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Vesa Linnamo

Motor Unit Activation and Force Production during Eccentric, Concentric and Isometric Actions

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Academic Dissertation

Neuromuscular Research Center,
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ABSTRACT

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The aim of the present series of studies was to examine force and myoelectrical activity in human forearm flexors and knee extensors during dynamic and isometric muscle actions. The main purposes were 1) to clarify the methodological issues regarding the measurements of maximal force, EMG and EMG power spectrum in eccentric, concentric and isometric conditions, 2) to examine the motor unit activation patterns during dynamic and isometric actions by following the behavior of the EMG power spectrum and by utilizing selective intramuscular fine wire electrodes, and 3) to examine the effects of fatigue on force production, aEMG and EMG power spectrum in eccentric and concentric actions. The results showed that eccentric force measured after the onset of the stretch is higher than the isometric preactivation force preceding the movement regardless of the stretching velocity or of the joint angle. However, due to possible inhibition during maximal eccentric action the maximal eccentric force measured in the middle part of the movement may in some situations be exceeded by separately measured isometric force. Lower median frequency (MF) during eccentric than in concentric actions would not support the concept that fast motor units would be selectively recruited during eccentric action. In concentric actions MF increased with increased movement velocity which could indicate increased activation of fast motor units. A more detailed examination of MF showed, however, that window placement of Fast Fourier Transformation (FFT) and the part of the signal chosen for the analysis may be of crucial importance. Intramuscular spike-amplitude frequency (ISAF) analysis suggests that in eccentric actions with isometric preactivation all motor units may become recruited at lower relative force level than in isometric and in concentric actions and the additional force is achieved by increased firing rate of the active units. Despite possible inhibition in eccentric actions the relative force decrease after fatiguing maximal eccentric and concentric exercise can be similar after both exercise types provided that the movement is always started with maximal isometric preactivation.

Key words: Eccentric, concentric, isometric, force, aEMG, median frequency, motor unit recruitment

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This book is dedicated to my parents

CONTENTS

ORIGINAL PAPERS

This thesis is based on the following papers, which will be referred to by their Roman numerals.

I Komi P.V., Linnamo V., Silventoinen P., Sillanpää M. (2000) Force and EMG power spectrum during eccentric and concentric actions. Med. Sci Sports Exerc. 32(10): 1757-1762

II Linnamo V., Bottas R., Komi P.V. (2000) Force and EMG power spectrum during and after eccentric and concentric fatigue. J. Electromyogr. Kinesiol. 10(5): 293-300

III Linnamo V., Newton R.U., Häkkinen K., Komi P.V., Davie A., McGuigan M., Triplett-McBride T (2000) Neuromuscular responses to explosive and heavy resistance loading. J. Electromyogr. Kinesiol. 10 (6): 417-424

IV Linnamo V., Strojnik V., Komi P.V. (2001) Electromyogram power spectrum and features of the superimposed maximal M-wave during voluntary isometric actions in humans at different activation levels. Eur. J. Appl. Physiol. 86: 28-33

V Linnamo V., Strojnik V., Komi P.V. (2001) EMG power spectrum and features of the superimposed maximal M-wave during voluntary eccentric and concentric actions at different activation levels. Eur. J. Appl. Physiol. In Press.

VI Linnamo V., Strojnik V., Komi P.V. (2001) Maximal force and EMG during eccentric and isometric actions. Submitted

VII Linnamo V., Moritani T., Nicol C., Komi P.V. (2001) Motor unit activation during eccentric and concentric actions with and without preactivation. Submitted.

ABBREVIATIONS AND DEFINITIONS

aEMG	average amplitude of the rectified surface electromyography
CE	concentric exercise
CK	creatine kinase
CV	muscle fiber conduction velocity
CV%	coefficient of variation
EE	eccentric exercise
EMG	Electromyography
EXE	explosive exercise
FFT	Fast Fourier Transformation
HRE	heavy resistance exercise
ISAF	intramuscular spike-amplitude-frequency
MF	median frequency
MPF	mean power frequency
MVC	maximal force produced either in isometric or during eccentric or concentric action
M-wave	muscle compound action potential
SD	standard deviation
SE	standard error
10-RM	10 repetition maximum

1 INTRODUCTION

An increase in the muscle force can be achieved by recruiting additional motor units and by increasing the firing rate of the active units. According to Henneman et al (1965 a, 1965b) the neurons with small slowly conducting axons innervating slowly contracting fatigue-resistant muscle fibers appear to be recruited before neurons with large rapidly conducting axons innervating rapidly contracting fatigable muscle fibers. This size principle has been shown to be valid both in isometric (DeLuca et al. 1982, Duchateau & Hainaut 1990, Freund et al. 1975, Milner-Brown et al. 1973a) and in dynamic (Garland et al. 1996, Kossev & Christova 1998, Sogaard et al. 1996) situations. In eccentric actions, however, selective activation of high threshold fast motor units has been reported (Nardone et al. 1989) and it has been suggested that there may be a change in activation with an increase in movement velocity (Citterio & Agostoni 1984, Grimby & Hannerz 1977, Muro et al. 1983).

Despite possible selective activation of fast motor units, increased movement velocity in concentric actions is accompanied by a decrease in muscle force (e.g. Asmussen et al. 1965, Komi 1973, Wilkie 1950). In eccentric actions, the force is greater and it is less affected by changes in velocity in comparison to concentric actions (Colliander & Tesch 1989, Komi 1973). These high forces may be a reason that some neural inhibition has been observed in maximal eccentric actions (Westing et al. 1990) and it may be difficult to maintain maximal eccentric force throughout the motion. Therefore, when the value of maximal eccentric force is taken from the middle part of the motion and compared to separately measured maximal force at the corresponding joint angle, the maximal isometric force can sometimes be similar or even exceed the maximal eccentric force (Singh & Karpovich 1966, Strojnik et al. 1998, Westing et al. 1988). Measurements with single muscle fibers show, however, that immediately after stretching the fiber, the force always increases above the pre-stretched level (e.g Edman et al 1978). With regard to EMG activity during concentric and eccentric actions, the maximal EMG activity has been at the same level (Komi 1973, Komi & Rusko 1974, Komi & Buskirk 1972), greater in concentric actions (Eloranta & Komi 1980, Tesch et al. 1990, Westing et al 1991) or greater in eccentric actions (Grabiner & Kasprisin 1997) depending on the muscles, joint angles and protocols used.

The different behavior in force and EMG between eccentric and concentric actions in non-fatiguing conditions may play a role also during fatigue. Indeed, fatigue studies with maximal eccentric and concentric actions have shown that muscle force may decrease more either in eccentric (Komi & Rusko 1974, Komi & Viitasalo 1977) or in concentric exercise (Grabiner & Owings 1999, Gray & Chandler 1989, Hortobagyi et al. 1996, Pasquet et al. 2000, Tesch et al. 1990). If the movement is started with maximal isometric preactivation in eccentric fatigue the force has reported to decrease by 30-50% (Brown et al. 1997, Day et al. 1998, Komi & Rusko 1974, Komi & Viitasalo 1977, Newham et al. 1987). Eccentric exercise, due to higher mechanical loading can lead to a higher amount of muscle damage and muscle soreness than concentric exercise and thus also to a longer recovery period (Howell et al.1993, Day et al. 1998, Lieber & Friden 1988, Komi & Viitasalo 1977, Newham et al. 1987.

While average EMG is affected by both motor unit recruitment and changes in the firing rate of the active units, EMG power spectrum may be sensitive specifically to motor unit recruitment (Moritani & Muro 1987, Solomonow et al 1990). Frequencies of the EMG power spectrum are related to the average conduction velocity (CV) of the active muscle fibers (Arendt-Nielsen & Mills 1985) and CV is higher for fast twitch fibers (Andearssen & Arendt-Nielsen 1987). A shift of power spectrum towards higher frequencies may therefore indicate an increase in the CV and thus increased activation of fast motor units. EMG power spectrum has also been used as an indicator of fatigue. Decreased CV may cause a shift towards lower frequencies. This shift during fatigue is generally greater with subjects possessing a greater relative number of fast twitch fibers (Viitasalo & Komi 1978, Komi & Tesch 1979) and it may be greater during concentric exercise as compared to eccentric one (Tesch et al. 1990) or it may remain unaltered immediately after both eccentric and concentric exercise (Komi & Viitasalo 1977).

Much of the controversy regarding force and EMG behavior between different studies may possibly be explained by methodological differences. One main purpose of this thesis was to clarify these methodological issues so that the obtained results would not be misinterpreted. The other main purpose was to examine the motor unit activation patterns during dynamic and isometric actions. The behavior of the EMG power spectrum was examined during eccentric and concentric fatigue as well as in the non-fatiguing situation, with different movement velocities and activation levels. Special emphasis was placed on the EMG power spectrum in isometric situation in which the signal is assumed to be stationary and the frequency component should remain unchanged if the force level is kept stable. To obtain more detailed information about the motor unit activation patterns, intramuscular recordings were also utilized. Selective fine wire electrodes were used to examine the recruitment order and firing rates of motor units during eccentric and concentric actions starting from several different preactivation levels.

2 REVIEW OF THE LITERATURE

2.1 Motor unit activation

2.1.1 Motor unit

A motor unit consists a motor neuron, its motor axon and the muscle fibers it innervates (Burke 1981). The size of a motor neuron 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. The greater the values of these properties, the larger the motor neuron (Stuart & Enoka 1983). Motor neurons supplying fast twitch muscles appear to be larger than those innervating slow twitch fibers (Enoka 1994). Based on contraction time and fatigue resistance, motor units can be classified into three groups (Burke 1981) - slow-contracting, fatigue resistant (type S); fast-contracting, fatigue resistant (type FR); and fast-contracting, fast to fatigue (type FF). Gydikov & Kosarov (1973,1974) classified two types of motor units, tonic and phasic, on the basis of the dependence between the level of the isometric muscle tension and the discharge frequency, the threshold and the size of the summated equivalent potential. Tonic motor units generate smaller action potentials, are recruited at lower forces and are less fatigable than the phasic ones. Classification can also be based on histochemical and biochemical measurements of muscle fibers. The distinction between type I and II is based on the ATPase reactivity patterns and type II can be further separated to IIa and IIb (Brooke & Kaiser 1974) or in humans to IIa and IIx (e.g. Bottinelli & Reggiani 2000). Type I represents the slow twitch and type II the fast twitch muscle fibers. Other scheme of classification by Peter et al. (1972) considers patterns of metabolic enzymes, contraction speed, aerobic and anaerobic capacity and employs the terms slow twitch oxidative (type SO), fast twitch oxidative-glycolytic (type FOG) and fast twitch glycolytic (type FG). In general type I fibers are the same as type SO belonging to a type S motor unit, Type IIa fibers correspond to type FOG belonging to type FR motor unit and type IIb fibers are the same as type FG fibers belonging to a type FF motor unit (Enoka 1994). All the muscle fibers in a motor unit are the same type (Edström & Kugelberg 1968, Nemeth & al 1986).

2.1.2 Factors influencing motor unit activation

The tension output of a muscle is controlled by regulation of the number and identity of the active motor units - recruitment and the rate and pattern of motor unit firing - discharge rate or rate coding (eg. Kukulka & Clamann 1981, Milner-Brown et al. 1973a and b, Moritani & Muro 1987). In most motor functions, there seems to be an orderly recruitment of motor units. According to Henneman's size principle, the neurons with slowly conducting axons innervating slowly contracting fatigue-resistant muscle fibers appear to be recruited before neurons with rapidly conducting axons innervating rapidly contracting fatigable muscle fibers (Hennenman & al. 1965a, 1965b). It appears that some morphological (e.g. number of dendrites, axon diameter, innervation ratio), biophysical (e.g. input resistance, rheobase, afterhypolarization) and input (e.g. Renshaw shell pool, group Ia afferent) characteristics vary with motor neuron size so that the smallest motor neurons can be excited more easily (Enoka 1994). 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 motor units are recruited up to 50% - 80% MVC depending on the muscle (DeLuca et al. 1982, Kukulka & Clamann 1981, Milner-Brown et al. 1973a and b) after which the additional increase in force is accomplished with increased firing rate of the active units (Deluca et al. 1982, Gydikov & Kosarov 1973, 1974, Milner-Brown et al. 1973a and b). At higher force levels this increase is mainly due to increased firing rate of the fast (phasic) motor units, which may increase almost linearly up to 100% MVC while slow (tonic) motor units reach a saturation frequency of discharge at lower force levels of approximately 60% - 80% MVC (Gydikov & Kosarov 1973, 1974).

2.1.2.1 Type of muscle action

It has been shown by several investigators that motor units are recruited according to the size principle in isometric condition (e.g. DeLuca & al 1982, Duchateau & Hainaut 1990, Milner-Brown & al 1973a, Freund & al 1975). The same size principle appears to be valid in concentric actions (Bawa & Jones 1999, Garland et al 1996, Kossev & Christova 1998, Sogaard et al 1996) but some controversy exists regarding the recruitment order of the motor units in lengthening conditions. Nardone et al (1989) showed selective recruitment of fast motor units in triceps surae muscle in lengthening condition as opposed to shortening condition. Similar findings, but only in selective portion of the examined motor units, has been reported in first dorsal interroseus muscle (Howell et al. 1995). Most of the studies, however, have reported the recruitment order to be similar in eccentric as in isometric or in concentric actions (Bawa & Jones 1999, Garland et al 1996, Kossev & Christova 1998, Laidlaw et al. 2000, Sogaard et al 1996, Stotz & Bawa 2001). In contrast, the recruitment threshold in dynamic actions has been shown to be lower compared with isometric actions (Ivanova et al 1997, Tax et al. 1989). Although the same motor units may be recruited in concentric, eccentric and isometric actions, the mean firing rate is generally higher in concentric compared with eccentric and isometric actions (Ivanova et al 1997, Moritani et al. 1987, Sogaard et al. 1996). The mean firing rate may increase at shorter muscle lengths (Christova et al. 1998), where the difference in the mean firing rate between concentric and eccentric condition has shown to be even more substantial than at longer muscle lengths (Moritani et al. 1987).

2.1.2.2 Contraction velocity

There is some evidence that as the movement velocity increases, the activation of the muscles containing mainly fast twitch fibers may be augmented as the slow muscles become silenced. Smith et al (1980) demonstrated selective recruitment of fast gastrocnemius muscle of a cat during rapid paw shaking. A similar change in the activation of soleus and gastrocnemius as the movement velocity increased, has been observed in some human studies (Moritani et al. 1991a & b, Nardone & Schieppati 1988). Based on surface EMG, some studies have suggested that fast motor units may be selectively activated within the same muscle as the movement velocity increases (Citterio & Agostoni 1984, Muro et al. 1983, Strojnik et al. 1997). Single motor unit studies in humans, however, give support to this concept in few cases only (Grimby & Hannerz 1977, Gimby 1987). Instead, several studies have shown that the recruitment order in fast contractions remains the same as in the slow ones (Desmedt & Goudaux 1977, 1978, Ivanova et al 1997, Thomas et al. 1987, Van Cutsem et al. 1998). The recruitment threshold in brisk ballistic contractions, however, becomes lower and the instantaneous firing frequency increases (Desmedt & Goudeaux 1977, Ivanova et al. 1997, Van Cutsem et al 1998). It seems that in brisk movements the recruitment threshold in slow muscles, such as soleus, is reduced even more than for muscles containing both fast and slow motor units (Desmedt & Godeaux 1978).

2.1.3 Assessment of motor unit activation as it relates to the present study

2.1.3.1 Intramuscular EMG recordings

According to Basmajian & DeLuca (1985) the most common indwelling electrode is the needle electrode and in particularly the “concentric” electrode, first described and used by Adrian & Bronk (1929). Intramuscular EMG recordings with needle electrodes in humans have generally been made in isometric situations (e.g De Luca et al. 1982, Desmedt & Godeaux 1977, 1978, Duchateau & Hainaut 1990, Milner-Brown et al. 1973a and b) or in dynamic condition with slow movement velocity and with low force levels (Sogaard et al 1996).

Another often used intramuscular electrode type is the wire electrode popularized by Basmajian & Stecko (1962). In that technique, the bipolar wire electrodes form a hook that enables the electrodes to remain in the muscle once the needle is withdrawn. The advantage of the fine wire electrode is that they are painless and easily implanted and withdrawn and can be used also during movement. At present, wire electrodes may even be more commonly used than needle electrodes. The use of wire electrodes has been well documented in isometric situation (e.g. Jonsson & Bagge 1968, Jonsson & Reichmann 1968, Jonsson & Komi 1973, Komi & Buskirk 1970) but the technique has been successfully used also with concentric and eccentric actions (Komi 1973) as well as with repetitive fatigue situation (Komi & Rusko 1974). To record single motor units, diffferent techniques to make the wire electrodes more selective have been developed. Using the technique described by Basmajian & Stecko (1962), but attaching the two wires together thus minimizing the inter-electrode distance, Moritani et al (1985b) analyzed the behavior of a selected population of motor units with intramuscular spike-amplitude-frequency (ISAF) histograms. Intramuscular spikes were isolated and counted according to their amplitude in 100μV increments. The mean spike amplitude and frequency together with standard deviations were then used for statistical comparisons between different conditions (Moritani et al. 1985b).

An even more selective approach is a subcutaneous branched wire electrode by Gydikov et al. (1986). This technique has been successfully used in several investigations to study single motor unit activation patterns during concentric and eccentric as well as in isometric actions (e.g. Garland et al. 1996, Ivanova et al. 1997, Kossev & Christova 1998) The electrode consists of two isolated parallel wires with two leading-off areas in one wire and the third on the other across from the midpoint between the first two. This type of electrode has a high selectivity and stability against mechanical displacement (Enoka et al. 1988).

A common approach in single motor unit studies is that motor units are identified according to their amplitude and shape. In a technique called spike triggered averaging, the action potentials from single motor unit firing are used as “spike triggers” to extract the force generated by that particular motor unit by averaging the force signal. This technique allows to study the contractile properties of individual motor units activated by voluntary recruitment and to examine the recruitment threshold at which the motor unit is activated. Although spike triggered averaging has mainly been used in isometric situation (e.g Desmedt & Godeaux 1977, 1978, Duchateau & Hainaut 1990, Milner-Brown et al. 1973a and b) attempts have been made to apply it also for dynamic conditions (Thomas et al 1987).

2.1.3.2 EMG power spectrum

It has been suggested that the frequency component of the EMG power spectrum can be used as an indicator of motor unit recruitment (Moritani & Muro 1987, Solomonow et al 1990). This assumption gets support from the findings that the average conduction velocity of the active muscle fibers is higher for fast twitch than for slow twitch fibers (Andearssen & Arendt-Nielsen 1987) and that the muscle fiber conduction velocity is related to the frequencies of the EMG power spectrum (Arendt-Nielsen & Mills 1985). Furthermore, Solomonow et al. (1990) showed a linear increase in median frequency (MF) with motor unit recruitment, while the changes in the firing rate of the active units did not affect the MF. Therefore, a shift in the power spectrum to high frequencies would represent an increase in the average conduction velocity and thus greater use of fast units. There is also some evidence that a high relative number of fast twitch fibers results in higher frequency values of the EMG power spectrum (Gerdle et al. 1988, Moritani et al. 1985a).

The results reported on the behavior of the EMG power spectrum with increasing isometric force are, however, somewhat controversial. Some authors report an increase of MF or MPF up to 60%-80% MVC (Bilodeau et al. 1990, Moritani & Muro 1987), some up to 25%-60% MVC (Bernardi et al. 1995, Gerdle et al. 1990, Hagberg & Ericson 1982) and some report hardly any changes at all (Bazzy et al. 1986, Merletti et al. 1984, Petrofsky & Lind 1980, Viitasalo & Komi 1978). Interelectrode distance and skin acting as a low pass filter (Bilodeau et al. 1990, Moritani & Muro 1987), small differences in muscle fiber diameter between slow and fast fibers (Miller et al. 1993, O’Hagan et al 1995), electrode location (Komi & Viitasalo 1976, Roy et al. 1986) and type of action; ramp vs. step-wise (Bilodeau et al. 1991) may have caused some of the differences in the results obtained between different studies.

2.2 Maximal force and aEMG during eccentric, concentric and isometric action

2.2.1 The effect of joint angle and type of action

Experiments with single muscle fibers have shown that when the fiber is stretched after isometric preactivation, the force immediately after the stretch exceeds the force at the pre-stretched level (e.g Edman et al 1978). When maximal eccentric force is compared with separately measured maximal isometric force at the corresponding joint angle, the isometric force is usually lower than the eccentric one (e.g. Asmussen et al. 1965, Doss & Karpovich 1965, Komi 1973). There are also some opposite results, however, in which the isometric force has exceeded the eccentric one (Singh & Karpovich 1966, Strojnik et al. 1998, Westing et al. 1988). This could be due to neural inhibition that has been suggested to occur during maximal eccentric action (Westing et al.

1990) causing the subjects to have difficulty to maintain a high eccentric force throughout the motion. In contrast, maximal EMG activity, when comparing eccentric and concentric actions, may be at the same level (Komi 1973, Komi & Buskirk 1972, Komi & Rusko 1974), greater in concentric actions (Eloranta & Komi 1980, Tesch et al. 1990, Westing et al. 1991) or greater in eccentric actions (Grabiner & Kasprisin 1997).

2.2.2 The effect of movement velocity

The classical force-velocity curve in concentric situation shows that the muscle force decreases as the shortening velocity increases. The shape of the relation has been shown to be similar both in isolated muscle (Hill 1938) and in single muscle fiber (Edman et al. 1978) studies as well as in human intact muscle groups (e.g. Asmussen et al. 1965, Komi 1973, Wilkie 1950). In eccentric actions, the force is greater and is less affected by changes in velocity in comparison to concentric actions (Asmussen et al. 1965, Colliander & Tesch 1989, Komi 1973). In isolated muscle fibers, however, the force is greater at higher the stretching velocities (Edman et al 1978). During eccentric actions, the movement velocity does not seem to affect the aEMG (Aagaard et al. 2000, Komi 1973) while in concentric actions higher aEMG has been observed as the movement velocity has increased (e.g. Aagaard et al. 2000, Strojnik et al. 1998). It has been suggested that neural inhibition that can occur during eccentric actions and may occur also in concentric actions with low movement velocities, although the exact mechanisms responsible for this inhibition in neuromuscular activation are still unknown (Aagaard et al. 2000).

2.3 Eccentric and concentric fatigue

2.3.1 Force and aEMG during eccentric and concentric fatigue

Controversial results have been reported in the literature regarding the decrease in force after repeated maximal eccentric and concentric actions. It seems that muscle force due to fatigue may decrease more either in eccentric (Komi & Rusko 1974, Komi & Viitasalo 1977) or in concentric exercise (Grabiner & Owings 1999, Gray & Chandler 1989, Hortobagyi et al 1996, Pasquet et al. 2000, Tesch et al. 1990) depending on a protocol and the muscles used. In some eccentric fatigue studies the eccentric force has decreased by 30-50% (Brown et al. 1997, Day et al. 1998, Komi & Rusko 1974, Komi & Viitasalo 1977, Newham et al. 1987) while in some others there were hardly any changes in the eccentric force (Hortobagyi et al. 1996, Tesch et al. 1990). Although the changes in force have not been similar after eccentric and concentric exercise, no major differences have been reported in the changes in the average EMG (Komi & Rusko 1974, Komi & Viitasalo 1977, Tesch et al. 1990). The recovery after eccentric exercise is generally longer than after concentric exercise because repeated eccentric actions are associated with delayed muscle soreness and structural muscle damage (Friden et al 1983, Howell et al. 1993, Lieber et al 1991, McCully & Faulkner 1985, Newham et al 1987). An indirect marker of muscle damage, serum creatine kinase (CK) has been shown to increase and reach the highest value several days after eccentric exercise (Felici et al. 1997, Newham et al. 1986, 1987, Nosaka & Clarkson 1997) as well as after exercises utilizing stretch shortening cycle (Avela et al. 1999, Horita et al. 1996, Nicol et al. 1996). The recovery after repeated lengthening of the muscle may take more than a week as indicated by the increased stiffness and swelling (Howell et al. 1993).

2.3.2 EMG power spectrum during eccentric and concentric fatigue

During fatigue a shift of the EMG power spectrum towards lower frequencies has been observed both in isometric (e.g. Arendt-Nielsen & Mills 1985) and in dynamic condition (e.g. Komi & Tesch 1979). The shift during fatigue is generally greater in subjects possessing greater relative number of fast twitch fibers (Komi & Tesch 1979, Viitasalo & Komi 1978). The frequency component of the power spectrum has been found to be well correlated with the muscle fiber conduction velocity (Arendt-Nielsen & Mills 1985), which is higher in fast motor units than in the slow ones (Andearsen & Arendt-Nielsen 1987). It has been suggested that a decrease in conduction velocity is related to proton [H^+] accumulation (Lindström et al. 1970) and it has been shown that lactate concentration is correlated to the mean power frequency (Tesch 1980, Viitasalo & Komi 1978). As power spectrum recovery may take place very fast (Kirsch & Rymer 1987, Vestergaard-Poulsen et al. 1995) it seems possible, however, that proton or blood lactate accumulation is not primarily responsible for the spectral changes of surface EMG. Instead, an impairment of the excitation-contraction coupling has been suggested as a cause of the change (Vestergaard-Poulsen et al. 1995). Mean power frequency may remain unaltered immediately after both eccentric and concentric exercise (Komi & Viitasalo 1977) or the decrease may be greater in concentric exercise (Tesch et al. 1990). During delayed recovery after maximal eccentric exercise the frequency component of the EMG power spectrum may be significantly lower than before the exercise (Day et al. 1998, Felici et al. 1997). Fast twitch fibers may be selectively damaged after repeated lengthening of the muscle as shown by Lieber & Friden (1988) and could thus be reflected in the behavior of the EMG power spectrum.

3 PURPOSE OF THE STUDY

Based on measurements with isolated muscle fibers (e.g. Edman et al. 1978) eccentric force is higher than the isometric one. The same concept is generally valid also in human muscle groups. However, due to possible inhibition that may occur during maximal eccentric action and due to methodological differences the isometric force can in certain conditions exceed the eccentric one. The force output is regulated by motor unit recruitment and firing rate of the active units. In most motor functions the slow motor units appear to be recruited before the fast ones but there is some evidence that during eccentric actions and in very rapid movements this may not be the case. EMG power spectrum has been widely used in connection with motor unit recruitment but the results regarding its behavior in different conditions have been controversial. This study had three main purposes: 1) to clarify the methodological issues regarding the measurements of maximal force, EMG and EMG power spectrum in eccentric, concentric and isometric conditions so that the results are not misinterpreted, 2) to examine the motor unit activation patterns by following the behavior of the EMG power spectrum and by utilizing selective intramuscular fine wire electrodes during both dynamic and isometric actions, and 3) to examine the effects of fatigue on force production, aEMG and EMG power spectrum in eccentric and concentric actions. The more detailed aims and hypothesis of this thesis were as follows:

1) Based on measurements with isolated muscle fibers, eccentric force should be higher than isometric and concentric forces. It seems, however, that inhibition may depress the ability to maintain maximal eccentric force throughout the whole range of motion. The first aim of the project therefore examines muscle force and average EMG (aEMG) during eccentric, concentric and isometric muscle actions following the model used in isolated situation where the movement starts with isometric preactivation (I, V and VI). It was hypothesized that eccentric force, measured immediately after the stretch, is higher than isometric and concentric force at the corresponding joint angles. Maximal EMG activity

should be similar in all conditions, although due to possible inhibition in eccentric action it may decrease towards the end of the motion.

2) There is some evidence that selective recruitment of fast motor units may occur during submaximal eccentric actions and possibly during rapid movements. It has been suggested that changes in the frequency component of the EMG power spectrum, such as median frequency (MF), may be used in assessment of motor unit recruitment. It was hypothesized that MF would increase along with an increase in force or in movement velocity and that MF would be higher during eccentric compared with concentric actions. The second aim of the study was therefore to examine the behavior of median frequency (MF) of the EMG power spectrum during eccentric, concentric and isometric muscle actions and to determine if the frequency component of the EMG power spectrum measured with surface electrodes is a valid tool for assessment of motor unit recruitment (I, III, IV and V). To obtain more detailed information about the recruitment patterns, intramuscular recordings with wire electrodes were also used (VII).

3) Neuromuscular fatigue in dynamic situation depends on the protocol and on the type of loading. Maximal concentric heavy resistance exercise may lead to more dramatic neuromuscular changes than maximal concentric “explosive” exercise, which is performed with low weights (30-50% MVC) but with highest possible movement velocity. The literature, however, is somewhat controversial regarding eccentric and concentric fatigue. It was expected that if during repetitive maximal eccentric and concentric fatigue protocol all dynamic actions begin with maximal isometric preactivation, the decrease in force would be similar after both eccentric and concentric exercise or even greater after eccentric exercise. It was hypothesised that MF would decrease in a similar manner after both eccentric and concentric exercises and that after concentric explosive exercise the decrease in MF would be more substantial than after concentric explosive exercise. However, because muscle damage induced by eccentric fatigue occur primarily in the fast twitch fibers, it was expected that during recovery period several days after the eccentric exercise MF would be lower than after concentric exercise (II, III).

4 RESEARCH METHODS

4.1 Subjects

The total number of subjects in six different experiments was 53. The subjects were well motivated basketball players and physical education students. The same subjects often participated in more than one experiment. The subjects were well informed about the possible risks associated with the experiments and all the studies were approved by the Ethics Committee of the University of Jyväskylä, Finland (I, II, IV, V, VI, VI, VII) and Southern Cross University, Australia (III). The physical characteristics of the subjects are presented in Table 1.

TABLE 1 Physical characteristics of the subject groups (Mean ± SD)

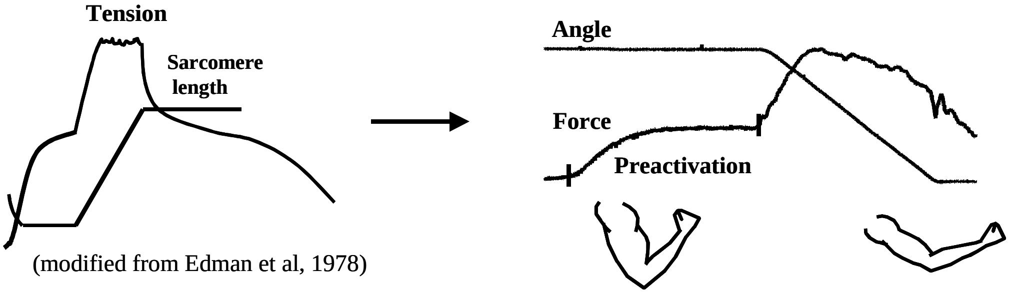
Exp. No	Age (years)	Height (m)	Body mass (kg)	Body fat (%)	Original paper
1 (N = 9)	23.2 ± 3.2	1.87 ± 7.8	78.8 ± 9.9	10.9 ± 0.9	I
2 (N = 8)	26.1 ± 2.8	1.81 ± 6.0	77.3 ± 9.9	11.9 ± 1.9	II
3 (N = 8)	27.1 ± 2.2	1.81 ± 3.8	74.4 ± 9.9	12.9 ± 1.9	III
4 (N = 10)	21.6 ± 3.6	1.85 ± 6.4	77.2 ± 8.7	11.9 ± 1.6	IV, V
5 (N = 10)	25.6 ± 3.6	1.82 ± 4.5	76.1 ± 5.2	12.6 ± 2.2	VI
6 (N = 8)	24.8 ± 4.4	1.85 ± 7.2	80.4 ± 8.8	12.8 ± 3.3	VII

4.2 Experimental design

Altogether six separate experiments were performed. Experiments 1, 2 and 3 resulted in original articles I, II and III, respectively. Experiment 4 resulted in articles IV and V and experiments 5 and 6 in articles VI and VII, respectively.

4.2.1 Experiment 1 (Exp. 1)

To investigate the effect of muscle action type and movement velocity on motor unit activation and force production, maximal force, aEMG and median frequency (MF) of the EMG power spectrum were analyzed from elbow flexors at different movement velocities of eccentric and concentric actions. The subjects were seated in a dynamometer chair and their supinated right forearm was fixed to a lever arm. The range of motion in eccentric (ECC) actions was from 55° to 165° and in concentric (CONC) from 165° to 55° elbow angle (180° = full extension). In eccentric actions the subjects were told to resist the movement of the machine and in concentric actions to assist the lever arm movement. Four different velocities (1 rad·s^{-1}, 2 rad·s^{-1}, 3 rad·s^{-1} and 4 rad·s^{-1}) were used in both conditions. All actions were performed maximally all the way throughout the movement and started with maximal isometric preactivation similar to the model of Edman et al. (1978) with isolated muscle fibers (fig. 1). Trials were performed in a random order with two consecutive attempts at each condition and with a resting period of 2 minutes between the trials.



(modified from Edman et al, 1978)

FIGURE 1 Activation mode with isolated muscle fibers (left) and with the present human forearm flexors (right).

4.2.2 Experiment 2 (Exp. 2)

As motor unit activation patterns may be different between eccentric and concentric actions and because eccentric fatigue is associated with delayed muscle damage, it was of interest to examine the fatigue effects of the different action types. Eccentric and concentric force, aEMG and median frequency of the EMG power spectrum, along with blood lactate concentration and serum creatine kinase (CK) activity, were followed during and immediately after maximal eccentric (EE) and concentric (CE) exercise and during the recovery period of one week. Similar setup as in Exp. 1 was used except that the range of motion of the elbow joint during the movement was from 40° to 170° in the eccentric actions and from 170° to 40° in the concentric actions. Angular velocity was kept at 2 rad·s^{-1} in both conditions and one repetition lasted approximately 1.1 s. All actions were performed maximally throughout the movement with approximately 0.5 s maximal preactivation phase. The two exercise protocols, EE and CE, were performed at four weeks interval. In EE, after a short warm-up, the subjects first performed two maximal eccentric and concentric actions with a recovery of 1min followed by 100 maximal eccentric actions. The recovery between eccentric actions during the exercise was 2 seconds, of which 0.5 s was used for preactivation. Therefore, the total time for the exercise was approximately five minutes. The actual work period lasted three minutes including the isometric preactivation phases. Two maximal concentric actions were performed immediately after the termination of the exercise. The CE followed the same protocol except that it started with two maximal concentric and eccentric actions then followed by 100 maximal concentric actions and two maximal eccentric actions immediately after the exercise. After a period of half an hour, two days and seven days after both exercises the subjects performed two maximal eccentric and concentric actions. The subjects were asked not to perform any arm exercises during the 7-day follow-up period.

4.2.3 Experiment 3 (Exp. 3)

Exp. 3 studied how different concentric movement velocities affect the EMG activity patterns and the force production of the leg extension muscles before and after fatigue. Maximal force, aEMG, median frequency of the EMG power spectrum and blood lactate concentration were measured during two maximal concentric leg press exercises using different movement velocities. Muscle biopsies were taken prior to the exercises to determine the muscle fiber composition. The two exercises: 1. Explosive Exercise (EXE) and 2. Heavy Resistance Exercise (HRE) were performed separately so that there was a recovery period of at least two weeks after the explosive exercise, which was administered first. The subjects were allowed to continue their normal physical activities throughout the experimental period but were instructed to have a full day of rest preceding the testing sessions. The EXE protocol consisted of 5 x 10 repetitions of bilateral concentric leg extensions on an inclined leg press machine (Kolossal, Sydney) with a hip angle of 110°. The subjects extended their legs from a starting position of a 100° knee angle to full extension as fast as possible. The computer-controlled braking system caught the press and lowered it (Wilson et al. 1993) so that the subjects did not perform any eccentric work. During EXE the weight corresponded to 40 ± 6% of the isometric maximum at a 100° knee angle. The recovery period between the sets was one minute. The HRE was performed using the same protocol and apparatus as EXE and the number of sets and repetitions was the same in both exercises. However, in HRE extra weights were added so that the loads for the first set corresponded to about 70% (67 ± 7%) of the isometric maximum at a 100° knee angle. During HRE the weights were either added or removed so that the subject was always able to just finish the required ten repetitions. In addition, the subjects performed one maximal bilateral isometric leg extension followed by three single concentric actions with submaximal loads of 40%, 55% and 70% of the isometric maximum at a 100° knee angle before and after both fatigue protocols. Also an isometric fatigue test was administered before and after the actual exercise. In the isometric fatigue test subjects started at the force level of 10% MVC holding the force on the required target which was displayed on the computer screen. The target force was increased after every tenth second by increments of 10% until the subject was no longer able to maintain the required force level. A ten second work period was always followed by a five second rest period. All the isometric actions were performed with a knee angle of 120°.

4.2.4 Experiment 4 (Exp. 4)

Both median frequency (MF) of the EMG power spectrum and the duration of the maximal M-wave have been used to indicate the conduction velocity of the muscle fibers. As the muscle fiber conduction velocity may be affected by the activation level of the muscle and by the muscle fiber length it was of interest to examine if possible changes in the MF and M-wave would follow the same time course. Therefore, myoelectric activity (aEMG), MF of the EMG power spectrum and the behaviour of maximal M-wave were analysed from isometric, eccentric and concentric knee extension performed with different voluntary activation levels. The subjects were seated in a specially built dynamometer with knee and hip angles of 45° and 110°, respectively in isometric situation, while in eccentric actions the range of motion was from 25° to 90° knee angle and in concentric actions from 90° to 25° (0° = full extension) with the movement velocity of 2 $rad \cdot s^{-1}$. After a standardised 5 min warm-up on a bicycle ergometer, maximal isometric, eccentric and concentric knee extension force (MVC) of the right leg were measured. Subsequently, 40%, 60% and 80% MVC was calculated and then displayed on an oscilloscope to the subject. Subjects performed the required force levels in a random order with a 1.5 minute pause between the trials to avoid fatigue. Several additional attempts were performed in order to measure maximal M-wave during the isometric and dynamic actions at each force level and also in a relaxed condition. Some of the measurements were repeated after one week as the effect of different movement velocity was examined using the same subjects. However, only the results of the movement velocity of 2 $rad \cdot s^{-1}$ in maximal concentric and eccentric actions regarding force and aEMG will be reported in the present thesis.

4.2.5 Experiment 5 (Exp. 5)

The force increases above the maximal pre-isometric level if the active muscle is stretched. However, the separately measured maximal isometric force may sometimes exceed maximal eccentric force if the force is obtained from the middle part of the eccentric action. Exp. 5 examined how the preactivation level, stretching velocity and range of motion affect muscle activity and force production. Maximal isometric and eccentric force and aEMG were measured at different joint angles and with different eccentric movement velocities using the same dynamometer as in exps. 1 and 2. Maximal isometric force was measured in random order at 80°, 95°, 110°, 125° and 140° of elbow angle. During eccentric action, the elbow joint motion ranged from 80° to 140° or from 110° to 140° (full extension = 180°) with movement velocities of 1 $rad \cdot s^{-1}$, 2 $rad \cdot s^{-1}$, and 4 $rad \cdot s^{-1}$. All eccentric actions were performed maximally throughout the movements starting from preactivation levels of 50%, 80% and 100% of separately measured isometric MVC at the corresponding joint angle. The movement started a few hundred milliseconds after stable isometric force in 100% condition and almost immediately after 50% or 80% preactivation level were reached as shown in figure 2 at 2 rad·s^{-1} condition. Trials were performed in a random order with a resting period of 2 minutes between the trials.

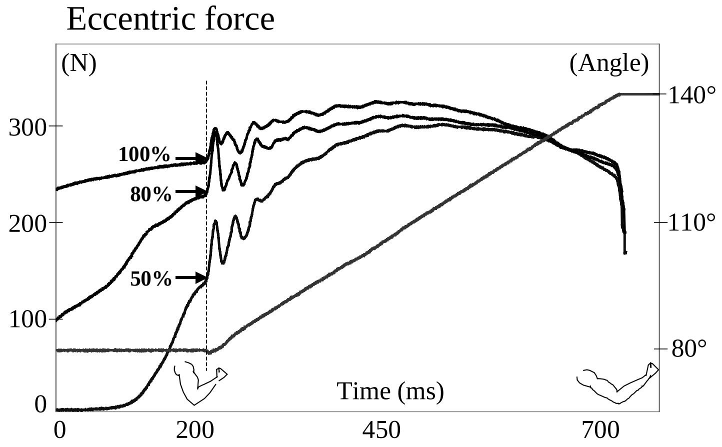


FIGURE 2 Absolute eccentric force curves at 2 rad·s^{-1} from 80° to 140° elbow angle starting from 50%, 80% and 100% preactivation (mean of 10 subjects).

2.4.5 Experiment 6 (Exp. 6)

In the final experiment of this thesis motor unit recruitment patterns were examined at different force levels of eccentric and concentric actions which were performed with and without isometric preactivation. The measurements began with recording of the maximal isometric force (MVC) at 100° and maximal eccentric and concentric force curves. Using the similar set up as in experiments 1, 2, and 5 during eccentric action, the range of motion of the elbow was from 100° to 140° and during concentric mode from 100° to 60° (full extension = 180°). The movement velocity was 2 rad·s^{-1} in all dynamic conditions. All concentric and eccentric actions were started from the same 100° joint angle either without any isometric preactivation (figs 3 and b) or after a few hundred milliseconds of steady isometric 20%, 40%, 60% or 80% MVC preactivation (figs 4 a and b). The lowest force levels were performed first but the preactivation level (zero vs. submax) and the direction of the movement (concentric vs. eccentric) were randomized. The subjects were instructed to maintain the required submaximal force level throughout the movement so that the shape of the force curve would be similar to that of the maximal attempts which had been measured first. The shape of the force curve was examined immediately after from the oscilloscope and the attempts that were not satisfactory were rejected and repeated.

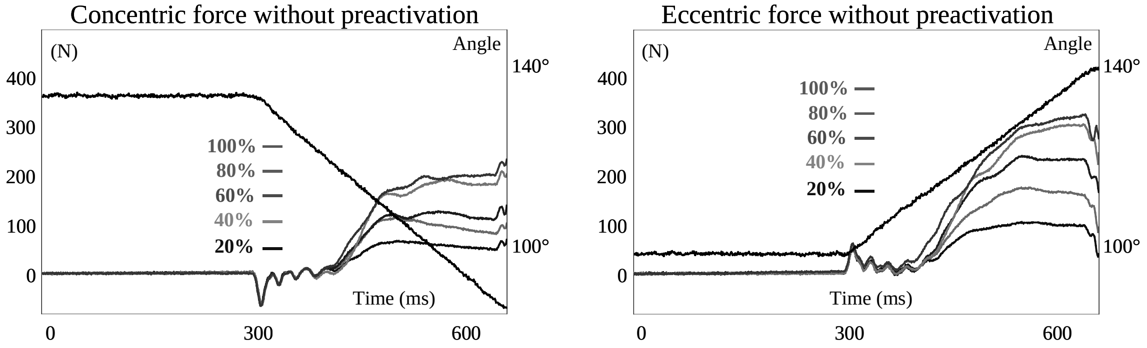


FIGURE 3 Force curves during concentric (a) and eccentric actions (b) without preactivation at different force levels (mean of 8 subjects).

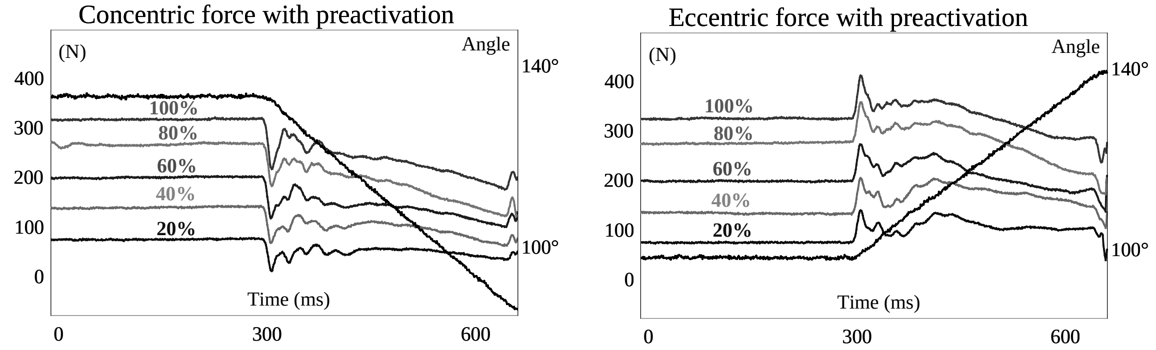


FIGURE 4 Force curves during concentric (a) and eccentric (b) with preactivation at different force levels (mean of 8 subjects).

4.3 Recording procedures and analyses

4.3.1 Force measurements

A specially built machine designed to record dynamic and isometric forces was used in all experiments (except for Exp. 3). The present ergometer can be used for both elbow and knee joint movements and can involve both flexors and extensors (fig. 5). It is driven by a powerful servomotor, which has necessary feedback control for position and velocity. The range for effective constant angular velocity is from 0 to 13 rad·s^{-1}. The lever arm is equipped with the strain gauge transducer to measure the force applied on the wrist and ankle, respectively for elbow and knee flexion/extension. The maximum recorded torques (force x distance of the transducer form the rotational axis) can be as high as 480 Nm. The high angular acceleration of 100 rad·s^{-2} assures reaching of the constant selected angular velocity in a very short period of time. No gravity correction has been installed in the dynamometer. The position of the lever arm and thus the joint angle can be recorded directly from the machine.

FIGURE 5 The ergometer subject system for recording eccentric, concentric and isometric forces for elbow flexors. The lever arm position can be changed for similar measurements for the knee joint.

In Exp. 3 (III) maximal isometric force and the forces during the concentric actions were determined using a Kistler force platform (Type 9287, Kistler, Switzerland) which was fixed to the leg press. A rotary encoder (Omron Corporation, Japan) which was attached to the press and interfaced with the computer, measured the position of the leg press apparatus. This allowed the calculation of movement time.

4.3.2 Force analyses

In Exp. 1, maximal force was recorded with a force transducer throughout the motion. In isometric action maximal force was measured in the middle of this movement range at a 110° elbow angle and at 55° and 165°, which correspond to the starting angles of the eccentric and concentric actions, respectively. The range of motion was divided into five 22-degree sections (fig. 6) for further analyses (I).

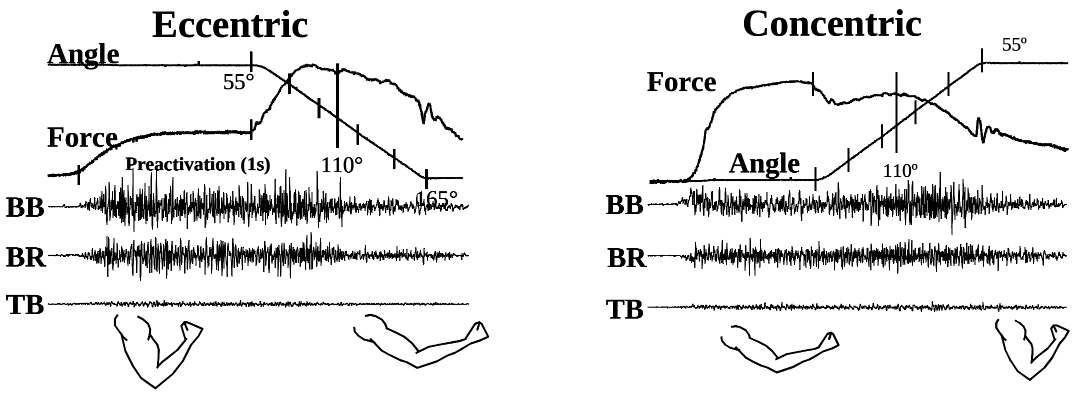


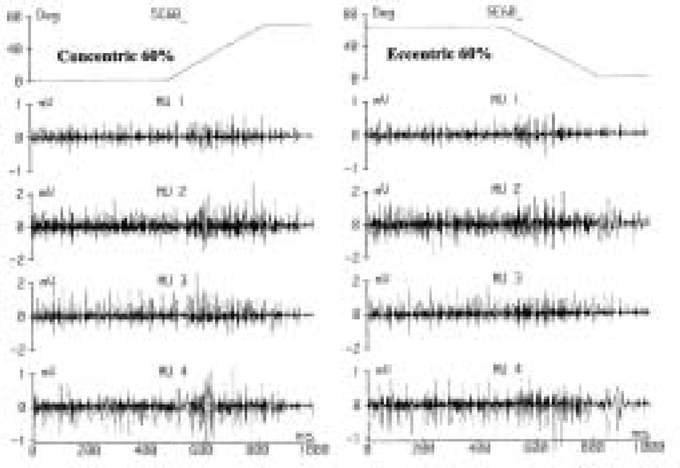
FIGURE 6 An example of (a) eccentric and (b) concentric actions in Exp. 1 showing the isometric preactivation phase and the range of motion divided into five sections and the interference EMG form biceps brachii (BB), brachioradialis (BR) and triceps brachii (TB) muscles.

In Exp. 2 which consisted of 100 maximal eccentric or concentric actions, the average force recorded throughout the motion was taken for analysis. The average of 97th – 99th repetition was then used as an “after” value in eccentric action in eccentric exercise and in concentric action in concentric exercise. Before the exercises and during recovery the average of two maximal eccentric or concentric actions for each subject and during the exercises the average of 29th – 31st (3rd set), 49th - 51st (5th set) and 97th – 99th (10th set) repetition were used for further analysis (II). In Exp. 3 both the maximal peak force and average force as well as the maximal rate of rise of force production ($N \cdot s^{-1}$) were calculated both in isometric and in dynamic actions (III). In Exp. 5 the maximal force was calculated both in the absolute and relative scales. For the relative scale, the isometric preactivation phase just prior to the stretch was used as a predominator. In addition, a movement of the lever arm was performed at all the movement velocities with the subject sitting passively without resisting the movement. This was done to estimate the effect of inertia on the measured force. The force measured in the relaxed condition was then subtracted from the forces measured during active resistance (VI).

4.3.3 EMG measurements

Surface EMG was recorded from the biceps brachii (BB), brachioradialis (BR) and triceps brachii (TB) muscles of the right arm (I, II, VI) and from the vastus lateralis (VL), vastus medialis (VM), and rectus femoris (RF) muscles of the right leg (IV and V) using bipolar Beckman miniature sized electrodes. According to the recommendation by SENIAM (1999), a 20-mm inter-electrode distance was employed. Constant inter-electrode distance was ensured by the use of a special plastic housing into which the electrodes were built. In experiment 3 (III) surface EMG was recorded from the vastus medialis (VM) muscles of both legs with silver/silver chloride surface electrode modules. Each electrode module consisted of two active electrodes and a third reference electrode, all equidistant at 2 cm. In all experiments the electrodes were placed longitudinally on the muscle approximately halfway between the motor point area and the distal part of the muscle. The skin under the electrodes was shaved, abraded and cleansed with alcohol to reduce inter-electrode resistance. Surface EMG signals were recorded telemetrically (Glonner Biomes 2000, Germany) with a bandwidth of 3-360 Hz (I, II, VI, VII) or directly (Neuropack Four Mini, MEB-5304K, Japan) with a high-pass filter of 20Hz (IV, V). Preamplifiers (Quantec, Australia) were incorporated in Exp. 3 into the electrode modules with the signal being further amplified with amplifiers (Quantec, Australia) at a low-pass filter setting of 1000 Hz and a high-pass at 3 Hz (III). Sampling frequency was either 1000 Hz (I, III), 2000 Hz (II), 2016 Hz (VI, VII) or 2520 Hz (IV, V).

For intramuscular recordings, four pairs of bipolar wire electrodes were used (VII). The two 50 μm polyureathane insulated wires were glued together cutting one wire 2 mm shorter than the other one. The insulation was then mechanically removed from the longer wire over ½ mm distance from the tip. A hook was formed to the end of the wires to ensure the fixation during the measurements. The wire electrode pairs were inserted approximately 2 cm from the skin surface into the muscle near the surface EMG electrode with a 27 gauge needle. The needle was subsequently withdrawn. Intramuscular signals were amplified (Neuropack Four Mini, MEB-5304K, Japan, 100 – 10kHz) and digitized at a sampling rate of 20 kHz. Fig. 7 shows an example of the interference EMG signal recorded with four wire electrodes in eccentric and concentric forearm 60% MVC flexion starting with preactivation.



	MSA (μV)	MSF (Hz)
Iso Con	319 ± 159	15.4 ± 4.7
Con	394 ± 156	14.2 ± 4.3
Iso Ecc	316 ± 118	19.2 ± 5.6
Ecc	334 ± 129	16.0 ± 2.0

FIGURE 7 Intramuscular recordings and mean spike amplitude (MSA) and mean spike frequency (MSF) ± S.D values of four different motor unit pools during 60% MVC concentric(Con) and eccentric (Ecc) elbow flexion with isometric preactivation (Iso).

4.3.4 EMG analyses

4.3.4.1 Average EMG

To calculate average EMG (aEMG), the signal was fullwave rectified and average amplitude of the signal was calculated. (I, II, III, IV, V, VI, VII). In Exp. 1 the range of motion (110°) was divided into five 22-degree sections (fig 1.), which were then used for further analyses of aEMG (I). In Exp. 2, the range of motion was slightly larger (130°) and aEMG was calculated for the whole range of motion as well as for five 26-degree sections (II). In Exp. 3, aEMG for the concentric actions was calculated over the whole range of motion, which was always the same (80°) regardless of the angular velocity (III). In Exp. 4, aEMG in isometric condition was calculated over 1 s period of stable force in each activation level (IV), while in eccentric and concentric condition the range of motion (65°) was divided into nine equal sections (V). In Exp. 5, the range of motion during eccentric action was divided either into equal six or three 10-degree sections (depending on the range of motion) for further aEMG analyses while in isometric action the EMG measurements were taken from a specific joint angle during a plateau phase of the isometric force (VI).

4.3.4.2 EMG power spectrum

In Exp. 1, Fast Fourier transformation (FFT) was performed with Mega Electronics (Kuopio, Finland) software so that the window overlap was 50%. To cover the whole range (110°) of motion the window length was set according to the movement velocity. At 4 $\mathrm{rad{\cdot}s^{-1}}$ it was 128 data points (9 windows), at 3 $\mathrm{rad{\cdot}s^{-1}}$ and at 2 $\mathrm{rad{\cdot}s^{-1}}$ 256 data points (6 and 8 windows) and at 1 $\mathrm{rad{\cdot}s^{-1}}$ 512 data points (7 windows). Median frequency (MF) was calculated for each window. The average of the three windows at the halfway point of the movement was used for further analyses (I). In Exp. 2, two FFT windows of 1024 data points with 10% overlap were used to analyze the whole range (130°) of motion. The mean MF value of the two windows was used for further analysis (II). To analyze the same range of motion both in explosive and heavy resistance exercise in Exp. 3 FFT windows of 128 (explosive) and 256 data points (heavy resistance) were used in concentric actions. A window of 1024 data points was used in isometric actions to calculation of MF and mean power frequency (MPF). In dynamic actions, the window was placed at the start of the movement, and in maximal isometric actions the window was placed at the plateau phase of the peak force. During the isometric fatigue test, the window was placed at the midpoint of each ten second work period (III). In Exp. 4, both in isometric and dynamic situations, MF was calculated for each of the overlapped FFT windows (1024 data points) so that a new window was moved for one data point to the right. In isometric condition, 1 s time period of isometric plateau phase at each force level while in dynamic condition the whole range of angular motion was chosen for the analyses. The mean value of the obtained MF values for each muscle was used for further analyses (IV, V).

4.3.4.3 Measurement and analysis of the maximal M-wave

For measurement of the M-wave in Exp. 4 the subjects performed additional isometric and dynamic actions at similar force levels as in pure voluntary conditions. A supramaximal electrical stimulus was given to the femoral nerve (Neuropack Four Mini, MEB-5304K) just distal of the inguinal ligament during the steady force phase. The electrical stimulus was 1 ms long and had a rectangular shape. The anode (5 x 5 cm) was placed over the hip of the stimulated leg and the cathode (1 cm diameter) over the nerve. Maximal electrical stimulation intensity was defined as the current level when a further increase was not reflected in a M-wave amplitude increase. The actual stimulation intensity was further increased by 50% to secure supramaximal stimulation intensity. The cathode was additionally pressed against the nerve to secure supramaximal stimulation in all conditions. The maximal M-wave was analysed for its latency (defined as the time from the start of the electrical stimulus to the first peak of the M-wave), peak-to-peak amplitude and the duration between the negative and positive peaks of the M-wave (fig. 8) (IV, V).

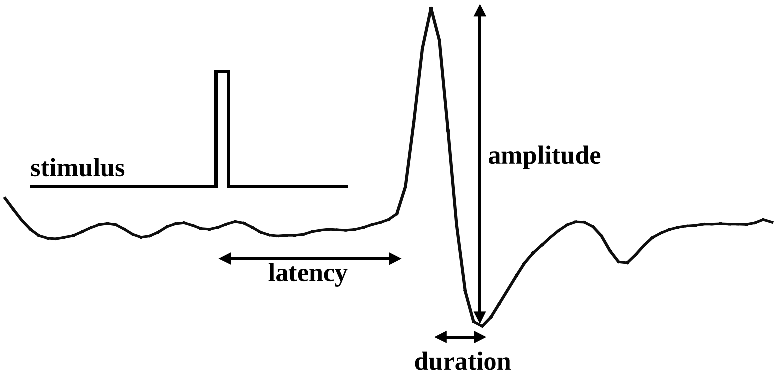


FIGURE 8 An example of the latency, amplitude and duration of the maximal M-wave.

4.3.4.4 Intramuscular spike-amplitude-frequency analyses

In Exp. 6, the behavior of a selected population of motor units was obtained by constructing the intramuscular spike-amplitude-frequency (ISAF) histograms according to Moritani et al. (1985). Intramuscular spikes were isolated and counted according to their amplitude in 100 µV increments and mean spike amplitude and frequency together with standard deviations were used for statistical comparisons between different conditions. A total of 32 motor unit populations obtained from 8 different subjects were recorded. From these 28 had no noise problems and were accepted for further analysis. ISAF histograms were analyzed throughout the whole range of movement with a 350 ms window in each condition and for 350 ms from the isometric preactivation phase preceding the movement at each force level (VII). Figure 9 shows an example of the ISAF histogram from one subject.

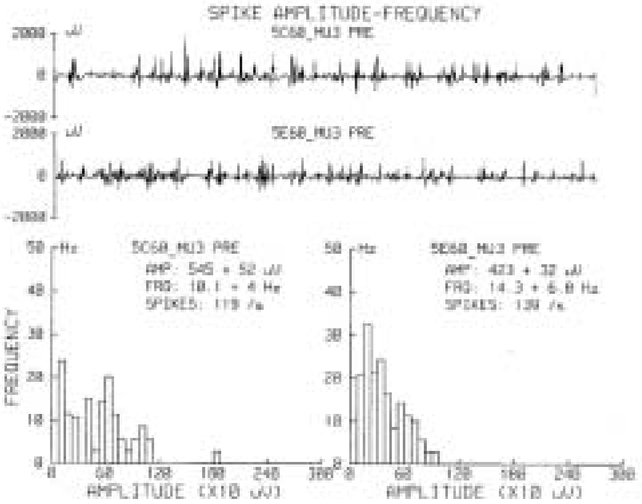


FIGURE 9 An example of ISAF histogram in concentric and eccentric 60% MVC elbow flexion starting with isometric preactivation.

4.3.5 Blood sampling and analyses

In Exp. 2, blood lactate concentration was determined (Biochemica Boeringer GmbH, Germany) from the fingertip blood drawn before, immediately after and half an hour after both eccentric and concentric exercise. To determine serum Creatine kinase activity (CK) (Boehringer Mannheim, Germany), the blood samples were drawn from ulnar vein before, immediately after, half an hour after, 2 days and 7 days after both exercises (II). In Exp. 3, blood was drawn from a canula was inserted into the antecubital vein of each subject before the exercise. Blood was subsequently drawn before the exercises, and after the second, fourth and last sets in both exercises and analyzed using a YSI 1500 SPORT L-LACTATE ANALYSER (Yellow Springs Instrument Co, Ohio, USA) (III).

4.3.6 Muscle biobsies and fiber typing

In Exp. 3, muscle biobsies were taken before the exercise to determine the fiber type composition. Muscle biopsies were obtained from the vastus lateralis muscle from six subjects by a standard procedure involving a double-chop and suction method (Bergrström 1962, Evans et al. 1982). Muscle fibers were then aligned, mounted on small pieces of cork, frozen in isopentane pre-cooled in liquid nitrogen, and stored at -80^{o} C for later analysis. Standard histochemical analysis was performed to determine fiber type distribution (Brooke & Kaiser 1970, Green et al. 1982). Muscle samples were serially cross-sectioned (10 µm) and mounted on cover slips. Samples were assayed for mATPase activity after pre-incubation either at pH 4.34 (1.5-2 minutes, 25° C) or pH 10.3 (5-7 minutes, 37° C). In addition, other samples were also stained for NADH-tetrazolium reductase (Halkjaer-Kristensen & Ingemann-Hansen 1979). Samples were then mounted on slides (Aquamount, BDH Laboratories, Poole, England) and photographed (Olympus BH-2 Imaging System, OLYMPUS America Inc., Melville, USA). Fiber typing was performed by manually counting approximately 100 (90-153) fibers for each sample and then cross-referencing the pH 4.34, pH 10.3 and NADH stained samples to determine the proportion of type I to type II fibers (III).

4.3.7 Statistical methods

All statistical analyses were done by the SPSS™ program (SPSS Inc, USA). Means and standard deviations (SD) or standard errors (SE) were first calculated. ANOVA with METHOD/UNIQUE (also called sums of squares TYPE III) which uses regression method to partition sums of squares was used. Multiple comparisons were made between velocities and between types of work (I), before and after fatigue and between types of work (II, III), between activation levels and types of work (IV, V, VI, VII) and between joint angles (I, V, VI) according to Bonferroni’s method with a significance level of $P<0.05$. When appropriate, comparisons of means were performed by Student's paired t-test with the significance level of $P<.05$ (two-tailed). To test the reliability of the measurements correlations (Pearson) and coefficients of variation (CV) were calculated for each variable between two consecutive attempts. CV was expressed as a percentage (CV% = $100\sqrt{\Sigma d_i^2 / 2n} / x$), where d is the difference between the two results in each individual, n is the number of subjects and x is the mean obtained from all the subjects (Madsen 1996) (I, III).

4.3.8 Reproducibility of the measurements

In Exp. 1, the reproducibility of different parameters were tested by calculating the coefficient of variation between attempts. The CV% was usually smallest and the correlation highest at the slowest velocities and at the elbow angle in the middle part of the movement. The range of CV% at the 110° elbow angle of two consecutive attempts for the average force, aEMG and MF in different conditions is shown in table 2. The correlation between two attempts was significant for force ($P<.001$), for aEMG ($P<.01$) and for MF ($P<.05$) for all the muscles at all the conditions with a few exceptions regarding MF in the BB muscle. In Exp. 3 the CV% of MF between the second and third repetitions of the first set was 8.7% in EXE and 9.9% in HRE.

TABLE 2 Lowest and highest CV% of maximal force, aEMG and MF at the elbow angle of 110°

	Lowest CV%	Condition	Highest CV%	Condition
Max force	3.1%	ECC 1 rad·s^{-1}	6.8%	CONC 4 rad·s^{-1}
aEMG BB	7.7%	CONC 3 rad·s^{-1}	17.4%	ECC 2 rad·s^{-1}
aEMG BR	0.6%	ECC 1 rad·s^{-1}	24.8%	CONC 2 rad·s^{-1}
MF BB	6.5%	CONC 4 rad·s^{-1}	12.0%	CONC 3 rad·s^{-1}
MF BR	5.7%	ISOM	16.8%	CONC 2 rad·s^{-1}

In Exp. 6 no significant differences were observed either in the mean spike amplitude or in the mean frequency in the isometric preactivation phase between concentric and eccentric actions at any force level. The mean of the two curves has been used to represent the isometric preactivation phase in figs 27 and 28.

5 RESULTS

The main findings from the present experiments are presented below. For more details the original papers (I-VII) should be consulted.

5.1 Maximal force and aEMG in eccentric, concentric and isometric actions

5.1.1 Effects of the joint angle, type of action and movement velocity

The results of Exp. 1 with elbow flexors (fig. 10) as well as of Exp. 4 with knee extensors (figs. 11a and b) indicated an angle specific response of maximum force. Maximal concentric force was almost identical in a second test measured a week after the first test (Fig 11a) while a considerable increase was observed in the maximal eccentric force (fig. 11b). The force in all conditions was generally the greatest in the middle of the movement regardless of velocity and direction.

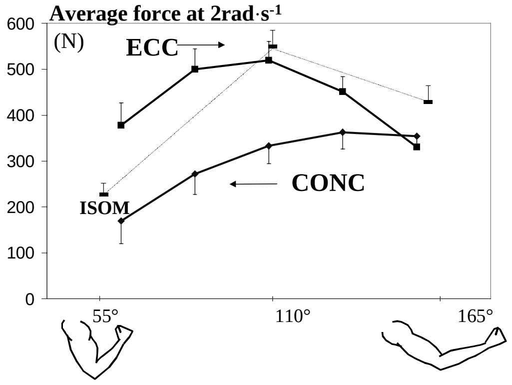


FIGURE 10 Average force (±SE) in maximal eccentric (ECC), isometric (ISOM), and concentric (CONC) elbow flexion at 2rad·s^{-1} (mean of 9 subjects).

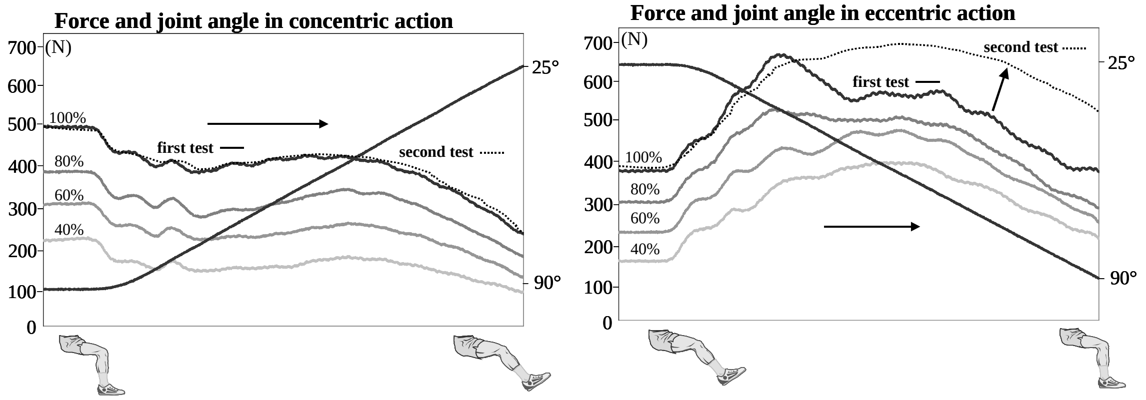


FIGURE 11 Force during concentric (a) and eccentric (b) knee extension at different activation levels (mean of 10 subjects).

At the 110° elbow angle, which represents the middle portion of the movement (see Fig. 4), the average force for elbow flexors was significantly lower (P<.001) in the CONC in comparison with the ECC and the ISOM at all velocities and lower in the ECC than in ISOM at 3 rad·s^{-1} and at 4 rad·s^{-1} (fig. 12). In the CONC actions the force was the greatest at the slowest velocity and the effect of velocity was significant (P<.001), while the ECC forces, when averaged for the 110° point, were not velocity dependent. aEMG of the BB, when compared at this same 110° angular position, was significantly higher (p<.001) in the CONC compared with the ECC at all velocities and higher (p<.05) than in the ISOM at the three slowest velocities (fig. 12).

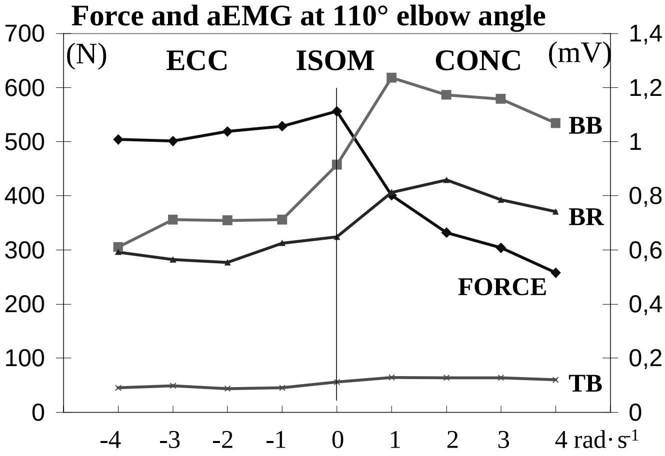


FIGURE 12 Force and aEMG of biceps brachii (BB), brachioradialis (BR) and triceps brachii (TB) with different movement velocities in eccentric, isometric and concentric elbow flexion action at elbow angle 110° (mean of 9 subjects).

Although EMG activity was generally greater in concentric actions than in eccentric actions in the middle part of the motion, this was not the case for the angle that corresponded to the beginning of the eccentric action and the end of concentric action as seen in fig. 13 for elbow flexors.

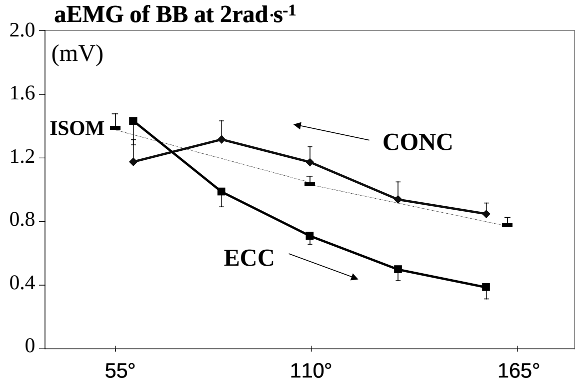


FIGURE 13 aEMG of biceps brachii (BB) (±SE) in eccentric, isometric and concentric elbow flexion at 2 rad·s^{-1} (mean of 9 subjects).

aEMG of the knee extensors in maximal concentric situation was higher than in the eccentric one in the first test. However, this was no longer the case in the second test (figs 14a and b)

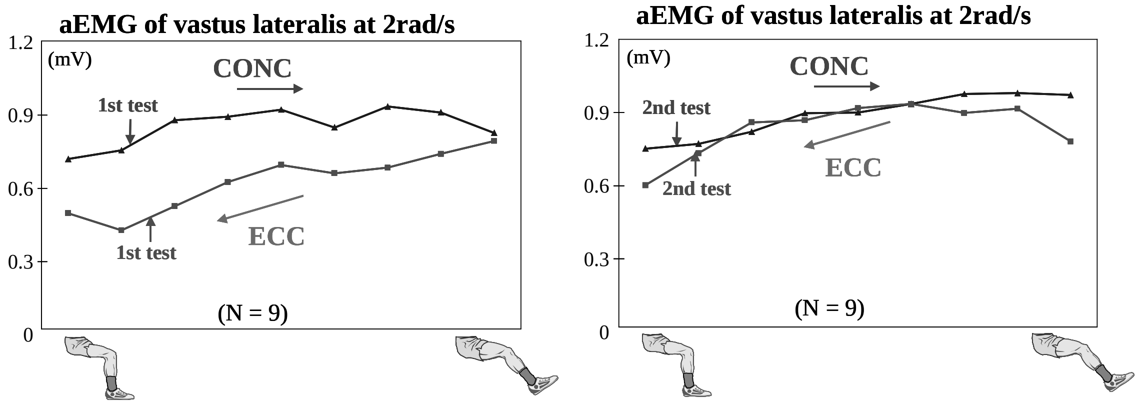


FIGURE 14 aEMG of vastus lateralis (VL) muscle during maximal eccentric and concentric knee extension at 100% force level in the first (a) and in the second (b) test (mean of 10 subjects).

5.1.2 The effect of preactivation

The results indicate clearly that the force enhancement as well as the maximum force level in eccentric action was dependent on the prehistory of the eccentric mode. Although the separately measured isometric force may exceed the eccentric force at the joint angle representing the middle part of the motion, the eccentric force after the onset of the movement was higher than the isometric preactivation force as seen from experiments 1 and 4 (figs. 6 and 11b). In Exp. 5, this phenomenon was examined in more detail and the results showed that maximal eccentric force during the first ten degrees of the movement for elbow flexors was significantly higher (P<.001) than the maximal isometric preactivation force both in 80° and in 110° starting position at all three velocities. The relative force increase after 100% preactivation level was significantly lower throughout the motion (P<.01) during 1 rad·s^{-1} as compared with 2 rad·s^{-1} and 4 rad·s^{-1} starting either from the 110° (P<.01) or, as shown in figure 15, from 80° (P<.05) elbow angle.

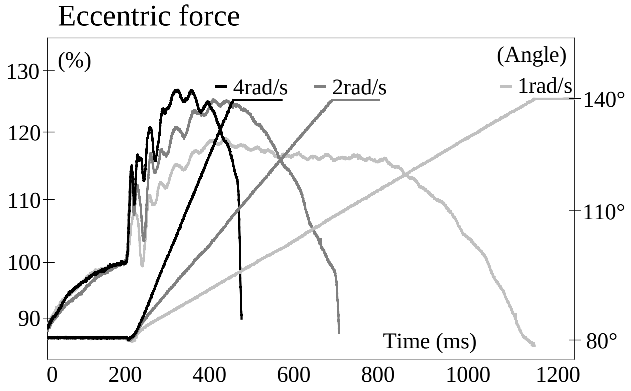


FIGURE 15 Relative eccentric force curves at 1rad·s^{-1}, 2rad·s^{-1} and 4rad·s^{-1} from 80° to 140° elbow angle starting from maximal preactivation (mean of 10 subjects).

No major differences in relative force enhancement between velocities were observed either with 50% or 80% starting level. Tables 1 and 2 summarize the relative force increases throughout the whole range of motion from both starting positions. As seen in fig. 2 when the comparisons between different preactivation levels were made using the absolute scale, the maximal force and the average force throughout the whole range of motion were lower when the eccentric action was started from 50% preactivation level as compared with 80% and 100% (P<.001) preactivation levels and regardless of the starting position.

The force curves obtained in Exp.6 show that the difference either in maximal or average eccentric force is even more substantial if the comparison is made between zero and maximal preactivation (fig 17). The same phenomenon was observed also in concentric actions (fig. 18).

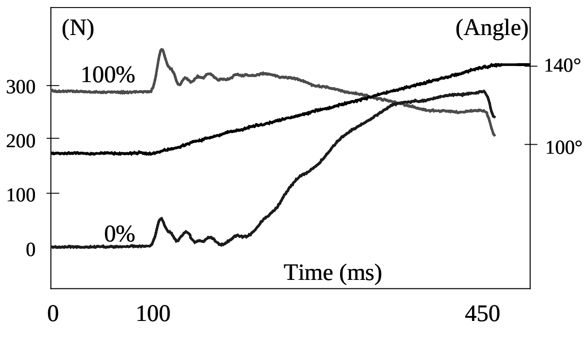


FIGURE 17 Absolute eccentric elbow flexion force curves at 2rad·s^{-1} from 100° to 140° elbow angle starting from 0% and 100% preactivation (mean of 8 subjects).

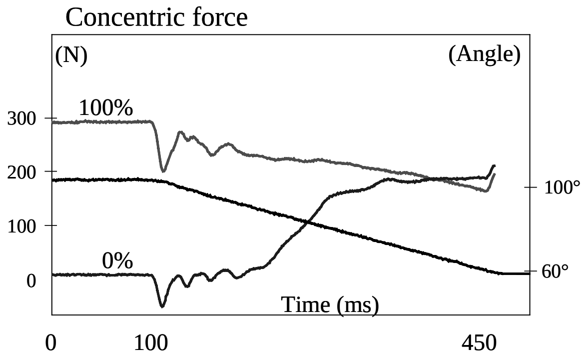


FIGURE 18 Absolute concentric elbow flexion force curves at 2 rad·s^{-1} from 100° to 60° elbow angle starting from 0% and 100% preactivation (mean of 8 subjects).

5.2 EMG power spectrum in eccentric, concentric and isometric actions

5.2.1 The effect of joint angle and movement velocity

In Exp. 1, the median frequency (MF) in the biceps brachii (BB) muscle was significantly higher (P<.01) at 66° compared with the 154° elbow angle in the eccentric condition at all velocities and in the concentric at 1 rad·s^{-1}. However, no significant differences were observed in MF of the BB in the ISOM at different joint angles (fig. 19). Fig. 19 also shows MF of BB in concentric and eccentric actions with the velocity of 2 rad·s^{-1}.

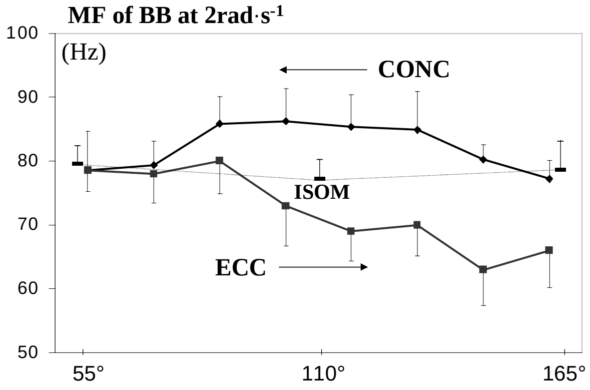


FIGURE 19 Median Frequency (MF) (±SE) of biceps brachii in isometric and in eccentric and concentric elbow flexion at 2 rad·s^{-1} (mean of 9 subjects).

MF decreased towards the end of the maximal eccentric action also for knee extensors and was higher in concentric compared with eccentric action as measured in experiment 4. (fig. 20).

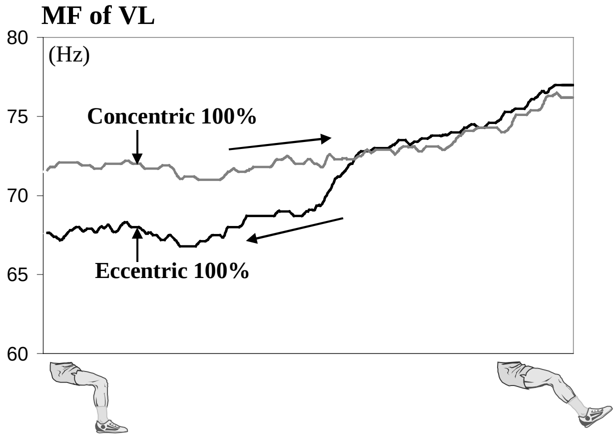


FIGURE 20 MF of vastus lateralis muscle during maximal eccentric and concentric knee extension at 2rad·s^{-1} (mean of 10 subjects).

Figure 21 shows that when the middle part (110°) was taken as a reference angle, MF of the BB was significantly lower (P<.05) in the ECC than in the CONC at the three fastest velocities, while no differences were observed when comparing either CONC or ECC to ISOM. In the CONC, MF of BB was higher (P<.05) in 4 rad·s^{-1} than in 1 rad·s^{-1} (fig. 21)

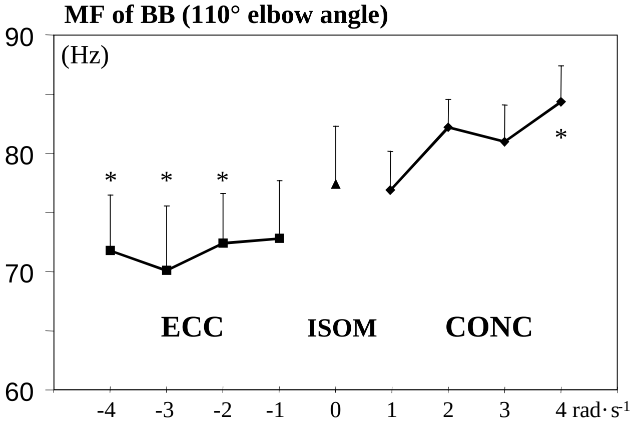


FIGURE 21 Median Frequency (MF) (±SE) of biceps brachii (BB) with different movement velocities in eccentric, isometric and concentric elbow flexion at elbow angle 110°. (* P<.05).

In Exp. 3, higher MF (P<.05) values were also observed with higher movement velocity (Fig 22) but only when MF was calculated as an average of several repetitions throughout explosive and heavy resistance exercise. However, in single concentric actions of different angular velocity no significant changes were seen in the MF.

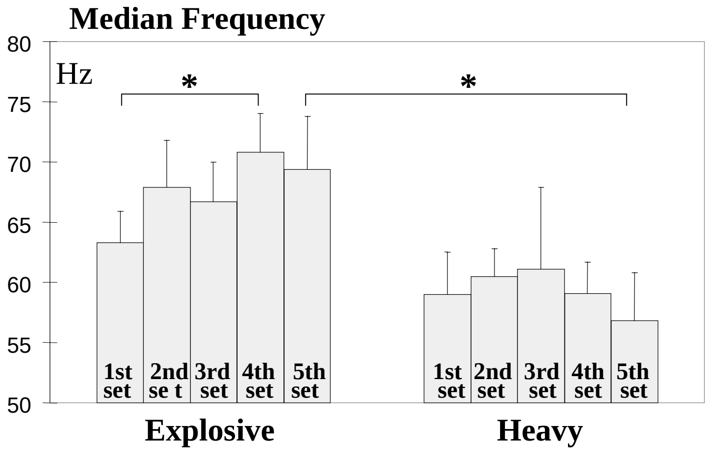


FIGURE 22 Median Frequency (+ SE) in concentric knee extension during Explosive and Heavy Resistance Exercise. (* P<.05).

5.2.2 The effect of activation level to MF and to the maximal M-wave

In the isometric condition, the duration of the M-wave decreased as the force level increased in all three muscles (P<.05) (fig. 23). However, no significant changes were observed in MF across different force levels in any of the muscles during voluntary actions. No consistent differences were observed in the amplitude and in the latency of the maximal M-wave in any of the conditions.

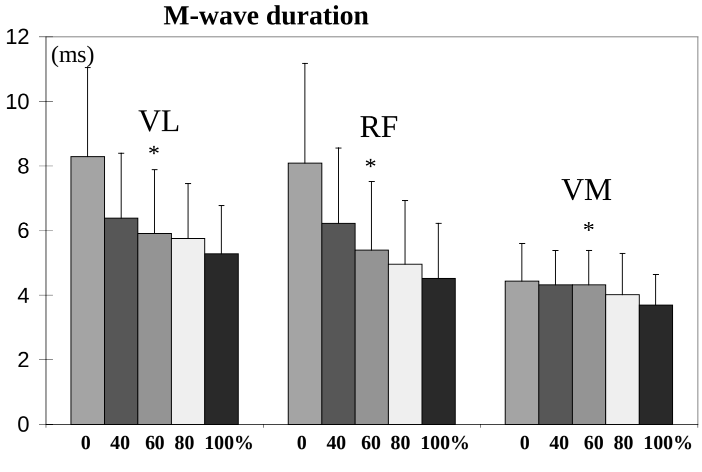


FIGURE 23 Duration (+SD) of the M-wave of VL, RF and VM muscle in knee extension at different isometric force levels. (* P<.05).

When comparing the duration of the M-wave between eccentric and concentric actions, the only significant differences were found in relaxed condition and at 40% force in VL muscle where the duration was shorter (P<.05) in eccentric action as compared to concentric. However, as the force level increased, the duration of the M-wave decreased significantly (P<.01) both in eccentric and concentric actions. The differences were greatest in VL muscle (fig. 24) but the same trend was observed also in RF and VM muscles.

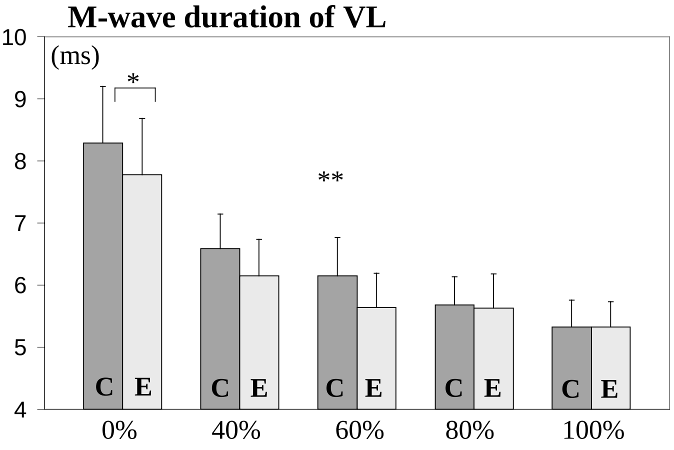


FIGURE 24 Duration (+SD) of the M-wave of VL muscle at different force levels in eccentric (E) and concentric (C) knee extension. (* P<.05, ** P<.01).

MF in concentric action tended to be somewhat higher (N.S) in concentric than in eccentric action when averaged over all the overlapping FFT windows. No major differences were observed in MF between the force levels in either type of action. The results, however, depend on which part of the motion is chosen to for inspection.

5.2.3 The effect of FFT window placement

When analyzed with overlapping FFT windows, the mean curves of all 10 subjects over a 1s time period of stable isometric force showed remarkable variation in MF over the chosen time period (fig. 25). The same phenomenon was observed also in eccentric and concentric situation (figs. 26 a and b).

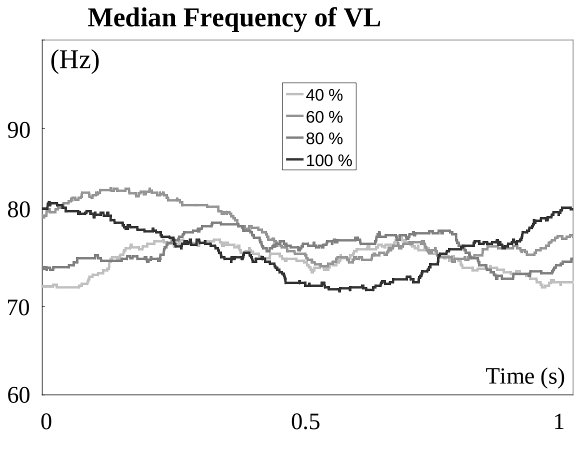


FIGURE 25 MF of VL muscle in knee extension over 1s time at different isometric force levels (mean of 10 subjects).

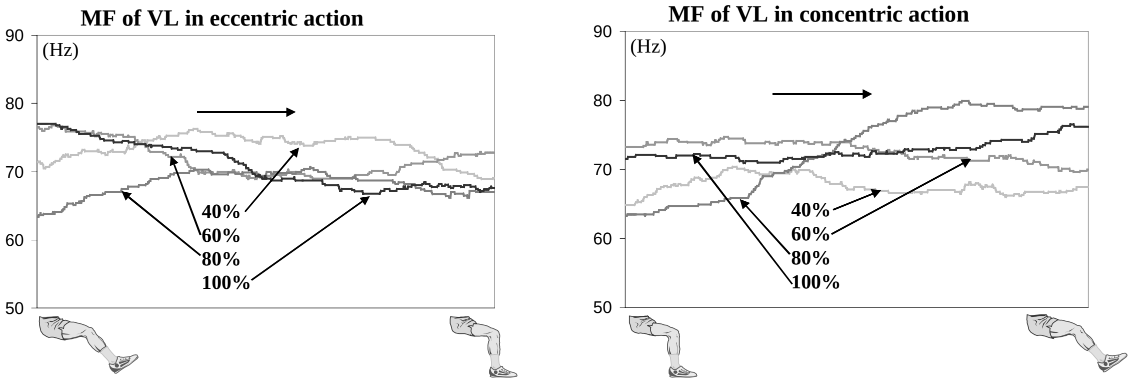


FIGURE 26 MF of VL muscle during eccentric (a) and concentric (b) knee extension at different activation levels (mean of 10 subjects).

When considering the individual subjects the variation was even greater. Table 3 shows the mean -, smallest and greatest range (highest MF – lowest MF) in MF of VL muscle over time (1s) in isometric condition for all subjects at different force levels.

TABLE 3 The range of variation of MF in VL over 1s time at different isometric force levels (10 subjects).

	40%	60%	80%	100%
Mean ± SD	21,9 ± 9,9 Hz	20,7 ± 8,5 Hz	16,7 ± 8,4 Hz	23,2 + 7,9 Hz
Min	10 Hz	8 Hz	7 Hz	14 Hz
Max	37 Hz	35 Hz	35 Hz	35 Hz

5.2.4 Motor unit activation

In all conditions both the mean spike amplitude (P<.001) and the mean spike frequency (P<.01) increased with force. The mean spike amplitude was lower in the isometric preactivation phase than in the consequent concentric action at all the force levels (P<.01) and lower than in the consequent eccentric action at 40% and 60% levels (P<.001) (fig. 27). The mean spike amplitude increased significantly (P<.001) up to 80% in isometric and in the consequent concentric actions while in eccentric actions with preactivation the significant increase continued up to 60% (P<.01). When the movements were started without preactivation, however, the mean spike amplitude in eccentric actions increased up to 80% (P<.05).

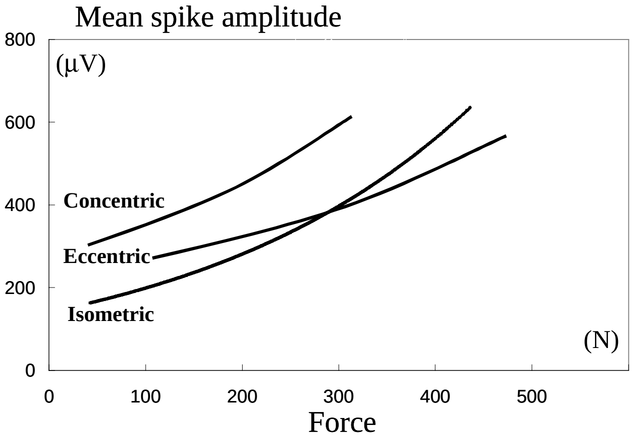


FIGURE 27 The mean spike amplitude of biceps brachii and absolute force in isometric preactivation phase and in concentric and eccentric elbow flexions with preactivation.

The mean spike frequency was higher in isometric than in the consequent concentric and eccentric at all the force levels (P<.05) (fig. 4). The mean spike frequency in isometric preactivation and in the consequent concentric action at the 20% force level was lower (P<.01) than at the other force levels, but no major differences were observed between the other force levels while in eccentric action with preactivation the increase between the force levels was significant (P<.01) up to 60% (fig 28). When the movements were started without preactivation, the mean spike frequency increased in concentric up to 40% (P<.05) and in eccentric up to 60% (P<.01).

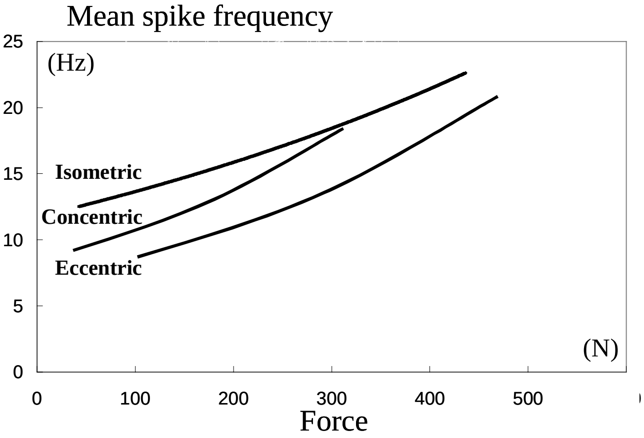


FIGURE 28 The mean spike frequency of biceps brachii and absolute force in isometric preactivation phase and in concentric and eccentric elbow flexions with preactivation.

At 20% and at 40% force level started without preactivation the mean spike amplitude was higher (P<.01) in eccentric action compared with concentric, whereas, at 60% (P<.01) and at 80% (N.S) the situation was the opposite (fig 6). When the movement was started with preactivation, no major differences in the mean spike amplitude were observed between concentric and eccentric actions at the three lowest force levels but at 80% level the mean spike amplitude in concentric was higher (P<.01) than in the eccentric actions. The mean spike frequency at 40% (P<.001) and at 60% (P<.05) level without preactivation and at 40% (P<.05) with preactivation was higher in concentric than in eccentric actions (fig 29).

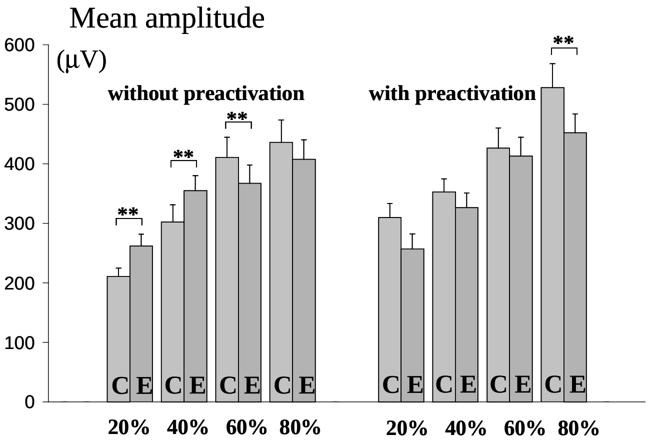


FIGURE 29 The mean spike amplitude (±SE) of biceps brachii in concentric (C) and eccentric (E) actions without and with preactivation at different force levels. (* P<.05, ** P<.01).

5.3 The effect of eccentric and concentric fatigue

5.3.1 Force and aEMG

In Exp. 2, when comparing maximal eccentric and concentric actions before the exercises, the average force was higher (P<.001) in eccentric than in concentric but the average EMG (aEMG) values were the same in the two types of action. During fatiguing eccentric exercise (EE) the average eccentric force at all the joint angles decreased significantly (P<.001) throughout the exercise (fig. 30). Similar behavior (P<.001) was observed in average concentric force at all the joint angles during fatiguing concentric exercise (CE) (fig. 31). No major differences were observed in aEMG in either exercise.

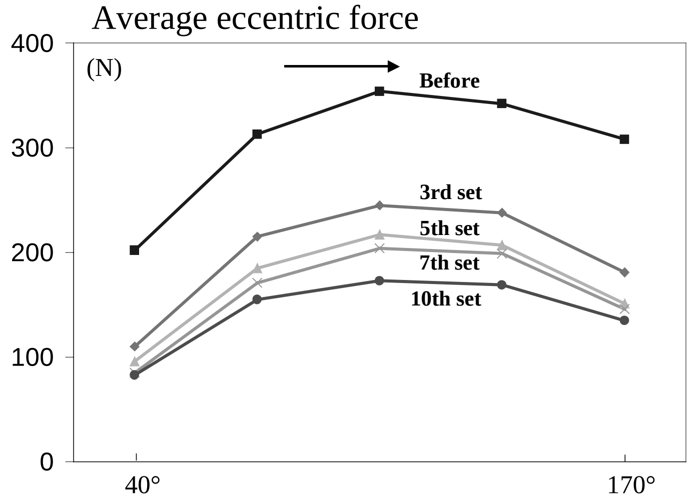


FIGURE 30 Eccentric force (mean of 9 subjects) during fatiguing eccentric exercise with elbow flexors.

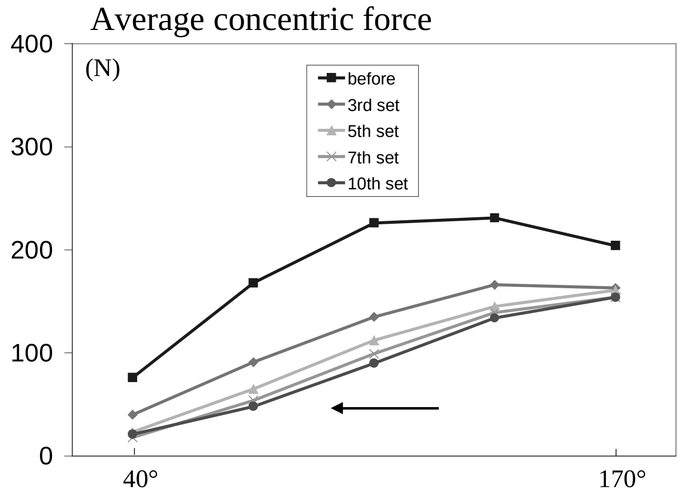


FIGURE 31 Concentric force (mean of 9 subjects) during fatiguing concentric exercise with elbow flexors.

The average eccentric force of the whole range of motion (130°) decreased after both EE and CE (P<.001) (fig. 32). The decrease was greater (P<.001) and the recovery slower after EE in which the average force was still significantly lower (P<.001) seven days after the exercise, whereas the recovery was complete already within two days after CE (fig. 32a). The average concentric force decreased after both concentric and EE (P<.001) and the decrease was greater after CE (P<.01) (fig 32b). Table 4 summarizes the relative changes in force after both exercises and during recovery.

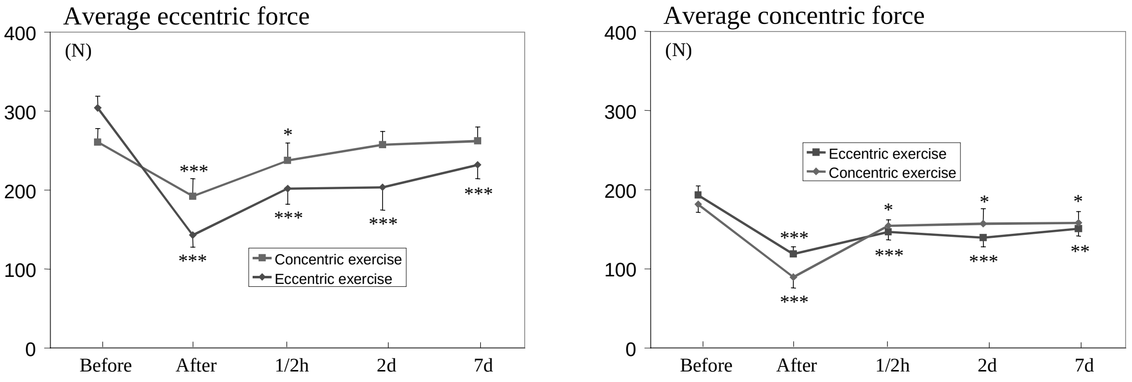


FIGURE 32 Average eccentric (a) and concentric (b) force (± SE) from 40° to 170° elbow angle in eEccentric and concentric exercise. (* P<.05, ** P<.01, *** P<.001).

TABLE 4 Relative changes (Δ%)(± S.E) in eccentric and concentric elbow flexion force in eccentric exercise (EE) and concentric exercise (CE)

	Eccentric force	Concentric force
EE Δ% after	-53,3 ± 3,5	-38,4 ± 4,0
Δ% 1/2h after	-34,0 ± 4,6	-23,3 ± 4,5
Δ% 2d after	-33,7 ± 8,1	-23,6 ± 10,1
Δ% 7d after	-23,8 ± 3,8	-21,5 ± 6,7
CE Δ% after	-30,6 ± 6,4	-49,9 ± 6,6
Δ% 1/2h after	-9,7 ± 3,7	-13,7 ± 7,1
Δ% 2d after	-0,6 ± 3,3	-12,0 ± 8,6
Δ% 7d after	0,9 ± 2,8	-11,6 ± 7,4

In another fatigue experiment with knee extensor muscles (Exp. 3) the average time of one concentric repetition was 347 ms in the explosive exercise (EXE) and 670 ms in the heavy resistance exercise (HRE), and corresponding average forces were 1121 N and 1556 N, respectively. The average power was approximately 39% higher during EXE than during HRE. During HRE the average time of one concentric repetition increased by 11.6 ± 4.4% (P<.05) from the first set to the last set, while there was no change during EXE (Table 8). No significant changes were observed in peak force, maximal rate of force production or average force from a 100° to 180° knee angle during concentric actions of either exercise (Table 5) or in aEMG.

TABLE 5 Force characteristics (± S.E) during concentric actions of explosive exercise (EXE) and heavy resistance leg extension exercise (HRE) and their relative changes (Δ%)

	Maximal peak force	Maximal rate of force production	Average force 100°-180°	Repetition time 100°-180°
EXE 1st set	1307 ± 41N	11485 ± 905N/s	1118 ± 27N	345 ± 111ms
5th set	1266 ± 47N	11575 ± 877N/s	1125 ± 28N	350 + 117ms
Δ%	-3.2 ± 1.7%	3.0 ± 7.7%	0.8 ± 1.8%	1.4 ± 1.8%
HRE 1st set	1790 ± 89N	9529 ± 1221N/s	1595 ± 72N	638 ± 129ms
5th set	1703 ± 90N	8972 ± 823N/s	1517 ± 76N	704 ± 119ms
Δ%	-4.5 ± 3.3%	1.4 ± 12.9%	-4.6 ± 3.7%	11.6 ± 4.4% *

5.3.2 EMG power spectrum

In Exp. 2, MF of biceps brachii (BB) in eccentric action decreased during both EE (P<.01) and CE (P<.05). It recovered within two days after the exercises but was lower again (P<.01) seven days after EE. In concentric action MF of BB decreased during CE (P<.01), while no changes were observed in EE (fig. 33a and b).

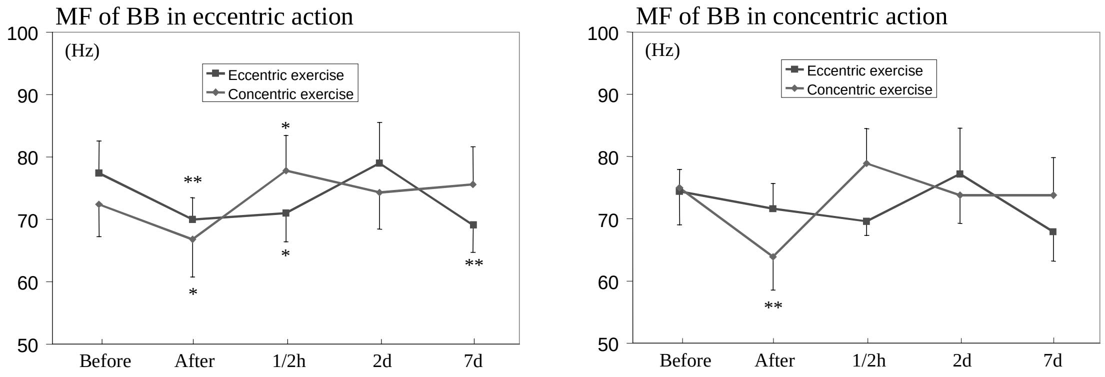


FIGURE 33 MF of BB (± SE) in eccentric (a) and in concentric (b) elbow flexion in eccentric and in concentric exercise. (* P<.05, ** P<.01).

5.3.3 Metabolic changes during fatigue

In Exp. 2, blood lactate concentration increased (P<.001) in both exercises but it was higher after the CE (P<.05) than after the EE (fig. 34).

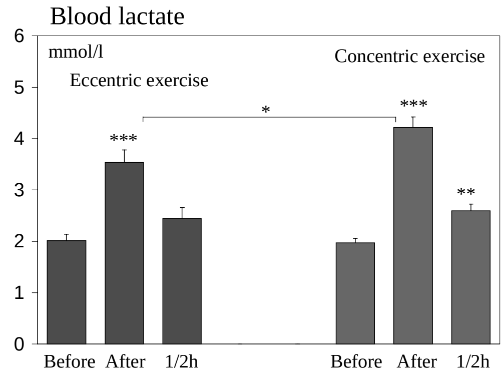


FIGURE 34 Blood lactate concentration (+ SE) in EE and in CE. (* P<.05, ** P<.01, *** P<.001).

Serum CK was significantly higher (P<.001) seven days after EE than before, while no changes occurred after CE (fig. 35). On a scale from zero to five the subjects rated the soreness they felt to 4.1 + 0.7 (SD) which occurred 2.3 + 0.5 days (SD) after the EE.

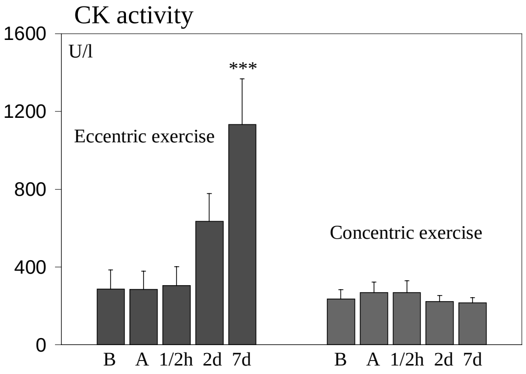


FIGURE 35 Serum CK (+ SE) in EE and in CE. (* P<.05, ** P<.01, *** P<.001).

In Exp. 3 blood lactate increased from 1.00 + 0.22 to 3.09 + 0.55 mmol/l during EE (P<.05) and from 0.79 + 0.09 to 4.95 + 0.81 mmol/l during HRE (P<.01). The increase during HRE was significantly greater (P<.05) than that of EE and was correlated significantly with the change in MPF in HRE (r = -.73, P<.05).

5.4 Muscle fiber composition and its relation to MF and blood lactate

In Exp. 3, the relative number of fast twitch fibers correlated significantly with the change in blood lactate in HRE (r = .87, P<.05), while in EE it was not significant (r = .70, P = .118). No significant correlations between the relative number of fast twitch fibers and MF or MPF were found before or after either exercise, although MF was somewhat lower after HRE (r = -.72, P = .105)

6 DISCUSSION

The main findings in the present study were as follows:

1) Maximal eccentric force measured after the onset of movement exceeded the maximal isometric preactivation force. This was true regardless of the starting joint angle, movement velocity or of muscle group (elbow flexors and knee extensosrs) used in the present study. When the movement was started from the lower preactivation levels of 0%, 50% and 80% MVC, the maximal eccentric force was lower than in 100% MVC preactivation condition.
2) Maximal eccentric force in the middle part of the motion was in most cases lower than the isometric force measured separately at the corresponding joint angle. This difference between isometric and eccentric force was more substantial with knee extensors than with elbow flexors. For the elbow flexors, the lowest maximal eccentric force occurred at the slowest movement velocity.
3) Maximal EMG activity was lower in eccentric compared with concentric and isometric conditions. However, at the joint angle corresponding to the beginning of the eccentric and the end of the concentric motion the aEMG was similar. Although there was a joint angle dependency in the aEMG in isometric situation, the aEMG in the maximal eccentric action decreased towards the end of the motion more than the concentric or isometric aEMG at the corresponding joint angle.
4) Median frequency (MF) was lower in maximal eccentric action compared with maximal concentric one when measured from the middle part of the motion. In eccentric action, MF decreased towards the end of the motion, which was not the case in concentric actions. In concentric actions, MF increased as the movement velocity increased while no velocity dependence was observed in eccentric actions.
5) The duration of the M-wave decreased as the force level increased in the isometric, eccentric and concentric conditions suggesting changes in the muscle fiber conduction velocity. No differences in the M-wave duration

were observed between eccentric and concentric actions. Furthermore, there were no differences in MF when calculated as an average of consecutive Fast Fourier Transformation (FFT) windows over 1s of stable force in isometric or over the range of motion in dynamic condition. Instead remarkable variations were observed in the individual MF values and thus the results depended very much on which part of the signal was chosen for the FFT analyses.

6) Based on the intramuscular spike-amplitude-frequency (ISAF) analysis and on the changes in the mean spike amplitude the recruitment threshold may be lower in dynamic as compared to isometric actions. The recruitment of high threshold motor units, which are likely to be fast units, may continue to higher force levels in isometric and in concentric as in eccentric actions. On the other hand, eccentric actions, as indicated by increased the mean spike frequency, seem to achieve the higher forces by increasing the firing rate of the active units. At the lower force levels mean spike amplitude was higher in eccentric than in concentric actions which might indicate selective activation of fast motor units. This was, however, the case only when the movements were started without isometric preactivation.
7) Force decrease after fatiguing eccentric exercise was greater in absolute terms compared with the force decrease after concentric exercise, but the relative change in force was similar. Eccentric force decreased more than the concentric force after fatiguing eccentric exercise, whereas the situation was opposite after fatiguing concentric exercise. Eccentric exercise led to muscle soreness and increased serum CK activity several days after the exercise, suggesting possible muscle damage. MF, after decreasing during both exercises, recovered rapidly after concentric exercise but remained low for several days after eccentric exercise. The relative number of fast twitch fibers correlated significantly with the change in blood lactate in concentric heavy resistance exercise but was not strongly related with the changes in MF.

6.1 Maximal EMG activity and eccentric, concentric and isometric force

When maximal eccentric force is compared to maximal isometric force, it is of crucial importance how the force was measured and which part of the signal is chosen for the analysis. If the force is measured immediately after the stretch under maximal preactivity condition similar to what has been shown with isolated muscle fibers or sarcomeres (Edman et al. 1978), the eccentric force will exceed the preactivated isometric force. This phenomenon was well supported by the results of the present study. Regardless of the starting angle, movement velocity or preactivation level, the maximal isometric preactivation force was always lower than the subsequent eccentric force. However, this protocol has not always been used in these kind of studies. Comparisons are often made between eccentric, concentric and isometric performance at a joint angle representing the middle part of the motion. Maximal isometric force is then measured separately at the corresponding joint angle. With such an approach, the differences between maximal eccentric and isometric force were not so clear and somewhat opposite to those reported earlier for the elbow flexors (Komi 1973). However, similar results have been reported for the knee extensors (Strojnik et al. 1998, Westing et al. 1988) and for the elbow extensors (Singh & Karpovich 1966).

In certain situations in the present study, the maximal eccentric force did not exceed the separately measured maximal isometric force. It has been suggested that there may be some neural inhibition and therefore the subjects have difficulty in maintaining the maximal eccentric force throughout the motion (Westing et al. 1990). In the present series of studies, isometric force was 7% higher for the elbow flexors and 17% higher for the knee extensors than the eccentric force at the corresponding joint angle, thus suggesting that inhibition may be greater for the knee extensors. The concept of inhibition is consistent with the decrease in maximal EMG towards the end of the eccentric action. In the joint angle corresponding the beginning of the eccentric action and the end of the concentric action the aEMG was in the same level, but towards the end of the eccentric action the aEMG was lower in eccentric as compared with concentric condition. The existence of this neural regulatory mechanism that limits the recruitment and/or discharge of motor units during maximal voluntary eccentric actions, has been suggested to occur, however, also during concentric actions, in particular with low movement velocities (Agaard et al. 2000).

Our recent unpublished findings indicate, however, that there may also be some supraspinal effects involved and the subjects may be afraid to perform maximally, in particular in maximal eccentric knee extension. The same subjects as in Exp.4 participated a week later in another study in which the effect of the movement velocity on maximal eccentric and concentric force was examined. At the same movement velocity (2rad/s) as one week before, there was no longer any difference in the aEMG between eccentric and concentric action and the dramatic decrease in maximal eccentric force as seen in fig. 7b had disappeared. Surface EMG may also be influenced by cancellation of the negative and positive phases of motor unit action potentials as they sum to form the interference EMG (Day & Hulliger 2001). Changes in action potential shape e.g. due to motor unit synchronization can affect the amount of cancellation in different conditions (Yao et al. 2000). The synchronization may be greater for eccentric actions compared with concentric and isometric actions (Semmler et al. 2001). Therefore, the amount of cancellation and thus the quantity of EMG activity may be influenced more during eccentric compared with concentric or isometric actions. On the other hand, there is also evidence that the average amplitude of the surface EMG may increase due to synchronization (Yao et al 2000). What may also be of importance are the depth of the motor unit under the skin surface and the radial distance i.e. the distance from the recording electrode to the active muscle fibers which can both affect the amplitude of the recorded potential (Roelevald et al. 1997a and b). In intramuscular recordings an attempt was made to avoid this problem by inserting the electrodes to different depths into the muscle.

Besides possible inhibition, motivational problems, synchronization and radial distance, low maximal eccentric forces may be related to the measurement protocol. If the movement is started with maximal preactivation as in Komi (1973), the eccentric force is higher than the isometric one. The present results show that if the maximal eccentric action is started from 80%, 50% or 0% MVC, there may not be enough time to even reach the true maximum, especially with higher movement velocities. If the movement starts from zero preactivation, as is often the case, the maximal eccentric force and the average force from the whole range of motion will remain lower than the maximal preactivation level. It is also relevant to examine how much time is used to develop the maximal isometric force and which part of the isometric force curve is chosen for the analysis. The peak force in an isometric action may be reached within 1.5 –2.5 s, which is much longer than the time usually given for maximal preactivation before the stretch. This slow increase in isometric force could be due to increased activation of some other muscles trying to assist in increasing the force. As shown in the Exp. 5 of the present study, the aEMG of biceps brachii muscle was fully activated already during the first peak whereas the activity of brachioradialis increased significantly towards the second peak. In cases where the separately measured maximal isometric force was similar to the maximal preactivation force it was always exceeded by the maximal eccentric force. Therefore, whether the maximal eccentric force is higher than the separately measured isometric force seems to depend also on which part of the isometric curve is chosen for the analysis.

6.2 Motor unit activation

6.2.1 EMG power spectrum

The frequency component of the EMG power spectrum in maximal conditions followed the same pattern as that of aEMG. At the flexed position, no difference in MF was observed between eccentric and concentric actions but in the middle of the movement MF was significantly lower during eccentric action. MF decreased during maximal eccentric mode both in elbow flexors and in knee extensors throughout the motion, which suggests that changes had occurred in the muscle fiber conduction velocity. It has been proposed that the EMG power spectrum is more susceptible to changes in motor unit recruitment than changes in the firing frequency of the individual motor units (Solomonow et al. 1990). The power spectrum could also be affected by muscle length (Moritani et al 1987). An increase in muscle length leads to a decrease in the conduction velocity of the muscle fiber (Rau et al. 1997) which has been shown to be related to the frequencies of the EMG power spectrum (Arendt-Nielsen & Mills 1985). If fast twitch units are selectively recruited in eccentric actions (Nardone et al. 1989), however, an increase in MF could be expected because muscle fiber conduction velocity is higher for fast twitch fibers (Andearssen & Arendt-Nielsen 1987). Several reports have, however, found no proof of selective activation of fast motor units in lengthening condition (Bawa & Jones 1999, Garland et al 1996, Kossev & Christova 1998, Sogaard et al 1996, Stotz & Bawa 2001). Instead, there may even be occasional silencing of the active motor units occurring immediately after the stretch (Stotz & Bawa 2001). When considering the middle part of the motion, our results are similar to others who have reported lower or equal frequencies during eccentric compared with concentric actions either in submaximal (Christensen et al. 1995, Moritani et al 1987) or in maximal (Tesch et al. 1990, Tyler et al. 1997) situations. On the other hand, possibly greater amount of synchronization during eccentric actions (Semmler et al. 2001) may increase the power in the low-frequency domains of the EMG power spectra (Yao et al 2000). This may also explain the lower median frequencies observed during eccentric compared with concentric actions.

The EMG power spectrum has been used also to evaluate changes in muscle activation at different movement velocities. The shift of the EMG power spectrum towards higher frequencies with higher movement velocities has been suggested to be due to differences in activation patterns (Muro et al. 1983, Strojnik et al. 1997). The significant increase in MF observed in the present study with the highest velocity concentric actions would give further support that some changes in the activation may have occurred. Because the skin acts as a low-pass filter (Lindström et al. 1970) it is possible that some of the highest frequencies may have been attenuated. Whether the changes in the power spectrum are due to derecruitment of slow units or recruitment of additional fast units is difficult to estimate with the present methodology.

While there was an increase in aEMG both in isometric and in dynamic situation as the force level increased no changes were observed in the MF. This was unexpected because the decreased duration of the M-wave suggests that the CV had increased along with the force level. As the force level increases in voluntary isometric action, bigger and faster motor units are recruited up to 50% - 80% MVC, after which the additional increase in force is accomplished with increased firing rate of the active units (e.g. Deluca et al. 1982, Gydikov & Kosarov 1973, 1974, Kukulka & Clamann 1981, Milner-Brown et al. 1973a and b). Therefore if recruitment is the major factor affecting the MF (Solomonow et al. 1990), an increase in MF should have been observed at least between the lowest force levels. With shorter inter-electrode distance the frequency content of the EMG signals could have been more sensitive to changes in force; if the inter-electrode distance is too long the high frequency content of the signal may be suppressed (Bilodeau et al. 1990; Moritani & Muro 1987). It has recently been suggested that because of the random motor unit locations in the muscle, the correlation between MF and CV during recruitment may be poor (Farina et al 2002). Although the mean CV may increase independently on the motor unit location, the influence on the EMG power spectrum may be small.

The EMG power spectrum has previously been shown to be rather reliable in isometric situation even for measurements repeated over separate days (Bilodeau et al. 1994, Daanen et al. 1990, Viitasalo & Komi 1975). In the first experiments (I, III) of the present study, the high correlations between two consecutive attempts and rather low coefficient of variations were observed. This was especially true in the middle part of the motion and with low movement velocities, suggested that the EMG power spectrum is reproducible in dynamic situations as well. However, when the MF was calculated by overlapping the FFT window data point by data point, rather large variations in MF were observed both in isometric and in dynamic conditions. In dynamic situations the electrode position in relation to innervation zone area may change, which can explain the changes in MF (Roy et al. 1986). In isometric situation this variation in MF is surprising because during stable isometric force the EMG signal is generally considered to be stationary. Similar phenomenon but with 50% overlapping windows has, however, been reported also previously (Pincivero et al. 2000, 2001). Whether these variations in MF reflect some true physiological phenomena or if they represent some methodological artefacts is not clear at the moment. In any case it does suggest that one should be very cautious when interpreting the behavior of MF in different conditions.

6.2.2 Maximal M-wave

Even though there was no change in MF between the force levels, the duration of the M-wave decreased as the force increased indicating increased CV. Because there were no significant differences in the latencies, it seems that the axonal conduction velocity remained the same regardless of the force level and thus the only observable changes occurred along the muscle fibers. The duration of the M-wave decreased even at the highest force levels between 80% and 100% MVC. This would be in line with previous studies showing that in voluntary situation the CV does increase up to 100% MVC (e.g. Broman et al 1985, Zwarts & Arendt-Nielsen 1988). The increased CV may be difficult to explain though by recruitment of fast motor units or by increased firing rate because during electrical stimulation all the motor units may be activated simultaneously. One explanation for the increased CV could be that the excitability of muscle membranes may be affected by the preceding action potential (Morimoto & Masuda 1984) and the activity of the Na+-K+ pump can increase due to repetitive activation of muscle fibers (Hicks & McComas 1989). Fast (phasic) motor units which may increase their firing frequency almost linearly up to 100% MVC while slow (tonic) motor units reach a saturation frequency of discharge at lower force levels of approximately 60% - 80% MVC (Gydikov & Kosarov 1973, 1974). Increased firing rate of fast motor units affecting the activity the Na+-K+ pump could thus play a role in the increased CV. The reason why the amplitude of the M-wave did not change could be related to the absolute refractory period of the action potential during which another potential cannot be elicited by electrical stimulation (Farmer et al. 1960).

At higher force levels it is more likely that more motor units are in this refractory phase than at lower force levels.

As discussed in connection with MF change, CV may also be affected by the muscle fiber length. It has been shown that the CV is higher at shorter muscle lengths (Rau et al 1997). In isometric situation, the fascicle length of the vastus lateralis muscle may shorten by 10-35% from rest to MVC depending on a joint angle (Ichinose et al. 1997). Besides some exceptions at low force levels, no consistent changes were observed in the duration of the M-wave between the action types in the present study. If the muscle fiber length is different during concentric and eccentric actions, it would seem likely that the changes in muscle fiber membrane excitability would be the major factor affecting the duration of the M-wave and thus the CV, whereas the changes in the fiber length do not seem to be so important. However, recent experiments from our laboratory indicate that whether the fascicle length in eccentric situation is greater than in the concentric situation depends on the movement velocity and on which part of the motion is chosen for the analysis. The greatest fascicle length differences in VL muscle between eccentric and concentric actions appear to be towards the end of eccentric action at the flexed position of the knee (Finni 2001). Because we chose the middle part of the motion in our experiment it is possible that the fascicle length in eccentric action may not have been much different from that of concentric one.

6.2.3 Intramuscular recordings

As the individual motor units were not analyzed in the present study but rather pools of several motor units, direct conclusions about the recruitment order of slow and fast motor units are difficult to make. Nevertheless, the present methodology offers a chance to examine the behavior of several motor unit pools and thus give more information than would be available with surface EMG. Although an increase in the amplitude of a single motor unit action potential alone does not necessarily indicate that the motor unit is of higher threshold, it appears that the mean spike amplitude can increase as faster motor units are recruited. It has been shown in numerous experiments that in isometric situation as the force increases the motor units are recruited starting from small and slow motor units followed then by the larger and faster ones (e.g. De Luca 1982, Freund et al. 1975, Milner.Brown et al. 1973). In the biceps brachii muscle the recruitment has been suggested to continue up to 80% MVC (Kukulka & Clamann 1981). The increase in the mean spike amplitude of the intramuscular EMG recordings along with an increase in isometric force up to similar 80% MVC force level in a study of Moritani & Muro (1987) as well as in the present study may therefore represent recruitment of larger and faster motor units. As a consequent, the possible amplitude differences between concentric and eccentric actions when performed at the same relative force level could then also be related to differences in motor unit recruitment. Almost identical mean amplitude values in the isometric preactivation phase before the onset of concentric and eccentric actions suggest that the method is valid and the observed differences are not due to possible position shifts of the recording electrodes. It seems highly unlikely that if the electrodes would move they would then return to their original position after the movement.

In the present study, the mean spike amplitude increased significantly up to 80% MVC in isometric preactivation phase and in the subsequent concentric action. This would support the recruitment of bigger and faster motor units even at such high force levels. In eccentric conditions, however, the increase in the mean spike amplitude leveled off after 60% suggesting fuller recruitment of motor units at lower relative force levels. However, in eccentric actions the mean spike frequency increased after 60% MVC. This was in contrast to isometric and concentric conditions in which the mean spike frequency increased only up to 40% MVC. The differences in the observed activation patterns could be partly explained by the different joint angles and thus by muscle length differences between concentric and eccentric actions. The mean firing frequency was generally higher in concentric than in eccentric actions, which is in line with some of the previous studies showing that the firing rate may be higher at shorter muscle lengths (Christova et al 1998, Moritani et al. 1987). Whether the joint angle may have affected the mean amplitude is also not clear. It has previously been suggested that the same motor units would be active during both concentric and eccentric action although the firing rate may be different (Sogaard et al. 1996, Moritani et al. 1987). In the present study, this same concept is supported by the finding that with the preactivated mode no major differences were observed in the mean spike amplitude between concentric and eccentric actions. The mean spike amplitude, however, was higher in dynamic conditions than in the preceding isometric phase. Possible explanation for this could be that the motor unit recruitment thresholds in isometric and dynamic actions are not similar. The recruitment threshold in dynamic actions has been shown to be lower than in the isometric ones (Ivanova et al 1997, Tax et al 1981) and therefore the high threshold units may get to be recruited at lower relative force level.

As already mentioned the higher mean spike amplitude in eccentric and concentric action as compared with the isometric one may mean that the recruitment threshold in dynamic conditions has decreased. An alternative explanation would be that the fast motor units have been preferentially recruited instead of the slow ones (Nardone et al. 1989). In eccentric actions without preactivation at lower force levels the mean spike amplitude in the present study was significantly higher than in corresponding concentric actions. This can thus indicate that either the recruitment threshold was even lower in eccentric action or some selective activation of fast motor units may have occurred as shown by Nardone et al (1989). The higher mean spike amplitudes in eccentric as compared with concentric actions were, however, observed only in the conditions where the movement started without isometric preactivation. In the preactivated condition no differences in the mean amplitude were observed between concentric and eccentric actions which would be in line with previous studies failing to show any preferential recruitment of fast motor units in lengthening conditions (Bawa & Jones 1999, Garland et al 1996, Kossev &

Christova 1998, Sogaard et al 1996, Stotz & Bawa 2001). On the other hand, Stotz & Bawa (2001) reported that some or all of the active motor units ceased to fire during lengthening condition depending on the velocity. With fast velocity, an immediate silencing of the background units was first observed followed then by phasic recruitment of motor units midway through the lengthening. With slower movement velocities the lengthening phase was made up of successive steps (“hesitations”), which were suggested to result from small but fast shortening contractions (Stotz & Bawa 2001).

One possible reason why the fast motor units would be recruited more easily might be related to the motoneuron pool excitability in different conditions. H-reflex response has been shown to be lower in lengthening compared with shortening conditions (Romano & Schieppati 1987, Nardone & Schieppati 1988). As suggested by Nardone & Schieppati (1988) the fast motor units may be more free to discharge during the lengthening conditions as the slow motor units are subjected to the largest presynaptic inhibition (Zengel et al. 1983) and the H-reflex mainly tests the excitability of the slow motor units (Buchtal & Schmalbruch 1970). As the H-reflex has been shown to increase with increasing isometric force levels (Mynark & Koceja 1997) the preactivation level before the movement may thus also affect the recruitment pattern. Due to increased gamma-motoneuron activity in isometric preactivation phase, the H-reflex response may be larger with higher force levels and the slow motor units would receive less presynaptic inhibition than with zero preactivation. Consequently no selective activation of fast motor units would take place. Because the activation of fast motor units may cause derecruitment of slow motor units it may be methodologically difficult to differentiate if the fast motor unit had really been recruited before the slow one or do they simply appear earlier due to larger axonal (Henneman et al 1965a and b) and muscle fiber (Andearsen & Arendt-Nielsen 1987) conduction velocity. Furthermore, the derecruitment of the slow motor units could be explained by the larger motor units contributing more excitation to Renshaw cells than the small ones (Cullheim & Kellerth 1978, Hultborn et al 1988a). The recurrent inhibition may primarily activate the smaller units (Friedman et al. 1981, Hultborn et al. 1988b).

6.3 Effects of fatigue

6.3.1 The effect of type of exercise

The results reported in the literature regarding eccentric and concentric fatigue are quite controversial. In some studies, the fatigue response is equal or even greater after eccentric compared with concentric exercise (Komi & Rusko 1974, Komi & Viitasalo 1977), whereas in other studies the decrease in force was more substantial after concentric than after eccentric exercise (Hortobagyi et al. 1996, Tesch et al. 1990). The studies in which the eccentric action is started with maximal isometric preactivation appear to result in a considerable fatigue effect. The present study showed that when the eccentric action was started either from 50% or 0% preactivation, the maximal and average eccentric force remained lower compared with when maximal preactivation was used (figs 20 and 21). Therefore, if in the fatigue protocol the eccentric mode is started with zero preactivation (e.g Hortobagyi et al. 1996, Tesch et al. 1990) it is natural to expect that the overall eccentric loading is less than the full preactivated mode (Komi & Rusko 1974, Komi & Viitasalo 1977). In the latter case, the mechanical loading (duration) in the eccentric is much higher and the fatigue response is usually of greater magnitude than after concentric exercise. Equal metabolic loading between eccentric and concentric exercise in these conditions are in line with this observation as indicated by almost similar glycogen depletion (Komi & Viitasalo 1977), oxygen consumption (Komi & Rusko 1974) and blood lactate values (Komi & Viitasalo 1977). In contrast, the same phenomenon regarding force levels between zero and maximal preactivation modes occurs also in concentric actions (fig 24), yet the fatigue response after concentric exercise using zero preactivation mode is generally quite dramatic (e.g Hortobagyi et al. 1996, Tesch et al. 1990). In concentric actions, the difference in the absolute force levels between zero and full preactivation mode is most likely not as great as in corresponding eccentric conditions. This may at least partly explain why the subjects are able to fatigue themselves better with concentric as compared to eccentric action with zero preactivation mode.

The level of muscular activity (EMG) may also play a role in the fatigue response. Although maximal preactivation was used, Pasquet et al. (2000) found a greater force decrease after concentric than after eccentric exercise. It seems that in their study the aEMG was lower in eccentric actions than in concentric, whereas in the present study no differences in aEMG was observed between the two action types. This would suggest that the subjects were capable fully activating their muscles also in the eccentric mode. aEMG decreased slightly in both exercises but the changes were not dramatic. These rather small changes in aEMG are in line with previous studies (Day et al. 1998, Komi & Rusko 1974, Komi & Viitasalo 1977, Tesch et al. 1990) suggesting that fatigue may be more of peripheral origin. Coactivation of the antagonist muscle should not be responsible for the force reduction either because the aEMG of triceps brachii muscle decreased during the exercises. The specificity of the fatigue was seen in the eccentric/concentric force relationship which decreased after eccentric exercise and increased after concentric exercise. This agrees with the study of Komi & Buskirk (1972), which showed that for a long-term adaptation it is beneficial to exercise “eccentrically” to improve eccentric force and “concentrically” to improve concentric force. The effect of eccentric actions was more substantial in a sense that concentric force decreased more after EE than eccentric force after concentric.

6.3.2 The effect of movement velocity

The neuromuscular fatigue effects in two leg extensor exercises performed with different movement velocities were examined in Exp. 3 (III). Based on glycogen depletion of different type muscle fibers it seems that during lower exercise intensities type I fibers would be preferentially recruited, whereas during heavier submaximal exercise both type I and type II fibers seem to be equally depleted from glycogen (Andersen & Sjogaard 1976, Vollestad & al 1984). In contrast, an exhaustive one minute bicycling (Tabata & al. 1985) as well as pedalling with higher frequency (Ahlquist & al. 1992) resulted in greater type II depletion. How closely the glycogen depletion actually reflects the motor unit activity is not entirely clear. However, based on electromyographical studies, it has been suggested that fast motor units may be selectively activated with higher movement velocities (Citterio & Agostoni 1984, Muro et al. 1983, Strojnik et al. 1997). It was expected that if this selective activation should take place in the explosive concentric exercise it would be seen in the fatigue response. The present data showed, however, that the signs of fatigue in the two concentric exercise modes were much smaller than could be expected based on another study between heavy resistance and explosive leg extension exercise with the same number of sets and repetitions (Linnamo et al. 1998). During explosive exercise there was hardly any change or in some occasions a small increase in the force parameters, and even during heavy resistance exercise the decreases were not substantial. Although in the heavy resistance exercise the same protocol (5 x 10RM) was used as previously (Linnamo et al. 1998), a smaller range of motion and consequently shorter duration of action time and a lack of eccentric work could partly explain why the changes after the exercise were so small. Another thing of importance is that in the present study a constant resistance machine was used, which has been shown to lead to a less dramatic fatigue response compared with variable resistance machines (Häkkinen et al. 1987).

6.3.3 EMG power spectrum and metabolic changes

As with simple force measurements, the literature shows that the results regarding EMG power spectrum in eccentric and concentric fatigue are also controversial. There are studies that have found a decrease in force and MPF only during concentric exercise (Tesch et al. 1990) or when measured in isometric situation, a decrease in force but no change in MPF after eccentric exercise (Day et al. 1998) or after both eccentric and concentric exercise (Komi & Viitasalo 1977). In the present study, MF decreased during both exercises but the decrease was somewhat greater during concentric exercise. A decrease of MF during fatigue has been attributed to decreased conduction velocity of the active muscle fibers (e.g. Arendt-Nieslen & Mills 1985, Lindström et al. 1970). Decreased muscle fiber conduction velocity has been suggested to be related to proton (H+) accumulation (Lindström et al. 1970, Mortimer et al 1970). Generally, MF may decrease more if the blood lactate concentration is high (Karlsson et al. 1981, Tesch 1980). However, changes in MF have been observed also in the absence of blood lactate and impairment of the excitation-contraction coupling has been suggested to be responsible for the changes in MF (Vestgaard-Poulsen et al. 1995). In the present study, heavy resistance exercise caused a decrease in MF and MPF, wheras during explosive exercise the change was in the opposite direction. A negative correlation with the change in MPF and blood lactate was found in the present study during heavy resistance exercise, although blood lactate concentration was extremely low compared with previous studies of heavy resistance protocols (e.g. Häkkinen 1994, Kraemer et al. 1987, Linnamo et al. 1998, Tesch et al. 1989). Another candidate to affect MF could be synchronization of motor units which may occur during fatigue and cause a shift of the MF towards lower frequencies (Bigland-Ritchie et al. 1981).

The recovery of performance was faster after CE than after EE. This is in complete agreement with the study of Komi & Viitasalo (1977). Delayed muscle soreness and elevated serum CK values after EE indicate that muscle damage may have occurred. The subjects reported feeling of the greatest soreness 2-3 days after EE, in accordance to other studies (e.g. Brown et al. 1997, Newham et al. 1987). Serum CK values showed rather large inter-subject variability, which has been reported also before (e.g. Nosaka & Karlsson 1996). The highest serum CK values in the present study were observed seven days after the exercise. According to Clarkson (1997), the CK increase peaks 4-5 days after the exercise. Therefore it is possible that in the present study CK, although still elevated, was already on its recovery phase. Although the changes in force and MF are not necessarily in phase with the increase in CK (Felici et al. 1997), the differences might have been more clear, if the follow-up measurements would have been done also between days 2 and 7. The recovery rate may be different depending on a measured variable (Horita et al. 1999). Increased stiffness can remain elevated four days after eccentric exercise while the arm swelling may last as long as nine days (Howell et al. 1993). In any case, seven days after EE MF was again decreased which is in line with studies of Felici et al. (1997) and Day et al. (1998) who also observed a decrease in MF and MPF during recovery. Because the fast twitch fibers can be selectively damaged after eccentric work (Lieber & Friden 1988), the possible damage may have affected the muscle fiber conduction velocity and the activation of the fast motor units as well.

6.4 Subject background

The subjects chosen for the present study were physically active physical education students and basketball players. They were familiar with maximal weight exercises but did not represent any specific (e.g. power vs. endurance) athletic background. They were also fit and possessed relatively low body fat percentage, which can be of importance when EMG power spectrum is used. Skin acts as a low pass filter and therefore with high amounts of apidose tissue the high frequencies of the signal may be filtered (e.g Lindström et al. 1970). MF behavior may be related also to the fiber type composition being higher with the subjects possessing higher relative value of fast twitch fibers (Geerdle et al. 1988, Moritani et al 1985b). In particular during fatigue studies, the subject background may be of importance as the fast/slow fiber composition of the exercised muscle (Holten et al. 1975, Thorstensson & Karlsson 1976, Viitasalo & Komi 1978) as well as the athletic background (Häkkinen & Myllylä 1990) can affect the fatigue response. Because the fiber type composition was analyzed only in Exp.3, it is not clear how much the results would have changed had the subject groups been different.

7 PRIMARY FINDINGS AND CONCLUSIONS

The main findings and conclusions of the present study can be summarized as follows

1) This study showed clearly that regardless of movement velocity or joint angle, maximal eccentric force measured after the onset of movement is higher than the preceding isometric preactivation force. This same phenomenon, which has previously been demonstrated with isolated muscle fibers, is thus valid for whole muscle groups in human subjects. As in isolated muscle preparations, the initial increase in force appears to be velocity dependent being higher with higher stretching velocities. If the eccentric movement is not preceded by maximal preactivation, it can be difficult to even reach the true maximal force, in particular with high movement velocities.

2) Due to possible inhibition or fear of performing maximal eccentric actions, maximal EMG activity may decrease towards the end of the eccentric action and therefore be lower than the corresponding EMG activity in maximal concentric action. As a result of this decreased muscle activity, the eccentric force measured in the middle part of the movement may sometimes be lower than separately measured maximal isometric force at the corresponding joint angle. It seems that maintaining the maximal eccentric force is more difficult with knee extensors than with elbow flexors.

3) The behavior of the median frequency during eccentric and concentric actions does not support the concept that fast motor units are selectively recruited in eccentric actions. Increased median frequency (MF) along with increased movement velocity during concentric actions could indicate increased activation of fast motor units. An analysis technique where Fast Fourier Transformation (FFT) windows were moved data point

by data point revealed, however, that even in stable isometric condition there can be remarkable variations in the median frequency depending on the placement of the FFT window. This suggest that the results regarding MF should be interpreted with caution.

4) The activation patterns when the force level is increased appears to be different between isometric, concentric and eccentric actions. Based on the increased mean spike amplitude the recruitment of fast motor units may continue to higher force levels in isometric and concentric actions. In contrast, eccentric actions may rely more on the increased firing rate of the active units to achieve the highest forces. The concept of selective recruitment of fast motor units in eccentric versus concentric actions was not supported when the dynamic actions were started with preactivation. At lower force levels, however, when the eccentric and concentric actions were initiated without preactivation the mean spike amplitude was higher in eccentric than in concentric actions. This could indicate selective activation of fast motor units.

5) The immediate fatigue response of eccentric and concentric exercises were rather similar. This was achieved in the protocol in which the movement always started with maximal isometric preactivation and when aEMG levels were the same in the two conditions. On an absolute scale, the force decrease after eccentric exercise may be even greater than after concentric exercise. Eccentric fatigue led to muscle soreness possibly associated with muscle damage, resulting in a longer recovery compared with concentric fatigue. Lower MF during recovery after eccentric exercise may be related to selectively damaged fast twitch muscle fibers.

YHTEENVETO

Motoristen yksiköiden aktivointi ja lihasten voimantuotto eksentrisessä, konsentrisessa ja isometrisessä lihastyössä

Lihaksen tuottamaa voimaa säädellään rekrytoimalla uusia motorisia yksiköitä ja/tai muuttamalla jo aktiivisten yksiköiden syttymistiheyttä. Motorisia yksiköitä jaotellaan koon ja voimantuotto-ominaisuuksien mukaan siten, että pienemmät motoriset yksiköt ovat hitaampia, tuottavat vähemmän voimaa ja kestävät paremmin väsymystä kuin isommat ja nopeammat motoriset yksiköt. Useimmissa tapauksissa näyttää siltä, että tuotettaessa voimaa motoristen yksiköiden rekrytoiminen tapahtuu kokojärjestyksessä pienimmistä isompiin. Poikkeuksena tästä saattaa kuitenkin olla eksentrinen lihastyö sekä nopeat liikkeet, joissa on esitetty nopeiden motoristen yksiköiden aktivoituvan ennen hitaita. Rekrytointijärjestystä ja muutoksia syttymistiheydessä voidaan tutkia selektiivisten lanka- tai neulaelektrodien avulla. Myös pinta-EMG:tä on käytetty arvioimaan motoristen yksiköiden aktivoitumismalleja. EMG teho-tiheys spektrin taajuuskomponentti, esim median frequency (MF), on tutkimusten mukaan yhteydessä keskimääräiseen johtumisnopeuteen solukalvolla. Koska nopeilla motorisilla yksiköillä on korkeampi solukalvon johtumisnopeus kuin hitailla, saattaa teho-tiheys spektrin taajuutta kuvaava MF siirtyä korkeammille taajuuksille rekrytoitaessa lisää nopeita motorisia yksiköitä. Tutkimustulokset liittyen MF:n muutoksiin lisääntyneen voimatason myötä ovat kuitenkin ristiriitaisia.

Tuotettu lihasvoima on suurempaa eksentrisessä lihastyössä kuin konsentrisessa, jossa voima laskee liikenopeuden kasvaessa. Useissa tutkimuksissa eksentrinen voima ylittää myös vastaavalla nivelkulmalla erikseen mitatun isometrisen voiman, vaikka päinvastaisiakin tuloksia on raportoitu. Eristetyillä lihassoluilla tehdyt tutkimukset kuitenkin osoittavat, että kun lihassolua stimuloidaan sähköisesti isometrisessä tilanteessa ja sitten äkillisesti venytetään, nousee eksentrinen voima välittömästi venytyksen jälkeen isometrisen esiaktiivisuustason yläpuolelle. Koska myös luonnollisessa liikkumisessa eksentristä vaihetta edeltää esiaktiivisuus, on tätä aktivointimallia käytetty tässä väitöskirjassa tutkittaessa erilaisia liike-suorituksia. Esiaktivoinnilla ennen varsinaista liikettä saattaa olla vaikutusta myös vaihteleviin tutkimustuloksiin, joita on raportoitu verrattaessa eksentristä ja konsentrista väsymystä keskenään.

Tämän väitöskirjaprojektin päätarkoituksina oli 1) tutkia missä määrin mittaustilanteen metodologiset eroavaisuudet vaikuttavat käsivarren koukistaja- ja polven ojentajalihasten tuottamaan maksimivoimaan ja maksimaaliseen lihasaktiivisuuteen eksentrisessä, konsentrisessa ja isometrisessä lihastyössä, 2) tutkia motoristen yksiköiden aktivoitumismalleja erilaisissa lihastyötavoissa ja eri liikenopeuksilla tarkastelemalla EMG teho-tiheys spektrin taajuuskomponentin (MF) käyttäytymistä eksentrisessä, konsentrisessa ja isometrisessä lihastyössä, 3) tutkia väsymyksen vaikutuksia voimantuottoon, aEMG:hen ja MF:ään eksentrisessä ja konsentrisessa lihastyössä. Koska pinta-EMG:llä saadut tulokset EMG teho-tiheysspektrin taajuuskomponentin käytöstä motoristen yksiköiden rekrytoinnin mittaamisessa näyttävät ristiriitaisilta, tarkoituksena oli selvittää liittyykö siihenkin metodologisia ongelmia. Yksityiskohtaisemman tiedon saamiseksi käytettiin myös selektiivisempiä lihaksen sisään laitettavia lankaelektrodeita. Vapaaehtoisina koehenkilöinä mittauksissa toimi miespuolisia (20-30v) opiskelijoita/koripalloilijoita. Voimamittaukset tehtiin Neuromuscular Research Centerissä, liikuntabiologian laitoksella rakennetulla voimadynamometrillä.

Tulokset osoittavat, että samoin kuin eristetyssä tilanteessa yksittäisellä lihassolulla, myös ihmisellä kokonaisilla lihasryhmillä eksentrinen voima on korkeampi kuin isometrinen esiaktiivisuusvoima, mikäli voima mitataan lähes välittömästi liikkeen alkamisen jälkeen. Tämä näyttää pitävän paikkansa riippumatta liikenopeudesta ja lähtökulmasta. Sen sijaan keskivaiheilla liikettä maksimaalinen eksentrinen voima voi olla alhaisempi kuin erikseen samalla nivelkulmalla mitattu maksimaalinen isometrinen voima, mahdollisesti johtuen vaikeudesta ylläpitää maksimaalista eksentristä voimaa yllä koko liikkeen ajan. Väsymyksen osalta havaittiin, että mikäli liikettä edeltää maksimaalinen isometrinen esiaktiivisuusvaihe ja eksentrisen ja konsentrisen liikesuorituksen välillä ei ole eroa lihasaktiivisuudessa, on voiman suhteellinen lasku samankaltaista sekä eksentrisen että konsentrisen harjoituksen jälkeen.

Alempi MF maksimaalisessa eksentrisessä verrattuna konsentriseen ei viittaa nopeiden motoristen yksiköiden selektiiviseen aktivoitumiseen eksentrisen liikkeen aikana. Alhaisemmilla voimatasoilla tämä saattaa kuitenkin olla mahdollista, jota tukisi myös lankaelektrodeilla mitatut korkeammat keskimääräiset amplitudit eksentrisen vaiheen alussa verrattuna konsentriseen ja isometriseen, kun liike alkaa ilman esiaktiivisuutta. Dynaamisessa lihastyössä motorisilla yksiköillä saattaa olla alhaisempi syttymiskynnys kuin isometrisessä. Uusien motoristen yksiköitten rekrytoituminen näyttää jatkuvan korkeammille voimatasoille konsentrisessa ja isometrisessä lihastyössä verrattuna eksentriseen, jossa voiman nousu korkeilla voimatasoilla tapahtunee enemmänkin syttymistiheyttä kasvattamalla. MF:n nousu liikenopeuden myötä konsentrisessa suorituksessa voisi viitata nopeiden motoristen yksiköiden lisääntyneeseen aktivoitumiseen. EMG teho-tiheys spektrin tarkempi analysointi osoitti kuitenkin, että MF saattaa vaihdella merkittävästi riippuen valitusta Fast Fourier Transformation (FFT) analysointi-ikkunan paikasta. Koska vaihtelua tapahtui myös tasaisen isometrisen voiman aikana, kyseenalaistaa se teho-tiheys spektrin käyttöä, tai ainakin antaa aihetta varovaisuuteen tulosten tulkinnassa. Motoristen yksiköiden aktivoitumismallien tarkemmaksi selvittämiseksi tulisi jatkossa pystyä kehittämään lankaelektrodeita vielä selektiivisemmiksi, jotta voitaisiin eristää ja tunnistaa yksittäisiä motorisia yksiköitä luotettavasti liikkeen aikana ja myös korkeimmilla voimatasoilla.

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