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Inhomogeneous activation of skeletal muscles

Investigated by multi-channel surface electromyography

Thesis for the degree philosophiae doctor

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Norwegian University of Science and Technology
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Inhomogen aktivering av skjelettmuskler studert med multi-kanals overflate elektromyografi

Bakgrunn
Anatomisk komplekse muskler er foreslått å være aktivert, kontrollert og inneha en fordeling av fysiologiske karakteristikker ulik fra muskler med enklere arkitektur. Siden anatomisk komplekse muskler (for eksempel trapezius) er av betydelig fysiologisk og klinisk interesse var hovedmålet med avhandlingen å undersøke aktivering, kontroll og fordeling av fysiologiske karakteristikker i anatomisk komplekse muskler med en fler-kanals overflate elektromyografi (MCsEMG) teknikk.

Metode
MCsEMG målinger fra biceps brachii og øvre trapezius ble gjort under isometriske kontraksjoner med langsomme endringer i kraft og vedvarende lave kraft nivåer. Den brukte MCsEMG teknikken bestod av 13 x 10 elektroder som dekte 6 x 4.5 cm av hudens overflate over muskelen. Endringer i fordeling av aktivitet over musklene med endret kraft og tretthet ble kvantifisert for å få representativ informasjon angående aktiveringssekvensen til grupper av motoriske enheter. Gjentakende skifter i relativ aktivitet mellom det lange og korte hodet til biceps brachii ble undersøkt under en vedvarende kontraksjon inntil utmattelse. En nylig utviklet metode basert på endringer av MCsEMG signalene ved synkronisering av motoriske enheter ble brukt til å undersøke fordelingen av felles synaptisk tilførsel til motoneuronene til biceps brachii. Informasjon angående karakteristikker til muskelfibrene (ledningshastighet og orientering) ble estimert basert på propagering av aksjonspotensialer langs muskelfibrene registrert med MCsEMG teknikken.

Hovedfunn
Endringene i fordeling av aktivitet over biceps brachii var konsistent innad og mellom individer ved kraftregulering. Kvantifisering av endringer i fordeling av aktivitet gir dermed informasjon angående aktiveringssekvensen av grupper av motoriske enheter. Endringene i fordeling av aktivitet over øvre trapezius var lik ved regulering av kraft og tretthet. Dette indikerer en velordnet aktiveringssekvens av grupper av motoriske enheter i øvre trapezius under vedvarende kontraksjoner. Den observerte skiftende relative aktiviteten mellom det lange og korte hodet til biceps brachii under vedvarende kontraksjoner indikerer en delvis selektiv kontroll av hodene. Skiftene i relativ aktivitet mellom hodene til biceps brachii var ikke positivt relatert til evnen å motstå tretthet under den vedvarende kontraksjonen. Graden av synkronisering mellom motoriske enheter var forskjellig mellom hodene til biceps brachii. Dette funnet indikerer en ujevn fordelig av felles synaptisk tilførsel til motoneuronene som innerverer biceps brachii. I samsvar med studier av menneskelige kadavre var muskelfiber karakteristikkene avhengig av hvor registreringen ble gjort over øvre trapezius. Disse funnene indikerer at muskel aktivering, kontroll og fysiologiske karakteristikker er romlig avhengig innen anatomisk komplekse muskler.

Preface

This thesis was carried out at the Human Movement Science Programme, Faculty of Social Sciences and Technology Management, Norwegian University of Science and Technology. The thesis is a result of research conducted in collaboration with fellow researchers, Stefan J. Karlsson and Christer Grönlund from the Department of Biomedical Engineering and Informatics, University Hospital, Umeå, Sweden.

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List of papers

This thesis is based on the following papers, referred by their Roman numerals in the text.

Paper I Holtermann A, Roeleveld K, and Karlsson JS (2005) Inhomogeneities in muscle activation reveal motor unit recruitment. *Journal of Electromyography and Kinesiology,* 15: 131-137.

Paper II Holtermann A, and Roeleveld K (2006) EMG amplitude distribution changes over the upper trapezius muscle are similar in sustained and ramp contractions. *Acta Physiologica,* 186: 159-168.

Paper III Holtermann A, Grönlund C, Karlsson JS, and Roeleveld K (2007) Differential activation of regions within the biceps brachii muscle during fatigue. *Acta Physiologica, In Press.*

Paper IV Holtermann A, Grönlund C, Karlsson JS, and Roeleveld K (2007) Motor unit synchronization during fatigue: Described with a novel sEMG method based on large motor unit samples. *Journal of Electromyography and Kinesiology, In Press.*

Paper V Holtermann A, Grönlund C, Karlsson JS, and Roeleveld K (2007) Spatial distribution of active muscle fibre characteristics in the upper trapezius muscle and its dependency on contraction level and duration. *Journal of Electromyography and Kinesiology, In Press.*

Abstract

Background

The current understanding of neuromuscular control is based on the related characteristics of the motoneuron (size) and its belonging muscle fibers resulting in a stereotyped activation of all motor units within a muscle. This “size principle” was originally founded on the anatomical and histochemical non-complex soleus muscle of decerebrated cats. However, deviations from this stereotyped control are observed during voluntary contractions in anatomical complex muscles. The main objective of this thesis was to investigate intra-muscular spatial dependency of activation, control and physiological characteristics of the anatomical complex biceps brachii and trapezius muscle with a multi-channel surface electromyographical (MCsEMG) technique.

Methods

MCsEMG recordings from the biceps brachii and the trapezius muscle were performed during isometric slow force modulation and sustained sub-maximal contractions. The applied MCsEMG grid consists of 13 by 10 surface electrodes covering 6 x 4.5 cm of the skin surface. To obtain information about recruitment of motor unit populations from a large fraction of the muscles, changes in spatial distribution of activity with force modulation and fatigue were quantified by correlating the root-mean-square amplitude from all electrodes at different time-epochs within and between contraction types. Frequency and duration of repeated shifts in activity between intra-muscular regions (differential activation) were investigated by calculating the average activity level from (electrodes situated above) the two heads of the biceps brachii, respectively, throughout a sustained sub-maximal contraction until exhaustion. To examine the distribution of common synaptic input to motoneurons innervating the biceps brachii with fatigue, a descriptor for motor unit synchronization was quantified based on changes in the monopolar MCsEMG signals during a sustained contraction. To attain *in vivo* information about intra-muscular distribution of physiological characteristics, the muscle fiber conduction velocity and fiber orientation were estimated based on detection of propagating motor unit action potentials from large fractions of the biceps brachii and the upper trapezius muscle with the MCsEMG technique.

Main findings and conclusions

The biceps brachii and the trapezius muscle were inhomogeneously activated during force regulation and fatigue due to recruitment of differently located motor units within the muscles. The changes in spatial distribution of biceps brachii activity with force gradation were consistent within and between subjects, indicating that changes in spatial distribution of intra-muscular activity are suited to attain information about recruitment of motor unit populations. The changes in spatial distribution of upper trapezius activity were similar during sustained and ramp contractions, indicating an orderly recruitment sequence of motor unit populations during sustained contractions. The regions (long and short head) of the biceps brachii were differentially activated during a sustained contraction, indicating a partially selective control of intra-muscular regions. However, this region-dependent activation of the biceps brachii muscle was not associated with time to exhaustion at a contraction level of 25 % of maximal voluntary contraction. The motor unit synchronization descriptor was different between regions within the biceps brachii muscle with fatigue, indicating an uneven distribution of common synaptic input to the motoneurons of the muscle. Consistent with studies of human cadavers, the muscle fiber characteristics were dependent on the intra-muscular regions of the upper trapezius muscle. The findings from this thesis support an intra-muscular spatial dependency of the activation, control and physiological characteristics of the biceps brachii and the trapezius muscle.

Introduction

Based on observations of foremost the anatomical non-complex and histochemical homogeneous soleus muscle of decerebrate cats in the 1960's, Henneman and colleagues proposed a fundamental principle of the organization and control of the neuromuscular system based on the "size" of the motoneuron in the spinal cord. The core of the principle was that the load of controlling muscle actions upon the central nervous system is relieved by a co-variation of the characteristics of the muscle fibers and the motoneurons innervating them. By this organization, the properties (size) of the motoneurons determine which muscle fibers to be activated and to what extent, based on the degree of input to all motoneurons innervating a muscle. Since these classical publications of Henneman (Henneman et al. 1965b; Henneman et al. 1965a; Henneman 1965), the size principle has been a fundament for the understanding of the activation, control and organization of the neuromuscular system.

Mechanisms and deviations from the size principle have been extensively examined during different types of voluntary contractions in humans (Denier van der Gon et al. 1985; Desmedt and Godaux 1977; Nardone et al. 1989; Ter Haar Romeny et al. 1984; Thomas et al. 1978). In constrained tasks, the control has been reported to be in accordance with the size principle (Desmedt and Godaux 1977; Grimby and Hannerz 1977; Milner-Brown et al. 1973). However, deviations from the principle have been observed in eccentric contractions (Nardone et al. 1989) and during isometric force generation in different directions (Desmedt and Godaux 1981; Ter Haar Romeny et al. 1984; van Zuylen et al. 1988). Deviations from the size principle are typically observed in anatomically complex and often histochemical uneven muscles like the trapezius and biceps brachii muscle (Ter Haar Romeny et al. 1984; Westad et al. 2003).

Electromyography (EMG) is commonly applied to attain information about the activity, control and state of skeletal muscles. The EMG technique measures the electrical activity originating from the muscle fibers when activated. The most commonly used EMG technique in clinical neurophysiology and research of the neuromuscular system is invasive EMG, providing temporal information from relatively few motor units. In this thesis, a multi-channel surface EMG (MCsEMG) technique was applied. In contrast to invasive EMG, this technique enables spatiotemporal insight into

the activity, control and physiological characteristics of large motor unit populations within a muscle.

The introduction of this thesis is divided into four sections constituting the organization of the neuromuscular system, neuromuscular force regulation, control of anatomical complex muscles, and investigation of the neuromuscular system based on EMG. In this thesis, the term *neuromuscular system* is considered as the motoneurons in the spinal cord, their axons, constituting muscle fibers and muscle afferents. The term *organization of the neuromuscular system* implies how the structures of the neuromuscular system are coupled, interrelated and topographically distributed in the spinal cord and within a skeletal muscle. The term *physiological characteristic* is regarded to involve physiological properties (e.g. muscle fiber type and cross-sectional area) and topographical distribution (e.g. muscle fiber orientation) of the structures of the neuromuscular system.

Organization of the neuromuscular system

The architectural, histochemical and functional variety of skeletal muscles is astonishing (Peters 1989). Some muscles are composed of uniarticular and unipinnate fibers having a single action upon the skeleton (e.g. the soleus muscle). Other muscles comprise widely distributed and multi-pinnate fiber orientations (e.g. the trapezius muscle) or anatomically separate “heads” often oriented in parallel (e.g. the biceps brachii muscle). Activation of different intra-muscular parts of muscles with multi-pinnate fibers (e.g. the trapezius muscle) generates different actions upon the skeleton (Johnson et al. 1994; Johnson and Pandyan 2005). In contrast, activation of different parallel-oriented intra-muscular heads (i.e. the short and long head of the biceps brachii) is considered to impose only minor dissimilar actions upon the skeleton (Ettema et al. 1998), and can therefore generate a similar mechanical output with different relative activity-levels between the heads of the muscle.

In this thesis, muscles composed of uniarticular and unipinnate fibers are defined as *anatomical non-complex muscles*. Muscles comprising fibers with broad multi-pinnate orientations or separate anatomical heads are termed *anatomical complex muscles*. Intra-muscular parts are termed *muscle regions*, designating parts of a single muscle on basis of anatomical orientation (e.g. long and short head of biceps brachii).

The smallest functional entity of a muscle, activated by the nervous system is the motor unit. The motor unit comprises a motoneuron, its axon and the muscle fibers innervated by the axon. Despite of considerable overlap, motoneurons innervating a single muscle are located in a restricted region of the longitudinal column in the rostrocaudal axis of the spinal cord (Romanes 1951; Vanderhorst and Holstege 1997), termed a *motoneuron pool*. The morphological and electrophysiological properties of individual motoneurons constituting a motoneuron pool vary over a wide range. The property that has received most publication is the motoneuron size (i.e. surface area of the soma and dendrites). The size is closely associated with other electrophysiological properties of the motoneuron (e.g. input resistance, rheobase, axonal conduction velocity) determining its susceptibility to discharge (Binder et al. 1996). Thus, the net excitatory input needed to depolarize a motoneuron is positively related to the motoneuron size (Henneman et al. 1965b). The motoneuron is connected to several muscle fibers by a motor axon. The area of the muscle fiber connected to a single motor axon is called the *innervation zone*. It is oriented approximately halfway between the tendons of a muscle with some muscular and inter-individual variations (Masuda and Sadoyama 1991).

All muscle fibers innervated by a single motoneuron, *termed muscle unit* are histochemically similar and limited to one anatomical muscle (Burke et al. 1973). In accordance with the varying properties of the motoneurons within a pool, the muscle fibers comprising skeletal muscles vary considerably in biochemical, morphological and mechanical properties (Burke et al. 1971). As a result, muscle fibers within a muscle compose different functional characteristics like contraction speed, force-generating capacity and resistance to fatigue (Kernell 1983). An important aspect of the organization of the neuromuscular system is the interdependent properties of the motoneuron and their muscle units (Burke 1981). By this means, the net synaptic input needed to depolarize a motoneuron is matched with the contraction speed, force generating capacity and fatigue resistance of their muscle unit. Therefore, the largest motoneurons with highest discharge threshold innervate fast-twitch muscle fibers with large cross-sectional area and high susceptibility to fatigue, termed fast-fatigable or type IIb fibers. The smallest and most excitable motoneurons consist of thin and slow-twitch fatigue resistant fibers, termed slow or type I fibers. Moreover, the motoneurons of

intermediate size and threshold for discharge supply fibers with intermediate properties termed fatigue-resistant or type IIa fibers (Burke 1981).

Prolonged stimulation of a single motoneuron or motor axon in cats depleting the glycogen content of its muscle fibers has shown that the muscle fibers belonging to a single motoneuron are limited to a fraction of the muscle (Bodine-Fowler et al. 1990), termed *motor unit territory*. Consistent findings are reported from human muscles by electrophysiological analyses (Buchthal et al. 1959; Stälberg and Antoni 1980). However, a region of a muscle is not only occupied by fibers from a single motor unit, but shared by fibers of different motor units (motor unit overlap) (Burke and Tsairis 1973). In summation, it is well-known how the muscle fiber diversity is organized by means of the motor units. Contrary, how the motor unit diversity within the spinal cord and single muscles are organized has been a debated topic for several decades (Burke 2002; Cohen 1953; Enoka and Fuglevand 2001; Kernell 1989; Swett and Eldred 1959).

Motoneurons with different properties are traditionally considered to be randomly intermingled throughout a motoneuron pool (Burke et al. 1977; Clamann and Kukulka 1977). However in anatomical complex muscles, motoneurons are shown to be aggregated in distinct rostrocaudal regions connected to individual primary axonal branches (Weeks and English 1985; Weeks and English 1987). The primary branch of an axon innervates selected non-overlapping regions within a muscle, defined as a *neuromuscular compartment* (English and Letbetter 1982). For instance, the location of motoneurons innervating the medial gastrocnemius is always situated more caudally in the spinal cord than motoneurons innervating the lateral gastrocnemius (Luscher et al. 1980). Therefore, motoneurons within a pool of anatomical complex muscles are observed to be topographically related to the muscle fibers within the muscle (Burke and Tsairis 1973; Donselaar et al. 1985; Swett et al. 1970; Swett and Eldred 1959).

Accordingly, systematic variation in distribution of different fiber types are well documented in anatomical complex muscles of animals (De Ruiter et al. 1995; English and Letbetter 1982; Wang and Kernell 2000), termed *muscle fiber regionalization* (Kernell 1998). For example, type I fibers tend to predominate deep regions within single muscles, while the more superficial regions tend to contain a greater portion of type II fibers (Johnson et al. 1973; Kernell 1998; Travnik et al. 1995). Due to the close relation between muscle fiber and motoneuron properties, low-threshold motor units are

observed to predominate regions with most type I fibers (Clamann 1970; English and Letbetter 1982; Knight and Kamen 2005).

Single human anatomical complex muscles (i.e. the biceps brachii) have been observed to consist of separate neuromuscular compartments (Segal 1992). Similarly, the descending region of the trapezius muscle is innervated by a single branch of the accessory nerve, whereas the middle and low regions are innervated by both the accessory nerve and branches of the cervical plexus (Kierner et al. 2001). Moreover, *in vitro* investigations of the trapezius muscle have revealed an uneven distribution of fiber types, and cross-sectional fiber area of the fiber types among different regions of the muscle (Lindman et al. 1991; Lindman et al. 1990).

Neuromuscular force regulation

Muscle force is regulated by a combination of varying the number of active motor units (recruitment) and their rate of discharge (Adrian and Bronk 1929). The concept of motor unit recruitment was first introduced by Sherrington (Liddell and Sherrington 1925). A few years later, Sherrington's student Denny-Brown (1929) demonstrated that small and weak motor units were always recruited before larger and more powerful motor units in contractions with gradual force increase. Nevertheless, the current understanding of the determinants for recruitment of motor units is based on the classical work of Henneman and colleagues (Henneman et al. 1965a). They declared that the susceptibility of a motoneuron to discharge was grounded on the physical size of the motoneuron or closely related intrinsic properties (Henneman et al. 1965a). Originally, Henneman and colleagues observed that a net excitatory input to a motoneuron pool led to recruitment of motor units in order of increasing action potential amplitude of small ventral root filaments, from which they extrapolated motoneuron size (Henneman et al. 1965b). Based on this observation, they proposed that the recruitment sequence of motoneurons occurred in an orderly manner in accordance to their size (Henneman et al. 1965a), later termed *Henneman's size principle*. Due to the close relation between the electrophysiological properties of the motoneurons and the mechanical and histochemical properties of the muscle fibers, the smallest, slowest, weakest, and most fatigue resistant motor units are always activated prior to larger,

faster, stronger, and fatigable motor units with increasing net excitatory input to all motoneurons in a pool (Fleshman et al. 1981; Stephens and Usherwood 1977).

A functional advantage of the stereotyped orderly recruitment is that neuromuscular output is controlled by the intensity of input to all motoneurons within a pool in which the different electrophysiological properties of the motoneurons provide a functional mechanical and histochemical sequence of recruitment (Henneman et al. 1974). This spinally based control scheme relieves higher centre of the nervous system from the responsibility to individually select motoneurons for each task at hand (Enoka 1995). A second functional advantage is that the orderly recruitment sequence leads to a convenient means of force regulation, referred to as “proportional control” (Kernell 1992), i.e. the enhanced force with recruitment is proportional to the force already present. In specific, when the force output of a muscle is small, force is increased by recruitment of additional weak motor units. As force increases, the motor units remaining to be recruited are progressively more powerful. Another functional advantage is that the capacity to perform a sustained contraction is improved by the greater fatigue resistance of the earliest recruited motor units (Enoka and Stuart 1992).

The other mechanism of neuromuscular force regulation is variation in rate and pattern of action potentials sent to the muscle fibers from the motoneuron. The relation between the net excitatory input to a single motoneuron and the discharge rate is approximately linear in a certain range (Kernell 1992). Therefore, the discharge rate of all active motor units increases monotonically with increasing force output (Milner-Brown et al. 1973; Tanji and Kato 1972). The homogeneous changes in discharge rate of motor units imply that the discharge rate is not individually controlled (De Luca et al. 1982b), but modulated by the net excitatory input to the motoneuron pool.

Not only the discharge rate, but also the pattern of discharge influences the force output. The synaptic input to a motoneuron pool comes from numerous sources (Binder et al. 1996; Edgerton et al. 1985). Therefore, motor units commonly generate action potentials randomly in time. However, more often than expected by chance, motor units simultaneously discharge action potentials (Sears and Stagg 1976). This pattern of discharge is termed *motor unit synchronization*. Since the degree of motor unit synchronization depends on the degree of shared synaptic input between motoneurons (Kirkwood et al. 1982), the temporal dependency of discharges between motor units

provides information about the distribution of common input to a motoneuron pool (Datta and Stephens 1990; Nordström et al. 1992). An effect of motor unit synchronization has been claimed to be involuntary fluctuations in neuromuscular output, defined as *tremor* (Halliday and Redfearn 1956; Hortobagyi et al. 2003; Mendell and Henneman 1971; Yao et al. 2000). This statement is contradicted by several experimental studies (Dietz et al. 1976; Logigian et al. 1988; Semmler et al. 2000; Semmler and Nordström 1995). Therefore, the impact of motor unit synchronization on tremor remains a debated issue (Enoka et al. 2003; Semmler 2002).

The relative contribution of motor unit recruitment and discharge rate to modulate force varies between muscles. For most muscles (e.g. the biceps brachii and tibialis anterior), recruitment of motor units occurs until at least 80% of maximal force (De Luca et al. 1982a; Kukulka and Clamann 1981; Van Cutsem et al. 1997). Whereas in some hand muscles, the upper limit of MU recruitment is about 50% of maximal force (Duchateau and Hainaut 1988; Milner-Brown et al. 1973). The increase in muscle force beyond the upper limit of motor unit recruitment is accomplished entirely by enhanced discharge rate.

The activity and control of the neuromuscular system described in this section is foremost based on anatomical and histochemical non-complex muscles (e.g. the soleus muscle) during involuntary activity or constrained voluntary slow ramp contractions. However, the activity and control of anatomical complex muscles during voluntary contractions have been reported to deviate from the described stereotyped control of the neuromuscular system (Desmedt and Godaux 1981; Herrmann and Flanders 1998; Stephens et al. 1978; Ter Haar Romeny et al. 1982; Wyman et al. 1974).

Neuromuscular control of anatomical complex muscles

Before Henneman's proposal of a regular and stereotyped control of the neuromuscular system, Denny-Brown argued that anatomical complex muscles are not controlled in such stereotyped manner: "*individual muscles are used in different ways in different movements… there are separate pools of units first activated in biceps brachii for flexion of the elbow and supination, but that in a combined movement yet a third set is first used*" (Denny-Brown 1949, p.120). In accordance with this notion, the orderly recruitment of motor units has repeatedly been studied and contradicted during different

tasks in anatomical complex muscles (Desmedt and Godaux 1981; Herrmann and Flanders 1998; Stephens et al. 1978; Ter Haar Romeny et al. 1982; Westad et al. 2003; Westgaard and De Luca 1999).

Divergence from the stereotyped activation of motor units within a muscle is observed in studies of cats (Chanaud et al. 1991; English 1984; Hensbergen and Kernell 1992; Hoffer et al. 1987; Hutchison et al. 1989; Kanda et al. 1977; Wyman et al. 1974) and pigs (Anapol and Herring 2000; Herring and Wineski 1986). These studies demonstrated that regions within a single muscle constituting different histochemical or mechanical properties could be selectively activated depending on the task. For example, the deeply located regions of the gastrocnemius (English 1984), semitendinosus and tibialis anterior (Chanaud et al. 1991), composed of mainly type I fibers, were active during slow contractions whereas the superficial regions were active during fast contractions. Furthermore, selective control of regions within histochemically non-regionalized, but mechanical complex muscles (i.e. cat sartorius muscle) during different voluntary contractions are also demonstrated (Hoffer et al. 1987). The observed selective control of regions within a muscle is termed *differential activation* (Chanaud et al. 1991; English 1984).

Deviations from the stereotyped control of motor units are also observed in human muscles during different tasks (Desmedt and Godaux 1981; Jongen et al. 1989; McMillan and Hannam 1992; Nardone et al. 1989; Riek and Bawa 1992; Ter Haar Romeny et al. 1982; Thomas et al. 1978; van Zuylen et al. 1988; Westad et al. 2003). In particular, recruitment of motor unit populations located in different regions of the long head of the human biceps brachii has been documented to depend on the direction of the force (Desmedt and Godaux 1981; Jongen et al. 1989; Ter Haar Romeny et al. 1984; van Zuylen et al. 1988). Moreover, motor units with initially higher threshold are observed to be recruited to replace lower-threshold motor units that have stopped firing during sustained fatiguing contractions (Westad et al. 2003; Westgaard and De Luca 1999). These observations have confirmed and strengthened the early idea of a different control scheme for motor units within anatomical complex compared to non-complex muscles (Denny-Brown 1949).

A plausible physiological explanation for the deviating control of motor unit populations in anatomical complex muscles is an intra-muscular topographical

dependency of Ia muscle afferents. Liddell and Sherrington (1924) and later Cohen (1953) showed that stimulation of the Ia afferents by stretching a single intra-muscular region caused selective muscle twitches in the same region being stretched. This finding initiated the proposal of the "sensory partitioning hypothesis" of Windhorst and co-workers (Cameron et al. 1981; Windhorst 1978; Windhorst et al. 1989), emphasizing the regionalization of afferent input to the motoneuron pool. Moreover, the anatomical description of "neuromuscular compartments" was described by English and colleagues (1982), highlighting the regionalization of the efferent system of anatomical complex muscles. Subsequently, in "the task group notion" Loeb and colleagues (1985) proposed that sub-populations of motor units within a muscle can be selectively activated in an orderly manner depending on the task.

Based on the work from these research groups, the physiological foundation for a selective control of regions within anatomical complex muscles was established. The critical physiological features for a selective control of intra-muscular regions were that 1) the motoneurons innervating an intra-muscular region (a neuromuscular compartment) are topographically clustered within the spinal cord (English and Weeks 1987; English and Weeks 1989) and, 2) the motoneurons innervating a neuromuscular compartment receive a selective synaptic input from afferent sources (Windhorst et al. 1989). Therefore, deviation from the stereotyped control of motor units in anatomical complex muscles is likely due to a selective synaptic input to motoneurons innervating a neuromuscular compartment (Ter Haar Romeny et al. 1984; Thomas et al. 1978). As a result, the control of motor units observed in anatomical complex muscles is not necessarily a deviation from the size principle. The orderly recruitment rather occurs within sub-populations of motoneurons receiving a common synaptic input than within all motoneurons of a motoneuron pool (Riek and Bawa 1992). To examine the recruitment sequence of motor unit populations from a representative fraction of an anatomical complex muscle, the trapezius muscle was studied during a sustained contraction (paper II).

Another afferent source, besides the Ia afferents that might provide uneven distributed input to a motoneuron pool is recurrent inhibition. Since the terminals from a renshaw cell do not cover the whole homologous motoneuron pool, but are restricted to a few nearby located motoneurons (Eccles et al. 1961; Romanes 1951), the recurrent

inhibitory input can be selectively distributed to motoneuron populations within a pool. Segregated synaptic input to a motoneuron pool may also originate from the central nervous system. Although descending corticospinal input is generally considered to be evenly distributed within a motoneuron pool (Bawa and Lemon 1993), the lower motor unit synchronization between than within regions of anatomical complex muscles indicates a selective synaptic input from descending systems to a motoneuron pool (Bremner et al. 1991a; Keen and Fuglevand 2004; Reilly et al. 2004). In this thesis, the distribution of common synaptic input to motoneurons within the biceps brachii muscle was investigated by analyses of motor unit synchronization of different intra-muscular regions (paper IV).

It is well recognized that the described control of anatomical complex muscles may have a functional impact on local muscle fatigue during prolonged contractions (Enoka 1995). Already in 1922, Forbes proposed that "*Possibly a group of fibers in a shortened state…sends to a limited number of motor neurons the requisite proprioceptive impulses to establish reflex connection. The muscle fibers thus excited may be different from the first group…and so the fiber groups may take up the load in rotation and, for some reason, by this means attain an economy otherwise impossible"* (Forbes 1922, p. 404). Such rotation between active motor unit populations in anatomical complex muscles during monotonous contractions are generally considered to prevent local muscle fatigue and reduce the risk of muscle fiber overexertion (Mathiassen 1993). Especially in the biceps brachii muscle, in which rotation of activity between the different heads would cause minor changes in mechanical output (Ettema et al. 1998), load-sharing between muscle regions could occur during sustained or repetitive monotonous contractions. However, the impact of load sharing between active motor unit populations within anatomical complex muscles on local muscle fatigue remains uncertain. In this thesis, a study was performed to examine whether shifts in relative activity between regions (differential activation) within the biceps brachii muscle were related to time to exhaustion in a sustained contraction (paper III).

Examination of the neuromuscular system by electromyography (EMG)

EMG is an acquisition technique for the study of activation, control, state and properties of motor units. The invasive EMG is regarded as the golden standard for investigation

of single motor unit behaviour. The advantages of the invasive technique are the short distance from the source of the motor unit action potential (MUAP) to the electrode and the small pickup area around the tip of the electrode. These aspects permit recording of the MUAPs waveform (envelope) before it is distorted by the surrounding biological tissue (volume conduction) or MUAPs from other motor units. Based on identification of the specific waveform of a MUAP from an individual motor unit, the recruitment threshold and firing characteristics of single motor units can be retrieved (motor unit decomposition). However, the advantage of the small pickup area with the invasive EMG techniques also constricts the attained information to a small number of motor units. As a consequence, invasive EMG technique recordings may not be representative for the overall motor unit behaviour within a muscle (Ertas et al. 1995).

Detailed information of motor unit behaviour is not easily retrieved with conventional non-invasive surface EMG (sEMG). This is mainly due to the relatively large distance with biological tissue between the source of the MUAP (sarcolemma) and the recording electrode (Basmajian and De Luca 1985). Thus, the myoeletric signal recorded at the skin surface consists of compound activity from a high number of motor units (interference pattern) with low spatial resolution. Moreover, the distance from the fiber to the recording electrode also influences the amplitude and duration of the recorded MUAP waveform (Blok et al. 2002). For example, a thicker subcutaneous fat layer or increased depth of a motor unit in the muscle generates a decreased signal amplitude and increased spatial spread above the muscle (Gath and Stälberg 1979; Roeleveld et al. 1997). Consequently, it is difficult to extract detailed information about single motor unit behaviour from conventional sEMG recordings.

The number of electrodes placed on the skin above the muscle has a profound impact on the information attained from sEMG. A sEMG registration with one electrode placed on the skin above a muscle is called a monopolar recording. The drawback of this sEMG configuration is the contribution of electrical signals from sources other than the muscle being investigated. This limitation is overcomed by applying two electrodes at the skin above a muscle, each with respect to a reference electrode (bipolar configuration). The difference between the two signals is amplified, eliminating the common signal from electrical devices and more distant muscles. As a result, uncommon signals from muscle tissue close to the electrodes (from the investigated

muscle) are retrieved. This bipolar montage is the most common recording configuration in sEMG.

Application of additional surface electrodes enables extraction of more than barely the time-variation of the myoelectric signal. The main advantage of several recording locations above a muscle is the attained spatial information of motor unit activity. The MUAPs propagate along the muscle fibers from the innervation zone towards both ends with a typical velocity between 1.5 and 6.5 m/s (Stälberg 1986). The muscle fiber conduction velocity (MFCV) is related to and thereby provides information about the muscle fiber cross-sectional area (Blijham et al. 2006; Hakansson 1956), muscle fiber type (Kupa et al. 1995), and shifts in ion balance (local muscle fatigue) (Andreassen and Arendt-Nielsen 1987; Arendt-Nielsen and Zwarts 1989; Brody et al. 1991). The MFCV has been examined for a few decades using several linearly arranged sEMG electrodes (Nishizono et al. 1979). From this electrode setup (linear array), information about the location of the innervation zone based on the bidirectional propagation of MUAPs (Masuda et al. 1983) and the MFCV from the time of propagation of the MUAPs between the recording electrodes can be retrieved (Broman et al. 1985).

At present time, the state-of-the-art in sEMG is two-dimensional grids with densely-oriented multiple surface electrodes (MCsEMG). The many sites of recording above a muscle provide two-dimensional spatiotemporal information of the propagating MUAPs along the muscle fibers. Therefore, *in vivo* estimation of the muscle fiber orientation (MFO), MFCV (Grönlund et al. 2005a) and innervation zone (Lapatki et al. 2006; Östlund et al. 2007) can be attained with the MCsEMG technique. Correct estimates of MFCV require an electrode location parallel to the MFO, limiting recording of MFCV to muscles with parallel MFO (Merletti et al. 2001). However, this methodological limitation can be avoided by off line estimation of MFO, and subsequent assessment of MFCV along the estimated MFO (Grönlund et al. 2005a). In this thesis, MFO and MFCV were estimated from a large fraction of the the trapezius muscle to attain information of eventual region dependency of physiological characteristics (paper IV). Another advantage of the MCsEMG technique is the reduction of sources contributing to the sEMG signal with two-dimensional spatial filters (Disselhorst-Klug et al. 1997). The narrowed spatial view to near by sources

provides an improved focus on single motor unit activity. The individual spatial configurations (position, depth, innervation zone and MFCV) of the focused motor units (motor unit fingerprints) enable non-invasive detection of motor unit behavior with the MCsEMG technique (Kleine et al. 2000a).

The muscle fibers innervated by a motoneuron are limited to a fraction of a muscle (Bodine-Fowler et al. 1990). Therefore, the spatial activity detected on the surface of the skin from an active motor unit depends on its size, location and depth in the muscle (Monster and Chan 1980; Roeleveld et al. 1997). The consequent spatial dependency of electrode-location above the muscle on myoelectric signals is well known (Farina et al. 2002a; Hermans and Spaepen 1997; Hermens et al. 2000; Mademli et al. 2004; Roy et al. 1986). Traditionally, the spatial dependent activity above the muscle was considered a problem for both the validity and reliability of the sEMG technique. The methodological solution to the spatial variability in activity was to locate the sEMG electrodes on the muscle region with highest and most stable sEMG amplitude level (Jensen et al. 1993; Jensen et al. 1996). In the last decade, the spatial distribution of activity above a muscle has been used to attain information about motor unit location (Zwarts and Stegeman 2003) and depth (Roeleveld et al. 1997). Moreover, changes in spatial distribution of activity have been applied to attain information about the location of recruited motor units during force modulation (Scholle et al. 1992) and fatigue (Kleine et al. 2000b). In these studies, changes in spatial distribution of activity were described with two-dimensional profiles of the myoelectrical activity from all electrodes above the muscle (interference mapping). This mapping method is also useful to retrieve information about the innervation zone location (Masuda and Sadoyama 1988), visualized by highest activity with unipolar recordings (Kleine et al. 2000b) and lowest activity with bipolar configurations (Roeleveld et al. 1997). In this thesis, analyses of changes in spatial distribution of activity were carried out to attain information about recruitment of motor unit populations from a large fraction of the biceps brachii and upper trapezius muscles (paper I & II).

Aims of the thesis

The overall purpose of this thesis was to investigate neuromuscular activation, control and physiological characteristics of the biceps brachii and the trapezius muscle with the MCsEMG technique. The main aims were to 1) examine the recruitment sequence of motor unit populations, 2) study the activation and control of intra-muscular regions during sustained contractions, and 3) investigate the intra-muscular distribution of physiological characteristics. The biceps brachii and trapezius muscle were investigated because of observed deviations from the stereotyped control scheme of motor units, and reports based on dissections of human cadavers of architectural and histochemical regionalization of muscle fiber characteristics.

The specific aims in order to fulfill the overall purpose, outlined in paper I-V, were to:

I. Develop a MCsEMG based method to provide information of recruitment of large motor unit populations based on changes in spatial distribution of activity above a muscle.
II. Examine whether the recruitment sequence of motor unit populations is similar during sustained and ramp contractions in the upper trapezius muscle.
III. Investigate differential activation between intra-muscular regions within the biceps brachii muscle and its relation to fatigue during sustained contractions.
IV. Study fatigue induced changes in synchronization of large motor unit populations in different regions of the biceps brachii muscle.
V. Provide non-invasive *in vivo* information about intra-muscular distribution of physiological characteristics based on estimations of MFCV and MFO from different regions of the upper trapezius muscle during voluntary contractions.

Methods and materials

Study samples

A total of 91 subjects, 73 males and 18 females volunteered for these studies. The age ranged from 19 to 37 years. Recordings from 17 subjects were excluded due to low data quality. Thus, data from 74 subjects (64 males and 10 females) were applied in the results and statistics. The experiments were carried out in accordance with the Declaration of Helsinki. The protocols were approved by the Regional Committee for medical science and ethics, University hospital, NTNU, Trondheim, Norway.

Experimental protocols

Isokinetic dynamometers were used to standardize position and measure force production during voluntary contractions (paper I: KIN-COM 500H, Chattanooga Group, Inc., Hixson, TN, USA and papers II –V: BIODEX System 3 Pro; Biodex Medical Systems, Shirley, NY, USA) were used. MCsEMG was recorded from the upper trapezius muscle during isometric bilateral shoulder elevation with a standard closed chain system, converting linear motion of the arm to rotational motion at the shaft of the dynamometer (Figure 1A). From the biceps brachii muscle, MCsEMG was recorded during isometric unilateral elbow flexion (paper I, III, IV & V) (Figure 1B).

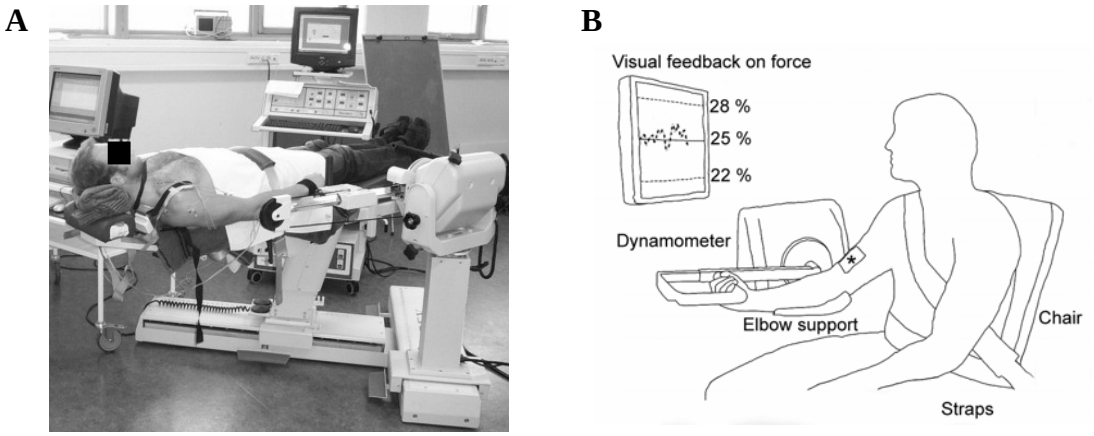

Figure 1. A) Picture of the experimental setup used for MCsEMG recordings from the upper trapezius muscle during isomtric bilateral shoulder elevation. B) Schematic illustration of the experimental setup for isometric unilateral elbow flexion.

To normalize force and MCsEMG, the subjects carried out three isometric maximal voluntary contractions (MVC) in all experiments (papers I-V). To investigate changes in spatial distribution of activity with force modulation, three sinusoidal contractions from 0 to 80 % MVC of 20 s duration (paper I), and three ramp contractions from 0 to 90 % MVC of 10 s duration (paper II) were carried out.

Sustained contractions at 25 % MVC of 3 min duration to compare changes in spatial distribution of activity during fatigue with the ramp contraction (paper II), and until exhaustion to examine differential activation and changes in motor unit synchronization with fatigue (paper III & IV) were performed. In addition, sustained contractions at 5 %, 10 %, 25 % MVC of 3 min duration and at 50 % MVC of 1 min duration were conducted with the biceps brachii and trapezius muscles to examine MFO and changes in MFCV with force modulation and fatigue (paper V). The subjects received force target and on-line feedback of the generated force on a monitor (Figure 1).

Force recordings and analyses

The analogue force signal at 1000 Hz was attained from the dynamometer. The force signal was low-pass filtered and divided in time-epochs of 500 ms throughout the whole contraction period (paper I - III). The maximal force during the MVC was determined as the epoch with highest detected value. In paper IV, the force signal was band-pass filtered (5^{th} order Butterworth) at 4-30 Hz (Semmler and Nordström 1995). Force tremor was quantified using the coefficient of variation (standard deviation (SD) / mean * 100) of the filtered force signal (Burnett et al. 2000). The force tremor was calculated in 10 s windows with 5 s overlap throughout the sustained contraction.

Multi-channel surface EMG recordings

Muscle activation and characteristics of the biceps brachii and the upper trapezius muscle were recorded with a MCsEMG grid consisting of 13 by 10 gold covered active pin electrodes (modified ActiveOne, BioSemi, Amsterdam, Netherlands). The grid covers 6 x 4.5 cm of the skin surface, with 1.5 mm electrode diameter and 5 mm inter electrode distance. sEMG was recorded from all electrodes with a common reference (monopolar recording), at a sampling frequency of 2048 Hz.

The base of the electrode-grid device is concave and semiflexible and fits well with the convex area of recording of both the upper trapezius and the biceps brachii muscle. On the upper trapezius muscle, the center of the MCsEMG grid was firmly placed in middle of the line between processus spinosus of the C7 vertebra and the lateral edge of acromion (Figure 2). To prevent movement of the electrodes and secure a stable pressure onto the skin, the MCSEMG grid was held in place by two elastic straps around the shoulder and torso of the subject fastened to each corner of the electrode grid (Figure 1A).

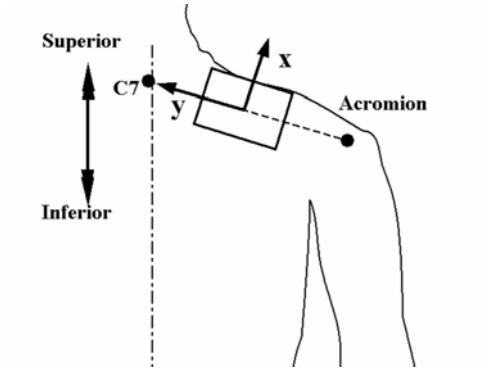

Figure 2. A schematic drawing (posterior view) of the MCsEMG grid placement and the alignment of the detection system coordinates on the upper trapezius muscle.

Above the biceps brachii muscle, the middle of the MCsEMG grid was placed on the partition of the two heads (based on palpation). To avoid the innervation zone running approximately midway between the origin and insertion of the biceps brachii (Masuda et al. 1985), the MCsEMG grid was situated at the distal part of the muscle. The grid was firmly fixed with two elastic straps fastened to each corner of the grid and strapped around the upper arm of the subject.

Multi-channel surface EMG analyses

The quality of the MCsEMG signals from the 130 electrodes was determined by visual inspection (paper I) and an automatic method (paper II - V) described by Grönlund et al (2005b). The automatic method calculates the standard deviation (SD) of the signal from each electrode in two time-windows with different lengths. The frequency of each signal having extreme SD values as compared to the bulk of the signals (defined as outlier) was used to determine the signal quality. Signals from electrodes detected as

outliers more than 5 % of the time within 1s were defined as low quality (Grönlund et al. 2005b).

The monopolar signals with acceptable signal quality were either band-pass filtered at 20 – 400 Hz (paper I & II) or high-pass filtered at 10 Hz (8^{th} order Butterworth) (paper III & IV). Subsequently, bipolar leadings were calculated in the medial-lateral direction in parallel with the line between C7 and acromion for the upper trapezius muscle (paper II & V) (Figure 2), and in the proximal-distal direction in parallel with the humerus for the biceps brachii muscle (paper I, III & V). Root-mean-square (RMS) values of all bipolar signals were calculated in 500 ms non-overlapping time-windows throughout the entire contraction length (paper I, II, III and V). The RMS values were normalized to the maximal RMS of the signals attained during the MVC recordings. To evaluate the level of local muscle fatigue during the sustained contraction, the median frequency (MF) of the power density spectrum was computed in epochs of 500 ms (paper II).

EMG amplitude distribution

In short, changes in spatial distribution of muscle activity were calculated by correlating the RMS values of all electrodes at one time-epoch, with the RMS values of the same electrodes at another time-epoch (paper I & II). Therefore, the correlation coefficient provides quantitative information of the degree of change in spatial distribution. In specific, a low correlation indicates large change in spatial distribution, while a high correlation indicates a small change in spatial distribution. Since recruitment of differently located motor units in a muscle changes the spatial distribution of activity (Roeleveld et al. 1997), the correlation provides information about recruitment of motor unit populations from a large fraction of a muscle. Because the applied correlation method is influenced by relative changes in RMS between electrodes only, the method is suited to examine recruitment of motor unit populations. Moreover, the method is not influenced by the specific anatomical location in which changes in activity occurs in the muscle. Due to the unknown location and scattering of individual motor units in a muscle, this is a necessary feature of the method.

To examine recruitment of motor unit populations during force modulation, correlations were obtained for each individual time-epoch throughout the contraction

and a single time-epoch (e.g. with highest generated force or 25% MVC) (paper I & II). To enable comparison of changes in spatial distribution of activity during ramp and sustained contractions, correlations between RMS values of all electrodes at each time-epoch of the sustained contraction and RMS values of the same electrodes at each time-epoch of the ramp contraction were calculated, respectively (Figure 3).

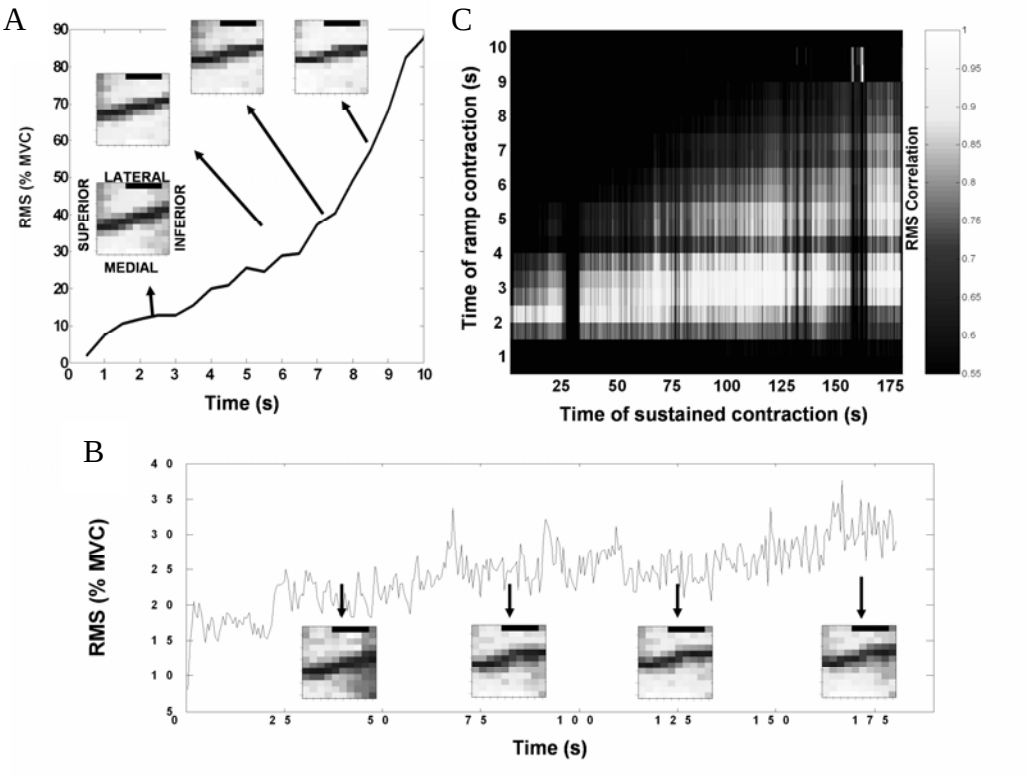

Figure 3. A typical recording from the upper trapezius muscle of A) the change in average RMS from all electrodes during the ramp contraction with RMS distribution maps displayed at different levels of RMS, B) the change in average RMS during the sustained contraction with RMS distribution maps displayed at different time-epochs of the sustained contraction, C) changes in RMS correlation when the RMS values from all electrodes at each time-epoch throughout the sustained contraction (X-axis) is correlated with all RMS values from the same electrodes of each time-epoch of the ramp contraction (Y-axis). The grayscale illustrates the correlation-values. Bright areas of the RMS distribution maps indicate high activity and dark areas indicate low activity. The five black electrodes in the upper row of the RMS distribution maps are automatically removed electrodes due to low signal quality.

Differential activation between intra-muscular regions

Information of changes in relative activity between regions within the biceps brachii muscle was attained from electrodes of the MCsEMG grid located above the short and long heads of the muscle. RMS was calculated each 500 ms from bipolar electrode

leadings located above each respective region throughout the contraction. The RMS values from electrodes above each respective muscle region were temporally de-trended (linear), and normalized to the 99 % highest RMS value of the contraction. The relative difference between RMS values from each intra-muscular region was quantified. The frequency and duration with relative difference in muscle activity of more than 33 % (regarded as differential activation) were calculated (paper III). The threshold was set at 33 % to attain a measure of activity of individual muscle regions, not recruitment of randomly located single motor units in the muscle.

Motor unit synchronization

Motor unit synchronization was estimated with a recently developed sEMG method (Grönlund et al. 2007). The stochastic characteristics of the sEMG signal is modified with motor unit synchronization (De Luca 1979). Therefore, a descriptor for motor unit synchronization was estimated with a continuous wavelet transform by filtering the monopolar sEMG signal at a sub-band with highest sensitivity with motor unit synchronization (and least sensitivity with MFCV), and subsequent calculation of the skewness of the signal (the sub-band skewness) (Grönlund et al. 2007).

In order to assess the general association between motor unit synchronization and force tremor, the correlation coefficient (R) was calculated between the motor unit synchronization descriptor and force tremor for each subject. The association between fluctuations in the motor unit synchronization descriptor and force tremor was assessed based on correlation of both de-trended and not de-trended versions of the motor unit synchronization descriptor and force tremor throughout the sustained contraction. In specific, the motor unit synchronization descriptor and its association with force tremor was assessed from 1) different intra-muscular regions from electrodes located 1 cm from the innervation zone and, 2) electrodes located along the muscle fibers.

Since muscle activity *per se* not provides direct information about distribution of common synaptic input within a motoneuron pool, this information was attained by estimation of the motor unit synchronization descriptor from electrodes located above the short, long and partitioning of the heads of the biceps brachii muscle. The most commonly used technique to estimate motor unit synchronization utilizes needle EMG and histograms of the cross-correlation of pairs of single MUAP trains (Nordström et al.

1992). However, only a small number of motor units is examined when estimating motor unit synchronization by needle EMG (Semmler and Nordström 1999). Therefore, motor unit synchronization was estimated with the MCsEMG technique to attain representative information from the biceps brachii muscle. On the other hand, sEMG-based methods of motor unit synchronization (Del Santo et al. 2006; Farina et al. 2002b; Kleine et al. 2001) depend on MFCV, and are therefore constricted to un-fatigued muscle contractions. Hence, the motor unit synchronization was estimated with a method based on large motor unit populations being minimally dependent on MFCV (Grönlund et al. 2007).

Muscle fiber conduction velocity and muscle fiber orientation

Both the velocity (MFCV) and orientation (MFO) of propagating MUAPs along muscle fibers can be attained with MCsEMG recordings. In paper V, the MFCV and MFO from the upper trapezius and biceps brachii muscle were calculated with a method developed by Grönlund and colleagues (2005a). The method detects MUAPs as moving high-potential (amplitude) regions on the electrodes oriented at the surface of the skin above the muscle, providing a trajectory for each detected MUAP (Figure 4). A 3-D regression model was applied to estimate the MFCV and MFO based on the neighbour electrodes to the detected trajectories (Figure 4). At higher contraction levels, the spatial amplitude distribution of the propagating MUAP is contaminated with other MUAPs, impairing the estimates of MFCV and MFO. However, by using the spatial distribution of MFCV and MFO, single or populations of active motor units were separated as individual density regions with a 2-D density estimation technique (Figure 4D). The local maximal values of MFCV and MFO of each individual density region were subsequently calculated. To study changes in spatial distributions of MFCV with force generation, local maximal values in the spatial distribution of MFCV were examined for each subject at each contraction level (marked by crosses in Figure 4D).

The MFCV is correlated with muscle fiber type and cross-sectional area (Kupa et al. 1995; Sadoyama et al. 1988), and were therefore estimated to attain information of the cross-sectional area and muscle fiber types from different regions of the trapezius muscle.

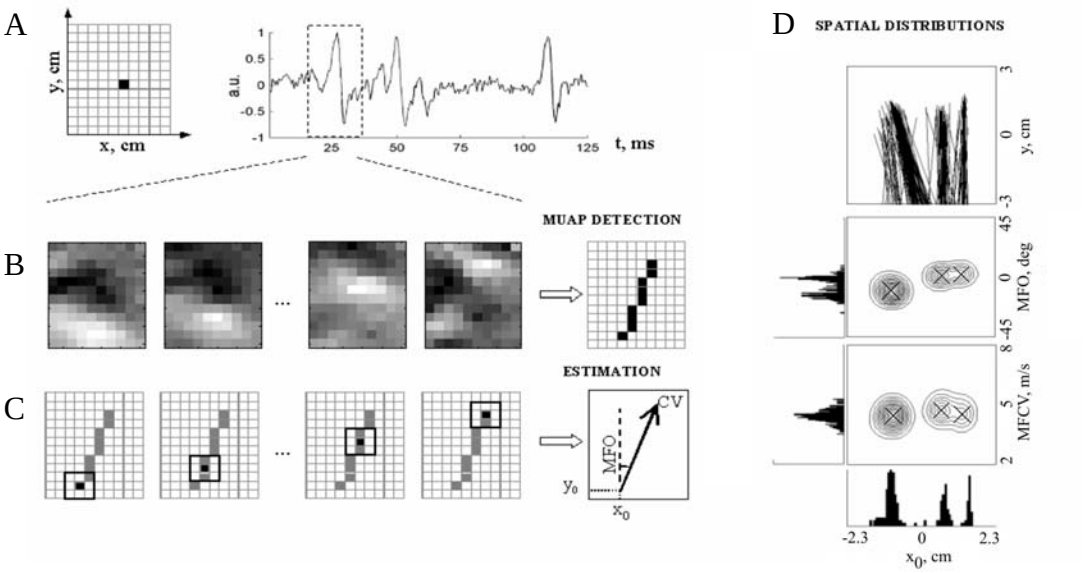

Figure 4. Overview of the applied method to estimate MFCV and MFO. A) The MCsEMG grid representing the 13 by 10 electrodes, covering the skin's surface, and an experimental time signal from one of the electrodes (dark square). B) A sequence of spatial amplitude distributions, showing propagation of high amplitude regions (light color), and the MUAP trajectory detected by the method. C) Precision of the MUAP trajectory is improved by a 3-D regression model on the neighbour electrodes to the trajectory providing the MFCV and MFO of the propagating MUAP. D) Construction of the spatial distributions: thin lines represent examples of the MUAP trajectory estimates (top) over the skin's surface above the biceps brachii muscle during a 15 s period at 25 % MVC. Each detected propagating MUAP was used to estimate individual density distributions of MFCV and MFO, respectively (marked by crosses).

Summary of results

Paper I: Inhomogeneities in muscle activation reveal motor unit recruitment.

To investigate whether recruitment of motor unit populations can be retrieved from changes in spatial distribution of muscle activity, correlation coefficients between RMS values of all electrodes at different force levels from 0 to 80 % MVC were calculated. In general, the spatial distribution of biceps brachii activity changed in a consistent manner with force modulation (Figure 5A). The spatial distribution of muscle activity was not different between contractions 1-3 or ascending and descending contraction levels when quantified with respect to the reference epoch at 80 % MVC (Figure 5A). When calculated with respect to the reference epoch at 25% MVC, the spatial distribution of activity was different between the first two and the last contraction, and between the ascending and descending contraction levels (Figure 5B). The observed consistent changes in spatial distribution of activity between subjects and contractions support that spatial inhomogeneities in muscle activation provide information of recruitment of motor unit populations.

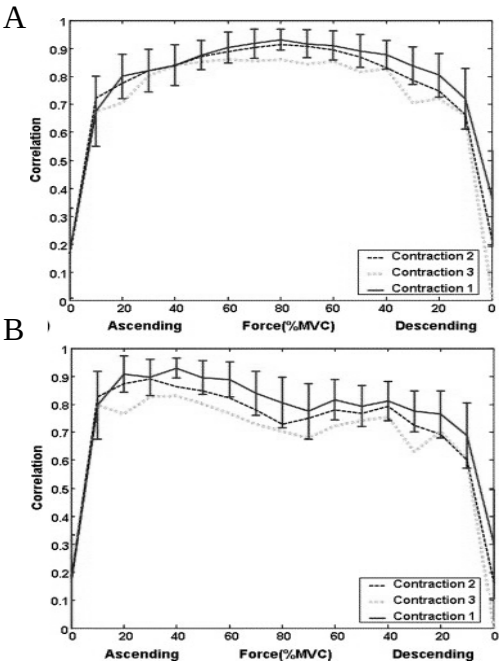

Figure 5. Mean changes in correlation from all subjects with generated force (% of MVC) of the three contractions calculated with respect to reference epoch at 80% A) and 25% B) of MVC. 95% confidence intervals are included to the results of the first contraction.

Paper II: EMG amplitude distribution changes over the upper trapezius muscle are similar in sustained and ramp contractions.

The purpose of the study was to investigate whether the recruitment sequence of motor unit populations in the upper trapezius muscle is similar during sustained and ramp contractions. Motor unit recruitment was quantified by comparing changes in spatial distribution of activity above the muscle in the two different types of contractions. A non-uniform spatial distribution of activity was observed above the upper trapezius muscle at all investigated time-epochs of both the sustained and ramp contractions (see insets with RMS distribution maps in Figure 3). The distribution of muscle activity throughout the sustained contraction became more similar to the activity distribution at progressively higher force levels of the ramp contraction (see typical example Figure 3). The spatial distribution of activity above the upper trapezius muscle in the start of the sustained contraction was most similar to the time-epoch of the ramp contraction with similar force level. At the end of the sustained contraction, the spatial distribution progressed to be most similar to the time-epoch of the ramp contraction corresponding to a force level of 52 % MVC. The spatial distribution of upper trapezius activity remained similar to the best fitting time-epochs of the ramp contraction throughout the sustained contraction (mean correlation of 0.87). In conclusion, the spatial distribution of activity from the upper trapezius muscle changed in a similar manner in the ramp and sustained contraction.

Paper III: Differential activation of regions within the biceps brachii during fatigue.

The aim of the study was to examine differential activation between the long and short heads of the biceps brachii muscle and its relation to fatigue during a sustained contraction. While the subjects produced the prescribed force at 25 % MVC (Figure 6A), the average activity of the biceps brachii increased from 15 (5.4) to 34 (12.8) % of maximal RMS from the first (0-25 %) to the last (75-100 %) time segment of the sustained contraction (Figure 6B).

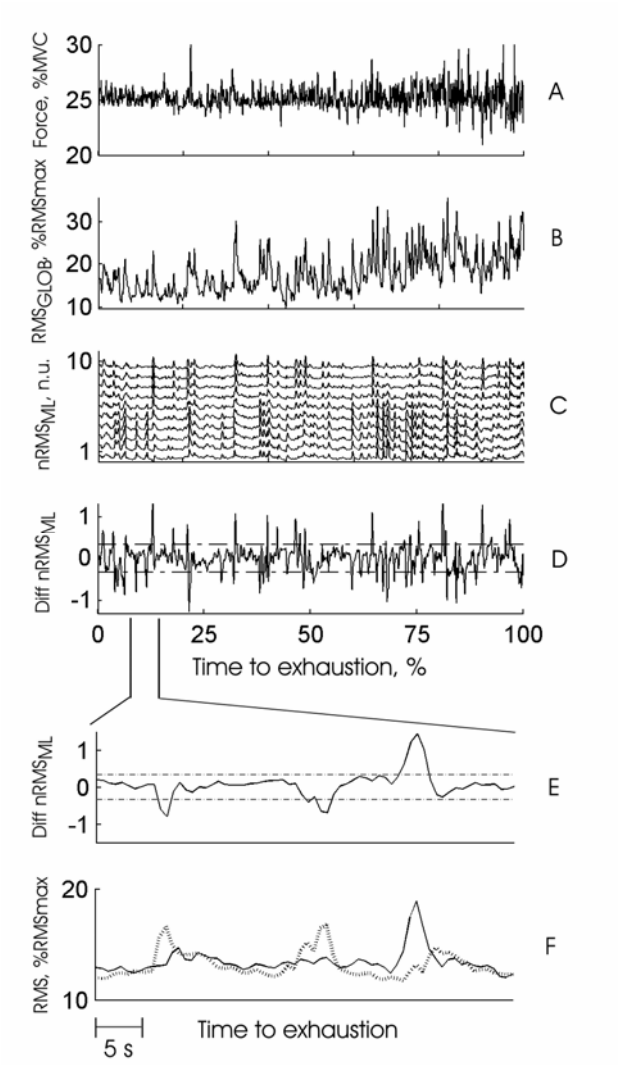

Figure 6. Results of a typical recording from one subject of the 25 % MVC isometric elbow flexion contraction until exhaustion. A) Force signal normalized to MVC. B) RMS amplitude (average of signals from all electrodes) normalised to maximal RMS amplitude during MVC. C) Normalized average RMS from signals of each column of electrodes along the fiber orientation from the lateral (electrodes 1-5) to the medial (electrodes 6-10) heads of the biceps brachii. D) The difference in activation between the heads of the biceps brachii (electrode columns medial – lateral) calculated for each time instant of 0.5 seconds throughout the contraction. The horizontal dashed lines illustrate the 33% threshold set for detection of periods with differential activation. X-axis is contraction time normalised to time to exhaustion. E) A zoomed segment of the signal in D. F) The corresponding RMS signals from electrodes of column 2 (Medial head: dotted), and column 9 (Lateral head: solid).

Differential activation between regions of the biceps brachii was observed in 30 of 33 subjects. The frequency of differential activation increased from the first to the last time segment of the sustained contraction, while the mean duration of periods with differential activation remained stable. Periods with differential activation constituted about 25% of the total contraction time. The association between frequency of periods with differential activations and time to exhaustion did not reach significance in the first time segment of the contraction. In the last three time segments, a significant negative relation between frequency of differential activations and time to exhaustion was observed. There was no significant association between mean duration of differential activations and time to exhaustion in any time segment. In conclusion, differential activation occurs between intra-muscular regions of the biceps brachii, but does not prevent local muscle fatigue at a sustained contraction at a force level of 25 % MVC.

Paper IV: Motor unit synchronization during fatigue: Described with a novel sEMG method based on large motor unit samples.

The aim of this study was to apply a novel sEMG descriptor for motor unit synchronization based on large motor unit populations to examine changes in motor unit synchronization with fatigue at different sites of a muscle and its relation to tremor. Both the motor unit synchronization descriptor and force tremor increased throughout the sub-maximal contraction. There was a general association between the motor unit synchronization descriptor and force tremor (R = mean 0.6, SD 0.21), but not between fluctuations in the de-trended motor unit synchronization descriptor and force tremor throughout the contraction (R = mean 0.13, SD 0.09). Changes in the motor unit synchronization descriptor with fatigue (motor unit synchronization index) were different between the medial and lateral regions of the biceps brachii muscle (Figure 7B). Moreover, the association between the motor unit synchronization descriptor and force tremor was lower at the partitioning of the heads as compared to the medial and lateral regions, respectively (Figure 7D). The motor unit synchronization descriptor and its association with force tremor decreased with increasing distance from the innervation zone.

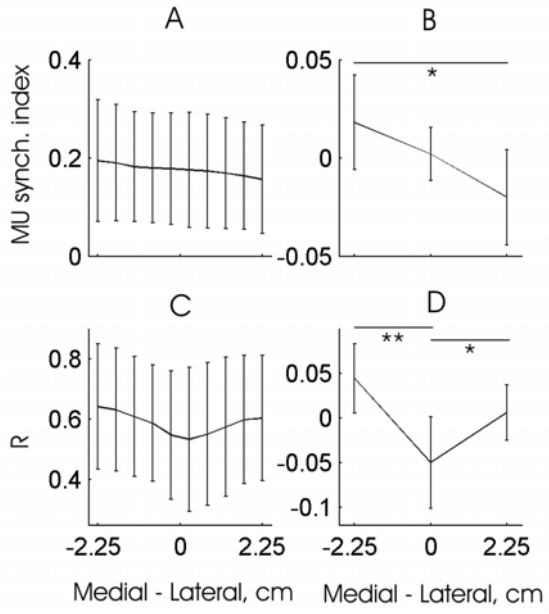

Figure 7. Illustration of distribution of the motor unit synchronization descriptor along the innervation zone (between regions). In A and C, the average and SDs of the distribution of the motor unit synchronization index and the R statistics are presented, respectively, for all subjects (N = 24). Figures, B and D demonstrate the average and 95 % confidence intervals of the distribution of normalized motor unit synchronization index and R statistic values, respectively. Normalization was obtained by subtraction of the average of the motor unit synchronization index and R, respectively, from the three positions of each subject (-2.25, 0 and 2.25 cm with respect to the partitioning of the two heads of the biceps brachii). Symbols of significance levels: *** $p<0.001$, ** $p<0.01$, * $p<0.05$.

Paper V: Spatial distribution of active muscle fiber characteristics in the upper trapezius muscle and its dependency on contraction level and duration.

The study was conducted to provide non-invasive *in vivo* information about the physiological characteristics from a large fraction of the trapezius muscle during voluntary contractions. A previously developed MCsEMG method (Grönlund et al. 2005a) was applied to detect propagating MUAPs and to estimate their corresponding MFO and MFCV. In order to demonstrate the impact of changes in MFCV at different force levels and fatigue in the upper trapezius muscle, the findings were compared with recordings from the biceps brachii. The MFCV was spatial unevenly distributed above the upper trapezius muscle depending on force level (Figure 8) and fatigue.

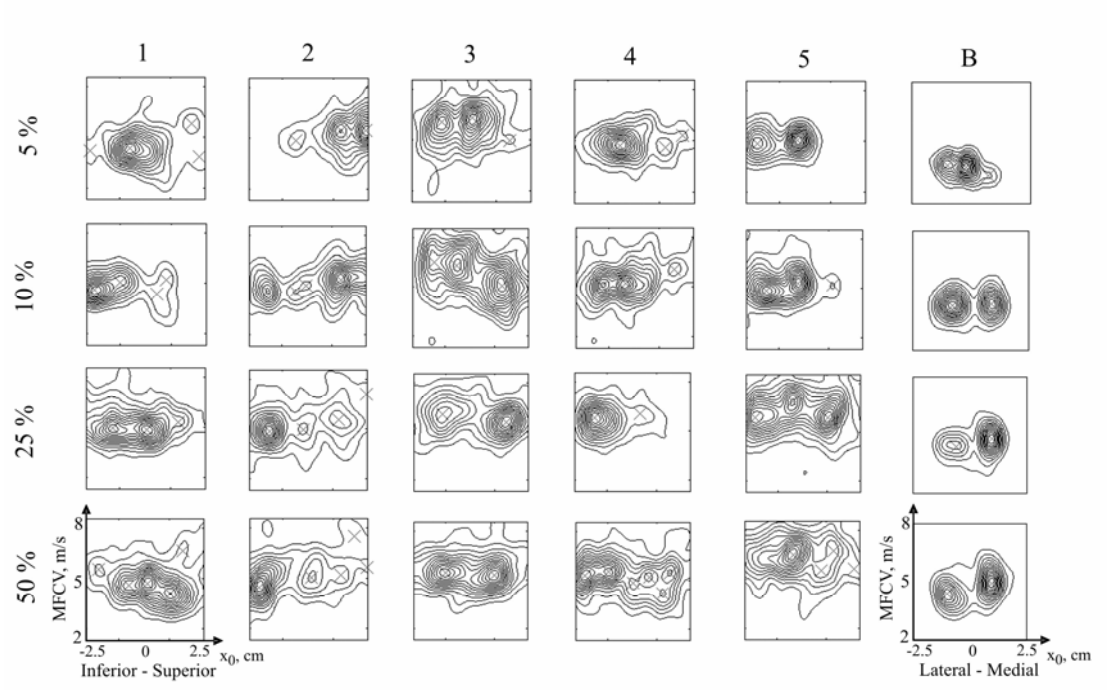

Figure 8. Spatial distributions of MFCV at 5, 10, 25 and 50 % MVC. Dense lines indicate high probability (incidence). Numbers 1-5 are results of recordings at the upper trapezius muscle from different subjects, whereas 'B' presents results from a typical measurement from the biceps brachii muscle. For the trapezius recordings, x_0 corresponds to the inferior – superior position relatively to the anatomical midpoint of a line between C7 and the lateral edge of acromion. For the biceps case, x_0 corresponds to the partitioning between the short and long head of the muscle.

No consistent relation between average MFCV and force level was observed in the upper trapezius muscle when considering the whole spatial recording area (Figure 8). In contrast, the average MFCV increased between 5 and 50 % MVC for all subjects

in the inferior part. There was a tendency to a different increase in MFCV between the superior and inferior part of the upper trapezius muscle with enhancing force levels (p=0.06). In the biceps brachii, the average MFCV increased between 5 and 50 % MVC for all subjects. The increase in MFCV from 5 % to 50 % MVC force was higher in the biceps brachii compared to the upper trapezius muscle. The MFCV decreased throughout the 25 and 50 % MVC contractions, depending on the spatial location at the upper trapezius muscle.

The MFO from muscle fibers with origin superior to C7 in the trapezius muscle was on average 6° more descending oriented than fibers with origin inferior to C7.

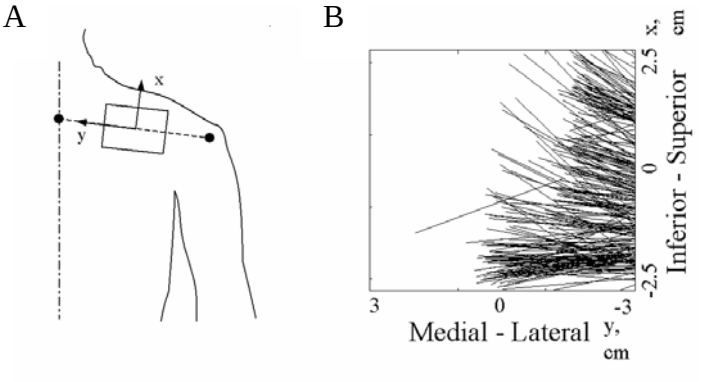

Figure 9. A) Schematic drawing at a posterior view of the electrode-device placement and the alignment of the detection system coordinates on the upper trapezius muscle. B) The estimated MUAP trajectories and their spatial distributions of MFO from the upper trapezius.

Discussion

The recently developed MCsEMG methods applied in this thesis enabled new spatial related information about the activation, control and physiological characteristics of the biceps brachii and the upper trapezius muscle during slow force modulation and sustained contractions. The main findings were the consistent changes in intra-muscular spatial distribution of activity with recruitment of motor unit populations (paper I), being similar during sustained and ramp contractions (paper II). Regions within the biceps brachii muscle were differentially activated during a sustained contraction, but these region-dependent shifts in activity between the long and short head were not positively associated with the ability to prevent local muscle fatigue (paper III). Consistent with the inhomogeneous intra-muscular activation, the motor unit synchronization descriptor differed above the biceps brachii muscle (paper IV). In accordance with previous studies of human cadavers, the physiological characteristics of the upper trapezius muscle were dependent on the region of the muscle (paper V). The observed intra-muscular spatial dependency of activation, control and physiological characteristics of the biceps brachii and trapezius muscle will be discussed. Moreover, considerations regarding the applied MCsEMG methods will be addressed.

Spatial dependency of intra-muscular activation and control

The spatial distribution of activity above the biceps brachii and the upper trapezius muscle was demonstrated to change with force modulation and fatigue (paper I & II). This finding is consistent with previous reports of changes in spatial distribution of activity above anatomical complex muscles with force modulation (Grassme et al. 2003; Kleine et al. 2000b; Scholle et al. 1992), fatigue (Farina et al. 2006; Kleine et al. 2000b), different tasks (Jensen and Westgaard 1997), changed limb posture (Jensen and Westgaard 1995; Mathiassen and Winkel 1990) and experimental muscle pain (Falla et al. 2007; Madeleine et al. 2006).

Changes in spatial distribution of activity above the trapezius muscle have been hypothesized to be a result of partial selective control of intra-muscular regions (Jensen and Westgaard 1997; Jensen and Westgaard 1995). For example, Farina and colleagues (2006) demonstrated redistribution of activity from inferior to superior regions of the

trapezius muscle with fatigue. Although changes in spatial distribution of muscle activity could be due to a partial selective control of intra-muscular regions, the relocation of activity towards the superior region can be explained by the higher frequency of type II fibers in the superior than the inferior region of the upper trapezius muscle (Lindman et al. 1990). A regular recruitment sequence of motor units with fatigue would therefore change the distribution of activity from inferior to superior regions of the upper trapezius muscle. The similar change in spatial distribution of activity with force modulation and fatigue (paper II) supports that redistribution of muscle activity can be induced by an orderly recruitment sequence. Further, the observed changes in spatial distribution of MFCV with force modulation (paper V) support that motor units with dissimilar physiological characteristics are located in different regions within the upper trapezius muscle. In conclusion, the findings of papers II and V indicate that the inhomogeneous spatial activity above the upper trapezius muscle is mediated by recruitment of divergently located motor unit populations in a regular manner, not a selective control of intra-muscular regions.

Region-dependency of motor unit recruitment (differential activation) has been shown to depend systematically on direction of force in the biceps brachii muscle (Desmedt and Godaux 1981; Jongen et al. 1989; Ter Haar Romeny et al. 1984; van Zuylen et al. 1988). During unchanged biomechanical conditions (i.e. sustained contractions), differential activation between intra-muscular regions has not been previously reported. However, this may depend on the operationalization of differential activation. Initially, differential activation was regarded to involve relative changes in activity between regions within a muscle throughout a contraction period (English 1984). Accordingly, redistribution of activity between compartments in cat lateral gastrocnemius muscle with increasing walking speed was considered as differential activation (English 1984). Due to muscle fiber regionalization of the lateral gastrocnemius muscle (English and Letbetter 1982), changes in relative activity between muscle regions were most likely due to orderly recruitment of additional motor units with increased walking speed. Consequently, differential activation compatible with the definition by English (1984) does not require a selective control of regions within a muscle. Subsequently, differential activation was defined as reciprocal reversals of activity between regions within a muscle (Chanaud et al. 1991). In specific,

differential activation required a significant burst of EMG activity in one intra-muscular region whereas the other region either declined, or not changed activity over a series of trials (Dunbar and Macpherson 1993). In this thesis, the definition of differential activation proposed by Chanaud and colleagues (1991) was used. Generally, differential activation observed during the sustained contraction involved significant bursts of EMG activity in one region with no change in activity in the other region (paper III). Because reciprocal reversals of activity (increase - decrease) between intra-muscular regions was rarely seen, complete selective control of regions within the biceps brachii cannot be claimed based on the observations in paper III.

Partial selective control of intra-muscular regions requires an uneven synaptic input to motoneurons innervating regions of a muscle (Chanaud et al. 1991). Several sources have been documented to provide uneven synaptic input to motoneurons innervating a single muscle (Cameron et al. 1981; Hamm et al. 1985; Stuart et al. 1988; Windhorst et al. 1989). The best documented source is the Ia excitatory input from the homologous muscle. The synaptic input from these muscle afferents is shown to be more effective to motoneurons situated in the same region as the Ia spindle than motoneurons in other regions of the muscle (Cohen 1953). Therefore, the Ia afferents can provide a more or less selective synaptic input to groups of motoneurons within a pool (Hamm et al. 1985), activating a single region within anatomical complex muscles (Windhorst et al. 1989). Furthermore, the terminals from a renshaw cell do not cover the whole homologous motoneuron pool, but are restricted to a few nearby located motoneurons (Eccles et al. 1961; Romanes 1951). The recurrent inhibitory input from renshaw cells can therefore be unevenly distributed to motoneurons within a pool. Moreover, the observed differential activation requires repeated shifts in distribution of synaptic input throughout a sustained contraction. A plausible source to such changes in synaptic input is the inhibitory effect from small muscle afferents (group III and IV) on renshaw cells (Windhorst et al. 1997) and Ia muscle afferents (Kniffki et al. 1981). The group III and IV afferents are sensitive to accumulation of fatigue associated metabolites (Bigland-Ritchie et al. 1986; Hayward et al. 1991), and shown to induce region-dependent changes in activity within the trapezius muscle (Falla et al. 2007; Madeleine et al. 2006). As a result, shifts in accumulation of metabolites between intra-

muscular regions could provide repeated changes in distribution of synaptic input to the motoneuron pool.

Direct recordings of motoneuron discharges from the spinal cord cannot be carried out in humans. Therefore, knowledge about distribution of synaptic input to a motoneuron pool is restricted. An indirect method for attaining this information is to quantify the degree of synchronization between motor units located within versus between regions of a single muscle (Bremner et al. 1991a). The synchronization between motor units located at different intra-muscular regions is normally similar to the synchronization between motor units from different functionally related synergistic muscles (Bremner et al. 1991a; Huesler et al. 2000), and half of the synchronization between motor units within a single muscle region (Keen and Fuglevand 2004; McIsaac and Fuglevand 2007). Thus, these observations indicate that intra-muscular regions can be selectively controlled to the same degree as synergistic muscles (Bremner et al. 1991b), enabling differential activation of intra-muscular regions (Keen and Fuglevand 2004; McIsaac and Fuglevand 2007). The motor unit synchronization is generally considered to be of mainly descending origin (Semmler et al. 1997). This assumption is based on observations of a normal degree of motor unit synchronization in patients with peripheral deafferentation (Farmer et al. 1993) and muscles without afferent spindles (De Luca et al. 1993), while patients with central lesions have modified degree of motor unit synchronization (Datta et al. 1991; Farmer et al. 1993).

To attain information of the distribution of synaptic input to the motoneuron pool of the biceps brachii, motor unit synchronization was investigated with a novel method (Grönlund et al. 2007) at different locations of the muscle. Consistent with previous studies from other anatomical complex muscles (Bremner et al. 1991a; Keen and Fuglevand 2004; McIsaac and Fuglevand 2007; Reilly et al. 2004), the motor unit synchronization was observed to depend on the location of recording above the biceps brachii muscle (paper IV). This finding indicates that the synaptic input to the motoneuron pool of the biceps brachii muscle is unevenly distributed. An exciting experimental design would be to investigate whether complete selective control of intra-muscular regions can be achieved with appropriate biofeedback on muscle activity from the different regions.

Effects of region-dependent muscle activity on local muscle fatigue

An inevitable consequence of prolonged contractions is local muscle fatigue. Variations in muscle activity are generally considered to reduce the risk of muscle fiber overexertion and accumulation of metabolites in prolonged sustained or repetitive contractions (Mathiassen 1993). In anatomical complex muscles, variations in muscle activity during sustained isometric contractions can be achieved by redistribution of activity between intra-muscular regions (Farina et al. 2006). Therefore, redistribution of activity within anatomical complex muscles has been hypothesized to prevent local muscle fatigue (van Dieen et al. 1993).

Farina and colleagues (2006) observed that the degree of redistribution of spatial activity above the trapezius muscle was positively related to the ability to prevent local muscle fatigue during a sustained sub-maximal contraction. In this thesis, the frequency of differential activation between regions of the biceps brachii was observed to be negatively related to time to exhaustion in a sustained contraction at 25% of MVC (paper III). Several factors could have mediated this finding. The relatively high force level (25% MVC) during the sustained contraction could have a significant impact on the finding. The muscle activation at the end of the sustained contraction (34% maximal RMS) was lower than required for a complete ischemic condition in the biceps brachii (>50% MVC) (Sadamoto et al. 1983). In theory, re-distribution of intra-muscular activation could therefore influence the intra-muscular pressure and blood flow to different regions of the muscle throughout the sustained contraction (Sjögaard et al. 1986). However, parallel modifications in muscle activation and local circulation during sustained contractions are demonstrated to be restricted to very low force levels (<7.5% MVC) (Kouzaki et al. 2003; Kouzaki et al. 2002). Consequently, the sustained force level at 25 % MVC could be too high to provide parallel modifications in local blood flow with differential activation between the intra-muscular regions. The effect of redistribution of intra-muscular activity on blood flow and local muscle fatigue could therefore be limited to prolonged monotonous low level contractions, like computer work.

Augmented blood flow during sustained contractions requires temporary reductions in activity levels (reciprocal activation) (Kouzaki et al. 2003), decreasing the intra-muscular pressure below average arterial pressure (Sjögaard et al. 1986). The

observed differential activation (paper III) involved repeated burst of activity in one region while the activity of the other region remained similar. Previous studies demonstrating a positive relation between degree of redistribution of intra-muscular activity and fatigue resistance observed a reciprocal activation between regions of the upper trapezius muscle (Falla and Farina 2007; Farina et al. 2006). Consequently, a positive effect of intra-muscular inhomogeneous activation on local muscle fatigue is likely to require reciprocal distribution of activity between intra-muscular regions during sustained contractions.

The negative relation between frequency of differential activation and time to exhaustion could be a result of inter-individual differences in muscle fiber type. Type II fibers are more susceptible to fatigue than type I fibers (Enoka and Stuart 1992). Therefore, subjects with high percentage of type II fibers are likely to be more fatigable in sustained contractions at a similar percentage of MVC compared to subjects with low percentage of type II fibers. Since the frequency of differential activation increased throughout the contraction, the differential activation could be a result of local muscle fatigue. Consequently, high frequency differential activation and short time to exhaustion would be likely in subjects with high percentage of type II fibers, explaining the negative relation between the variables.

A promising approach to improve the understanding about mechanisms related to inhomogeneous muscle activity is simultaneous recording of muscle activity (e.g. MCsEMG), local circulation (e.g. near infrared spectroscopy), muscle metabolism (e.g. nuclear magnetic resonance spectroscopy), muscle characteristics (e.g. functional ultrasound) and accumulation of metabolites (microdialysis) from different intra-muscular regions during different tasks. In specific, investigation of effects from differential activation between intra-muscular regions during repetitive or sustained low contraction-levels (~ 5% MVC) would be an interesting theme for future studies.

Region-dependency of physiological characteristics

Muscle fiber characteristics of the upper trapezius muscle are of considerable physiological and clinical interest due to the commonly reported pain and discomfort in the neck and shoulder region (Hagberg and Wegman 1987; Woods 2005). Studies of human cadavers have revealed a different distribution of muscle fiber types and relation

between muscle fiber type and cross-sectional area between regions within the upper trapezius muscle (Johnson et al. 1973; Lindman et al. 1990; Polgar et al. 1973). Due to the invasiveness and induced pain of the muscle biopsy technique, distribution of fiber type and cross-sectional area from different regions of the upper trapezius muscle from living humans is scarce. Non-invasive *in vivo* information of muscle fiber characteristics from a large fraction of the trapezius muscle would therefore be of particular value to ensure representative information (Hägg 2000). Further, such recordings would enable investigations of the association between the distribution of muscle fiber characteristics and muscle activity of intra-muscular regions during different experimental tasks or muscle pain.

In this thesis, analyses of the distribution of MFCV and MFO from a large fraction of the upper trapezius muscle were used to provide *in vivo* and non-invasive information about the region-dependency of muscle fiber characteristics during different experimental tasks. The relative influence of muscle fiber cross-sectional area and dissimilar membrane properties of the muscle fiber types on MFCV has been a debated theme (Blijham et al. 2006; Hakansson 1956; Kupa et al. 1995; Sadoyama et al. 1988). Due to the close relation between cross-sectional area and muscle fiber type in most muscles (e.g. the biceps brachii) (Polgar et al. 1973), the relative influence of these characteristics on MFCV has been difficult to reveal. In the biceps brachii and the inferior region of the upper trapezius muscle, a positive relation between MFCV and generated force was shown (paper V). Whereas in the superior region of the upper trapezius, no consistent changes in MFCV with force modulations was observed (paper V). These findings are in accordance with the unsystematic relation between muscle fiber cross-sectional area and fiber type in the superior region of the upper trapezius muscle, and the positive relation between these muscle fiber characteristics in the biceps brachii and the inferior region of the upper trapzius muscle (Lindman et al. 1990; Polgar et al. 1973). If MFCV is primary determined by fiber type, the MFCV would be expected to increase in both regions of the muscle, i.e. with recruitment of higher threshold motor units with progressively more similar membrane properties as type II fibers. Therefore, the observed changes in MFCV of the biceps brachii and regions of the trapezius muscle with force modulation support that MFCV is mainly determined by

muscle fiber cross-sectional area in an un-fatigued state (Blijham et al. 2006; Hakansson 1956).

Moreover, the general positive relation between motor unit recruitment threshold (motoneuron size) and muscle fiber cross-sectional area (Burke 1981) have led several authors to use MFCV as an indirect descriptor for motor unit recruitment (Andreassen and Arendt-Nielsen 1987; Houtman et al. 2003). The observed inconsistent relation between generated force and MFCV in the superior region of the upper trapezius signify that the MFCV is not an appropriate parameter for determining motor unit recruitment in this region of the trapezius muscle.

The trapezius muscle is characterized by its broad multi-pinnate fiber architecture. The present knowledge of the fiber orientation of the upper trapezius muscle is based on cadaver studies (Johnson et al. 1994). The developed MCsEMG method enabled *in vivo* information about the orientation of active muscle fibers from a large fraction of the trapezius muscle. The observed MFO of the upper trapezius muscle (paper V) was generally in accordance with previous reports from human cadavers (Johnson et al. 1994). This finding supports that the applied method can be used to attain *in vivo* information of muscle fiber architecture during voluntary contractions (Lapatki et al. 2006).

Methodological aspects and considerations

As illustrated in this thesis, the MCsEMG technique enables unique non-invasive and *in vivo* insight into intra-muscular activation, control, state and physiological characteristics. The numerous recording-locations from large fractions of a muscle with the MCsEMG technique are crucial for retrieval of representative information of the activity level from skeletal muscles (Staudenmann et al. 2005). The findings from this thesis highlight that multiple recording locations not only provide representative information, but are also essential for gaining insight into the region-dependent activation, control and distribution of physiological characteristics within anatomical complex muscles. Due to the novelty of the applied MCsEMG methods, several methodological aspects need consideration.

The base of the used MCsEMG grid is concave and semiflexible and fits well with the convex area of the upper trapezius and the biceps brachii muscle. However,

only 56 % of the recordings from female subjects, and 88 % of the recordings from male subjects were considered to be of sufficient signal quality. The problem of attaining MCsEMG data of good quality, especially in female subjects is well known (Sjögaard et al. 2006). The often reported low signal quality of sEMG recordings is attributed to smaller muscle dimensions or thicker subcutaneous fat-layers in females compared to males (Hägg 1993). Thus, the lower signal quality in female subjects in this thesis could partly be explained by smaller muscle dimensions reducing the number of electrodes with appropriate skin contact. However, good signal quality could neither be obtained from several females with minimal subcutaneous fat-layer thickness. Therefore, the problem with low sEMG signal quality in females cannot be attributed to thicker subcutaneous fat-layers only.

Changes in spatial distribution of activity above the biceps brachii and the upper trapezius muscle with modulating force and local muscle fatigue were interpreted to be due to recruitment of motor unit populations. Since motor unit recruitment is not the only factor determining the spatial distribution of activity above a muscle, influences from other factors require consideration. The distance from the motor unit to the recording electrode has a profound impact on the spatial distribution of activity above a muscle (Roeleveld et al. 1997). Both the thickness of the subcutaneous fat-layer (Solomonow et al. 1994) and the motor unit depth (Roeleveld et al. 1997) are positively related to spatial spread of activity, and negatively related to the signal peak amplitude at the surface of the skin. As a result, the subcutaneous fat-layer thickness and motor unit depth influence the sensitivity of the methods applied in paper I, II and III, causing an inter-individual bias. However, intra-subject comparisons in paper I and II are not influenced by this bias. Plausible effects of inter-individual differences in subcutaneous fat-layer thickness or motor unit location on the quantification of differential activation (paper III) were reduced by excluding electrodes located near the partitioning of the heads of the biceps brachii muscle.

The spatial distribution of activity could also be affected by relative movements of the MCsEMG grid and the underlying muscle. Relative movements could be caused by relocation of the MCsEMG grid on the skin and changes of the muscle-shape (i.e. fascicle length, muscle thickness) during contractions. To minimize this influence, the MCsEMG recordings were performed during isometric contractions. Nevertheless,

changes in muscle-shape occur even during isometric contractions (Finni et al. 2003; Hodges et al. 2003). Changes in muscle-shape during force modulation would most likely cause a relative relocation of the innervation zone with respect to the MCsEMG grid. However, in accordance with previous reports (Kleine et al. 2000b) the location of the innervation zone remained similar during the contractions indicating no significant changes in muscle-shape. Moreover, the reproducible changes in spatial distribution of activity within and between subjects with force modulation in the biceps brachii muscle (paper I) and the similar changes in spatial distribution of activity with force modulation and fatigue in the upper trapezius muscle (paper II) indicate a consistent location of the MCsEMG grid relative to the muscle during the contractions. However, relocation of the MCsEMG grid occurred in some subjects between the ramp and the sustained contractions, indicated by a dissimilar spatial distribution at same force level in un-fatigued state (paper II). This methodological problem of relocation of the MCsEMG grid on the skin could be solved by applying adhesive MCsEMG electrodes (Lapatki et al. 2004; Lapatki et al. 2006).

Although the sEMG amplitude is influenced by both the number of active motor units and their firing rate, the changes in spatial distribution of activity were considered to be due to recruitment of motor unit populations (paper I & II). This interpretation was based on the observed monotonous increase in discharge rate of active motor units with force modulation (Milner-Brown et al. 1973; Tanji and Kato 1972) and minor changes during sustained contractions (Garland et al. 1994; Westgaard and De Luca 2001). Consequently, the discharge rate was expected to influence the average sEMG amplitude of the muscle, but not the spatial distribution of muscle activity.

The applied method for estimation of motor unit synchronization has been shown by simulations to have a sensitivity of 0.1 units pr 5 % change in motor unit synchronization (Grönlund et al. 2007). Moreover, changes in MFCV (within a range of 3-5 m/s) cause a bias of the motor unit synchronization descriptor of 0.1 units at most. The observed difference in motor unit synchronization index (0.05 units) between the medial and lateral regions of the biceps brachii muscle is therefore less than the “reliable” sensitivity of the method. However, the decreased MFCV in the biceps brachii muscle with local muscle fatigue was observed to be quite homogeneous above the entire muscle (i.e. < 0.5 m/s difference between the long and short head) (paper V).

Thus, the observed different motor unit synchronization index between the regions of the biceps brachii is most likely not caused by inhomogeneous changes in MFCV above the muscle. Since the novel descriptor for the first time was used on experimental data to describe changes in MU synchronization with fatigue, final physiological conclusions concerning distribution of common synaptic input to the motoneuron pool and association between MU synchronization and force tremor cannot be drawn from this study alone.

An important aspect of the applied method to retrieve MFCV and MFO (paper V) is that the estimates are based on spatial density regions of populations of detected MUAPs (Figure 4D). Single physiological incorrect MFCV or MFO will therefore be suppressed, not significantly influencing the estimated MFCV and MFO.

In conclusion, a methodological take-home message from this thesis is that retrieval of information of muscle activity, control, state and physiological characteristics of anatomical complex muscles ought to be based on recordings from a substantial area of the muscle (i.e. several recording locations above respective intra-muscular regions).

Conclusions

The main objective of this thesis was to investigate the spatial dependency of the activation, control and the physiological characteristics within the biceps brachii and the upper trapezius muscle with the MCsEMG technique. The conclusions based on the findings from this thesis are summarized as follows:

1) The biceps brachii and the upper trapezius muscle are inhomogeneously activated during force regulation and fatigue due to recruitment of different located motor unit populations within the muscles.
2) The recruitment sequence of upper trapezius motor unit populations is similar during sustained and ramp contractions, indicating an orderly recruitment sequence of motor unit populations during sustained contractions.
3) Regions within the biceps brachii muscle are differentially activated during sustained contractions, indicating a partially selective control of intra-muscular regions of the muscle.
4) The differential activations between regions within the biceps brachii are not positively associated with time to exhaustion during a sustained contraction at 25% MVC.
5) The region-dependency of the motor unit synchronization descriptor indicates an uneven distribution of common synaptic input to the motoneuron pool of the biceps brachii muscle.
6) Consistent with previous reports from human cadavers, the physiological characteristics of the upper trapezius muscle are dependent on the intra-muscular region of the muscle.

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Paper I

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Inhomogeneities in muscle activation reveal motor unit recruitment

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Inhomogeneities in muscle activation reveal motor unit recruitment

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Abstract

This paper presents a novel method to quantify spatial changes in muscle activation pattern by multi-channel surface electromyography (MCSEMG) in order to investigate motor unit recruitment variation. The method is based on non-uniform distributions of motor units that cause spatial inhomogeneous muscle activation. To evaluate the method, 15 subjects performed three isometric elbow flexion contractions consisting of slow sinusoidal changes in force ranging from 0% to 80% of the maximal voluntary contraction. MCSEMG electrodes were placed in a 10×13 grid over the *biceps brachii* muscle. From all channels, root mean square (RMS) values of bipolar leadings were computed over 0.5 s epochs over the whole recording. Thereafter, correlation coefficients were calculated between the RMS values at one epoch, with the RMS values at another epoch. Results showed consistent spatial changes in the distribution of RMS at different contraction levels up to 80% of maximal voluntary contraction and when comparing increasing and decreasing contractions at the same force level. These findings are reproducible within and between subjects, and in agreement with physiological phenomena and therefore indicate that the spatial inhomogeneities of motor unit properties in the *biceps brachii* muscle can be used to study changes in motor unit recruitment.

Keywords: Inhomogeneous muscle activation; Multi-channel surface electromyography; Spatial RMS distribution; Motor unit recruitment

1. Introduction

In many fields of study, like neurology, ergonomics and sports, it is of major interest to be able to investigate motor unit (MU) recruitment strategies. The most commonly used techniques to study muscular activation patterns consist of needle and wire electrode electromyography (EMG) (e.g. [25]). In addition, it is possible to use the median frequency of the surface EMG (sEMG) power spectrum to obtain some information about this topic [22]. Recently, different techniques based on multi-channel sEMG (MCSEMG) were presented and used for this purpose (e.g. [20,5,8]). An advantage of MCSEMG, compared to other methods to investigate MU recruitment, besides its non-invasiveness, is that it is not constrained to analyze recruitment of only a few MUs, but can investigate MU recruitment in a large spatial area of a muscle. Although single MU activity can be assessed through MCSEMG [16,12,5], to date this technique is not automatic, time consuming and only applicable in a few subjects.

Changes in the EMG amplitude distribution obtained with MCSEMG have revealed spatial inhomogeneous activation of muscles in isometric contractions at different force levels [19,13,6]. In other words, different parts of a muscle are dominantly active as a function of the force level. Such inhomogeneities can be explained by the observation that muscle fiber types are not randomly distributed, but organized in regions, with different histochemical muscle fiber composition [2]. Then, recruitment of MUs according to the size principle [7] would,

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in a muscle with these characteristics, cause a spatial inhomogeneous activation in a single task with changing force levels.

Studies applying MCSEMG to examine spatial intramuscular activation have applied three main techniques to describe this phenomenon: (1) by reporting the change in the root mean square (RMS) distribution over the muscle by topographical visualization, called mapping [19,20], (2) by illustrating mapping of MU action potentials with triggered averaging [12], (3) by calculating and displaying the cross-correlation of each individual channel related to a selected reference channel [6,18].

This paper presents a novel method to quantify spatial variations in muscle activation patterns due to MU recruitment modulation. Like the above-mentioned papers, this technique is based on spatial inhomogeneities and the application of MCSEMG, but it gives objective and quantitative results, involves all electrodes simultaneously, and is a relative easy applicable. In short, the amplitude distribution over the skin during one epoch is compared with the amplitude distribution over the skin during another epoch by calculating the correlation coefficient between all sEMG amplitudes in the two epochs. A low correlation coefficient then indicates a large change.

To evaluate the method, 15 subjects performed isometric elbow flexions with slowly changing contraction levels between 0% and 80% of maximal voluntary contraction (MVC) with MCSEMG electrodes placed in a 10×13 grid over the *biceps brachii* muscle. The *biceps brachii* muscle was chosen because spatial inhomogeneities have been found previously [11,15,19], it has been reported to have an uneven fiber type distribution [10], an architectural and nervous compartmentalization [21], and recruitment of MUs occurs almost throughout the complete range of force output in this muscle [14]. If the muscle is inhomogeneously activated, it is expected that (1) the amplitude distribution changes with contraction level because of recruitment of additional MUs, and (2) the amplitude distribution at the same force level during increasing compared to decreasing force generation differ, since MU recruitment strategies differ between increasing and decreasing force tasks [4]. Furthermore, it is expected that these changes in amplitude distribution are reproducible and show changes in the correlation coefficient.

2. Method

2.1. Subjects

Fifteen subjects voluntarily participated in the experiment. All subjects were males, between 24 and 37 years of age, with no prior injury in the upper extremities. The protocol was approved by a medical ethical committee and the subjects signed an informed consent prior to the experiment.

2.2. Equipment

An isokinetic dynamometer (KIN-COM 500H, Chattanooga Group, Inc., Hixson, TN, USA) was used to standardize position and measure force production. The force signal was sampled at 1 kHz using a wearable wireless DAQ system [9] and synchronized with the EMG recordings.

The force signal from the dynamometer was also fed to a visual feedback device in real-time. This device consisted of three columns of diodes, each with 80 elements representing force between 0% and 100% MVC. Enlightened elements in the middle column represented the force produced by the subject. Enlightened elements in the two most outer columns represented the target force.

A multi-channel system (ActiveOne, Biosemi Biomedical Instrumentation, the Netherlands) with a 130-channel grid was used to acquire sEMG data. The multi-electrode array consisted of 13×10 gold covered pin electrodes placed at a holder of 7×5 cm. The inter-electrode distance was 5 mm. Data were recorded with a common reference (unipolar recordings) at a sampling rate of 2048 Hz/channel, and converted with 16 bit resolution. The input range was ±66 mV. Anti-aliasing filter had a fifth-order sinc response with a -3 dB point at 1/5th of the sample rate. A trigger signal at the beginning of each test was used to synchronize the sEMG and force recordings.

2.3. Procedure

After informing the subjects about the procedure, they were placed in the dynamometer with their hip and back strapped to the chair. The right arm and wrist of the subject were attached to the lever arm foundation of the dynamometer. The elbow support was attached to the lever arm such that the motor axle center coincided with the elbow rotation center of the subject. The wrist support was adjusted to each subject ensuring a proper grip of the handle without diverging the elbow and motor rotation center. The dynamometer chair position (forward–backward) and lever arm foundation (right–left and height) was adjusted for each subject to sit in a comfortable position. The other parameters were held constant, affording all muscle contractions to be isometric with approximately 130° in the elbow joint. To determine MVC, the subjects performed two maximal contractions, lasting two seconds each, with a recovery period of 3 min between each contraction. The subjects received visual feedback of the force generation during the task. The force data recorded during the MVC of each subject was filtered using a 0.2 s moving average

window. The MVC was determined as the highest obtained value after averaging.

Subsequently, the subjects were instructed to perform three contractions with sinusoidal force modulations between 0% and 80% of MVC. The subjects followed the force tracking displayed on the feedback system. Each sinusoid started at its lowest point (target force of 0, phase shift of -0.5π and lasted 20 s, with 20 s (target force 0) rest between each sinusoid. The total test period was thus 100 s (three 20-s sinusoids with two 20-s brakes). Three contractions with both increasing and decreasing force modulations were performed to be able to investigate the consistency and reliability in this method. Contraction levels from 0% to 80% of MVC were applied to investigate the range where recruitment of MUs in *biceps brachii* muscle occurs [14].

2.4. Data analyses

The force data were low-pass filtered (15 Hz), and divided in epochs of 500 ms. The average force of each epoch was calculated.

The analyses of the sEMG data started with removal of the EMG-channels of poor quality (due to bad electrode to skin contact) by visual inspection. Subsequently, bipolar configurations were calculated of the remaining channels by taking the difference between channels in proximal-distal direction. Thereafter, the sEMG data were band-pass filtered (20–400 Hz). Root mean square (RMS) values of all bipolar sEMG signals were calculated over epochs of 500 ms (the same epochs as the force data). The channel with median RMS of each subject was applied to illustrate changes in activation of the muscle. Thereafter, in order to quantify RMS distribution changes, correlation coefficients were calculated between RMS values of all electrode pairs at one time epoch, with the RMS values of the same electrode pairs at another time epoch. Correlation coefficients were obtained for all possible combinations within the recording epoch (100 s), resulting in a matrix of 200×200 correlations. In this way, a change in correlation in time compared to any other time epoch was obtained.

Because the RMS values were calculated from epochs of 0.5 s, and no visual delay between force and RMS was present (Fig. 1), the electromechanical delay was not calculated and applied in the analyses. All analysis of the RMS correlation changes were done relative to mean quantified force.

2.5. Statistics

The correlation coefficients between the RMS distribution at the first epoch with 25% and 80% of MVC and all other time epochs were used for statistical analysis. To test whether changes in RMS distribution occurred, the 95% confidence intervals of these signals were determined. Since the RMS distribution must be tested at same force levels in all subjects, and the subjects did not precisely follow the target force, interpolated correlation values were taken at force levels of 0–80% MVC in steps of 10% using a hermite interpolant fit between the normalized force and RMS correlation.

The Levene test for homogeneity of variance was applied to test whether the correlation coefficients were Gaussian distributed. General linear model with repeated measurements was applied to test whether the RMS distribution changed with force, was different between the three contractions, and whether a divergence in RMS correlation between the ascending and descending contraction levels was present.

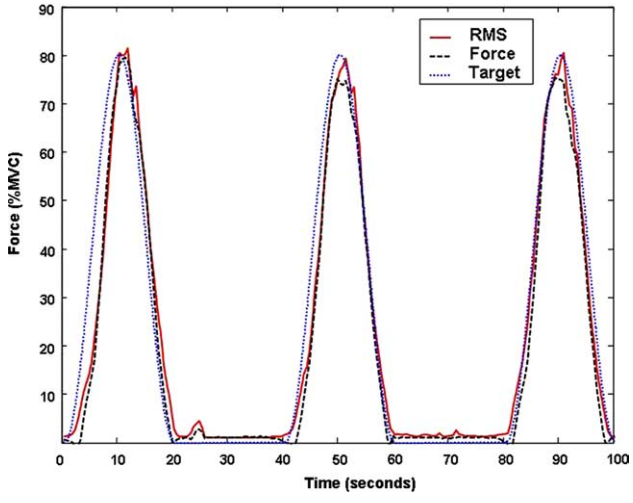

Fig. 1. Mean changes in time of target force, generated force and RMS.

3. Results

Visual inspection of Fig. 1 reveals that the subjects managed to follow the target force, except for a time delay during the first contraction. The EMG amplitude expressed as the median RMS value of all EMG channels, roughly followed the force curve in all subjects (Fig. 1). No significant differences were found in force or in RMS between the three trials or between ascending and descending forces.

Fig. 2 shows typical examples of the RMS distribution at 10% of MVC and 70% of MVC of one subject. The correlation coefficient of the RMS of the electrodes at these two force levels is $r = 0.6$. The black spots represent removed electrodes due to poor connection. In this subject, the high RMS distribution seems to be more spatially clustered and laterally distributed at high contraction levels than at lower contraction levels.

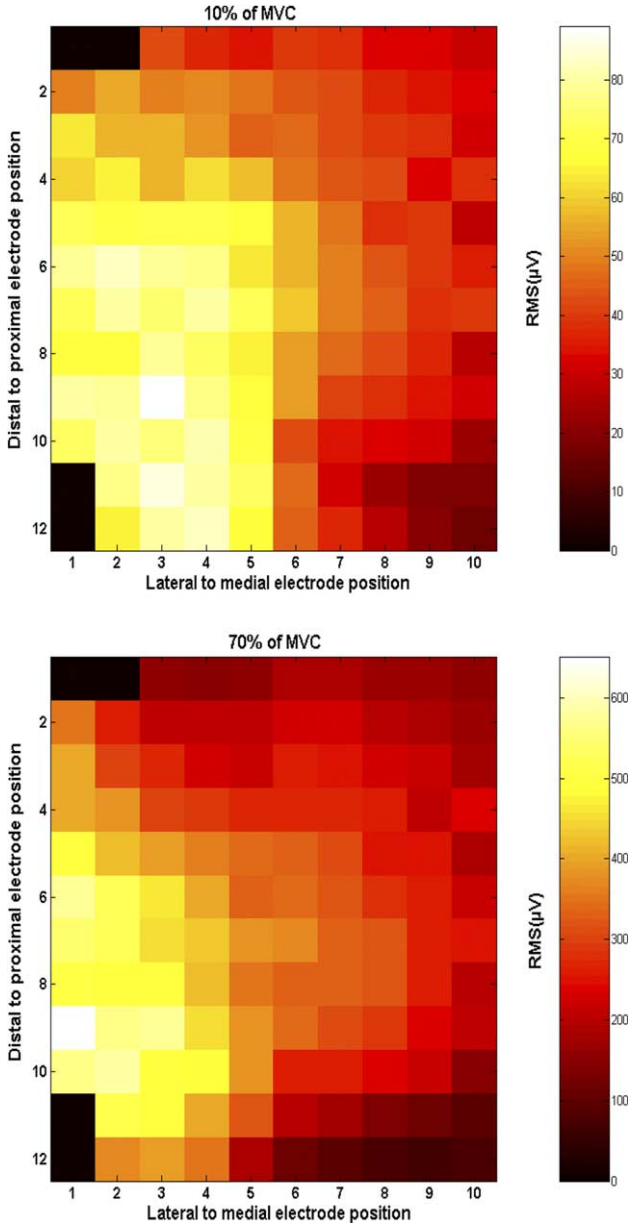

Fig. 2. A typical example of RMS distribution over *m. biceps brachii* at 10% and 70% of MVC of one subject. The bright areas illustrate high RMS values and the dark areas illustrate low RMS values.

The mean and 95% confidence intervals of the correlation between RMS values at 80% and 25% of MVC and all other time epochs are shown in Figs. 3(a) and (b), respectively. The time scale is the same as in Fig. 1. Non-overlapping 95% confidence intervals demonstrate a change in RMS correlation with time and different contraction levels.

Figs. 4(a) and (b) illustrate the mean change in RMS correlation with modification in target force in the three contractions of all subjects with respect to the reference epochs. For the first contraction cycle, the 95% confidence interval is shown. Investigating the correlations with respect to the reference epoch 80% MVC (Fig. 4(a)), no significant differences between the three trials or between ascending and descending contraction levels were found. However, investigating the correlations with respect to the reference epoch 25% MVC, there was a difference in RMS correlation between the first two and the last contraction ($p < 0.05$), and between ascending and descending contraction levels ($p < 0.05$). In agreement with Fig. 3(a), Fig. 4(a) illustrates that changes in RMS correlation occur in contraction levels up to 80% of MVC.

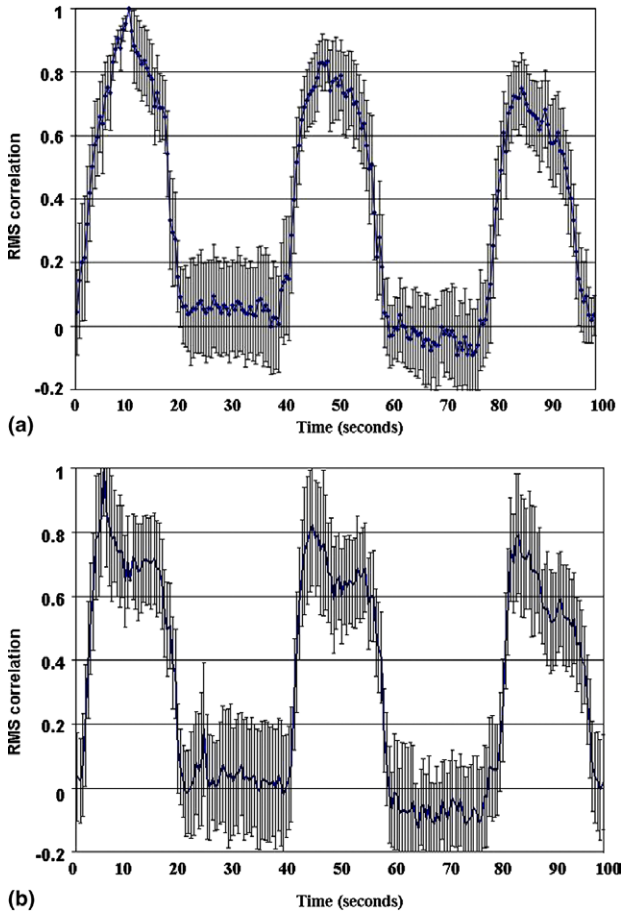

Fig. 3. The mean RMS correlation with 95% confidence intervals calculated with respect to a reference epoch at 80% (3a) and 25% (3b) of MVC.

Figs. 5(a) and (b) express the relationship between the mean force generation and mean RMS correlation of all subjects from 0% to 80% of MVC in all three contraction cycles. The RMS correlations in Figs. 5(a) and (b) are calculated relative to the 80% and 25% MVC reference epoch, respectively. The RMS correlation, calculated from the reference epoch of 80% of MVC, was not different between ascending and descending force generation (Fig. 5(a)). The RMS correlation, calculated from the reference epoch of 25% of MVC, was divergent at ascending and descending force generation ($p < 0.05$; Fig. 5(b)).

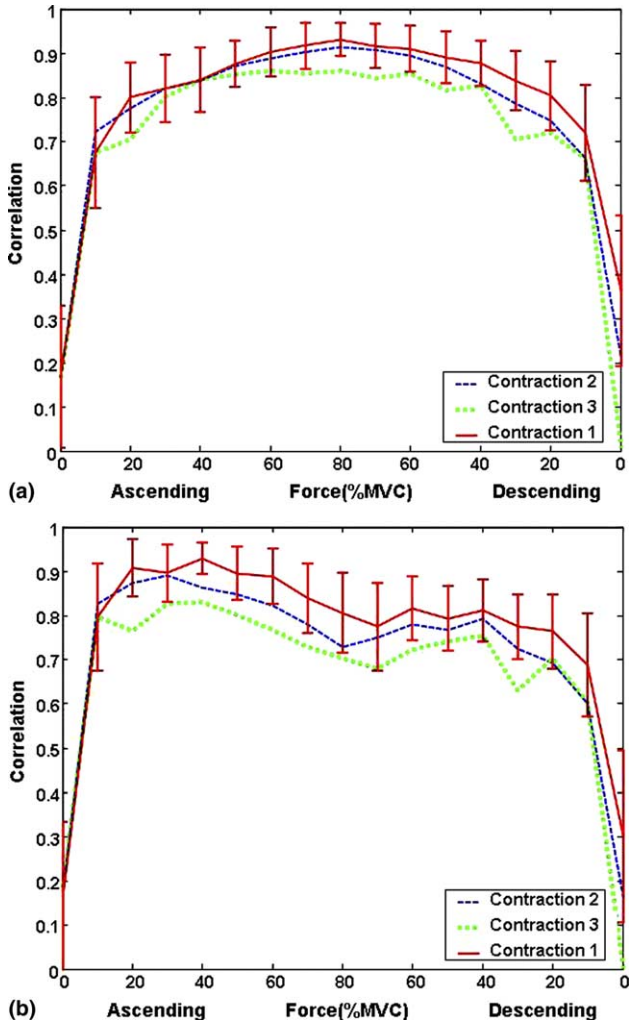

Fig. 4. The mean change in RMS correlation with generated force (% of MVC) of the three contractions calculated with respect to reference epoch at 80% (4a) and 25% (4b) of MVC. 95% confidence intervals are included to the results of the first contraction. The confidence intervals of the two other contractions were approximately the same as in the first contraction.

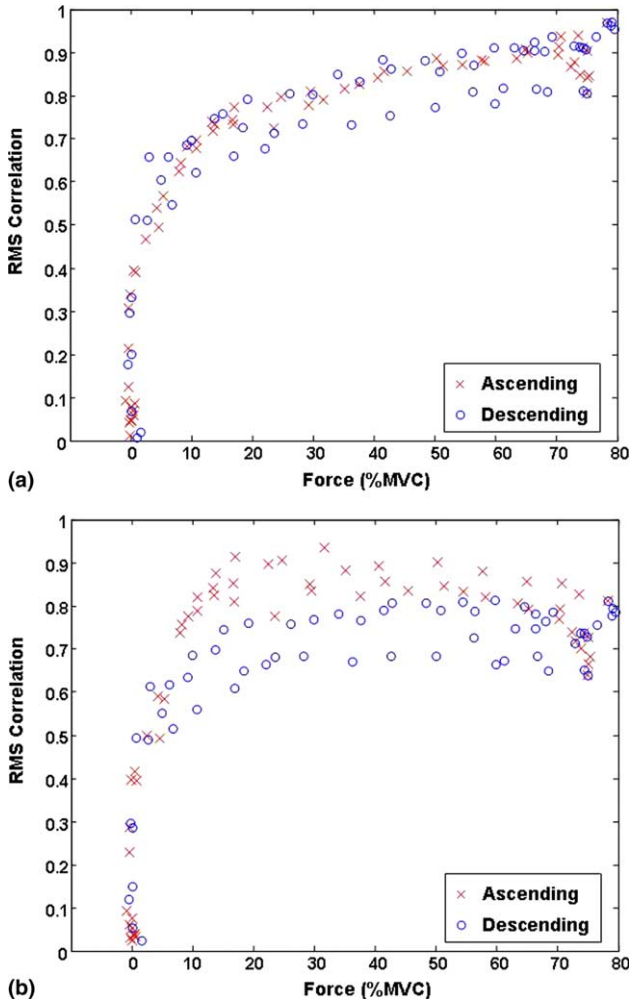

Fig. 5. The relationship between the mean generated force (% of MVC) at ascending (x) and descending (o) force levels and mean RMS correlation calculated with respect to a reference epoch at 80% (5a) and 25% (5b) of MVC.

4. Discussion

The results show (1) that the calculated RMS correlations varied in a consistent manner with altered contraction levels, (2) that changes in RMS correlation are present throughout the total range of force generation from 0% to 80% of MVC and (3) that the RMS correlation deviated between ascending and descending contraction levels.

The modification in RMS correlations with alternating force production supports that recruitment of MUs are not randomly scattered, but evolve in distinct regions in the *biceps brachii* muscle. This finding is in accordance with results from other studies applying MCSEMG with isometric contractions with changing contraction levels [13,19].

Current methods to study spatial activation patterns with MCSEMG have described the intra-muscular changes that occur at different contraction levels [6,13]. The quite consistent changes in RMS correlation with altering contraction levels, seen in Figs. 3(a) and (b), indicate that this method is reliable, and can be applied to quantify intra-muscular spatial activation patterns.

The high RMS correlation between equivalent force levels during the first two trials indicates a stable and low variation in MU recruitment during one specific task. This illustrates that the inhomogeneous activation of *m. biceps brachii*, in this constrained task, is quite consistent. A reproducible recruitment order and recruitment thresholds of MUs are earlier observed in isometric contractions at a particular elbow angle of *m. biceps brachii* [23]. The unvarying inhomogeneous activation of *m. biceps brachii* is in agreement with the size principle, where the recruitment of MUs not occurs

in a random and fluctuating order in a motor neuron pool, but in a regular manner [7].

Despite general consistent RMS correlation changes with force, a different pattern was found in the descending force phase of the third contraction (Fig. 4(b)). One plausible explanation for this change in amplitude distribution is fatigue since the subject performed high contraction levels with short rest periods. Moreover, previously similar changes in the distribution of activation have been observed in prolonged contractions in the *trapezius* muscle [13].

The modulation of force generation of a muscle is accomplished by a combination of rate coding of individual MUs and recruitment of more and larger MUs. The range where recruitment of new MUs contributes to produce force is very different from muscle to muscle, where recruitment almost occurs throughout the complete range of force output in *m. biceps brachii*, but only participates in force generation until 50% of MVC in *m.* adductor pollicis [14]. The modification in RMS correlation even at contraction levels of 80% of MVC (Fig. 4(a)) is in agreement with findings that MU recruitment occurs almost throughout the complete force generation range in *m. biceps brachii* [14].

A few studies have documented a deviation between recruitment and derecruitment of MUs [3,17,4]. Romaiguere et al. [17] have demonstrated that mean thresholds of MUs during derecruitment is lower than during recruitment, indicating that there are more active MUs at decreasing than at increasing force generation. Another aspect is that the discharge rate of the active MUs tends to rapidly stabilize during contraction, and subsequently decrease below this level, with the consequence that the mean discharge rate of the active MUs is higher at each contraction level when the force is augmented than when it is decreased [17]. The deviating recruitment and rate modulation during ascending and descending force generation could be a motor control strategy to counteract the effects of muscle fatigue, perhaps by drawing the active MUs closer to recruitment threshold, initiating a substitution in recruited MUs [24]. The asymmetrical RMS correlations from the reference epoch of 25% of MVC between ascending and descending contraction levels (Figs. 4(b) and 5(b)) support the presence of dissimilar force gradation mechanisms in ascending and descending force generation.

In this paper, the change in amplitude distribution was interpreted to be due to recruitment of MUs, despite that the sEMG amplitude is influenced by both the number of active MUs and their firing rate. Theoretically, differences between active MUs in the relative firing rate changes with force level could also cause this type of change in amplitude distribution. However, the change in firing rate with force level is almost equal for the different MUs [4]. Therefore, the firing rate is expected to influence the absolute sEMG amplitudes, but not it's distribution.

5. Conclusion

The modification in RMS correlations with alternating force production of all subjects implies that recruitment of MUs are not randomly scattered, but evolve in distinct regions in *m. biceps brachii*. The high RMS correlation between equivalent force levels indicates a stable MU recruitment sequence during this specific task. The changes in RMS correlation throughout the performed force generation range from 0% to 80% of MVC, indicates that recruitment of MUs contributes to force generation at high contraction levels in *m. biceps brachii*. The asymmetrical RMS correlations in the ascending and descending contraction levels indicate a presence of dissimilar force gradation strategies. The consistent alteration in RMS correlation in accordance with theory on recruitment modulation [1,17] implies that this is a reliable and valid method to study spatial inhomogeneous muscle activation in humans.

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Paper II

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EMG amplitude distribution changes over the upper trapezius muscle are similar in sustained and ramp contractions

by

Holtermann A, and Roeleveld K

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Paper III

Acta Physiologica (2007) In Press

Differential activation of regions within the biceps brachii muscle during fatigue

by

Holtermann A, Grönlund C, Karlsson JS, and Roeleveld K

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Paper IV

Journal of Electromyography and Kinesiology (2007) In Press

Motor unit synchronization during fatigue: Described with a novel sEMG method based on large motor unit samples

by

Holtermann A, Grönlund C, Karlsson JS, and Roeleveld K

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Motor unit synchronization during fatigue: Described with a novel sEMG method based on large motor unit samples

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Abstract

The amount of documented increase in motor unit (MU) synchronization with fatigue and its possible relation with force tremor varies largely, possibly due to inhomogeneous muscle activation and methodological discrepancies and limitations. The aim of this study was to apply a novel surface electromyographical (EMG) descriptor for MU synchronization based on large MU populations to examine changes in MU synchronization with fatigue at different sites of a muscle and its relation to tremor. Twenty-four subjects performed an isometric elbow flexion at 25% of maximal voluntary contraction until exhaustion. Monopolar EMG signals were recorded using a grid of 130 electrodes above the biceps brachii. Changes in MU synchronization were estimated based on the sub-band skewness of EMG signals and tremor by the coefficient of variation in force. The synchronization descriptor was dependent on recording site and increased with fatigue together with tremor. There was a general association between these two parameters, but not between their fluctuations. These results are in agreement with other surface EMG studies and indicate that the novel descriptor can be used to attain information of synchronization between large MU populations during fatigue that cannot be retrieved with intra-muscular EMG.

Keywords: Force tremor; Electrode location; Multi-channel surface EMG; Motor unit synchronization; Fatigue

1. Introduction

Motor unit (MU) synchronization is defined as a higher occurrence of simultaneous discharge of action potentials from different MUs than expected by chance. The consequences of this communality of MU activity have been a topic for debate in several decades (Bigland and Lippold, 1954; Buchthal and Madsen, 1950; Milner-Brown and Lee, 1975; Sears and Stagg, 1976). In particular, MU synchronization has been claimed to cause involuntary fluctuations in motor output, defined as tremor (Halliday and Redfearn, 1956; Hortobagyi et al., 2003; Mendell and Henneman, 1971; Yao et al., 2000).

Studies inducing MU synchronization experimentally by stimulation (Allum et al., 1978) or by applying computer modelling (Yao et al., 2000) have shown that MU synchronization increases the amplitude of tremor, and is the most likely cause to tremor (Taylor et al., 2003). On the contrary, most experimental studies have failed to attain an association between MU synchronization and tremor (Dietz et al., 1976; Logigian et al., 1988; Semmler et al., 2000; Semmler and Nordstrom, 1995; Semmler and Nordstrom, 1998). Consequently, the role of MU synchronization in generation of tremor is poorly understood (Enoka et al., 2003; Semmler, 2002).

Under normal conditions, MU synchronization and tremor are weak in healthy individuals (Dietz et al., 1976;

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Semmler and Nordstrom, 1995; Semmler and Nordstrom, 1998). Muscle fatigue, however, is known to induce tremor also in healthy subjects (Arihara and Sakamoto, 1999; Hunter and Enoka, 2003; Loscher et al., 1994). Like other types of tremor, such fatigue induced tremor has been associated with increased MU synchronization (Lloyd, 1971; Mori, 1973). However, due to MU synchronization not is observed to increase with fatigue when recorded directly by cross correlating firings of individual MUs (cross-correlation method) (Nordstrom et al., 1990), the association between MU synchronization and tremor is without experimental evidence. The lack of consistent experimental support for the relation between MU synchronization and tremor might be due to several methodological limitations in the estimation of MU synchronization.

First, MU synchronization has been estimated directly by the cross-correlation method obtained by needle or wire electromyography (EMG) or by using changes in signal characteristics of surface EMG (sEMG). The main problem with the application of needle or wire EMG lies in the low number of investigated MUs from a small part of the muscle (Semmler and Nordstrom, 1995). This makes the estimated level of MU synchronization not necessarily representative for the entire muscle (Semmler, 2002) and might blur the association with force tremor. On the other hand, the methods to obtain MU synchronization from the sEMG signal (Del Santo et al., 2006; Farina et al., 2002; Kleine et al., 2001) are dependent on muscle fiber conduction velocity (MFCV) and therefore constricted to un-fatigued contractions since MFCV is affected by fatigue (Arendt-Nielsen et al., 1989). Recently, we developed a new method to quantify changes in level of MU synchronization using sEMG (Grönlund et al., accepted). This method has a demonstrated low dependency on MFCV and is therefore suitable to apply during fatiguing contractions.

Second, the association between MU synchronization and force tremor might be influenced by and thus vary with the location of recording within a compartmentalized muscle. Like many other activation characteristics (Holtermann et al., 2005; Ter Haar Romeny et al., 1984), the level of MU synchronization has been shown to depend on the localization of the MUs within single compartmentalized muscles (Keen and Fuglevand, 2004; Reilly et al., 2004). Therefore, its relation with tremor might also depend on the recording location.

Another factor that might explain the discrepancies between computer models and experimental studies is the effect of electrode location with respect to the innervation zone (IZ). The time-dependency of action potentials between MUs will be influenced by the recording distance from the IZ due to the different MFCV of the MUs. However, this methodological issue has not been previously examined in experimental studies.

The aim of this study was to examine how the novel sEMG descriptor for MU synchronization from large MU populations changes with fatigue at different sites of a muscle and how it is related to force tremor. For this reason, multi-channel sEMG signals were acquired from a 6×4.5 cm area at the distal part of the biceps brachii during a sub-maximal contraction of elbow flexion at 25% of maximal voluntary contraction (MVC) until exhaustion. MU synchronization was estimated using a method proven to be minimally dependent on MFCV (Grönlund et al., accepted) and subsequently correlated with fluctuations in force throughout the fatiguing contraction. The variables were calculated in 10 s windows, and thus only information on fluctuations at frequencies less than 0.1 Hz were obtained.

2. Methods

2.1. Subjects

Thirty-nine male subjects participated in the study (mean age 22.6, standard deviation 2.8). None of the subjects had previous injuries of the upper limbs and all participated regularly in different exercises and sports. The study was approved by the Regional Committee for medical science and ethics, University hospital, NTNU, Trondheim, Norway.

2.2. Exercise protocol

The subjects performed isometric elbow flexion with the dominant arm using a dynamometer (BIODEX System 3 Pro, Biodex Medical Systems, Shirley, New York, USA). The experimental setup is illustrated in Fig. 1.

The subjects performed three sessions of isometric force modulation to get familiarized with the experimental setting. To determine MVC, the subjects carried out three maximal contractions of 4 s duration, with at least 1 min recovery period

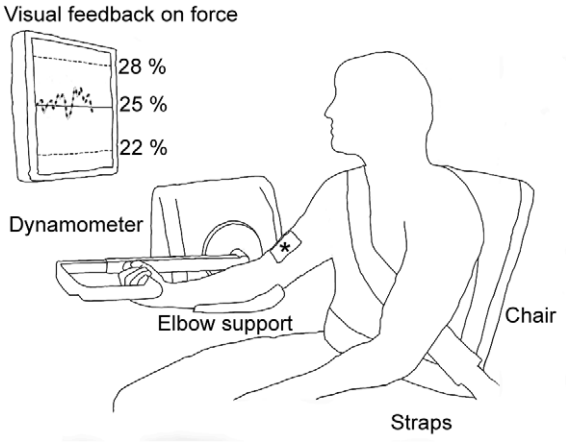

Fig. 1. Schematic illustration of the experimental setup. The dynamometer was adjusted to the subject to ensure a maintained stereotype position throughout the experiment (the hip, back and shoulder strapped to the chair). The anatomical center of rotation of the elbow joint of the dominant arm was positioned on an elbow support aligned with the center of rotation of the arm foundation of the dynamometer. The subject held a firmly fixed handle with a supinated position of the forearm to reduce influence of the brachioradialis muscle. The lever arm foundation of the dynamometer was adjusted to obtain 120 degrees of the elbow joint and ensuring a proper grip of the handle.

between each contraction. The subjects received visual feedback of the force generation during the task from a monitor. The highest force from the three trials was considered as maximal force and used to calculate force target during the sub-maximal contraction.

At least 10 min after the MVC, an isometric sub-maximal fatiguing contraction of elbow flexion was performed at 25% of MVC until exhaustion. The subject received target and feedback of the generated force in the range 20–30% of MVC on a monitor straight in front of the subject. The force target was shown as a solid line at 25% MVC. In addition, two dashed lines were displayed at 22% and 28% of MVC. The instant feedback of the generated force was displayed as horizontal dotted markers. The target and feedback was displayed 15 s after and the target 15 s before real time. The instruction to the subject was to generate a steady force as close as possible to the target without changing the position of the hand, elbow or shoulder until complete exhaustion. The orientation of the hand, elbow and shoulder was carefully inspected. Exhaustion was determined when the generated force was below the dashed line at 22% of MVC for more than 1 s. The subject did not receive any verbal encouragement during the sub-maximal contraction (see Fig. 2).

2.3. Force and surface EMG acquisition

The force signal was acquired by sampling the analogue force signal output from the dynamometer at 1000 Hz (converted from a range of ±5 V with 16 bit resolution). The dynamometer output signal was ±5 V, at a range of 0–172 Nm, presenting 29 mV/Nm.

sEMG signals were recorded using an electrode-grid device (modified ActiveOne, BioSemi, Amsterdam, The Netherlands) consisting of 13 by 10 active electrodes with 1.5 mm electrode diameter and 5 mm inter electrode distance, covering 6 × 4.5 cm of skin surface (Fig. 1). The electrode grid was placed on the skin above the biceps brachii muscle of the dominant arm in parallel with the humerus, distal to the innervation (IZ) zone running medial to lateral midway between the origin and insertion of the biceps (Masuda et al., 1985). The middle of the electrode grid was precisely placed on the partitioning of the two heads (based on palpation) in order to obtain signals from both the medial and lateral heads, respectively. To prevent movement of the electrodes and generate a stable pressure on the skin, the electrode grid was firmly fixed to the skin with two elastic straps fastened to each corner of the electrode grid and taping to the upper arm of the subjects. Signals were recorded from all electrodes with a common reference placed on the seventh cervical vertebra (monopolar recordings), converted from a range of ±33 mV with 16 bit resolution at a sampling frequency of 2048 Hz. The anti-aliasing filter was a 5th-order Bessel with −3 dB gain at 512 Hz. The force and sEMG acquisition was synchronized in time by a common trigger pulse.

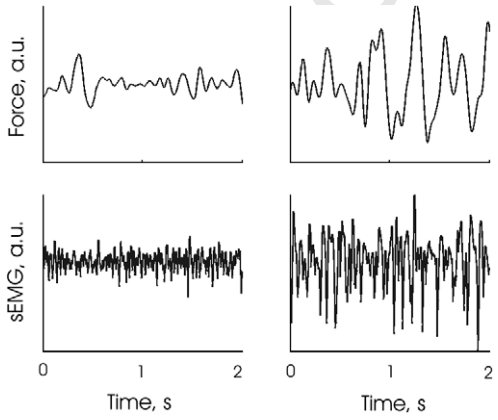

Fig. 2. Example of force signals and sEMG signals from initial and final parts of a 25% MVC isometric fatiguing contraction. The amplitude of the oscillations is prominently increased in the force signal while both amplitude and distribution is changed in the sEMG signal.

2.4. Data quality check

Low quality recordings with poor electrode-skin contact and heavy power-line interference were identified automatically (Grönlund et al., 2005) and omitted from further processing. The method calculates the standard deviation (SD) of each of the 130 signals in two time windows with different lengths. Signals having extreme SD values as compared to the bulk of the signals are classified as outliers (Grönlund et al., 2005). A recording was discarded if more than 10% of its total 130 signals had classified outliers more than 5% of the time.

2.5. Motor unit synchronization index, force tremor and their association

Motor unit synchronization was quantified using the descriptor proposed by Grönlund et al. (accepted). The descriptor, *the sub-band skewness*, was applied since it has proven low dependency of changes in MFCV (e.g. manifested during muscle fatigue) and thus can distinguish between a change in MU synchronization and change in MFCV. It is calculated by sub-band filtering the monopolar sEMG signal and subsequently calculating the skewness statistic. Since the sub-band skewness is negatively correlated to MU synchronization level (Grönlund et al., accepted), the polarity was inverted to ease interpretation of changes in MU synchronization (positive correlation). Prior to sub-band skewness calculation, the sEMG signals were high-pass filtered at 10 Hz using a 8th-order Butterworth filter in order to reduce movement artifacts and down-sampled to 1024 Hz.

Changes in MU synchronization with fatigue was estimated using a MU synchronization index. This was defined as the difference between final and initial values of a recording in sub-band skewness (Fig. 3c) as proposed by Grönlund et al. (accepted). The rationale for this was to remove the subject-dependent bias component of the sub-band skewness (due to different signal-to-noise levels and volume conduction properties, etc.) (Grönlund et al., accepted). The variation in sub-band skewness was quantified using the coefficient of variation (100 * SD of the de-trended (linear) sub-band skewness/mean of the sub-band skewness during the first 25% of the contraction).

The force signal was band-pass filtered (5th-order Butterworth) at 4–30 Hz (Semmler and Nordstrom, 1995), prior to further analyses. Force tremor was quantified using the coefficient of variation (SD/mean * 100) of the filtered force signal (Burnett et al., 2000). Both the force tremor and the sub-band skewness were calculated in 10 s windows and 5 s overlap throughout the whole contractions (Fig. 3b and c). A window length of 10 s was used because a stable quantification of MU synchronization requires a large number of MUAPs. Thus, only information on

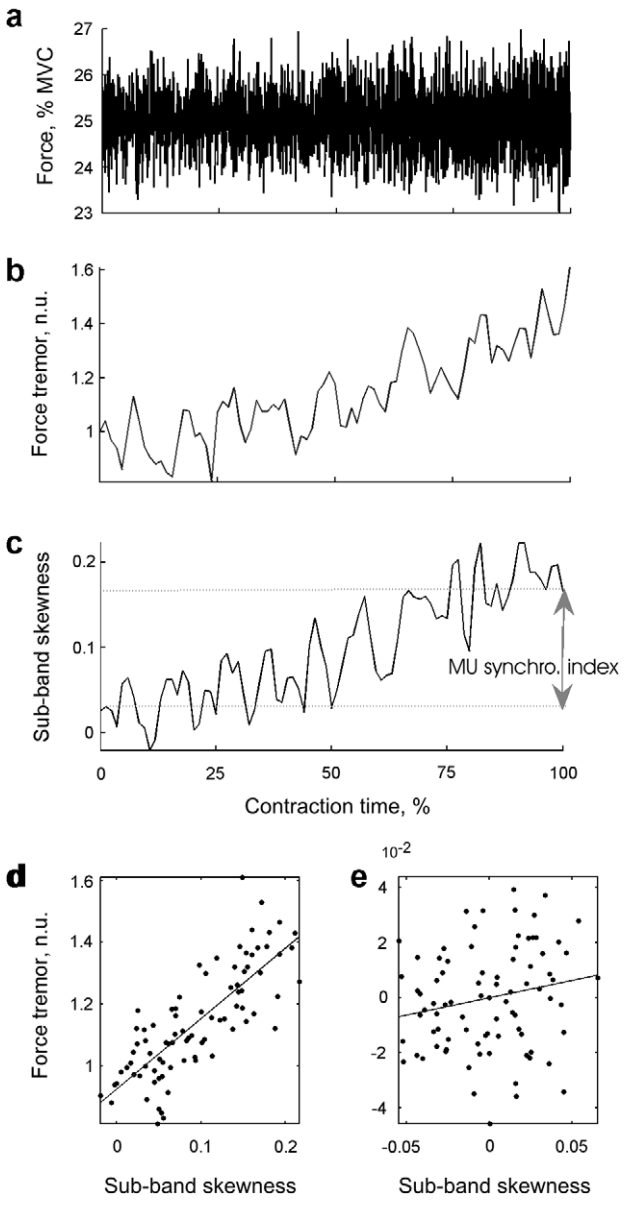

Fig. 3. Typical results from a subject performing a 25% MVC isometric contraction of the biceps brachii until exhaustion. (a) Presents the force (b) coefficient of variation of the force signal (force tremor), (c) sub-band skewness calculated from medial region of a biceps brachii muscle, (d) the corresponding relation between the force tremor and sub-band skewness ($R = 0.79$), and (e) the relation between de-trended versions of force tremor and sub-band skewness ($R = 0.19$). The variables were calculated in 10 s intervals with 5 s overlap. A MU synchronization index was used to quantify the level of imposed MU synchronization, using the difference between the final and initial sub-band skewness values of a recording (c).

fluctuations occurring at frequencies less than 0.1 Hz could be obtained.

In order to assess the general association between MU synchronization and force tremor, the correlation coefficient (Pearsons's), R, was calculated between the sub-band skewness and force tremor for each subject (Fig. 3d). The association between fluctuations in MU synchronization and force tremor was assessed based on correlation of the corresponding de-trended versions of sub-band skewness and force tremor (Fig. 3e).

2.6. Selection of subgroup of subjects with spatial narrow IZ

Estimation of MU synchronization has been suggested to depend on the recording location along the muscle fibres (Kleine et al., 2001). This is likely due to different MFCVs of the active MUs causing increasing time-lags between fast and slow propagating MUAPs with increasing distance along the fibres. Thus, correct estimation of MU synchronization requires (at least theoretically) recording at a location near the IZ of all active MU. Since the location of the IZ of the biceps brachii varies between subjects and can differ up to 2 cm between the heads of the muscle (Masuda and Sadoyama, 1988; Masuda and Sadoyama, 1991), the location of the IZ was examined using a visual inspection procedure proposed by Masuda and Sadoyama (1991) based on bipolar differentiated signals. The IZ position was defined at the electrode where the bidirectional propagating action potentials had minimal amplitude with different polarity and similar MFCV at both sides (Masuda and Sadoyama, 1991). If no IZ could be detected, it was assumed to be located on the proximal electrode of the electrode grid.

Since the applied method is based on monopolar signals, cross-talk of myoelectrical signals between the heads of the biceps brachii muscle is most likely present. Therefore, a recording location near (and at a constant distance to) the IZ of all active MUs contributing to the detected myoelectric signal is not plausible in subjects with large deviation of IZ between the heads of the Biceps Brachii. Accordingly, a correct estimation of MU synchronization requires a spatial even (homogeneous) IZ within the muscle, enabling a constant distance from the recording electrode to the IZ. Consequently, subjects having a difference between the IZ centers in the biceps brachii of more than 1 cm were excluded from further analyses. In order to minimize the effect of different MUAP shape above the IZ as compared to the shape of a propagating MUAP, the signals from all electrodes located at least 1 cm distal from the IZ were retained for further analysis.

2.7. Analysis of MU synchronization distribution and electrode position along-fibre effects

The general fatigue induced changes in MU synchronization was assessed in terms of average, SD and range of estimated force tremor, and quantified MU synchronization of the signals from electrodes located 1 cm distal the IZ (Fig. 4).

In specific, the MU synchronization (MU synchronization index) and its general association with force tremor (R) was assessed in terms of:

(1) The intra-muscular (medial–lateral) distribution of MU synchronization (MU synchronization distribution) of signals from electrodes located 1 cm from the IZ (Fig. 4, row A) and
(2) Effect of electrode location along the muscle fibres (proximal–distal) on the MU synchronization quantification (along-fibre electrode location effects). Signals from electrodes located at the medial side of the muscle (Fig. 4, column B) were used. This location was chosen because it is least effected by ~~lateral~~ cross-talk from the brachioradialis muscle.

The MU synchronization distribution and electrode location along-fibre effects were tested independently of each other. The

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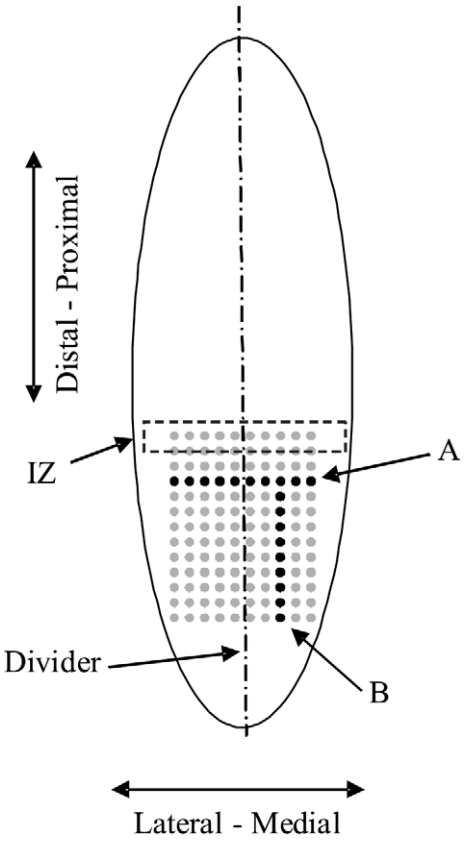

Fig. 4. Schematic drawing of the placement of the 13×10 electrode grid (gray points) on the muscle biceps brachii. Signals from electrodes indicated in A (1 cm distal the IZ), were selected for intra-muscular MU synchronization analysis, and signals from electrodes (as given in B) were used to assess effects on electrode location along fibre orientation. The location of the IZ was determined using a visual inspection procedure based on bipolar differentiated signals (Masuda and Sadoyama, 1991).

MU synchronization distribution was tested using three signals originating −2.25 (medial), 0 (intermediate) and 2.25 (lateral) cm from the partitioning of the two heads (Fig. 4). To test the along-fibre electrode location effects, signals originating 1, 3 and 5 cm distal to the IZ were selected (Fig. 4). Prior to statistical testing, the variables were normalized by subtracting the average of each variable of MU synchronization distribution and along-fibre electrode location effects, respectively. This was carried out to remove inter-individual bias of the variables which could mask actual spatial dependencies.

2.8. Statistics

To test for dependency of MU synchronization distribution and along-fibre electrode location effects on the variables, one-way MANOVA tests were performed prior to subsequent 1-way ANOVA analysis with concluding pairwise post hoc tests, using Student's t test with Bonferroni correction. Significance level was set to $p = 0.05$. MANOVA requirements were checked in terms of independency in observations equality of covariance and variance matrices (tested using Box' M-test and Levene's test, respectively) and multivariate normality (tested using mulitple univariate Lilliefors tests).

3. Results

3.1. Drop-outs due to poor signal quality and wide IZ

Five subjects were omitted due to poor quality of the sEMG recording. Ten of the remaining 34 subjects had a difference between the IZ centers in the biceps brachii muscle of more than 1 cm. Hence, 24 subjects with good recording quality and narrow IZ were included in the further analyses.

3.2. General findings

The duration of the sub-maximal contraction was 5.4 (3.3) min. The sub-band skewness increased from 0.03 (0.06) units (range −0.1 to 0.15), to 0.20 (0.11) units throughout the contraction ($p < 0.01$). The corresponding MU synchronization index was 0.18 (0.11) units, (range 0.01–0.52). The force tremor increased from 1.2% (0.6) to 2.6% (1.5) throughout the contraction ($p < 0.01$). The coefficient of variation of the sub-band skewness was on average 0.36 (0.14) and did not change during the contraction ($p < 0.01$). The correlation (R) between force tremor and sub-band skewness was on average 0.6 (0.21). The correlation (R) between the de-trended force tremor and sub-band skewness was on average 0.13 (0.09).

3.3. MU synchronization distribution

Fig. 5a and c illustrate the MU synchronization index and its association with force tremor (R) at the medial, intermedial and lateral regions of the biceps brachii muscle 1 cm from the IZ. The normalized MU synchronization index was about 0.05 units higher in the medial as compared to the lateral position of the biceps brachii muscle ($p < 0.05$) (Fig. 5b). The normalized R was about 0.1 and 0.05 units lower in the intermediate as compared to the medial ($p < 0.01$) and lateral regions ($p < 0.05$), respectively (Fig. 5d). These pairwise tests were justified by a preceding one-way MANOVA test ($p < 0.001$) and one-way ANOVA tests on MU synchronization index and R, respectively (both $p < 0.01$).

3.4. Electrode position along-fibre effects

Fig. 6a and c presents the MU synchronization index and R calculated at different distances from the IZ. The normalized MU synchronization index and R decreased about 0.10 and 0.15 units ($p < 0.01$), respectively, with increasing distance from the IZ (Fig. 6b & d). These pairwise tests were justified by a preceding unbalanced one-way MANOVA test ($p < 0.001$) and one-way ANOVA tests on MU synchronization index and R, respectively (both $p < 0.001$).

4. Discussion

The main findings of this study were (1) both the MU synchronization descriptor and force tremor increased

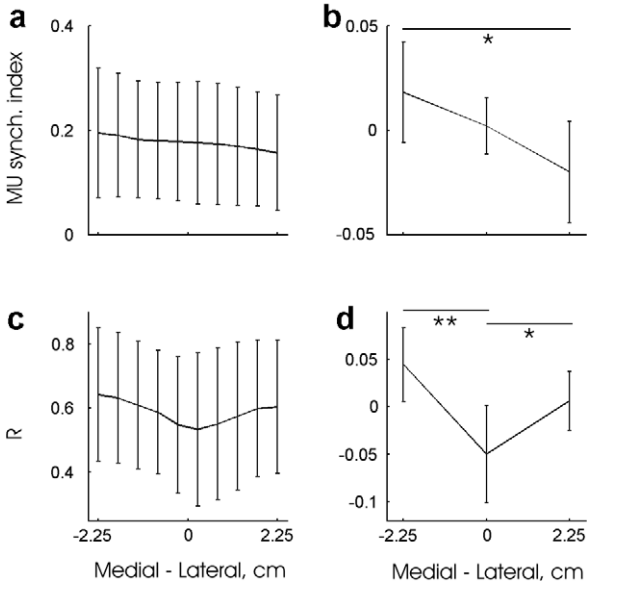

Fig. 5. This figure presents the results on MU synchronization distribution along the IZ (medial–lateral). In a and c, the average and SDs of the distribution of the MU synchronization index and the R statistics is presented, respectively, for all subjects ($N = 24$). Figures, b and d demonstrate the average ± 95% confidence intervals of the distribution of normalized MU synchronization index and R statistic values, respectively. Normalization was obtained by subtraction of the average of MU synchronization index and R, respectively, from the three positions of each subject (−2.25, 0 and 2.25 cm with respect to the division of the two heads of the biceps brachii). Symbols of significance levels: $***p < 0.001$, $**p < 0.01$, $*p < 0.05$.

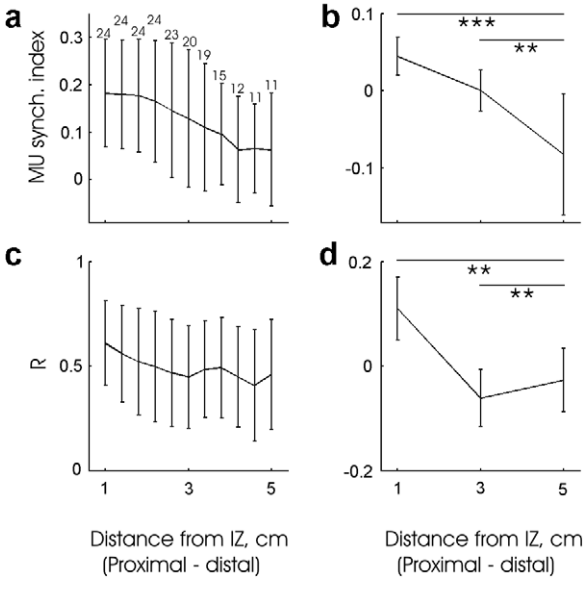

Fig. 6. This figure demonstrates the influence on MU synchronization assessment of electrode location distal to the IZ along the fibre orientation (proximal–distal, medial region). In a and c, the average ± SD of MU synchronization index and R statistic is presented, respectively. The numbers present the number of subjects for each electrode position; a consequence of different IZ positions of the subjects. In b and d, the average ± 95% confidence intervals of normalized MU synchronization index and R statistic values are presented, respectively. Normalization was accomplished by subtracting the average values of MU synchronization index and R statistic, respectively, of each subject. Symbols of significance levels: $***p < 0.001$, $**p < 0.01$, $*p < 0.05$.

throughout the fatiguing contraction, (2) there was a general association between the MU synchronization descriptor and force tremor, but not between fluctuations in these two parameters, (3) the MU synchronization descriptor and its association with force tremor ~~depended~~ on the location at the muscle. In the following, possible physiological correlates of these findings will be discussed.

4.1. Increased MU synchronization descriptor with fatigue

The MU synchronization descriptor increased throughout the sub-maximal contraction until exhaustion. This is in agreement with other studies investigating EMG signals of large MU populations during fatigue, showing grouping of MU activity, bursting of sEMG amplitude (Hunter and Enoka, 2003) and large periodic oscillations in the EMG signal (Mori, 1973). On the other hand, a previous study investigating the amount of synchronization from a few MUs by the cross-correlation method did not observe consistent increases with fatigue (Nordstrom et al., 1990). The latter might be explained by methodological limitations of the cross-correlation method requiring very stable MU activity (Semmler and Nordstrom, 1999) and being based on a very small sample of the MU population (Semmler, 2002).

4.2. Intra-muscular distribution of the MU synchronization descriptor

The MU synchronization descriptor was dependent on the spatial location of recording above the biceps brachii muscle (Fig. 5a). This finding is in accordance with observations of a spatial dependency of MU synchronization within a single muscle of the hand, obtained with intramuscular recordings (Bremner et al., 1991a; Bremner et al., 1991b; Keen and Fuglevand, 2004; Reilly et al., 2004) and by the observation of excitatory post synaptic potentials in only a fraction of motoneurons constituting a single muscle with cortical stimulation (Jankowska et al., 1975). Such a location dependency of MU synchronization indicates that the pre-synaptic projections are not uniformly distributed across the entire motoneuron pool, but segregated to different regions of the muscle.

4.3. Association between the MU synchronization descriptor and force tremor

Increased force tremor throughout sub-maximal fatiguing contractions is a well-documented finding (Hunter and Enoka, 2003; Loscher et al., 1994; Semmler et al., 2000). Contrary, the mechanisms behind the increased force tremor with fatigue have been an issue for debate (Elble, 1996). The association between MU synchronization and

force tremor in previous studies applying the cross-correlation method has been very low or not present at all (Dietz et al., 1976; Halliday and Redfearn, 1956; Logigian et al., 1988; Semmler and Nordstrom, 1995; Semmler and Nordstrom, 1998). In contrast, studies inducing MU synchronization experimentally by stimulation (Allum et al., 1978) or by computer modelling (Yao et al., 2000) have indicated a positive relation between MU synchronization and force tremor. In addition, several studies have documented an association between MU activity and tremor in the frequency domain (Elble and Randall, 1976; Halliday et al., 1999; Lippold, 1970; Matthews and Muir, 1980; McAuley et al., 1997; Mori, 1973), suggesting that MU synchronization accounts for a significant part of the tremor.

The MU synchronization descriptor was generally associated with force tremor throughout the fatiguing contraction (Fig. 5c). However, no significant relation was observed between fluctuations in the de-trended MU synchronization descriptor and force tremor. Although final physiological conclusions cannot be drawn from this study alone applying an indirect descriptor for MU synchronization for the first time, these findings indicate that the observed general positive association between the variables is mainly due to enhanced levels of both variables with fatigue, and not a causal dependency. Therefore, the findings of this study applying an indirect measure of synchronization from large MU populations are in accordance with previous reports using the cross-correlation method based on a few single MUs. These experimental findings undermine the possible causality between MU synchronization and force tremor (Dietz et al., 1976; Halliday and Redfearn, 1956; Logigian et al., 1988; Semmler and Nordstrom, 1995; Semmler and Nordstrom, 1998), and leave the phenomenon of fatigue induced tremor unresolved.

4.4. Spatial dependency of the association between the MU synchronization descriptor and force tremor

Fig. 5b illustrates that the general association between the MU synchronization descriptor and tremor with fatigue was dependent on the intra-muscular location of recording. The correlation between MU synchronization and force tremor was lower in the intermediate location compared to the medial region of the muscle (Fig. 5c and d). This finding is a result of the observed dependency of the MU synchronization descriptor above the biceps brachii muscle.

4.5. Along-fibre electrode position effects

The MU synchronization index and the general association between the MU synchronization descriptor and force tremor decreased with increasing recording distance from the IZ along the muscle fibres (Fig. 6a and b). This finding indicates that the time-dependency between action potentials of different MUs is dependent on electrode position away from the IZ. This is most likely due to different MFCV of different MUs (Arendt-Nielsen et al., 1989). A common synaptic input to two MUs with different MFCV would be estimated as a high level of MU synchronization near the IZ and progressively decreased levels of MU synchronization with increasing distance from the IZ. Consequently, the distance from the electrode location to the IZ has an impact on all techniques estimating MU synchronization. The observed variation between subjects in location and spatial disparity of IZ of up to 2 cm between the heads of the biceps brachii in this and other studies (Masuda and Sadoyama, 1988; Masuda and Sadoyama, 1991) emphasizes the need for detection of the IZ with multi-channel sEMG or other techniques to obtain an appropriate electrode location for recording of MU synchronization.

4.6. Methodological aspects

The applied method has previously been proven to be minimally dependent on changes in MFCV. Using simulations, Grönlund et al. (accepted) showed that the MU synchronization index has a general sensitivity of 0.1 units/5% MU synchronization. In addition, a change in MFCV (within the range 3–5 m/s) resulted in a bias of the MU synchronization index of 0.1 units at most. Therefore, the sub-band skewness "reliably" distinguishes changes in MU synchronization if they are larger than 5% MU synchronization. The observed difference in MU synchronization index (0.05 units, $p < 0.05$) between the medial and lateral regions of the biceps brachii muscle (Fig. 4B) is therefore less than the "reliable" sensitivity of the method, and could be an effect of inhomogeneous MFCV in the muscle. However, the documented homogeneous decrease in MFCV (<0.5 m/s) between regions in the biceps brachii muscle with fatigue (Holtermann et al., 2007) indicates that the observed different MU synchronization index is a result of different MU synchronization and not MFCV between the regions of the muscle.

Fat layers and skin properties (influencing myoelectric volume conduction and electrode-skin impedance) vary considerably between subjects. These subject-dependent factors influence (bias) the sub-band skewness of the signal, but not the change in sub-band skewness of a subject in time (Grönlund et al., accepted). As a result, single values of the sub-band skewness will likely not reflect the actual MU synchronization level. However, the MU synchronization index (the relative change between final and initial sub-band skewness values of a contraction) avoids the subject-dependent bias providing a valid estimate of the actual change in MU synchronization level. Therefore, in this paper the MU synchronization was investigated using the MU synchronization index, calculated as the difference between the final and initial sub-band skewness values.

An estimate of the MU synchronization level imposed during the sub-maximal contractions in this study can be obtained using the inverse of the sensitivity constant (0.10 units sub-band skewness per 5% MU synchronization level) reported by Grönlund et al. (accepted). Thus, the estimated MU synchronization level was 50 times the

obtained change in sub-band skewness units. Using this approach, imposed MU synchronization with fatigue was on average: 10% (SD = 6.5%), with a range from (0.5% to 25%). These numbers are calculated using the assumptions (simulated conditions) of 260 recruited MUs and a firing rate of about 14 Hz.

Modulation of firing rate can also affect the MU synchronization descriptor. A very high firing rate decreases the bias and sensitivity (Grönlund et al., accepted). Thus, a heavily increased firing rate could cause under-estimation of the MU synchronization descriptor during very high contractions levels and during fatiguing contractions. However, the change in average firing rate in the biceps brachii during sub-maximal contractions is generally small (Garland et al., 1994) and should not have influenced our results.

Recruitment of many MUs (from 50% to 100% of MU pool) reduces the bias and increased the sensitivity of the method. However, monotonic MU recruitment with fatigue has a small influence on the MU synchronization index, where the effect of decreased bias and increased sensitivity cancel each other out (Grönlund et al., accepted).

Generally, spatial filters are used to reduce cross-talk and enhance the spatial selectivity (Disselhorst-Klug et al., 1999). However, it has been shown that temporal filtering also partly suppresses cross-talk (Dimitrova et al., 2002; Grassme et al., 2003) and increases spatial selectivity (Dimitrov et al., 2003; Grassme et al., 2003). In particular, the sub-band filtering approach on the monopolar signal (wavelet scale 3 is related to a sub-band center frequency of about 85 Hz) should therefore likely reduce cross-talk and enhance the spatial selectivity as compared to bipolar signals.

5. Conclusions

The novel descriptor was for the first time used on experimental data to describe changes in MU synchronization with fatigue at different sites of a muscle and its relation to tremor. The main advantage of the descriptor is the quantification of synchronization from large MU populations with minimal dependency on MFCV. The MU synchronization descriptor was observed to be dependent on recording site and increased with fatigue together with tremor. The location dependency of the MU synchronization descriptor above the muscle illustrates the need for quantification of synchronization based on large MU samples from different intra-muscular regions. Moreover, detection of the IZ with multi-channel sEMG or other techniques to determine electrode-localization is recommended. Although final physiological conclusions cannot be drawn from this study alone applying an indirect descriptor for MU synchronization for the first time, the findings indicate that the observed general positive association between the variables is mainly due to enhanced levels of both variables with fatigue, and not a causal dependency. The findings from this study are in agreement with other surface EMG studies, indicating that the novel descriptor can be used to attain information of synchronization between large MU populations during fatigue that cannot be retrieved with intra-muscular EMG.

6. Uncited reference

Yue et al., 199[illegible] Q3

Acknowledgements

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Paper V

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Spatial distribution of active muscle fibre characteristics in the upper trapezius muscle and its dependency on contraction level and duration

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Abstract

The aim of this study was to provide direct in vivo information of the physiological and structural characteristics of active muscle fibres from a large part of the upper trapezius muscle. Two-dimensional (2-D) multi-channel surface electromyography recordings were used, with 13×10 electrodes covering 6×4.5 cm of the skin's surface. A previously developed method was applied to detect individual propagating motor unit action potentials and to estimate their corresponding muscle fibre conduction velocity (MFCV) and muscle fibre orientation (MFO). Using these estimates, spatial distributions of MFCV and MFO were examined for five male subjects performing isometric shoulder elevation at different force levels. The main results were: (1) the general relationship between MFCV and force generation was non-systematic, with a positive relationship at the inferior part of the muscle, (2) the spatial distribution of MFCV at different force levels and fatigue was inhomogeneous and (3) the MFO was slightly different (6°) of the muscle fibres with origin superior compared to inferior to the C7 vertebra. These findings provide new information of the MFO of contracting muscle fibres and knowledge of the physiological characteristics of a large part of the upper trapezius muscle that previously was based on observations from human cadavers only.

Keywords: Muscle fibre conduction velocity; Muscle architecture; Inhomogeneous activation; Multi-channel surface EMG; Fatigue

1. Introduction

Despite many years of scientific effort, several physiological aspects of specific human skeletal muscles are still unknown. Especially from the trapezius muscle, the present knowledge of some important aspects is only based on observations from human cadavers (Johnson et al., 1994). In the present study, some of these aspects of the upper trapezius muscle will be investigated in vivo, namely the spatial distribution of (1) co-variation between fibre size and type, (2) fibre fatigability and (3) fibre orientation.

The smallest fraction of a muscle that can be voluntary activated is the motor unit (MU) constituting a single motoneuron and its belonging muscle fibres. Enhanced generation of force requires recruitment of additional MUs with larger size (Henneman, 1957). The larger MUs generally innervate fast, strong and fatigable type II muscle fibres with superior cross-sectional area (Burke, 1981). Such a co-variation of MU properties is thought of as highly functional in the movement control (Enoka, 1995; Kernell, 1992).

However, a histochemical study on human cadavers by Lindman et al. (1990) showed that in contrast to the large cross-sectional area of type II compared to type I muscle fibres in most human skeletal muscles (Jennekens et al.,

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1970; Polgar et al., 1973), an unsystematic relationship between the type of muscle fibres and cross-sectional area is observed in male upper trapezius muscle (Lindman et al., 1990). More specific, the different fibre types are unevenly distributed in this muscle, with a non-consistent relationship between fibre type and cross-sectional area in the superior part and a positive relationship in the inferior part of the upper trapezius muscle.

The muscle fibre conduction velocity (MFCV) of action potentials, travelling from the endplate along the membrane of the muscle fibres can be studied to investigate the characteristics and state of the active muscle fibres (Andreassen and Arendt-Nielsen, 1987; Arendt-Nielsen and Zwarts, 1989; Houtman et al., 2003; Kupa et al., 1995). Due to a positive relationship between MFCV and muscle fibre cross-sectional area (Hakansson, 1956) and percentage type II fibres (Kupa et al., 1995), higher force generation is often accompanied by an increased MFCV (Andreassen and Arendt-Nielsen, 1987; Masuda and De Luca, 1991). An inconsistency between fibre type and cross-sectional area will disrupt the positive relationship between MFCV and force generation. Moreover, since muscle fibres of one MU are observed to be clustered in limited spatially distributed territories (Buchthal et al., 1957), a spatial dependency of changes in MFCV with force generation would indicate a spatially uneven distribution of fibre size and type co-variation.

Another well documented finding is the decrease in MFCV throughout sustained contractions (Arendt-Nielsen et al., 1989). Since high-threshold MUs are most susceptible to fatigue (Henneman and Olson, 1965), and a marked impairment of action potential propagation is observed in these MUs only (Enoka et al., 1992), the amount of decrease in MFCV with fatigue provides information of active MU types in the muscle. An uneven distribution of MFCV changes with contraction time would indicate an unevenly distribution of different fibre types.

Another aspect of the upper trapezius muscle that has attained attention is its complex fibre orientation (Johnson et al., 1994). The trapezius muscle fibre orientation (MFO) with origin superior to the seventh cervical vertebra (C7) has been illustrated in several textbooks of anatomy to have a major degree of downward (descending) orientation (Basmajian and Slonecker, 1989; Romanes, 1964). Contrary, these muscle fibres of cervical origin are also reported to be approximately transversally oriented relatively to the spine (Hollinshead, 1982; Johnson et al., 1994).

Because of the considerable physiological and clinical interest of the upper trapezius muscle and the limited information of the physiological characteristics based on in vivo recordings, the aim of this study was to examine physiological characteristics of the upper trapezius muscle based on the spatial distributions of MFCV and MFO. The hypotheses of this study are: (1) the MFCV is generally not positively related to force generation, (2) the MFCV is spatially inhomogeneously distributed with force modulation and fatigue, and thus dependent on the spatial location of the electrodes on the muscle and (3) the MFO of the active muscle fibres originating superior and inferior to C7 are different.

In order to demonstrate the impact of changes in MFCV in the upper trapezius muscle, the findings were compared with recordings from the biceps brachii. This muscle is generally considered to have larger cross-sectional area of type II fibres as compared with type I (e.g. Polgar et al., 1973), and muscle fibres in parallel with the humerus (Murray et al., 2000).

2. Methods

2.1. Subjects

Recordings from the upper trapezius of five men (age 24.4 ± 3.7) were used in this study. Data from the biceps brachii muscle was collected from seven other male subjects (age 28.4 ± 4.5). None of the subjects had experienced any pain or injury of the upper extremities. The subjects signed an informed written consent prior to participation. The Regional Committee for medical science and ethics, University hospital, NTNU, Trondheim, Norway, approved the study.

2.2. Exercise protocol

The five subjects performed shoulder elevation using a dynamometer (BIODEX System 3 Pro, Biodex Medical Systems, Shirley, New York, USA). The experimental setup is illustrated in Fig. 1. Subjects were placed in a fully extended, supine position and secured by body straps in the dynamometer chair. A standard closed chain system, converting linear motion of the arm to rotational motion at the shaft of the dynamometer, in parallel with the straight right arm and torso of the subject was used for the experimental setup. The subject had a fixed, pronated grip with the right hand at a handle of the closed chain system. The left hand was oriented in the same manner as the right hand, holding

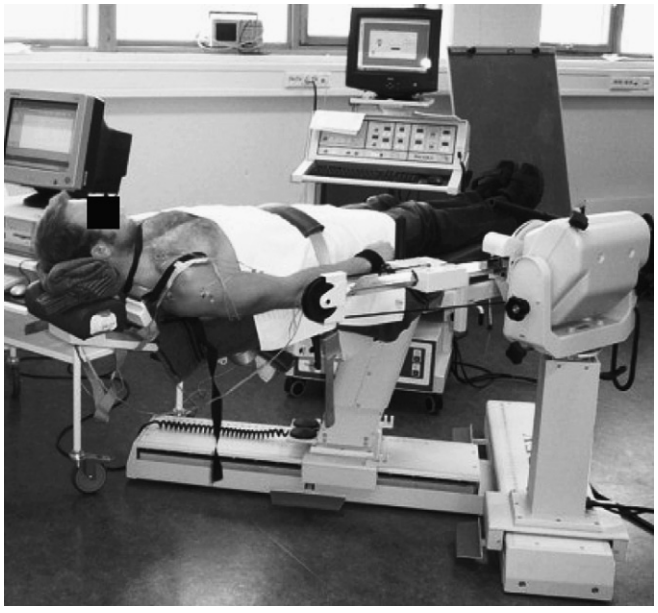

Fig. 1. Picture of the experimental setup.

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a handle with no force recording. The force was generated with bilateral shoulder elevation. The head of the subjects was slightly elevated, positioned on a pillow in a constant stabilized resting position.

The other seven subjects performed isometric elbow flexion with the right arm. The right arm and wrist were attached in a supinated position, with 130° in the elbow joint, to the lever arm foundation of the dynamometer. The hip and back of the subjects were strapped to the chair, and the wrist support was adjusted to each subject ensuring a proper grip of the handle.

The experimental protocol was identical in shoulder elevation and elbow flexion. To determine maximal voluntary contraction (MVC), the subjects carried out three maximal contractions of 4 s duration, with 3 min recovery period between each contraction. The subjects received direct visual feedback of the force generation during the task from a monitor. The force data recorded during the MVC of each subject was analyzed in epochs of 0.5 s, where MVC was determined as the highest obtained value. Isometric sub-maximal contractions were performed at 5%, 10%, 25% and 50% MVC in periods of 3, 3, 3 and 1 min, respectively. The recovery period between each contraction was 3 min. The force signal was sampled at 100 Hz.

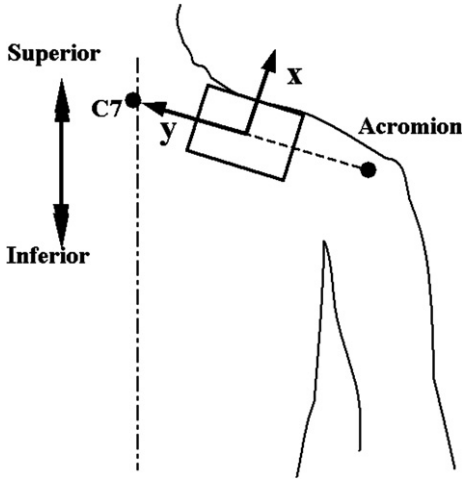

Fig. 2. A schematic drawing of the posterior view of the electrode-device placement and the alignment of the detection system coordinates on the upper trapezius muscle. The electrode-grid device was placed in parallel with a straight line between the acromion and the C7 (dashed line). The spatial location of the electrodes were described using x and y co-ordinates, corresponding to the two directions with 10 and 13 electrodes, with origin at the center of the grid.

2.3. Surface EMG acquisition

Multi-channel surface electromyographical (MCSEMG) data were recorded using a 13 by 10 active electrode-grid device (modified ActiveOne, BioSemi, Amsterdam, The Netherlands) with 1.5 mm electrode diameter and 5 mm inter electrode distance, covering 6×4.5 cm of skin surface. The base of the electrode-grid device is concave and semiflexible and thereby fits well with the convex recordings area of the upper trapezius muscle. Data were recorded from all channels with a common reference (unipolar recordings), converted from a range of ± 33 mV with 16 bit resolution, at a sampling frequency of 2048 Hz. The anti-aliasing filter was a 5th order Bessel with -3 dB gain at 1/4th of the sample rate.

On the skin above the right trapezius muscle the center of the MCSEMG grid was firmly placed in the middle of the line between processus spinosus of the C7 vertebra and the lateral edge of acromion (Fig. 2). The electrode grid was placed at this location to obtain an appropriate estimate of the MFO of the three parts of the upper trapezius muscle. Consequently, the electrode grid will be located above the innervation zone (Holtermann and Roeleveld, 2006). This may introduce a bias in MFCV estimates (e.g., Gydikov et al., 1986; Roy et al., 1986), however not effect changes in MFCV with fatigue and different force levels, which is investigated in this study. To prevent movement of the electrodes and generate a stable pressure on the skin, the MCSEMG grid was firmly fixed to the skin above the upper trapezius muscle and held in place by two elastic straps around the shoulder and torso of the subject fastened to each corner of the electrode grid. The reference electrode was placed at the olecranon of the right arm.

On the skin above the right biceps brachii muscle, the MCSEMG grid was placed on the middle of the distal end of the muscle bulk in parallel with the humerus (y-axis in parallel with the humerus). The grid was fixed with two straps around the upper arm of the subjects. The reference electrode was placed on the C7 vertebra.

2.4. Surface EMG analysis

Data analysis was performed off-line using MATLAB® 6.5 (The MathWorks Inc., Natick, USA). Monopolar signals were high-pass filtered using an eight-order Butterworth filter with a cut-off frequency of 10 Hz, prior to bipolar spatial filtering. Channels with low signal quality due to poor electrode-skin contact and heavy power-line interference were identified automatically (Grönlund et al., 2005b), and omitted from further processing. This method calculates the standard deviation (SD) of each channel in two time windows with different lengths. Channels having extreme SD values as compared to the bulk of the channels are classified as outliers (Grönlund et al., 2005b). When channels are detected as outliers more than 5% of the time within 1 s, they are likely low quality signals, and consequently omitted from further processing.

The EMG amplitude was calculated for each channel using the root-mean-square (RMS) over the first 15 s at each contraction level. In order to obtain a global measure of the muscle activation, the median RMS of all channels was used.

MFCV and MFO values were calculated using the algorithm developed by Grönlund et al. (2005a). The method utilizes the 2-D electromyograms to estimate MFCV and MFO of propagating MU action potentials (MUAPs). These potentials are detected as moving high-potential regions across the skin's surface, and results in a trajectory for each detected MUAP (Fig. 3b). The trajectories are then used to cut out spatio-temporal windows containing sequences of the propagating MUAPs. Finally, MFCV, MFO and initial position of propagation (x_0, y_0) of each MUAP are simultaneously estimated using a 3-D regression model on the windowed sequence data (Fig. 3c). Detected MUAPs were omitted from further processing if either of it's estimates were classified as an outlier (if further than 1.5 times the inter-quartile range from the median). This retains 99% of a normally distributed variable.

Spatial distributions of MFCV and MFO were found using the 2-D distributions of MFCV and initial position estimates, and

MFO and initial position estimates, respectively (Fig. 3d). These were generated by smoothing the corresponding estimates' 2-D histograms, calculated from 15 s time-windows (for all subjects and force levels), using 100 by 100 bins. Time window length was set on empirical basis to obtain averaged distributions and such that minimal fatigue manifestations would occur. In addition, for visualization purposes, only the estimates of MFCV, MFO and initial position in the ranges 2–8 m/s (as generally reported to be the extremes), −45 to 45°, and −2.3 to 2.3 cm, respectively, were used. The smoothing procedure was obtained by convoluting the 2-D histograms with a Gaussian kernel (Fan and Marron, 1994; Silverman, 1986). The kernel was set symmetric with a bandwidth of 12 (bins) at half the height. This was an empirical choice which was not critical for our results but, for visualization purposes, gave nice representations of the distributions.

Using the spatial distributions, single or populations of active MUs were separated as individual density regions (Fig. 3D). Local maxima of MFCV and MFO at individual density regions were calculated for all subjects and contractions. Only regions belonging to the 95% most probable estimates were retained. These were used in the following calculations:

(1) To examine the muscle architecture of the muscle fibres with origin superior and inferior to the C7, the average and standard deviation (SD) of MFO density region estimates inferior and superior to C7 were calculated during the first 15 s at 25% MVC. This contraction level was chosen on the basis that many MUs should be recruited.
(2) To study the changes in the spatial distributions of MFCV with force generation, the density peaks in the MFCV spatial distributions were examined for each subject during the first 15 s at each contraction level. The average and SD of the corresponding MFCV estimates were calculated for the whole detection volume and the inferior and superior positions, respectively. In addition, the maximal and minimal density region MFCV estimate was assessed within the detection volume.

The decrease in MFCV for each subject was calculated at 50% MVC, as the difference between the average MFCV estimates during the last and first 15 s, divided by the contraction duration. Student's t-tests were used for statistical testing. Significance level was set to $p = 0.05$.

3. Results

The EMG amplitude estimated from the upper trapezius muscle increased with enhanced force generation during shoulder elevation in all subjects (Fig. 4).

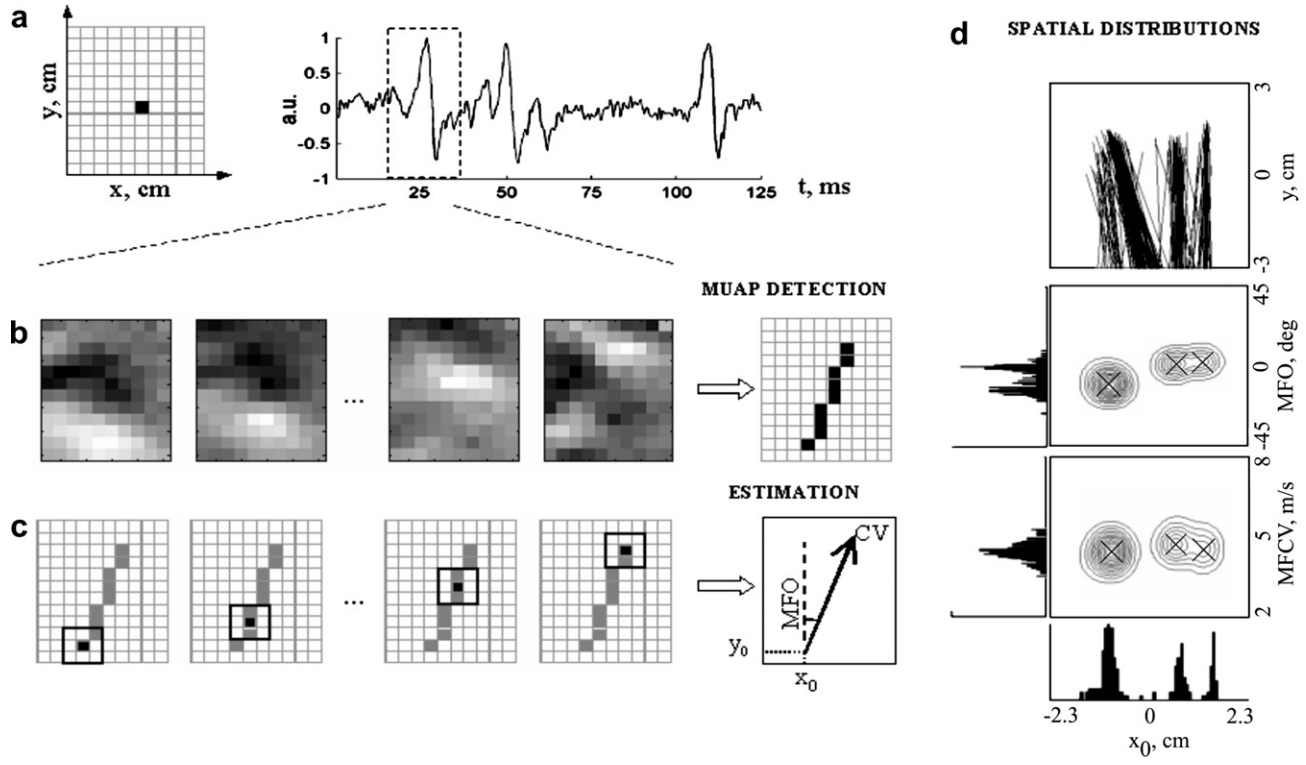

Fig. 3. Overview of the methodology. (a) The grid representing the 13 by 10 electrodes, covering the skin's surface, and an experimental time signal from one of the channels (dark square). (b) A sequence of spatial amplitude distributions, showing propagation of high amplitude regions (light color), and the MUAP trajectory detected by the method. (c) The trajectory is then used to cut out local spatial regions. The data from these regions are then applied to a 3-D regression model, and results in estimation of the propagating MUAP's MFCV, MFO and initial position of propagation, x_0. (d) Construction of the spatial distributions: thin lines represent examples of the MUAP trajectory estimates (top) over the skin's surface during a 15-s period at 25% MVC isometric biceps recording. The estimates from each detected propagating MUAP were used to create joint distributions of MFCV and MFO, respectively, against initial position of propagation. The example illustrates that such spatial distribution reveals density regions of individual or populations of MUAPs. The density region peaks were detected (marked by crosses) and were used for statistical analysis.

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3.1. Spatial distribution of MFCV

Fig. 5 shows the spatial distribution of MFCV at different force levels from five upper trapezius muscles and a typical example of the biceps brachii muscle. The graphs present the 2-D spatial distributions of MFCV against initial position of MUAP propagation. All graphs show that the MFCVs of the density regions are dependent on the position, with no obvious inter subject similarities, illustrating a spatially uneven MFCV distribution. The difference between the maximal and minimal MFCV of the different density peaks of a contraction could be as high as 1.9 m/s (subject 1, 50% MVC), but was on average 1.4 (0.5) m/s for all contractions and subjects.

3.2. MFCV vs. force relationship

No consistent relationship was observed between average MFCV and force level in the upper trapezius muscle (Fig. 5) over the whole recording area. The average MFCV slightly increased in subject 1, 4 and 5 with higher force levels, and decreased or remained stable in the other subjects (average increase was 0.3 (0.6) m/s (range: −0.25 to +1.2 m/s; $p = 0.33$)) between 5% and 50% MVC. In contrast, the average MFCV estimates increased between 5% and 50% MVC of all subjects in the inferior part 0.6 (0.4) m/s (range: 0.3 to +1.2 m/s; $p < 0.05$). The estimates over the recording area of the superior part showed no such increase 0.1 (0.9) m/s (range: −0.8 to +1.6 m/s; $p = 0.89$). There was a tendency although not significant, in divergent MFCV increase between the superior and inferior part with enhancing force levels ($p = 0.06$).

In the biceps brachii muscle, illustrated by a typical example in Fig. 5, the average increase in MFCV was 0.9 (0.4) m/s (range: 0.5 to +1.5; $p < 0.01$) between 5% and 50% MVC of all subjects. The increase in MFCV from 5% to 50% MVC force was significantly higher in the biceps compared to the trapezius muscle ($p < 0.05$).

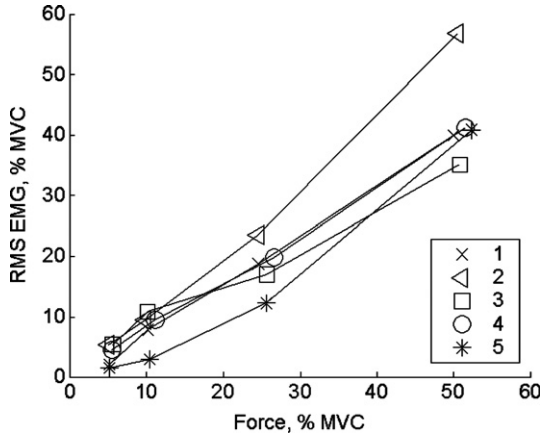

Fig. 4. The relation between generated force and median RMS EMG amplitude of all electrodes calculated during the first 15 s of each contraction of the upper trapezius muscle. Each subject is separately presented with different symbols.

3.3. Changes in spatial distribution of MFCV with fatigue

Throughout the contractions at different force levels, the MFCV did not decrease at any of the contractions in the biceps brachii muscle or in the upper trapezius muscle at 5% and 10% of MVC. However, the MFCV decreased 0.3 m/s min ($p < 0.01$) and 1.32 m/s min ($p < 0.01$), respectively, for the trapezius, and 0.18 m/s min ($p < 0.05$) and 1.62 m/s min ($p < 0.05$), respectively, for the biceps brachii, during the 25% and 50% MVC contractions.

Fig. 6 illustrates the changes in the spatial distributions of MFCV with fatigue at 50% MVC for the upper trapezius of all subjects and for one typical biceps brachii measurement. The decrease in MFCV was observed to depend on the spatial location of the upper trapezius muscle. The positions of density regions with the highest decrease were inconsistent between the subjects. For example, the decrease in MFCV of subject 2 with fatigue is larger in the inferior than the superior part of the muscle. In contrast, subject 1 showed a larger decrease in MFCV in the superior as compared the inferior part of the muscle.

3.4. Muscle fibre architecture superior vs. inferior

Fig. 7a illustrates the estimated trajectories of the detected MUAPs in the upper trapezius muscle. In Fig. 7b the angle, relative to the line between the C7 and acromion, of the recorded MFO estimates is presented. The average MFO with origin superior to C7 was 14 (4), range 9 to +18° with respect to a line between C7 and acromion. Fibres with origin inferior to C7 had on average an orientation of 8 (2), range 5 to +11°. The average difference between superior and inferior MFO was 6 (3), range 0 to +13 ($p < 0.05$) degrees. In the biceps brachii measurements, the fibre direction was on average −1 (3), range −5 to +2 ($p < 0.05$) degrees.

4. Discussion

The main findings of this study of the upper trapezius muscle are that (1) the MFCV is spatially unevenly distributed and dependent on force levels and fatigue, (2) the general relationship between force generation and MFCV is non-systematic, with a positive relationship at the inferior part of the muscle and (3) the muscle fibres with an origin superior to C7 are on average 6° more descending oriented than fibres with origin inferior to the C7 processus. In the remaining of this discussion, these results will be compared with existing knowledge of the characteristics of the upper trapezius muscle from human cadavers. In addition, methodological implications and considerations will be discussed.

4.1. MFCV vs. force relationship

A positive relationship between MFCV and force generation was present in all biceps brachii muscles studied ($p < 0.01$). This result is in accordance with observations of enhanced MFCV with increasing force generation at

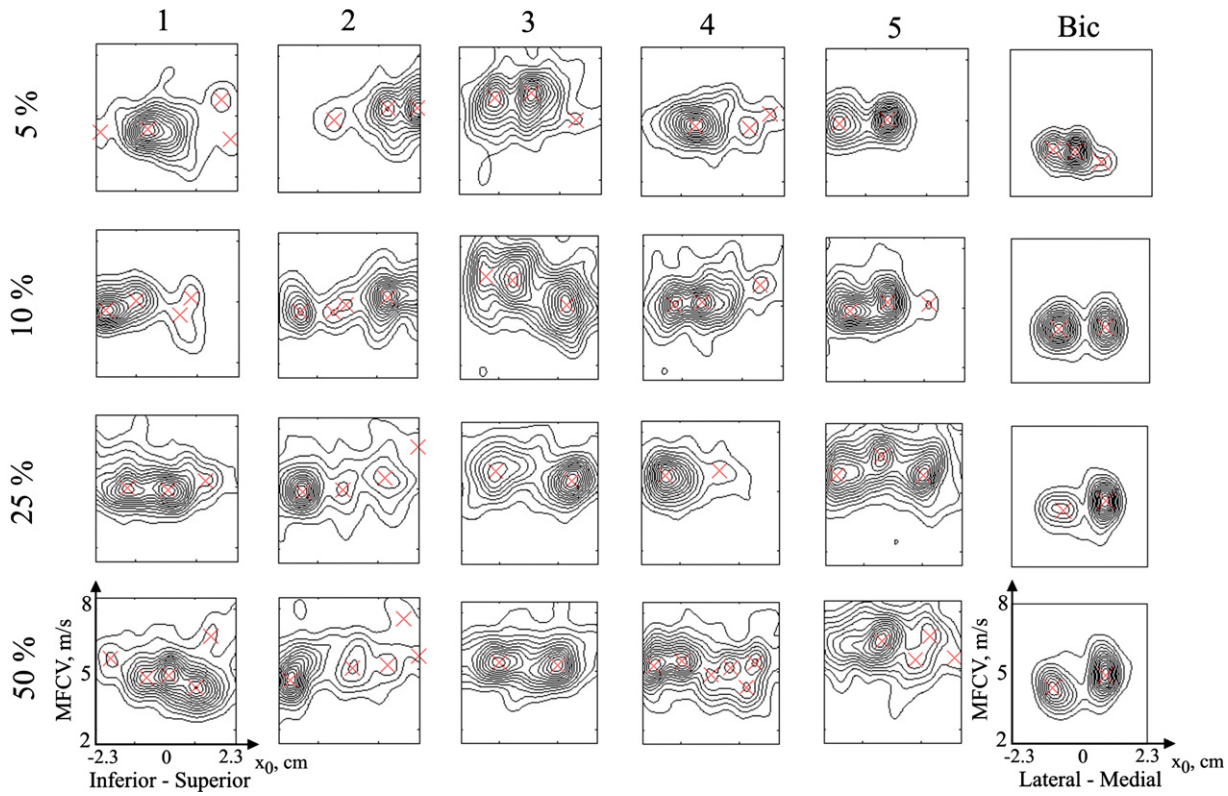

Fig. 5. Spatial distributions of MFCV at 5%, 10%, 25% and 50% MVC. Dense lines indicate high probability (incidence). Numbers 1–5 are the results from the upper trapezius muscle recordings of the different subjects, whereas 'Bic' presents results from a typical measurement from the biceps brachii muscle. For the trapezius recordings x_0 corresponds to the inferior–superior position relatively to the anatomical midpoint of a line between the processus spinosus on the C7 vertebra and the lateral edge of acromion. For the biceps case, x_0 corresponds to the lateral–medial position relative to the humerus. The density region peaks used for statistical analyses are marked by crosses.

skeletal muscles, i.e. tibialis anterior and biceps brachii (Andreassen and Arendt-Nielsen, 1987; Broman et al., 1985; Farina et al., 2002; Masuda and De Luca, 1991), that constitutes larger cross-sectional areas of type II than type I muscle fibres (Polgar et al., 1973).

Even though the RMS increased with enhancing force levels in both investigated muscles, in the upper trapezius muscle, the MFCV did not significantly increase with enhancing force generation. When spatially dividing the upper trapezius in two parts, a positive relationship between the force generation and the average MFCV was observed in the inferior part of the upper trapezius in all subjects ($p < 0.05$), whereas an unsystematic relationship was found in the superior part of the muscle ($p = 0.89$). This finding can be explained by a larger cross-sectional area of type II than type I muscle fibres in the inferior part of the upper trapezius, and an unsystematic relationship between cross-sectional area and fibre type in the superior part of the upper trapezius muscle as observed in a cadaver study (Lindman et al., 1990).

Furthermore, in other human muscles with no systematical difference in cross-sectional area between the fibre types, i.e. vastus lateralis (Polgar et al., 1973), no clear relationship between MFCV recorded at MVC and cross-sectional fibre area is observed (Sadoyama et al., 1988). One implication of this is that the use of MFCV as a size-principle parameter in muscles with clear distinction in cross-sectional area between the different fibre types, like tibialis anterior (Andreassen and Arendt-Nielsen, 1987; Polgar et al., 1973), cannot be directly generalized to the upper trapezius muscle.

Some studies have questioned the generally established view of muscle fibre cross-sectional area as the main determinant for MFCV, and indicated that the muscle fibre type proportions also have a considerable impact on MFCV (Kupa et al., 1995; Sadoyama et al., 1988). This is supported by observation of different intracellular action potential characteristics in muscle fibres of different types (Wallinga-De Jonge et al., 1985), indicating divergent fibre type dependent membrane properties. However, the coherent findings between the force – MFCV relationship and prior reports of the cross-sectional area of the different fibre types (Lindman et al., 1990; Polgar et al., 1973) in the biceps brachii and the inferior and superior part of the upper trapezius muscle, support the argument of the muscle fibre cross-sectional area as the main contributor to the MFCV in a non-fatigued state.

4.2. Spatial distribution of MFCV

In accordance with the diversion in fibre type distribution of the trapezius muscle (Lindman et al., 1990), the

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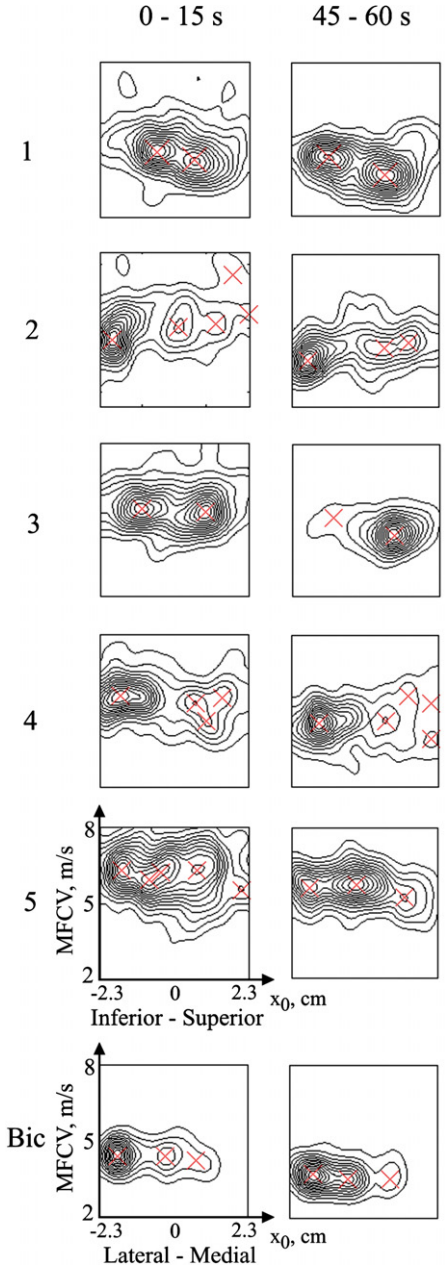

Fig. 6. Spatial distributions of MFCV for the inferior-superior position (x) calculated during the first and last 15 s of the 1 min lasting contractions at 50% MVC. Recordings from the upper trapezius muscle are presented for each subject. The inferior–superior position (x_0) is given relatively to the anatomical midpoint of a line between the processus spinosus on the C7 vertebra and the lateral edge of acromion for the trapzius muscle. For the biceps case, the lateral–medial position (x_0) is related to the elongation of the humerus. The density region peaks used for statistical analyses are marked by crosses.

recorded MFCV varied over the spatial area of the muscle (Fig. 5). The spatial dependency of the change in MFCV at different force levels demonstrates that the upper trapezius muscle is unevenly (inhomogeneously) activated (Fig. 5). This finding corresponds with the observation that muscle fibres of one MU are located in a limited territory of the muscle (Buchthal et al., 1957).

Because the MFCV estimated from the superior and inferior part of the upper trapezius muscle varies, the recorded MFCV depends on the electrode placement of the muscle. However, since the recorded MFCV was inconsistent between subjects, electrode placement recommendations for MFCV estimation at the upper trapezius muscle cannot be given.

4.3. Changes in spatial distribution of MFCV with fatigue

Consistent with the uneven fibre type distribution of the upper trapezius muscle (Lindman et al., 1990), and the spatially inhomogenious MFCV distribution, the decrease in MFCV throughout the sustained contraction of 50% MVC was dependent on the recording position (Fig. 6). This is in accordance to earlier findings of variable susceptibility to fatigue of different MUs in cats (Clamann and Robinson, 1985; Enoka et al., 1992) and muscle fibre types in human patients (Linssen et al., 1991). Because the general unspecific relationship between muscle fibre type and cross-sectional area in male trapezius muscles (Lindman et al., 1990) makes absolute MFCV inappropriate for classification of muscle fibres, the spatial dependent decrease in MFCV with fatigue can be used to reveal the characteristics of the muscle fibres located in different areas of the muscle.

4.4. Muscle fibre architecture superior vs. inferior

The 2-D analyses of the MUAPs propagation provided information of the fibre orientation of the active muscle fibres of the upper trapezius and biceps brachii muscle in vivo. As expected, the MFO of biceps brachii muscle was found to be parallel with respect to the humerus and is in accordance with observations from human cadavers (Murray et al., 2000). In the upper trapezius muscle, the results show that the active muscle fibres superior to C7 are only slightly descending oriented. This descending fibre orientation of the muscle fibres superior to C7, and the minor difference of 6° between the fibres with origin superior and inferior to C7 are in accordance with previous reported radiographical observations (Johnson et al., 1994).

In contrast, the descending fibre orientation of 8° in muscle fibres inferior to C7 is larger than previous reported (Johnson et al., 1994). However, this finding could be influenced by a relative motion of the scapula and its constituting muscle fibres in the isometric contraction at 25% MVC, whereas the fibre orientation has been previously recorded under resting conditions (Johnson et al., 1994). In addition, it should be noted that, since this method only estimates the fibre orientation of active muscle fibres, this finding might be influenced by selective recruitment of MUs with a suitable descending fibre orientation to perform shoulder elevation.

4.5. Methodological limitations

Since muscle fatigue reduces the MFCV (Arendt-Nielsen et al., 1989), and the contractions at ascending force

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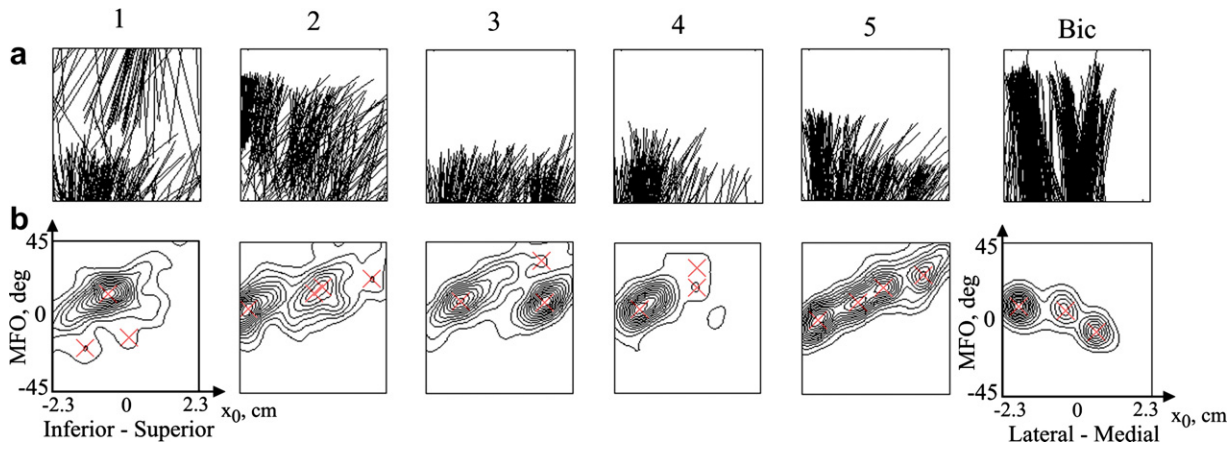

Fig. 7. Results of the estimated MUAP trajectories and their spatial distributions of MFO from the upper trapezius for the subjects (1–5) performing 25% MVC isometric shoulder elevation. One typical biceps measurement is also presented (Bic). The estimates are calculated during the first 15 s of contraction. (a) Propagating MUAPs detected within the 6×4.5 cm surface area above the upper trapezius muscle's innervation zone. The straight solid lines demonstrate the spatial location of propagation and their corresponding MFO. For the trapezius recordings the inferior–superior position (x_0) is presented relatively to the anatomical midpoint of a line between the processus spinosus on the C7 vertebra and the lateral edge of acromion. For the biceps case the lateral–medial position (x_0) is related to the humerus. (b) Spatial distributions of the MFO against initial position of propagation (x_0) for the detected MUAPs. Dense lines indicate high probability (incidence). Positive MFO values correspond to descending fibre orientation and negative to ascending orientation with respect to the orientation of the line between the processus spinosus on the C7 vertebra and the lateral edge of acromion. The density region peaks used for statistical analyses are marked by crosses.

levels were not randomized, the decreased MFCV throughout the contraction at 25% of MVC could influence the MFCV in the start of the 50% MVC contraction. However, since the decrease in MFCV was similar in both muscles (0.3 and 0.18 m/s min) and the subjects rested 3 min between each contraction, fatigue did not affect the conclusions of this study.

Recording MFCV and mean frequency close to innervation zones (IZ) and tendons generally results in biased estimates (e.g., Gydikov et al., 1986; Roy et al., 1986). To get representative information of the upper trapezius muscle, the electrode-grid device was placed in middle of the line between processus spinosus of the C7 vertebra and the lateral edge of acromion, i.e., above the IZ. This could explain the slightly higher MFCV estimates of the MU populations as compared to estimates reported by other papers (e.g., Farina et al., 2006; Schulte et al., 2006) where MFCV was recorded laterally from the IZ. However, the absolute MFCV values were not a focus in this study. Moreover, the IZ locations were approximately the same with respect to the detection system, and therefore the bias should be the same for all subjects. In addition, the location of the IZ does not change with respect to the electrode system during isometric contractions at force levels up to 50 % MVC of the upper trapezius muscle (Kleine et al., 2000). For the biceps recordings, the electrode-grid device was placed distal to the IZ and these MFCV estimates was in the same range as reported in other papers (e.g., Schulte et al., 2003).

A clinical limitation of this study is the more prominent shoulder pain in females than males (Norman et al., 2004). The use of MCSEMG techniques to estimate MFCV from the trapezius muscle has been shown to be challenging in females (Sjøgaard et al., 2006), and has been attributed to a smaller muscle dimension or more subcutaneous fat in females than males (Hagg, 1993). However, there should be no problem to apply the proposed method on females as long as sufficient signal quality can be established.

An important aspect of the applied method is that physiological information is not based on individually detected MUAP trajectories, but rather on the whole population of detected MUAPs (the spatial distributions). Therefore, individual MUAP trajectories might be physiologically incorrect, but will be suppressed by the applied method.

The method detected few MUAPs in the medial part of the trapezius muscle (Fig. 7). In general, the electrodes located in the medial-superior part had poorer electrode-skin contact (and these electrodes were consequently omitted from the analysis). Moreover, the broad aponeurosis of the trapezius muscle located between the sixth cervical to the third thoracic vertebra (Gray, 1977) might be responsible for the failed detection of propagating MUAPs in the medial-inferior part of the muscle.

5. Conclusions

This study provides direct in vivo information of both the physiological characteristics and activation of the male trapzius muscle. By applying a method for estimation of the spatial distribution of MUAPs in the upper trapezius muscle, we obtained new information of the spatial dependent relationship between MFCV and force and thereby the relationship between muscle fibre type and cross-sectional area, the spatial distribution of different MUs with divergent properties, and the muscle fibre architecture from the large, flat and multi-pennate trapezius muscle. The in vivo findings of this study provide knowledge of the

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physiological characteristics of the upper trapezius muscle that previously was based on observations from human cadavers.

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