked twitch contraction and relaxation times.
2. Power training induced a significant increase in twitch post-activation potentiation capacity in plantarflexor muscles, whereas endurance training did not induce similar changes.
3. High-intensity short-term isokinetic knee extension exercise induced an acute neuromuscular fatigue with lowered isometric voluntary and electrically evoked tetanic contraction force-generating capacity of knee extensor muscles.
4. Power-lifters fatigued faster during repetitive maximal isokinetic knee extensions compared to untrained subjects. The recovery of isometric voluntary and electrically evoked tetanic contraction characteristics of knee extensor muscles after fatiguing exercise was more delayed in power-lifters.
5. High-frequency direct submaximal percutaneous electrical stimulation induced posttetanic potentiation in knee extensor muscles with small increase at 1–5 min followed by small decrease at 10 min. Twitch maximal rates of force development and relaxation seem to be more sensitive indicators of post-tetanic potentiation than twitch peak force.

REFERENCES

- Aagaard P. Training-induced changes in neural function. *Exer Sport Sci Rev*, 2003, 31: 61–67.
- Abbate F., Van Der Velden L., Stienen G. J., Haan A. Post-tetanic potentiation increases energy cost to a higher extent than work in rat fast skeletal muscle. *J Muscle Res Cell Motil*, 2001, 22(8): 703–710.
- Allman B.L., Rice C.L. Neuromuscular fatigue and aging: central and peripheral factors. *Muscle Nerve*, 2002, 25(6): 785–796.
- Alway S.E., Hughson R.L., Green H.J., Patla A.E., Frank J.S. Twitch potentiation after fatiguing exercise in man. *Eur J Appl Physiol*, 1987, 56: 461–466.
- Alway S.E., MacDougall J.D., Sale D.G., Sutton J.R., McComas A. J. Functional and structural adaptations in skeletal muscle of trained athletes. *J Appl Physiol*, 1988, 64: 1114–1120.
- Alway S.E., MacDougall J.D., Sale D.G. Contractile adaptations in human triceps surae after isometric exercise. *J Appl Physiol*, 1989, 66: 2725–2732.
- Agbonjinmi, A.P., Amusa, L.O. & Toriola, A.L. Anthropometric and tissue characteristics of an elite power athlete in Botswana. *J Sports Stud*, 2001, 6(1): 9–17.
- Asmussen G., Schmalbruch I., Soukup T., Pette D. Contractile properties, fiber types, and myosin isoforms in fast and slow muscles of hyperactive Japanese waltzing mice. *Exp Neurol*, 2003, 184(2): 758–766.
- Barany M. ATPase activity of myosin correlated with speed of muscle shortening. *J Gen Physiol*, 1967, 50: 197–218.
- Baudry S., Duchateau J. Postactivation potentiation in human muscle is not related to the type of maximal conditioning contraction. *Muscle Nerve*, 2004, 30(3): 328–336.
- Behm D.G. Neuromuscular implications and applications of resistance training. *J Strength Cond Res*, 1995, 9: 264–274.
- Belanger A.Y., McComas A.J. Contractile properties of human skeletal muscle in childhood and adolescence. *Eur J Appl Physiol*, 1989, 58: 563–567.
- Bellemare F., Woods J.J., Johansson R.S., Bigland-Ritchie B. Motor-unit discharge rates in maximal voluntary contractions of three human muscles. *J Neurophysiol*, 1983, 50: 1380–1392.
- Bigland-Ritchie B., Woods J.J. Changes in muscle contractile properties and neural control during human muscle fatigue. *Muscle Nerve*, 1984, 7: 691–699.
- Bigland-Ritchie B., Johansson R., Lippold O.J., Woods J.J. Contractile speed and EMG changes during fatigue of sustained maximal voluntary contractions. *J Neurophysiol*, 1983a, 50: 313–324.
- Bigland-Ritchie B., Johnson R., Lippold O.T., Smith S., Words J.J. Changes in motoneurone firing rates during sustained maximal voluntary contractions. *J Physiol (Lond)*, 1983, 340: 335–346.
- Blanc F.X., Coirault C., Salmeron S., Chemla D., Lecarpentier Y. Mechanics and crossbridge kinetics of tracheal smooth muscle in two inbred rat strains. *Eur Respir J*, 2003, 22(2): 227–237.
- Bosco C. Stretch-shortening Cycle in Skeletal Muscle Function. Academic Dissertation. Jyväskylä, 1982.

- Bosco C. Strength training for volleyball players. Slightly abbreviated translation from *Leitungssport*, 1988: 18–20.
- Brasil-Neto J.P., Cohen L.G., Hallet H. Central fatigue as revealed by postexercise decrement of motor evoked potentials. *Muscle Nerve*, 1994, 17: 713–719.
- Brocherie F., Babault N., Cometti G., Maffiuletti N., Chatard J.C. Electrostimulation training effects on the physical performance of ice hockey players. *Med Sci Sports Exerc*, 2005, 37: 455–460.
- Brody L.R., Pollock M.T., Ruy S.H., DeLuca C.J., Celly B. pH – induced effects on median frequency and conduction velocity of the myoelectric signal. *J Appl Physiol*, 1991, 71: 1878–1885.
- Brooke M.H., Engel W.K. The histographic analysis of human muscle biopsies with regard to fiber types. I. Adult male and female. *Neurology*, 1969, 19: 221–233.
- Brown A.B., McCartney N., Sale D.G. Positive adaptations to weight-lifting training in the elderly. *J Appl Physiol*, 1990, 69: 1725–1733.
- Brown S.J., Child R.B., Day S.H., Donnelly A.E. Exercise-induced skeletal muscle damage and adaptation following repeated bouts of eccentric muscle contractions. *J Sports Sci*, 1997, 15: 215–222.
- Brown I.E., Loeb G.E. Postactivation potentiation – A clue for simplifying models of muscle dynamics. *Amer Zool*, 1999, 38: 743–754.
- Bruton J.D., Lännegren J., Westerblad H. Mechanisms underlying the slow recovery of force after fatigue: importance of intracellular calcium. *Acta Physiol Scand*, 1998, 162: 285–293.
- Burke R.E. Motor units: anatomy, physiology, and functional organization. In: Brooks V. B. (ed) *The Nervous System, Motor Control. Handbook of Physiology*, vol 2, part 1. American Physiological Society, Bethesda, 1981, 345–422.
- Cady E.B., Elshore H., Jones D.A., Moll A. The metabolic causes of slow relaxation in fatigued human skeletal muscle. *J Physiol (Lond)*, 1989, 418: 327–337.
- Caiozzo, J.V., Perrine, J.J., Edgerton, R.V. Training induced alteration of the in vivo force-velocity in human muscle. *J Appl Physiol*, 1981, 51: 750–754.
- Campbell M.J., McComas A.J., Petito F. Physiological changes in aging muscles. *J Neurol Neurosurg Psychiatry*, 1973, 36: 174–182.
- Carolan B., Cafarelli E. Adaptations in coactivation after isometric resistance training. *J Appl Physiol*, 1992, 73: 911–917.
- Carroll T.J., Riek S., Carson R.G. Neural adaptations to resistance training: implications for movement control. *Sports Med*, 2001, 31(12): 829–840.
- Cavagna G.A., Dusman B., Margaria R. Positive work done by a previously stretched muscle. *J. Appl. Physiol.*, 1968, 24: 21–32.
- Chan K.M., Doherty T.J., Brown W.F. Contractile properties of human motor units in health, aging, and disease. *Muscle Nerve*, 2001, 24(9): 1113–1133.
- Costill D.L., Fink W.J., Pollock M.L. Muscle fiber composition and enzyme activities of elite distance runners. *Med Sci Sports*, 1976, 8:96–100.
- Coyle E.F., Feiring D.C., Rotkis T.C., Cote R.W., Roby F.B., Lee W., Wilmore J.H. Specificity of power improvements through slow and fast isokinetic training. *J Appl Physiol*, 1981, 51(6):1437–1442.
- Darques J.L., Dendaham D., Roussel M., Giannesini B., Tagliarini F., Le Fur Y., Cozzone J., Jammes Y. Combined in situ analysis of metabolic and myoelectrical

- changes associated with electrically induced fatigue. *J Appl Physiol*, 2003, 95:1476–1484.
- Davies C.T.M., Young A. Effects of training at 30 and 100% maximal isometric force (MVC) on the contractile properties of the triceps surae in man. *J Physiol (London)*, 1982, 336: 22–23P.
- Davies C.T.M., White M.J. Contractile properties of elderly triceps surae. *Gerontology*, 1983, 29: 19–25.
- Davies C.T.M., Dooley P., McDonagh M.N., White M.J. Adaptation of mechanical properties of muscle to high force training in man. *J Physiol (Lond)*, 1985, 365: 277–284.
- Dawson M.J., Gadian D.G., Wilkie D.R. Muscular fatigue investigated by phosphorus nuclear magnetic resonance. *Nature*, 1978, 274(5674): 861–866.
- Desmedt J.E., Godaux E. Ballistic contractions in man: Characteristic recruitment pattern of single motor units of the tibialis anterior muscle. *J Physiol (Lond)*, 1977, 264: 673–693.
- Dietz, V., Noth, J., Schmidtbleicher, D. Interaction between pre-activity and stretch reflex in human triceps brachii during landing from forward falls. *J Physiol (Lond)*, 1981, 311: 113–125.
- Drachman D.B., Johnston D.M. Development of mammalian fast muscle: dynamic and biochemical properties correlated. *J Physiol (Lond)*, 1973, 234: 29–42.
- Duchateau J., Hainaut K. Isometric or dynamic training: differential effects on mechanical properties of a human muscle. *J Appl Physiol*, 1984, 56: 296–301.
- Dyer R.F., Enna C.D. Ultrastructural features of adult human tendon. *Cell and Tissue Research*, 1976, 6, 168(2): 247–259.
- Edwards R.T. Human muscle function and fatigue. In: Porter R., Whelan J. editors. *Human Muscle Fatigue: Physiological Mechanisms*. London: Pintman Medical, 1981, pp. 1–18.
- Elder G.B., Bradbury K., Roberts R. Variability of fiber type distributions within human muscle. *J Appl Physiol*, 1982, 53: 1473–1480.
- Eloranta V, Komi P.V. Function of the quadriceps femoris muscle under maximal concentric and eccentric contractions. *Electromyogr Clin Neurophysiol*. 1980, 20(2): 159–154.
- Emerson J.C.P. Molecular genetics of myosin. *Ann Rev Biochem*, 1987, 56: 695–726.
- Engel W.K. The essentiality of histo- and cytochemical studies of skeletal muscle in the investigation of neuromuscular disease. *Neurology*, 1962, 12: 778–784.
- Enoka R. *Neuromechanical Basis of Kinesiology*. Human Kinetics, Champaign, 1988.
- Enoka R. M. Neural adaptations with chronic physical activity. *J Biomech*, 1997, 30: 447–455.
- Feiereisen P., Duchateau J., Hainaut K. Motor unit recruitment order during voluntary and electrically induced contractions in the tibial anterior. *Exp Brain Res*, 1997, 114: 117–123.
- Feinstein B., Lindegard B., Nyman E., Wohlfart G. Morphologic studies of motor units in normal human muscles. *Acta Anat*, 1955, 23: 127–142.
- French D.N., Kraemer W., Cooke C.B. Changes in dynamic exercise performance following a sequence of preconditioning isometric muscle actions. *J Strength Cond Res*, 2003, 17: 678–685.

- Freund, H.J., Büdingen, H.J., Dietz, V. Activity of single motor units from human forearm muscle during voluntary isometric contractions. *J Neurophysiol*, 1975, 38: 933–956.
- Froese E.A., Houston M.E. Torque-velocity characteristics and muscle fiber type in human vastus lateralis. *J Appl Physiol*, 1985, 59: 309–314.
- Fry A.C., Webber J.M., Weiss L.W., Harber M.P., Vaczi M., Pattison N.A. Muscle fiber characteristics of competitive power lifters. *J Strength Cond Res*, 2003, 17: 402–410.
- Fukashiro S., Itoh M., Ishinose Y., Kawakami Y., Fukunaga T. Ultrasonography gives directly but noninvasively elastic characteristics of human tendon in vivo. *Eur J Appl Physiol*, 1995, 71: 555–557.
- Gandevia S.C. Spinal and supraspinal factors in human muscle fatigue. *Physiol Rev*, 2001, 81(4): 1725–1789.
- Gandevia S.C., Allen G.M., Butler J.E., Taylor J.L. Supraspinal factors in human muscle fatigue: evidence for suboptimal output from the motor cortex. *J Physiol (Lond)*, 1996, 490: 529–536.
- Garland S.J., Enoka R.M., Serrano L.P., Robinson G.A. Behaviour of motor units in human biceps brachii during submaximal fatiguing contractions. *J Appl Physiol*, 1994, 76: 2411–2419.
- Garner S.H., Hicks A.L., McComas A.J. Prolongation of twitch potentiation mechanism throughout muscle fatigue and recovery. *Exp Neurol*, 1989, 103: 277–281.
- Gerdle B., Karlsson S., Crenshaw A., Friden J., Nilsson L. Characteristics of the shift from the fatigue phase to the endurance level (breakpoint) of peak torque during repeated dynamic maximal knee extensions are correlated to muscle morphology. *Isokin Exerc Sci*, 1998, 7: 49–60.
- Gollnick P.D., Sjödin B., Karlsson J., Jansson E., Saltin B. Human soleus muscle: a comparison of fiber composition and enzyme activities with other leg muscles. *Pflügers Arch*, 1974, 348: 247–255.
- Graig B.W., Lucas J, Pohlman R. Effects of running, weightlifting and a combination of both on growth hormone release. *J Appl Sport Sci Res*, 1991, 5: 198–203.
- Grange R.W., Vandenboom R., Houston M.E. Physiological significance of myosin phosphorylation in skeletal muscle. *Can J Appl Physiol*, 1993: 18: 229–242.
- Green H.J., Daub B., Houston M.E., Thomson J.A., Fraser I., Ranney D. Human vastus lateralis and gastrocnemius muscles. A comparative histochemical and biochemical analysis. *J Neurol Sci.*, 1981, 52: 201–210.
- Green H. Neuromuscular aspects of fatigue. *Can J Sports Sci*, 1987, Suppl. 17S–19S.
- Green H.J., Jones S.R. Does post-tetanic potentiation compensate for low frequency fatigue? *Clin Physiol*, 1989, 9: 499–514.
- Gregor R.J., Edgerton V.R., Rozenek R., Castelman K.R. Skeletal muscle properties and performance in elite track athletes. *Eur J Appl Physiol*, 1981, 47: 355–364.
- Gregorevic P., Plant D.R., Stupka N., Lynch G.S. Changes in contractile activation characteristics of rat fast and slow skeletal muscle fibres during regeneration. *J Physiol (Lond)*, 2004, 558(2): 549–560.
- Gross M.T., Hoffman G.M., Phillips C.N., Wray J.A. Intramachine and intermachine reliability of the Biodex and Cybex II for knee flexion and extension peak torque and angular work. *J Orthop Sports Phys Ther* 1991, 13: 329–335.

- Güllich A., Schmidtbleicher D. MVC-induced short-term potentiation of explosive force. *N Stud Athlet*, 1996, 11: 67–81
- Gydikov A., Kossev A., Christova L. Influence of the interstimulus interval on the extraterritorial potentials of the motor units. *Electromyogr Clin Neurophysiol*, 1982, 22(7): 563–577.
- Gydikov A., Kosarov D. Influence of various factors on the length of the summated depolarized area of the muscle fibres in voluntary activating of motor units and electrical stimulation. *Electromyogr Clin Neurophysiol*, 1974, 14(1):79–93.
- Hainaut K., Duchateau J. Neuromuscular electrical stimulation and voluntary exercise. *Sports Med*, 1992, 14: 100–113.
- Hamada T., Sale D.G., MacDougall J.D. Postactivation potentiation in endurance-trained male athletes. *Med Sci Sports Exerc*, 2000, 32: 403–411.
- Hamada T., Sale D.G., MacDougall J.D., Tarnopolsky M.A. Interaction of fibre type, potentiation and fatigue in human knee extensor muscles. *Acta Physiol Scand*, 2003, 178: 165–173.
- Henneman E., Somjen G., Carpenter D.O. Excitability and inhibitability of motoneurons of different sizes. *J Neurophysiol*, 1965, 28(3): 599–620.
- Hicks A.L., Fenton J., Garner S., McComas A.J. M wave potentiation during and after muscle activity. *J Appl Physiol*, 1989, 66: 2606–2610.
- Hoh J.F. Muscle fiber types and function. *Curr Opin Rheumatol*, 1992, 4(6): 801–808.
- Houston M.E., Grange R.W. Torque potentiation and myosin light-chain phosphorylation in human muscle following a fatiguing contraction. *Can J Physiol Pharmacol*, 1991, 69: 269–273.
- Hultman E., Greenhaff P.L., Ren J. M., Soderlund K. Energy metabolism and fatigue during intense muscle contraction. *Biochem Soc Trans*, 1991, 19(2): 347–353.
- Hultman E., Sjöholm M. Electromyogram, force and relaxation time during and after continuous electrical stimulation of human skeletal muscle in situ. *J Physiol (Lond)*, 1983, 339: 33–40.
- Häkkinen K., Komi P.A. Neuromuscular, anaerobic and aerobic performance characteristics of elite power athletes. *Eur J Appl Physiol*, 1984, 53: 97–105.
- Häkkinen K., Keskinen K.L. Muscle cross sectional area and voluntary force production characteristics in elite strength- and endurance-trained athletes and sprinters. *Eur J Appl Physiol*, 1989, 59: 215–220.
- Häkkinen K. Neuromuscular fatigue and recovery in male and female athletes during heavy resistance training. *Int J Sports Med*, 1993;14: 53–59.
- Häkkinen K. Neuromuscular fatigue in males and females during strenuous heavy resistance loading. *Electromyogr Clin Neurophysiol*, 1994, 34(4): 205–214.
- Häkkinen K., Kraemer W.J., Newton R.U., Alen M. Changes in electromyographic activity, muscle fibre and force production characteristics during heavy resistance/ power strength training in middle-aged and older men and women. *Acta Physiol Scand*, 2001, 171(1): 51–62.
- Ishida K., Moritani T., Itoh K. Changes in voluntary and electrically induced contractions during strength training and detraining. *Eur J Appl Physiol*, 1990, 60: 244–248.

- Ivy J.L., Withers R.T., Brose G., Maxwell B.D., Costill D.L. Isokinetic contractile properties of the quadriceps with relation to fiber type. *Eur J Appl Physiol*, 1981, 47: 247–255.
- Izquierdo M., Häkkinen K., Gonzales-Badillo J.J., Ibáñez J., Gorostiaga E.M. Effects of long-term training specificity on maximal strength and power of the upper and lower extremities in athletes from different sports. *Eur J Appl Physiol*, 2002, 87: 264–271.
- Jaric S. Muscle strength testing. Use of normalisation for body size. *Sports Med*, 2002, 32(10): 615–631.
- Jenkins W.L., Thackaberry C., Killian C. Speed-specific isokinetic training. *J Orthop Sports Phys Ther*, 1984, 6: 181–183.
- Johansson C., Lorentzon R., Sjöström M., Fagerlund M., Fugl-Meyer A.R. Sprinters and marathon runners: isokinetic knee extensor performance reflect muscle size and structure? *Acta Physiol Scand*, 1987, 130: 663–670.
- Johnson M.A., Polgar J., Weightman D., Appleton D. Data on the distribution of fibre types in thirty-six human muscles. An autopsy study. *J Neurol Sci.*, 1973, 18: 111–129.
- Josephson R.K. Extensive and intensive factors determining the performance of striated muscle. *J Exp Zool*, 1975, 194: 135–154.
- Kanda K., Hashizume K. Changes in the properties of the rat medial gastrocnemius motor units in aging rats. *J Neurophysiol*, 1989, 61: 737–746.
- Kent-Brown J.A. Noninvasive measures of central and peripheral activation in human muscle fatigue. *Muscle Nerve*, 1997, 5: 98–101.
- Kirkendall D.T. Mechanisms of peripheral fatigue. *J Med Sci Sports Exerc*, 1990, 22(4): 444–449.
- Kitai T.A., Sale D.G. Specificity of joint angle in isometric training. *Eur J Appl Physiol*, 1989, 58: 744–748.
- Klein C.S., Ivanova T.D., Rice C.L., Garland S.J. Motor unit discharge rate following twitch potentiation in human triceps brachii muscle. *Neurosci Lett*, 2001, 316: 153–156.
- Klitgaard H., Ausoni S., Damiani E. Sarcoplasmic reticulum of human skeletal muscle: age-related changes and effect of training. *Acta Physiol Scand*, 1989, 137: 23–31.
- Klug G.A., Botterman B.R., Stull J.T. The effect of low frequency stimulation on myosin light chain phosphorylation in skeletal muscle. *J Biol Chem*, 1982, 257 : 4688–4690.
- Klug G.A., Leberer E., Leisner E., Simoneau J.A., Pette D. Relationship between parvalbumin content and the speed of relaxation in chronically stimulated rabbit fast twitch muscle. *Pflügers Arch*, 1988, 411: 126–131.
- Knaflitz M., Merletti R., De Luca C.J. Inference of motor unit recruitment order in voluntary and electrically elicited contractions. *J Appl Physiol*, 1990, 68: 1657–1667.
- Knapik J.J., Wright J.E., Mawlsly R.H., Braun J.M. Isokinetic, isometric and isotonic strength relationships. *Arch Phys Med Rehabil*, 1983, 64: 77–80.
- Komi P.V. Neuromuscular performance: factor influencing force and speed production. *Scand J Sport Sci*, 1979, 1(1): 2–15.

- Komi P.V. Physiological and biomechanical correlates of muscle function: Effects of muscle structure and strength-shortening cycle on force and speed. *Exerc Sport Sci Rev*, 1984, 12: 81–122.
- Komi P.V., Tesch P. EMG frequency spectrum, muscle structure and fatigue during dynamic contractions in men. *Eur J Appl Physiol*, 1979, 42: 41–52.
- Komi P.V. Stretch-shortening cycle: a powerful model to study normal and fatigued muscle. *J Biomech*, 2000, 3(10): 1197–1206.
- Konstantinov I.M., Filippova S.N., Vavilin V.A., Panov A.V., Liakhovich V.V. Changes in oxidative phosphorylation in rat liver mitochondria during the development of cholestasis. *Vopr Med Khim*, 1980, 26(4): 498–502.
- Krarup C. Electrical and mechanical responses in the platysma and in the abductor pollicis muscle in normal subjects. *J Neurol Neurosurg Psychiatry*, 1977, 40: 234–240.
- Krarup C, Horowitz SH. Evoked responses of the elbow flexors in control subjects and myopathy patients. *Muscle Nerve*, 1979, 2: 465–477.
- Krenács T., Molnár E., Dobó E., Dux L. Fibre typing using sarcoplasmic reticulum Ca^{2+} -ATPase and myoglobin immunohistochemistry in rat gastrocnemius muscle. *Histochem*, 1989, 21: 145–155.
- Kroll W., Clarkson P., Kamen G., Lambert J. Muscle fiber type composition and knee extension isometric strength fatigue patterns in power and endurance trained males. *Res Quart Exer Sport*, 1980, 51: 323–333.
- Kugelberg E., Thornell L-E. Conduction time, histochemical type, and terminal cisternae volume of rat motor units. *Muscle Nerve*, 1983, 6: 149–153.
- Kyröläinen H., Komi P.V. Neuromuscular performance of lower limbs during voluntary and reflex activity in power- and endurance-trained athletes. *Eur J Appl Physiol*, 1994, 69: 233–239.
- Lacour J.R. Physiological analysis of qualities in sprinting. *New Studies in Athletics*, 1996, 2–3: 59–62.
- Larsson L., Moss R.L. Maximum velocity of shortening in relation to myosin isoform composition in single fibres from human skeletal muscles. *J Physiol (Lond)*, 1993, 472: 595–614.
- Lattier G., Millet G.Y., Maffiuletti N.A., Babault N., Lepers R. Neuromuscular differences between endurance-trained, power-trained, and sedentary subjects. *J Strength Cond Res*, 2003, 17: 514–521.
- Leveritt M., Abernethy P.J., Barry B.K., Logan P.A. Concurrent strength and endurance training. *Sports Med*, 1999, 28: 413–427.
- Lewis D.M., Al-Almood W.S., Rosendorff C. Stimulation of denervated muscle: what do isometric and isotonic recordings tell us? In: Nix W. A., Vrbova G. *Electrical Stimulation and Neuromuscular Disorders*. Springer Verlag, Berlin, 1986, 101–113.
- Lexell J. Human ageing, muscle mass, and fiber type composition. *J Gerontol*, 1995, 50(A): 11–16.
- Li J.L., Wang X.N., Fraser S.F., Carey M.F., Wrigley T.V., McKenna M.J. Effects of fatigue and training on sarcoplasmic reticulum Ca^{2+} regulation in human skeletal muscle. *J Appl Physiol*, 2002; 92: 912–922.
- Linnamo V., Häkkinen K., Komi P. V. Neuromuscular fatigue and recovery in maximal compared to explosive strength loading. *Eur J Appl Physiol*, 1998; 77: 176–181.

- Liu Y., Schlumberger A., Wirth K., Schmidtbleicher D., Steinacker J. M. Different effects on human skeletal myosin heavy chain isoform expression: strength vs. combination training. *J Appl Physiol*, 2003, 94: 2282–2288.
- Malatesta D., Cattaneo F., Dugnani S., Maffiuletti N.A. Effects of electromyostimulation training and volleyball practice on jumping ability. *J Strength Cond Res*, 2003, 17: 573–579.
- McComas A.J., Thomas A.C. Fast and slow twitch muscles in man. *J Neurol Sci*, 1968, 7: 301–307.
- McComas A.J., Galea V., Einhorn R.W. Pseudofacilitation: a misleading term. *Muscle Nerve*, 1994, 17: 599–607.
- McComas A.J. *Skeletal Muscle: Form and Function*. Human Kinetics, Champaign, 1996.
- MacDougall J.D., Elder G.C.B., Sale D.G., Moroz J.R., Sutton J. R. Effects of strength training and immobilization on human muscle fibres. *Eur J Appl Physiol*, 1980, 43: 25–34.
- MacDougall J.D., Sale D.G., Alway S.E., Sutton J.R. Muscle fiber number in biceps brachii in bodybuilders and control subjects. *J Appl Physiol*, 1984, 57: 1399–1403.
- MacDougall J.D., Sale D.G., Elder G.C.B., Sutton J.R. Muscle ultrastructural characteristics of elite powerlifters and body builders. *Eur J Appl Physiol* 1982, 48: 117–126.
- MacDougall J.D., Sale D.G., Moroz J.R., Elder G.C.B., Sutton J. R., Howald H. Mitochondrial volume density in human skeletal muscle following heavy resistance training. *Med Sci Sports Exer*, 1979, 11: 164–166.
- MacDougall J.D. Morphological changes in human skeletal muscle following strength training and immobilization. In: Jones N., McCartney N., McComas A. *Human Muscle Power*. Human Kinetics Publishers, 1986, 78–99.
- MacIntosh B.R., Gardiner P.F. Posttetanic potentiation and skeletal muscle fatigue: interactions with caffeine. *Can J Physiol Pharmacol*, 1987, 65: 260–268.
- MacIntosh B.R., Grange R.W., Cory C.R., Houston M.E. Myosin light chain phosphorylation during staircase in fatigued skeletal muscle. *Pflügers Arch*, 1993, 425: 9–15.
- Madsen O.R. Torque, total work, power, torque acceleration energy and acceleration time assessed on a dynamometer: reliability of knee and elbow extensor and flexor strength measurements. *Eur J Appl Physiol*, 1996, 74: 206–210.
- Maffiuletti N.A., Martin A., Babault N., Pensini M., Lucas B., Schieppatti M. Electrical and mechanical Hmax – to – Mmax ratio in power- and endurance-trained athletes. *J Appl Physiol*, 2001, 90: 3–9.
- Mc Donagh M.J.N., Hayward C.M., Davies C.T.M. Isometric training in human elbow flexor muscles. *J Bone Joint Surg*, 1983, 65: 355–358.
- Mc Kay, W.B., Tuel, S.M., Sherwood, A.M., Stonic, D.S., Dimitrijevic, M.R. Focal depression of cortical excitability induced by fatiguing muscle contraction: a transcranial magnetic stimulation study. *Exp Brain Res*, 1995, 105: 276–282.
- Mero, A., Luhtanen, P., Viitasalo, J., Komi, P.V. Relationship between the maximal running velocity, muscle fibre characteristics, force production and force relaxation of sprinters. *Scand J Sports Sci*, 1981, 3: 16–22.

- Metzger J., Moss R. pH modulation of the kinetics of a Ca^{2+} sensitive cross-bridge state transition in mammalian single skeletal muscle fibers. *J Physiol (Lond)*, 1990, 428: 751–764.
- Milner-Brown H.S., Stein R.B., Lee R.G. Synchronization of human motor units: possible roles of exercise and supraspinal reflexes. *Electroencephalogr Clin Neurophysiol*, 1975, 38: 245–254.
- Moore R.L., Stull J.T. Myosin light chain phosphorylation in fast and slow skeletal muscles in situ. *Am J Physiol*, 1984, 245: C462–C471.
- Moritani T., de Vries H.A. Neural factors versus hypertrophy in the time course of muscle strength gain. *Am J Phys Med*, 1979, 58: 115–130.
- Narici M.V., Hoppeler H., Kayser B., Landoni L., Claassen H., Gavardi C., Conti M., Cerretelli P. Human quadriceps cross-sectional area, torque and neural activation during 6 months strength training. *Acta Physiol Scand*, 1996, 157: 175–186.
- Newham D.J., Jones D.A., Clarkson P.M. Repeated high-force eccentric exercise: effects on muscle pain and damage. *J Appl Physiol*, 1987, 63: 1381–1386.
- Newham D.J., McCarthy T., Turner J. Voluntary activation of human quadriceps during and after isokinetic exercise. *J Appl Physiol*, 1991, 71: 2122–2126.
- O'Hagan F., Tsunoda N., Sale D.G., Mac Dougall J.D. Elbow flexor evoked twitch contractile properties in untrained men and women and male bodybuilders. *Eur J Appl Physiol*, 1993, 66: 240–245.
- O'Leary, D.D., Hope, K., Sale, D.G. Posttetanic potentiation of human dorsiflexors. *J Appl Physiol*, 1997, 83: 2131–2138.
- Paavolainen L., Häkkinen K., Nummela A., Rusko H. Neuromuscular characteristics and fatigue in endurance and sprint athletes during a new anaerobic power test. *Eur J Appl Physiol*, 1994, 69: 119–126.
- Palmer, B.M., Moore, R.L. Myosin light chain phosphorylation and tension potentiation in mouse skeletal muscle. *Am J Physiol Cell Physiol*, 1989, 257: C1012–C1019.
- Pampus B., Lehnertz K., Martin D. The effect of different load intensities on the development on maximal strength and strength endurance. *Leistungssport*, 1989, 19: 20–25.
- Pasquet B., Carpentier A., Duchateau J., Hainaut K. Muscle fatigue during concentric and eccentric contractions. *Muscle Nerve*, 2000, 23(11): 1727–1735.
- Pavlat D.J., Housh T.J., Johnson G.O., Eckerson J.M. Electromyographic responses at the neuromuscular fatigue threshold. *J Sports Med Phys Fitness*, 1995, 35(1): 31–37.
- Perrin D.H. *Isokinetic Exercise and Assessment*. Champaign, Human Kinetics, 1993, 41–67.
- Persechini A., Stull J.T., Cooke R. The effect of myosin phosphorylation on the contractile properties of skinned rabbit skeletal muscle fibers. *J Biol Chem*, 1985, 260: 7951–7954.
- Peter J.B., Barnard R.J., Edgerton V.R., Gillespie C.A., Stempel K.E. Metabolic profiles of three fiber types of skeletal muscle in guinea pigs and rabbits. *Biochemistry*, 1972, 11: 2627–2633.
- Petrella R.J., Cunningham D.A., Vandervoort A.A., Paterson D.H. Comparison of twitch potentiation in the gastrocnemius of young and elderly men. *Eur J Appl Physiol*, 1989, 58: 395–399.

- Pincivero D.M., Gandaio C.B., Ito Y. Gender-specific knee extensor torque, flexor torque, and muscle fatigue responses during maximal effort contractions. *Eur J Appl Physiol*, 2003, 89: 134–141.
- Pincivero D.M., Gear W.S., Sterner R.L. Assessment of the reliability of high-intensity quadriceps femoris muscle fatigue. *Med Sci Sports Exer*, 2001, 33: 334–338.
- Pincivero D.M., Lephard S.M., Karunakara R.G. Reliability and precision of isokinetic strength and muscular endurance for the quadriceps and hamstrings. *Int J Sports Med*, 1997, 18: 115–119.
- Putman C.T., Xu X., Gillies E., MacLean I.M., Bell G.J. Effects of strength, endurance and combined training on myosin heavy chain content and fibre-type distribution in humans. *Eur J Appl Physiol*, 2004, 92: 376–384.
- Pääsuke M., Ereline J., Gapeyeva H. Neuromuscular fatigue during repeated exhaustive submaximal static contractions of knee extensor muscles in endurance-trained, power-trained and untrained men. *Acta Physiol Scand*, 1999, 166: 319–326.
- Pääsuke M., Ereline J., Gapeyeva H. Changes in twitch contractile characteristics of plantarflexor muscles in post-activation potentiation condition during repeated fatiguing submaximal static contractions. *Biol Sport*, 2000a, 17: 169–177.
- Pääsuke M., Ereline J., Gapeyeva H. Twitch contraction properties of plantar flexor muscles in pre- and postpubertal boys and men. *Eur J Appl Physiol*, 2000b, 82(5–6): 459–464.
- Pääsuke M., Ereline J., Gapeyeva H., Sander P., Sirkel S. Twitch potentiation capacity of plantarflexor muscles in women with increasing age. *Biol Sport*, 2002, 19(3): 213–223.
- Raastad T., Hallen J. Recovery of skeletal muscle contractility after high- and moderate intensity strength exercise. *Eur J Appl Physiol*, 2000, 82: 206–214.
- Rassier D.E., Herzog W. The effects of training on fatigue and twitch potentiation in human skeletal muscle. *Eur J Sports Sci*, 2001, 1: 1–8.
- Rice C.L., Cunningham, D.A., Paterson D.H., Dickinson J.R. Strength training alters contractile properties of the triceps brachii in men aged 65–78 years. *Eur J Appl Physiol*, 1993, 66: 275–280.
- Rusko H., Rahkila P. Effect of training on aerobic capacity of female athletes differing in muscle fibre composition. *J Sports Sci*, 1983, 1: 185–194.
- Rusko H. Effect of training on aerobic power characteristics of young cross country skiers. *J Sports Sci*, 1987, 5: 273–286.
- Sacco P., Thickboom G., Thompson M.L., Mastaglia F.L. Changes in corticomotor excitation and inhibition during prolonged submaximal muscle contraction. *Muscle Nerve*, 1997, 20: 1158–1166.
- Sahlin K., Tonkonogi M., Söderlund K. Energy supply and muscle fatigue in humans. *Acta Physiol Scand*, E and FNSpon, 1998, 162: 261–276.
- Sahlin K. Muscle fatigue and lactic acid accumulation. *Acta Physiol Scand*, 1986, 128: Suppl. 556: 83–91.
- Sale D.G. Neural adaptation to resistance training. *Med Sci Sports Exer*, 1988, 20: 135–145.
- Sale D.G. Postactivation potentiation: role in human performance. *Exerc Sport Sci Rev*, 2002, 30: 138–143.

- Sale D.G., McComas A.J., MacDougall J.D., Upton A.R.M. Neuromuscular adaptation in human thenar muscles following strength training and immobilization. *J Appl Physiol*, 1982a, 53: 419–424.
- Sale D.G., Quinlan J., Marsh E., McComas A.J., Belanger A Y. Influence of joint position on ankle plantarflexion in humans. *J Appl Physiol*, 1982b, 52: 1632–1642.
- Sale D.G., Upton A.R.M., McComas A.J., Mac Dougall J.D. Neuromuscular function in weight-trainers. *Exp Neurol*, 1983, 82: 521–531.
- Saltin B. The physiology of competitive c.c. skiing across a four decade perspective; with a note on training included adaptations and role of training at medium altitude. In: *Science and skiing*, 1997, pp. 435–469.
- Salviati G., Sorenson M.M., Eastwood A.B. Calcium accumulation by sarcoplasmic reticulum in two populations of chemically skinned human fibres. *J Gen Physiol*, 1982, 79: 603–632.
- Saugen E., Vollestad N.K., Gibson H., Martin P.A., Edwards R.H.T. Dissociation between metabolic and contractile responses during intermittent isometric exercise in man. *Exp Physiol*, 1997, 82: 213–226.
- Schmidtbleicher D., Haralambie G. Changes in contractile properties of muscle after strength training in man. *Eur J Appl Physiol*, 1981, 46: 221–228.
- Schmidtbleicher D., Golhofer A., Frick U. Effects of a stretch-shortening type training on the performance capability and innervation characteristics of leg extensor muscles. In: De Groot G., Hollander A.P., Huijing G.J. von Ingen Schenau (eds.) *Biomechanics XI-A*. Free University Press, Amsterdam, 1988, 185–189.
- Schwendner K.I., Mikesky A.E., Wiggleworth J.K., Burr D.B. Recovery of dynamic muscle function following isokinetic fatigue testing. *Int J Sports Med*, 1995, 16(3): 185–189.
- Scott C. Strength training for endurance runners. *J Track Coach*, 2000, 152: 4841–4848.
- Sherrington C.S. Some functional problems attaching to convergence. *Proc Roy Soc Lond, B*, 1929, 105: 332–362.
- Sinacore D.R., Delitto A., King D.S., Rose S.J. Type II fiber activation with electrical stimulation: a preliminary report. *Phys Ther*, 1990, 70: 416–422.
- Sjøgaard G., Houton M.E., Nygaard L., Saltin B. Subgrouping of fast fibers in skeletal muscles of men: a critical appraisal. *Histochemistry*, 1978, 58: 79–87.
- Sjöholm H., Sahlin K., Edström L., Hultman E. Quantitative estimation of anaerobic and oxidative energy metabolism and contraction characteristics in intact human muscle in response to electrical stimulation. *Clin Sci*, 1983, 3: 227–239.
- Sleivert G.G., Backus R.D., Wenger H.A. Neuromuscular differences between volleyball players, middle distance runners and untrained controls. *J Sports Med*, 1995, 16: 390–398.
- Strojnik V., Komi P.V. Neuromuscular fatigue after maximal stretch-shortening cycle exercise. *J Appl Physiol*, 1998, 84(1): 344–350.
- Stuart D.S., Lingley M.D., Grange R.W., Huston M.E. Myosin light chain phosphorylation and contractile performance of human skeletal muscle. *Can J Physiol Pharmacol*, 1988, 66: 49–54.
- Suter E., Herzog W., Sokolosky J. P., Macintosh B.R. Muscle fiber type distribution as estimated by Cybex testing and muscle biopsy. *Med Sci Sports Exerc*, 1993, 25: 363–370.

- Sweeney H.L., Stull J.T. Alteration of cross-bridge kinetics by myosin light chain phosphorylation in rabbit skeletal muscle: implications for regulation of actin-myosin interaction. *Proc Natl Acad Sci USA*, 1990, 87(1): 414–418.
- Sweeney H.L., Bowman B.F., Stull J.T. Myosin light chain phosphorylation in vertebrate striated muscle: regulation and function. *Am J Physiol*, 1993, 264: C1085–C1095.
- Takamori M., Gutmann L., Shane S.R. Contractile properties of human skeletal muscle. *Arch Neurol*, 1971, 25: 535–546.
- Tesch P.A., Karlsson J. Muscle fiber types and size in trained and untrained muscles of elite athletes. *J Appl Physiol*, 1985, 59: 1716–1720.
- Tesch P.A. Skeletal muscle adaptations consequent to long-term heavy resistance exercise. *Med Sci Sports Exer*, 1988; 20: 132–138.
- Thepaut-Mathieu C., van Hoecke J., Maton B. Myoelectrical and mechanical changes linked to length specificity during isometric training. *J Appl Physiol*, 1988, 64: 1500–1505.
- Thomas C.K., Nelson G., Than L., Zijdewind I. Motor unit activation order during electrically evoked contractions of paralyzed or partially paralyzed muscles. *Muscle Nerve*, 2002, 25(6):797–804.
- Thorstensson A., Karlsson J. Fatigability and fiber composition of human skeletal muscle. *Acta Physiol Scand*, 1976, 98: 318–322.
- Thorstensson A., Grimby G., Karlsson J. Force-velocity relations and fiber composition in human knee extensor muscles. *J Appl Physiol*, 1976, 40: 12–16.
- Tiidus P.M., Shoemaker J.K. Effluage massage, muscle blood flow and long-term post exercise strength recovery. *Int J Sports Med*, 1995, 16: 478–483.
- Tis L.L., Maxwell T. The effect of positioning on shoulder isokinetic measures in females. *Med Sci Sport Exerc*, 1996, 28(9): 1188–1192.
- Toniolo L., Patrino M., Maccatrozzo L., Pellegrino M.A., Canepari M., Rossi R., D'Antona G., Bottinelli R., Reggiani C., Mascarello F. Fast fibres in a large animal: fibre types, contractile properties and myosin expression in pig skeletal muscles. *J Exp Biol*, 2004, 207(11): 1875–1886.
- Vandenboom, R., Grange, R.W., Huston, M.E. Threshold for force potentiation associated with skeletal myosin phosphorylation. *Am J Physiol*, 1993, 265: C1456–C1462.
- Vandervoort A.A., McComas A.J. Contractile changes in opposing muscles of the human ankle joint with aging. *J Appl Physiol*, 1986, 61: 361–367.
- Vandervoort A.A., Hayes K.C. Plantarflexor muscle function in young and elderly women. *Eur J Appl Physiol*, 1989, 58: 389–394.
- Vandervoort A.A., Quinlan J., McComas A.J. Twitch potentiation after voluntary contraction. *Exp Neurol*, 1983, 81: 141–152.
- Vandervoort A.A., McComas A.J. A comparison of the contractile properties of the human gastrocnemius and soleus muscles. *Eur J Appl Physiol Occup Physiol*, 1983, 51: 435–440.
- Van Cutsem M., Duchateau J., Hainaut K. Changes in motor unit behaviour contribute to increase in contraction speed after dynamic training in humans. *J Physiol (Lond)*, 1998, 513: 295–305.

- Vollestad N.K., Sejersted O.M., Bahr R. Motor drive and metabolic responses during repeated submaximal contractions in human. *J Appl Physiol*, 1988, 64: 1421–1427.
- Westerblad H., Allen D.G., Bruton J.D., Andrade F.H., Lännergren J. Mechanisms underlying the reduction in isometric force in skeletal muscle fatigue. *Acta Physiol Scand*, 1998, 162: 253–260.
- Westerblad H., Lännergren J., Allen D.G. Slowed relaxation in fatigued skeletal muscle fiber of *Xenopus* and mouse: contribution $[Ca^{2+}]$ and cross-bridges. *J Gen Physiol*, 1997, 109: 385–399.
- Wilkie D.R. Generation of protons by metabolic processes other than glycolysis in muscle cells: a critical view. *J Mol Cell Cardiol*, 1979, 11(3): 325–330.
- Yang Z., Stull J.T., Levine R.J.C., Sweeney H.L. Changes in interfilament spacing mimic the effects of myosin regulatory light chain phosphorylation in rabbit psoas fibers. *J Struct Biol*, 1998, 122: 139–148.
- Zhong N., Zucker R.S. Roles of Ca^{2+} , hyperpolarization and cyclic nucleotide-activated channel activation, and actin in temporal synaptic tagging. *J Neurosci*, 2004, 24(17): 4205–4212.
- Zhou S., Lawson D.L., Morrison W.E., Fairweather I. Electromechanical delay in isometric muscle contractions evoked by voluntary, reflex and electrical stimulation. *Eur J Appl Physiol*, 1995, 70: 138–145.

SUMMARY IN ESTONIAN

SKELETILIHASTE KONTRAKTIILSED OMADUSED: SPORTLIKU TREENINGU, VÄSIMUSE JA POST-TETAANILISE POTENTSEERUMISEGA SEOTUD ASPEKTID

Sissejuhatus

Skeletilihaste spetsiifiliseks reaktsiooniks erutumisel on kontraktsioon. Lihaskontraktsioonid on aluseks organismi mitmekesisele motoorsele tegevusele, alustades keha ja selle osade asendi säilitamisest raskusjõu väljas ja lõpetades kõige keerulisemate mootorsete aktidega spordis, tööprotsessis või olmetingimustes. Lihaste kontraktiilsete omaduste uurimine põhineb elektromüostimulatsiooni meetodil. Seejuures lihaste kontraktiilsete omaduste määramine elektrostimulatsiooni tingimustes võimaldab närvi-lihassüsteemi funktsioonide uurimisel eristada lihastes toimuvaid funktsionaalseid nihkeid muutustest lihaseid juhtivates mootorsetes keskustes. Supramaksimaalse elektrostimulatsiooniga esile kutsutud isomeetrilise üksikkontraktsiooni parameetreid on sageli kasutatud adaptiivsete muutuste uurimisel inimese närvi-lihasaparaadis süstemaatilise kehalise treeningu tingimustes, samuti lihasväsimuse uurimisel. Vähe on aga andmeid lihaste kontraktiilsete omaduste iseärasuste kohta sportlastel, kes treenivad erinevaid kehalisi võimeid: jõudu, kiirusjõudu või vastupidavust. Vastavad uuringud võimaldavad hinnata adaptiivsete nihete iseärasusi närvi-lihassüsteemis erineva iseloomuga sportliku treeningu tingimustes. Üheks skeletilihaste kontraktiilsete omadustega seotud nähtuseks on üksikkontraktsiooni jõuparameetrite potentseerumine, mis avaldub nii tugeva tahtelise pingutuse järel (aktiivsusejärgne potentseerumine) kui ka elektromüostimulatsiooniga esile kutsutud tetaanilise kontraktsiooni järel (post-tetaaniline potentseerumine). Nimetatud nähtus kujutab endast skeletilihaste kontraktsioonijõu ja -kiiruse suurenemist pärast mõjutust võrreldes lähtetasemega. Post-tetaanilise potentseerumise nähtust on uuritud põhiliselt supramaksimaalse elektrostimulatsiooni tingimustes, mis põhjustab tugeva valuaistingu. Samas on seda nähtust taastusravis ja sportliku treeningu protsessis sageli kasutatava submaksimaalse direktse (transkutaanse) elektrostimulatsiooni tingimustes vähe uuritud.

Käesoleva töö eesmärgiks oli uurida lihaste kontraktiilsete omaduste iseärasusi sportlastel sõltuvalt treeningu iseloomust, samuti hinnata lihaste kontraktiilsete omaduste muutusi lokaalsel maksimaalsel dünaamilisel tööl areneva lihasväsimuse tingimustes ning post-tetaanilise potentseerumise tingimustes pärast lühiajalist submaksimaalset direktset elektrostimulatsiooni.

Uurimistöö ülesanded

1. Hinnata sääre kolmpealihase tahtelist isomeetrilist maksimaaljõudu ja supramaksimaalse elektrostimulatsiooniga esile kutsutud üksikkontraktsiooni karakteristikuid kiirusjõudu ja vastupidavust treenivatel sportlastel ning mittetreenitud vaatlusalustel.
2. Hinnata sääre kolmpealihase aktiivsuse järgse potentseerumise iseärasusi pärast lühiajalist tahtelist maksimaalset pingutust kiirusjõudu ja vastupidavust treenivatel sportlastel ning mittetreenitud vaatlusalustel.
3. Hinnata reie nelipealihase tahtelise isomeetrilise maksimaaljõu ja elektrostimulatsiooniga esile kutsutud submaksimaalse tetaanilise kontraktsiooni karakteristikute muutusi lokaalsel maksimaalse intensiivsusega dünaamilisel tööl jõutõstjatel ning mittetreenitud meestel.
4. Hinnata post-tetaanilise potentseerumise iseärasusi reie nelipealihases pärast lühiajalist kõrge sagedusega (100 Hz) submaksimaalset direktset elektrostimulatsiooni mittetreenitud vaatlusalustel.

Uuritavad ja kasutatav metoodika

Uuringus osales kokku 97 meest ja 25 naist vanuses 19–28 aastat. Vaatlusalusteks olid kiirusjõudu treenivad mees- ja naissportlased (sprinterid, hüppajad), meessoost jõutõstjad, pikamaajooksjad ning mittetreenitud mehed ja naised. Kõik uuritud sportlased kuulusid Eesti paremikku.

Sääre kolmpealihase ja reie nelipealihase tahtelise isomeetrilise jõu ja kontraktilsete omaduste määramiseks kasutati spetsiaalseid elektromehaanilisi dünamomeetrilisi seadmeid. Sääre kolmpealihase isomeetrilise üksikkontraktsiooni karakteristikute määramiseks kasutati supramaksimaalset indirektset (*n. tibialis*'e ärritamise kaudu teostatud) elektromüostimulatsiooni, kasutades ristkülikimpulssi kestusega 1 ms. Uuritavad skeetilihase üksikkontraktsiooni parameetrid (maksimaaljõu, kontraktsiooni- ja lõõgastusfaasi kestus, jõugradiendid, määratuna kontraktsiooni- ja lõõgastusfaasis) määrati dünamogrammilt, mis saadi vaatlusaluse labajala mittetahtelise surve muutuse tulemusena vastu spetsiaalselt konstrueeritud pedaali. Antud parameetrid fikseeriti kahes seisundis: puhkeolekus ning potentseerunud olekus, so. vahetult pärast 5-sekundilist tahtelist maksimaalset pingutust. Määrati reie nelipealihase elektrostimulatsiooniga esile kutsutud submaksimaalse tetaanilise kontraktsiooni (25% tahtelisest maksimaaljõust, mis kutsuti esile sagedusega 50 Hz) karakteristikud enne ja pärast doseeritud lokaalset dünaamilist tööd. Post-tetaanilise potentseerumise uurimisel määrati reie nelipealihase supramaksimaalse indirektse elektrostimulatsiooniga esile kutsutud üksik- ja tetaanilise kontraktsiooni (10 Hz) parameetrid enne ja pärast 7-sekundilist submaksimaalset tetaanilist

kontraktsiooni (25% tahtelisest maksimaaljõust), mis kutsuti esile direkte kõrge sagedusega (100 Hz) elektrostimulatsiooniga. Seejuures istus vaatlusalune spetsiaalsel dünamograafilisel pingil, kus ta fikseeriti mansettide abil pingi seljatoe külge selliselt, et nurk uuritava jäsme põlveliigeses oli ligikaudu 90° ja puusaliigeses 110°. Sääre distaalsele osale sääreluu keskmisest ja pindluu külgmisest peksist umbes 1 cm ülespoole kinnitati tensodünamomeetriga ühendatud mansett. Lihase pingutamisel tekitas sääre surve mansetile, mis omakorda kandus üle dünamomeetrile. Reie nelipealihase doseeritud lokaalse dünaamilise töö teostamiseks kasutati Cybex II (USA) tüüpi moderniseeritud isokineetilist dünamomeetrit. Käesolevas töös kasutati nurkkiirust $1.57 \text{ rad}\cdot\text{s}^{-1}$. Testimisel anti vaatlusalusele ülesanne teostada 30 maksimaalselt kiiret ja tugevat sääre sirutus- ja painutusliigutust. Määrati võimsuse langus protsentides ning sooritatud töö hulk. Pärast tööd määrati uuritud lihaste kontraktiilsed karakteristikud 10-minutilise taastumisperioodi jooksul.

Järeldused

1. Kiirusjõudu treenivatel sportlastel olid sääre kolmpealihase tahtelise isomeetrilise jõu ja elektrostimulatsiooniga esile kutsutud üksikkontraktsiooni jõu ning kiiruse näitajad oluliselt suuremad võrreldes vastupidavust treeninud sportlastega. Seejuures nii kiirusjõu kui ka vastupidavustreeningu tagajärjel nähtus lihaste kontraktsiooni ja lõõgastuse aja lühenemine.
2. Kiirusjõu treening põhjustas isomeetrilise üksikkontraktsiooni aktiivsuse järgse potentseerumise suurenemise sääre kolmpealihases, vastupidavustreeningu tagajärjel seda ei täheldatud.
3. Lühiajalise isokineetilises režiimis sooritatud maksimaalse intensiivsusega töö tulemusel tekkis reie nelipealihases perifeerne (lihase-)väsitus, mis väljendus elektrostimulatsiooniga esile kutsutud tetaanilise kontraktsiooni jõu parameetrite languses ning lõõgastuse aja pikenemises.
4. Jõutõstjad väsisid reie nelipealihase lühiajalise isokineetilises režiimis sooritatud maksimaalse intensiivsusega töö tagajärjel kiiremini kui mittetreenitud mehed. Samuti nähtus neil reie nelipealihase kontraktiilsete omaduste näitajate aeglasem tööjärgne taastumine.
5. Lühiajaline kõrge sagedusega transkutaanne submaksimaalne elektrostimulatsioon kutsus esile olulise post-tetaanilise potentseerumise reie nelipealihases 1–5 minutit pärast mõjutust. Kontraktsiooni ja lõõgastusfaasis registreeritud isomeetrilise üksikkontraktsiooni jõugradiendid osutusid post-tetaanilise potentseerumise suhtes tundlikumaks kui maksimaaljõud.

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PUBLICATIONS

Pääsuke M., Ereline J., Gapeyeva H.

Twitch potentiation capacity of plantarflexor muscles in endurance and power athletes. *Biology of Sport*, 1998, 15 (3): 171–178.

Pääsuke M., Ereline J., Gapeyeva H. Twitch contractile properties of plantar flexor muscles in power and endurance trained athletes. *European Journal of Applied Physiology and Occupational Physiology*, 1999, 80 (5): 448–451.

Pääsuke M., Ereline J., Gapeyeva H., Torop T.
Twitch contractile properties of plantarflexor muscles
in female power-trained athletes.
Medicina dello Sport, 2002, 55 (4): 279–286.

Ereline J., Gapeyeva H., Pääsuke M.
Contractile changes in knee extensor muscles
after repetitive maximal isokinetic contractions
in male power-lifters and untrained subjects.
Medicina dello Sport, 2004, 57 (1): 29–39.

Requena B., Ereline J., Gapeyeva H., Pääsuke M.
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