Influence of Muscle Length on Maximal Rate of Tension Development in Frog Skeletal Muscle

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Abstract

The effect of muscle length on parameters concerning the force generating processes at both the early tension development and the subsequent tension plateau phase in isometric tetanic contractions was studied in whole-muscle preparations of frog sartorius. The maximal rate of tension development (dP/dt_{max}) and the peak tension (Po) were measured at lengths ranging from 70 to 120% of the optimum length for tension generation (Lo). The length–peak tension relation agreed with those reported for single muscle-fibers. The length–dP/dt_{max} relation appeared to be similar to the length–peak tension relations in that they showed a maximum at Lo, but had steeper ascending limb. Greater values of Po-to-dP/dt_{max} ratio at lengths far shorter than Lo indicated that higher peak tension was produced than expected from the preceding tension rising phase at these lengths. The results were discussed at both macroscopic and microscopic levels.

Introduction

In isometric tetanic contractons, the force generating process consists of two phases;*i.e.*, the early tension development, and the following steady state with maintained tension.

To characterize the early tension rising phase, the rate of tension development has often been investigated. Some studies have made an attempt to use it as a substitutional index for the maximal velocity of shortening (V_{max})[6,43], while others have used it more frequently to compare the contractile properties of different types of muscle fibers[5,6,45], and to describe functional changes of muscles under various conditions, such as those following fatigue[11,17,18,21], disuse[16,46] and exercise training[17].

In many of these studies, the rate of tension development has been regarded as a parameter representing "the contracting speed of the muscle", because it presumably relates to the speed of motion. In the isometric contraction, however, what the rate of tension development actually means is the tension generated per unit time, so that it would not necessary represent the dynamic properties of muscle. Contrary, it would give important information about the force generating processes during the early phase of the isometric contraction.

From the early studies[2,14,37], the phenomenon that peak tetanic tension measured during a steady phase of isometric contraction varies as a function of muscle length is well known as the length–tension relationship. In contrast, there have been few studies[12,42,47] which examined the tension generating capacity during the early tension rising phase over a wide range of muscle length.

The purpose of this studey is to learn the effect of muscle length on the rate of isometric tension development during the early tension development and to compare it to that on the peak tension attained in the following steady state.

Methods

Materials and Apparatus

A pair of m.sartorii of *Rana catesbeiana* (270-350g body wt. ; NIPPON BIO-SUPPLY CENTER, Tokyo) was dissected out with both their attachments to the pelvic bone and the innervation of sciatic nerve left intact. Paired muscles were fixed together vertically, with distal tendons clamped closely to the end of muscle fibers as possible, while the fragment of pelvic bone was immobillized on a lower clamp with a bolt. Muscle length was measured with a caliper as the distance between both ends of fibers, which were visually determined. The upper clamp was connected to a force transducer (Model UT-1K ; SHINKOH TSUSHIN ; natural frequency of oscilation, 980Hz), and the muscle length was changed by displacing the transducer with a micrometer at a minimal step of 0.01mm.

Muscles were placed in a bath containing Ringer solution (95.0mM NaCl, 2.5mM KCl, 20.0mM $NaHCO_3$, 1.0mM $CaCl_2$, 1.0mM $MgCl_2$, and 5mM glucose, pH=7.2) aerated with 95% O_2-5%CO_2. The temperature of the solution was maintained at 12.0±0.5℃. Trunks of sciatec nerves were hung gently above the solution by hook-shaped Ag:AgCl electrodes and kept wet throughout the experiment by dripping the solution on them.

Stimulation

Electrical stimulations with the trains of rectangular pulses of 0.1-0.2ms duration were given at a supramaimal intensity by an electronic stimulator (Model SEN-7203 ; NIHON KOHDEN) via sciatic nerve at intervals of 15 to 30min. Muscles were repeatedly stimulated at a frequency of 50Hz for 800-1,000ms until reproducible isometric contractions were observed. At this frequency, both tension and tension differentiated

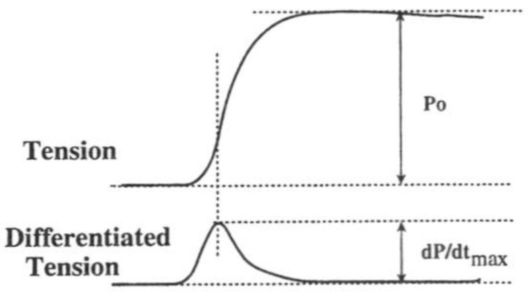

Fig.1 Recording parameters.

recordings did not show any visible ripple.

In each series of experiments, several contractions before being fully equilibrated were excluded from analysis, and the first analyzed record was used as a control for fatigue.

The effect of fatigue was carefully examined by stimulating the musle at the initial length every seven contractions to compare tension with that of the control. If there appeared any sign of fatigue such as the reductions in peak tension, rate of tension development and/or rate of relaxation, the period of time to rest the muscles was prolonged and the control contraction was re-examined. When the decay of the peak tension reached 5% of the initial peak tension, the preparation was discarded.

Data Recording

Measurements at various lengths were made in a random order but data at near the optimum length of tension generation (Lo) were obtained precedently than at other lengths to avoid irreversible damage of the muscle (dalta state[37]). Data from 12 preparations were analyzed. Tension records from individual tetanus were amplified and digitized with A/D converter (Model DM-7000 ; IWATSU) at a sampling rate of 0.5ms, and stored on disk. Stimulation signals were also digitized and stored simultaneously. A custom software was used to measure the peak tetanic tension (Po) in each digitized tetanus. The maximum rate of tension development (dP/dt_{max}) was also obtained from the positive peak of differentiated tension (Fig.1).

For normalizing Po and the dP/dt_{max}, muscle cross–sectional area (CSA) was estimated by dividing the muscle weight with the product of muscle fiber length at Lo[7,47] and density. Fiber length was determined by multiplying Lo by fiber-to-muscle length ratio of 0.9[7], and the density was assumed to be 1.056[33].

$$\mathrm{CSA}=\frac{\text{muscle weight}}{\text{muscle fiber length}\times\text{density}}=\frac{\text{muscle weight}}{\mathrm{Lo}\times 0.9\times 1.056}$$

Muscle lengths were normalized for Lo.

The values in text and table are expressed as mean ± SE.

Results

The frog used in the present study, *Rana catesbeiana*, had large sartorius muscles (744.3±46.3mg), which therefore, exerted the five to tenfold greater Po (4.41±0.21 N) at Lo than in other species of frog. When normalized, Po and dP/dt_{max} at Lo were 32.66±0.61 N/cm² and 456.34±23.68N/cm²/s, respectively.

The values of mean Po per unit CSA thus far reported for muscle or muscle fiber are around 25N/cm² [10,15,19,27,31], with a large deviation[13]. Furthermore, the normalized Po values in whole muscle preparations appear to deviate a greater deal (*e.g.*, ranging from 439 to 831 g/gwt in 'control' muscles in ref. 36) and our data were all within this range. Values for Po similar to ours were reported in frog sartorius 〔3.325±0.265kg/cm²〕[8], frog semitendinosus 〔3.7kg/cm²〕[9] and mouse foot muscle 〔375±56kPa〕[29].

There are few reported values of dP/dt_{max} which can be used for the comparison with ours because it is sensitive to temperature[12,38,39,41] and pH[39,43]. The dP/dt_{max} value of 43.88±2.81kg/cm²/s for toad sartorius[43] under the

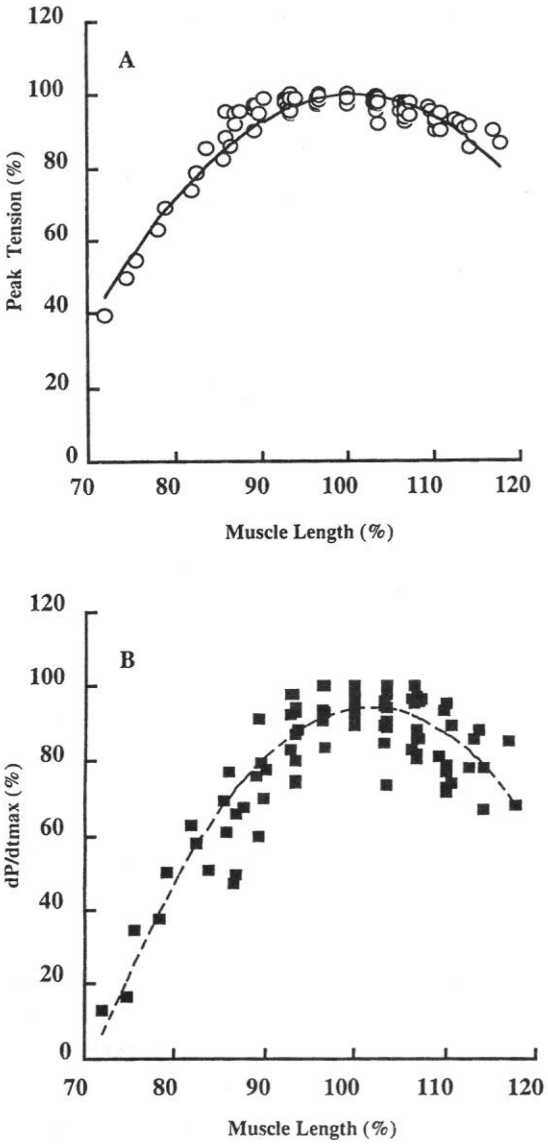

Fig.2 (A) length−peak tension and (B) length−maximal rate of tension development relations from 12 muscles. Values of peak tension (○) and the maximal rate of tension development (■) have been normalized in each preparation to their highest values, respectively, obtained at Lo. Lines are regression curves for all data (n=97).

similar condition (at 15℃, pH=7.0) was smaller than ours by about 15%. When dP/dt_{max} was expressed as relative to peak tension[22], the present study gave 1.39%Po/ms, which was similar to the value previously reported for rat EDL at 15℃ (ref.12, Fig 1).

Fig. 2A shows the length−tension (L−%Po) relations obtained from 12 muscles in which Po were normalized with respect to the maximal tension in each preparation. The shape of the L−%Po curve was similar to those reported for whole skeletal muscles of frog[2,14].

The relation between length and $\%dP/dt_{max}$ ($L-\%dP/dt_{max}$) obtained from the same preparations is shown in Fig.2B, in which dP/dt_{max} were normalized with respect to the maximal rate of tension development in each preparation. $\%DP/dt_{max}$ was also a function of length as did tension, and exhibited the highest value at Lo.

The optimum length for $\%dP/dt_{max}$ was within ±3% of Lo determined from the L−%Po for each preparation. No significant difference was shown between these two optima by the paired t-test ($p>0.05$).

Fig. 2A and B showed that the $L-\%dP/dt_{max}$ curve is steeper at both sides of Lo than L−%Po curve. Since no difference in length dependency was observed between Po and dP/dt_{max} in twitch contractions[28,45], the difference observed in the present results could be derived from the repetitive stimulation in tetanic contractions.

To quantify their length dependency, both the L−%Po and the $L-\%dP/dt_{max}$ relationships were subjected to least-squares regressions to the following polynomial equation :

$$y=Ax^2+Bx+C \quad (1)$$

where y is $\%dP/dt_{max}$ or %Po, x is normalized muscle length, and A, B and C are constants.

The values of constant A, index for the curvature, for the $L-\%dP/dt_{max}$ and the L−%Po curves were −0.100±0.007 and −0.068±

Table 1. Values of the constants of A, B, and C for regression curves of L-%dP/dt_{max} and L-%P_o.

	A	B	C	R2
length-%dP/dt_{max}	-0.100 ±0.007	20.33 ±1.33	-938.66 ± 63.59	0.7932 (n=97)
length-%P_o	-0.068 ±0.003	13.68 ±0.49	-585.91 ± 23.32	0.9160 (n=97)

Values are means + standard error of the mean (SE).

0.003, respectively (Table 1). Two-sample test for the equality of the regression coefficients revealed that the constant A of regression curve was significantly greater in the L−%dP/dt_{max} curve than in the L−%Po curve ($p<0.005$). This implies that dP/dt_{max} depends more strongly on muscle length than does Po.

When the ratio between Po and dP/dt_{max} in the same contraction was plotted against muscle length, it was smallest around Lo and increased at lengths distant from Lo, especially at shorter lengths (Fig.3).

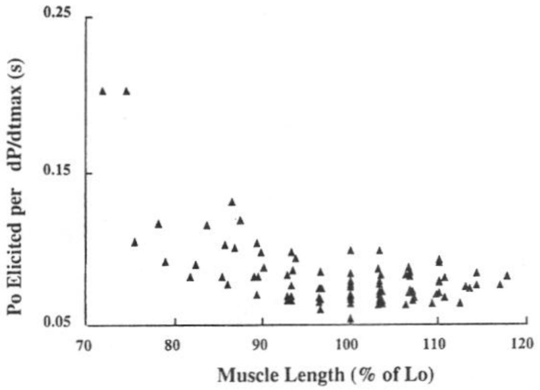

Fig.3 Ratios of peak tension and maximal rate of tension development at various lengths in 12 muscles. Note that the ratio is greater at distant lengths from the optimum length (Lo).

Discussion

When the length of muscle fibers (L_f) is less than the overall length of muscle (L_m), a length change in whole muscle would cause a greater length change in muscle fibers with a inverse factor of L_f/L_m. For example, 10.0% length change from Lo in a whole muscle would cause 11.1% length change in muscle fibers, assuming the mean L_f/L_m ratio is 0.9 (Fig. 4). Thus, relative muscle lengths in the present study could be re-calculated into relative muscle fiber lengths (L_f) by dividing the length changes from Lo by 0.9[8]. The L_f−%Po curve obtained in this way was found to be in good accordance with the sarcomere length−tension curve (Gordon et al. ; 1966)[20] when their sarcomere lengths were normalized to the midst among the range of optimal lengths, 2.125μm (Fig. 5).

In most of previous studies which investigated the influence of muscle length on the mechanical properties of isometric tetanic contractions, only peak tension values have been focused on. The present results indicated that the muscle length also affects the maximal rate of tension development.

A few studies have observed the length dependence of dP/dt_{max} of isometric tetanic contraction in a single motor unit[42] and in a whole muscle stimulated by either direct[12] or indirect[42,47] stimulation. On the other hand, Julian and Morgan (1979)[26] reported that the

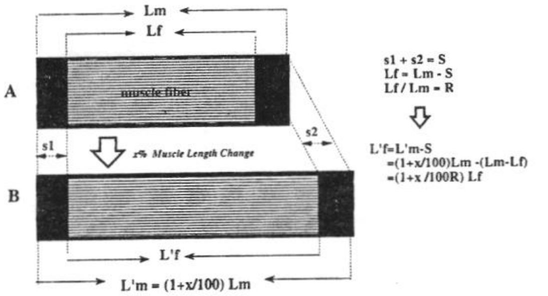

Fig.4 Schematic diagram illustrating length change of muscle fiber within a muscle. A), The standard muscle length (L_m) at witch the lengths of non-fiber components (s_1, s_2, and S as a total) and the muscle fiber to the overall muscle length ratio (R) are defined. B), A new muscle length (L'_m) with a relative length change x in L_m, assuming length change in non-fiber area is much smaller than in muscle fiber length and negligible. Note that it is also valid when the muscle shortens with negative x in the equation.

L_m, overall muscle length ; L_m, muscle fiber length ; x, relative length change in L_m. L' represents a new length changed from the standard.

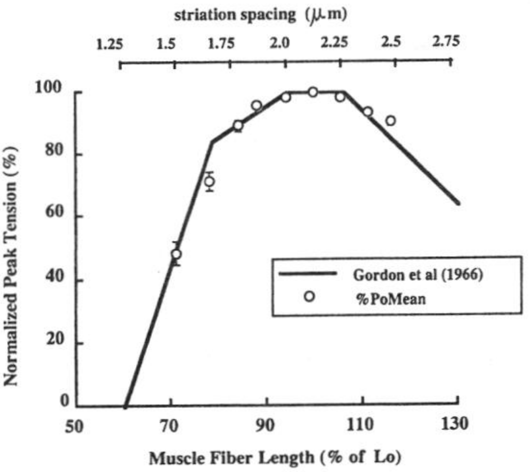

Fig.5 Length−tension diagram replotted on the axis corrected for the muscle fiber length. Symbols are mean±SE obtained in the present study. Line is the length-tension diagram for single fibers based on Gordon et al. (1966)[20].

initial rate of rise of tension in a fixed-end tetanic contraction of a single muscle fiber was constant over a range of sarcomere lengths from 1.7μm to beyond 3.0μm. In the results by Ramsey and Street (1940;in their fig.8)[37], however, there seems to be differences in the rate of tension development at the lengths of 82, 100 and 136% of Lo.

It is not clear whether the length dependence of the dP/dt_{max} does exist in a single muscle fiber, since dP/dt_{max} values were not shown in relation to lengths in those studies made on a single muscle fiber. If dP/dt_{max} is held constant against the fiber length change, the length dependence of dP/dt_{max} observed in the present study is the property of a whole muscle or muscle fibers placed within a muscle (*i.e.*, those in a motor unit). There may be morphological effects to be considered (*e.g.*, fiber-to-muscle length ratio, and the elastic component surrounding the fibers).

The difference between the curvature of $L-\%dP/dt_{max}$ and that of $L-\%Po$ relation implies that muscle length affects differently on the tension rising and the plateau phases. We found that the effect was greater on the former than on the latter. For example, dP/dt_{max}, a parameter for tension rising phase, could exert only 52% of its maximum capacity achieved at Lo, while Po, a parameter for plateau phase, exerted 71% of its maximum at 80% Lo ; 81% and 93% for dP/dt_{max} and Po, respectively, at 110%Lo (Fig. 2A and 2B). Fig. 3 indicates that at lengths more distant from Lo, the greater tension is generated than expected from the preceding tension-rising phase.

It is considered that inward spread of activation along the transverse tubular(T) system is interrupted at short fiber lengths (Huxley and Taylor, 1958[24]). Taylor and co-workers found inactivated wavy myofibrils in the core of the fiber[44] and the decrease in the release of Ca^{2+} from sarcomplasmic reticulum[3] when a muscle fiber was allowed to shorten up to $1.6\mu m$ of sarcomere spacing. Such a structure-related inactivation, however, does not seem to recover through a contraction, thus the similar effects should work on Po. In fact, Rome et al. (1985) indicated that the insufficient activation of the muscle fiber with a low-rate stimulation made the tension depressed especially at shorter lengths and that it recovered by adding the potentiating agent[40]. Since the $L_f-\%Po$ relation (Fig. 5) in the present study did not show such a tension depression at shorter lengths, insufficient level of intercellular calcium does not seem to explain the depression occurred only in dP/dt_{max}, hence, the difference of length dependency between dP/dt_{max} and Po.

If sartorius muscle contains, as is thought to do, parallel and same sized fibers running from tendon to tendon, the mechanical properties of a whole muscle could be obtained by simply summing those of individual muscle fibers. There should be, however, a variation of lengths among muscle fibers and shorter muscle fibers would be more sensitive to muscle length changes. Julian and Morgan (1978) have reported a delay prior to the tension rise at sarcomere lengths below $2.0\mu m$[26]. Such a length would correspond to 94%Lo in the present study. Below this muscle length, therefore, the retarded tension rise in some shorter fibers may be responsible for the lower rate of tension development. Furthermore, the decrease in the initial rate of tension rise observed below sarcomere length of $1.6\mu m$[26] (corresponding to approximately 75%Lo in our preparations) would accelerate the decrease in dP/dt_{max} of a whole muscle at the shortest length in our experiment. Since such retards would be reflected on only dP/dt_{max} and not on Po, the difference of the length dependency between dP/dt_{max} and Po might consequently appear lead in a whole muscle.

For above optimum length, one might be able to explain this phenomenon, at least partly, by a mechanism called 'creep'. In fixed-end tetanic contractions at higher lengths above Lo, initial rapid tension rise is followed by a slower 'creeping' rise of tension described for the first time by Hill (1953)[23]. This creep tension has been considered to be correlated with the development of non-uniformities in sarcomere lengths[25,30,35]. That is, during a creep, sarcomeres in series interact to each other with a small proportion of sarcomeres near ends of the fiber shorten, increasing their tension generating capacity, and stretching the rest, which bear the extra tension in accord with the stretch part of the force−velocity relationship[26]. Such phenomenon occurring in individual fiber will be added in whole muscle. Thus, the greater is the total creep tension, the greater would become the Po to dP/dt_{max} ratio. Furthermore, polyneuronal innervations often seen in frog sartorius muscle fibers[32] might promote the growth of non-uniformities among sarcomeres by causing a subtle mismatch in the onset of contraction along the same fiber. In addition, if there are fibers arranged in series[1], interactions among fibers might generate gradually longer extra force as the sarcomeres in series within a fiber do during 'creep'. Indeed, in Fig.5, Po above Lo seems to slightly exceed the sarcomere length−tension curve predicted from Gordon et al.[20].

It could not be known whether the difference of the length dependency between dP/dt_{max} and Po is an intrinsic property of individual muscle fiber. However, it would give an important information about the feature of isometric contraction when the muscular activity *in vivo* is to be described. That is, isometric contractions performed at various muscle lengths are differ not only in their peak tension but also in their rate of tension development. This indicates that the time course of tension generating processes itself is greatly affected by length, giving consequently different shapes of contraction curves at different lengths even after normalization.

In recent biochemical studies, Brenner (1987)[4] and Metzger et al.(1989)[34] have suggested that the peak dP/dt reflects the rate of transition in actomyosin binding from a weakly bound low-force-state to a strongly bound high-force-state. On the other hand, tension generating and maintaining capability would depend on the reverse transition, so that the slower is the net reaction rate represented by dP/dt, the larger is the tension maintaining capacity. We could not correlate directly our results to theirs, since their experiments were carried out on tension re-development after quick release in activated muscle fibers. However, it should be still worth to mention.

Providing tension generating capacity per unit time during the tension rising phase was more length dependent than tension maintaining capacity, it is suggested that the slowed net reaction rate in the transition of crossbridge states plays an important role in "compensating" the lower rate of tension development for achieving higher peak tension. But such an argumentation needs further investigations.

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