

THE UNIVERSITY OF CALGARY

**The EMG-Force Relation of the Cat Soleus Muscle**

by

Antonio Carlos S. Guimaraes

A DISSERTATION

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES  
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE  
DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF MEDICAL SCIENCE

CALGARY, ALBERTA

DECEMBER, 1993

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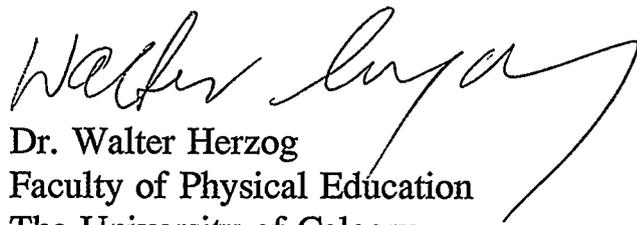
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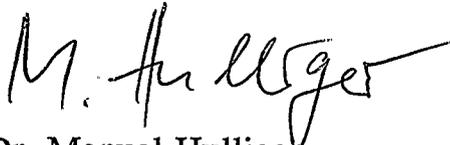
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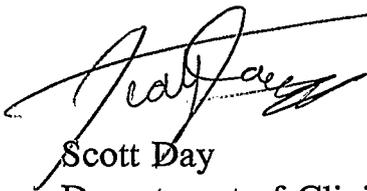
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# Chapter 4

## Declaration

As a co-author of the paper entitled "EFFECTS OF MUSCLE LENGTH ON THE EMG-FORCE RELATION OF THE CAT SOLEUS MUSCLE USING NON-PERIODIC STIMULATION OF VENTRAL ROOT FILAMENTS" I declare that I am aware that this paper is part of the Ph.D. thesis of Antonio Carlos Guimaraes.

I give my consent for this paper to be microfilmed along with other contents of that thesis.

Calgary, August/17/1993.



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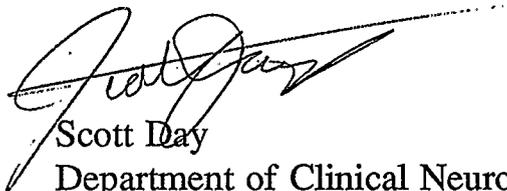
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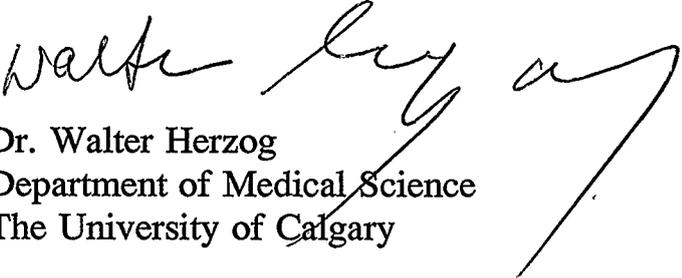
# Chapter 5

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As a co-author of the paper entitled "The EMG-force relation of the cat soleus muscle during locomotion, and its association with contractile conditions" I declare that I am aware that this paper is part of the Ph.D. thesis of Antonio Carlos Guimaraes.

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# Chapter 5

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# Chapter 5

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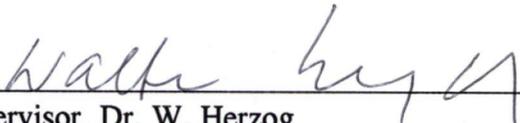
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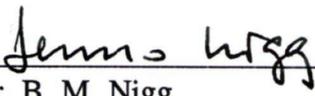


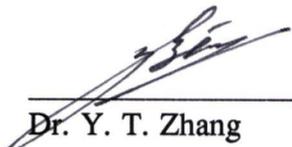
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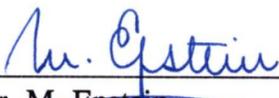
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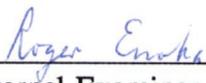
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a dissertation entitled "The EMG-Force Relation of the Cat Soleus Muscle" submitted by Antonio Carlos S. Guimaraes in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

  
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# Abstract

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This project was aimed at gaining a better understanding of the relationship between electromyographic (EMG) and force signals of the cat soleus muscle. Distributed stimulation of ventral root (VR) filaments and pseudo-random inter-pulse intervals were used, respectively, to: (1) assess the isometric EMG-force relation, and (2) determine the effects of changes in muscle length on the EMG signals, force, and EMG-force relation; and an attempt was made to (3) describe, and (4) understand the dynamic EMG-force relation on the basis of instantaneous contractile condition during locomotion. Indwelling (wire) electrodes and tendon force transducers were used. A protocol consisting of addition and rate modulation of eight or ten VR filaments ( $N = 3$ ) produced EMG and force records similar to those obtained during voluntary contractions, and yielded non-linear (sigmoid) relations between integrated rectified EMG (IEMG) and mean force. In an intermediate (physiological) stimulation region the IEMG-mean force relation was virtually linear. Similar results were found in most cases for four different muscle lengths ( $N = 2$ ). Effects of muscle length on EMG were

likely to be associated to movement of the recording electrodes relative to each other and to the active motor units. Mean forces increased with increasing muscle length and stimulation. Mean force-length relations obtained using submaximal stimulation levels appeared to be shifted towards longer muscle lengths compared to the force-length relation obtained using supramaximal nerve stimulation. The mean EMG-force relations obtained during locomotion were highly non-linear, but similar in shape across cats ( $N = 3$ ) and five different speeds. The theoretically predicted activation-time plots (Allinger and Herzog, 1993) and the experimentally measured IEMG-time plots tended to have two bursts. The first IEMG burst was usually higher than the second one, and it appeared to be associated with the initial priming of the muscle for force production at paw contact, and with the peak force observed early during the stance phase. The second IEMG burst appeared to be an attempt to produce the force required to complete the stance phase, when the contractile conditions of the soleus muscle for force production were highly unfavourable.

# Preface

---

The chapters 3, 4 and 5 of this dissertation project are based, respectively, on the following three manuscripts:

Guimaraes, A.C., Herzog, W., Hulliger, M., Zhang, Y.T. and Day, S. (in press). EMG-force relation of the cat soleus muscle studied with distributed and non-periodic stimulation of ventral root filaments. Submitted to *J. exp. Biol.* (reprinted with permission).

Guimaraes, A.C., Herzog, W., Hulliger, M., Zhang, Y.T. and Day, S. Effects of muscle length on the EMG-force relation of the cat soleus muscle using non-periodic stimulation of ventral root filaments. Submitted to *J. exp. Biol.*

Guimaraes, A.C., Herzog, W., Allinger, T.L. and Zhang, Y.T. EMG-force relation of the cat soleus muscle during locomotion, and its association with contractile conditions. Submitted to *J. exp. Biol.*

The theoretically predicted maximal possible force and activation values of the cat soleus muscle used in chapter 5 were provided by the following authors, and based on the following publication:

Allinger, T.L. and Herzog, W. (1993). Calculated activation of cat soleus muscle during locomotion. In *Abstracts of XIV ISB Congress*, vol. I, pp. 82-83. Paris.

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**to Denise, Carlos and Alice**

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# List of Abbreviations

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AJA:	ankle joint angle
CMUAP:	compound motor unit action potential
EMG:	electromyographic
ENMS:	electro-neuro-muscular stimulation
H:	high
I:	intermediate
IEMG:	integrated EMG
L:	low
L7:	seventh lumbar vertebra
MVC:	maximal voluntary contraction
PMPF:	predicted maximal possible force

pps:	pulses per second
RMS:	root mean square
S1:	first sacral vertebra
VR:	ventral root

# Chapter 1

## Introduction

---

The knowledge of how much force a muscle can exert during a voluntary contraction is relevant to basic and applied research. This knowledge may, for example, help in the understanding of aspects associated with motor control, and it may be used in areas such as muscle transplants, muscle rehabilitation, and control of prosthesis. Researchers in biomechanics can estimate joint moments by making assumptions regarding the location of the centre of mass and moment of inertia of the segments of the system of interest, and by using the inverse dynamics approach (Andrews, 1974). Beyond that point, further assumptions are needed in order to estimate how much force each muscle of a synergistic group generates during a given motor task, because the number of unknown muscle forces is typically higher than the number of equations that describe joint movements. This problem of redundancy of the musculoskeletal system is sometimes referred to as the distribution problem in biomechanics (Crowninshield and Brand, 1981), and the mathematical description of this problem is indeterminate (Hof, 1984). The distribution problem remains one of the main challenges in

biomechanics.

Different strategies have been used to solve the distribution problem in biomechanics: mathematical optimization (Seirig and Arvikar, 1973; Pedotti et al. 1978; Crowninshield, 1978; Crowninshield and Brand, 1981; Dul et al. 1984; Herzog, 1987); neural networks (Sepulveda and Vaughan, 1993); and the association between electromyographic (EMG) and force/moment signals (Milner-Brown and Stein, 1975; Komi and Viitasalo, 1976; Hof and Berg, 1977).

The work presented here will focus on the approach that attempts to describe and explain the relation that may exist between EMG signals and muscle force.

The relationship between EMG and force signals has attracted the attention of scientists for several decades (Inman et al. 1952; Liberson et al. 1962; Stevens et al. 1973; Moritani and Muro, 1987; Smith and Stokes, 1993). The mechanical outcome of muscle contraction (i.e. force) is always preceded by electrical activity. This is true at the muscle fibre level, the motor unit level, and the entire muscle level. At the motor unit level, an action potential represents the temporal and spatial summation of action potentials of all muscle fibres comprised in a motor unit, and the force output represents the summation of the forces produced by the same muscle fibres. At the muscle level, EMG signals represent the temporal and spatial summation of all motor unit action potentials, and force represents the summation of the forces produced by all active motor units. EMG signals can be recorded using electrodes and conventional electronic equipment (Basmajian and De Luca, 1985), and muscle forces can be

recorded using force transducers. However, difficulties associated with EMG (Basmajian and De Luca, 1985) and force (Bouisset, 1973) measurements have prevented a systematic and complete study of the EMG-force relation.

A large number of experimental investigations aimed at establishing the EMG-force relation has been conducted using human subjects and voluntary isometric contractions (Lippold, 1952; Vredenbregt and Rau, 1973; Seyfert and Kunkel, 1974; Komi and Viitasalo, 1976; Hof and Berg, 1977). One of the main limitations of these studies, is associated with the fact that EMG signals recorded (supposedly) from a single muscle were related to the resultant forces or joint moments generated by a group of muscles, rather than with the force generated exclusively by the muscle of interest. This limitation is hard to overcome in human subjects, because direct muscle force measurements require invasive techniques.

The EMG-force relation has been investigated much more extensively for isometric contractions than for dynamic contractions; and furthermore, dynamic contractions that have been studied, typically involved isokinetic contractions rather than unrestrained, normal voluntary movements (Bigland and Lippold, 1954; Close et al. 1960; Heckathorne and Childress, 1981; Dolan and Adams, 1993).

In some studies of animal locomotion, EMG and force signals have been measured directly from a single muscle (Hodgson, 1983; Whiting et al. 1984; Abraham and Loeb, 1985; Gregor et al. 1988), however, the aim of these studies was not centered on establishing the EMG-force relation. The exception to this rule is the work of Sherif et

al. (1983).

Electroneuromuscular stimulation (ENMS) techniques have been applied to a nerve (Bigland et al. 1953); or to ventral root (VR) filaments (Lam et al. 1979) to study the EMG-force relation. Although it has been possible to reproduce successfully the process of recruitment of motor units according to the size principle as described by Henneman et al. (1965), using ENMS (Petrofsky, 1978; Solomonov et al. 1987; Fang and Mortimer, 1991), it has not been possible to mimick the asynchronous process of firing rates of motor units (De Luca and Forrest, 1973) as it occurs under physiological conditions (Gydikov and Kosarov, 1974; Monster and Chan, 1977). Therefore, approaches using ENMS have typically being limited to producing signals of a periodic and synchronous nature, and they have rarely been used to study the EMG-force relation explicitly (Solomonov et al. 1987; Solomonov et al. 1990).

When attempting to predict muscle forces from the corresponding EMG signal, it is necessary to make assumptions about the relation between the two signals. EMG, or the active state of muscle, has often been related linearly to force, and the experimental non-linearities of the dynamic EMG-force relation were accounted for by the contractile properties of the muscle (Bogert et al. 1988; Hof and Berg, 1981a). Sometimes, the inherent relation between EMG and muscle force has been assumed to be non-linear (Ruijvens and Weijs, 1990; Hof and Berg, 1981b). These assumptions are likely to be responsible for the discrepancies in the predicted forces or moments obtained from different models.

The relation between EMG and force has been reported to depend on the fibre-type distribution of a muscle (Bigland-Ritchie et al. 1980) and the mechanism of force modulation (i.e. recruitment versus firing rates of motor units, Lawrance and De Luca, 1983). These factors should not influence the EMG-force relation of a given muscle, however, there are cases where different relations have been found for the same muscle. For example, the relation between EMG and force (moment) of the human rectus femoris has been reported to be linear (Thorstensson et al. 1976; Komi and Viitasalo, 1976) and non-linear (Smith and Stokes, 1993). These discrepancies may either be genuine and represent actual differences between subjects, or they may reflect the different procedures adopted in these studies.

For dynamic contractions, the EMG-force relation is believed to depend on the contractile properties of the muscle; the force-length (Gordon et al. 1966) and the force-velocity (Hill, 1938) relations. These properties are usually obtained for maximal levels of stimulation (Edman, 1979; Heslinga and Huijing, 1993), and under these conditions, the force-length and force-velocity properties of skeletal muscles are quite well understood. However, normal movements are performed using submaximal levels of muscle excitation. Submaximal force-length and force-velocity properties appear to differ significantly, and in a complex way, from the corresponding properties obtained for maximal levels of stimulation; they are not well understood; and experimental data are scarce (Rack and Westbury, 1969; Heckman et al. 1992). It appears, therefore, that an important piece of information may be missing to allow for a complete understanding of the EMG-force relation during voluntary movements.

In this project an attempt was made to explore systematically some of the aspects of the EMG-force relation that have not been studied systematically: (a) ENMS incorporating non-synchronized and pseudo-random stimulation of VR filaments was used to study the relation between EMG and force in a controlled laboratory setting; and (b) direct EMG and force measurements of the target muscle were performed in a freely moving animal model to investigate the EMG-force relation under normal movement conditions. An animal model (the cat soleus muscle) was chosen for all tests because it was necessary to measure force signals directly from the muscle of interest during free locomotion. The animal model also allowed direct stimulation of VR filaments.

The cat soleus muscle was selected in this investigation of the relation between EMG and force, because it is a homogeneous muscle comprised of slow twitch fibres (Ariano et al. 1973). The EMG-force relation of uniform slow twitch fibered muscles has been reported to be linear for isometric contractions (Close et al. 1960; Woods and Bigland-Ritchie, 1983), and therefore, could be compared with the isometric EMG-force relations obtained in this study using ENMS. Furthermore, the ENMS approach adopted in this project could not be used to recruit motor units according to the size principle (Henneman et al. 1965). It was believed that this limitation of the ENMS technique was less severe in a muscle containing slow twitch fibres exclusively, compared to a muscle containing a mixed fibre population.

The general purpose of this project was to gain a better understanding of the EMG-force relation of the cat soleus muscle. The specific objectives were: (1) to assess the EMG-force (isometric) relation of the cat soleus muscle, using ENMS of

VR filaments. Particular attention was given to the stimulation of VR filaments using asynchronous and non-periodic pulse trains (chapter 3); (2) to determine the effects of changes in muscle length on EMG signals, muscular force, and on the resulting EMG-force relation of the isometrically contracting cat soleus muscle, using asynchronous and non-periodic stimulation of VR filaments (chapter 4); (3) to describe the EMG-force relation of the cat soleus muscle during locomotion at different speeds (chapter 5); and (4) to attempt to understand the EMG-force relation of the cat soleus muscle during locomotion, on the basis of instantaneous contractile conditions as calculated by Allinger and Herzog (1993) (chapter 5).

## **Project**

In order to accomplish the general and specific purposes stated in the previous paragraph, three studies were conducted using two different approaches. Initially, aspects associated with the EMG-force relation of the cat soleus muscle were assessed using acute preparations (i.e. experiments in which the surgery, data acquisition and the final force calibration were performed within a period no longer than 24 hours, and the animal was maintained under the effects of anesthesia during this entire period). This approach was adopted so that, the nerve roots that supply the cat soleus muscle, could be exposed and subdivided into ten VR filaments. These VR filaments were subsequently submitted to independent stimulation using pseudo-random interpulse intervals. The contractions elicited in response to this type of stimulation were recorded using indwelling EMG electrodes and a tendon force transducer. These

procedures are schematically illustrated in Figure 1 (see chapter 3). Using the methods that have just been described, the EMG-force relation was quantified during isometric contractions performed at a single muscle length for three animals, and this first study is reported in chapter 3.

In the second study (chapter 4), stimulation of VR filaments was used to assess the EMG-force relation of the cat soleus muscle during isometric contractions performed at four different muscle lengths for two animals.

In the third study (chapter 5), the EMG-force relation of the cat soleus muscle was assessed during treadmill locomotion using chronic preparations (i.e. experiments in which data acquisition and force calibration were performed approximately one week after the surgical implantation of a tendon force transducer and indwelling EMG electrodes). Experiments using this approach were performed at different speeds including walking and trotting. Measurements were performed on five animals, three of which could be analyzed.

## Chapter 2

### Review of Selected Literature as Reported

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Selected studies aimed at investigating the EMG-force (moment) relation are reviewed in this chapter. These studies were classified into the following categories: (1) isometric contractions, elicited voluntarily; (2) dynamic contractions, elicited voluntarily; (3) stimulation elicited contractions; and (4) muscle models. The studies reviewed in each of these categories are introduced in chronological order. A summary of the literature reviewed is presented at the end of the chapter.

#### Isometric Contractions Elicited Voluntarily

Inman et al. (1952) measured EMG and force signals of eleven subjects having one or more cineplastic tunnels. The pectoral, triceps brachii, and forearm muscles were studied, and recordings were also made for the tibialis anterior of one normal subject. The subjects performed isometric contractions at different muscle lengths. EMG was obtained using surface, needle, and wire electrodes. Force was measured directly from each muscle using a metal apparatus instrumented with strain gauges.

The rectified and filtered EMG was found to be parallel to the force recordings of all muscles. The magnitude of EMG was reduced as the muscle was taken from a short to a long length, during the execution of maximal voluntary contractions. The three different types of electrodes gave the same results, provided that the electrodes were placed in or over the central mass of the muscle.

Lippold (1952) monitored the EMG activity of the gastrocnemius and soleus muscles of thirty human subjects as they performed isometric contractions at a fixed muscle length. A dynamometer was used to measure the force produced during plantar flexion exercises. The integrated EMG (IEMG) was found to be linearly related to force. Correlation coefficients between the IEMG and force were found to range from 0.93 to 0.99. The results obtained were consistent across all subjects, however, the slopes of the regression lines approximating the EMG and force data differed amongst subjects, and also differed for the same subject when two tests were conducted on different days.

Lenman (1959) determined the EMG-force relation of the biceps brachii or of the triceps brachii of healthy individuals ( $N = 12$ ), and of patients with weak muscles due to neurological or muscular disease ( $N = 26$ ). The subjects executed isometric contractions. EMG signals and force were measured using surface electrodes and a strain gauge dynamometer, respectively. Linear EMG-force relations were obtained for both groups, however, patients had EMG-force relations that were considerably steeper than those of the healthy subjects.

Close et al. (1960), studied the association between action potential counts and the isometric force produced by the human soleus muscle of six young subjects. Wire electrodes were used to record the EMG signals. Direct force measurements were made by attaching a force gauge to the subject's calcaneus using a pin. Tests were conducted for seven different muscle lengths. Linear relations were observed for different muscle lengths when action potential counts were expressed as a function of the isometric force. The slope of the EMG-force relation tended to decrease as muscle length increased.

Liberson et al. (1962) obtained EMG-force relations for the biceps brachii of ten human subjects using surface electrodes and a tensiometer. The subjects performed isometric exercises at a fixed elbow joint angle. The IEMG was found to be linearly correlated with the recorded tension.

Zuniga et al. (1970) investigated the influence of the location of the electrodes on the relationship between EMG and force signals of the human biceps brachii muscle. Three subjects performed isometric elbow flexion contractions, and three subjects performed isometric supination contractions of the radio-ulnar joint. Muscle forces were assessed using external force measurements obtained from a dynamometer. The protocol consisted of increasing force from zero up to the maximal voluntary contraction (MVC) level in a period of five seconds (ramp force). Nine monopolar surface electrodes were placed parallel to the muscle fibres of the long head of the biceps brachii, and five monopolar electrodes were placed transverse to the muscle fibres, around the muscle. Non-linear EMG-force relations (EMG increasing proportionally more than

force) were reported for the elbow flexion exercises; for all the electrodes placed along, and transverse to the muscle fibres. The highest EMG values of both, longitudinal and transverse electrodes were observed from the electrodes placed in the middle of the muscle.

Komi and Buskirk (1972) used isometric EMG-force relations to assess the effects of different strength training programs. Surface electrodes were used to record the activity of the biceps brachii of 31 human subjects, and a strain gauge dynamometer was used to measure the external force produced by isometric exercises. The subjects were classified into three groups, which were submitted to: (a) a concentric exercise program; (b) an eccentric exercise program; and (c) no exercise. The relationship between the IEMG and the external forces was non-linear (IEMG increasing proportionally more than force) for the isometric contractions performed by all subjects in the pre-training tests. In the post-training tests, however, the IEMG-force relation was close to linear for the two groups of subjects submitted to the exercise program, but remained non-linear for the control group.

Stevens et al. (1973) used surface electrodes to record EMG signals from several muscles (i.e. biceps brachii, brachialis, brachioradialis, triceps brachii, coracobrachialis and deltoid) of forty seven male and female human subjects. The subjects performed isometric contractions at four different efforts. A dynamometer was used to obtain the tension exerted during each contraction. The mean amplitude of the EMG signals was calculated for each test. The results showed, in most cases, a linear trend between the quantified myoelectric signal and tension, although there were cases (mostly females)

in which the mean action potential did not respond to tension as the effort was increased from 75 % to 100 %.

Vredenbregt and Rau (1973) determined the isometric EMG-force relation of the biceps brachii of one subject for different muscle lengths. The force component parallel to the alignment of the biceps brachii was measured at the wrist using a dynamometer, and surface electrodes were used to record EMG signals. The slope of the rectified IEMG over a period of 100 ms was used to quantify the EMG signals. The biceps brachii showed a non-linear relation between EMG and isometric tension, with EMG increasing proportionally more than force. Different curves were found for different muscle lengths. These relations were reported to reflect the changing involvement of the brachialis, brachioradialis, and biceps brachii at different elbow angles. The authors suggested that for a given EMG level, the absolute force that the muscle can exert is dependent of muscle length.

Seyfert and Kunkel (1974) investigated the EMG-force relationship of the biceps brachii and vastus medialis muscles. Twenty subjects performed isometric elbow flexor and knee extensor contractions. The elbow and knee joints were kept at an angle of 90 degrees during testing. EMG measurements were made using needle electrodes and force measurements were obtained using known weights. The mean amplitude of the EMG signals was calculated for each trial. The results indicated that the mean amplitude of the EMG signals were related linearly with force, although in some instances the relation was described by two lines instead of one.

Lindstrom et al. (1974) investigated the influence of external loads on the myoelectric signals of several different muscles (lateral head of the biceps brachii, brachioradialis, medial and lateral heads of the triceps brachii, extensor digitorum communis, extensor carpi radialis longus, deltoid, and trapezius). Thirty subjects performed isometric contractions using known weights. The EMG activity of all muscles was monitored using needle electrodes; and additional surface electrodes were used on the lateral head of the biceps brachii, and medial and lateral heads of the triceps brachii. The total power was used to quantify the EMG signals. All muscles were found to have a linear EMG-force relation, and different types of electrodes did not influence the results. The average correlation coefficients obtained between total power and external load of all muscles ranged between 0.96 and 0.99.

Milner-Brown and Stein (1975) obtained EMG-force relations from the first dorsal interosseous muscle of six subjects. Surface electrodes were used to record the EMG activity, and a force transducer was used to measure the external force generated during isometric contractions. The force transducer did not completely prevent other muscles from contributing to the movement. The peak-to-peak amplitude of the action potentials increased approximately as the square root of the force threshold.

Thorstensson et al. (1976) assessed the influence of eight weeks of training on the EMG signals of the rectus femoris and vastus lateralis muscles of six male subjects. Surface electrodes were used for EMG recordings. Maximal and submaximal voluntary knee isometric extension exercises were performed at fixed joint angles, prior to and after the training period. The results showed a non-linear relation between IEMG

and force. The data obtained for both muscles were best described by three straight lines with steeper slopes as force increased. The first line approximated the EMG-force relation from 0 % to about 40 % of maximal force, the second line from 40 % to 90 %, and the third line from 90 % until maximal force. No significant alterations in EMG were observed when the data obtained before the training period was compared to the data obtained after the training period.

Komi and Viitasalo (1976) studied twelve subjects in order to obtain EMG-force relations. Knee isometric contractions at standardized knee and hip joint angles were performed on a dynamometer chair, at levels of 20, 40, 60, 80, and 100 % effort. A visual feedback was provided to the subjects to help them to obtain the desired effort. EMG signals of the rectus femoris muscle were obtained using surface electrodes. It was found that IEMG increased in a slight non-linear fashion when expressed as a function of muscle force. The IEMG tended to increase proportionally more than force.

Hof and Berg (1977) studied the association between EMG and the torque generated at the ankle joint. The activities of the medial gastrocnemius, lateral gastrocnemius, combined medial and lateral gastrocnemius, and soleus muscles were monitored using individual pairs of surface electrodes. The contribution of other muscles to the ankle plantar-flexion torque was considered negligible. A strain gauge instrumented footplate was used to measure the isometric torque about the ankle joint. Variations in the knee joint angle were used to regulate the contribution of the gastrocnemius muscle to the ankle torque. Evaluation of cross-talk allowed the calculation of the

EMG activity of individual muscles. The results indicated that the mean rectified EMG-torque relation was linear for all muscles.

Moritani and deVries (1978) investigated the relationship between EMG signals and isometric force of the biceps brachii. Twenty-six male subjects performed elbow flexion exercises on a hydraulic dynamometer over the full range of force. Fatigue, muscle length, and co-contraction variables were controlled. Surface electrodes were used in a monopolar and in a bipolar configuration. IEMG was found to be linearly related to the external force, for the data obtained using the monopolar configuration (the correlation coefficients of individual subjects were greater than 0.97), however, a curvilinear relationship was found between the same two variables (EMG increasing proportionally more than force) for the bipolar configuration.

Bigland-Ritchie et al. (1980) examined the possibility that anatomical and physiological properties of muscles influence the EMG-force relation. In order to examine this possibility, they followed precisely the procedures that were described in selected previous studies. The EMG-force relations were found to be linear for the adductor pollicis, soleus, first interosseous and quadriceps muscles; whereas two straight lines with different slopes were required (discontinuity occurring at about 30 % of the maximal voluntary contraction) to approximate the data of the biceps brachii, triceps brachii, and brachioradialis. The authors observed that: (a) muscles comprised predominantly of slow twitch fibres (soleus and adductor pollicis), and muscles that tend to depend mainly on the firing rate of motor units for force modulation (adductor pollicis and first dorsal interosseous) had linear EMG-force relations; and (b) muscles that

depend mainly on the recruitment of motor units for force modulation had non-linear EMG-force relations.

Lunnen et al. (1980) studied the effects of changing the muscle length of the biceps femoris on the EMG signals and on the torque generated during isometric knee flexion exercises performed on a Cybex dynamometer. The hip joint angle was varied in order to test four different lengths of the biceps femoris, thus avoiding changes in the line of action of the muscle, and consequently in its moment arm about the knee. Surface electrodes were placed on the long head of the muscle, and the IEMG was calculated. The results obtained indicated that muscle torque increased, and that IEMG decreased, in response to increasing muscle length.

Heckathorne and Childress (1981) obtained the EMG-force relation of the cineplastic biceps brachii of one subject, at three different muscle lengths. Surface electrodes were used to obtain the EMG signals. A testing apparatus (consisting of a beam instrumented with a strain gauge, a steel cable, and a turnbuckle assembly connected to the muscle by a pin) was used to measure the force of the muscle directly. The IEMG-force relations were fit by third order polynomials (the lowest order polynomial to describe the data appropriately). The IEMG increased as muscle length decreased.

Lawrance and De Luca (1983) studied the effects of training level and rate of force production on the relation between EMG and force signals of different human muscles (biceps brachii, deltoid, and first dorsal interosseous). Four groups of subjects

(3 pianists; 4 long distance swimmers; 3 power lifters; and 6 normals) performed voluntary isometric contractions up to 80 % of the MVC (ramp force), at rates of 10, 20, and 40 % of the MVC/s. Surface electrodes were used for recording the EMG signals. External forces were measured using dynamometers instrumented with force transducers. EMG signals were quantified by means of the root mean square (RMS). The EMG-force relations were found to be: (a) independent of the rates of force production; (b) quasilinear for the first dorsal interosseous; and the same for all groups of subjects; and (c) non-linear (EMG increasing proportionally more than force) for the biceps brachii and deltoid. For the biceps brachii the relation was similar for all groups, however, some differences were observed between the groups for the deltoid. The authors suggested that the EMG-force relation is primarily determined by the muscle to be studied, and that this relation may be associated with the mechanisms of recruitment and firing rates of motor units during force modulation.

Woods and Bigland-Ritchie (1983) investigated the possibility that factors such as (a) the type of the muscle; (b) the location of the recording electrodes; and (c) the configuration of the recording electrodes affected the relation between EMG and force signals. The following muscles were studied: adductor pollicis, soleus, first dorsal interosseous, vastus lateralis, biceps brachii, triceps brachii, and brachioradialis. Twenty subjects participated in the study. The protocol consisted of a MVC, and a series of isometric contractions performed at efforts ranging between 10 and 90 % of the MVC. The exercises were performed using dynamometers instrumented with strain gauges, specifically designed to test each muscle. EMG signals were obtained

using surface electrodes; they were full-wave rectified and smoothed; and the IEMG was calculated. Variations in the configuration of the electrodes and in the location of the electrodes did not affect the findings. The results showed linear EMG-force relations for the adductor pollicis, soleus, first dorsal interosseous, and vastus lateralis (6 out of 8 subjects); and non-linear EMG-force relations for the biceps brachii, triceps brachii, brachioradialis, and vastus lateralis. Muscles that have a predominantly uniform fibre type composition (i.e. adductor pollicis and soleus), and muscles that depend primarily on the firing rates of motor units for force modulation (adductor pollicis and first dorsal interosseous) were associated with linear EMG-force relations; whereas muscles comprised of mixed fibre type composition (biceps brachii, triceps brachii, brachioradialis and vastus lateralis), and muscles that recruit motor units throughout the entire range of force modulation (biceps brachii) were associated with non-linear EMG-force relations.

Moritani and Muro (1987) tested twelve subjects to study the relation between parameters associated with the frequency power spectrum of the EMG signals, and the recruitment and firing rates of motor units. The triceps brachii was monitored using wire and surface electrodes; and subjects performed isometric contractions at increasing levels of force ranging from 0 % to 80 % of the MVC (ramp force) in a period of five seconds. A strain gauge system was used to measure the external forces, and visual feedback was provided to the subjects to help them obtain the desired effort in the appropriate time. The RMS of the EMG signals was calculated for the data obtained using the surface electrodes, and RMS was found to be related curvilinearly

with force (RMS increasing proportionally more than force). The mean of the power frequency spectrum of the EMG signals increased linearly with force. The results obtained using wire electrodes indicated that the mean amplitude of the motor unit action potentials and the respective firing frequencies increased significantly during the ramp force protocol.

Vogt and Pfeifer (1990) used macro EMG recording and spike triggered averaging techniques to study the relation between the EMG and force signals of single motor units of the human first dorsal interosseous muscle. Six subjects performed isometric contractions, and data from fifty single motor units were collected. The results indicated that the twitch force increased exponentially when expressed as a function of the IEMG. The non-linear EMG-force relation obtained in this study was attributed to the fact the signals were recorded from single motor units as opposed from the entire muscle.

Dolan and Adams (1993) obtained a linear relationship between the EMG (full wave-rectified and averaged) and the corresponding extensor moment of the erector spinae muscles, during isometric extension exercises performed by ten subjects. EMG and force signals were obtained using surface electrodes and a load cell, respectively.

Smith and Stokes (1993) quantified the relation between the EMG and force signals of the human rectus femoris muscle. Twenty subjects performed isometric knee extension exercises. The contractions were made at five different levels of effort (10, 25, 50, and 75 % of the MVC), and the external forces exerted during each contraction

were recorded using a strain gauge instrumented apparatus. The knee and hip joint angles were fixed at 90 degrees. The electrical activity of the rectus femoris was monitored using surface electrodes. The IEMG-force relation was found to be linear ( $r = 0.99$ ).

## **Dynamic Contractions Elicited Voluntarily**

### *Isokinetic Contractions*

Bigland and Lippold (1954) investigated the relation between EMG and force signals during dynamic plantar flexion exercises (concentric and eccentric) performed by five human subjects at constant velocities. EMG signals were recorded using surface suction electrodes placed on the gastrocnemius muscle, and force measurements were obtained using a dynamometer. A linear relationship was found between the IEMG and the external force, however, the slope of the relation was steeper for concentric than for the eccentric contractions. Different subjects had different slopes of the regression lines approximating the IEMG-force data, and different slopes were also seen for different measurements made on a given subject.

Knowlton et al. (1956) obtained 56 EMG recordings from normal biceps brachii muscles, and 214 recordings from muscles affected by poliomyelitis. Surface electrodes were used to obtain the EMG signals, and known loads were used to perform lifting exercises. Details about the speed of execution of the exercises were not reported. EMG signals (average maximal peak-to-peak amplitude) were found to be

linearly related to the external load for the normal muscles as well as for the muscles affected by poliomyelitis. The slopes approximating the EMG-force relations obtained for the muscles affected by poliomyelitis were steeper than those obtained for the normal muscles.

Close et al. (1960) studied the EMG-force relation of the human soleus muscle of six subjects. Dynamic (concentric) contractions were performed at a constant velocity using progressively increasing loads, which were connected to the calcaneus through a cable and a pin. EMG signals were measured using wire electrodes. The action potential counts of the EMG signals were non-linearly related to the external loads (i.e. external load increased proportionally more than EMG counts).

Komi (1973) studied the relation between EMG signals and the tension of the biceps brachii, brachialis and brachioradialis muscles of ten human subjects, during concentric and eccentric exercises at different constant speeds. Wire electrodes were used on the brachialis and brachioradialis muscles whereas surface electrodes were used on the biceps brachii. A dynamometer was used to record tension. All muscles showed a linear relation between IEMG and tension for both, concentric and eccentric exercises, however, the slopes of these relations tended to be steeper for the concentric than for the eccentric contractions.

Bigland-Ritchie and Woods (1974) used surface electrodes to monitor the EMG activity of the quadriceps muscles as three subjects exercised on a bicycle ergometer at a constant speed. The pedals of the bicycle were designed to minimize the involve-

ment of the gastrocnemius muscles to the bicycling action, and the current drawn by the motor of the ergometer was directly related to the imposed load. Frictional and inertial forces were accounted for. Visual feedback was provided to the subjects to aid them to maintain a constant speed of pedalling. Quantification of the EMG signals was made by calculating the IEMG. A linear relation was found between the IEMG and the forces exerted on the pedal. The correlation coefficients between these two variables were found to be greater than 0.92 for all subjects.

Heckathorne and Childress (1981) determined the EMG-force relation of the cineplastic biceps brachii of one subject, during dynamic exercises. Surface electrodes were used to obtain the EMG signals. Concentric and eccentric contractions were performed in a testing apparatus consisting of a weight assembly attached to steel cables, and to a pin attached to the muscle. The IEMG-force relations were described by third and fourth order polynomials (concave-convex) when the speed of the exercise was kept constant and the load was varied. Tests conducted using a constant load and variable velocity indicated that the IEMG was relatively independent of the velocity of the eccentric exercises; and also that the IEMG obtained during the concentric contractions tended to be greater than those obtained during the eccentric contractions, for any given force.

*Locomotion*

Walmsley et al. (1978) implanted EMG wire electrodes and tendon force transducers simultaneously in the soleus and medial gastrocnemius muscles of three cats; and in the medial gastrocnemius only, of four other cats. Posture, treadmill locomotion (speeds from 0.6 to 3.0 m/s), and jumping were studied. From the perspective of the relationship between EMG and force signals, these authors observed that there was a good correspondence between the mean peak IEMG and the mean peak force of the two muscles during locomotion. However, they emphasized that accurate predictions of force from IEMG values could not be made due to the variability of the IEMG for different steps.

Sherif et al. (1983) studied the EMG-force relation of the cat medial gastrocnemius muscle during unrestrained treadmill locomotion. Indwelling EMG electrodes and a tendon force transducer were chronically implanted in one animal. Recordings were made for an unspecified number of steps at speeds of 0.67 and 2.2 m/s. The direct force measurements were expressed as a function of the RMS of the EMG signals, which were calculated for intervals of 25 ms. The results obtained showed that EMG had two bursts during each step cycle. The relation between EMG and force (without introducing an electromechanical delay) was found to be highly non-linear and similar for the two speeds tested. The authors proposed that the first EMG burst may be associated with a predominantly central neuro control, and that the second EMG burst may be associated with a local control at the sarcomere level.

## Stimulation Elicited Contractions

Bigland et al. (1953) stimulated the nerve that supplies the anterior tibial muscle of rabbits using supramaximal shocks every five seconds. EMG signals were recorded by wire electrodes. A strain gauge attached to the muscle tendon was used to measure the isometric tension produced by stimulation. The number of active fibers responding in each twitch was controlled by slowly infusing tubocurarine into the jugular vein of the animal, until no force was produced in response to stimulation. A linear relation was found between the action potentials and the twitch tension.

Lam et al. (1979) used synchronous and distributed stimulation of the sciatic nerve of cats ( $N$  appears to be equal to 2) to produce isometric contractions of the soleus muscle. In one experiment laminectomy was performed in order to dissect and stimulate the ventral nerve roots of the seventh lumbar (L7) and first sacral (S1) vertebrae. Surface electrodes (wires around the whole muscle) and five pairs of indwelling (wire) electrodes were used for EMG recordings. A force transducer was implanted on the soleus tendon, and muscle length was set for maximum twitch tension. The results obtained using the summed records of all paired electrodes produced less fluctuation of the data compared to the results obtained using the single pairs of electrodes. The sum of the IEMG of the five pairs of electrodes was found to be linearly related to tension. The IEMG calculated for signals obtained using surface electrodes was found to be non-linearly related to force, and distinct curvatures were observed beyond 75 % of the maximal force. Distributed stimulation of VR filaments showed less fluctuations in the

IEMG obtained from the different pairs of electrodes than synchronous stimulation of VR filaments and gross nerve stimulation.

Solomonov et al. (1987) used synchronous nerve stimulation to assess the influence of different strategies of recruitment and firing rate of motor units on the EMG-force relation of the soleus and medial gastrocnemius muscles of nine cats. Two independent stimulators were connected to two independent nerve cuff stimulation electrodes. One stimulator delivered pulse trains of linearly decreasing voltage at a frequency of 600 Hz to the nerve. This procedure caused the smallest motor units to escape the blockage due to the high stimulation frequency first, and the largest motor units to escape last. The other stimulator delivered pulses with linearly increasing frequencies, and was it used to control the firing frequency of the active motor units. The minimal and maximal stimulation frequencies delivered to the two muscles were between approximately 8 and 56 Hz. EMG signals were recorded using wire electrodes, and force measurements were made directly from the tendon of the muscles using force transducers. Restricting the recruitment of motor units to force levels up to 50 % of the maximal force for the medial gastrocnemius, and up to 40 % of the maximal force for the soleus produced linear EMG-force relations. Recruitment of motor units beyond these force levels, respectively, produced EMG and force signals to be non-linearly related. The authors proposed (a) that the cat soleus muscle may depend on the recruitment of motor units up to or less than 50 % of the maximal tetanic force, and that modulation of force beyond 50 % of the maximal force was associated with changes in the firing rates of motor units exclusively; and (b) that the

cat medial gastrocnemius may depend on the recruitment of motor units as the primary mechanism of force generation.

### **Muscle Models**

Coggshall and Bekey (1970) developed a model to predict the force produced by the triceps brachii during time varying isometric contractions. A linear relationship was assumed between the force and the full wave-rectified myoelectric signals. Surface electrodes were placed on the long head of the triceps brachii of two human subjects, and the activity of the antagonist, biceps brachii, was monitored. The triceps brachii was assumed to be the main muscle in forearm extension, and the external force produced in each trial was measured at the wrist. When the measured force was compared to the predicted force, the mean difference was found to be zero, however, the instantaneous error was significant when force changed rapidly.

Sherif et al. (1983) developed a "black box" model in order to predict the instantaneous force generated by the cat medial gastrocnemius muscle during unrestrained treadmill locomotion. EMG and force measurements were obtained directly from the muscle using implanted EMG electrodes and a force transducer. The model consisted of an intervention analysis based on an autoregressive-integrated moving average process, and it was applied to predict the force-time history of three steps of one animal. The model relied completely on the first of the two observed EMG bursts during the stance phase. The results of the predicted force and the measured force were similar, in terms of the shape and magnitude.

Olney and Winter (1985) presented a deterministic model to predict the instantaneous moments about the ankle and knee joints during human locomotion. The model incorporated processed EMG, and the contractile properties of force-length (based on joint ankle) and force-velocity (based on angular velocity) of the ankle dorsi-flexor (tibialis anterior) and plantar-flexor (soleus) muscles; and of the knee extensor (rectus femoris and vastus lateralis) and flexor (medial gastrocnemius and medial hamstrings) muscles. Relations between the EMG signals and the isometric moments were determined experimentally from the subjects, and were submitted to a linear regression analysis. The ankle joint flexors and extensors were represented by the tibialis anterior and soleus muscles, respectively; and the knee flexors and extensors were represented by the rectus femoris/vastus lateralis and medial hamstring/medial gastrocnemius muscles. The predicted resultant moments about each joint were compared to the corresponding resultant moments calculated using the inverse dynamics approach. The RMS errors between the predicted and the calculated resultant moments were reported to be low.

Hof et al. (1987) developed a model in which the moment of human calf muscles during walking and stepping was predicted from EMG, muscle length, and contractile and elastic properties. The EMG activity of the soleus and gastrocnemius were recorded using surface electrodes. The ankle moments predicted using the model were compared to the moments obtained from kinematic and kinetic information provided by a SELSPOT system, an electrogoniometer, and a force platform. The results of five subjects showed RMS differences between 7 and 54 Nm (mean = 22 Nm). When the

predicted and calculated ankle moments were normalized with respect to the RMS, the range of the differences was found to be between 0.13 and 0.51 (mean = 0.22). These differences were explained primarily by antagonistic activity.

Dowling (1987) predicted the force of the four major individual muscles that cross the human elbow joint (i.e. biceps brachii, brachialis, brachioradialis, and triceps brachii). The model included muscle activation (EMG), and contractile properties (i.e. force-length relation, force-velocity relation, and series elasticity). Predicted muscle forces were multiplied by their respective instantaneous moment arms (obtained from the literature) and summed with the passive moment, which resulted in the predicted net elbow moment. The predicted net elbow moments obtained from three subjects performing isometric and dynamic (anisotonic) flexion and extension exercises of the elbow joint at different speeds and loads were compared to the calculated corresponding moments obtained from kinematic and kinetic information. Comparisons between the predicted and the calculated net moments indicated that the RMS error was generally less than 25 % for isometric exercises and 45 % for dynamic exercises. Based on multiple linear regression analysis, the discrepancies between the predicted and the calculated moments were found to be mostly related to the anatomical or skeletal aspects (i.e. the size of muscles and the moment arms) of the model.

Bogert et al. (1988) developed a model to predict the force of the deep digital flexor muscle of the hind limb of the horse during regular and interrupted walking. The force-length relation was incorporated in the model, and force was assumed to be proportional to the active state (EMG). A linearly damped element was included into

the mechanical model as a first order approximation of all velocity dependent effects. Geometrical parameters were obtained from radiographs. The experimental procedures included the use of surface electrodes, a force transducer implanted in the tendon of the muscle, high speed film, and a force platform. In order to verify the accuracy of the predictions, the output of the model (instantaneous force) was compared to direct force measurements. A good agreement was found between the predicted and the measured force, although the peak force was systematically underestimated. Large errors were produced during the swing phase of the step cycle, when the muscle did not produce force.

Buchanan et al. (1993) proposed a model to predict the isometric force produced by muscles crossing the wrist joint of five subjects. The model used EMG and anatomical parameters obtained from the literature, and magnetic resonance imaging as input. The following muscles were studied: extensor carpi radialis longus, extensor carpi radialis brevis, extensor carpi ulnaris, flexor carpi ulnaris, and flexor carpi radialis. Other muscles were considered not relevant, provided that the thumb and fingers were relaxed. The wrist joint was modelled as a skewed universal joint. A three-dimensional load cell was used to decompose the force exerted during isometric contractions into extension/flexion; abduction/adduction, and supination/pronation components. The relation between EMG and force signals was assumed to be linear. The estimated forces of individual muscles were compared with the corresponding measured torques. This procedure was thought to eliminate the problem due to mechanical redundancy, assuming that each joint moment was produced by the action of a single

muscle (the extensor carpi radialis brevis and extensor carpi radialis longus were modelled together). The authors concluded that the forces of the wrist muscle could be estimated with reasonable accuracy, although they did not measure forces directly from the muscles.

### **Summary of the Review of Selected Literature**

The brief review of the literature given above indicates that the majority of the experimental EMG-force studies focused on isometric contractions. In a few studies, the EMG-force relations were assessed for isometric contractions at different muscle lengths (Close et al. 1960; Vredenburg and Rau, 1973). These studies revealed that the shape of the EMG-force relation was independent of the length of the muscle, however, the equations that described the relations for different muscle lengths had different coefficients.

Studies aimed at investigating the EMG-force relation for dynamically contracting muscle are rare compared to those investigating isometrically contracting muscle. Furthermore, most studies of dynamic muscular contractions concentrated on contractions performed at a given constant rate of change of muscular length. Despite the fact that force transducers (as well as indwelling electrodes) can, and have been implanted chronically in animal models for other purposes, this type of approach has rarely been used in studies aimed at determining the EMG-force relation of dynamically contracting muscle (Sherif et al. 1983). It is thought that the dynamic EMG-force relation may be studied the best in animal models, where EMG and force can be measured

directly from the target muscle during unrestrained movements of the animals. This approach has not received the attention it should, possibly due to the technical difficulties that it imposes.

Although in most cases the isometric EMG-force relations were found to be linear, there are cases where this relation was reported to be non-linear. It has been argued that the methodology employed to study the association between EMG and force signals may have affected the results of these investigations (Moritani and deVries, 1978). However, a study designed to assess the influence of different ways of recording EMG and force signals on the EMG-force relation, did not support the preceding argument (Woods and Bigland-Ritchie, 1983). There is evidence suggesting that the fibre type composition of a muscle (Bigland-Ritchie et al. 1980), and that muscles comprised primarily of slow twitch fibres tend to have a linear EMG-force relation whereas muscles comprised of a mixed fibre type composition tend to have a non-linear relation. Furthermore, it has also been suggested that the strategy used to modulate force (i.e. recruitment and firing rate of motor units), may determine whether the EMG-force relation is linear or non-linear. For example, Lawrance and De Luca (1983) found that muscles which recruit new motor units throughout the entire range of force production, showed a non-linear EMG-force relation. In contrast, muscles which do not recruit motor units throughout the entire range of force production, and that rely primarily on the firing rate of motor units for force modulation, had a linear EMG-force relation. Interestingly, the EMG-force (moment) relation of a single muscle such as the rectus femoris has been reported to be linear (Smith and Stokes, 1993) as well

as non-linear (Thorstensson et al. 1976; Komi and Viitasalo, 1976), and discrepancies like this one are not easily understood.

Most often, EMG-force relations were obtained using voluntary contractions performed by human subjects. The advantage of this approach is that it reflects the normal physiological conditions. The main disadvantage of this approach is that individual forces and EMG signals cannot be obtained readily. Instead of measuring individual muscle forces in these situations, it has been assumed that the external force/moment of force of an entire synergistic group of muscles (e.g. the knee extensor muscles) reflects accurately the force contribution of an individual muscle (e.g. the rectus femoris). This assumption is not supported by direct force measurements of two or more muscles in animal models (Walmsley et al. 1978; Hodgson, 1983; Herzog et al. 1991, 1992, 1993; Fowler et al. 1993). The EMG-force relations obtained from voluntary human contractions, therefore, represent the association between the EMG signals obtained (presumably) from a single muscle, and the force/moment signals produced by a group of muscles. Direct force measurements from a single muscle in human subjects have been made in isolated cases where the muscles were not functioning in their normal way (Inman et al. 1952; Close et al. 1960; Heckathorne and Childress, 1981). The difficulty of measuring force directly from a single human muscle has been considered to be one of the biggest limitations of studies aimed at identifying a meaningful EMG-force relation (Bouisset, 1973). Another disadvantage of studies conducted using human subjects and voluntary contractions is that there is only limited control over the excitation process, and therefore, identical contractions cannot be

produced repeatedly. Excitation to a skeletal muscle, has, however, been replaced by ENMS approaches which have been used to investigate the EMG-force relation in animal models. Using such an approach muscle forces can be measured directly, and stimulation can be controlled and repeated precisely. ENMS has been used successfully to reproduce the process of recruitment of motor units (Solomonov et al. 1987) according to the size principle as described by Henneman et al. (1965), but the process of independent firing and pseudo-random inter-pulse intervals of motor units (Basmajian and De Luca, 1985) has not been accounted for experimentally. Studying the EMG-force relation while simulating experimentally the independent nature of motor unit firing and the pseudo-random rate of firing of individual motor units may provide new insight into the basic aspects of the relation between EMG and force.

Muscle models using EMG as input have been used to predict the force or the moment produced by a given muscle or group of muscles. Usually, these models incorporate the force-length and the force-velocity properties along with the active state (EMG) of the target muscle (e.g. Hof et al. 1987; Bogert et al. 1988). These models are based on the assumption that the EMG-force relation of the target muscle is known. Furthermore, the force-length and force-velocity properties of the muscles are assumed to be known for all levels of activation, or are assumed to be linearly scaled for all submaximal levels of activation from the "known" properties at maximal levels of stimulation. There is evidence indicating that the force-length and force-velocity relations at submaximal levels of force production are not just linearly scaled-down versions of the force-length and force-velocity properties obtained for maximal

contraction (Rack and Westbury, 1969; Heckman et al. 1992). However, there is only a small amount of data on the force-length and force-velocity relations of submaximally contracting skeletal muscle available. Finally, models aimed at predicting individual muscle forces/moments from measured EMG signals have not been validated, most often, because they lack the possibility of direct force measurements (Coggshall and Bekey, 1970; Olney and Winter, 1985; Dowling, 1987; Hof et al. 1987; Buchanan et al. 1993).

From the above considerations, it appears that substantial new insight into the EMG-force relation of skeletal muscle may be gained (a) using an ENMS technique that allows for independent and pseudo-random stimulation of motor units (or groups of motor units); (b) studying the relation between EMG-force-length; and (c) determining the EMG-force relation during animal locomotion where EMG and force can be measured directly. This project is an attempt to address each one of the points listed above.

### **Evaluation of the Literature**

At least two main factors appear to affect the linearity of the relationship between the EMG and force signals during isometric contractions; namely: the fibre type distribution and the mechanism of force modulation (i.e. recruitment and rate modulation of motor units). The mechanism of force modulation used by the cat soleus muscle during changing of isometric forces is not known; however, this muscle is comprised essentially of slow twitch fibres. Based on the fact that muscles with this type of fibre

composition have been reported to have a linear EMG-force relation it is the author's opinion that the EMG-force relation of the cat soleus muscle will turn out to be linear in this study for isometric contractions performed at a single muscle length.

When tested at different muscle lengths, the EMG-force relation of a skeletal muscle should be affected by the force-length property. Possible effects of changing muscle length on the interelectrode distance, and consequently on the EMG-force relation are expected to be relatively small, compared to the effects of the force-length relation. Therefore, the EMG-force relation of the cat soleus muscle is expected to be linear for isometric contractions at different muscle lengths, however, the relation should have different slopes due, primarily, to the influence of the force-length property.

Aside from the two factors that appear to be relevant in determining the shape of the isometric EMG-force relation of skeletal muscle (i.e. the strategy of force modulation and the fibre type), at least two other properties of skeletal muscle must be taken into account when one thinks about the EMG-force relation during dynamic voluntary contractions; namely: the force-length relation and the force-velocity relation.

Considering the enormous amount of afferent information that the central nervous system is supplied with via different sensors (e.g. golgi tendon organs and muscle spindles), the central nervous system should be aware of the local contractile conditions of the muscle at any given instant in time during the movement. Considering further that the local contractile conditions are dependent on the combined properties

of force-length and force-velocity, the excitation that is sent to the muscle may be modulated by the local contractile conditions. In other words, excitation to a muscle may be low when the muscle is capable of generating high force levels, relative to the force levels that are required to successfully execute the movement; and excitation to a muscle may be high when the muscle's capability of generating force is relatively low compared with the amount of force that it is required to accomplish the motor task.

Assuming that the excitation that is sent to the soleus muscle is represented by the EMG signals, the behaviour of the combined force-length-velocity property is expected to affect the EMG signals, and therefore, the EMG-force relation of the cat soleus muscle during locomotion.

Based on the previous considerations it is hypothesized that:

- (1) the EMG-force relation of the cat soleus muscle is linear for isometric contractions at a single muscle length;
- (2) the EMG-force relation of the cat soleus muscle is linear for isometric contractions performed at different muscle lengths, however, it should have different slopes that reflect the influence of the force-length relation on the EMG-force relation;
- (3) the EMG-force relation of the cat soleus muscle is non-linear for the dynamic contractions performed during locomotion;
- (4) the EMG-force relation of the cat soleus muscle is influenced by the instantaneous contractile conditions during locomotion.

## Chapter 3

### EMG-Force Relation: Stimulation of VR Filaments

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Experiments conducted by Galvani in 1791 showed that electrical stimulation of skeletal muscles produced contraction and force (Basmajian and De Luca, 1985). It has been a theory of many scientists that EMG signals and muscular force are related. Although the literature most often describes a linear relation between EMG and force (e.g. Lippold, 1952; Liberson et al. 1962; Seyfert and Kunkel, 1974; Hof and van den Berg, 1977), there is experimental evidence suggesting that the relation may be non-linear (e.g. Komi and Viitasalo, 1976; Vredenburg and Rau, 1973). The different results reported in the literature may be explained partly by (a) difficulties in obtaining direct force (Bouisset, 1973) and EMG records from a single muscle, (b) differences in fibre type composition of the muscles studied (Bigland-Ritchie et al. 1980), and (c) different mechanisms of force modulation of different muscles (Woods and Bigland-Ritchie, 1983; Lawrance and De Luca, 1983). With regard to the last point, Solomonov et al. (1987) obtained either linear or non-linear EMG-force relations in skeletal muscle depending on the strategy of recruitment employed to activate motor units.

EMG-force relations may be studied using two basic approaches: voluntary contractions or ENMS. Physiological conditions are best studied using voluntary contractions but under these conditions it is difficult to measure EMG signals without cross-talk from neighbouring muscles, and it is difficult to obtain direct measurements of muscular forces in humans. Studies using ENMS techniques in animal models can overcome these limitations, and in addition, allow for precise control of stimulation. Present ENMS techniques have been successfully used to reproduce the process of recruitment of motor units according to the size principle as described by Henneman et al. (1965) (e.g. Petrofsky, 1978; Solomonov et al. 1987; Fang and Mortimer, 1991). However, muscular force is also modulated by the firing rates of active motor units (Milner-Brown et al. 1973) which to date has not been reproduced successfully using ENMS (e.g. Petrofsky, 1978; Solomonov et al. 1987). When using ENMS to simulate the process of motor units firing in a muscle, four factors should be considered: (a) motor units fire asynchronously (Basmajian and De Luca, 1985); (b) firing rates at initial recruitment range between 6 to 12 pulses per second (pps) (Burke, 1981); (c) firing rates of active motor units increase as new motor units are recruited (Gydikov and Kosarov, 1974; Monster and Chan, 1977); and (d) firing rates are non-periodic (De Luca and Forrest, 1973).

Ideally, ENMS techniques should be capable of combining recruitment of motor units according to the size principle, with independent rate modulation of motor units as described above. Such techniques are presently not available, but by choosing a muscle comprised of relatively homogeneous motor unit size, the possible effects of

recruitment according to the size principle on the EMG-force relation might be reduced to some extent.

The purpose of this study was to assess the EMG-force relation of the cat soleus muscle using ENMS, with particular attention being paid to simulate experimentally the complex behaviour of motor unit firing using VR filaments.

The cat soleus muscle was used for several reasons: (a) it is comprised exclusively of slow twitch fibres of homogeneous size (Ariano et al. 1973), thus, recruitment strategies were considered of relative less importance in force and EMG modulation, (b) the EMG-force relation of muscles with predominantly slow motor units has been reported to be linear (Close et al. 1960; Bigland-Ritchie et al. 1980); and (c) EMG and force records of cat soleus muscle during locomotion can be found in the literature for comparison (Walmsley et al. 1978; Hodgson, 1983; Gregor et al. 1988).

## **METHODS**

### **Animals**

Five animals were used in three different tests. Three cats (masses = 3.8, 3.3 and 4.2 kg) were used in the main test, designed to investigate the combined effects of addition and rate modulation of VR filaments on the EMG-force relation of cat soleus muscle during isometric contractions. A fourth animal (mass = 4.3 kg) was used exclusively to study the effects of addition of VR filaments on the EMG-force relation,

and a fifth animal (mass = 4.0 kg) was used to study the effects of systematic increases in stimulation rates of single VR filaments on the EMG-force relation.

### **Animal Preparation**

All animals were anesthetized using either an injection of Nembutal or Somnotol. Cannulation of the left superficial jugular vein was performed to allow intravenous injections of drugs. Tracheal intubation allowed the use of artificial respiration if necessary. Cannulation of the carotid artery was performed to monitor blood pressure continuously, and blood pressure was maintained using injections of 2 to 4 ml of Macrodex (6 % Hausmann, St. Gallen) when required. After cannulation and intubation, the animals were placed in a prone position on a thermostatically controlled pad. Body temperature was continuously monitored and kept at approximately 38 degrees C throughout the experiments.

Myotomy of the back muscles and laminectomy was performed to expose the nerve roots L7 and S1 in a way similar to that described by Rack and Westbury (1969). The cristae iliacae were removed bilaterally to create space for the stimulation electrodes. The VRs L7 and S1 which contain alpha motoneurons to the soleus muscle were identified and separated from the corresponding dorsal roots. A microscopic dissection was performed to split the VRs of L7 and S1 into either eight or ten filaments that produced comparable force when stimulated at a fixed rate of 30, 50, or 60 pps (i.e. stimulation rates were different in each experiment). VR filaments were rank ordered according to force production (except in the experiment designed to

assess the effects of addition of VR filaments on the EMG-force relation) and were placed on hook-like individual stimulation electrodes. Each VR filament prepared in this way contained an unknown number of alpha motoneurons.

The soleus muscle of the left hindlimb was exposed with its innervation and blood supply being maintained. Nerve supply to other muscles and cutaneous territories of the same hindlimb was severed. A relation between ankle joint angle (AJA) and soleus length was established using a goniometer and a linear scale with the muscle attached at its original insertion (an AJA of 0 degrees was defined as the angle that would be obtained if the foot was forced into plantar flexion up to the point where it would be perfectly aligned with the shank). Dorsi-flexion of the ankle joint increased the AJA. The tendon of the soleus muscle was then detached from its insertion with a remnant piece of the calcaneus. This piece of bone was firmly tied to the longitudinal arm of an electromagnetic motor which served to adjust muscle length to the desired position. The motor was instrumented with a transducer to record soleus force (Entran, ESU-60-350, semi-conductor strain gauge). The pelvis and the left hindlimb of the animals were firmly fixed to a rigid frame using steel pins.

Paraffin pools were prepared to cover the exposed areas on the back and left hindlimb. The leg pool was continuously supplied with a carbogen-oxygen mixture (Medigas, 5% CO<sub>2</sub>, and 95 % O<sub>2</sub>) and the soleus muscle was regularly moistened with oxygenized Ringer's solution (pH 7.4).

The stability of the preparation was assessed on-line at regular intervals throughout the testing session by stimulating each VR filament at a fixed rate, and comparing its force output to the value obtained at the start of the experiment. Experiments were terminated when more than 10 % of the initial force was lost.

### **Stimulation, EMG, and Force Measurements**

Stimulation of VR filaments was performed using rectangular pulses (duration of 1 ms) with an amplitude of two to three times threshold levels. Each VR filament was placed on a separate silver wire electrode of a multi-electrode array (Figure 1).

Stimulation trains consisted of pulses with pseudo-random intervals (coefficient of variation of 12.5 %) based on a Gaussian distribution (Zhang et al. 1992). Eight VR filaments were stimulated directly from digital memories of a hybrid signal generator. Pulses of two of these generators were delayed 10 to 20 ms and applied to two further VR filaments. VR filaments were stimulated using ten independent voltage-controlled stimulators. Stimulation for each trial started two to three seconds prior to data collection. Eight of the ten VR filaments could be stimulated independently at different nominal mean rates, and these rates could be varied between trials.

Recordings were made using indwelling (wire) electrodes (Loeb and Gans, 1986) with 1 to 2 mm of exposed tips. The interelectrode distance was approximately 10 mm. Raw EMG signals were pre-amplified and then further amplified using a band-pass filter with cut-off frequencies of 3 Hz and 1 kHz (Figure 1).

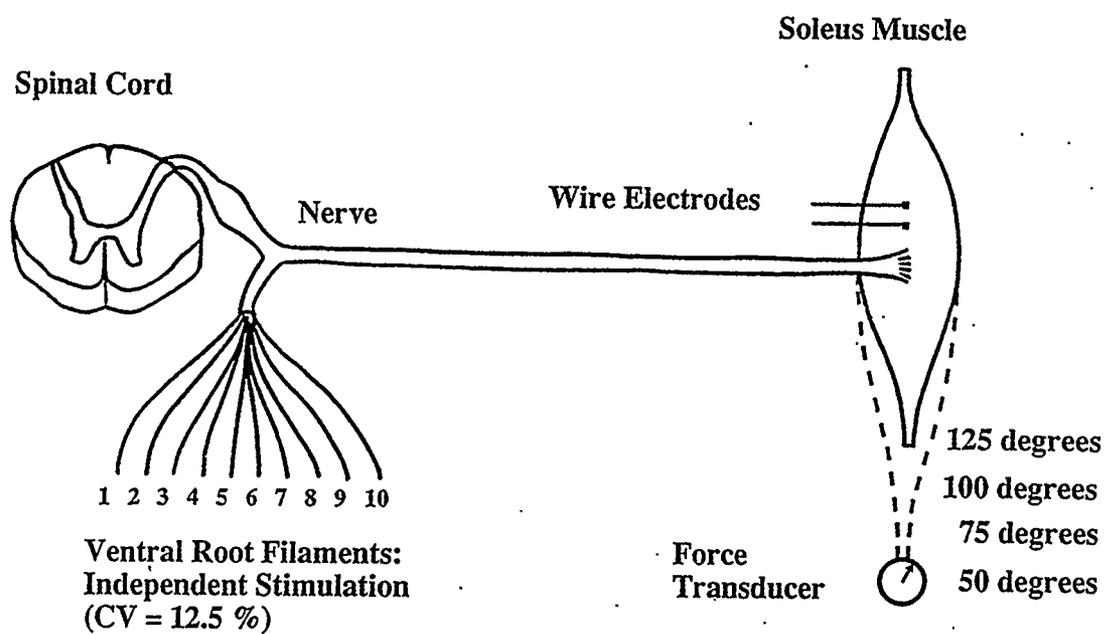


Figure 1. Schematic representation of the procedures used during the acute experiments. CV = coefficient of variation. Muscle length was adjusted by changing the ankle joint angle.

Force signals were amplified and low-pass filtered with a cut-off frequency of 100 Hz. Calibration of the strain transducer was linear ( $r^2 = 1.0$ ) for the range of forces produced during the experiments.

### **Data Acquisition and Treatment**

EMG and force data were collected for 2 seconds in each trial and were digitized at 2100 and 350 samples per second, respectively, using an analog to digital board and an LSI computer. The IEMG (i.e. the area under the full-wave rectified EMG) and the mean force were calculated for each 2 second period.

### **Protocols**

The protocols designed to study the effects of (a) simultaneous addition and rate modulation of VR filaments; (b) addition of VR filaments; (c) rate modulation of single VR filaments; and (d) the procedures used to assess the EMG-force relation of isolated VR filaments will be described separately. All protocols were tested for a fixed muscle length corresponding to an AJA of 105 degrees.

#### *Simultaneous Addition and Rate Modulation of VR Filaments*

In order to study the effects of simultaneous addition and rate modulation of VR filaments on EMG, force, and the EMG-force relation of cat soleus muscle, the protocol shown in Table 1 was used in two experiments. The active VR filaments in each

Table 1. Protocol designed to study the simultaneous effects of addition (trials 1 to 10) and rate modulation (trials 1 to 27) of ten VR filaments on the EMG-force relation. Mean stimulation rates of active VR filaments are indicated for each trial in pps. Coefficient of variation of stimulation trains = 12.5 %.

Trial #	Ventral Root Filament #									
	1	2	3	4	5	6	7	8	9	10
1	3									
2	3	3								
3	5	5	3							
4	5	5	3	3						
5	7	7	5	5	3					
6	9	9	7	7	5	3				
7	11	11	9	9	7	5	3			
8	13	13	11	11	9	7	5	3		
9	15	15	13	13	11	9	7	5	3	
10	17	17	15	15	13	11	9	7	5	3
11	19	19	17	17	15	13	11	9	7	5
12	21	21	19	19	17	15	13	11	9	7
13	23	23	21	21	19	17	15	13	11	9
14	25	25	23	23	21	19	17	15	13	11
15	27	27	25	25	23	21	19	17	15	13
16	29	29	27	27	25	23	21	19	17	15
17	31	31	29	29	27	25	23	21	19	17
18	33	33	31	31	29	27	25	23	21	19
19	35	35	33	33	31	29	27	25	23	21
20	37	37	35	35	33	31	29	27	25	23
21	39	39	37	37	35	33	31	29	27	25
22	41	41	39	39	37	35	33	31	29	27
23	43	43	41	41	39	37	35	33	31	29
24	45	45	43	43	41	39	37	35	33	31
25	47	47	45	45	43	41	39	37	35	33
26	49	49	47	47	45	43	41	39	37	35
27	51	51	49	49	47	45	43	41	39	37

trial are identified by their mean stimulation rates in pps. From trial 1 to trial 10, muscle force was modulated simultaneously by stimulating additional VR filaments and by increasing the mean stimulation rates of previously active VR filaments. From trial 11 to trial 27, force modulation was accomplished exclusively by increasing the mean stimulation rates of all VR filaments.

A similar but shorter protocol than the one shown in Table 1 was adopted in one additional experiment. In this experiment, mean stimulation rates similar to those used from trial 5 to trial 19 in Table 1 were accommodated into ten trials.

#### *Addition of VR Filaments*

Addition of VR filaments without concomitant increases in stimulation rates was tested in one experiment (Table 2). The active VR filaments in each trial are identified by their mean stimulation rates in pps. In addition to the protocol shown in Table 2, each VR filament was stimulated by itself at the assigned mean rate shown in Table 2. The raw EMG and force recordings obtained from single VR filament stimulation were added algebraically in the same order as VR filaments were added experimentally (Table 2). Thus, calculated IEMG and calculated mean force values could be compared to the corresponding values obtained for each of the experimental trials.

Table 2. Protocol designed to study the effects of the addition of eight VR filaments on the EMG-force relation. Mean stimulation rates of active VR filaments are indicated for each trial in pps. Coefficient of variation of stimulation trains = 12.5 %.

Trial #	Ventral Root Filament #							
	1	2	3	4	5	6	7	8
1	5							
2	5	9						
3	5	9	12					
4	5	9	12	19				
5	5	9	12	19	16			
6	5	9	12	19	16	30		
7	5	9	12	19	16	30	23	
8	5	9	12	19	16	30	23	27

### *Rate Modulation of Single VR Filaments*

In order to assess the effects of rate modulation on the EMG-force relation, two single VR filaments from one animal were studied independently by stimulating them at nominal mean rates ranging from 5 to 50 pps, with increments of 5 pps.

### *EMG-Force Relation of Isolated VR Filaments*

In order to test if the IEMG of single compound motor unit action potentials (CMUAPs) was related to the corresponding tetanic force, CMUAPs elicited when VR filaments were stimulated separately were extracted from raw data, and their IEMGs were calculated and plotted versus tetanic force. These calculations were made for two experiments, when VR filaments were stimulated either at 50 pps or 60 pps.

## **RESULTS**

EMG signals produced using asynchronous, independent stimulation of VR filaments (Hulliger et al. 1987) and pseudo-random inter-pulse intervals (Zhang et al. 1992) were similar to EMG signals in the time (Figure 2a) and frequency domains obtained during voluntary contractions. The adoption of pseudo-random stimulation trains produced typical effects of force summation (Copper and Eccles, 1930) when a small number of VR filaments was stimulated at relatively low rates (Figure 2b).

The results will be presented in the following order: (a) simultaneous addition and rate modulation of VR filaments (main protocol); (b) addition without rate modulation

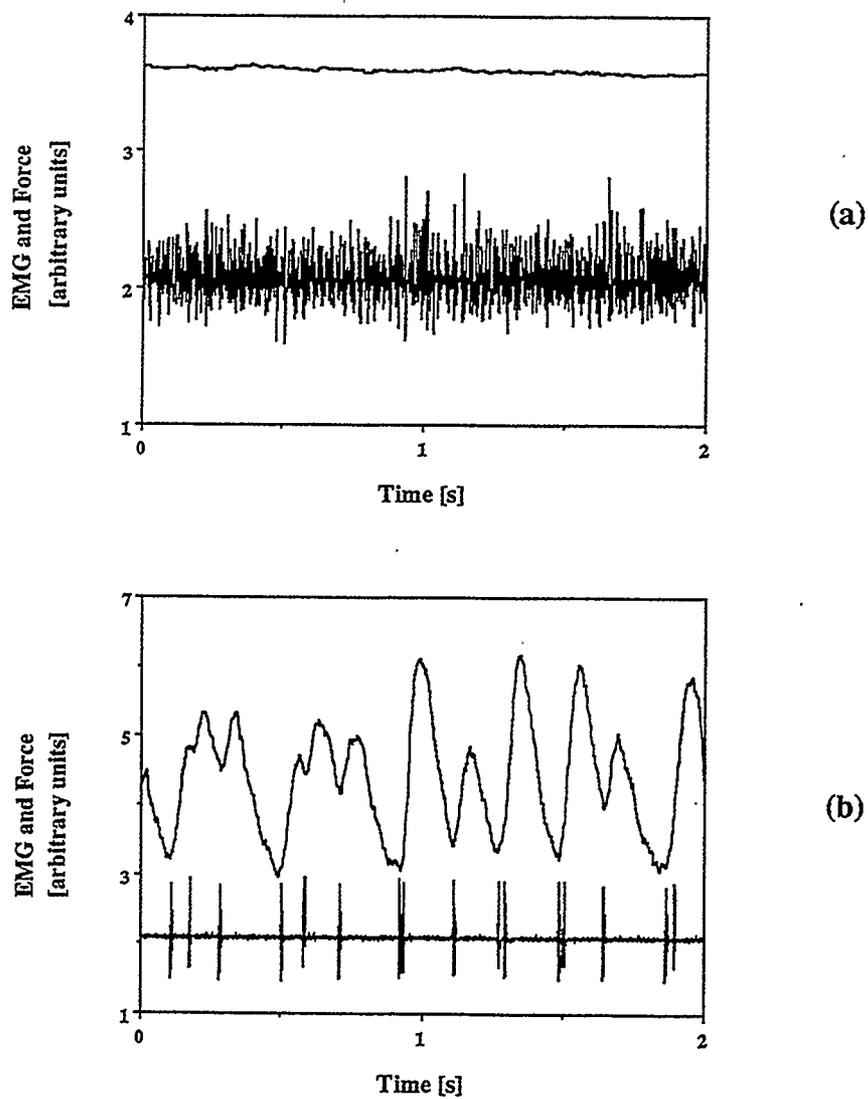


Figure 2. Typical raw EMG and force signals are shown in arbitrary units (a) when ten VR filaments were stimulated at high rates and (b) when a small number of VR filaments (e.g. three) was stimulated at low rates, both using pseudo-random inter-pulse intervals with a coefficient of variation of 12.5 %.

of VR filaments; (c) rate modulation of single VR filaments; and (d) EMG-force relation of isolated VR filaments. Unless otherwise specified IEMG and mean force results were normalized with respect to the values obtained in the last trial of the protocol. There were no signs of fatigue or of deterioration of the preparation in any of the tests reported here.

### **Simultaneous Addition and Rate Modulation of VR Filaments**

Figures 3, 4, and 5 show the effects of simultaneous addition and rate modulation of VR filaments on IEMG, mean force, and IEMG-mean force relation. The results shown in Figures 3 and 4 were obtained using the long protocol given in Table 1, whereas the results in Figure 5 correspond to the short protocol (i.e. approximately trials 5 to 19 in Table 1).

Using the long protocol, IEMG appeared to saturate beyond trial 22 in one experiment (Figure 3a) but not in the other (Figure 4a). The mean duration of CMUAPs were estimated to be approximately 19 ms (SD = 2 ms) and 11 ms (SD = 2 ms) for the experiments shown in Figures 3a and 4a, respectively.

Using the long protocol, mean force behaviour as a function of increasing stimulation through addition and rate modulation of VR filaments was similar in both animals (Figures 3b and 4b). In the initial trials (i.e. trials 1 to 4 in Figure 3b, and trials 1 to 5 in Figure 4b) mean force did not increase substantially with increasing stimulation. In the intermediate part of the protocol, however, (i.e. trials 5 to 16 in

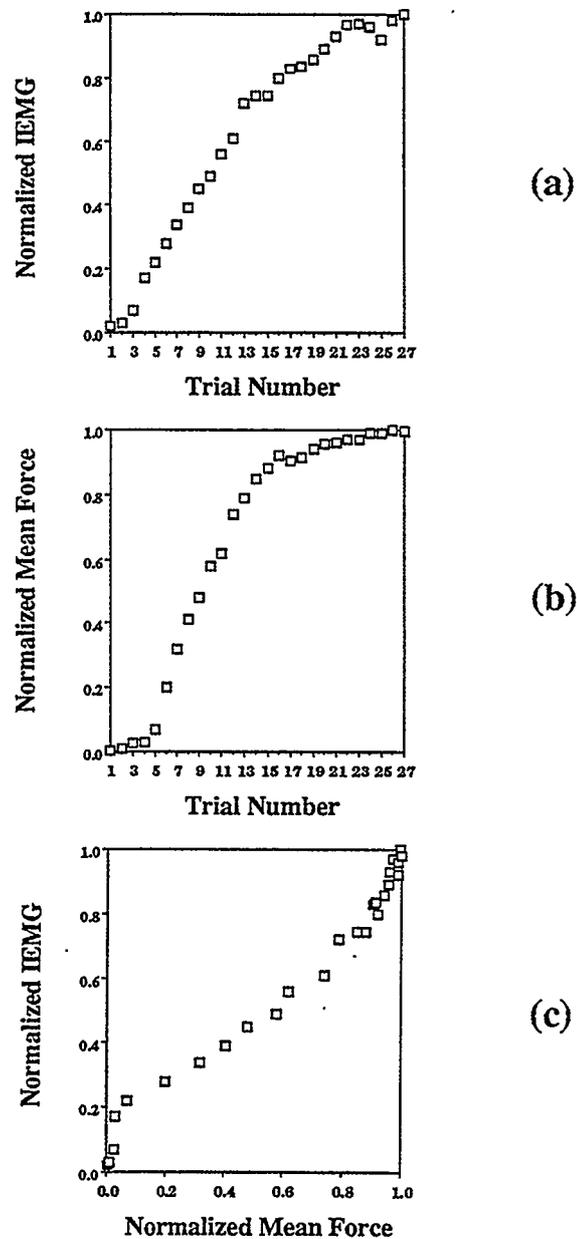


Figure 3. (a) IEMG and (b) mean force responses to addition and rate modulation of VR filaments (i.e. trial number, Table 1); and (c) the corresponding IEMG-mean force relation obtained from one experiment (three regions identified: low (L), intermediate (I), and high (H)). IEMG and mean force were normalized relative to the highest values obtained. Maximal mean force measured = 23.3 N. Single VR filaments produced mean forces from 1.9 N to 3.7 N when stimulated at 50 pps.

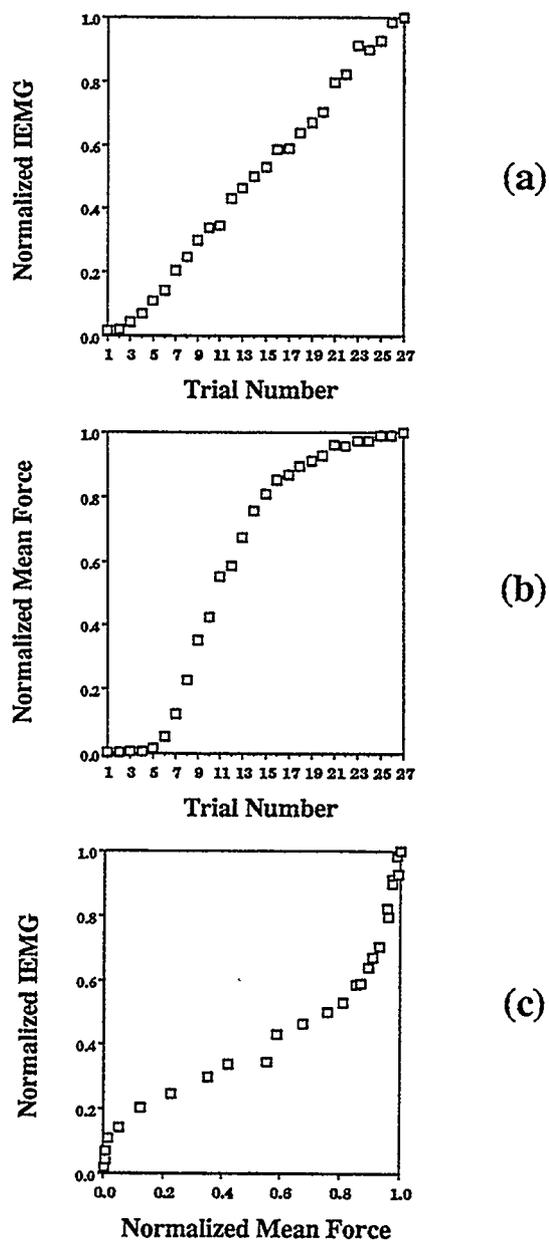


Figure 4. (a) IEMG and (b) mean force responses to addition and rate modulation of VR filaments (i.e. trial number, Table 1); and (c) the corresponding IEMG-mean force relation obtained from one experiment (three regions identified: low (L), intermediate (I), and high (H)). IEMG and mean force were normalized relative to the highest values obtained. Maximal mean force measured = 29.3 N. Single VR filaments produced mean forces from 2.0 N to 3.9 N when stimulated at 60 pps.

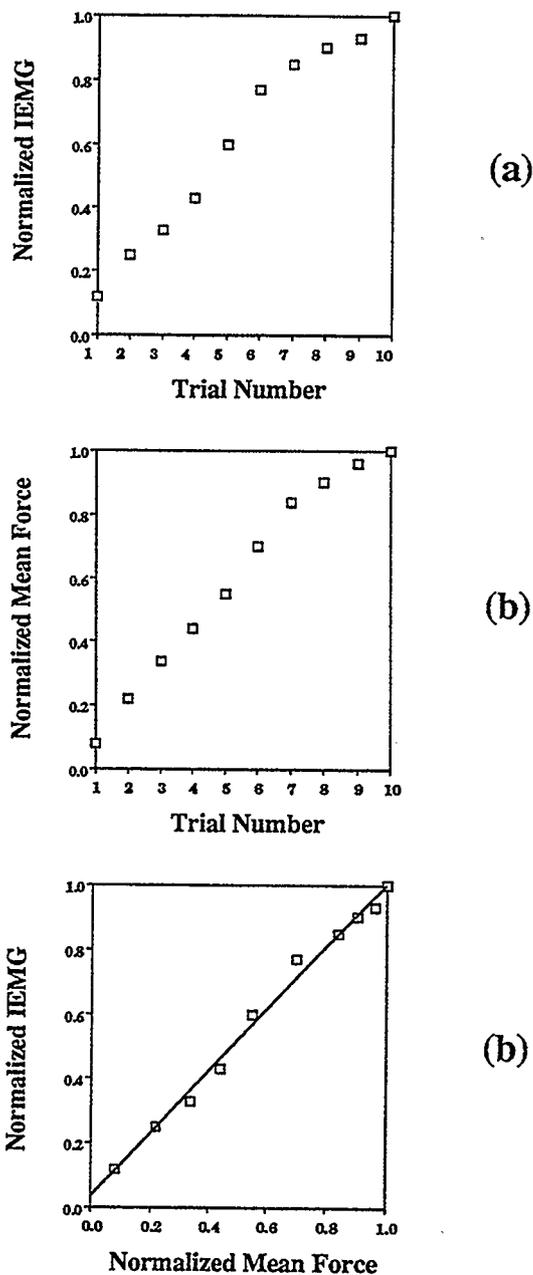


Figure 5. (a) IEMG and (b) mean force responses to addition and rate modulation of VR filaments (i.e. trial number, short protocol); and (c) the corresponding IEMG-mean force relation obtained from one experiment. IEMG and mean force were normalized relative to the highest values obtained. Maximal mean force measured = 35.6 N. Single VR filaments produced mean forces from 1.4 N to 4.8 N when stimulated at 30 pps.

Figure 3b, and trials 6 to 16 in Figure 4b) mean forces increased substantially. Beyond trial 16 (i.e. for a range of mean stimulation rates of 15 to 29 pps) increments in mean force decreased in both experiments. As a consequence of these results, the IEMG-mean force relations showed three distinct regions that will be referred to hereafter as low (L), intermediate (I), and high (H), according to the stimulation levels with which they are associated (Figures 3c and 4c).

In the L and H stimulation regions, IEMG increased fast compared to mean force; in the I region, mean force increased fast compared to IEMG. In the I region, the IEMG-mean force relations could be approximated adequately with straight line models ( $r^2 = 0.98$  and  $0.99$  in Figures 3c and 4c, respectively).

Using the short protocol, IEMG (Figure 5a) and mean force values (Figure 5b) increased substantially from trials 1 to 7, showing signs of saturation beyond trial 7. The relation between IEMG and mean force was close to linear for this protocol ( $r^2 = 0.99$  in Figure 5c).

In order to compare the IEMG-mean force relations for the three animals shown in Figures 3, 4, and 5, all results were normalized relative to the values obtained in each experiment when all ten VR filaments were stimulated simultaneously at 50 pps (Figure 6).

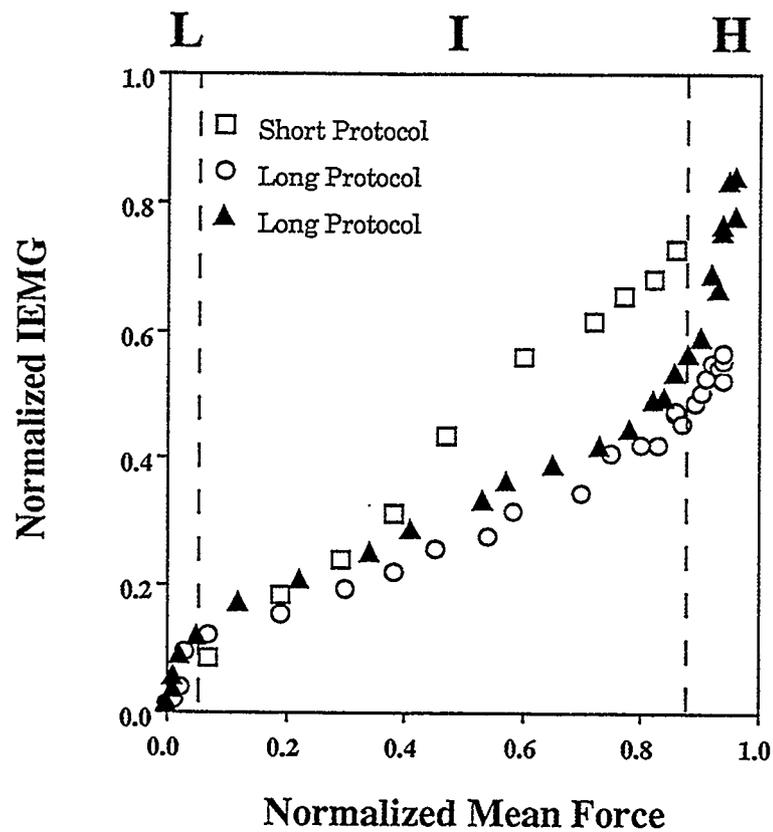


Figure 6. Summary of IEMG-mean force relations obtained from three experiments. Three regions are identified: low (L), intermediate (I), and high (H). Addition and rate modulation of ten VR filaments were implemented using the protocol in Table 1 in two experiments and its short version in one experiment. IEMG and mean force were normalized relative to values obtained when all ten VR filaments were stimulated simultaneously at 50 pps.

### **Addition of VR Filaments**

Calculated IEMG and mean force values (obtained after raw signals of individual VR filaments were added algebraically) are shown versus measured IEMG and mean force values (Table 2) in Figures 7a and 7b, respectively. Calculated and experimentally determined IEMG and mean force values were virtually identical ( $r^2 = 0.99$  in both figures).

### **Rate Modulation of Single VR Filaments**

The results obtained from stimulation of single VR filaments at nominal mean rates ranging from 5 to 50 pps are shown in Figures 8 and 9. IEMG was linearly related to mean stimulation rate for both VR filaments tested ( $r^2 = 0.99$  in both Figures 8a and 9a).

The mean force response to changes in stimulation rate was similar for both VR filaments (Figures 8b and 9b). Mean force increments were large for increases in mean stimulation rates up to 25 pps. Beyond 25 pps, mean forces increased only slightly (Figure 8b) or not at all (Figure 9b). Consequently, a non-linear IEMG-mean force relation was found for both VR filaments, with IEMG increasing faster than mean force at high rates of stimulation (Figures 8c and 9c).

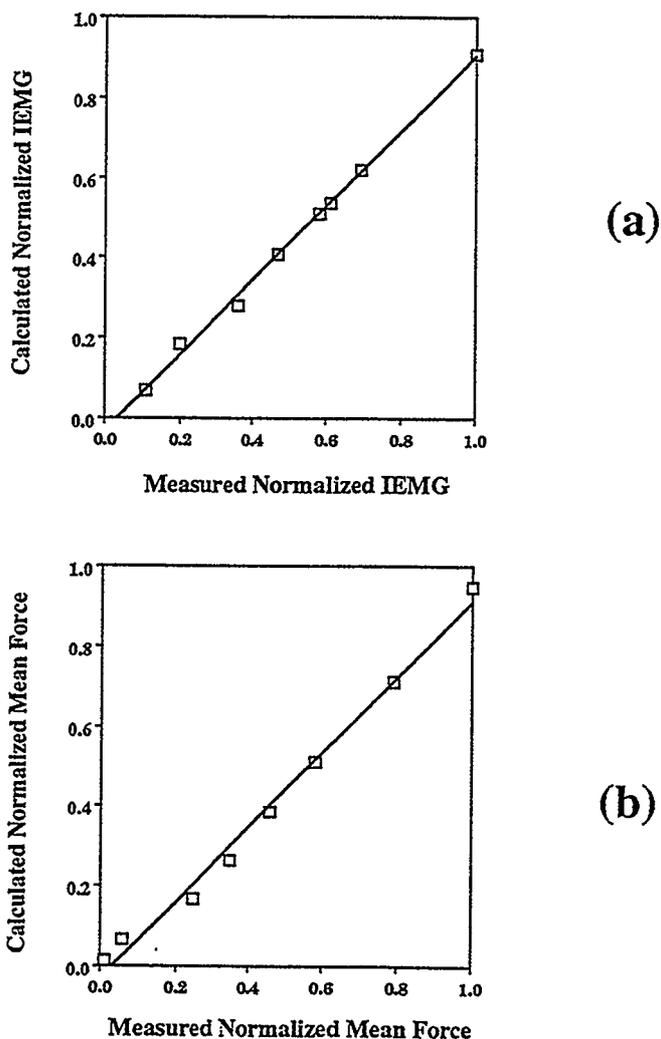


Figure 7. Calculated versus measured (a) IEMG and (b) mean force. Calculated values were obtained after summing raw signals produced when single VR filaments were stimulated according to the protocol shown in Table 2. Measured values were obtained experimentally using the protocol shown in Table 2. Calculated and measured IEMG and mean force were normalized relative to maximal measured values, respectively. Maximal mean force measured = 20.6 N; maximal mean force calculated = 19.5 N.

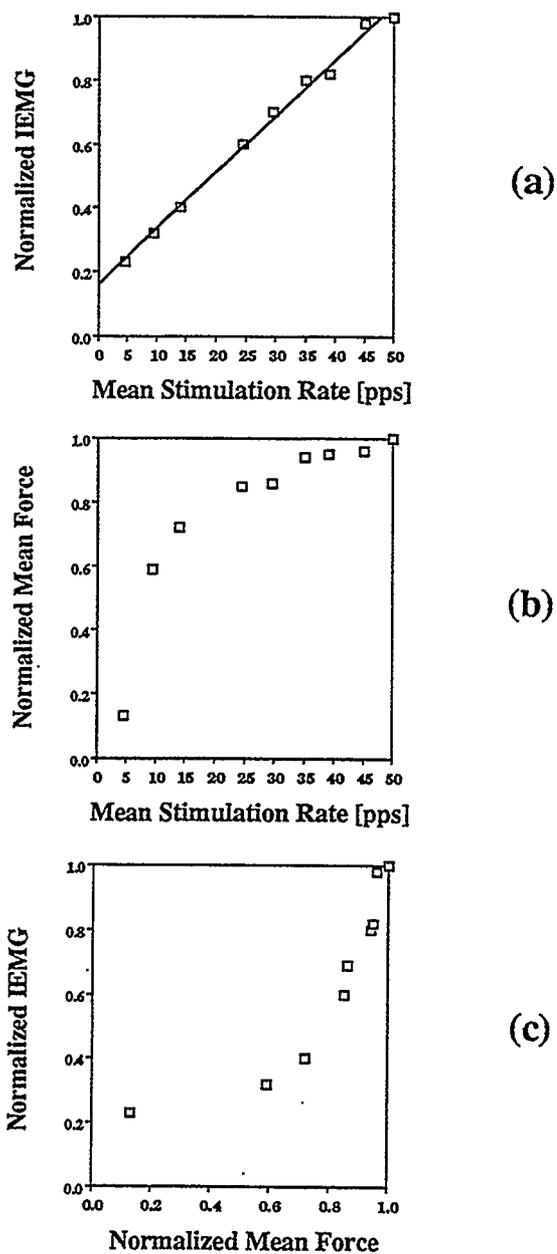


Figure 8. (a) IEMG, and (b) mean force response of a single VR filament as a function of actual mean stimulation rates; and (c) the corresponding IEMG-mean force relation. IEMG and mean force were normalized relative to the highest values obtained. Maximal mean force measured = 2.3 N.

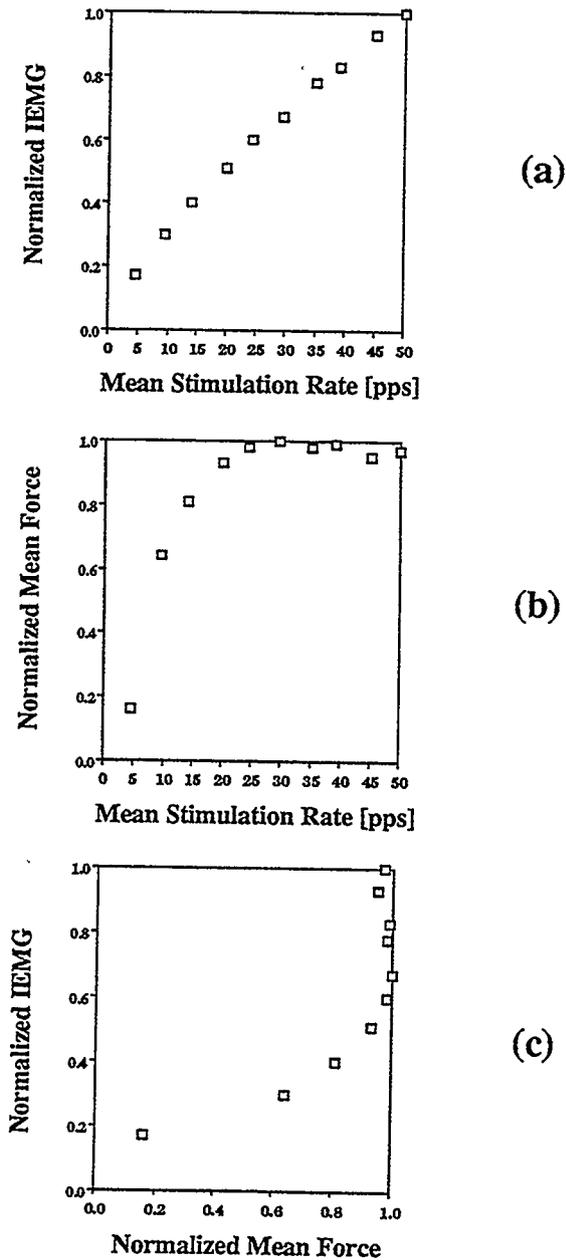


Figure 9. (a) IEMG, and (b) mean force response of a single VR filament as a function of actual mean stimulation rates; and (c) the corresponding IEMG-mean force relation. IEMG and mean force were normalized relative to the highest values obtained. Maximal mean force measured = 3.5 N.

## EMG-Force Relation of Isolated VR Filaments

Figures 10a and 10b show the relation between the IEMG of single CMUAPs (extracted from raw data) and the corresponding tetanic forces obtained when VR filaments were stimulated at 50 pps (Figure 10a) and 60 pps (Figure 10b) in two different experiments.

## DISCUSSION

Using a protocol for graded muscular contractions (i.e. stimulation) under isometric conditions (Table 1), we obtained a sigmoid relation between IEMG and mean force (Figures 3c and 4c). The cat soleus is a muscle with uniform fibre composition (Ariano et al. 1973), and muscles of this type have been associated with linear EMG-force relations (e.g. Close et al. 1960; Bigland-Ritchie et al. 1980). Therefore, the three different regions of the IEMG-mean force relations (i.e L, I, and H, Figures 3c and 4c) that make up the sigmoid relation found in this study must be explained.

The L region of the IEMG-mean force relation (Figures 3c and 4c) produced forces below approximately 0.04 of maximal force and was characterized by a fast increase in IEMG and slow increase in mean force. This finding could be associated with any of the following points: first, weak VR filaments (stimulated first) may produce disproportionately large IEMG compared to the strong VR filaments (stimulated last). For example, Milner-Brown and Stein (1975) observed that action potentials of small motor units had large peak-to-peak amplitudes relative to their force threshold,

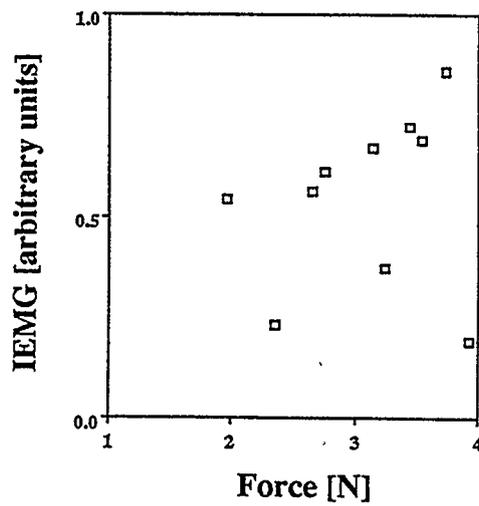
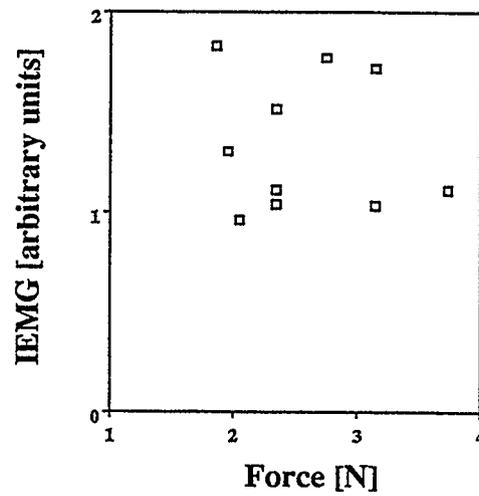


Figure 10. IEMG of single CMUAPs extracted from raw data versus tetanic force obtained when VR filaments were stimulated individually corresponding to experiments of (a) Figure 3, and (b) Figure 4.

compared to large motor units. In our study, motor units were not recruited according to size, since the motor units contained in a VR filament were not classified and separated. Possibly as a consequence of this design, no relation was found between IEMG of single CMUAPs and tetanic force of VR filaments (Figures 10a and 10b). Second, stimulating the VR filaments in a rank order from weakest to strongest caused low force production in the initial trials compared to the final trials; and third, the initial four trials (Table 1) contained maximal stimulation rates (i.e. 5 pps) that were lower than the initial firing rates that have been reported for motor units during voluntary contractions (i.e. 6 to 12 pps, Burke, 1981). Such low stimulation rates may have reduced the effects of force summation observed for higher stimulation rates. We believe that the combination of the two latter possibilities (i.e. weaker VR filaments being stimulated in early trials and at physiologically low rates) were the primary reasons for the fast increase in IEMG and slow increase in mean force observed in the L region. Figures 8b and 9b support this argument in part, showing that mean force increased almost four times when stimulation rates increased from 5 pps to 10 pps.

The I stimulation region of the IEMG-mean force relation (Figures 3c and 4c) produced mean force values between approximately 0.05 and 0.88 of maximal force. This region also contains the results of all trials in Figures 5a and 5b, (obtained using the short protocol), and was virtually linear for all three experiments (Figures 3c, 4c, and 5c). This linearity between IEMG and mean force in the middle region of the protocol may be explained in part by the linear behaviour between IEMG and rate of stimulation of individual VR filaments (Figures 8a and 9a). The linear relation between

IEMG and rate of stimulation, in turn, was expected and is based on the facts that the shape, amplitude and duration of CMUAPs (and thus IEMG) were independent of stimulation rate; and that the stimulation rates applied to single VR filaments in this study did not cause overlapping of CMUAPs. The linearity of the IEMG-mean force relation in the I region is also associated with the observation that IEMG and mean force values of individual VR filaments added algebraically (Figures 7a and 7b).

Mean stimulation rates, did not relate linearly to mean forces produced by single VR filaments (Figures 8b and 9b), not even in the region of concern here (i.e. below mean stimulation rates of 25 pps). However, deviations from linearity below stimulation rates of 25 pps were small and so, did not influence the linearity of the IEMG-mean force relation in the I region appreciably.

The H region of the IEMG-mean force relation produced mean force values above approximately 0.88 of maximal force (Figures 3c and 4c). This region is characterized by fast increases in IEMG and relatively slow increases in mean force for increasing stimulations. The mean stimulation rate of VR filaments at the transition between the I and H regions was approximately 25 pps. At this rate, mean forces (Figures 8b and 9b) but not IEMG (Figures 8a and 9a) obtained from single VR filaments were found to saturate. If the results found for these two single VR filaments are representative of the properties of other VR filaments and therefore, the entire muscle, the faster increase in IEMG relative to mean force observed in the H region may be explained with the saturation of force. Depending on the duration of CMUAPs, saturation of IEMG may occur at high stimulation rates. Relatively long duration of

CMUAPs produced some saturation in IEMG in one experiment (Figure 3a). This saturation however, was not sufficient to prevent the change in the relation between IEMG and mean force from the I to the H region. Therefore, the results of the H region of the IEMG-mean force relation can indeed be explained primarily on the basis of saturation of force levels as the mean stimulation rate calculated for all VR filaments exceeded 25 pps.

As discussed previously, the IEMG-mean force results corresponding to the L region (Figures 3c and 4c) were obtained using mean stimulation rates that were lower than the firing rates that have been observed at the point of recruitment of motor units (Burke, 1981). Therefore, it may be argued that stimulation patterns used in the L region do not reflect firing patterns of motor units during voluntary contractions.

The forces obtained in the H stimulation region were above 0.88 of the maximal isometric force. Peak soleus forces measured experimentally for cats of the size used in this study range from about 17 N and 22 N for locomotor and jumping activities (Herzog and Leonard, 1991; Walmsley et al. 1978). Corresponding isometric peak forces obtained using supramaximal stimulation of the tibial nerve typically exceed 30 N (Herzog et al. 1992). Thus, it appears that cat soleus muscle never produces more than about 60 % to 75 % of its isometric peak force potential, particularly when considering that maximal forces during locomotion are reached at the end of eccentric contractions of the muscle-tendon complex (Herzog et al. 1992). Therefore, the forces obtained in the H region of the stimulation protocol of this study are probably higher than any soleus force ever achieved by a cat during voluntary movements.

The overall results obtained in this study do not support the hypothesis raised in chapter 2 that the EMG-force relation of the cat soleus muscle is linear for isometric contractions performed at a single muscle length. However, neglecting the IEMG-mean force relation found here for the L and H regions on the basis of the preceding arguments, our results suggest that the IEMG-mean force relation of the cat soleus muscle is linear within the physiologic limits of stimulation parameters and force production, as hypothesized.

Results from three experiments showed a linear relation between EMG and force for a range of stimulations that is likely to occur during voluntary movement. We believe that the actual shape of the IEMG-mean force relation for voluntary contractions is similar to the one found here using stimulation of VR filaments. If individual motor units of the soleus muscle could be stimulated independently (rather than just ten VR filaments) one might expect a more pronounced and perhaps earlier onset of saturation of IEMG than that observed in this study, due to an increased amount of overlapping of motor unit action potentials. An earlier and more pronounced saturation of IEMG could cause the IEMG-mean force relation to remain linear even beyond the end of the I region (Figure 6), and therefore, would not compromise the findings reported here for the I region.

The relatively long duration of CMUAPs obtained in this study (19 and 11 ms for experiments in Figures 3a and 4a, respectively) may have compensated, to some extent, the overlapping that may have occurred had single motor units been stimulated instead of VR filaments. Single motor unit action potentials have been reported to last

between 1 to 13 ms (Basmajian and De Luca, 1985). The long duration of CMUAPs observed in this study is likely to be due to the spatial summation of several motor unit action potentials. Onset of action potentials of different motor units are likely to be shifted in time, as a consequence of differences in the length of the nerve branches that supply the muscle fibres; differences in the distances that the action potentials need to travel along the muscle fibres until they reach the recording electrodes; and differences in the velocity of conduction of the impulses along the nerve and muscle fibres. The differences seen in the duration of CMUAPs in this study may reflect, to some extent, different nerve and muscle conduction velocities of different animals; but could also have been affected by the difficulties associated with defining accurately where CMUAPs started and ended. It is important to acknowledge here that the amount of overlapping of action potentials is high when motor units are recruited (compared to the stimulation protocol that we adopted); and is also affected by motor unit size (Ray and Guha, 1983). In this study we were unable to stimulate individual motor units and control recruitment according to motor unit size. These limitations should be kept in mind when looking at the linear IEMG-mean force relations obtained here for the I region.

## SUMMARY

Independent stimulation of VR filaments and pseudo-random inter-pulse intervals were used to assess the EMG-force relation of the cat soleus muscle. This technique allowed for simulation of motor units firing patterns in accordance with findings from

studies using voluntary contractions. Physiologic recruitment according to the size principle was not implemented since each VR filament had an unknown number of motor units of different sizes. However, this (potential) limitation was expected to be reduced by studying a muscle that is known to contain motor units of relatively uniform size. Under these conditions, the EMG-force relation of the cat soleus muscle was found to be non-linear when tested using a wide range of stimulation rates, but linear within the range of stimulation rates corresponding to firing rates observed for motor units during voluntary conditions. The results of this study suggest that this approach may be useful for investigating electro-mechanical properties of skeletal muscle.

## Chapter 4

### EMG-force Relation: Effects of Muscle Length

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In the preceding chapter, we have assessed the relation between EMG and force signals of the cat soleus muscle (for a fixed muscle length) using distributed stimulation of VR filaments and irregular inter-pulse intervals. However, when performing isometric contractions at different muscle lengths, force will not depend solely on the excitation but also on the length of the muscle (e.g. Rack and Westbury, 1969; Herzog et al. 1992). In the case of dynamic contractions, predictions of force from EMG become still more complex and should not only take into account the force-length relation but also the force-velocity property (Hill, 1938).

Theoretical models have implicitly assumed that EMG is independent of muscle length, and furthermore, that the force-length relation obtained using supramaximal stimulation of a specific muscle can be linearly scaled to submaximal contraction levels (e.g. Bogert et al. 1988; Dowling, 1987). However, Woods et al. (1987) reported that the amplitude of action potentials may be affected by changes in muscle length; Lynn et al. (1978) predicted that changing muscle length may affect the conduction

velocity of action potentials across the muscle; and data from Gandevia and McKenzie (1988) suggest that muscular forces depend on the combination of muscle length and activation in a complex and non-linear way. Most experimental EMG-force studies tend to support that EMG is affected by changes in muscle length (e.g. Inman et al. 1952; Close et al. 1960; Lunnen, 1980; Heckathorne and Childress, 1981), although the opposite result has also been reported (e.g. Rosentwieg and Hinson, 1972; Vredendregt and Rau, 1973). The experimental studies cited above have used human subjects and voluntary contractions, and under these experimental conditions it is not possible to discriminate how changes in muscle length may influence the recorded signals. There are at least three factors that may affect EMG recording with changing muscle lengths: (a) changes in excitation to the muscle; (b) changes in mechanical or electrical properties of the muscle; and (c) changes in the location of the electrodes relative to the active motor units. The different observations made in experimental studies regarding the effects of changing muscle length on EMG might be due to a combination of these factors in different proportions, as a consequence of possible differences in the experimental conditions. It appears, therefore, that the complex behaviour of EMG and force as a function of muscle length is not understood completely.

The purpose of this study was to determine the effects of changes in muscle length on the EMG signal and muscular force first, and on the resulting EMG-force relation of the cat soleus muscle second, using distributed stimulation of VR filaments and irregular inter-pulse intervals. Such an approach allows to evaluate the effects of muscle length on the EMG-force relation without the interference of the central

nervous system.

## METHODS

Two cats (masses = 3.3 kg and 3.8 kg) were used in experiments designed specifically to assess the effects of muscle length on the EMG-force relation. Animals were anesthetized using an intraperitoneal injection of Somnotol (40 ml/kg), and submitted to a laminectomy in order to expose the VRs of L7 and S1 which contain the alpha motoneurons to the soleus muscle. Once exposed these nerve roots were divided into ten VR filaments.

The soleus muscle of the left hindlimb was exposed with its innervation being preserved. All other muscles of the experimental hindlimb were denervated. The insertion of the soleus muscle was detached along with a remnant piece of the calcaneus, and was rigidly fixed to a muscle puller instrumented with a strain transducer. Muscle lengths were adjusted using the muscle puller. Blood pressure, respiration and body temperature of the animals were continuously monitored throughout experiments.

Eight VR filaments were stimulated independently. Two further VR filaments were stimulated using pulse trains that were delayed 10 to 20 ms relative to two of the independently stimulated VR filaments. Inter-pulse intervals of stimulation trains were irregular and pseudo-random with a coefficient of variation of 12.5 % (Zhang et al. 1992). Stimulation could be reproduced identically at any time.

EMG signals were recorded using bipolar indwelling (wire) electrodes that were inserted into the mid-belly of the muscle without fixation (interelectrode distance = 10 mm, approximately), and with bipolar surface electrode of a patch type (interelectrode distance = 6 mm) which was sutured to the epimysium of the muscle. EMG and force signals were recorded at 2100 and 350 samples per second, respectively. VR filaments were stimulated for approximately 4 seconds in each trial with recordings starting about one second after the onset of stimulation and lasting for two seconds. The IEMG and the corresponding mean force were calculated for each trial.

The effects of changes in muscle length on IEMG, mean force, and the IEMG-mean force relation were assessed using two different tests.

#### **Test 1: 27 (or 15) Stimulation Levels, 4 Muscle Lengths**

In test 1, a stimulation protocol consisting of 27 different trials (Table 3) was applied to one animal, and a short version of this protocol (consisting of the 15 trials marked with an asterisk in Table 3) was applied to a second animal. These protocols were used at four different muscle lengths, corresponding to AJAs of 55, 80, 105, and 130 degrees, giving a total of 108 and 60 individual observations for this part of the study for animals 1 and 2, respectively. An AJA of 0 degrees was defined as the angle that would be obtained if the foot was forced into plantar flexion up to the point where it would be perfectly aligned with the shank. Dorsi-flexion of the ankle joint increased

Table 3. Protocol used in test 1, designed to implement addition (trials 1 to 10) and rate modulation (trials 1 to 27) of VR filaments. Trials marked with an asterisk identify the short version of the complete protocol. Trials 10, 17 and 24 are marked with arrows to identify the relatively low, medium and high stimulation levels adopted in test 2. Mean stimulation rate of active VR filaments is indicated in each trial in pps. Coefficient of variation of stimulation trains = 12.5 %.

Trial #	Ventral Root Filament #									
	1	2	3	4	5	6	7	8	9	10
1 *	3									
2 *	3	3								
3 *	5	5	3							
4 *	5	5	3	3						
5 *	7	7	5	5	3					
6 *	9	9	7	7	5	3				
7 *	11	11	9	9	7	5	3			
8 *	13	13	11	11	9	7	5	3		
9 *	15	15	13	13	11	9	7	5	3	
→ 10 *	17	17	15	15	13	11	9	7	5	3
11	19	19	17	17	15	13	11	9	7	5
12	21	21	19	19	17	15	13	11	9	7
13 *	23	23	21	21	19	17	15	13	11	9
14	25	25	23	23	21	19	17	15	13	11
15	27	27	25	25	23	21	19	17	15	13
16 *	29	29	27	27	25	23	21	19	17	15
→ 17	31	31	29	29	27	25	23	21	19	17
18	33	33	31	31	29	27	25	23	21	19
19 *	35	35	33	33	31	29	27	25	23	21
20	37	37	35	35	33	31	29	27	25	23
21	39	39	37	37	35	33	31	29	27	25
22 *	41	41	39	39	37	35	33	31	29	27
23	43	43	41	41	39	37	35	33	31	29
→ 24	45	45	43	43	41	39	37	35	33	31
25 *	47	47	45	45	43	41	39	37	35	33
26	49	49	47	47	45	43	41	39	37	35
27	51	51	49	49	47	45	43	41	39	37

the AJA. AJAs of 55 degrees and 130 degrees corresponded to the shortest and longest muscle lengths tested, respectively, and AJAs between 50 and 100 degrees have been reported for the stance phase of cat locomotion (Goslow et al. 1973).

The protocol shown in Table 3 was designed to add VR filaments from trials 1 to 10 and simultaneously increase the mean stimulation rates of the previously active VR filaments, whenever new VR filaments were stimulated. Beyond trial 10 the stimulation rates of all VR filaments were increased from one trial to the next, and no VR filaments were added. All IEMG and mean force measurements during test 1 were normalized with respect to the values obtained in the last trial of each protocol with the AJA at 105 degrees.

In order to assess the effects of increasing levels of stimulation on the force produced at different muscle lengths (test 1), the ratios between the mean forces produced at 55 degrees (short muscle length) and 105 degrees (long muscle length) were calculated for the long and short protocols of Table 3.

In order to test the reproducibility of the EMG and force recordings, test 1 was performed twice during one experiment for a fixed muscle length (i.e. AJA = 105 degrees), using the long protocol first and the short protocol second. Test and retest were separated by approximately 3.5 hours. The results thus obtained were normalized with respect to the highest values obtained for the initial test.

Theoretical calculations were made to illustrate the effects of muscle length on the interelectrode distance, and consequently on the IEMG of a single CMUAP. These

calculations were based on the following simplifications: (a) the action potential adopted was biphasic, and each phase had the shape of a triangle; (b) the initial muscle length was assumed to be 8.7 cm long, (based on unpublished observations); (c) the relative changes in the duration of the action potential were the same as the relative changes in muscle length (i.e. 0, 8.4, 16.8, and 23.2 % for AJAs of 55, 80, 105 and 130 degrees, respectively); and (d) the amplitude of the action potential was not affected by changes in the interelectrode distance. The changes in IEMG as a function of changes in muscle length were expressed relative to the value of IEMG at the shortest muscle length (AJA = 55 degrees). In addition, a single CMUAP obtained experimentally for four different muscle lengths was extracted for illustration of possible effects of changes in muscle length on the IEMG of a single CMUAP.

### **Test 2: 3 Stimulation Levels, 8 Muscle Lengths**

In test 2, three stimulation levels (i.e. the three trials marked with arrows in Table 3) were applied to eight different muscle lengths, corresponding to AJAs of 45, 55, 65, 75, 85, 95, 105, and 115 degrees, giving a further 24 observations per animal. AJAs of 45 and 115 degrees corresponded to the shortest and longest muscle lengths tested, respectively. The three stimulation levels adopted will be referred to, hereafter, as "low" (trial 10, Table 3), "medium" (trial 17, Table 3), and "high" (trial 24, Table 3). In one of the experiments the nerve to the soleus muscle was stimulated supramaximally at 75 pps (coefficient of variation = 25 %) for each of the muscle lengths. All measurements resulting from test 2 were normalized with respect to the values

obtained using the high stimulation level at an AJA 105 degrees.

In order to assess the effects of different stimulation levels on the force production at different muscle lengths, the ratio between the mean forces produced by the low, medium and high stimulation levels were calculated relative to the mean force levels obtained by nerve stimulation at 75 pps in one experiment.

Between stimulations, the muscle was taken to a short length and allowed to rest for at least one minute. The stability of the preparation was assessed by monitoring the force that each VR filament produced when stimulated independently at a fixed rate. These measurements were performed at the beginning and were repeated throughout the experiments.

## RESULTS

The results shown in this paper were obtained using indwelling electrodes and will be reported in sub-sections corresponding to tests 1 and 2 as described in the methods section. The results obtained using the patch-type surface electrodes corroborate the general findings obtained using indwelling electrodes.

### **Test 1: 27 (or 15) Stimulation Levels, 4 Muscle Lengths**

The results obtained when the entire protocol consisting of 27 trials (Table 3) was applied to four different muscle lengths of one animal are shown in Figure 11, and the corresponding results obtained applying the short version of that protocol to a second

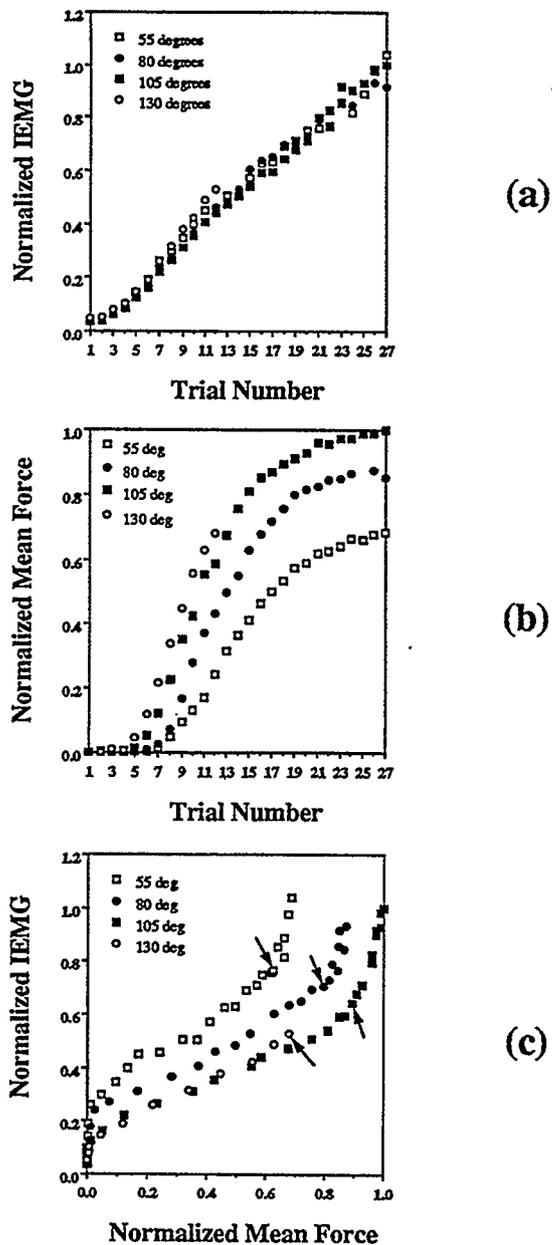


Figure 11. Effects of four different muscle lengths on the (a) IEMG, (b) mean force and (c) IEMG-mean force relation obtained in one experiment. VR filaments were stimulated according the long protocol shown in Table 3 (test 1). Last data points of each linear region are indicated with arrows. IEMG and mean force were normalized relative to values obtained in trial 27 with the AJA fixed at 105 degrees. Maximal mean force measured was 29.3 N.

animal are shown in Figure 12. Data points of the trials performed at an AJA of 130 degrees are missing beyond trial 12 in Figure 11, as the experiment was terminated due to lack of stability of the preparation.

When IEMG was expressed as a function of trial number (i.e. as a function of increasing stimulation levels, Table 3) it was found to be less affected by muscle length in one experiment (Figure 11a) compared to the other experiment (Figure 12a).

When mean force was expressed as a function of trial number, it showed the lowest values at the shortest muscle length (i.e. AJA = 55 degrees) and the highest values at the longest muscle length (i.e. AJA = 130 degrees) for all levels of stimulation (Figures 11b and 12b), except for the last four trials in Figure 12b where the mean forces of the two longest muscle lengths were about the same. Force results from both experiments indicated that higher stimulation levels were required at short muscle length compared to long muscle length in order to produce measurable forces. For example, soleus forces could be detected in trial 3 when the AJA was fixed at 130 degrees but only in trial 6 when the AJA was fixed at 55 degrees (Figure 12b). In both experiments mean force tended to saturate towards high levels of stimulation for all muscle lengths. Results obtained using the long protocol (Figure 11b) showed the effects of force saturation more clearly than the results obtained using the short protocol (Figure 12b) since the long protocol contained more trials in the region where saturation of force occurred.

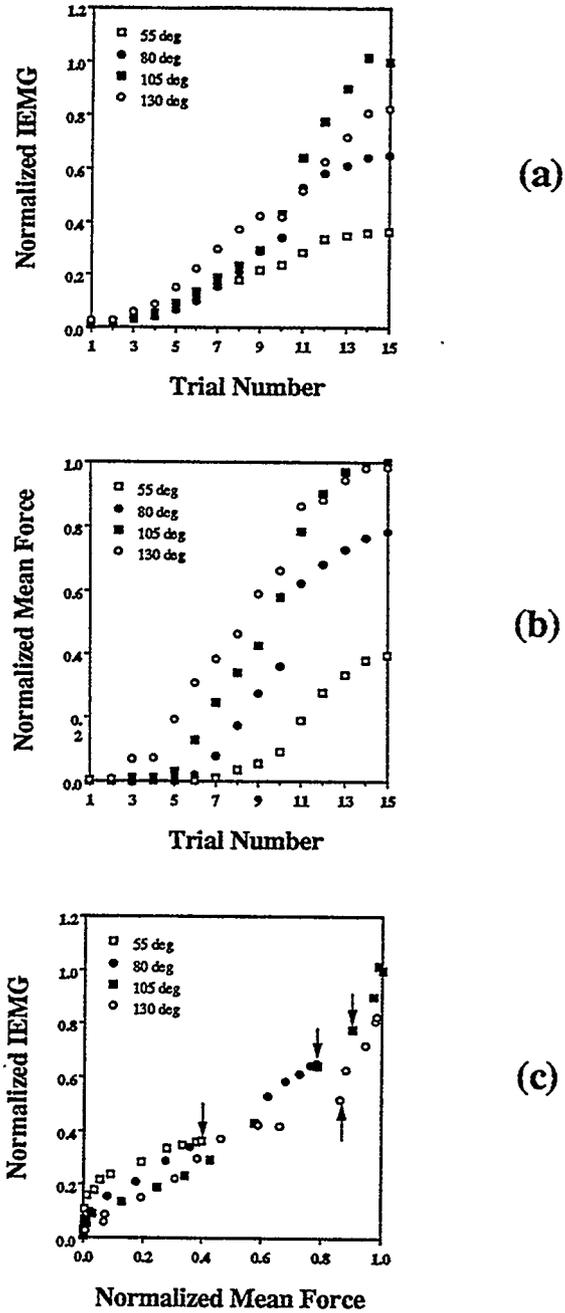
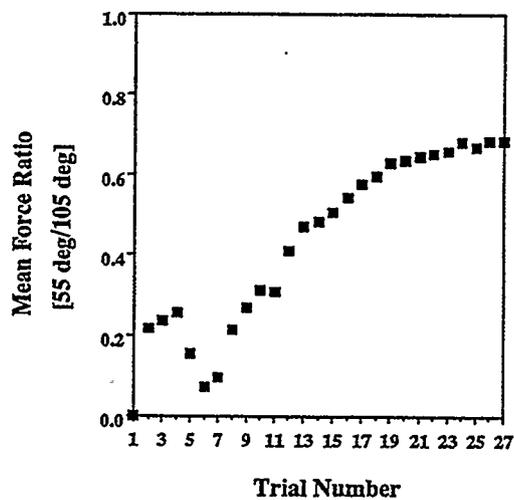


Figure 12. Effects of four different muscle lengths on the (a) IEMG, (b) mean force and (c) IEMG-mean force relation obtained from one experiment. VR filaments were stimulated according the short version of the protocol shown in Table 3 (test 1, trials marked with asterisks). Last data points of linear regions are indicated with arrows. IEMG and mean force were normalized relative to values obtained in trial 15 with the AJA fixed at 105 degrees. Maximal mean force measured was 23.3 N.

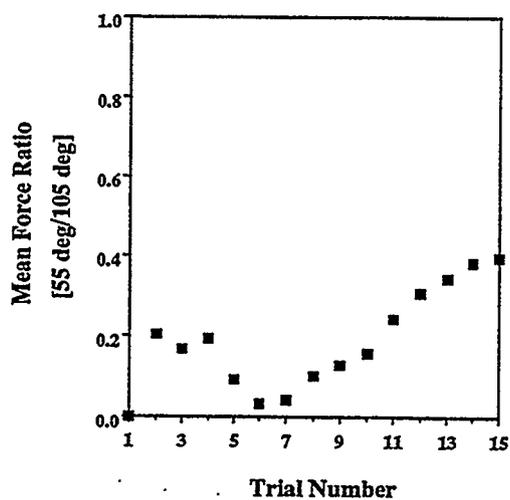
The ratio between the mean force values produced at an AJA of 55 degrees and the mean force values produced at an AJA of 105 degrees (from Figures 11b and 12b) are shown as a function of increasing levels of stimulation in Figures 13a and 14b for the long and short protocols, respectively. These ratios fluctuated in the initial trials; reached a local minimum for both protocols in trial 6; increased almost continuously until trials 19 and 15, respectively; and remained nearly constant beyond trial 19 in Figure 13a.

Except for relatively short muscle lengths (i.e. AJAs of 55 and 80 degrees) in Figure 12c, the IEMG-mean force relations were of sigmoid shape, containing an I region (Guimaraes et al. in press) that could be approximated well using least square fitted straight lines (in both, Figures 11c and 12c, the lowest  $r^2$  was equal to 0.87). Linear regions started at approximately 0.05 of the maximal mean force and ended at different mean force levels depending on the muscle length. The last data point of the linear region corresponding to each muscle length is indicated by an arrow in Figures 11c and 12c.

The results obtained when the protocol in Table 3 was tested and retested are shown in Figure 14, with data points corresponding to the same stimulation level connected by lines. Mean forces tended to be slightly smaller in the retest compared to the initial test for low levels of stimulation, and about the same for high levels of stimulation. IEMG was systematically lower in the retest compared to the initial test.



(a)



(b)

Figure 13. Ratio calculated by dividing the mean force values obtained at an AJA of 55 degrees by those obtained at an AJA of 105 degrees from experiments corresponding to (a) Figure 11b, and (b) Figure 12b.

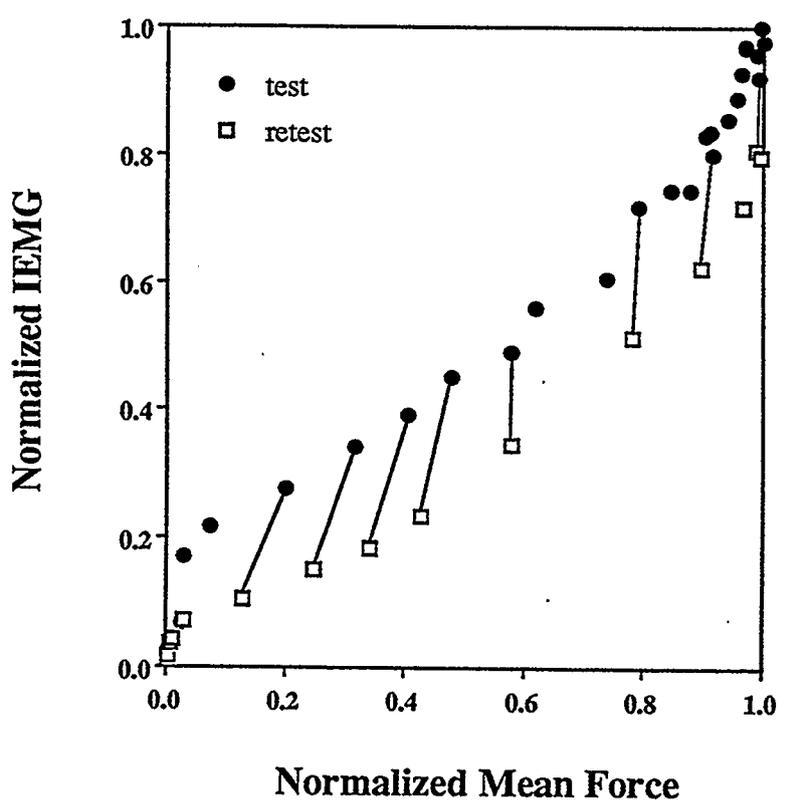


Figure 14. IEMG-mean force relations (test 1) obtained approximately 3.5 hour apart, from the same animal. AJA was fixed at 105 degrees. Test and retest were conducted utilizing the complete and short version of the protocol in Table 3, respectively. Corresponding data points are connected by lines. IEMG and mean force were normalized relative to values obtained for the test. Maximal mean force measured in both test and retest = 23.4 N.

Theoretical predictions of the changes in IEMG of a single CMUAP (assuming that the duration of the CMUAP increased in the same proportion as muscle length increased) associated with changing muscle lengths illustrate that the relative change in IEMG from the values obtained at the shortest muscle length are equal to the corresponding changes in muscle length (Figure 15). Experimental evidence showed that the duration of CMUAPs increased systematically with increasing muscle length (Figure 16).

### **Test 2: 3 Stimulation Levels, 8 Muscle Lengths**

The results obtained from experiments with two animals, applying low, medium and high stimulation levels (i.e. trials 10, 17 and 24 in Table 3, respectively) at eight muscle lengths (i.e. AJA from 45 degrees to 115 degrees, with 10 degree intervals) are shown in Figures 17 and 18. In both experiments IEMG increased with increasing stimulation levels from low to high. Furthermore, IEMG tended to be affected by changes in muscle length. These variations appeared to be random in one experiment (Figure 17a) and systematic in the other experiment, with IEMG increasing as muscle length increased (Figure 18a).

Passive forces tended to increase with increasing muscle length (Figures 17b and 18b). Total forces increased with increasing muscle length for all stimulation levels, indicating that the ascending limb of the force-length relation was tested. The results corresponding to the force-length relation obtained when the nerve to the soleus muscle was stimulated supramaximally at 75 pps for each of the different lengths are

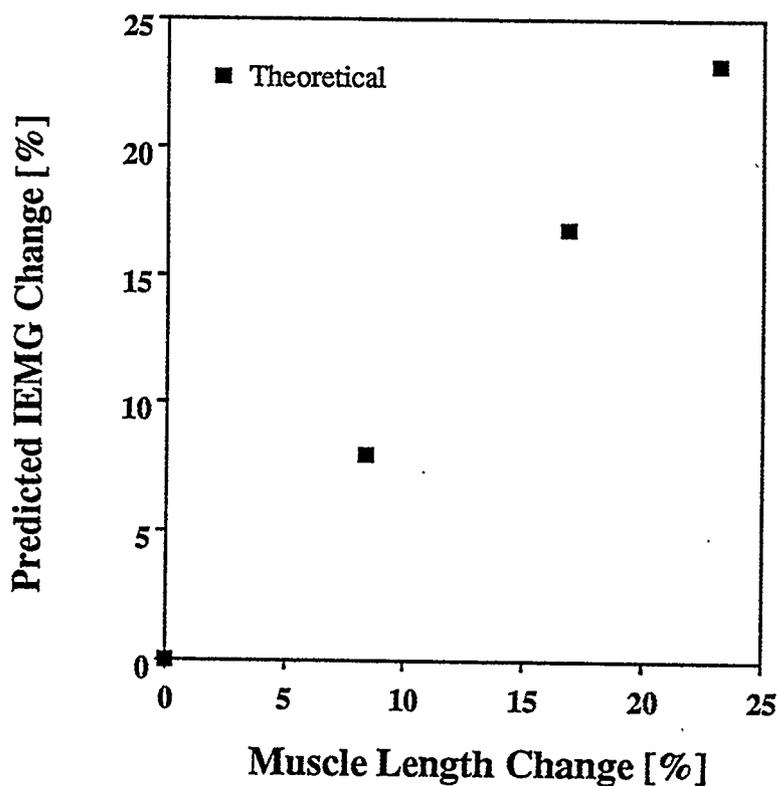


Figure 15. Theoretically predicted IEMG (of a single action potential) responses to increments in muscle length. For the calculation of IEMG the duration of the action potential was assumed to increase with the same relative increase of muscle length, and the amplitude of the action potential was assumed to be constant. Changes in predicted IEMG and changes in muscle length are expressed relative to respective measurements corresponding to the shortest muscle length (AJA = 55 degrees).

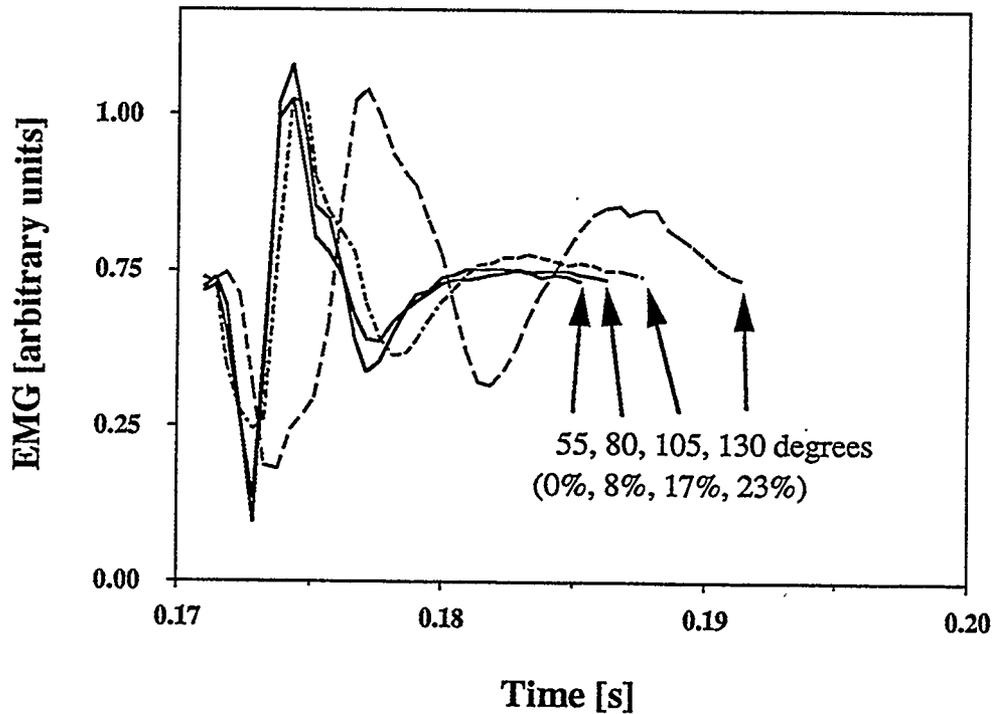


Figure 16. Single CMUAP (extracted from trial 1 of Table 3, experiment with the second animal) obtained for four muscle lengths (AJAs = 55, 80, 105, 130 degrees). Increases in muscle length are indicated relative to the shortest muscle length (AJA = 55 degrees).

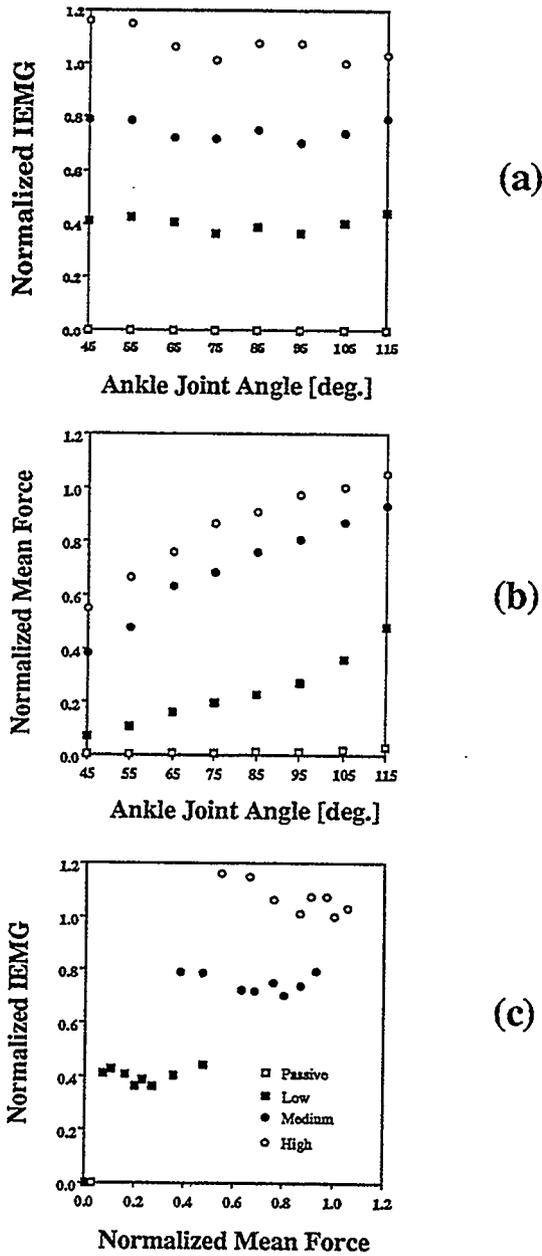


Figure 17. Effects of no-stimulation (passive) and three submaximal stimulation levels (low, medium and high, corresponding to trials 10, 17 and 24 in Table 3, respectively) on (a) IEMG, (b) mean force and (c) IEMG-mean force relation of eight different muscle lengths (AJAs from 45 to 115 degrees) of one animal. IEMG and mean force were normalized relative to values obtained applying the high stimulation level to an AJA of 105 degrees. Maximal mean force measured = 29.7 N.

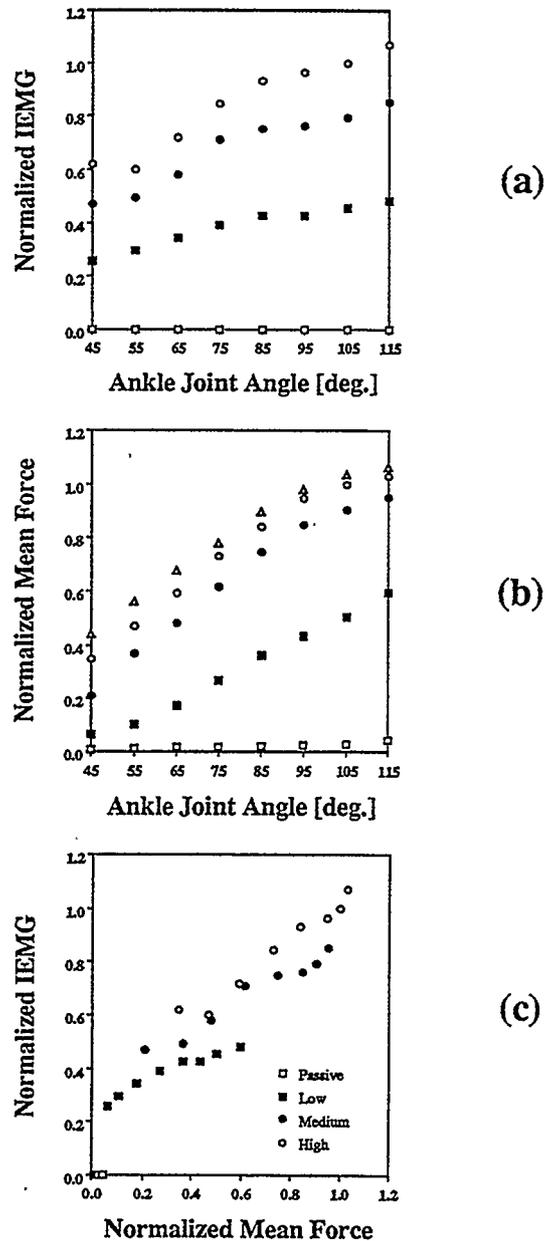


Figure 18. Effects of no-stimulation (passive) and three submaximal stimulation levels (low, medium and high, corresponding to trials 10, 17 and 24 in Table 3, respectively) on (a) IEMG, (b) mean force (also for nerve stimulation at 75 pps), and (c) IEMG-mean force relation of eight different muscle lengths (AJAs from 45 to 115 degrees) of one animal. IEMG and mean force were normalized relative to values obtained applying the high stimulation level to an AJA of 75 degrees. Maximal mean force measured = 25.3 N.

shown in Figure 18b.

IEMG-mean force relations (Figures 17c and 18c) were found to be affected by changes in muscle length in both experiments. In the first experiment, the IEMG-mean force relation was influenced strongly by the force-length relation of the soleus muscle and to a smaller extent by the random variations of EMG signals as a consequence of changes in muscle length (Figure 18c). In the second experiment the IEMG-mean force relations were strongly influenced by the force-length and IEMG-length relations (Figure 18c).

The ratio between the force values corresponding to each of the stimulation levels (i.e. low, medium, and high) and the mean force values obtained when stimulating the nerve at 75 pps are shown in Figure 19 for all muscle lengths tested. These ratios tended to increase from short (AJA = 45 degrees) to long muscle length (AJA = 115 degrees), indicating that submaximal stimulation levels resulted in muscular forces closer to the maximal possible forces at long compared to short muscle lengths. The shape of the relative force curves was close to linear for the low stimulation level, but highly non-linear for the medium and high stimulation levels.

## DISCUSSION

The sigmoid shaped IEMG-mean force relations obtained for cat soleus muscle at different muscle lengths in test 1 (Figures 11c and 12c) are consistent with our previous results obtained for a single muscle length (Guimaraes et al. in press). Sigmoid

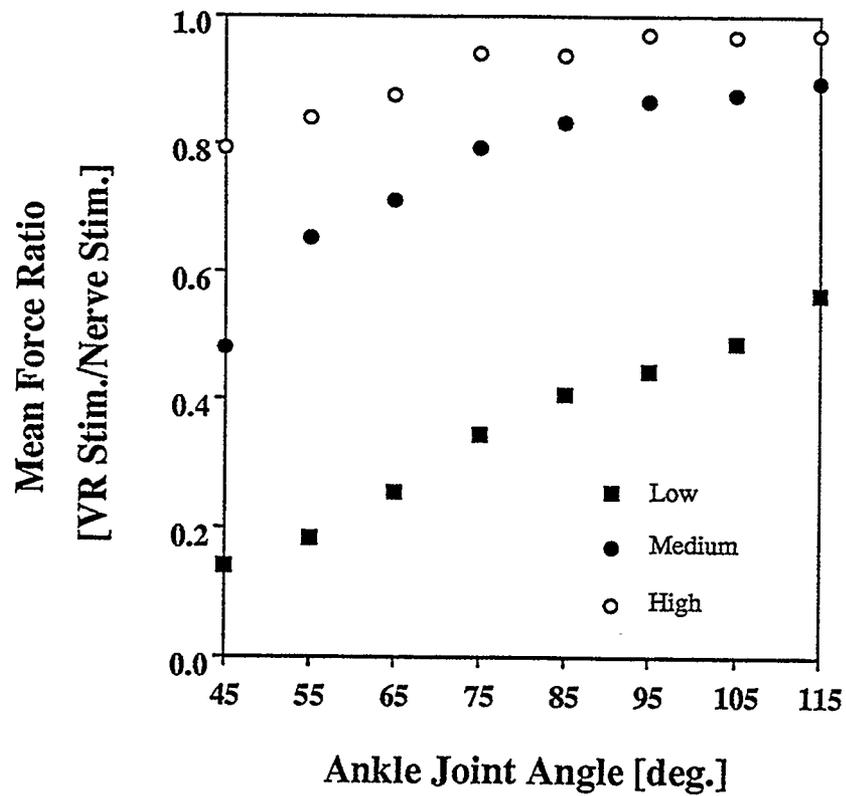


Figure 19. Ratio calculated by dividing the mean force values obtained using low, medium and high stimulation by those obtained using nerve stimulation at 75 pps for eight different muscle lengths. These results were derived from Figure 18b.

shaped relations did not come out as clear for two muscle lengths of one animal (i.e. AJAs of 55 and 80 degrees in Figure 12c), due to a pronounced saturation of IEMG and a smaller number of observations in this experiment compared to that shown in Figure 11c. As we reported previously for a single muscle length (Guimaraes et al. in press) the IEMG-mean force relations obtained at different muscle lengths displayed three distinct regions that, according to the levels of stimulation, were classified into L, I, and H. The shapes of the IEMG-mean force relations observed in Figures 11c and 12c were sigmoid, therefore, prevented the hypothesis raised in chapter 2 that the EMG-force relation of the cat soleus muscle is linear for different muscle lengths must be rejected. The different inclinations of the IEMG-mean force relations for different muscle lengths seen in Figure 11c show the expected effects of the force-length property. These effects were not as clear in the results of Figure 12c due to the additional effects of muscle length on the EMG signals observed in this experiment.

The rates of stimulation used in the L region were below the minimal firing rates observed in motor units during voluntary contractions (Burke, 1981); and the forces corresponding to the H region were higher than those obtained during voluntary contractions (Walmsley et al. 1978; Herzog and Leonard, 1991). In spite of the fact that the hypothesis of linearity between the EMG and force signals was rejected, the I region is of most interest from a functional point of view since it contains stimulation and force levels that do occur during normal voluntary contractions. The IEMG-mean force relations in the I region were virtually linear (Figures 11c and 12c). This finding extends our observation of a linear relation between IEMG and mean force for a single

muscle length (Guimaraes et al. in press) to muscle lengths covering basically the entire range encountered during normal locomotor activities of the cat (Goslow et al. 1973; Herzog et al. 1992). EMG and force signals of muscles consisting predominantly of slow motor units, such as the cat soleus, have been reported to be linear (Close et al. 1960; Bigland-Ritchie et al. 1980). Thus, the results here obtained using electroneuromuscular stimulation agree with the results reported for voluntary contractions.

EMG signals were influenced by changes in muscle length (Figures 11a, 12a, 17a, and 18a). The effects of muscle length on IEMG appeared to be random for tests 1 and 2 in one experiment (Figures 11a and 17a, respectively); systematic for three out of the four muscle lengths studied for test 1 (Figure 12a), and systematic for all muscle lengths for test 2 (Figure 18a) in the other experiment. Muscle length has been shown to affect the amplitude of action potentials (Woods et al. 1987), and fluctuations in EMG with changing muscle length may also be expected due to possible movement of recording electrodes relative to the active motor units (Basmajian and De Luca, 1985), and relative to themselves. The results obtained when test 1 was performed twice at a fixed muscle length in one experiment (Figure 14), provide evidence that there was indeed movement of electrodes relative to the muscle during the experimental protocol. IEMG values were systematically lower whereas mean forces were similar particularly at high force levels, from test to retest.

The systematic increase in IEMG with increasing muscle length seen in one experiment (Figures 12a and 18a), may have been caused by increases in the duration of CMUAPs as a consequence of systematic increases in the interelectrode distance, as

illustrated theoretically (Figure 15). The experimental results of Figure 16 (obtained from the experiment in which IEMG was found to increase systematically with increasing muscle length) show that increasing muscle length was associated with a perceived increase in the duration of the CMUAP, which is likely to be associated to a large extent, with changes in the interelectrode distance. Oscillations in the amplitude of the experimentally measured CMUAP obtained at different muscle lengths can be seen in Figure 16, therefore, the corresponding IEMGs were not compared to those predicted experimentally. Theoretically calculated IEMGs were obtained assuming a constant amplitude of the CMUAP at different muscle lengths. The oscillations in the amplitude of the CMUAP seen in Figure 16 appear to reflect problems associated with the sampling frequency, although EMG was recorded at 2100 samples per second.

The argument of the preceding paragraph is further supported by the results obtained using surface electrodes (not shown). The surface electrodes were of the patch type (Loeb and Gans, 1986), thus the interelectrode distance was fixed, and contrary to the results obtained using indwelling electrodes (Figures 11a, 12a, and 18a), the IEMG values obtained with surface electrodes did not change systematically with increasing muscle lengths.

The random variations produced by muscle length on IEMG seen in one experiment (Figures 11a and 17a) were likely associated with random displacements of the interelectrode distance since no attempts were made to fix the indwelling electrodes to the muscle.

Interestingly, the similar procedures adopted when inserting the indwelling electrodes in both experiments yielded different findings, suggesting that this type of electrode may or may not be affected systematically by changes in muscle length. One way of minimizing the undesirable systematic effects of interelectrode distance on EMG, is to insert the electrodes with a surgical needle into the mid-belly of the muscle; suture the electrodes in place at the entry and exit points of the needle; and reinforce the bipolar arrangement with medical grade silicone rubber tubing to reduce relative movement of the electrodes (Herzog et al. in press).

As expected, soleus forces increased with increasing stimulation levels and increasing muscle length (Figures 11b, 12b, 17b and 18b). These results indicated that the muscle lengths tested were within the range of the ascending limb of the force-length relation for the cat soleus muscle which is consistent with previous observations (Rack and Westbury, 1969; Herzog et al. 1992). Optimal length (i.e. the length at which the muscle can produce its maximal force) appeared to be shifted towards longer muscle lengths for the submaximal stimulations compared to supramaximal nerve stimulation (Figure 18b).

When predicting muscular forces from EMG signals in dynamic situations, the typical (and to our knowledge only) approach has been to multiply a measure of relative activation of the muscle (i.e. some measure of the EMG signal divided by the maximal value of this measure) with the relative force of the muscle, which at any given instant in time depends on the length and velocity of the contractile elements (e.g. Bogert et al. 1988; Dowling, 1987). This approach assumes implicitly that a given

stimulation will produce the same percentage of the maximal force for any contractile condition of the muscle (e.g. muscle length). The results of this study do not support this assumption (Figures 13a, 13b and 19). The relative forces produced for a given level of stimulation were clearly dependent on muscular length. Otherwise, the curves shown in Figure 19 would be horizontal for each of the different stimulation levels. Results similar to those in Figures 13a and 13b can be obtained if the force ratio between short and long muscle lengths is calculated using the findings of Gandevia and McKenzie (1988).

For a given level of stimulation, more relative force was produced at long compared to short muscle lengths, indicating that submaximal levels of stimulation may be used more efficiently for force production at long compared to short muscle lengths. Therefore, there appears to exist a mechanism that enhances force production at long muscle lengths. Ruedel and Taylor (1971) in skeletal muscle, and Fabiato and Fabiato (1975) in cardiac muscle, suggested that the calcium released from the sarcoplasmic reticulum is higher at long compared to short sarcomere lengths for constant stimulation. Since the free calcium in a muscle fibre is directly associated with force production, the observations made by Ruedel and Taylor (1971) may explain the relative force enhancement found here for cat skeletal muscle at long muscle lengths and submaximal stimulations. Similar changes in force-length properties as observed here have been reported for the entire cat soleus muscle (Rack and Westbury, 1969) and for single motor units of cat medial gastrocnemius muscle (Heckman et al. 1992).

The fact that force-length properties of cat soleus muscle obtained using submaximal levels of stimulation are not just a linear scaling down of the force-length relation obtained using supramaximal stimulation suggests that theoretical models will have to account for this non-linear behaviour. The force-length relation obtained using supramaximal stimulation protocols may not suffice to explain the force-length properties of submaximally contracting muscle. Since most physiologic contractions are submaximal, future research may focus on determining force-length properties for stimulation levels other than supramaximal.

## SUMMARY

IEMG-mean force relations of cat soleus muscle were of a sigmoid shape, with a linear I region that is associated with contractile levels that occur during voluntary movements. The results of this study directly extend our previous findings from a single muscle length to muscle lengths encountered during locomotion. EMG signals were influenced by changes in muscle lengths and these changes were thought to be predominantly associated with the displacement of electrodes caused by muscular movement. Soleus forces increased systematically with increasing muscle lengths, as expected from the known force-length relation, and were not linearly related to the force-length relation obtained for supramaximal stimulation. For given levels of submaximal stimulation, soleus forces were smaller at short compared to long muscle lengths. The results found here suggest that the predictions of isometric force from EMG must consider the variable changes in force-length behaviour of submaximally

stimulated muscle.

## Chapter 5

### EMG-Force Relation: Locomotion

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The relationship between EMG and force signals has been extensively documented for isometric contractions (e.g. Inman et al. 1952; Lippold, 1952; Seyfert and Kunkel, 1974; Smith and Stokes, 1993). Much less information is available for dynamic voluntary movements, which have typically been studied for contractions performed at a constant speed or load (e.g. Bigland and Lippold, 1954; Bigland-Ritchie and Woods, 1974; Heckathorne and Childress, 1981). EMG and force signals have been measured directly from single muscles during cat locomotion (e.g. Walmsley et al. 1978; Abraham and Loeb, 1985; Gregor et al. 1988) however, the relation between these two signals has rarely been studied in these investigations. The work of Sherif et al. (1983) appears to be the exception to this rule.

Reasonable predictions of instantaneous force (moment) during dynamic voluntary activities have been made using models that implement some form of processed EMG along with the force-length-velocity properties of the target muscle (e.g. Hof and Berg, 1981; Olney and Winter, 1985; Bogert et al. 1988 Ruijven and Weijjs, 1990). EMG-

force-length-velocity behaviour may be quantified by measuring EMG, force, and contractile conditions directly from a single muscle. Based on measurements made during locomotion, Sherif et al. (1983) proposed that the initial burst of EMG in the cat medial gastrocnemius was driven by the central nervous system, irrespective of the instantaneous contractile conditions of the muscle. These authors, however, did not present any information regarding how EMG signals were related to force-length-velocity properties.

The objectives of this study were (1) to investigate the EMG-force relation of the cat soleus muscle during locomotion at different speeds, and (2) to attempt to understand the EMG-force relation on the basis of instantaneous contractile conditions as predicted by Allinger and Herzog (1993).

This study is part of a project aimed at assessing the EMG-force relation of the cat soleus muscle. We have measured (i.e. using an ENMS technique) that EMG and force are linearly related for isometric contractions at different muscle lengths (Guimaraes et al. 1993). Given the introduction of the force-velocity property in dynamic movements, we expected to obtain non-linear EMG-force relations for the same muscle during locomotion.

## **METHODS**

### **Animals and Surgery**

Three male, adult cats (masses can be seen in Table 4) were anesthetized, and EMG electrodes and force transducers were implanted on the soleus muscle under strictly sterile conditions as described previously (Herzog et al. 1993). Briefly, bipolar indwelling (wire) electrodes were implanted in the soleus muscle of the left hindlimb, and an E-shaped stainless steel force transducer was fixed to the distal tendon of the soleus muscle. Leads from the EMG electrodes and the force transducer were passed subcutaneously to a backpack connector which was sutured to the skin in the lumbar region of the animal.

### **Experimentally Obtained EMG-force Relation**

Experiments were conducted approximately one week after implantation of the EMG electrodes and the tendon force transducer. During the experiments, the cats were enticed to walk and run on a motor-driven treadmill at the speeds shown in Table 4. All animals had been trained to walk and run on the treadmill for food rewards.

### *EMG and Force Measurements*

Details about the EMG, force and video recordings have been published previously (Herzog et al. in press). Briefly, EMG signals were pre-amplified on the back-

Table 4. Identification of cats, their respective masses and number of steps analyzed for each speed.

Cat	Mass (kg)	Speed (m/s)					# Steps
		0.4	0.8	1.2	1.5	1.8	
L	5.2	6	23	17	6	Na	52
M	4.6	15	14	18	Na	15	62
J	5.6	12	17	11	Na	Na	40
# Steps		33	54	46	6	15	154

pack of the animal and were further amplified and band-pass filtered (15-1000 Hz) in the main amplifier. EMG and force signals were transmitted on line through a cable from the backpack connector on the animal to an analog to digital board, and were stored on a 386 personal computer. EMG and force signals were sampled at 2240 Hz.

At the end of the experiment, the distal tendon of the soleus muscle was detached from the calcaneus, and a calibration of the force transducer was performed using known weights that exceeded the highest soleus force produced by the cat during testing. The coefficients of determination between the voltage output of the force transducer and the weights attached to the soleus distal tendon were always equal to or higher than 0.99.

#### *EMG and Force Analysis*

Data analysis was restricted to the phase from onset of soleus EMG to the end of the stance phase (Figure 20).

EMG signals were full-wave rectified, integrated over some time period that was calculated separately for each step, and the values obtained from the integration were approximated using an interpolation cubic spline function. The time period of integration was calculated based on the general idea that the processed EMG signals would have to contain frequency components similar to those of the force-time history of the soleus muscle. In order to satisfy this condition, the frequency contents of the force-time histories corresponding to the stance phase of each step were determined using a

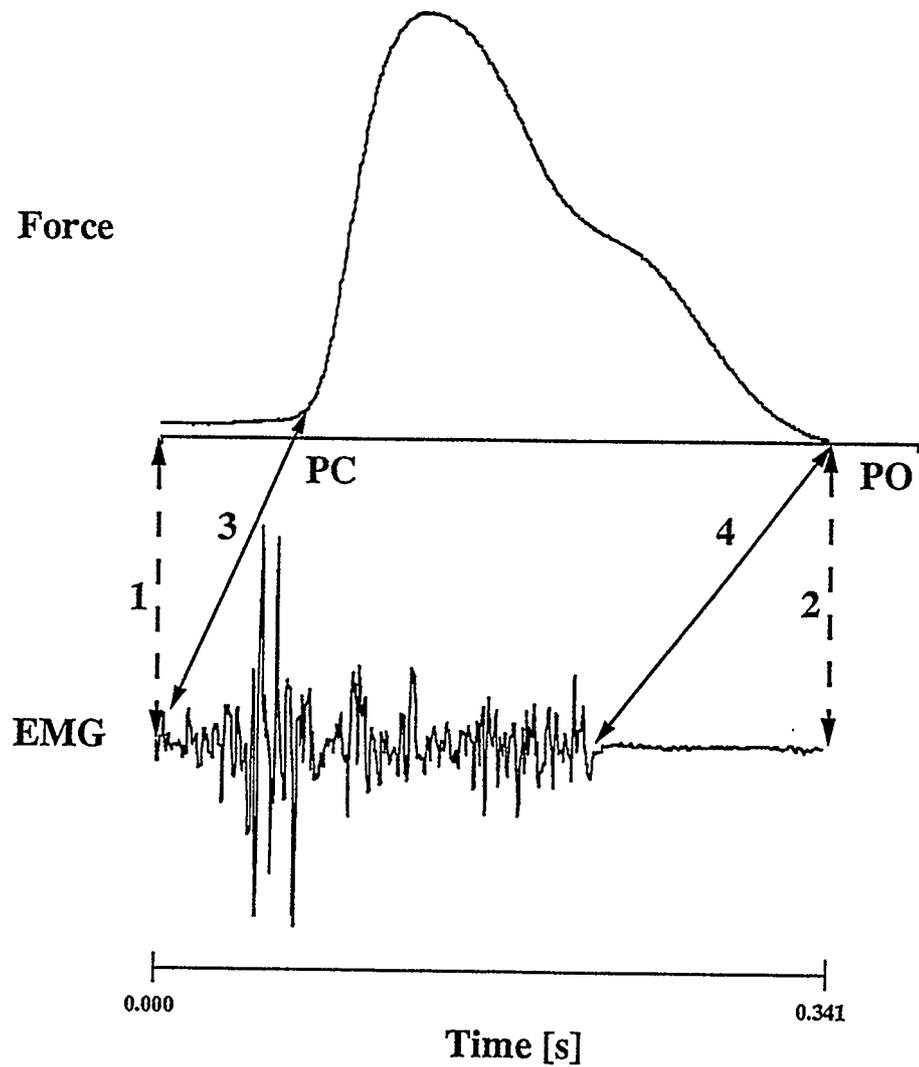


Figure 20. Procedure utilizing EMG and force signals as recorded in absolute time without any electromechanical delay is indicated by arrows 1 and 2. Procedure introducing a temporal shifting of the EMG signals and matching of EMG time and stance time is indicated by arrows 3 and 4. PC = paw contact; PO = paw-off.

Fast Fourier Transform algorithm. Once the highest relevant frequencies of the soleus force during the stance phase were established, the full-wave rectified signal was integrated over time periods corresponding to twice the highest relevant frequency of the force signals. According to the Nyquist theorem, the EMG-time curves obtained in this way should contain frequency components similar to those of the force-time curves. For example, for a maximal relevant frequency of the force signal of 16 Hz, the EMG signal was integrated over time periods of 0.0313 s ( $1 \text{ s}/32 \text{ Hz}$ ). For a typical stance phase of the step cycle, the shape of the processed EMG-time curve (envelope) was defined by seven or eight IEMG data points.

*Procedure 1: No Temporal Shifting of EMG signals Relative to Force Signals*

EMG and force signals were plotted against each other for some steps at the speed of 0.8 m/s, using values that corresponded in absolute time (Figure 20, arrows 1 and 2), and thus this procedure neglected any electromechanical delay (Cavanagh and Komi, 1979; Vos et al. 1990). For convenience of presentation of the results, EMG and force signals were normalized relative to their respective durations, and were expressed by 100 data points each.

*Procedure 2: Temporal Shifting of EMG Signals Relative to Force Signals*

In order to account for the electromechanical delay of the EMG and force signals, a temporal shift of the EMG signals relative to the soleus force was introduced. This procedure was applied to all steps, speeds, and animals (Table 4). A given speed of a

given animal will be referred to, hereafter as a test. First, the onset of the EMG signals was shifted in time to coincide with the value corresponding to the soleus force at the instant of paw contact (Figure 20, arrow 3). Second, the time of the EMG and force signals were normalized relative to their respective durations, and the corresponding relative times were matched and expressed by 100 values. This procedure forced the last datum point of the EMG signal to coincide with the last datum point of the force signal, which corresponded to the moment of paw-off (Figure 20, arrow 4). This second step was performed to account for the fact that the duration of the EMG signals was always less than the duration of the corresponding force signals. Although EMG and force signals differed in absolute time; and EMG signals preceded force signals, we will refer to EMG time and force time, hereafter, as stance time indistinctly.

### **Theoretically Calculated Activation**

In an attempt to understand the EMG behaviour on the basis of the contractile conditions of the soleus muscle, the processed EMG obtained experimentally was compared with a theoretically calculated activation (for the same cats, speeds and steps) which was based on the contractile conditions of the soleus muscle (Allinger and Herzog, 1993). Briefly, the instantaneous level of activation was calculated by dividing the measured force of the soleus muscle by the predicted maximal possible force (PMPF) that the muscle could exert at the same instant. The PMPF of soleus was calculated based on the instantaneous contractile conditions of the soleus fibres; the length and rate of change in length; and based on known force-length (Rack and Westbury, 1969;

Herzog et al. 1992) and force-velocity (Spector et al. 1980) properties of the soleus muscle. The length and rate of change in length of the soleus fibres were calculated as described by Allinger and Herzog (1992, 1993). The activation and PMPF values used in this study were calculated for the stance phases only, and were expressed for each one percent of the stance phase.

## RESULTS

### Procedure 1: No Temporal Shifting of EMG Signals Relative to Force Signals

IEMG-force plots obtained without introducing any time shift between the EMG and force signals are shown in Figure 21 for cats L, M, and J, for three non-consecutive steps at a fixed speed. Initially, IEMG increases steadily to the peak value and the corresponding soleus forces remain very small. After the peak IEMG values are reached, soleus forces increase fast and reach a peak while IEMG values tend to decrease in all cats. After the peak force has been reached, the IEMG-force loops progress somewhat differently; overall however, they show a decrease in force, and a corresponding general decrease in IEMG, that is sometimes interrupted by a slight increase in IEMG just after the peak force. When IEMG becomes zero late in the stance phase, corresponding soleus forces are still quite substantial (i.e. about 30 % to 80 % of the peak force). During the final period of the stance phase, IEMG values remain zero whereas forces steadily decrease and become zero, or very close to zero, at the instant of paw-off. The IEMG-force loops were similar for the different steps of

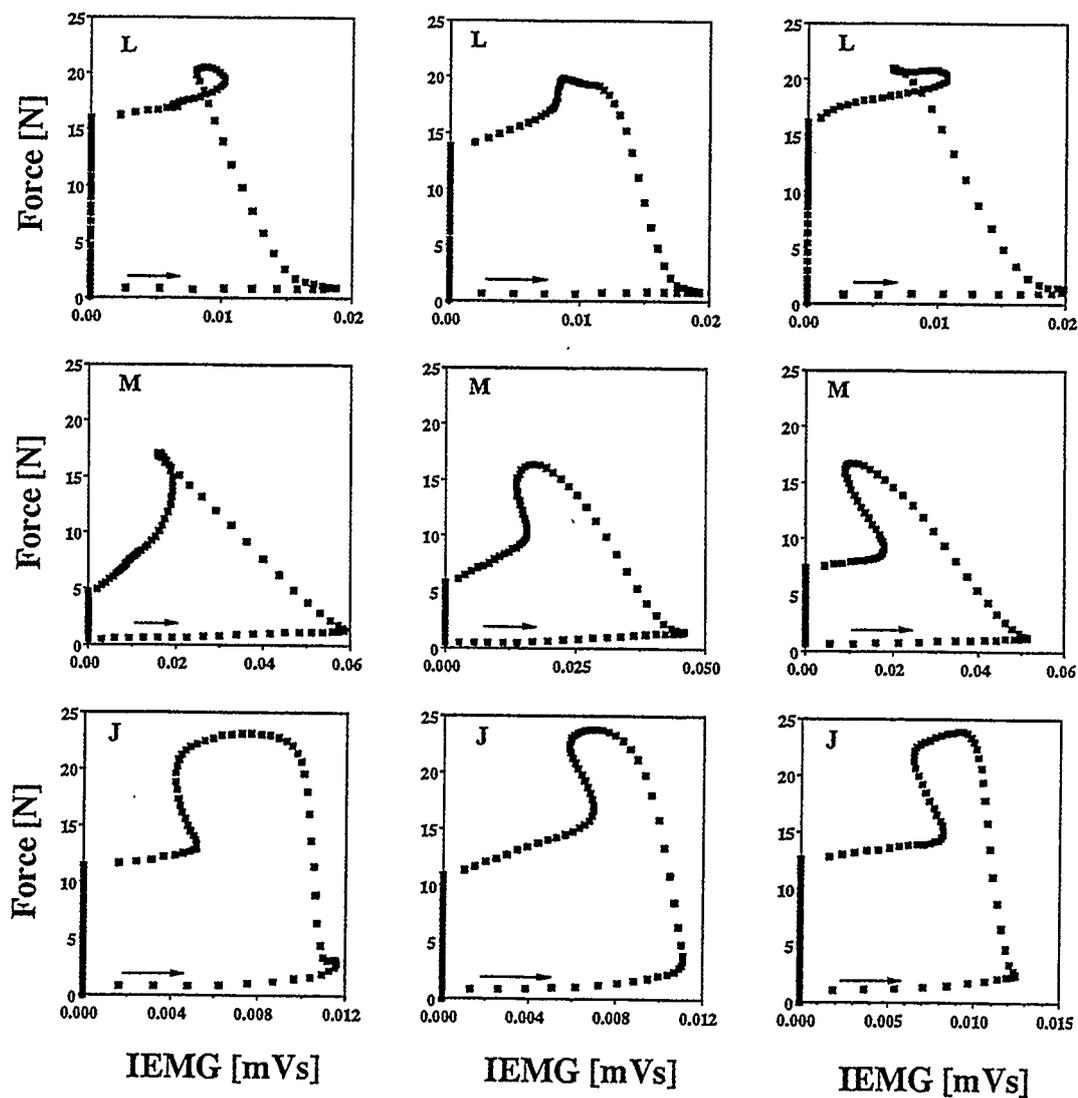


Figure 21. IEMG-force relations obtained when EMG signals were not shifted relative to force signals, for three non-consecutive steps of cats L, M, and J at 0.8 m/s. The progression of the loops is indicated with arrows from paw contact until paw-off, and each plot contains 100 data points.

one animal, and also revealed a common pattern for the different animals.

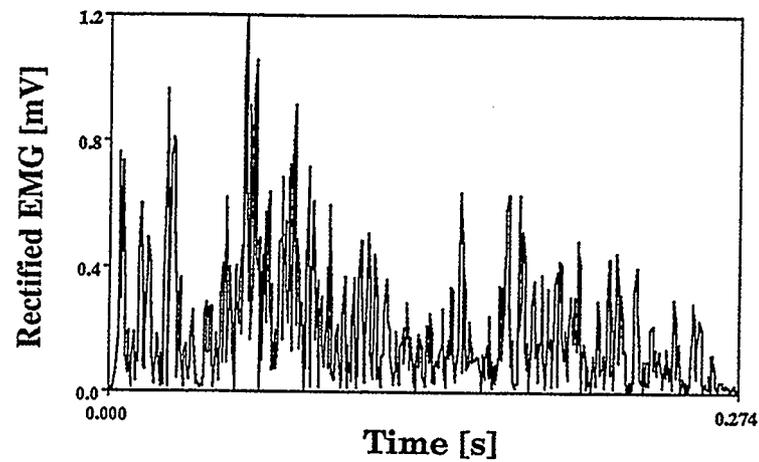
### **Procedure 2: Temporal Shifting of EMG Signals Relative to Force Signals**

The full wave rectified EMG signals (Figure 22a), the corresponding IEMG-time (Figure 22b), and force-time (Figure 22c) plots are illustrations of a typical step at a speed of 1.2 m/s (cat L). The rectified EMG shows a first burst between approximately 0 % and 50 %; and a second burst between approximately 50 % and 100 % the normalized stance time (Figure 22a). Both EMG bursts were reflected in the IEMG-time plot (Figure 22b). The first burst was usually higher than the second burst.

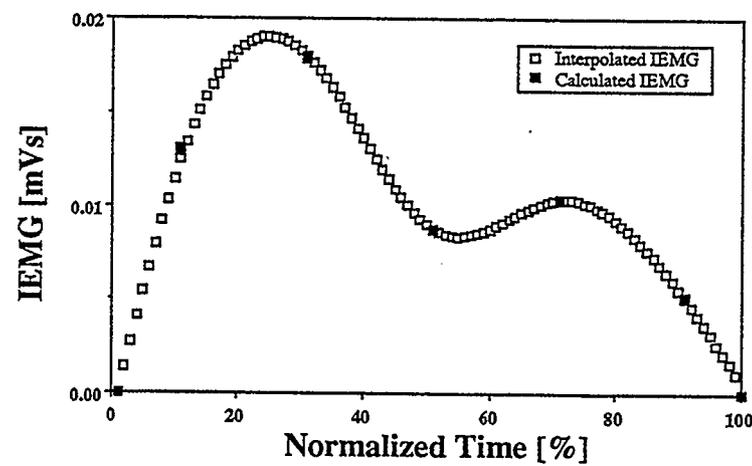
Force records of single steps had one local maximum, for speeds equal to or higher than 1.2 m/s (Figure 22c). Sometimes, a second local force maximum was observed for speeds slower than 1.2 m/s.

IEMG-force plots were highly non-linear for all animals and all speeds. IEMG-force plots are shown for a sequence of three consecutive steps of cats L (1.5 m/s), M (1.8 m/s), and J (0.4 m/s) in Figure 23. The progression of the loops is indicated with arrows from paw contact to paw-off.

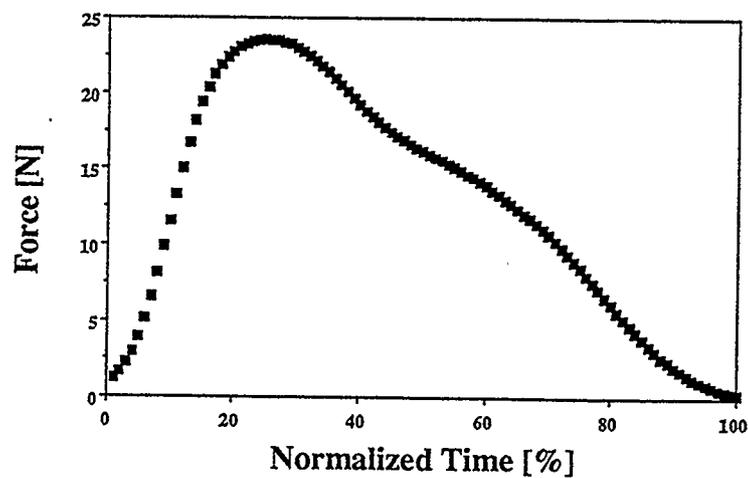
The IEMG-force curves obtained using a temporal shift to account for the electromechanical delay tended to have a similar basic pattern for different steps at a given speed for one animal (Figure 23), and also the mean IEMG-force curves were similar for a given speed of different animals and for different speeds of different animals (Figure 24).



(a)



(b)



(c)

Figure 22. Typical (a) full-wave rectified EMG of a single step at 1.2 m/s; (b) the corresponding calculated and interpolated IEMG; and (c) the corresponding force-time history. Interpolated IEMG in "b" and measured force in "c" were normalized relative to their respective times, and expressed by 100 data points each.

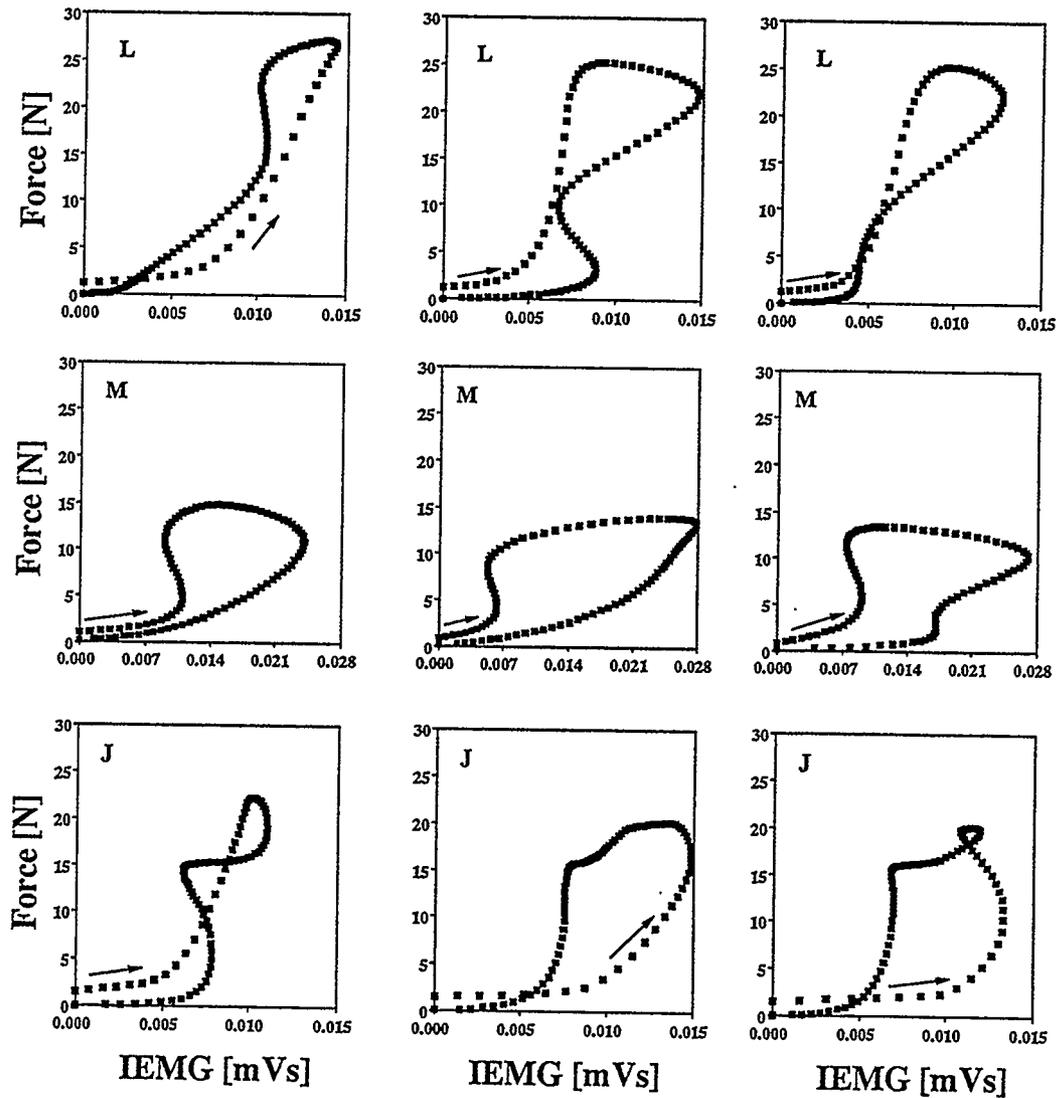


Figure 23. IEMG-force relations obtained when EMG signals were shifted relative to force signals, for three consecutive steps of cats L (1.5 m/s), M (1.8 m/s) and J (0.4 m/s). The progression of the loops is indicated with arrows from paw contact until paw-off, and each plot contains 100 data points.

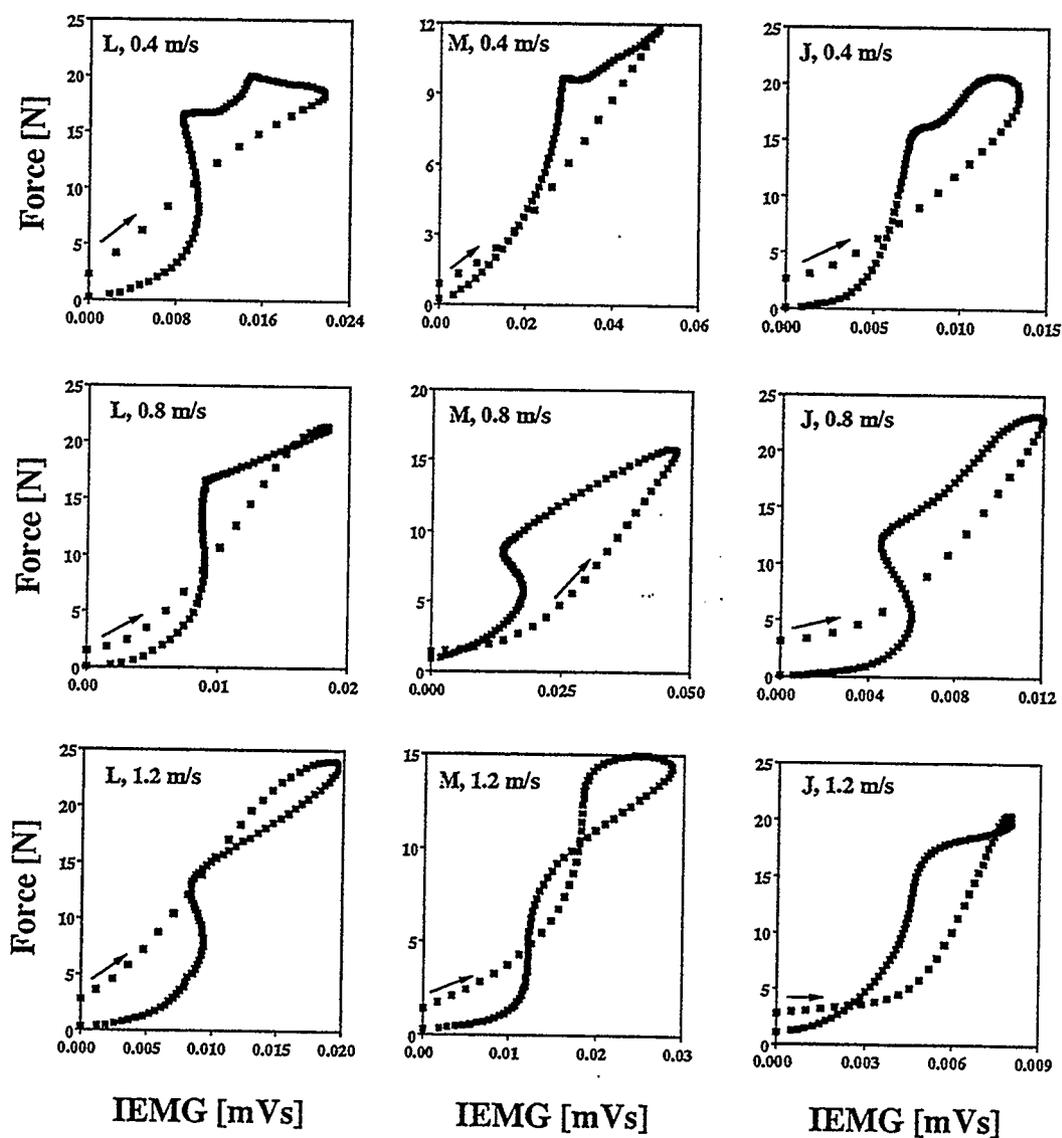


Figure 24. Mean IEMG-force relations obtained when EMG signals were shifted relative to force signals, calculated using all steps of cats L, M, and J at different speeds. The progression of the loops is indicated with arrows from paw contact until paw-off, and each plot contains 100 data points.

Figure 25 shows a series of plots summarizing the experimental measurements and the theoretical predictions that were made for the three animals walking at a speed of 1.2 m/s. The two rows of plots show: (a) the experimentally measured soleus force and the corresponding PMPF expressed as a function of normalized stance time; and (b) the measured normalized IEMG and the theoretically predicted activation expressed as a function of normalized EMG time and stance time, respectively. The amplitude of IEMG was normalized relative to its maximal value. Figure 26 shows (a) the relations between IEMG and the experimentally measured force; and (b) the relations between the theoretically predicted activation and the experimentally measured force obtained using the corresponding values of the three cats shown in Figure 25.

Early during the stance phase (i.e. between approximately 0 % and 20 %) the PMPF was much larger than the measured force (Figure 25a, all cats). Beyond about 20 % of the stance phase, PMPF decreased markedly, became similar to the measured force at 30 % to 40 % of the stance time, and remained close to the measured force for the rest of the stance phase for cats L and M. For cat J, the trend observed for the two other animals was also seen, except for a temporary increase in PMPF in the middle of the stance phase. For slow speeds of walking (i.e. 0.4 and 0.8 m/s) the measured force always remained smaller than the PMPF (results not shown). For speeds equal to or faster than 1.2 m/s the measured force was found to exceed PMPF for cats L and M during certain periods of the stance phase (Figure 25a).

Mean IEMG-time curves typically had two bursts (e.g. Figure 25b, cats L and J). The three bursts seen for cat M were an exception (Figure 25b). In some cases (i.e. in

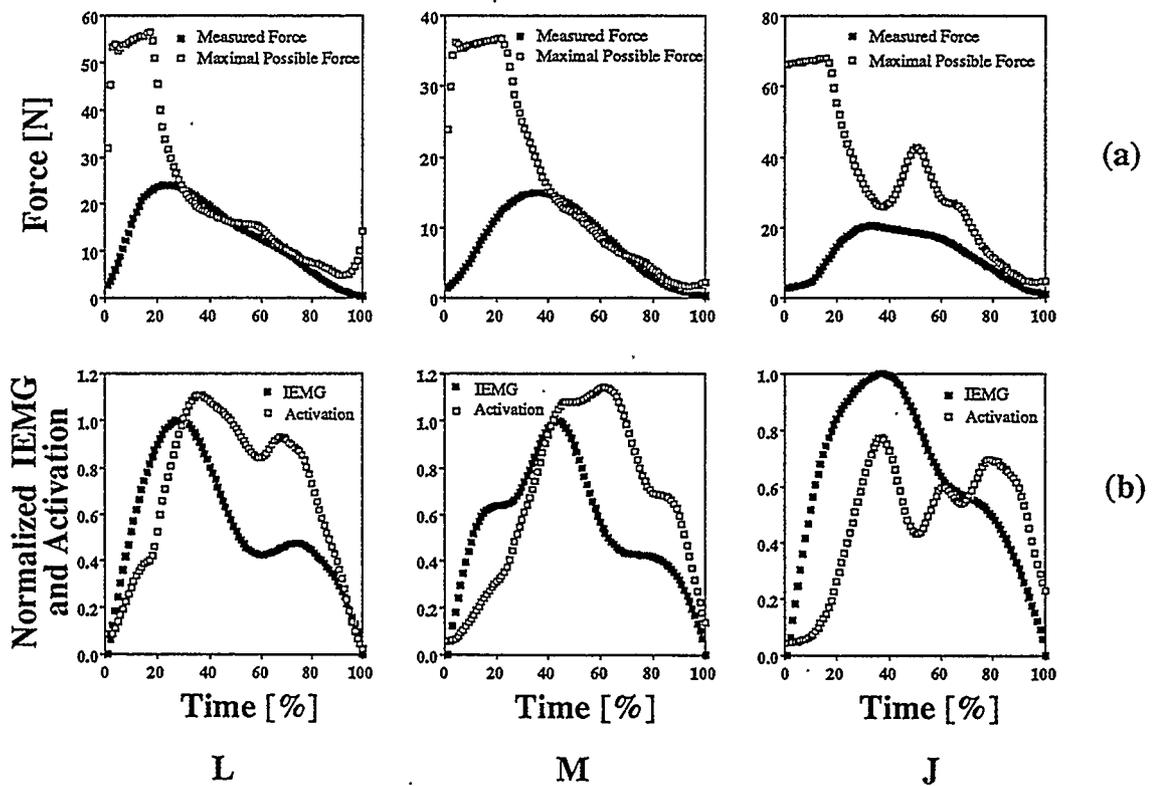


Figure 25. Measured values are means calculated using all steps of cats L, M, and J, at 1.2 m/s, when IEMG signals were shifted relative to force signals. (a) measured force and PMPF are plotted versus time; and (b) normalized IEMG and predicted activation are plotted versus time. Predicted values were calculated by Allinger and Herzog (1993). Each plot contains 100 data points.

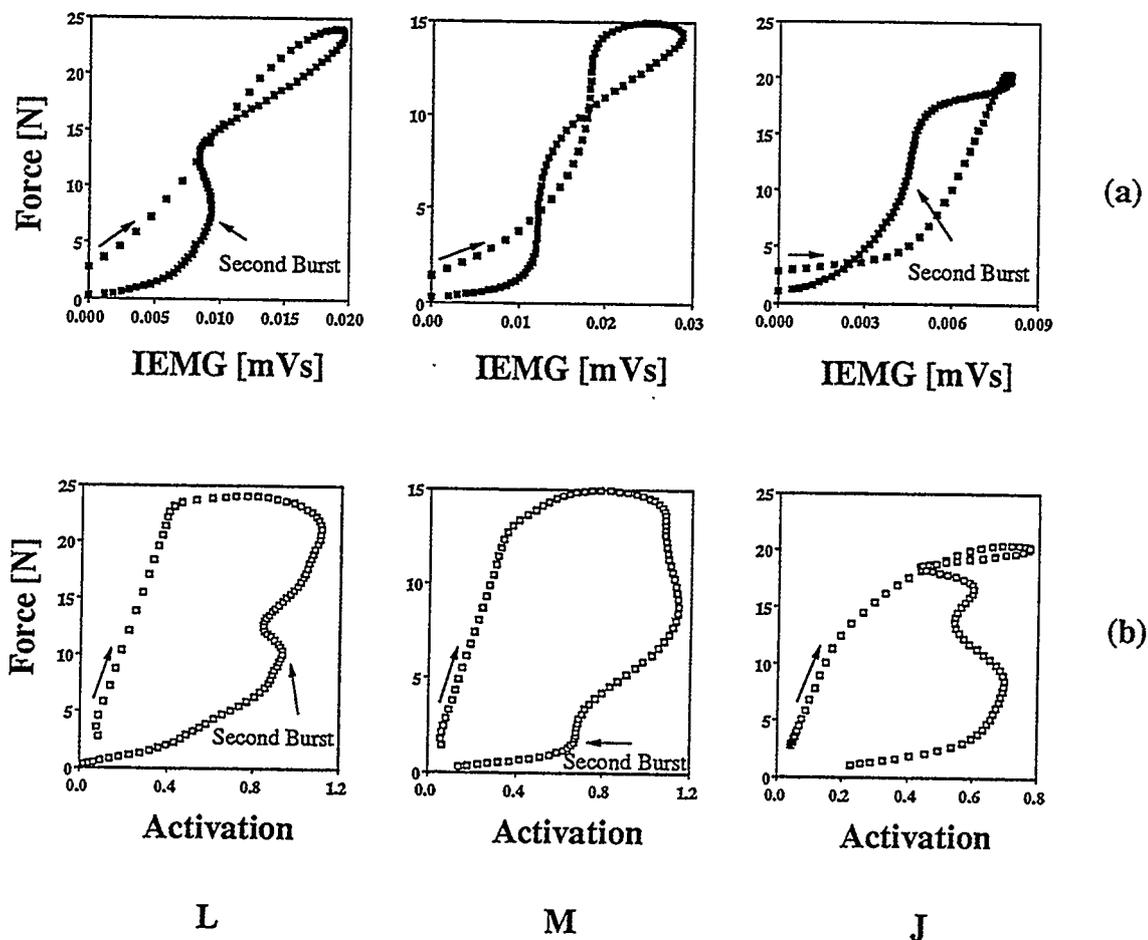


Figure 26. Measured values are means calculated using all steps of cats L, M, and J, at 1.2 m/s, when IEMG signals were shifted relative to force signals. (a) measured force is plotted versus IEMG; and (b) measured force is plotted versus predicted activation. Predicted values were calculated by Allinger and Herzog (1993). Each plot contains 100 data points.

four out of eleven tests) the entire predicted activation-time plots appeared to be shifted to the right on the time scale, compared to the corresponding IEMG-time plots (e.g. Figure 25b, cats M and J). In the remaining seven tests only the initial portion of the activation-time plots was shifted to the right on the time scale, compared to the corresponding IEMG-time plots (e.g. Figure 25b, cat L). Most often the shape of the theoretically predicted activation-time plots fluctuated more than the corresponding shape of the IEMG-time plots (e.g. Figure 25b, cat J).

The mean IEMG-force plots (Figure 26a) and the corresponding theoretically predicted activation-force plots (Figure 26b) were highly non-linear. The differences found between the IEMG-force loops and the activation-force loops reflected the differences obtained between the IEMG-time plots and the activation-time plots (Figure 25b). The IEMG-force loops were narrower than the activation-force loops (Figures 26a and 26b). In spite of this difference, certain general patterns were seen between the IEMG-force and the activation-force plots. For example, the second IEMG burst measured for cat L (Figure 25b), which is also seen in the corresponding IEMG-force plot (Figure 26a), was predicted by the theoretically calculated activation (Figure 25b) and is consequently seen in the corresponding activation-force plot (Figure 26b).

## DISCUSSION

All IEMG-force relations obtained for cat soleus muscles during dynamic contractions were found to be highly non-linear (Figures 23 and 24) as hypothesized in chapter 2. This is in contrast to our previous results for isometrically contracting cat

soleus muscle (using ENMS), where IEMG and force were found to be linearly related (Guimaraes et al. in press). Similar to cat soleus, EMG-force relations of human soleus muscle have also been reported to be linear for isometric contractions (Close et al. 1960). The cat soleus (Ariano et al. 1973) and the human soleus (Johnson et al. 1973) are muscles comprised primarily of slow twitch fibres, and muscles with this characteristic have been associated with linear isometric EMG-force relations (Bigland-Ritchie et al. 1980). It appears, therefore, that the non-linearities in the IEMG-force relations found in this study are a direct result of the dynamic contractile conditions of the muscle.

Qualitatively, the mean IEMG-force relations recorded in this study had a similar shape, across animals, and across speeds (Figure 24), although variations were observed from one step to the next (Figure 23). It appears, therefore, that all cats used a similar general motor control strategy during locomotion, and that this strategy provided some room for variations in the recruitment and the firing rate of motor units, which was reflected in the IEMG-force plots of the individual steps. The variations in the IEMG-force relations between steps appeared to be associated predominantly with variations of the IEMG and to a smaller extent with variations in soleus force. This result suggests that the recruitment of motor units in the cat soleus muscle may change for the same (or similar) soleus force production during a step. Human (Grimby, 1986) and cat (Hoffer et al. 1987) muscles comprised of mixed fibre types have been shown to recruit motor units according to the size principle (Henneman et al. 1965) during locomotion. The cat soleus, however, consists of uniform, slow motor units (Ariano et

al. 1973) which may be expected to have similar recruitment thresholds; thus, the recruitment of motor units may change somewhat from one step to the next. Reversals in the recruitment of motor units have been reported in the literature, although it has also been argued that these reversals could not be genuine, but rather reflect problems associated with the movement of wire electrodes (Basmajian and De Luca, 1985). In this study we were not able to evaluate the cause of the variations in IEMG of individual steps. One possibility for these variations may be that soleus forces are submaximal for much of the stance phase at the speeds of locomotion tested here (Hodgson, 1983; Herzog et al. 1992), and thus, changing the order of recruitment of motor units from one step to the next is possible and may prevent fatigue of specific motor units.

The theoretically calculated activation was based on the assumption that activation was high when the measured force was high relative to the PMPF; and that activation was low when the measured force was low relative to PMPF. Assuming that the theoretically predicted activation was a good measure of the actual excitation of the soleus muscle, and that the IEMG obtained experimentally reflected the same excitation process, it was hypothesized that the theoretical activation-time curves should be similar to the experimental IEMG-time curves during the stance phase of locomotion. In five out of the eleven tests, the shape and the frequency components of the activation-time histories were similar to those of the corresponding IEMG-time histories (e.g. Figure 25b, cat L); in the remaining six tests, the activation-time histories had higher frequency components than the corresponding IEMG-time histories (e.g. Figure 25b, cat J). Part of the differences observed between the IEMG-time and the

activation-time time history plots may be explained with the procedures which were used to obtain these curves. For example, the IEMG-time histories were determined in such a way that they contained approximately the frequencies observed in the corresponding force-time histories (i.e. 0 to 15 Hz), whereas measurements that affected the calculation of activation (e.g fibre length) were sampled at 60 Hz, and thus, the frequency contents of these curves may have been in the range from 0 to 30 Hz. Furthermore, the theoretical calculation of activation relied on the experimental quantification of the AJA and a model of the soleus muscle to calculate soleus fibre lengths (Allinger and Herzog, 1992); both of these procedures may have been sources for errors in calculating the instantaneous contractile conditions.

In spite of the differences in shape between the IEMG-time and the activation-time plots, some general and consistent observations were made.

The first burst of the IEMG occurred at about 0 to 50 % of the stance time, the second burst at about 50 to 100 % of the stance time (Figure 25b, cats L and J). In cases where the theoretically calculated activation had two bursts, the first activation burst tended to occur slightly after the corresponding IEMG burst (e.g. Figure 25b, cat L). In these cases, the second activation burst occurred at about the same time of the second burst of the IEMG.

Another consistent observation was that the theoretically predicted activation underestimated the IEMG values systematically, early during the stance phase (i.e. between approximately 0 % until 20 % or 30 % of the stance time, Figure 25b, all

cats). During this period, PMPF was high and the force exerted by the soleus muscle was relatively low (e.g. Figure 25a, all cats); therefore, the calculated activation was low. However, IEMG was high during this same period. This observation has two implications; first, the high EMG activity of the soleus muscle immediately preceding paw contact (Figure 20) may be associated with a "priming" of the muscle force production (note that in Figure 25b the IEMG results were shifted in time to offset the electromechanical delay). This "priming" includes a release of calcium from the sarcoplasmic reticulum, an activation of the thin filament through calcium binding to troponin C, and changes in the attachment of the cross-bridges from weak to strong binding sites (e.g. Gordon 1992). The "priming" of soleus causes muscular stiffness to be high, and thus, allows for a fast increase in force immediately following paw contact (Walmsley and Proske, 1981). The suggestion that the activation of the soleus preceding paw contact may enable the muscle to store energy (Sherif et al. 1983) cannot be supported because soleus forces are very low prior to paw contact (Walmsley et al. 1978; Hodgson, 1983; Herzog et al. 1993). Interestingly, the results of Figure 21 show that the fast increase in soleus force immediately following paw contact was associated with a decrease in IEMG, and it would be difficult to explain this observation, if it was not known that there is a delay between the EMG signals and the force of the muscle, which was not accounted for in Figure 21 (Cavanagh and Komi, 1979; Vos et al. 1990).

The second implication associated with the high IEMG values relative to the corresponding theoretically predicted activation values early in the stance phase, relates

to the motor control of the soleus muscle. The fact that IEMG was theoretically expected to be lower than it actually was early during the stance phase, suggests that excitation to the soleus muscle was not influenced by the favourable contractile conditions predicted for this period. Therefore, it appears that the initial and strong burst of IEMG was predominantly associated with a pre-programmed central neural control, and therefore, was independent of the instantaneous contractile conditions of the muscle, as suggested by Sherif et al. (1983).

During the period where the second burst of IEMG was observed, the contractile conditions of the soleus muscle became very unfavourable for force production due to relatively short muscle length (Rack and Westbury, 1969; Herzog et al. 1992) and high velocity of shortening of the muscle fibres (Spector et al, 1980). These conditions were reflected in the calculated activation, which tended to have a second burst, similar to the measured IEMG. The presence of the second IEMG burst, when the contractile conditions were unfavourable, and the observation that the measured soleus force decreased during this same period, may be used to speculate that the contractile conditions influenced excitation to the soleus muscle to partly offset the effects of the unfavourable contractile conditions for force production late during the stance phase.

Based on the observations made in this study, the hypothesis raised in chapter 2 that the EMG-force relation of the cat soleus muscle is influenced by the instantaneous contractile conditions is accepted for the late period during the stance phase, but not for the initial period of the stance phase. If it is correct that the contractile conditions do not influence excitation early in the stance phase, but influence excitation late in the

stance phase as argued above, it would be interesting to define the transition point at which the contractile conditions start to affect muscle excitation during locomotion. However, this was not attempted in this study.

In four out of the eleven tests, the predicted activation exceeded the theoretical maximum of 1.0. A value of activation larger than 1.0 means that the soleus force measured was larger than PMPF during locomotion. Since it may be assumed that the measured soleus forces are accurate within a margin of 5 %, it follows that the PMPF must have been underestimated when the theoretically predicted activation exceeded a value of 1.0. One possibility why PMPF may have been underestimated in this study is the fact that the force enhancement that occurs in a concentric contraction that is preceded by an eccentric contraction (Cavagna et al. 1968; Komi, 1986) was not taken into account in the calculation of PMPF (Allinger and Herzog, 1993). Activation values exceeding the theoretical maximum of 1.0 occurred in four out of the eleven tests, and were always obtained during concentric soleus contractions, which were preceded by an eccentric contraction, thus supporting the above speculation.

## **SUMMARY**

The major observations of this study were:

(1) The IEMG-force relation of the cat soleus muscle was highly non-linear during locomotion for speeds between 0.4 and 1.8 m/s. The mean IEMG-force relations were similar across speeds and across animals. This finding suggests that the mechan-

isms of motor control during locomotion were the same in all tested animals.

(2) IEMG-time histories and activation-time plots tended to have two bursts during the stance phase. The initial burst of the IEMG-time plots was higher than the second burst in all but one test; a similar trend was observed for most of the theoretically predicted activation-time plots. The first IEMG burst appeared to reflect the "priming" of the muscle for force production, possibly associated with a stiffening of the muscle. The second burst of the IEMG and the theoretically predicted activation appeared to reflect the fact that the contractile conditions (soleus fibre length, and particularly soleus fibre velocity of shortening) became very unfavourable for force production in the late period of the stance phase, and thus, an increased soleus excitation was required to produce the forces that are still observed in the muscle late in the stance phase.

# Chapter 6

## Summary and Conclusions

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This investigation was aimed at studying the EMG-force relation of the cat soleus muscle. All force measurements were made directly from the muscle using force transducers, and all EMG recordings were made using indwelling (wire) electrodes.

In the first project of this study the contractions of the cat soleus muscle were elicited in response to the independent and pseudo-random stimulation that was delivered to ten VR filaments. This approach allowed the implementation of a protocol in which addition and rate modulation of VR filaments (containing several motor units) could be combined simultaneously. Stimulating VR filaments asynchronously and using pulse trains containing pseudo-random interpulse intervals produced EMG signals that resembled the signals obtained during voluntary contractions, in the time and frequency domains. The effects of this type of stimulation could also be seen in the the force signals, which were different from the force signals obtained using periodic stimulation, particularly when a small number of VR filaments was stimulated at low rates.

Using the approach described in the previous paragraph, the relation between the EMG and force signals of the cat soleus muscle was found to be non-linear (sigmoid) for isometric contractions recorded at a single muscle length. An intermediate region of this sigmoid EMG-force relation (where the stimulation rates and the forces produced were compatible with physiological values), could be approximated well using a linear model. However, in the region where the stimulation rates of the ENMS approach were below those that have been observed in voluntary contractions, and in the region where the force levels were higher than those exerted by the cat soleus muscle during locomotion and jumping, EMG signals increased relatively faster than the corresponding force signals.

When tests were performed at different muscle lengths, the EMG-force relation was influenced primarily by the effects of the changes in muscle length on the force and only secondarily by the effects of changes in muscle length on the EMG. The influence of length changes on the EMG signals recorded were probably associated with the corresponding changes in the interelectrode distance. Thus, precautions in the design of the recording electrodes should be taken to assure that the interelectrode distance is not altered as a consequence of changes in muscle length, when studying the EMG-force relation for dynamically contracting muscle.

The EMG-force relation of the cat soleus muscle has not been described in the literature before; however, muscles comprised predominantly of slow twitch fibres, like the cat soleus, have been reported to have a linear EMG-force relation for voluntary contractions (Close et al. 1960; Bigland-Ritchie et al. 1980) Thus, the findings of this

investigation for the physiologically relevant (intermediate) region compare well with findings reported in the literature, and suggest that the isometric EMG-force relation of the cat soleus muscle is linear. It is important to keep in mind, however, that the procedures adopted in this part of the project utilized stimulation of VR filaments containing an unknown number of motor units, and for this reason, it was not possible to mimic the process of recruitment of motor units according to the size principle (Henneman et al. 1965), although VR filaments were "recruited" in a rank order (from small to large) of force production.

It is speculated that stimulating all motor units independently, rather than a group of motor units through the VR filaments, would most likely produce a greater amount of overlapping of the motor unit action potentials. This way of stimulating the muscle (which is the more physiological situation than the one that was used here) may cause a more pronounced and earlier saturation of the EMG signals, therefore, the linear relation between EMG and force would be extended further to force values beyond those reported here (Figure 5), since force also began to saturate in this region.

Force-length relations obtained using submaximal stimulation levels were not a simple scaled-down version of the force-length relation obtained using supramaximal stimulation, and they tended to be shifted towards relatively longer muscle lengths. For example, peak forces for a given level of submaximal stimulation occurred consistently at longer muscle lengths than peak forces obtained during supramaximal stimulation of the nerve, or all VR filaments. The lower the level of stimulation was, the more the peak force was shifted to longer muscle lengths. This finding should be

considered in the future, when theoretical models are used to predict force from EMG, in dynamically contracting skeletal muscle.

The stimulation technique used here is useful for studying the EMG-force relation, or other aspects associated with the EMG and force signals (e.g. decomposition of the EMG signals; control of muscle force). In contrast to existing stimulation techniques, which are typically periodic in nature and emphasize the process of recruitment of motor units, the stimulation of VR filaments, as it was done here, emphasizes the process of independent and non-periodic firing of VR filaments.

In the second project of this study, the EMG-force relation of the cat soleus muscle was determined during treadmill locomotion, at different speeds. For locomotion the EMG-force relation was found to be highly non-linear, in contrast to the linear relation measured previously for isometric contractions. Given the dynamic nature of the muscular contractions during locomotion, the combined force-length and force-velocity properties were expected to affect the EMG-force relation. These properties are non-linear, therefore, it was expected that the EMG-force relation was non-linear, as well. The EMG-force relations were similar across animals and across speeds, suggesting that motor control strategies for walking and trotting is similar across cats, and that EMG and force signals can be recorded consistently between animals.

During locomotion, the EMG of the soleus tended to have two bursts. The first burst was usually higher than the second burst, and it appeared to be associated with the initial priming of the muscle for force production at paw contact, and peak force

(Walmsley and Proske, 1981). The first burst of EMG occurred early during the stance phase, when the muscle was predicted to have contractile conditions that were favourable for force production (Allinger and Herzog, 1993). were favourable for force production. This finding suggests that the first EMG burst was pre-programmed, and that it was not influenced by the instantaneous contractile conditions.

The second burst of EMG occurred relatively late during the stance phase, when the contractile conditions were not favourable for force production, and when the soleus forces were close to the maximal predicted forces. Hence, the second EMG burst may represent an effort of the central nervous system, to at least partly off-set the unfavourable contractile conditions for force generation late during the stance phase. It seems that the magnitude of the IEMG was directly affected by the contractile conditions during the mid and late phase, but not during the initial period of the stance phase.

In summary, the main findings of this study were: (1) a linear EMG-force relation was measured for the cat soleus muscle at a single muscle length, during isometric contractions elicited by ENMS. This observation was made when the stimulation rates and the forces generated by the muscle were within the physiological range of the firing rates of motor units, and within the range of forces produced by the soleus muscle during locomotion and jumping; (2) similarly, linear but different EMG-force relations were found when using ENMS at different muscle lengths. The differences in the slopes of the EMG-force relations at different muscle lengths could partly be explained with the force-length properties of the cat soleus muscle (Rack and

Westbury, 1969; Herzog et al. 1992), and the possibility of increased interelectrode distance with increasing muscle length; and (3) highly non-linear EMG-force relations were measured for the cat soleus muscle for voluntary contractions during locomotion at different speeds. The patterns of the EMG-force relations obtained during locomotion were similar across speeds and animals.

It is suggested that in future work using the ENMS technique adopted here it should be attempted to reduce the number of motor units in each VR filament, by dividing the VR filaments L7 and S1 in to more than ten filaments. Another way of improving the ENMS technique used in this project would be, to combine the present technique with the the nerve stimulating technique that has been used by Solomonov et al. (1987), so that motor units can be recruited in a more physiological way compared to the addition of VR filaments.

It would be interesting to conduct experiments using ENMS of VR filaments, in which the muscle were submitted to shortening and lengthening at different rates of change of muscle length, and at ranges of muscle length other than the optimal range for force production. This type of experiment would complement the experiments conducted at different muscle lengths, and therefore may provide some relevant information regarding the mechanisms underlying the EMG-force relation.

It would also be interesting to study the EMG-force relation of the cat gastrocnemius muscle using the two different approaches adopted in this study (i.e. ENMS and voluntary elicited contractions). Since this muscle is comprised of both slow and

fast twitch fibres the addition of this variable (i.e. fibre type) may provide some further insight into the understanding of the EMG-force relation.

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Figure 8. (a) IEMG, and (b) mean force response of a single VR filament as a function of actual mean stimulation rates; and (c) the corresponding IEMG-mean force relation. IEMG and mean force were normalized relative to the highest values obtained. Maximal mean force measured = 2.3 N.

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Figure 9. (a) IEMG, and (b) mean force response of a single VR filament as a function of actual mean stimulation rates; and (c) the corresponding IEMG-mean force relation. IEMG and mean force were normalized relative to the highest values obtained. Maximal mean force measured = 3.5 N.

## Chapter 4



Chapter 5