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TETANIC TENSION AND MUSCLE LENGTH OF MOTOR UNITS IN CAT'S PERONEUS LONGUS

G. M. FILIPPI AND D. TROIANI

Istituto di Fisiologia Umana, Università Cattolica del S. Cuore, Largo F. Vito 1, 00168 Roma, Italy

INTRODUCTION

Muscle tension is related to muscle length as demonstrated by studies on the whole muscle (8) and on isolated muscle fibers (5). It is conceivable that the same ratio may also be applied to single motor units; however, only few, old and contradictory reports (1, 6, 7, 12) are available on the performance of single motor units at different muscle lengths. Usually the length at which the whole muscle develops its maximal twitch tension is considered coincident to the optimal length of the different motor units. We reinvestigated the topic and a first group of results was presented (4). In this paper we showed that length-tension curves obtained by applying single shocks to single motor units are shifted to longer muscle lengths compared to the whole muscle contraction. In the present paper active length-tension curves were built by using tetanic stimulations and the results are compared with the precedent ones.

METHODS

Experiments were carried out on 7 adult male cats, weighing 1.5-3 Kg. The animals were anesthetized with Nembutal in peritoneum initially (40 mg/Kg) and supplemental doses were provided i.v. when necessary. Blood pressure was monitored and body temperature was maintained at 38°C. The peroneus longus (PL) muscle was exposed and its length was measured at different functional articular angles. Then the ankle was blocked in order to avoid movements during motor unit contractions.

The hindlimb muscles were denervated, sparing the PL muscle whose nerve was isolated by microdissection, the tendon was cut and attached to isometric tension transducer (GRASS FT-03). The muscle and nerve were kept in a pool filled with paraffin oil maintained at 37°C temperature.

After laminectomy the lumbosacral cord was exposed and the dorsal and ventral roots were cut and protected in a pool of paraffin oil. L_7 ventral root was mounted on Ag-$AgCl_2$ electrode which was used as anode, the cathode being the body animal. An active length-tension curve was constructed by stimulating L_7 ventral root and it has been judged a complete survey of PL motor units considering the large number of alpha axons innervating PL contained in this root. The stimulation was performed by using single pulses, duration 0.05 ms, intensity 1.5 times the voltage necessary to induce the maximal contraction, at muscle lengths ranging between the minimum and maximum (steps ranged from 0.5 to 1 mm) ankle angles. For each length three twitch responses, separated by intervals of 13 s, were recorded and averaged to measure the twitch tension. As described for many muscles (8), also in present experiments the peaks of the curves coincided with the length at which all muscle slack components were removed and passive tension drastically increased.

The ventral roots were then split under oil into filaments and functionally isolated axons were identified according to the technique described in previous papers (9, 10). For each isolated motor unit a length-tension curve was built by applying a 0.5 s pulse train at a frequency of 125 Hz (10), 0.05 ms pulse duration and with a pulse intensity twice the threshold value to induce an evoked «all or none» response in the PL nerve.

At the end of experiments the motor unit types were identified as Slow (S), Fatigue Resistant (FR), Fast Fatiguable (FF) or Fast Intermediate (FI) according to the criteria (fatigue resistance and presence of «sag») introduced by Burke *et al.* (2).

All recorded data were digitalized off-line, and then analyzed.

RESULTS

Isometric tension developed by single motor units during tetanic stimulation was plotted as a function of muscle length. All the reported active length-tension curves were compared at the optimal length of the whole muscle at which the twitch contraction of PL muscle developed the maximal tension following stimulation of L_7 ventral root (*Lo*). Different results were obtained for Fatigue Resistant (FR) and Fast Fatiguable (FF) and Slow (S) motor units, and for tetanic or single twitches stimulations.

1. *Length-tension curves of Slow motor units.* — Data concerning S units are shown in Fig. 1A. Four S motor units, belonging to Exp. 3 and developing maximal

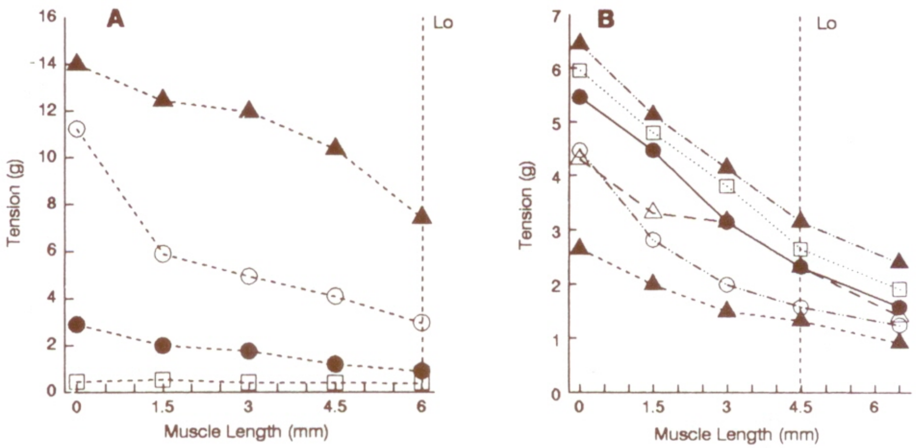

Fig. 1 – *Length-tension curves relative to 4 Slow motor units (A) and to 6 Slow units (B) studied in two different experiments.*

Each tension value was obtained by tetanically stimulating the correspondent alpha-axon with a train lasting 0.5 s, frequency 125 Hz, pulse width 0.05 ms, intensity twice the threshold value. *Lo* indicates the muscle length at which the whole muscle twitch contraction developed its maximal tension. Ordinates: peak tension in grams. Abscissae: muscle length in millimeters.

tetanic tension ranging between 0.52 and 14 g, presented their optimal length clearly below the length at which the whole muscle showed the maximal twitch tension (*Lo*). Only one unit (open squares) had its optimal length in the studied range (4.5 mm below *Lo*), the other three units exhibited their tension peak at lengths lower than *Lo*-6 mm. In this experiment, the minimum reported length (indicated by 0 mm in Fig. 1A) was 3.5 mm below the minimum physiological value.

In Fig. 1B, other 6 Slow units, studied in Exp. 4 developing tetanic tensions in a smaller range (2.6-6.4 g) than units of Fig. 1A, showed only the descending limb of their length-tension curves, being their optimal length presumably lower than *Lo*-4.5 mm. In this experiment PL muscle was shortened 2 mm below its minimum length value as measured on the normally inserted muscle.

2. *Length-tension curves of Fatigue Resistant and Fast Fatiguable motor units.* — The results obtained by the FR and FF motor units, which showed their optimal length at values nearer to *Lo* differed from these reported for the S units, as shown in Fig. 2, where the units were collected from the same experiment as in Fig. 1A. The peak of the length-tension curves, was within the analyzed range of lengths, although lower than *Lo*.

3. *Comparison between the Fatigue Resistant and the Fast Fatiguable and the Slow motor units' length-tension curves.* — The two groups of motor unit types (FR + FF and S motor units) presented also different shapes of their length-tension curves.

Concerning the Slow units, in most cases only the descending limb of the length-tension curves was analyzed and it generally showed a steep decrease of tension by increasing the muscle length. When very short muscle lengths, largely below

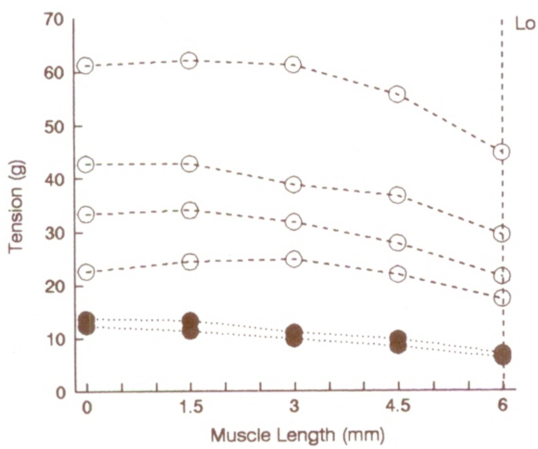

Fig. 2 - *Length-tension curves relative to 4 Fast Fatiguable motor units (open circles) and to 2 Fast Resistant motor units (closed circles).*

Stimulation parameters, abscissa and ordinate as in Fig. 1.

the minimum physiological value, were tested, the ascending limb of the curves was also analyzed and it resembled the descending one. The shapes of the curves, shown in Fig. 1A and B, are better evidenced in Fig. 3A and B, where the tension values of the two corresponding plots of Fig. 1 are expressed in percentage values. At the muscle length of 6 (Fig. 3A) and 6.5 mm (Fig. 3B), the tension was quite linearly reduced, to reach mean values of about 45% and 40%, respectively, of the peak value.

FR and particularly FF units presented different shapes of length-tension curves which appeared flat, both in the ascending and descending limb of the curves. Such a behavior, observed in Fig. 2, is even more evident in Fig. 4, where the normalization of values allows a better comparison between the different units. After 4.5 mm of muscle stretching, the tetanic tensions were reduced to 80% (FR) and to 90% (FF) of the initial values and, after 6 mm, to 50% (FR) and 72% (FF).

The results obtained from experiments in which the motor units' tetanic tension was studied are reported in Fig. 5. The histogram illustrates the tested motor units, divided in four groups, according to Burke's classification (2), and showing their distribution according to their optimal length. Slow motor units showed their peak at muscle lengths largely shorter than *Lo* and for 50% of the tested S units their maximal tension was recorded at muscle lengths 5-6 mm lower than the whole muscle optimal length (*Lo*). FR and FF motor units appeared more uniformly distributed along the scale of the muscle length, with a slight prevalence of FF units between *Lo* and -3 mm. However, as shown in the previous figures, for some units, particularly S units and some FR, the peak tetanic tension was

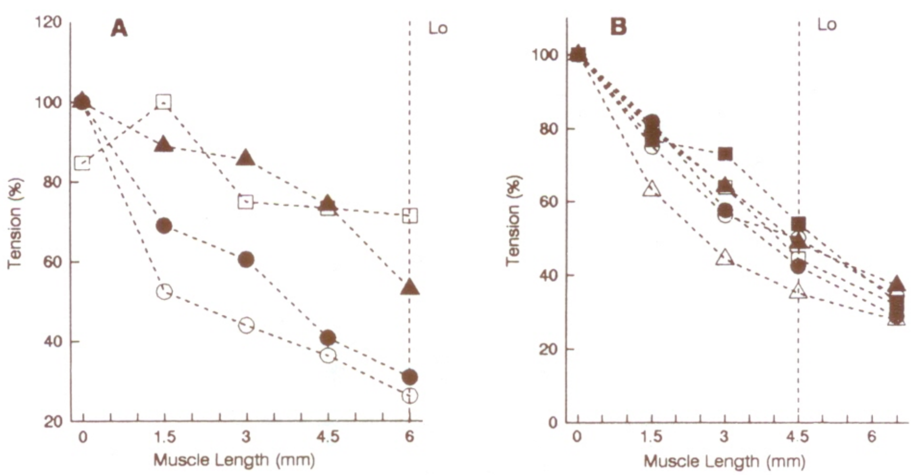

Fig. 3 – *Length-tension curves relative to 4 Slow motor units (A) and 6 Slow units (B) studied in two different experiments.*

Same units and stimulation parameters as in Fig. 1A and B. Ordinates: peak tension values normalized to their maxima. Abscissae: muscle length in millimeters.

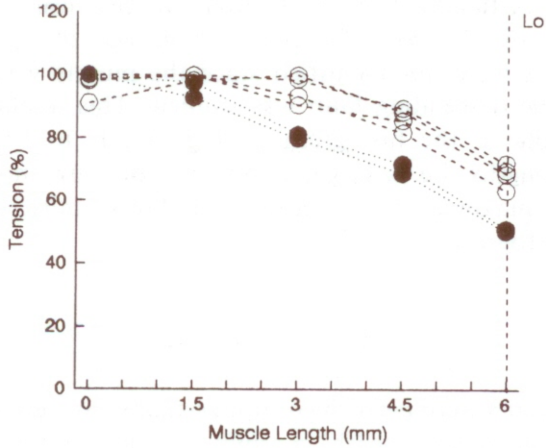

Fig. 4 – *Length-tension curves relative to 4 Fast Fatiguable motor units (open circles) and 2 Fast Resistant motor units (closed circles).*

Same units and stimulation parameters as in Fig. 2. Ordinate: peak tension values normalized to their largest amplitude. Abscissa: muscle length in millimeters.

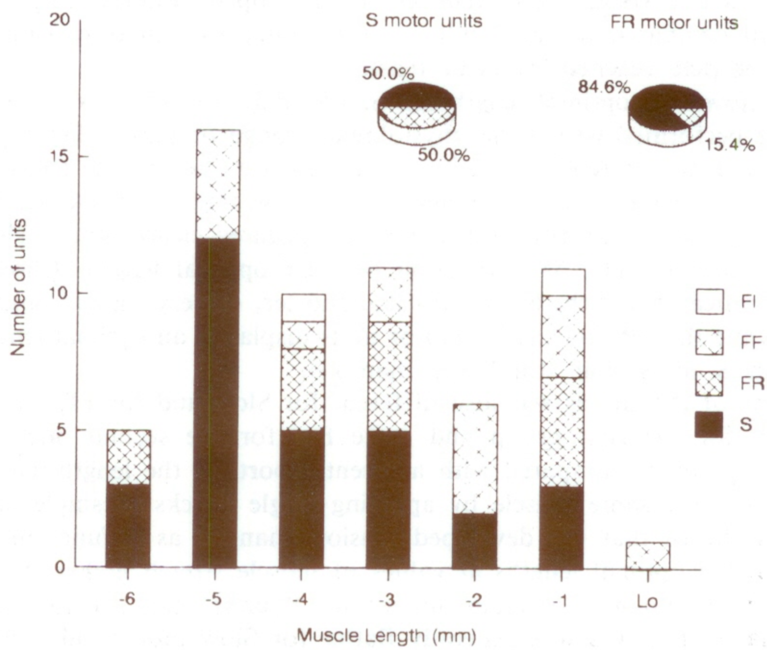

Fig. 5 – *Distribution of the optimal length for all the studied motor units.*

For each motor unit type, Slow (S), Fast Resistant (FR), Fast Fatiguable (FF) and Fast Intermediate (FI), the distribution of their optimal length is indicated. *Lo* represents the optimal length of the whole muscle. In the inset, the pie diagrams show, for the two populations of the tested Slow and Fatigue Resistant motor units, those groups (narrow crosshatch area) for which it was impossible to identify the peak of their length-tension curves.

not identified with certainty. The pie diagrams in the inset of Fig. 5 show that for 15 S units out of 30 and 2 FR motor units out of 13 the peaks of their length-tension curves were not identified since the muscle was too slack and for these curves only the descending limb was studied. This implies that the position of these motor units in the histogram of Fig. 5 has to be considered shifted at shorter muscle lengths, i.e. a larger population of Slow motor units and some FR developed their maximal tetanic tensions at shorter muscle lengths than those reported in the histogram.

DISCUSSION

The present experiments were performed to investigate the dependence of the motor unit force output on muscle length, a topic on which only a few reports have been so far published, as reported recently by Kernell (6). In order to allow a comparison of the present data with those reported in the literature, the motor units were characterized according to the now commonly used Burke classification (2).

The tetanic tension developed by single motor units, functionally isolated from PL muscle, was recorded at different muscle lengths. For each unit the muscle length at which maximal tetanic tension was developed (optimal length) was investigated and compared to the length (*Lo*) at which the length-tension curves of the whole muscle reached its peak tension.

Results show that optimal length for S, FR and FF units was lower than *Lo*. Trials were performed within the physiological range of muscle length, evaluated with the distal muscle tendon still inserted. However the off-line analysis of data showed that, in some cases, particularly for Slow units, optimal length had to be at a shorter muscle length, even if muscle appeared clearly slack. The distribution of the motor units, as a function of their optimal lengths (shown in Fig. 5), clearly indicates that the Slow units had shorter, or very shorter optimal length than *Lo*, while the FR and the FF motor units displayed an optimal length slightly longer than S units, but still lower than *Lo*.

The shape of the curves was also different for Slow and for FR plus FF units, being steep for the first group and quite flat for the second one.

These data can be compared with a recent report on the length-tension curves obtained from the same muscle by applying single shocks to single motor units (4). It was shown that the developed tension changed as a function of muscle length, showing optimal lengths at values of muscle stretch higher than *Lo*. The distance beyond *Lo* was generally longer for S units than for FR or FF units and the shape of curves was generally flatter for Slow motor units than for FR and FF ones.

It appears, therefore, that the two extreme values of frequency stimulation for alpha motor axons, i.e. single shocks and tetanic frequency, induce drastic changes in the length-tension curves, by shifting them along the «Y» and «X» axis. Old reports on the whole muscle stimulation (11) evidenced a progressive decrease in the optimal length values by stimulating the whole muscle at progressively higher frequencies. Moreover our results are in agreement with old reports showing different optimal lengths for tetani and twitches, the former being generally indicated as being shorter than the latter (1, 6, 7, 12).

Even if we attempted in our experiments to minimize passive components (see Methods), it must be supposed that these components are still largely operating, being the tetanic length-tension curves very different from those constructed by using single shocks (4). The drastic shift of the optimal lenghts to low or very low values produced by tetanic stimulations and the different shapes and optimal length values of the length-tension curves of FR and FF and S units suggest that mechanical muscle components might be also relevant in determining the resulting tension at the different lengths. Thus, the usually accepted idea that, during tetanic stimulation, the muscle or the group of muscle fibers reach their maximal degree of activation (3) could be, at least in our experimental conditions, reexamined because of the interaction of other factors.

Furthermore, the drastic increase of frequency stimulation (from single shocks to 125 Hz) suggests that the frequency of motor command to the muscle fibers could change their performance at different muscle lengths. Moreover, even if the discharge rate of the alpha motor neurons greatly differs under normal conditions from those induced by our stimulation, it is likely that at intermediate frequencies the optimal length of single motor units might be still different from the length values evidenced in our experiments. From a functional point of view the different mechanical performances of single motor units at different muscle length could have a relevance in the task-related motoneuron recruitment pattern, as recently suggested (6).

SUMMARY

Length-tension curves were constructed by stimulating tetanically single motor units belonging to the peroneus longus muscle. The lengths at which the motor units showed the maximal tension appeared to be shorter than the length at which the whole muscle developed the maximal twitch tension. Moreover, the optimal lengths appeared to be different for the different motor unit types, corresponding to very short muscle lengths for Slow units and to slightly higher lengths for the Fast Fatiguable and the Fatigue Resistant units.

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