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Muscle economy of isometric contractions as a function of stimulation time and relative muscle length

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Abstract. For rat medial gastrocnemius muscle economy (i.e. the ratio of time integral of force and total energy-rich phosphate consumption) was calculated. Muscles in situ at 35°C were stimulated to perform either one continuous or several repetitive isometric contractions at one muscle length in the range from 70% to 130% of optimum muscle length for force generation. Whereas during one continuous contraction economy increased, no differences in economy were found between 6, 12 or 18 successive contractions. Economy during intermittent exercise was always lower than during continuous exercise. The difference in economy is a result of different rates of metabolism, whereas no difference was found for force generation. Economy was highest at optimum muscle length for force generation and decreased at muscle lengths smaller as well as greather than optimum muscle length. Force-dependent energy consumption was calculated by substracting the force-independent part (obtained by extrapolation) from total energy consumption. The calculated force produced per µmol force-dependent energy-rich phosphate consumption was similar in muscles stretched beyond optimum length. In contrast, a decreasing amount of force per µmol force-dependent energy-rich phosphate consumption was observed at lengths smaller than optimum length.

Key words: Energy metabolism – Successive isometric contractions – Muscle length – Architecture

Introduction

Quantitative data of energy consumption by muscle during force-independent activation processes have been obtained from measurements of heat production (Homsher et al. 1972; Smith 1972). In these studies of isolated amphibian muscles heat production was measured at 0°C. These muscles were stimulated at very great lengths, where there is little overlap between actin and myosin filaments (Gordon et al. 1966a). The measured (force-independent) heat is produced by activation processes – predominantly by reactions related to calcium movements (Homsher and Kean 1978; Rall 1982). During conctraction only a fraction of the heat production can be explained by chemical changes (Curtin and Woledge 1978). Over the complete contraction-relaxation cycle, however all activation heat is derived from the enthalpy change of hydrolysis of ATP by the calcium pump (Homsher et al. 1972).

The total amount of force-independent energy utilized during a single tetanic contraction is a function of both the stimulation frequency and the number of applied stimuli (Homsher et al. 1972). Kushmerick and Paul (1977) showed that when a second brief tetanus was performed just after the first one less chemical energy was consumed. The difference in energy consumption was a function of the time interval between the tetani. From these results it may be expected that during several repetitive isometric contractions, the total amount of force-independent energy utilized will also vary as a function of the number of the contractions and the time intervals between the contractions.

For the relation between exerted force and energy consumption the term economy, defined as the ratio force produced/energy consumed (Goldspink 1978), is often used. During a maximal isometric tetanic contraction of rat quadriceps muscle, it has been observed that economy increases with the duration of contraction up to about 10 s but thereafter remains constant (Westra et al. 1985) This increase in economy with contraction duration may be explained by the relatively high amount of energy used for activation processes at the beginning of contraction.

In the present study muscle economy of rat skeletal muscle in situ at 35°C was calculated for several short-term repetitive isometric tetanic contractions and for one continuous isometric tetanic contraction. The effect on economy of changing the number of stimuli applied to the muscle was investigated in both conditions. It has been reported that economy is affected by muscle length in frog sartorius muscle at 0°C (Sandberg and Carlson 1966) and in rat gastrocnemius muscle at 20°C (de Haan et al. 1985b). We have therefore investigated the effect of muscle length on economy in the present preparation at 35°C. The data has been interpreted by reference to previous morphological studies carried out by our group using the same pennate muscle (see e.g. Woittiez et al. 1983, 1984). Finally we have investigated the effect of muscle length on the relation of force exerted and force-dependent energy consumption.

Methods and material

Male wistar rats about 60 days old (body weight 240–290 g) were anaesthetized with pentobarbital (i.p.; 60 mg · kg body weight^{-1}). After surgical preparation (about 40 min after the first anaesthesia) a second dose of pentobarbital (24 mg · kg body weight^{-1}) was administered. The medial

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Offprint requests to: A. de Haan at the above address head of the gastrocnemius muscle (GM) was carefully isolated in both legs. The non-stimulated GM of the left leg served as control. The origin of the right GM on the femur was left intact and the femur was fixed by means of a metal clamp. Distally the calcaneus was cut and connected to a force transducer (stiffness 721 N · cm^{-1}). Muscle ambient temperature was maintained at 35°C (its resting surface temperature) by a water saturated air flow.

Isometric contractions were induced by stimulation (Neurolog Systems (Welwyn Garden City, England); pulse height (1 mA; pulse width 0.5 ms) of the distal end of the severed tibial nerve, with only its branch to GM left intact. An electrical reset occurred just before each start of stimulation to zero the passive force signal. In this way active forces could be measured accurately, even with muscles at long lenths i.e. with high passive forces (see also Fig. 2).

Ten twitches (one each minute) at different muscle lengths were used in order to identify muscle optimum length (Lo = length with highest active twitch force). With the muscle set at Lo maximal isometric force was measured during a short tetanic contraction (duration 0.2 s; pulse frequency 100 Hz). Muscle length and most distal fibre bundle length were measured with a pair of compasses. Parameters of muscle morphology and physiology at Lo were used to characterise muscle preparations (Table 1).

Three series of experiments were carried out:

In series A (at Lo) the muscles were stimulated to produce either 6, 12 or 18 successive isometric contractions (0.35 s; one each second).

In series B (at Lo) the muscles performed one continuous tetanic contraction with the same total contraction time as in series A, i.e. 2.1, 4.2 or 6.3 s, respectively.

In series C effect of muscle length on economy was investigated. At any of five different muscle lengths, i.e. 0.70, 0.85, 1.00, 1.15 and 1.30 × Lo, 18 tetanic contractions (0.35 s; one each second) were performed.

The contralateral (control) GM was freeze-clamped first with a pair of tongs precooled in liquid nitrogen. Blood supply to the experimental muscle was interrupted by ligating the femoral artery and vein, about 10 s before start of the stimulation. In this way aerobic metabolism was minimized and leakage of metabolites out of the muscle during intermittent exercise was prevented. Clearly some slight replenishment of energy stores may still occurr during the stimulation as a result of O_2 trapped in the muscle. But this replenishment is likely to be very small. We have therefore made no attempt to correct for it. Within 1 s after completion of the stimulation, the experimental muscle was freeze-clamped. The frozen muscle tissue was weighed, thereafter it was ground in a precooled mortar, with continuous addition of liquid nitrogen, and freeze-dried (Virtis). Duplicate extractions occurred by homogenizing dry muscle tissue (25 mg) in 0.5 ml cold perchloric acid. The homogenate was centrifuged at 0°C (MSE Mistral 4L, 18,000 × *g*). The neutralized extract was centrifuged to remove potassium perchlorate (Eppendorf 10,000 rpm) and stored at −18°C till analysis. Enzymatic determinations of phosphocreatine (PC), creatine, ATP, ADP and lactate were performed as described by Bergmeyer (1970) on a double beam spectrophotometer (UV-190, Shimadzu, Tokyo, Japan). From the differences in concentrations of ATP phosphocreatine (PC) and lactate between experimental and contralateral (resting) GM, the total energy-rich phosphate consumption (EPC) was calculated for the whole muscle (EPC = $-\Delta PC - \Delta ATP + 1.5 \times \Delta$lactate). Muscle weights are given throughout the paper as wet muscle weight. In preliminary experiments the ratio dry weight/wet weight for GM was determined (0.23 ± 0.01; $n = 6$). This value was not different from the value previously reported for quadriceps muscle (de Haan et al. 1985a).

Table 1. Morphological and force parameters of M. gastrocnemius medialis of the rat ($n = 48$)

	Mean	SD
Rat weight (g)	258.6	11.4
Muscle weight (g)	0.73	0.04
Muscle length (at Lo) (mm)	34.6	1.1
Fibre length (most distal) (mm)	14.6	0.8
Index of architecture[a] (fibre length/muscle length)	0.42	0.02
Physiological cross-section (mm^2)[a]	46.1	2.8
Twitch force (at Lo) (*N*)	2.1	0.3
Tetanic force (at Lo) (*N*)	10.5	0.7

[a] Calculated according to Woittiez et al. (1983)

The areas under the force-time curve of the repetitive isometric contractions were added to obtain total force-time integral (FTI) of a muscle. Economy was calculated as FTI (Newtons × seconds; Ns) divided by EPC (μmoles energy-rich phosphate [~ P]).

Force-independent energy consumption can be calculated from experiments with muscles stretched to different lengths to decrease actin-myosin overlap (Homsher et al. 1972; Rall 1982). From the experiments with muscles stretched to and beyond Lo (series C), the regression line (least squares) between EPC and FTI was calculated and extrapolated to zero FTI to obtain an estimate of force-independent EPC. At all muscle lengths this force-independent energy consumption was substracted from the total energy consumption to obtain a force-dependent part.

Enzymes and nucleotides were supplied by Boehringer, Mannheim, FRG. The other chemicals were provided by BDH-Chemicals (UK) and Sigma Chemical Co, St. Louis, MO, USA.

Possible differences between continuous and intermittent exercise were tested with the two-tailed Student's *t*-test ($\alpha = 0.05$).

Results

Effects of the number of stimuli

Concentrations of muscle metabolites as well as FTI and calculated EPC and economy are presented in Fig. 1. ATP concentration only slightly decreased. Depletion of phosphocreatine occurred predominantly during the first 210 stimuli, where utilization of phosphocreatine accounted for about 70% of the total energy consumption during 210 stimuli. With increasing number of stimuli a greater fraction of the energy was supplied by glycolysis as indicated by the progressive increase in lactate concentration. The initial rate of isometric metabolism of GM was approximately 9 μmoles ~ P · g^{-1} · s^{-1}. This value is comparable with the initial rate for quadriceps muscle (7.4 μmoles · g^{-1} · s^{-1}; Westra et al. 1982) but somewhat higher than the 3.4 µmoles · g^{-1} · s^{-1} which can be calculated from the results of Aragon et al. (1980). However it should be noted that in the latter study a submaximal stimulus frequency (25 Hz) was used.

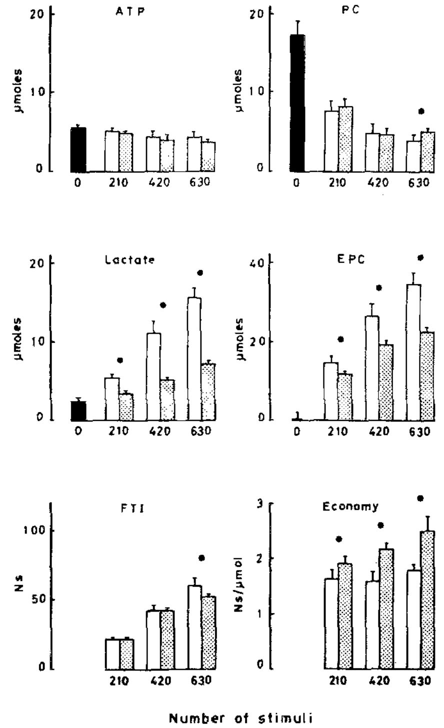

Fig. 1. Effect of number of stimuli applied to gastrocnemius muscle in situ on ATP, phosphocreatine (*PC*) and lactate concentration, energy-rich phosphate consumption (*EPC*), force-time integral (*FTI*) and economy. Mean values and standard deviations are presented for continuous stimulated (*shaded bars*; $n = 3$), intermittent stimulated (*light bars*; $n = 5$) and non-stimulated (*dark bars*; $n = 4$) muscles. For stimulation procedure: see Methods. * indicates a significant difference between continuous and intermittent stimulation ($P < 0.05$). Energy data are total values for the whole muscle

Intermittent stimulation (series A) induced a higher energy consumption, when compared to continuous stimulation (series B) with the same total contraction time (Fig. 1). However except for the largest number of stimuli there was no difference for FTI between continuous and intermittent exercise. Thus economy in one continuous contraction was higher than in several successive contractions of equal contraction time. Furthermore, the difference in economy between the two stimulation protocols became more pronounced with an increasing number of stimuli. This latter effect was the consequence of an increase in economy during the time course of a continuous contraction. This is in contrast to the situation in intermittent exercise where the economy of each component contraction remains the same and hence the economy of the series remains constant irrespective of the total number of contractions (Fig. 1).

Effect of muscle length

Figure 2 presents original force-time registrations at different muscle lengths (series C). At all muscle lengths isometric force of the last contractions was 75% ± 10% ($n = 25$) of the highest force for each muscle. The highest-force was obtained in the first contraction, except for muscles at 0.70 × Lo, where the highest force was found in the sixth contraction.

The influence of muscle length on FTI and EPC from 18 repetitive contractions is presented in Fig. 3. FTI was highest at optimum muscle length (Lo) and decreased at lengths smaller and greater than Lo. EPC decreased at lengths greater than Lo; at lengths shorter than Lo EPC was significantly lower at 0.70 × Lo but not at 0.85 × Lo (Fig. 3).

The combined effects of muscle length on FTI and EPC resulted in the highest economy occurring at Lo (Fig. 3). At lengths shorter and greater than Lo economy decreased. At extreme lengths economy was 17% ± 5% (at 0.70 × Lo) and 28% ± 8% (at 1.30 × Lo) of its value at Lo. In Fig. 4 EPC is presented in relation to FTI for the muscles at Lo and greater lengths where there would have been a decreased actin-myosin overlap. At zero FTI, (force-independent) EPC was calculated to be 14.2 µmoles. Force-dependent EPC was

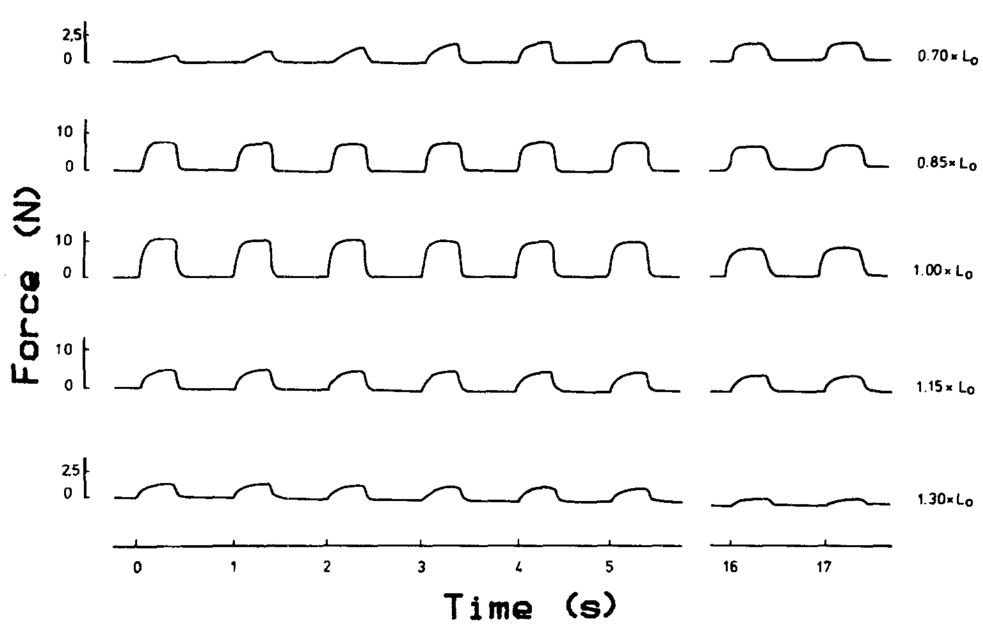

Fig. 2
Redrawing of the first six and last two contractions of gastrocnemius muscle in situ from original force registrations of typical experiments at the five different muscle lengths indicated. The muscles were stimulated (100 Hz; 0.35 s) to perform 18 isometric contractions ($1 \cdot s^{-1}$)

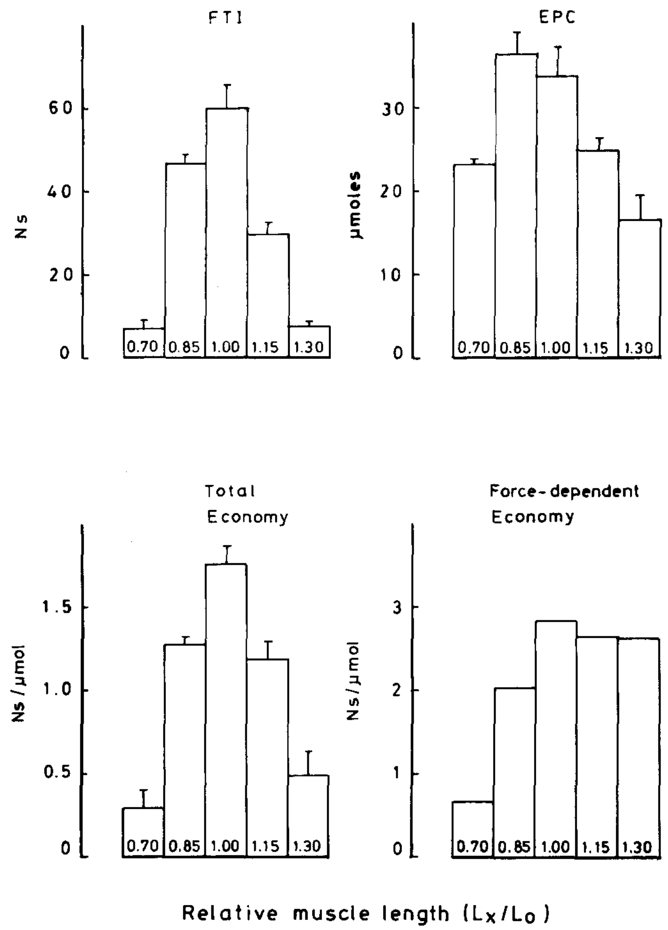

Fig. 3. Effect of relative mucle length on force-time integral (FTI), energy-rich phosphate consumption (EPC), total economy and force-dependent economy (ratio force-time integral / force-dependent energy consumption) of gastrocnemius muscle in situ. The muscles were stimulated (100 Hz; 0.35 s) to perform 18 isometric contractions ($1 \cdot s^{-1}$). Mean values and standard deviations from five experiments are presented. Energy data are total values for the whole muscle

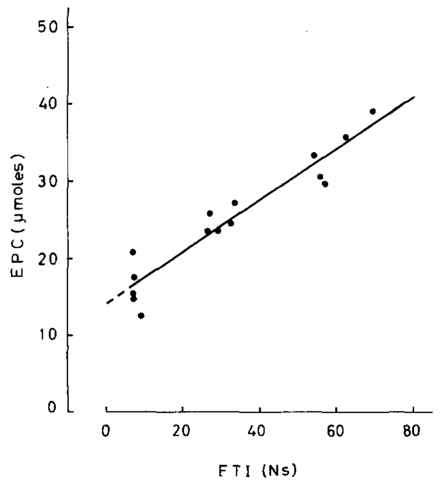

Fig. 4. Energy-rich phosphate consumption (*EPC*) as a function of force-time integral (*FTI*) of gastrocnemius muscle in situ. The muscles were stimulated (100 Hz; 0.35 s) to perform 18 isometric contractions ($1 \cdot s^{-1}$) at muscle lengths at and beyond optimum muscle length (*Lo*). Energy data are total values for the whole muscle, ($EPC = 0.33 \times FTI + 14.2$; $r = 0.95$; $n = 15$)

obtained by substracting force-independent EPC from the mean total EPC at each muscle length. The force-dependent economy (i.e. ratio of mean FTI to mean force-dependent EPC) at the different muscle lengths is presented in Fig. 3. At Lo and muscle lengths greater than Lo, similar force-dependent economies were found. However, at lengths smaller than Lo, force-dependent economy decreased in a similar fashion to total economy.

Discussion

Intermittent vs. continuous exercise

During one continuous contraction Westra et al. (1985) found an increasing economy with stimulation duration up to about 10 s. The present study confirm this finding for the first 6.3 s (Fig. 1). Economy in the experiments with intermittent stimulation show two differences when compared to continuous stimulation. Firstly, in contrast with an increasing economy with increasing number of stimuli, in continuous exercise the number of stimuli did not affect economy in intermittent exercise. Secondly, economy was lower intermittent exercise when compared to continuous exercise of equal number of applied stimuli. The lower economy was a result of a higher energy consumption, rather than changes in FTI which was not different between intermittent and continuous exercise after 210 and 420 stimuli (Fig. 1). These results are consistent with the observations of Marechal and Mommaerts (1963) who showed that the magnitude of the 'extra-metabolism' during intermittent exercise was proportional to the number of tetanic contractions. Kushmerick and Paul (1977) reported that, at 0°C, an interval of 200–400 s between two successive tetanic contractions was required before the second contraction utilized the same amount of energy as the first one. Shorter intervals caused decreased energy consumption during the second tetanic contraction. The explanation for the smaller amount of energy utilized during contractions produced after shorter intervals is that recovery processes are not completed with a resulting lower 'start-up-cost' for the following contraction (Rome and Kushmerick 1983). From our finding that economy was not dependent on the number of tetani during intermittent exercise we conclude that the intervals were long enough for complete recovery. The difference of time needed for total recovery between our results and those of Kushmerick and Paul (1977) can be explained by the difference in temperature (35°C vs. 0°C) (Q_{10} of the metabolic processes is about 3; Rall 1980). The higher energy-rich phosphate consumption during successive contractions when compared to one continuous contraction, as well as the constancy of economy with increasing number of contractions indicate that a fixed amount of 'start up cost' per contraction was utilized.

Effect of muscle length

While isometric force generation (FTI) showed a clear optimum at Lo, muscle length had a less pronounced effect on energy-rich phosphate consumption (EPC). The highest EPC occurred at 0.85 × Lo and at Lo but at extreme muscle lengths (0.70 and 1.30 × Lo), energy consumption was still high, while FTI was quite low (Fig. 3). This is in agreement with results of Sandberg and Carlson (1966) and de Haan et al. (1985b), who calculated energy consumption from one continuous tetanic contraction, indicating that the fashion of stimulation (intermittent vs. continuous) had no essential influence on the effect of muscle length. It has been suggested that muscles are at optimum length at that joint position where they are most often or most strongly electrically active (Herring et al. 1984). If this is so then it would appear that the greatest economy is also achieved at those joint angles which are most frequently used in vivo.

Economy is calculated by dividing FTI by total energy consumption. However, part of the energy is consumed by the calcium pump (Homsher and Kean 1978). Since this part of the energy consumption is independent of force generation, only a fraction of the energy consumption will vary with the amount of force generated. Hence, the observed decrease of economy at lengths smaller and greater than Lo (Fig. 3), does not imply that efficiency of actin-myosin interaction was decreased at lengths shorter and greater than Lo. Correction of energy consumption for its force-independent part demonstrates, that the force-dependent economy (i.e. ratio of integrated force over force-dependent energy consumption) did not change at lengths greater than Lo. Thus the lower total economy found at lengths greater than Lo is a result of the proportional decrease in force and force-dependent energy consumption combined with a constant force-independent energy consumption. However, at muscle lengths smaller than Lo the decrease of force-dependent economy indicate that less force could effectively be produced per μmol force-dependent ~P (Fig. 3). To explain the lower force-dependent economy at muscle lengths smaller than Lo the following considerations can be made:

1. From the work of Rall (1982) it was assumed that force-independent EPC was independent of muscle length, but if force-independent EPC was higher at smaller muscle lengths, this should result in a lower force-dependent EPC and thus increase the force-dependent economy at smaller muscle lengths. However the experiments of Blinks et al. (1970) indicated that calcium release was highest at optimum muscle length and slightly decreased with increasing as well as decreasing muscle lengths. Since force-independent EPC is supposed to be related to the calcium pump (Rall 1982) any tendency for increased force-independent EPC at small muscle lengts seems unlikely on these grounds.

2. Gordon et al. (1966b) argued that in active muscles at very small lengths collision of ends of thick filaments with the Z-lines may take place. This collision may cause high resistance to shortening and folding of the thick filaments, which would reduce the number of cross-bridges capable of generating force while still consuming energy. A diminished fraction of total cross-bridge cycling coupled to external force as suggested (Gordon et al. 1966b) could have occurred in our experiments at 0.70 × Lo. This phenomenon could have caused at least part of the steep decrease of the force-dependent economy and of total economy at this muscle length.

3. At the onset of an isometric contraction some energy will be used for internal work connected to changes of muscle morphology (Woittiez et al. 1984). Decreasing sarcomere length (Goldspink 1978) as well as increasing angle between fibre and muscle axis (Huijing and Woittiez 1986) contribute to this change of morphology in the very beginning of the contraction. As both shortening of sarcomeres and increase of fibre angle are more pronounced at small muscle length (Huijing and Woittiez 1986), the effect of this extra energy consumption on the force-dependent economy would be greater at smaller muscle lengths.

4. The measured force on the tendon is a product of the force exerted by the fibres and the cosine of the angle between fibre and muscle axis. The fibre angle is quite different in active GM at different muscle lengths (Woittiez et al. 1984). The greater fibre angle at small muscle lengths caused a greater difference between muscle force and the force generated by its fibres. When FTI was corrected to force generated by the fibres using the angles of Woittiez et al. (1984) there was a reduction in the magnitude of the difference between the force-dependent economy at smaller muscle lengths. Thus the effect of correction was to increase the force-dependent economy at 0.85 × Lo from 70% to 85% of the force-dependent economy at Lo. This illustrates that the differences in fibre angle to active GM at muscle lengths smaller than Lo will significantly affect both force-dependent economy and total economy. At 0.70 × Lo the small increase following correction of the force-dependent economy relative to its value at Lo (from 25% to 30%) indicates that even though fibre angle increases, the rapidly decreasing force at smaller muscle lengths has a greater effect.

These considerations lead us to conclude that when extrapolating data obtained from single fibres to whole mammalian muscle it is of vital importance to take account of the architecture of the active muscle as well as morphological changes occurring during contraction.

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