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# EMG–FORCE RELATIONSHIP OF THE CAT SOLEUS MUSCLE STUDIED WITH DISTRIBUTED AND NON-PERIODIC STIMULATION OF VENTRAL ROOT FILAMENTS

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## Summary

Distributed stimulation of ventral root (VR) filaments and pseudo-random interpulse intervals (based on a Gaussian distribution with a coefficient of variation of 12.5 %) were used to modulate electromyographic activity (EMG) and force of the cat soleus muscle to assess the EMG–force relationship. A protocol consisting of addition and rate modulation of ten VR filaments that contain alpha motoneurones to the soleus muscle was adopted. EMG was measured using indwelling electrodes and forces were measured at the distal tendon using a strain transducer. EMG records obtained using this approach were similar in the time and frequency domains to those obtained during voluntary contractions. Force records obtained from stimulation of single VR filaments showed summation effects typical of irregular interpulse intervals. The overall relationship between integrated rectified EMG (IEMG) and mean force was found to be non-linear. At low and high stimulation levels, IEMG tended to increase proportionally more than mean force. In the intermediate stimulation region (i.e. producing forces between approximately 5 % and 88 % of the maximal tetanic force), the IEMG–mean force relationship was virtually linear. Muscles with a homogeneous fibre type composition, such as the cat soleus muscle, have been reported to have a linear EMG–force relationship.

## Introduction

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 electromyographic (EMG) signals and muscular force are related. Although the literature most often describes a linear relationship 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 relationship may be non-linear (e.g. Komi and Viitasalo, 1976; Vredenbregt and Rau, 1973). The different results reported in the literature may be explained partly by (a) difficulties in measuring direct force (Bouisset, 1973) and EMG records from a single muscle, (b) differences in fibre type composition of the muscles studied (Bigland-Ritchie

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*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 both linear or non-linear EMG–force relationships in skeletal muscle depending on the strategy of recruitment employed to activate motor units.

EMG–force relationships may be studied using two basic approaches: voluntary contractions or electroneuromuscular stimulation (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 have 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 and 12 pulses $s^{-1}$ (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 made up of motor units of relatively homogeneous size, the possible effects of recruitment according to the size principle on the EMG–force relationship might be reduced to some extent.

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

The cat soleus muscle was used for several reasons: (a) it consists exclusively of slow-twitch fibres of homogeneous size (Ariano *et al.* 1973) so that recruitment strategies were considered to be relatively less important in force and EMG modulation, (b) the EMG–force relationship 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).

## Materials and 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 relationship of cat soleus muscle during isometric contractions. A fourth animal (mass 4.3 kg) was used exclusively to study the effects of the addition of VR filaments on the EMG–force relationship, 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 relationship.

### *Animal preparation*

All animals were anaesthetized using 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 2–4 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 ˚C throughout the experiments.

Myotomy of the back muscles and laminectomy were performed to expose the nerve roots of the seventh lumbar (L7) and first sacral (S1) vertebrae 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.Ventral roots L7 and S1, which contain alpha motoneurones to the soleus muscle, were identified and separated from the corresponding dorsal roots. A microscopic dissection was performed to split the ventral roots 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 pulses $s^{-1}$ (i.e. stimulation rates were different in each experiment). VR filaments were ordered in rank according to force production (except in the experiment designed to assess the effects of addition of VR filaments on the EMG–force relationship) and were placed on hook-like individual stimulation electrodes. Each VR filament prepared in this way contained an unknown number of alpha motoneurones.

The soleus muscle of the left hindlimb was exposed with its innervation and blood supply being maintained. The nerve supply to other muscles and cutaneous territories of the same hindlimb was severed. A relationship 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 ˚ 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. 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 %

$CO_2$ and 95 % $O_2$) 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 with 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 1 ms) with an amplitude of 2–3 times threshold levels. Each VR filament was placed on a separate silver wire electrode of a multi-electrode array.

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 hibrid signal generator. The pulses of two of these generators were delayed by 10–20 ms and applied to two further VR filaments. VR filaments were stimulated using ten independent voltage-controlled stimulators. Stimulation for each trial started 2–3 s 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 1–2 mm 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.

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 s in each trial and were digitized at 2100 and 350 samples $s^{-1}$, respectively, using an analog to digital board and an LSI computer. The integrated area under the full-wave rectified EMG (IEMG) and the mean force were calculated for each 2 s period. All protocols were tested for a fixed muscle length corresponding to an AJA of 105 °.

### *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 relationship of cat soleus muscle, the protocol shown in Table 1 was used in two experiments. The active VR filaments in each trial are identified by their mean stimulation rates in pulses $s^{-1}$. 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.

Table 1. *Protocol designed to investigate the simultaneous effects of addition (trials 1–10) and rate modulation (trials 1–27) of ten ventral root filaments on the EMG–force relationship*

| | Ventral root filament number | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Trial | 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 |

Mean stimulation rates of active ventral root filaments are indicated for each trial in pulses $s^{-1}$. Coefficient of variation of stimulation trains was 12.5 %.

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 pulses $s^{-1}$. 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).

Table 2. *Protocol designed to study the effects of the addition of eight ventral root filaments on the EMG–force relationship*

| | Ventral root filament number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Trial | 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 |

Mean stimulation rates of active ventral root filaments are indicated for each trial in pulses $s^{-1}$. Coefficient of variation of stimulation trains was 12.5 %.

Thus, calculated IEMG and calculated mean force values could be compared with the corresponding values obtained for each of the experimental trials.

*Rate modulation of single VR filaments*

In order to assess the effects of rate modulation on the EMG–force relationship, two single VR filaments from one animal were studied independently by stimulating them at nominal mean rates ranging from 5 to 50 pulses $s^{-1}$, with increments of 5 pulses $s^{-1}$.

*EMG–force relationship of isolated VR filaments*

In order to test whether 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 or 60 pulses $s^{-1}$.

## Results

EMG signals produced using asynchronous independent stimulation of VR filaments (Hulliger *et al.* 1987) and pseudo-random interpulse intervals (Zhang *et al.* 1992) were similar to EMG signals in the time (Fig. 1A) and frequency domains obtained during voluntary contractions.The adoption of pseudo-random stimulation trains produced visible effects of force summation (Copper and Eccles, 1930) when a small number of VR filaments were stimulated at relatively low rates (Fig. 1B).

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*

Figs 2, 3 and 4 show the effects of simultaneous addition and rate modulation of VR

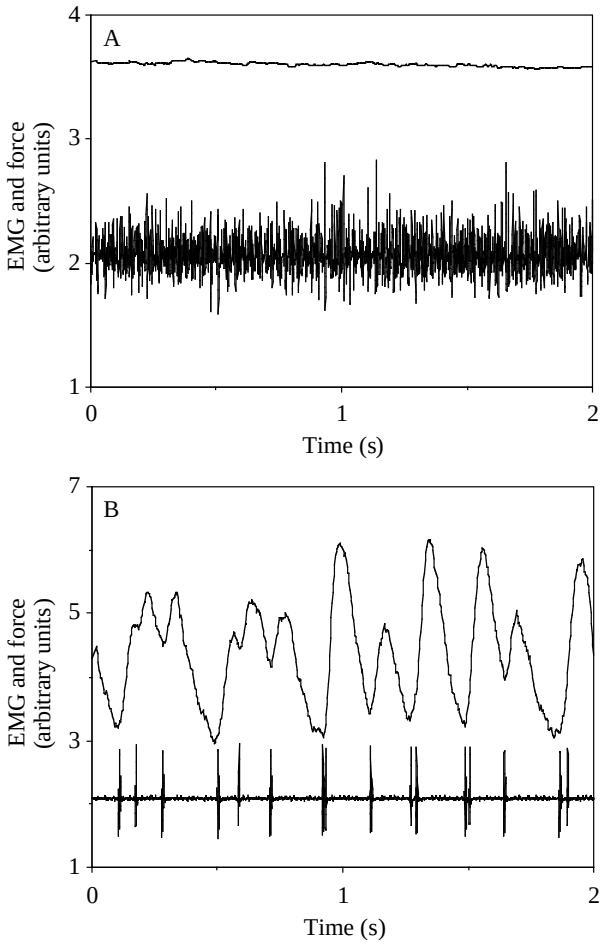


Fig. 1. Typical raw electromyographic (EMG) and force signals are shown in arbitrary units (A) when ten ventral root (VR) filaments were stimulated at high rates and (B) when a small number of VR filaments (e.g. three) were stimulated at low rates, both using pseudo-random interpulse intervals with a coefficient of variation of 12.5 %.

filaments on IEMG, mean force and IEMG–mean force relationship. The results shown in Figs 2 and 3 were obtained using the long protocol given in Table 1, whereas the results in Fig. 4 correspond to the short protocol (i.e. approximately trials 5–19 in Table 1).

Using the long protocol, IEMG appeared to saturate beyond trial 22 in one experiment (Fig. 2A) but not in the other (Fig. 3A). The mean durations of CMUAPs were estimated to be approximately 19±2 ms (S.D.) and 11±2 ms (S.D.) for the experiments shown in Figs 2A and 3A, 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 (Figs 2B and 3B). In the initial trials (i.e. trials 1–4 in Fig. 2B, and trials 1–5 in Fig. 3B),

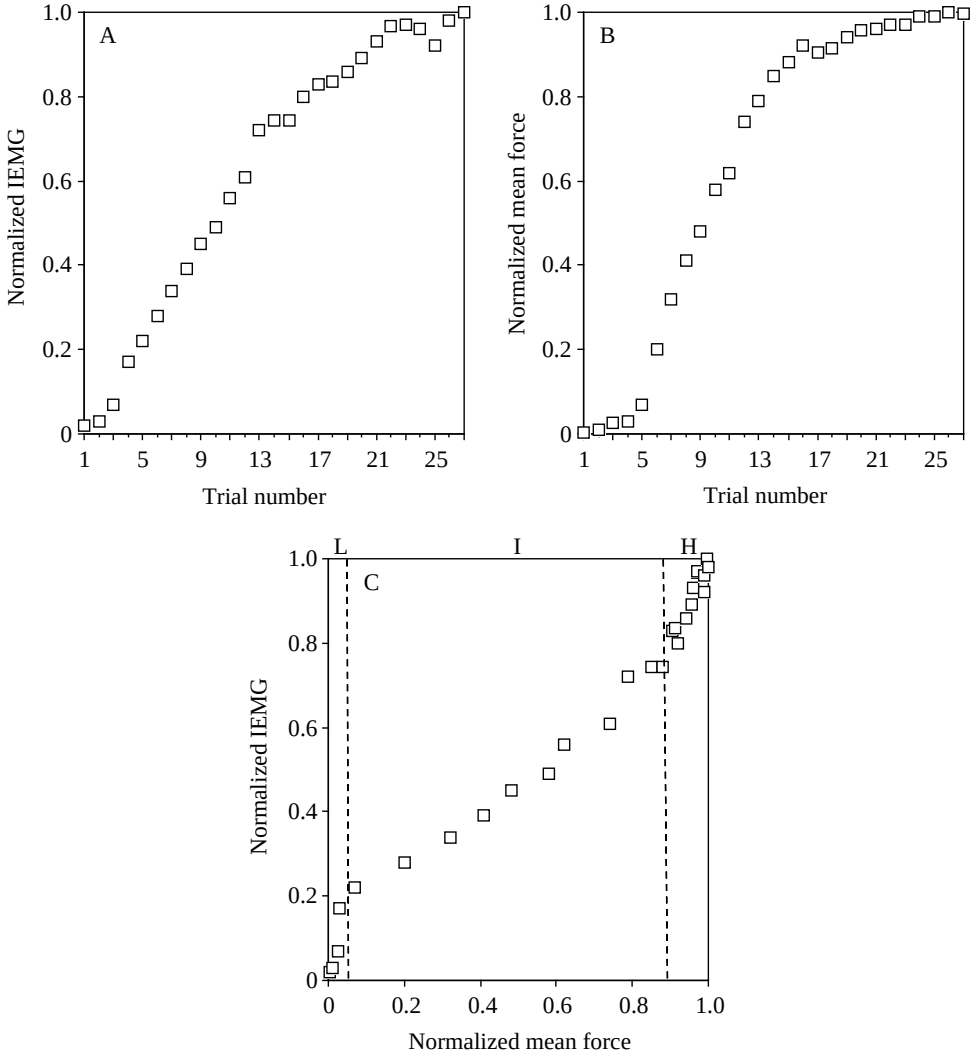


Fig. 2. (A) Integrated rectified EMG (IEMG) and (B) mean force responses to addition and rate modulation of VR filaments (i.e. trial number, Table 1) and (C) the corresponding IEMG–mean force relationship obtained from one experiment [three regions identified: low (L), intermediate (I) and high (H)]. IEMG and mean force were normalized relative to the highest values obtained. Maximal mean force measured was 23.3 N. Single VR filaments produced mean forces of 1.9–3.7 N when stimulated at 50 pulses $s^{-1}$.

mean force did not increase substantially with increasing stimulation. In the intermediate part of the protocol, however (i.e. trials 5–16 in Fig. 2B and trials 6–16 in Fig. 3B), mean forces increased substantially. Beyond trial 16 (i.e. for a range of mean stimulation rates of 15–29 pulses $s^{-1}$) increments in mean force decreased in both experiments. As a consequence of these results, the IEMG–mean force relationships

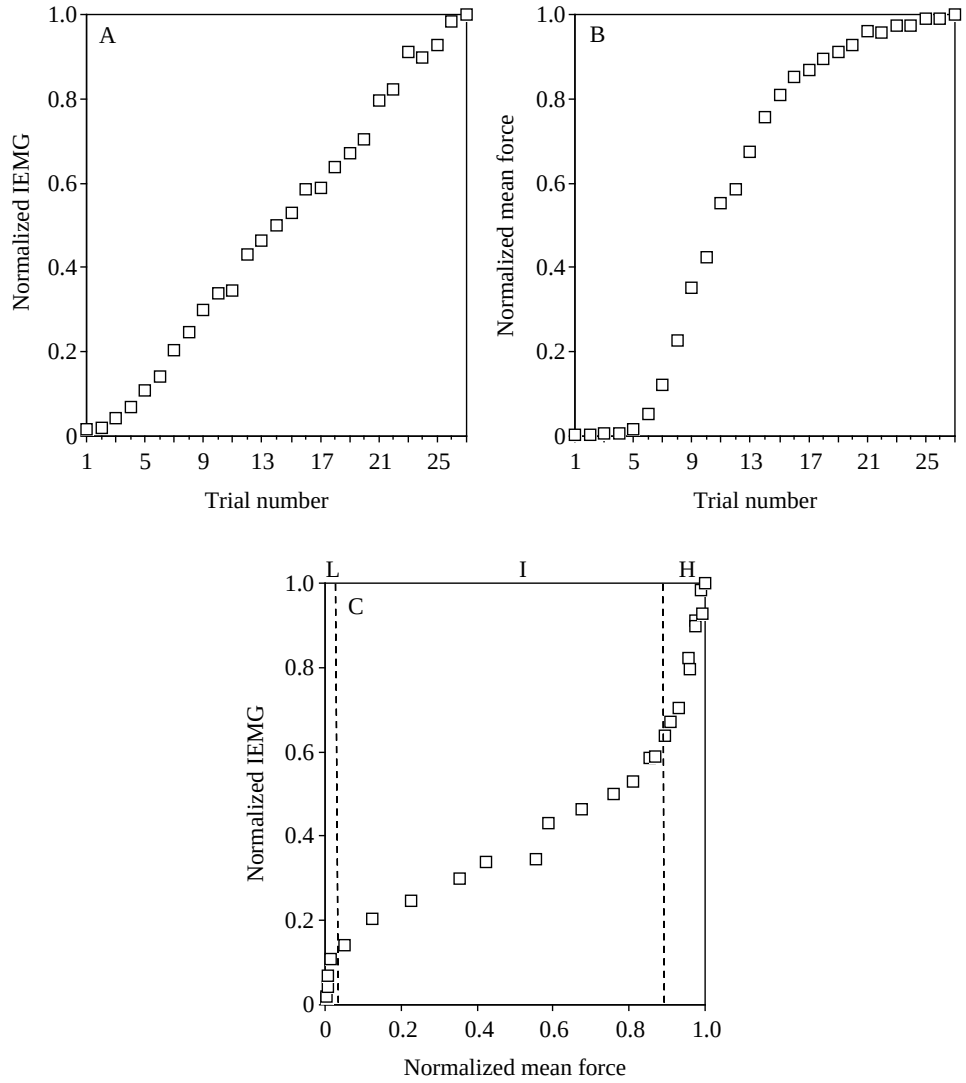


Fig. 3. (A) IEMG and (B) mean force responses to addition and rate modulation of VR filaments (i.e. trial number, Table 1) and (C) the corresponding IEMG–mean force relationship obtained from one experiment [three regions identified: low (L), intermediate (I) and high (H)]. IEMG and mean force were normalized relative to the highest values obtained. Maximal mean force measured was 29.3 N. Single VR filaments produced mean forces of 2.0–3.9 N when stimulated at 60 pulses $s^{-1}$.

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 (Figs 2C and 3C).

In the L and H stimulation regions, IEMG increased quickly compared with mean force; in the I region, mean force increased quickly compared with IEMG. In the I region,

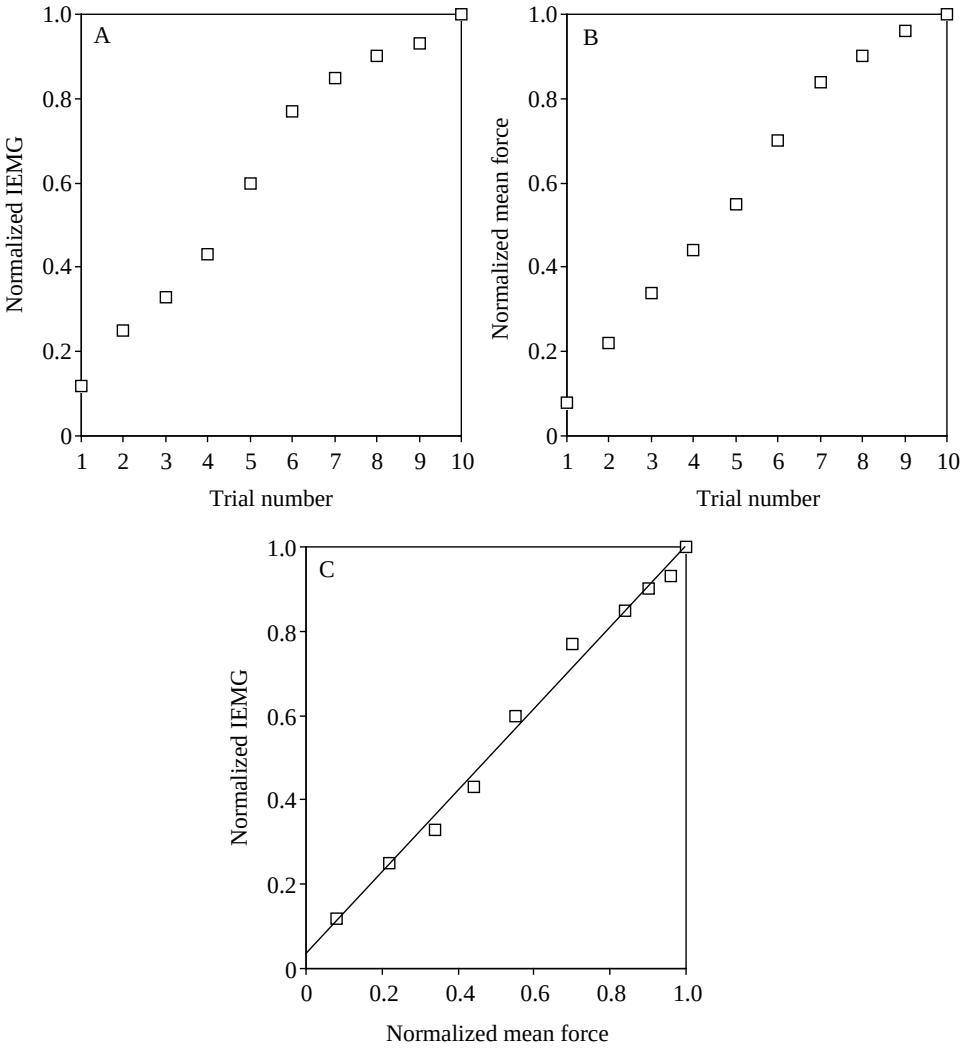


Fig. 4. (A) IEMG and (B) mean force responses to addition and rate modulation of VR filaments (i.e. trial number, short protocol) and (C) the corresponding IEMG–mean force relationship obtained from one experiment. IEMG and mean force were normalized relative to the highest values obtained. Maximal mean force measured was 35.6 N. Single VR filaments produced mean forces of 1.4–4.8 N when stimulated at 30 pulses $s^{-1}$.

the IEMG–mean force relationships could be approximated adequately with straight-line models ($r^2$=0.98 and 0.99 in Figs 2C and 3C, respectively).

Using the short protocol, IEMG (Fig. 4A) and mean force values (Fig. 4B) increased substantially from trial 1 to trial 7, showing signs of saturation beyond trial 7. The relationship between IEMG and mean force was approximately linear for this protocol ($r^2$=0.99 in Fig. 4C).

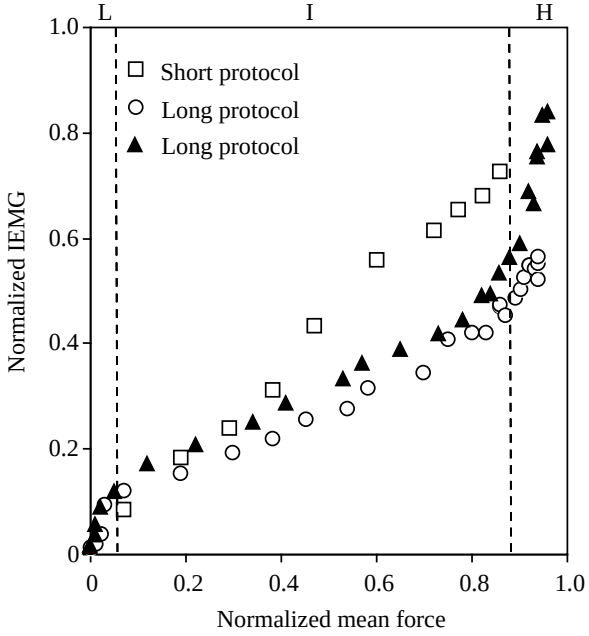


Fig. 5. Summary of IEMG–mean force relationships obtained from three experiments. Three regions are identified: low (L), intermediate (I) and high (H). Addition and rate modulation of ten VR filaments were implemented using the protocol in Table 1 in two experiments and its short version in one experiment. IEMG and mean force were normalized relative to values obtained when all ten VR filaments were stimulated simultaneously at 50 pulses $s^{-1}$.

In order to compare the IEMG–mean force relationships for the three animals shown in Figs 2, 3 and 4, all results were normalized relative to the values obtained in each experiment when all ten VR filaments were stimulated simultaneously at 50 pulses $s^{-1}$ (Fig. 5).

### *Addition of VR filaments*

Calculated IEMG and mean force values (obtained after raw signals of individual VR filaments had been added algebraically) are shown *versus* measured IEMG and mean force values (Table 1) in Fig. 6A,B, 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 pulses $s^{-1}$ are shown in Figs 7 and 8. IEMG was linearly related to mean stimulation rate for both VR filaments tested ($r^2$=0.99 in both Figs 7A and 8A).

The mean force response to changes in stimulation rate was similar for both VR filaments (Figs 7B and 8B). Mean force increments were large for increases in mean stimulation rates up to 25 pulses $s^{-1}$. Beyond 25 pulses $s^{-1}$, mean forces increased only

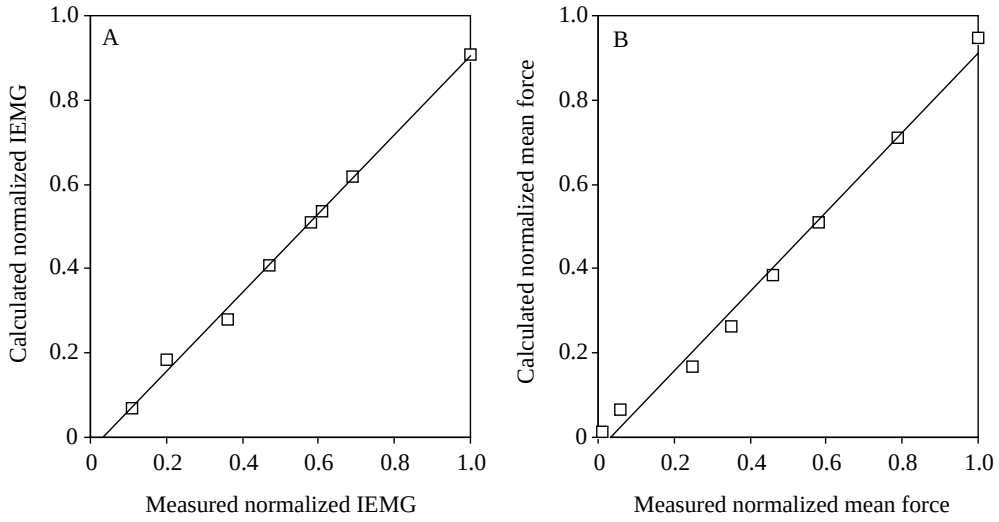


Fig. 6. Calculated *versus* measured (A) IEMG and (B) mean force. Calculated values were obtained after summing raw signals produced when single VR filaments were stimulated according to the protocol shown in Table 2. Measured values were obtained experimentally using the protocol shown in Table 2. Calculated and measured IEMG and mean force were normalized relative to their respective maximal measured values. Maximal mean force measured was 20.6 N; maximal mean force calculated was 19.5 N.

slightly (Fig. 7B) or not at all (Fig. 8B). Consequently, a non-linear IEMG–mean force relationship was found for both VR filaments, with IEMG increasing faster than mean force at high rates of stimulation (Figs 7C and 8C).

### *EMG–force relationship of isolated VR filaments*

Fig. 9A,B shows the relationship between the IEMG of single CMUAPs (extracted from raw data) and the corresponding tetanic forces obtained when VR filaments were stimulated at 50 pulses $s^{-1}$ (Fig. 9A) and 60 pulses $s^{-1}$ (Fig. 9B) in two different experiments.

## Discussion

Using a protocol for graded muscular contractions (i.e. stimulation) under isometric conditions (Table 1), we obtained a sigmoid relationship between IEMG and mean force (Figs 2C and 3C). 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 relationships (e.g. Close *et al.* 1960; Bigland-Ritchie *et al.* 1980). Therefore, the three different regions of the IEMG–mean force relationships (i.e. L, I and H, Figs 2C and 3C) that make up the sigmoid relationship found in this study must be explained.

The L region of the IEMG–mean force relationship (Figs 2C and 3C) produced forces below approximately 0.04 of maximal force and was characterized by a fast increase in IEMG and a slow increase in mean force. This finding could be associated with any of the

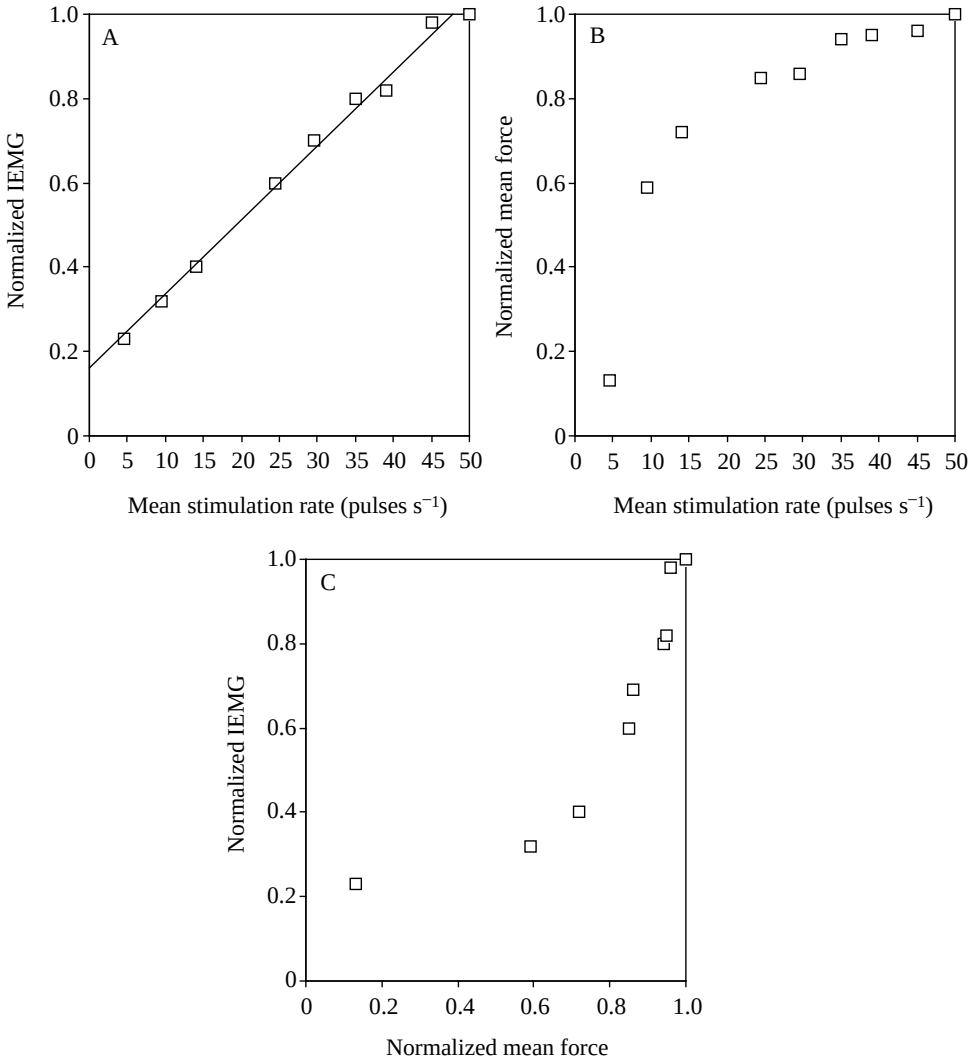


Fig. 7. (A) IEMG and (B) mean force response of a single VR filament as a function of actual mean stimulation rates and (C) the corresponding IEMG–mean force relationship. IEMG and mean force were normalized relative to the highest values obtained. Maximal mean force measured was 2.3 N.

following points. First, weak VR filaments (stimulated first) may produce disproportionately large IEMGs compared with 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 compared with large motor units. In our study, motor units were not recruited according to size, since the motor units contained in a VR filament could not be classified and separated. Possibly as a consequence of this design, no relationship was found between IEMG of

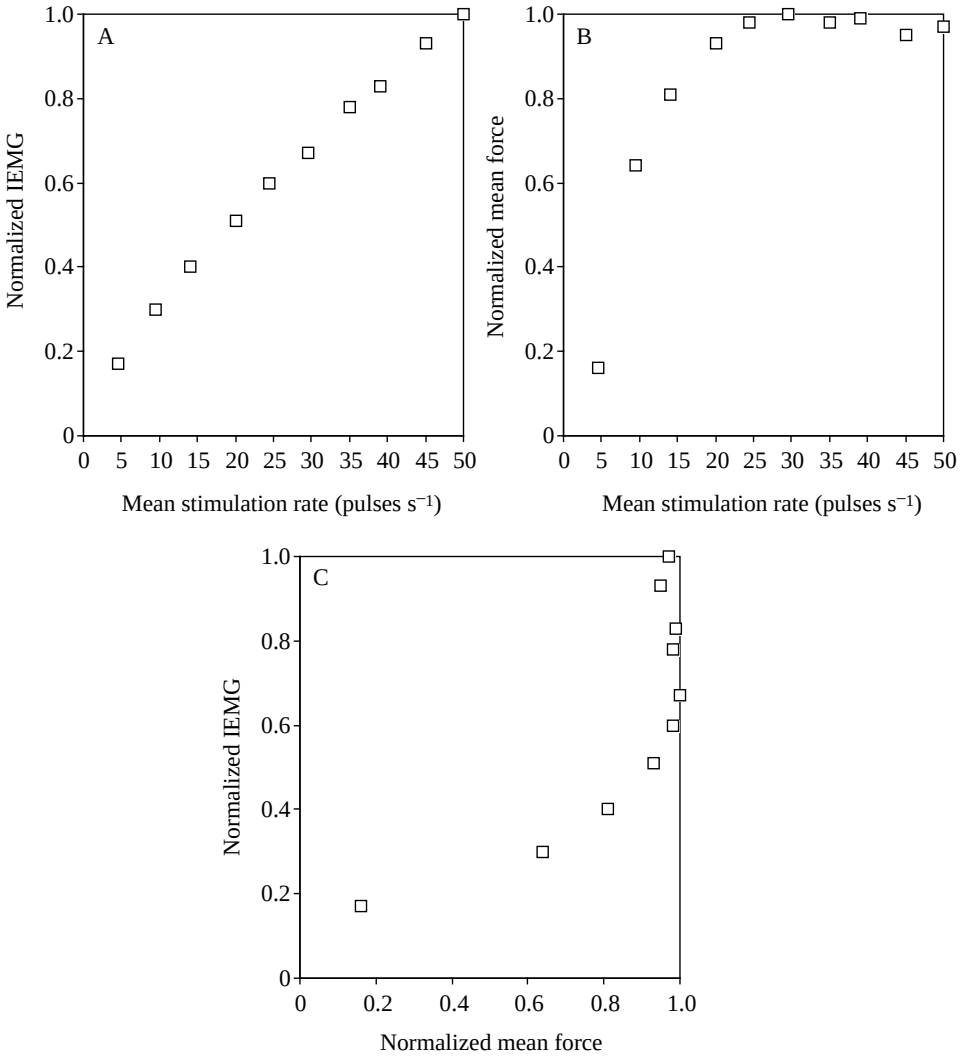


Fig. 8. (A) IEMG and (B) mean force response of a single VR filament as a function of actual mean stimulation rates and (C) the corresponding IEMG–mean force relationship. IEMG and mean force were normalized relative to the highest values obtained. Maximal mean force measured was 3.5 N.

single CMUAPs and tetanic force of VR filaments (Fig. 9A,B). Second, stimulating the VR filaments in rank order from weakest to strongest caused low force production in the initial trials compared with the final trials. Third, the initial four trials (Table 1) contained maximal stimulation rates (i.e. 5 pulses $s^{-1}$) that were lower than the initial firing rates that have been reported for motor units during voluntary contractions (i.e. 6–12 pulses $s^{-1}$, Burke, 1981). Such low stimulation rates may have reduced the effects of force summation observed for higher stimulation rates. We believe that the

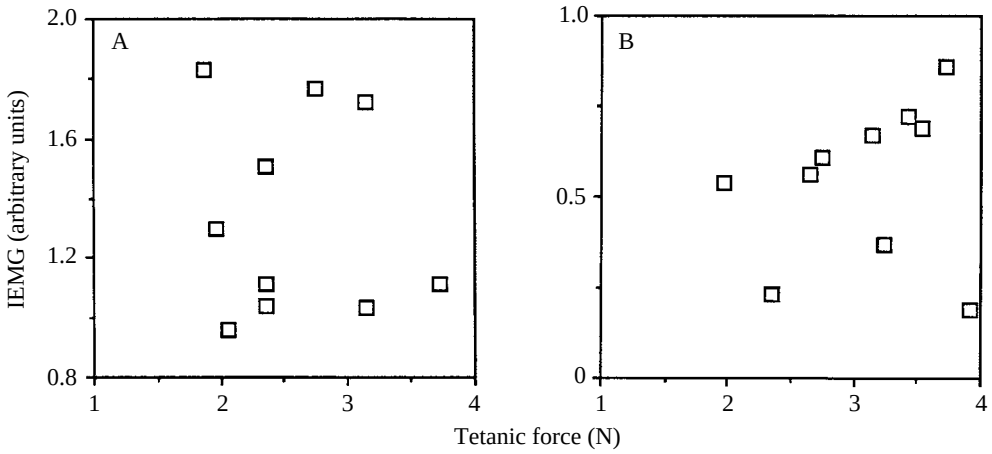


Fig. 9. IEMGs of single compound motor unit action potentials (CMUAPs) extracted from raw data *versus* tetanic force obtained when VR filaments were stimulated individually, corresponding to the experiments of (A) Fig. 2 and (B) Fig. 3.

combination of the two latter possibilities (i.e. weaker VR filaments being stimulated in early trials and at physiologically low rates) was the primary reason for the fast increase in IEMG and slow increase in mean force observed in the L region. Figs 7B and 8B support this argument in part, showing that mean force increased almost four times when stimulation rates increased from 5 to 10 pulses $s^{-1}$.

The I stimulation region of the IEMG–mean force relationship (Figs 2C and 3C) produced mean force values between approximately 0.05 and 0.88 of maximal force. This region also contains the results of all trials in Fig. 4A,B (obtained using the short protocol) and was virtually linear for all three experiments (Figs 2C, 3C and 4C). 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 (Figs 7A and 8A). The linear relationship between IEMG and rate of stimulation, in turn, was expected and is based on the observations that the shape, amplitude and duration of CMUAPs (and thus IEMGs) 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 relationship in the I region is also associated with the observation that IEMG and mean force values of individual VR filaments added algebraically (Fig. 6A,B).

Mean stimulation rates, did not relate linearly to mean forces produced by single VR filaments (Figs 7B and 8B), even in the region of concern here (i.e. below mean stimulation rates of 25 pulses $s^{-1}$). However, deviations from linearity below stimulation rates of 25 pulses $s^{-1}$ were small and so did not influence the linearity of the IEMG–mean force relationship in the I region appreciably.

The H region of the IEMG–mean force relationship produced mean force values above approximately 0.88 of maximal force (Figs 2C and 3C). 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 pulses $s^{-1}$. At this rate, mean forces (Figs 7B and 8B) but not IEMG (Figs 7A and 8A) 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 by the saturation of force. Depending on the duration of CMUAPs, saturation of IEMG may occur at high stimulation rates. Relatively long durations of CMUAPs produced some saturation in IEMG in one experiment (Fig. 2A). This saturation, however, was not sufficient to prevent the change in the relationship between IEMG and mean force from the I to the H region. Therefore, the results of the H region of the IEMG–mean force relationship can indeed be explained primarily on the basis of saturation of force levels, since the mean stimulation rate calculated for all VR filaments exceeded 25 pulses $s^{-1}$.

As discussed previously, the IEMG–mean force results corresponding to the L region (Figs 2C and 3C) were obtained using mean stimulation rates 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 60–75 % 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.

Neglecting the IEMG–mean force relationship found here for the L and H regions on the basis of the preceding arguments, our results suggest that the IEMG–mean force relationship of the cat soleus muscle is linear within the physiological limits of stimulation variables and force production.

Results from three experiments showed a linear relationship between EMG and force for the range of stimulation rates that is likely to occur during voluntary movement. We believe that the actual shape of the IEMG–mean force relationship 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, because of an increased amount of overlapping of motor unit action potentials. An earlier and more pronounced saturation of IEMG could cause the IEMG–mean force relationship to remain linear even beyond the end of the I region (Fig. 5) 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 Figs 2A and 3A, respectively) may have compensated, to some extent, for 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 and 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. The onset of action potentials of different motor units is probably 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 in 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 with 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 relationships obtained here for the I region.

Independent stimulation of VR filaments and pseudo-random interpulse intervals were used to assess the EMG–force relationship of the cat soleus muscle. This technique allowed for simulation of motor units firing patterns in accordance with findings from studies using voluntary contractions. Physiological 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 reduced by studying a muscle that is known to contain motor units of relatively uniform size. Under these conditions, the EMG–force relationship 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 the electromechanical properties of skeletal muscle.

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