

**THE SARCOMERE LENGTH DEPENDENCE OF THE
RATE OF HEAT PRODUCTION DURING ISOMETRIC TETANIC
CONTRACTION OF FROG MUSCLES**

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(Received 4 May 1984)

SUMMARY

1. Heat production and force have been measured as a function of sarcomere length between 1.6 and 3.0 μm during isometric tetani at 0 °C for two types of frog muscle: sartorius and extensor longus digiti iv (e.l.d. iv).
2. Stable heat rate declines linearly with increasing sarcomere length above 2.20 μm for both e.l.d. iv and sartorius muscles.
3. In sartorius muscle stable heat rate remains at or near its maximum value between 1.75 and 2.20 μm while force decreases.
4. In e.l.d. iv muscle, both stable heat rate and force decline linearly as sarcomere length decreases below 2.20 μm .

INTRODUCTION

The mechanical events of contraction in skeletal muscle, force, work and shortening, are generally considered to result from the interaction of cross-bridges (projections of the myosin molecules in the thick filaments) with the actin in the thin filaments (Huxley, 1974). As muscle length is increased above that which is optimum for the interaction between thick and thin filaments, force measured in length-clamped segments of muscle fibres varies with the number of active cross-bridges (Gordon, Huxley & Julian, 1966*a, b*; Edman & Reggiani, 1983). However, at lengths below this optimum the reasons for the fall in tension observed are not clear and may include the existence of an internal restoring force as well as a decline in the number of active sites (Julian & Morgan, 1979).

In the interaction between cross-bridges and thin filaments, ATP is split. A large part of the heat production in active frog muscle comes from this reaction, although significant quantities are also thought to be produced by ATP splitting by the calcium-ATPase pump in the sarcoplasmic reticulum and by other, unknown reactions (Curtin & Woledge, 1978). Heat production during an isometric tetanus can be resolved into two components, labile heat, which declines exponentially from the start of the tetanus and is over by about 5 s, and stable heat which is produced at a steady rate throughout the tetanus (Aubert, 1956). It is the stable heat which is

thought to be due to splitting of ATP (Curtin & Woledge, 1979). When a muscle is stretched sufficiently to prevent interaction between the thick and thin filaments, the rate of stable heat production and of ATP splitting is reduced to about 40% (Homsher & Kean, 1978) of that at a length optimum for actin-myosin interaction. This proportion of the heat production is therefore considered to come from ATP splitting by the calcium-ATPase pump in the sarcoplasmic reticulum which is thought to be independent of muscle length. Hence the remaining 60% of the stable heat rate represents ATP splitting by cross-bridges, and this part of the heat production would be expected to vary as the number of active cross-bridge sites is changed. If this interpretation is correct, measurement of stable heat rate can be used to investigate how the number of active sites varies with muscle length.

Many investigations have been carried out on the relation between heat rate and muscle length during isometric tetani for frog skeletal muscle (Hill, 1925; Fenn & Latchford, 1933; Aubert, 1956; Aubert & Gilbert, 1980). These experiments have shown that the maximum heat production occurs at a muscle length shorter than the optimum for force development, suggesting that, near the optimum length, tension is not proportional to the number of cross-bridge sites that are active. However, the relation of force to sarcomere length is not simple (Huxley & Peachey, 1961). This is because tension development, especially at long sarcomere lengths is often seen to have an initial fast rise followed by a slow increase, termed 'creep' (Hill, 1953). This creep phase has been associated with the fact that the sarcomeres at the ends of the fibres are shorter than those in the middle and therefore have more filament overlap. Creep therefore would not be expected at sarcomere lengths less than that at which overlap of thick and thin filaments is complete. However, at muscle lengths above the optimum, creep can cause the measured tension to be well above that of the expected isometric tension, based on the measurement of average resting sarcomere length, particularly when force is measured late in a tetanus. Therefore an interpretation of the length dependence of the heat rate requires also knowledge of the relation of heat rate to sarcomere length, which has not previously been studied. Therefore we have investigated the sarcomere length dependence of stable heat rate and force in isometric tetani, for frog skeletal muscle at 0 °C. We initially used extensor longus digiti iv (e.l.d. iv muscle) from *Rana temporaria*, as the variation of force and stable heat rate with muscle length was unknown in this muscle. We then extended the study to include sartorius muscle so we could compare our results with those of previous workers.

METHODS

Measurements of force and heat production were made at 0 °C on muscles from *Rana temporaria*. Either single e.l.d. iv or sartorius muscles, usually as pairs, were used. The Ringer solution contained (mM): NaCl, 115; KCl, 2.5; MgSO₄, 1.0; CaCl₂, 1.8; Na₂HPO₄, 2.0; NaH₂PO₄, 1.0. The muscles were stimulated directly via platinum electrodes by supramaximal square-wave pulses of 1–5 ms duration at 10–13 Hz. Tetani were of 7 s duration.

The relation between muscle length and sarcomere length was investigated in resting muscle before measurement of the heat production, by using diffraction of He-Ne laser light. Measurements were made at one to three places within the central 70% of the muscle. The mean sarcomere lengths expected during activity (mean estimated active sarcomere length) were estimated by taking account of the shortening of the muscle as it developed force against the compliance of the tendon

and the apparatus. This was measured by observing, under the microscope, the movement during tension development of gold-foil markers placed at the ends of the muscle. (For technical reasons sarcomere length could not be measured during the contractions used for observing heat production.)

Each muscle was used at either seven sarcomere lengths (between 1.8 and 3.0 μm or 1.6 and 2.5 μm) or at four lengths (1.6–2.2 μm). The initial length was chosen at random and muscle length was then increased or decreased in a series-and-return design such that two measurements were made at each sarcomere length. After a tetanus, the muscle was adjusted to the next length to be used, given a single stimulus, and then allowed to rest in Ringer solution for about 20 min before the next tetanus. Muscles were blotted and weighed at the end of the experiment. Heat-production results were normalized to the weight of the portion of the muscle overlying the active region of the thermopile, assuming the cross-section to be uniform.

Three thermopiles were used: an electroplated thermopile with an active region 11.2 mm long (Ricchiuti & Mommaerts, 1965) used for e.l.d. iv muscle, an evaporated metal thermopile (Mulieri, Luhr, Trefry & Alpert, 1977) with an active region of 5.8 mm also used for e.l.d. iv muscle, and an electroplated thermopile with which the active region could be varied, used for sartorius muscles. With this last thermopile, length of the active region was altered so as to record from approximately 90% of the muscle at each muscle length.

Heat loss was observed by Peltier heating or Joule heating (100 kHz). Where heat loss was exponential (all sartorius experiments and some e.l.d. iv experiments) heat-loss correction was carried out by the method described by Hill (1965). When two exponentials were required to describe the heat loss, the method of Curtin, Howarth & Woledge (1983) was used. Heat capacities of the part of the muscle over the thermopile were estimated for sartorius muscle, where the heat capacity of the thermopile and adherent Ringer is negligible, from the wet weight of the muscle, its length, and the length of the active region of the thermopile. In the case of e.l.d. iv muscle (which is about 20 times smaller than sartorius), the extra heat capacities are not negligible and the heat capacity had to be estimated from the initial slope of Peltier heating (Kretzschmar & Wilkie, 1975).

Stimulus heat was measured after making the muscle inexcitable with 10 mM-procaine. In most experiments, stimulus heat was negligible, but where it was not, the heat records were corrected appropriately.

RESULTS

Fig. 1 shows records of force and heat production (corrected for heat loss) at three different sarcomere lengths for both e.l.d. iv and sartorius muscles. The stable heat rate was measured by fitting a straight line to the heat production during the last few seconds of the tetanus. Labile heat is given by the positive intercept of this line at the start of the tetanus.

Force exerted was measured at 1.5 s for all experiments. This time was chosen because, at a sarcomere length of 2.2 μm where there should be little 'creep', maximum force had been reached in all the experiments by this time. Measurement of force at later times in the tetanus would have included an increasing proportion of the creep component for longer sarcomere lengths (Iwazumi, Pollack & Ter Keurs, 1977).

For each experiment, the mean of the two measurements of stable heat rate (h_b), labile heat (H_a) and force (P) at each sarcomere length were expressed relative to the maximum mean values for each of these variables. The mean results for all the experiments are shown in Table 1, with e.l.d. iv and sartorius muscle given separately. The table also shows the mean maximum stable heat rate, labile heat and normalized force measured for each type of muscle. Mean normalized tetanic force (force per cross-sectional area), stable heat rate and labile heat are all significantly lower ($P < 0.05$) for the e.l.d. iv muscle. These differences are unlikely to be due to the small

proportion of slow fibres contained in the e.l.d. iv muscle because they only occupy about 10% of the muscle volume (Gray, 1958). Nor are they likely to be due to the presence of a greater proportion of damaged muscle fibres in the e.l.d. iv muscle because this would reduce both heat rate and tension proportionately, whereas the ratio of heat rate to force is significantly greater in the e.l.d. iv muscle (Table 1). Hence

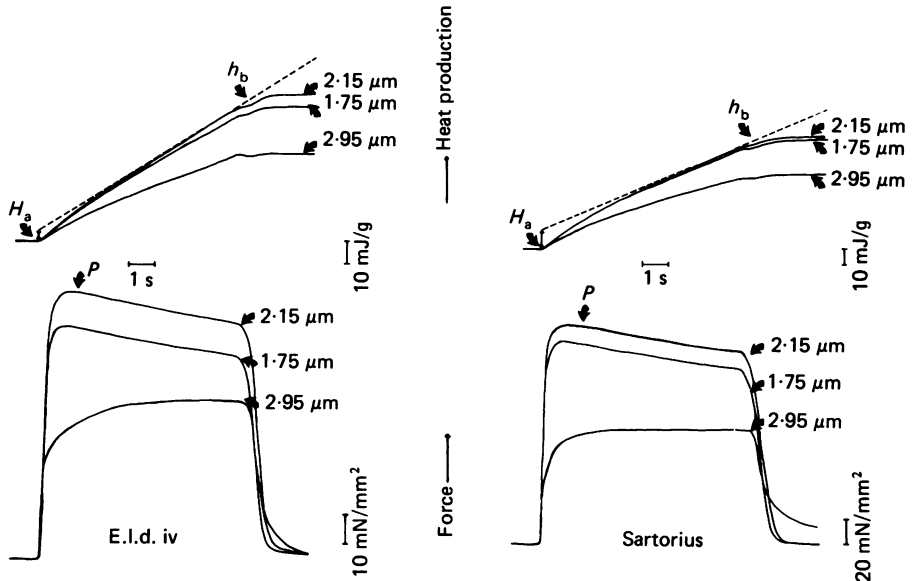


Fig. 1. Records of force and heat production for e.l.d. iv and sartorius muscle at three different sarcomere lengths (estimated mean sarcomere lengths during activity, see Methods). Heat production has been corrected for heat loss. The dashed lines are fitted to the last few seconds of the heat records for 2.15 μm sarcomere length. The slope of this line is the stable heat rate, and its intercept at the start of the tetanus is the labile heat. The arrows show the time at which the force was measured for Table 1.

there seem to be genuine differences between the different muscles, similar, for example, to differences in normalized force production found by Luff (1981), between inferior rectus and soleus muscles in the mouse.

The longest sarcomere length at which filament overlap should be maximal is 1.98–2.13 μm (for a summary of the evidence see the discussion by Huxley, 1980, pp. 54–56). It is found that at longer sarcomere lengths, heat rate declines in both muscles. The dotted line in Fig. 2A indicates the decline expected if 60% of the stable heat rate is proportional to filament overlap (this is the mid-point of the range of values given by Homsher & Kean (1978) based on their unpublished observation of the heat rate at a sarcomere length of 3.6 μm .) Our results appear compatible with this line. Force, however, does not decline with the decrease in filament overlap as indicated by the dashed line in Fig. 2B, but remains at its maximal value until a sarcomere length of about 2.35 μm is reached, before declining. This result is similar to those reported for sartorius muscle, for example by Close (1972) and for intact single

TABLE 1. Average values and standard errors (s.e. of mean) of normalized stable heat rate h_b , labile heat H_a and force P during isometric tetani. As the estimated mean sarcomere lengths used (see Methods) were not exactly the same for each experiment averaging has been done with interpolated values. Where necessary the sarcomere lengths used for this averaging were chosen to minimize the necessity for interpolation

E.l.d iv muscle

Estimated mean sarcomere length (μm)	$h_b/h_{b,\text{max}}$	S.E. of mean	P/P_{max}	S.E. of mean	$H_a/H_{a,\text{max}}$	S.E. of mean	n
1.75	0.764	0.042	0.653	0.088	0.625	0.055	8
1.93	0.890	0.033	0.841	0.041	0.679	0.052	9
2.15	0.981	0.005	0.966	0.010	0.726	0.050	9
2.33	0.953	0.016	0.971	0.018	0.785	0.058	9
2.54	0.869	0.027	0.879	0.029	0.767	0.059	9
2.74	0.818	0.035	0.752	0.027	0.858	0.040	9
2.94	0.731	0.048	0.646	0.043	0.869	0.054	9

Mean maximum stable heat rate for all muscles 12.3 ± 0.9 mJ/g. s.

Mean maximum force production for all muscles 126.3 ± 10.9 mN/mm²

Mean maximum labile heat for all muscles 13.0 ± 1.8 mJ/g.

Mean ratio $h_{b,\text{max}}/P_{\text{max}}$ for all muscles 0.110 ± 0.010 /s.

Sartorius muscle

Estimated mean sarcomere length (μm)	$h_b/h_{b,\text{max}}$	S.E. of mean	P/P_{max}	S.E. of mean	$H_a/H_{a,\text{max}}$	S.E. of mean	n
1.6	0.874	0.024	0.510	0.048	0.764	0.065	5
1.6*	0.860	0.053	0.519	0.021	—	—	4
1.75	0.948	0.012	0.732	0.032	0.832	0.048	8
1.96	0.969	0.007	0.900	0.024	0.828	0.059	8
2.15	0.954	0.012	0.974	0.013	0.924	0.027	8
2.36	0.891	0.040	0.953	0.020	0.987	0.080	5
2.50	0.845	0.043	0.872	0.032	0.970	0.010	3
2.76	0.797	0.024	0.780	0.091	0.907	0.052	3
2.96	0.703	0.043	0.633	0.141	0.870	0.056	3

Mean maximum stable heat rate for all muscles 14.7 ± 0.5 mJ/g. s.

Mean maximum force production for all muscles 172.3 ± 8.8 mN/mm².

Mean maximum labile heat for all muscles 25.2 ± 1.5 mJ/g.

Mean ratio $h_{b,\text{max}}/P_{\text{max}}$ for all muscles 0.087 ± 0.004 /s.

* Results for 1 mM-caffeine.

fibres by Ramsey & Street (1940) and is generally supposed to differ from the filament overlap curve because of 'creep' (Gordon *et al.* 1966*a,b*).

At sarcomere lengths below $2.20 \mu\text{m}$ the results are different for sartorius and e.l.d. iv muscles. In the latter, both the heat rate and force decline between 2.15 and $1.75 \mu\text{m}$. The relation between heat rate and force is the same in this range of sarcomere lengths as in the range 2.15 – $3.0 \mu\text{m}$ (Fig. 3). In sartorius muscle however, heat rate remains at or near its maximum value until $1.75 \mu\text{m}$, although force declines. At a sarcomere length of $1.6 \mu\text{m}$ however, a decline in heat rate is apparent. Thus,

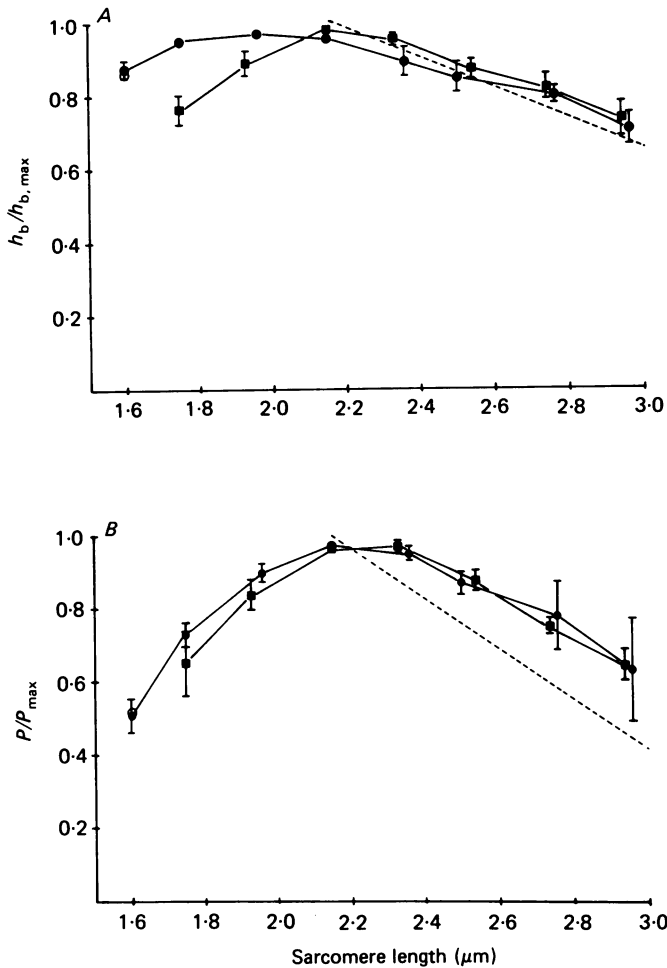


Fig. 2. The dependence of stable heat rate (*A*) and force (*B*) on estimated mean active sarcomere length (see Methods). Results from Table 1. ●, sartorius; ■, e.l.d. iv; ○, sartorius in 1 mM-caffeine. The dashed lines show: in *B* the dependence of filament overlap on sarcomere length and in *A* the expected heat rate if 40% of the rate is independent of sarcomere length and 60% of the rate is proportional to filament overlap.

the relation between heat rate and force in sartorius muscle is different at lengths below $2.2 \mu\text{m}$ than at longer lengths (Fig. 3).

Caffeine potentiates the release of calcium on activation of skeletal muscle and has been reported to increase tetanic force particularly at short sarcomere lengths (Rüdel & Taylor, 1971), but does not always produce this effect (Julian & Morgan, 1981). We therefore tested the action of caffeine (1 mM) in three experiments on sartorius muscle. This potentiated the twitch but had no significant effect on the length dependence of either heat rate or force (Table 1 and Fig. 2). The use of caffeine (0.1 mM) with three e.l.d. iv muscles gave a similar result for tetanic force production,

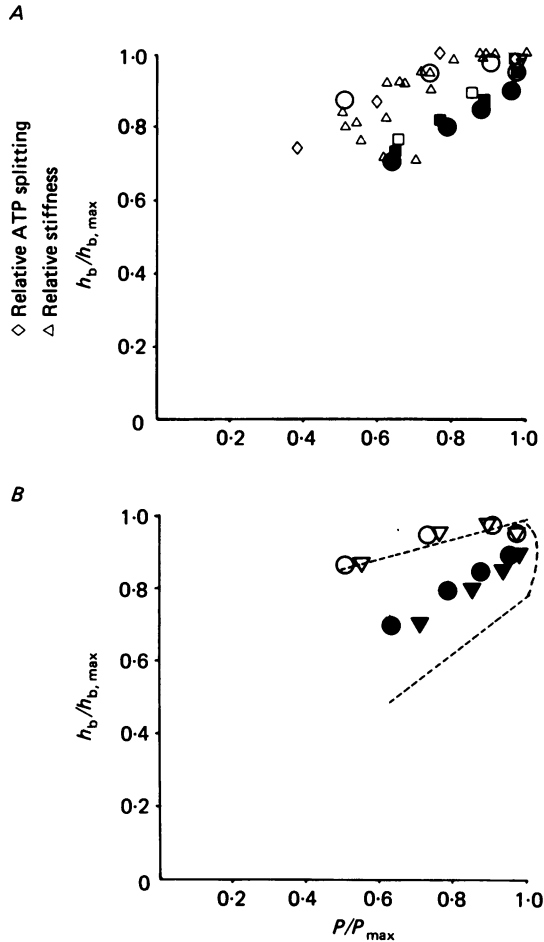


Fig. 3. Relation of normalized stable heat rate and normalized force. Results from Table 1. *A*: ●, sartorius muscle at sarcomere length $> 2.2 \mu\text{m}$; ○, sartorius muscle at sarcomere length $< 2.2 \mu\text{m}$; ■, e.l.d. iv muscle at sarcomere length $> 2.2 \mu\text{m}$; □, e.l.d. iv muscle at sarcomere length $< 2.2 \mu\text{m}$. Results of other workers are also shown as follows: △, stiffness relative to that at *in situ* muscle length. From the experiments of Bressler & Clinch (1975) on sartorius muscle of *Bufo bufo*; ◇, rates of ATP splitting relative to the maximum observed. From the experiments of Sandberg & Carlson (1966) on frog sartorius muscle. *B*: ○, sartorius muscle $< 2.2 \mu\text{m}$ (force measured at 1.5 s); ●, sartorius muscle $> 2.2 \mu\text{m}$ (force measured at 1.5 s); ▽, sartorius muscle $< 2.2 \mu\text{m}$ (force measured at 7 s); ▼, sartorius muscle $> 2.2 \mu\text{m}$ (force measured at 7 s). Dashed lines: normalized stable heat rate. From Aubert & Gilbert (1981), summary of their experiments on frog sartorius muscle.

although caffeine contractures developed at lower concentrations (0.5 mM) than with sartorius (2 mM). Heat production was not measured in these experiments on e.l.d. iv.

For sartorius muscle, the labile heat does not show any clear dependence on muscle length (Table 1), as previously noted by Aubert (1956) and Homsher, Mommaerts,

Ricchiuti & Walner (1972). In e.l.d. iv muscle, the labile heat was, in each of the eight experiments, greater at the longest muscle length used than at the shortest. However, within this range of lengths, the variation in labile heat with length was not consistent.

DISCUSSION

As sarcomere length is increased above $2.15 \mu\text{m}$, there is a decrease in overlap between actin and myosin filaments and fewer cross-bridges can form. As about 60% of the stable heat rate is thought to be due to splitting of ATP by cross-bridges, then this heat rate should decline as sarcomere length increases above $2.15 \mu\text{m}$. This study confirms that stable heat rate decreases in this way. Comparison with the results of Aubert & Gilbert (1981) is difficult; because these authors did not measure sarcomere length systematically, only the relation between force and heat rate in their experiment can be compared to ours. In our experiments force does not decrease in proportion to filament overlap, but remains at its maximum until a sarcomere length of about $2.35 \mu\text{m}$ before declining. This is presumably due to 'creep' and causes the relation between heat and force for long sarcomere lengths to be non-linear near the maximum (Fig. 3). Aubert & Gilbert report a similar, but much more extreme non-linearity (dashed line in Fig. 3*B*). They measured force at the end of a 9 s tetanus. We have therefore also measured force in a similar way: at the end of the 7 s tetani, for comparison. The results (Fig. 3*B*) are still quite different from those of Aubert & Gilbert. We cannot explain why this is so.

Heat production is recorded from the central part of the muscle, which is being slowly stretched by the ends of the muscle, as they shorten during creep. It is very likely that less than 10% of the muscle length is undergoing shortening (Huxley & Peachey, 1961). Within this region, the extent of the shortening during a 7 s tetanus might amount to as much as 10% of its length. The resulting amount of stretch in the central region would thus be no more than 1% of its length, over this period. The effect on the heat production during contraction of a slow stretch is to reduce it slightly. For example, Abbott & Aubert (1951) show that a stretch of 5% during an 8 s tetanus reduces the heat produced by about 5%. Although results with slower stretches have not been reported, it is unlikely that the effects on the heat production are larger than this. Thus, in contrast to force, heat rate is little affected by the phenomenon of creep.

For sartorius muscle, stable heat rate remains at or near its optimum value between 1.75 and $2.15 \mu\text{m}$. These results are similar to previous measurements of heat rate for muscle lengths below the length optimum for force development (Hill, 1925; Fenn & Latchford, 1933; Abbott, 1951; Aubert, 1956; Aubert & Gilbert, 1980). The simplest interpretation of this result is that the number of cross-bridges that can attach and split ATP does not change between sarcomere lengths of 1.75 and $2.15 \mu\text{m}$. We cannot of course, exclude the more complex possibility that the number of active cross-bridges does decrease, but there is a compensating increase in some other heat-producing process. This explanation is made to seem less likely if we consider measurements of two other quantities which are thought to indicate the number of active cross-bridge sites: stiffness and rate of ATP splitting, as shown in Fig. 3*A*. Both of these quantities also initially remain high as muscle length decreases below

the optimum (the stiffness of single frog muscle fibres also remains high for sarcomere lengths between 1.65 and 2.15 μm ; Julian & Morgan, 1981).

There are several reasons why the tension may decline as sarcomere length decreases below the optimum: there may be fewer active cross-bridges, on average each cross-bridge may be exerting a smaller force or some structure other than the cross-bridges might produce a force opposed to the cross-bridge force. The maximum speed of shortening does not change for sarcomere lengths between 1.65 and 2.7 μm (Edman, 1979; Julian & Morgan, 1981), so it seems that passive resistance to shortening does not increase over this range, thus excluding the last of these possibilities. If the number of cross-bridges which can attach and split ATP is decreasing between 1.75 and 2.15 μm , then stable heat rate would decrease also, but if the same number of cross-bridges were active, then the stable heat rate would remain high. The experimental results show that the latter is the case, in sartorius muscle, and so force production in this region of sarcomere lengths must decrease because, for some unknown reason, cross-bridges produce (on average) less force than they could at the optimum sarcomere length.

However, in the e.l.d. iv muscle, stable heat rate does not remain high for short sarcomere lengths but declines linearly with force in the same way that it does for long sarcomere lengths. Measurements of stiffness and rates of ATP splitting for short muscle lengths in e.l.d. iv muscle are not available, but the decline in heat rate suggests that fewer cross-bridges are able to attach and split ATP as sarcomere length is decreased below the optimum. This is not likely to be due to failure of activation, because the decline in force with decreasing sarcomere length below the optimum in e.l.d. iv muscle is similar to that seen in sartorius muscle which appears to be fully activated and because treatment with caffeine does not potentiate the force produced. Thus the number of cross-bridges which can attach to actin at sarcomere lengths below the optimum decreases in e.l.d. iv muscle, in contrast to what is thought to happen in sartorius muscle, perhaps because of some unknown structural difference between the two muscles.

M. Peckham is an M.R.C. Research Scholar.

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