

EFFECTS OF MUSCLE LENGTH ON THE EMG–FORCE RELATIONSHIP OF THE CAT SOLEUS MUSCLE STUDIED USING NON-PERIODIC STIMULATION OF VENTRAL ROOT FILAMENTS

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Summary

The effects of changing the length of the cat soleus muscle on electromyographic (EMG) signals, muscle force and the corresponding EMG–force relationship were assessed using distributed stimulation of ten ventral root filaments and irregular interpulse intervals. EMG–force relationships were first determined for four muscle lengths using a protocol of simultaneous addition and rate modulation of ventral root filaments. In the second test, three submaximal levels of stimulation were applied at eight muscle lengths. EMG signals were obtained using surface and wire electrodes, and force was measured using a strain transducer. For most muscle lengths, the relationships between integrated EMG and mean force obtained using wire and surface electrodes were sigmoid with a linear intermediate region. The effects of muscle length on EMG signals were likely to be associated with movement of the recording electrodes relative to each other and to the active motor units. Mean forces increased with increasing muscle length and with increasing levels of stimulation. Mean force–length relationships obtained using submaximal stimulation were not simply scaled down versions of the force–length relationship obtained using supramaximal stimulation of the soleus nerve, but appeared to be shifted towards longer muscle lengths.

Introduction

In the accompanying paper (Guimaraes *et al.* 1994), we assessed the relationship between electromyographic (EMG) signals and muscle force produced by the cat soleus muscle (for a fixed muscle length) using distributed stimulation of ventral root (VR) filaments and irregular interpulse intervals. However, during isometric contractions at different muscle lengths, force depends not only on the excitation but also on the length of the muscle (e.g. Rack and Westbury, 1969; Herzog *et al.* 1992). For dynamic contractions, predictions of force from EMG activity become still more complex and

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should take into account not only the force–length relationship but also the force–velocity relationship (Hill, 1938).

Theoretical models have implicitly assumed that EMG signals are independent of muscle length and, furthermore, that the force–length relationship obtained using supramaximal stimulation of a specific muscle can be linearly scaled to represent submaximal contractions (e.g. Cogshall and Bekey, 1970; van den Bogert *et al.* 1988; Hof, 1988; van Ruijven and Weijs, 1990). However, Woods *et al.* (1987) reported that the shape 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 the pattern of activation in a complex and non-linear way. Most experimental EMG–force studies tend to support the hypothesis that EMG signals are 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; Vredenburg and Rau, 1973). The experimental studies cited above have investigated voluntary contractions in human subjects and, under these experimental conditions, it is not possible to determine how changes in muscle length may influence the recorded signals. There are at least three factors that may affect EMG recordings as muscle length changes: first, there may be changes in excitation to the muscle; second, there may be changes in mechanical or electrical properties of the muscle; and third, there may be changes in the location of the electrodes relative to the active motor units. The differences between observations made in different studies of the effects of changing muscle length on EMG signals might result from various combinations of these factors, caused by differences in experimental conditions. It appears, therefore, that the complex changes in recordings and muscle force as a function of muscle length are not understood completely.

The purpose of this study was to determine, using distributed stimulation of VR filaments and irregular interpulse intervals, the effects of changes in muscle length on (a) the EMG signal and the muscular force, and (b) the resulting EMG–force relationship of the cat soleus muscle. This approach allowed us to evaluate the effects of muscle length on the EMG–force relationship without the interference of the central nervous system.

Materials and methods

A series of experiments was conducted to study the EMG–force relationship of the cat soleus muscle. Two cats (masses 3.3 and 3.8 kg) were used in experiments designed to assess the effects of muscle length on the EMG–force relationship. Approval for this study was obtained from the Committee on Animal Ethics at The University of Calgary. Animals were anaesthetized using an intraperitoneal injection of Somnotol (40 ml kg⁻¹) and submitted to a laminectomy in order to expose the ventral roots of L7 and S1, which contain the alpha motoneurons that innervate 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 intact. All

other muscles of the experimental hindlimb were denervated. The insertion of the soleus muscle was detached along with a piece of the calcaneus and was rigidly fixed to a muscle puller fitted with a strain transducer. Muscle lengths were adjusted using the muscle puller. The animals' blood pressure, respiration and body temperature were continuously monitored throughout the experiments.

Eight VR filaments were stimulated independently. Two further VR filaments were stimulated using pulse trains that were delayed by 10–20 ms relative to two of the independently stimulated VR filaments. Interpulse intervals of the stimulation trains were pseudo-random, with a coefficient of variation of 12.5% (Zhang *et al.* 1992). Identical trains of stimulus pulses could be reproduced at any time.

EMG signals were recorded using a patch-type bipolar surface electrode (inter-electrode distance, 6 mm) sutured to the epimysium of the muscle and with bipolar indwelling (wire) electrodes inserted into the mid-belly of the muscle without fixation (inter-electrode distance approximately 10 mm). EMG and force signals were digitised at 2100 and 350 Hz, respectively. VR filaments were stimulated for approximately 4 s in each trial, with recordings starting approximately 1 s after the onset of stimulation and lasting for 2 s. The integrated unsmoothed full-wave-rectified EMG (IEMG) and the corresponding mean force were calculated for each trial.

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

Test 1. 27 (or 15) stimulation levels, four muscle lengths

In test 1, a stimulation protocol consisting of 27 different trials (Table 1) was applied to one animal and an abbreviated version of this protocol (consisting of the 15 trials marked with asterisks in Table 1) was applied to the second animal. These protocols were used at four different muscle lengths, corresponding to ankle joint angles (AJAs) of 55, 80, 105 and 130°, 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° was defined as the angle that would be obtained if the foot were forced into plantar flexion up to the point where it would be perfectly aligned with the shank. Dorsiflexion of the ankle joint increased the AJA. AJAs of 55 and 130° correspond to the shortest and longest muscle lengths tested, respectively. AJAs between 50 and 100° have been reported for the stance phase of cat locomotion (Goslow *et al.* 1973).

The protocol shown in Table 1 was designed sequentially to increase the number of stimulated VR filaments during trials 1–10, while simultaneously increasing the mean rates of stimulation of previously activated VR filaments when new VR filaments were stimulated. Beyond trial 10, stimulation rates of all ten VR filaments were increased from one trial to the next but no new VR filaments were added. In this study, the phrase 'stimulus level' refers to the combination of stimulus frequency and number of activated VR filaments. All IEMG and mean force measurements obtained during test 1 were normalized with respect to the values obtained in the last trial of each protocol with the AJA set at 105°.

To assess the effects of increasing levels of stimulation on the force produced at different muscle lengths (test 1), the ratios between mean forces produced at 55° (short

muscle length) and 105 ° (long muscle length) were calculated for the full and abbreviated protocols of Table 1.

To test the reproducibility of EMG and force recordings, test 1 was performed twice during one experiment for a particular muscle length (i.e. AJA, 105 °), using the full protocol first and the abbreviated protocol second. The test and retest were separated by approximately 3.5h. The results thus obtained were normalized with respect to the highest values obtained during the initial test.

Theoretical calculations were made to illustrate the effects of muscle length on the inter-electrode distance and, consequently, on the IEMG of a single compound motor unit

Table 1. *Protocol used in test 1, designed to increase sequentially the number of stimulated ventral root filaments and the frequency of stimulation (trials 1–27)*

Trial	Ventral root filament number									
	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

Trials marked with asterisks identify the abbreviated version of the complete protocol, which was applied to animal 2.

Trials 10, 17 and 24 are marked with daggers to identify the relatively low, medium and high stimulation frequencies adopted in test 2.

Values in the table indicate the mean rate of stimulation of active ventral root filaments in each trial (Hz).

action potential (CMUAP). These calculations were based on the following simplifications: (a) the action potential was assumed to be biphasic, and each phase had the shape of a triangle; (b) the initial muscle length was assumed to be 8.7 cm; (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°, respectively); and (d) the amplitude of the action potential was not affected by changes in the inter-electrode distance. Changes in the IEMG as a function of changes in muscle length were expressed relative to the value of the IEMG at the shortest muscle length (AJA, 55°). In addition, a single CMUAP, obtained experimentally for four different muscle lengths, was extracted for illustration of the possible effects of changes in muscle length on the IEMG of a single CMUAP.

Test 2: three stimulation levels, eight muscle lengths

In test 2, three stimulation levels (trials marked with daggers in Table 1) were applied to the muscle set at eight different lengths, corresponding to AJAs of 45, 55, 65, 75, 85, 95, 105 and 115°, giving a further 24 observations per animal. AJAs of 45 and 115° corresponded to the shortest and longest muscle lengths tested, respectively. The three stimulation levels adopted will hereafter be referred to as 'low' (trial 10), 'medium' (trial 17) and 'high' (trial 24) frequencies. In one of the experiments, the nerve to the soleus muscle was stimulated supramaximally at 75 Hz (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 frequencies at an AJA of 105°.

To assess the effects of different stimulation frequencies on the force produced at different muscle lengths, the ratios between the mean forces produced by the low, medium and high stimulation frequencies were calculated relative to the mean force levels obtained by nerve stimulation at 75 Hz in one experiment.

Between trials, the muscle was rested at a short length for at least 1 min. 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. At the end of the experiments, the animals were killed using an overdose of barbiturate.

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 Materials and methods section. The results obtained using the patch-type surface electrodes corroborated the general findings obtained using indwelling electrodes and will be referred to whenever they provide additional information.

Test 1

The results obtained when the entire protocol consisting of 27 trials (Table 1) was applied to four different muscle lengths of one animal are shown in Fig. 1, and the corresponding results obtained by applying the abbreviated version of the protocol to a

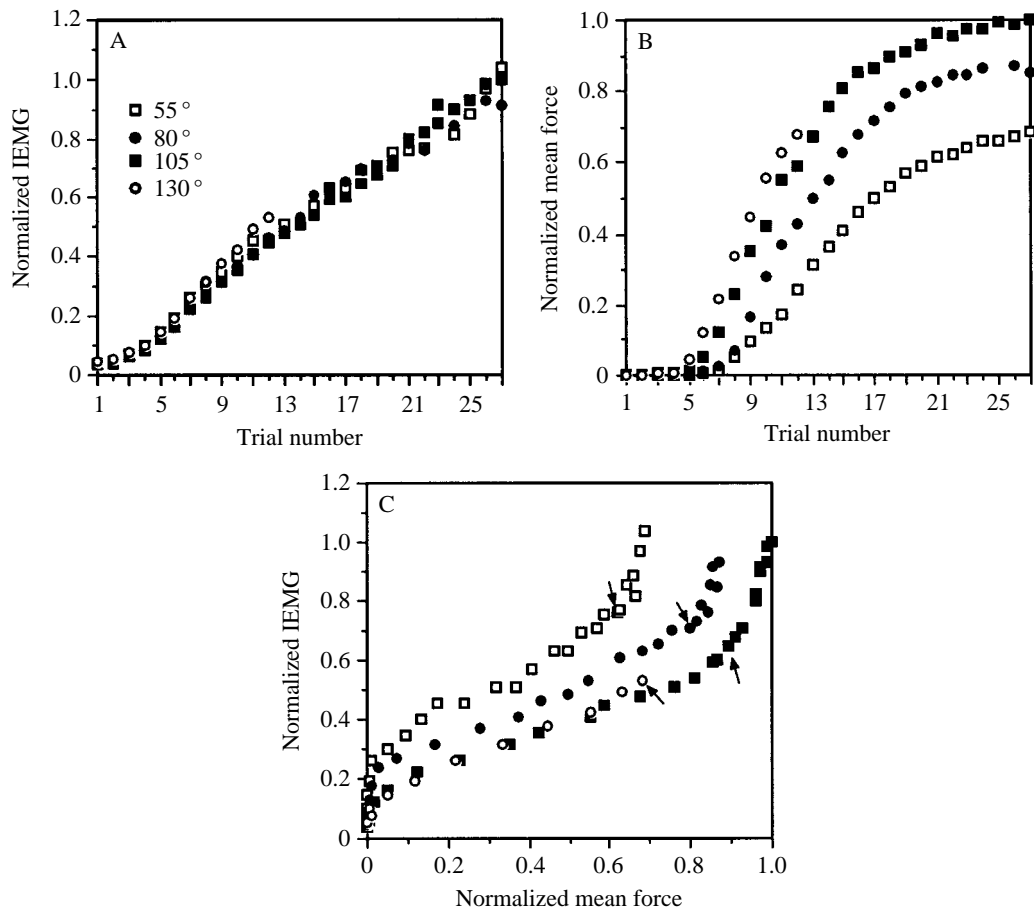


Fig. 1. Effects of four different muscle lengths on (A) IEMG values, (B) mean force and (C) the relationship between IEMG and mean force obtained in one experiment. Ventral root (VR) filaments were stimulated according to the full protocol shown in Table 1. The last data point of each linear region is indicated with an arrow. IEMG and mean force values were normalized relative to values obtained in trial 27 with the ankle joint angle (AJA) fixed at 105°. Maximal mean force was 29.3 N.

second animal are shown in Fig. 2. Only the first twelve trials were performed at an AJA of 130° (Fig. 1) because the preparation subsequently became unstable and the experiment was terminated.

When IEMG was expressed as a function of trial number (i.e. as a function of increasing stimulation level, Table 1), it was found to be less affected by muscle length in one experiment (Fig. 1A) than in the other (Fig. 2A).

The lowest values of mean force occurred at the shortest muscle length (AJA=55°) and the highest values occurred at the longest muscle length (AJA=130°) for all levels of stimulation (Figs 1B, 2B), except for the last four trials in Fig. 2B, where the mean forces of the two longest muscle lengths were approximately the same. In both experiments, higher stimulation levels were required at short muscle lengths than at long muscle

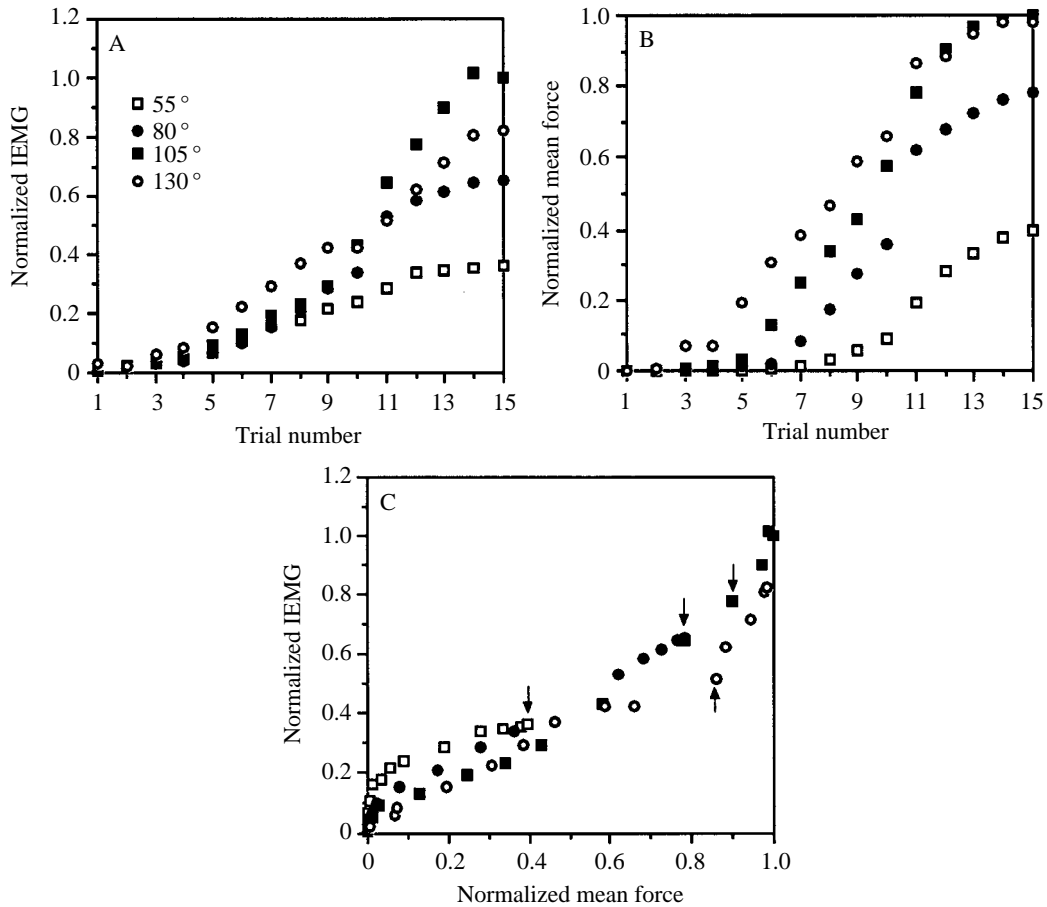


Fig. 2. Effects of four different muscle lengths on (A) IEMG values, (B) mean force and (C) the relationship between IEMG and mean force obtained from one experiment. VR filaments were stimulated according to the abbreviated version of the protocol shown in Table 1. The last data point of each linear region is indicated with an arrow. IEMG and mean force values were normalized relative to values obtained in trial 15 with the AJA fixed at 105°. Maximal mean force was 23.3 N.

lengths to produce measurable forces. For example, soleus forces could first be detected in trial 3 when the AJA was fixed at 130° but only in trial 6 (and subsequent trials) when the AJA was fixed at 55° (Fig. 2B). In both experiments, mean force tended to saturate towards high levels of stimulation for all muscle lengths. Results obtained using the full protocol (Fig. 1B) showed the effects of force saturation more clearly than did the results obtained using the abbreviated protocol (Fig. 2B) because the full protocol included more trials in the region where saturation of force occurred.

The ratios between the mean force values produced at an AJA of 55° and the mean force values produced at an AJA of 105° (from Figs 1B, 2B) are shown as a function of increasing levels of stimulation in Fig. 3A,B for the full and abbreviated protocols,

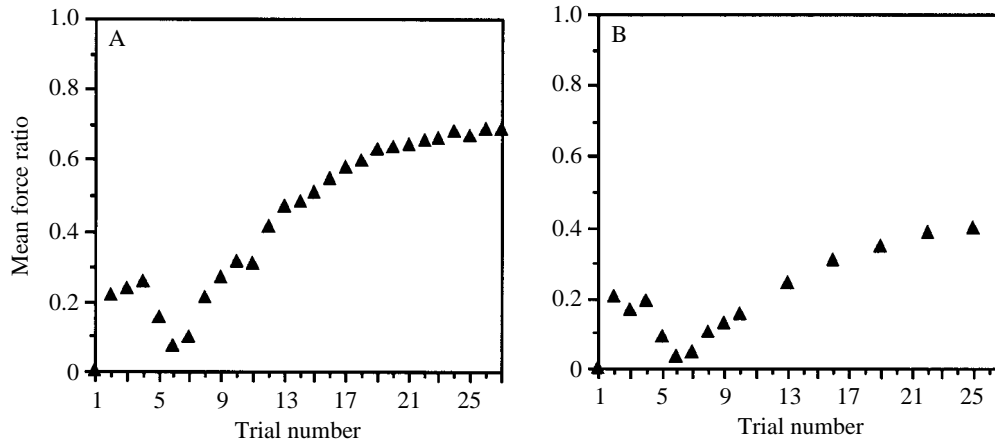


Fig. 3. Ratios obtained by dividing the mean force values obtained at an AJA of 55° by those obtained at an AJA of 105° from experiments corresponding to (A) Fig. 1B and (B) Fig. 2B.

respectively. These ratios fluctuated in the initial trials, reached a local minimum for both protocols in trial 6, and then increased steadily until the last trial.

Except for relatively short muscle lengths (AJAs of 55° and 80°) the relationships between IEMG and mean force were sigmoid, containing an intermediate region (Guimaraes *et al.* 1994) that could be approximated well using least-squares linear regression (r^2 , 0.85–1.0, Fig. 1C; r^2 , 0.99–1.0, Fig. 2C). 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 Figs 1C, 2C.

The results obtained when the muscle was tested and retested with the protocol in Table 1 are shown in Fig. 4, with data points corresponding to the same stimulation level being connected by lines. Mean forces tended to be slightly smaller in the retest than in the initial test for low levels of stimulation, but were approximately the same for high levels of stimulation. IEMG values were systematically lower in the retest than in the initial test.

Theoretical predictions of changes in the IEMG of a single CMUAP associated with changing muscle lengths (assuming that the duration of the CMUAP increased in proportion to muscle length) illustrate that the relative change in IEMG values from those obtained at the shortest muscle length are equal to the corresponding changes in muscle length (Fig. 5). Experimental evidence showed that the duration of CMUAPs increased systematically with increasing muscle length (Fig. 6).

Test 2

The results obtained from experiments with two animals, applying low, medium and high stimulation frequencies (trials 10, 17 and 24 in Table 1, respectively) at eight muscle lengths (AJA ranging from 45° to 115° , at 10° intervals) are shown in Figs 7, 8. In both experiments, IEMG values increased with increasing stimulation frequencies. IEMG values were unaffected by muscle length in one experiment (Fig. 7A), but showed a clear

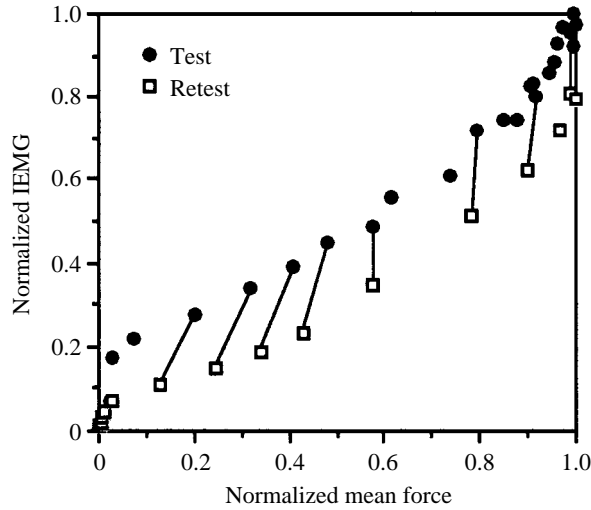


Fig. 4. The relationships between IEMG and mean force (test 1) obtained approximately 3.5 h apart from the same animal. The AJA was fixed at 105°. Test and retest were conducted utilizing the complete and abbreviated versions of the protocol in Table 1, respectively. Corresponding data points are connected. IEMG and mean force values were normalized relative to values obtained for the test. Maximal mean force was 23.4 N.

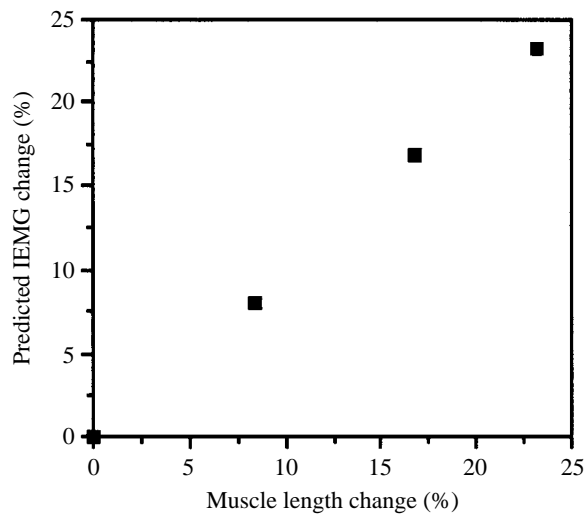


Fig. 5. Predicted changes in IEMG values (for single action potentials) in response to increments in muscle length. The duration of the action potential was assumed to increase in proportion to the increase in muscle length, and the amplitude of the action potential was assumed to be constant. Changes in predicted IEMG values and changes in muscle length are expressed relative to respective measurements corresponding to the shortest muscle length (AJA=55°).

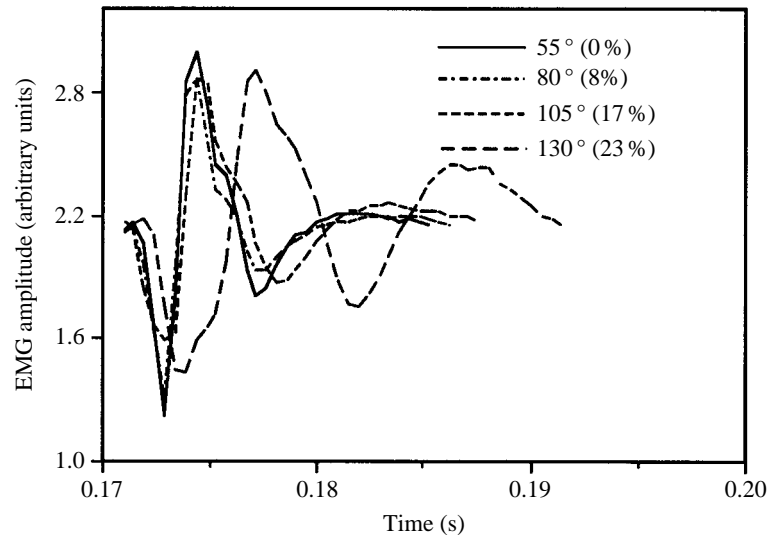


Fig. 6. Single compound motor unit action potentials (from trial 1 of Table 1, second animal) obtained at four muscle lengths (AJAs of 55, 80, 105 and 130°).

relationship with muscle length in the other, increasing as muscle length increased (Fig. 8A).

Passive forces increased with increasing muscle length (Figs 7B, 8B). Total forces increased with increasing muscle length for all stimulation frequencies, indicating that the ascending limb of the force-length relationship was tested. The results corresponding to the force-length relationship obtained when the nerve to the soleus muscle was stimulated supramaximally at 75 Hz for each of the different lengths are shown in Fig. 8B.

The relationships between IEMG and mean force (Figs 7C, 8C) were affected by changes in muscle length in both experiments. In the first experiment, the relationship was influenced strongly by the force-length relationship of the soleus muscle and, to a smaller extent, by the random variations of EMG signals as a consequence of changes in muscle length (Fig. 7C). In the second experiment, the relationships between IEMG and mean force were strongly influenced by the force-length and IEMG-length relationships (Fig. 8C).

The ratio between the force values corresponding to each of the stimulation protocols (i.e. low, medium, and high frequencies) and the mean force values obtained when stimulating the nerve at 75 Hz are shown in Fig. 9 for all muscle lengths tested. These ratios tended to increase as muscle length was changed from short (AJA=45°) to long (AJA=115°), indicating that submaximal stimulation frequencies resulted in muscular forces closer to the maximum possible forces at long rather than at short muscle lengths. The shape of the relative force curves was approximately linear for the low-frequency stimulation protocol, but non-linear for the medium- and high-frequency protocols.

Discussion

The sigmoid relationships between IEMG and mean force obtained for cat soleus muscle at different muscle lengths in test 1 (Figs 1C, 2C) are consistent with our previous

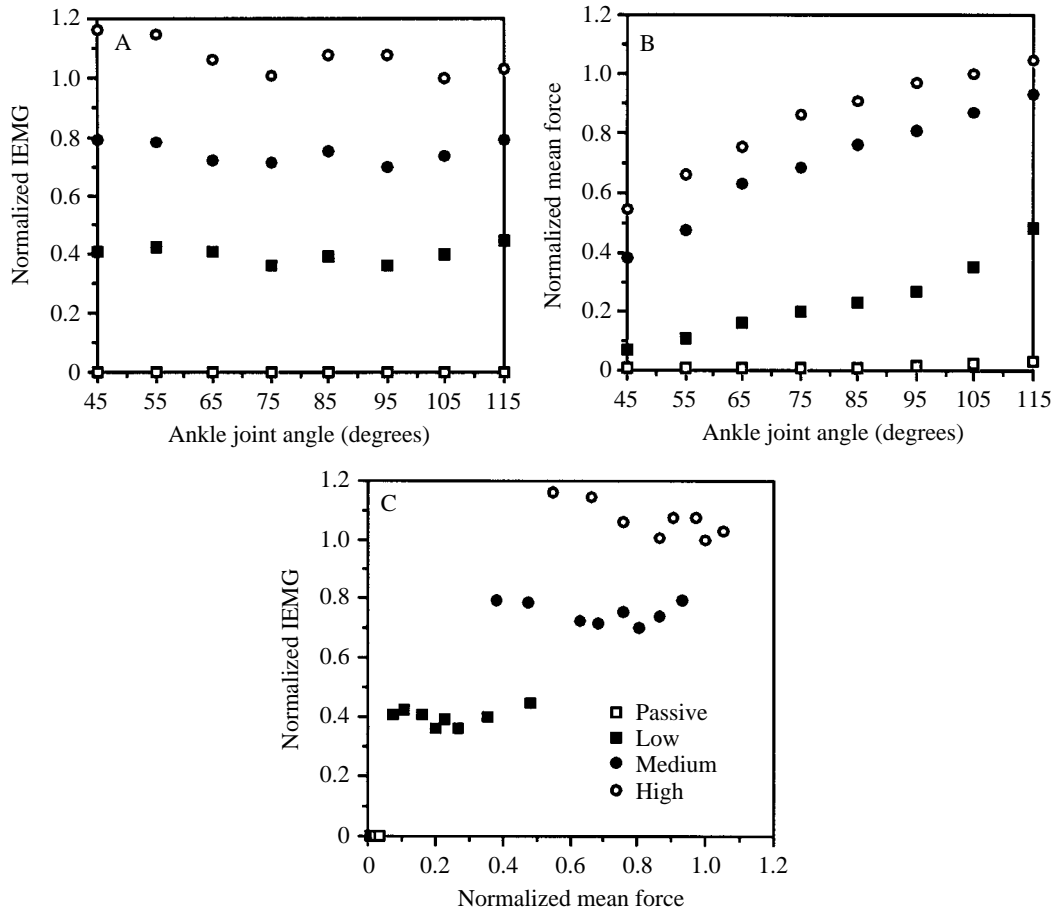


Fig. 7. Effects of no stimulation (passive) and three stimulation levels (low, medium and high frequencies, corresponding to trials 10, 17 and 24 in Table 1, respectively) on (A) IEMG values, (B) mean force and (C) the relationship between IEMG and mean force at eight different muscle lengths (AJAs ranging from 45 to 115°) for one animal. IEMG and mean force values were normalized relative to values obtained by applying the high stimulation level to the muscle set at an AJA of 105°. Maximal mean force was 29.7 N.

results obtained at a single muscle length (Guimaraes *et al.* 1994). Sigmoid relationships were not as clear for two muscle lengths of one animal (AJAs of 55 and 80° in Fig. 2C), because of a pronounced saturation of IEMG values and fewer observations in this experiment than in the one shown in Fig. 1C. As reported previously for a single muscle length (Guimaraes *et al.* 1994), the relationships between IEMG and mean force obtained at different muscle lengths displayed three distinct regions that were classified according to the levels of stimulation as low, intermediate and high.

The frequencies of stimulation used in the low region were below the minimal firing rates observed in motor units during voluntary contractions (Burke, 1981). The forces corresponding to the high region were higher than those obtained during voluntary

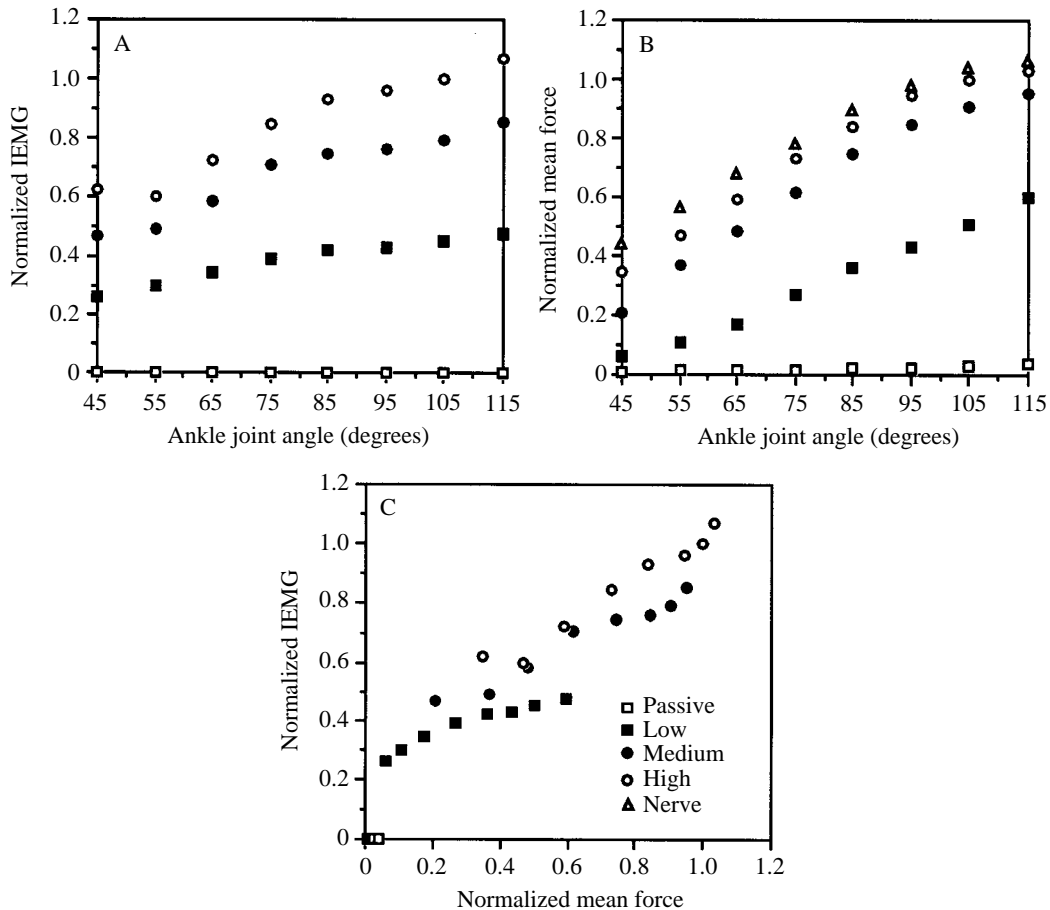


Fig. 8. Effects of no stimulation (passive) and three submaximal stimulation levels (low, medium and high frequencies, corresponding to trials 10, 17 and 24 in Table 1, respectively) on (A) IEMG values, (B) mean force (also for nerve stimulation at 75 Hz) and (C) the relationship between IEMG and mean force for eight different muscle lengths (AJAs ranging from 45 to 115°) for one animal. IEMG and mean force values were normalized relative to values obtained by applying the high stimulation level to an AJA of 75°. Maximal mean force was 25.3 N.

contractions (Walmsley *et al.* 1978; Herzog and Leonard, 1991). The intermediate region is therefore of most interest from a functional point of view since it contains stimulation and force levels that occur during normal voluntary contractions. The relationships between IEMG and mean force in the intermediate region were virtually linear (Figs 1C, 2C). This finding extends our observation of a linear relationship between IEMG values and mean force for a single muscle length (Guimaraes *et al.* 1994) to muscle lengths covering 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, such as the cat soleus, that consist predominantly of slow motor units have been reported to be linear

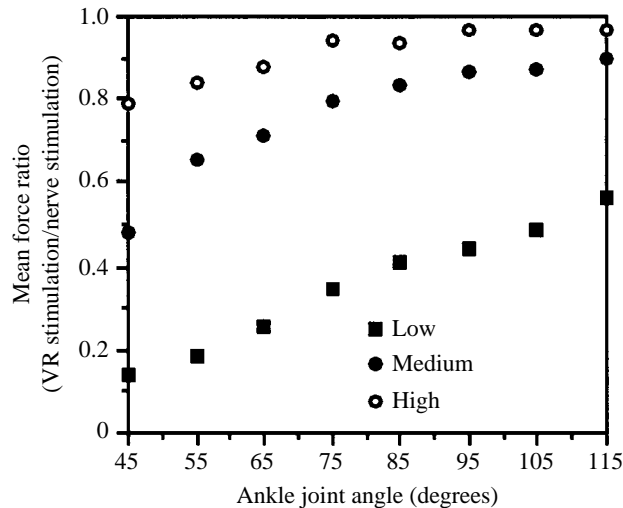


Fig. 9. Mean force ratio, obtained by dividing the mean force values obtained using low-, medium- and high-frequency stimulation by those obtained using nerve stimulation at 75 Hz, for eight different muscle lengths. These results were derived from Fig. 5B.

(Close *et al.* 1960; Bigland-Ritchie *et al.* 1980). Our results obtained using electroneuromuscular stimulation therefore agree with the results reported for voluntary contractions.

The effects of muscle length on IEMG values appeared to be random for tests 1 and 2 in one experiment (Figs 1A and 7A, respectively); but in the other experiment the effects were systematic for three out of the four muscle lengths studied for test 1 (Fig. 2A) and systematic for all muscle lengths for test 2 (Fig. 8A). Muscle length has been shown to affect the amplitude of action potentials (Woods *et al.* 1987), and fluctuations in EMG signals with changing muscle length may be caused by movement of the recording electrodes relative to the active motor units (Basmajian and De Luca, 1985) and relative to one another. The results obtained when test 1 was performed twice at one muscle length in one experiment (Fig. 4) provide evidence that there was indeed movement of electrodes relative to the muscle during the experimental protocol. IEMG values were systematically lower in the first test, whereas mean forces were similar (particularly at high force levels) in the two tests.

The systematic increase in IEMG values with increasing muscle length seen in one experiment (Figs 2A, 8A) may have been caused by increases in the duration of CMUAPs as a consequence of systematic increases in the inter-electrode distance, as illustrated theoretically (Fig. 5). The results illustrated in Fig. 6 (obtained from the experiment in which IEMG values were found to increase systematically with increasing muscle length) show that increasing muscle length was associated with an increase in the duration of the CMUAP, which is likely to be associated to a large extent with changes in the inter-electrode distance.

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) so the inter-electrode distance was fixed and, in contrast with the results obtained using indwelling electrodes (Figs 1A, 2A, 8A), the IEMG values obtained with surface electrodes did not change systematically with increasing muscle length.

The random variations in IEMG values produced by changes in muscle length in one experiment (Figs 1A, 7A) were probably associated with random changes in the inter-electrode distance since no attempts were made to fix the indwelling electrodes to the muscle. One way of minimizing the undesirable systematic effects of inter-electrode distance on EMG recordings is to insert the electrodes into the mid-belly of the muscle using a surgical needle, to suture the electrodes in place at the entry and exit points of the needle and to reinforce the bipolar arrangement with medical-grade silicone rubber tubing to avoid relative movement of the electrodes (Herzog *et al.* 1993).

As expected, soleus forces increased with increasing stimulation levels and increasing muscle length (Figs 1B, 2B, 7B, 8B). These results indicated that the muscle lengths tested were within the range of the ascending limb of the force-length relationship for the cat soleus muscle, which is consistent with previous observations (Rack and Westbury, 1969; Herzog *et al.* 1992). The 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 with supramaximal nerve stimulation (Fig. 8B).

When using EMG signals to predict muscular forces 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 maximum value of this measure) by the relative force of the muscle which, at any given instant, depends on the length and velocity of the contractile elements (e.g. van den Bogert *et al.* 1988; Hof, 1988; van Ruijven and Weijs, 1990). This approach assumes implicitly that a given stimulation will produce the same percentage of the maximum force for any contractile condition of the muscle (e.g. muscle length). The results of this study do not support this assumption (Figs 3A,B, 9). The relative forces produced at a given level of stimulation were clearly dependent on muscle length. If this were not the case, the curves shown in Fig. 9 would be horizontal for each of the different stimulation protocols. Results similar to those in Fig. 3A,B 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 than at short muscle lengths, indicating that submaximal levels of stimulation may be used more efficiently for force production at long than at short muscle lengths. Therefore, there appears to exist a mechanism that enhances force production at long muscle lengths. In skeletal muscle (Ruedel and Taylor, 1971) and in cardiac muscle (Fabiato and Fabiato, 1975) more calcium is released from the sarcoplasmic reticulum at long than at short sarcomere lengths during equivalent stimulation. The free calcium concentration in a muscle fibre is directly associated with force production, so 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 stimulation levels. Similar changes in force-length properties 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 observation that force-length properties of cat soleus muscle obtained using submaximal levels of stimulation are not simply a linear scaling down of the force-length relationship obtained using supramaximal stimulation suggests that theoretical models will have to account for this non-linear behaviour. The force-length relationship obtained using supramaximal stimulation protocols may not suffice to explain the force-length properties of submaximally contracting muscle. Since most physiological contractions are submaximal, future research should focus on determining force-length properties for stimulation levels other than supramaximal.

The relationships between IEMG and mean force of cat soleus muscle were sigmoid, with a linear intermediate region associated with muscle lengths and 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 length 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 relationship and were not linearly related to the force-length relationship obtained using supramaximal stimulation. For given levels of submaximal stimulation, soleus forces were smaller at short than at long muscle lengths. These results suggest that predictions of isometric force from EMG recordings must consider the variable changes in force-length behaviour of submaximally stimulated muscle.

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