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THE ENERGY LIBERATION OF FROG SKELETAL MUSCLE IN TETANIC CONTRACTIONS CONTAINING TWO PERIODS OF SHORTENING

BY M. IRVING* AND R. C. WOLEDGE

From the Department of Physiology, University College London, Gower Street, London WC1E 6BT

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SUMMARY

1. Heat and work production have been measured in pairs of frog sartorius muscles undergoing two periods of rapid isovelocity shortening at 0 °C. The first (conditioning) shortening occurred in the sarcomere length range 2·70–2·25 μm (as measured in resting muscles) and the second (test) shortening in the range 2·25–2·10 μm. The shortening heat associated with the test shortening was obtained as the difference in heat production between pairs of tetani which were identical except for the presence of the test shortening.

2. The shortening heat associated with the test shortening was reduced when it was preceded by the conditioning shortening; with no interval between shortenings its value was $52 \pm 3\%$ (mean $\pm$ S.E. of mean, $n = 6$) of that without the conditioning shortening. As the interval between shortenings was increased the shortening heat became larger; its recovery was more than half complete with an interval of 0·3 sec.

3. The work produced in the test shortening was also reduced in tetani which contained the conditioning shortening; its dependence on the interval between shortenings was similar to that of the shortening heat.

INTRODUCTION

When an active muscle shortens it produces more energy, both as heat and mechanical work, than in isometric contraction. The extra heat is known as the shortening heat (Hill, 1938). At moderate shortening speeds (when much of the extra energy appears as work) the rate of ATP hydrolysis by the muscle increases (Kushmerick & Davies, 1969; Curtin, Gilbert, Kretzschmar & Wilkie, 1974) and this may account for the additional energy liberation. However, during rapid shortening (when most of the extra energy appears as heat) the rate of ATP hydrolysis is *less* than that in isometric contraction (Kushmerick, Larson & Davies, 1969). Some other process must be responsible for the extra heat produced under these conditions. The results of Rall, Homsher, Wallner & Mommaerts (1976) and Homsher, Irving & Wallner (1981) suggest that this process may be reversed soon after shortening by

* Present address: Department of Physiology, Yale University School of Medicine, 333 Cedar Street, New Haven, CT 06510, U.S.A.

coupling to ATP hydrolysis. If this interpretation is correct, the substrate of the reaction producing the extra energy should be temporarily depleted following the shortening. A second shortening occurring at this time might therefore produce less extra energy than the first. Irving, Woledge & Yamada (1979) looked for such an effect in experiments with repeated periods of shortening, each in a separate tetanus. The minimum interval between shortenings was 5 sec, allowing time for the muscle to relax and be restretched to the original length between tetani. With this interval there was no effect of a 'conditioning' period of shortening on the shortening heat produced in subsequent shortenings. This may have been because the reversal process was already complete by the start of the second shortening. In the present experiments two periods of shortening were studied in a single tetanus, with intervals between shortening ranging from 0 to 1·7 sec.

Preliminary results of these experiments have been presented (Irving & Woledge, 1980).

METHODS

Pairs of sartorius muscles from *Rana temporaria* were used. Ringer solution contained (m-mole/l.) NaCl, 115·0; KCl, 2·5; $CaCl_2$, 1·8; $MgSO_4$, 1·0; NaH_2PO_4, 1·0; Na_2HPO_4, 2·0 (pH 7·0 at 0 °C) and was bubbled with O_2. Muscles were stimulated directly via gold or platinum electrodes with alternating-polarity capacitor discharges at 10 Hz.

The pelvic ends of the muscles were fixed by a bone clamp at the bottom of the thermopile. The tibial tendons were tied to one end of a connecting rod made partly of steel tube and partly of glass tube (to minimise heat conduction). The other end of the rod was connected to a light aluminium lever of the type described by Jewell & Wilkie (1958). Strain gauges mounted on the upper and lower surfaces of the lever were used to monitor muscle tension (Jewell, Kretzschmar & Woledge, 1967). The lever was also connected to a Ling 100 series vibration generator capable of 4 mm axial movement; this corresponded to 8 mm at the muscle because of the lever amplification. A length transducer of the type described by Jewell *et al.* (1967) was attached to the vibration generator and the length was made to follow a control signal by means of a feed-back network (Irving, 1979). The total compliance of the apparatus, measured at the muscle, was 0·50 mm/N.

Heat measurements were made with a Hill-Downing type thermopile (Hill, 1965), 28 mm long with twenty-eight flattened chromel-constantan thermocouples insulated with Kapton-Teflon laminar film, fused together in the gaps between the wires. Connections were made to the thermocouples at a number of points along the thermopile length, so that temperature measurements could be made from selected regions of the muscles. The thermopile was of small thermal capacity ('equivalent half thickness' 17 μm, Hill (1965)). No correction was necessary for the small conduction lag since the heat measurements were all made over a 1 sec interval. Simultaneous recordings of temperature were made from a 16 mm region near the pelvic end of the muscle pair and the adjacent 4 mm region towards the tibial end. The thermopile outputs from these regions were amplified, respectively, by a Kipp A80 galvanometer with photoelectric amplification (Hill, 1965) and an Ancom DC3a chopper amplifier. The difference between the two signals was used to correct the shortening heat measured from the 16 mm region for any longitudinal temperature gradients in the muscles; the details of this procedure are described by Irving *et al.* (1979) (method *A*). The mean value of the correction was only 7 % of the shortening heat. The sensitivity of each region of thermocouples was determined by the Peltier method (Kretzschmar & Wilkie, 1972, 1975). Heat loss from the muscles was exponential with time constants in the range 50–120 sec and was corrected for by the method of Hill (1965). Heat capacity of muscles and thermopile was determined by the method of Hill & Woledge (1962). Shortening heat and work values from different muscles were normalized by dividing by the isometric tension produced at muscle length 2·25 μm/sarcomere.

Work production was calculated by numerical integration of tension with respect to distance shortened with 0·1 mm intervals. The work exchange with series elastic structures was calculated from the tension changes assuming a net stiffness of 1·3 N/mm in series with the muscle sarcomeres.

This value was calculated from the stiffness of the transducers, feed-back network and connections (see above) and the stiffness of the elastic structures at the ends of sartorius muscles, which was assumed to be 100 P_0/l_0 (P_0 is maximum isometric tension; l_0 is standard muscle length) (Jewell & Wilkie, 1958).

Sarcomere lengths were measured in the unstimulated muscle by diffraction using a 2 mW He-Ne laser. Mean sarcomere length was calculated from the separation of the centres of the first-order diffracted beams. Measurements were made with the muscles in position on the thermopile at several points along the central 80% of the muscle length. Sarcomere length within the range 2·1–2·7 μm was linearly related to muscle length. Mean sarcomere length would be expected to decrease on stimulation by about 0·05 μm, based on the series compliance calculated above. Muscle lengths given below are expressed in terms of μm/sarcomere (from the sarcomere length measured in resting muscle); this quantity will thus overestimate the mean sarcomere length during a tetanus by about 0·05 μm.

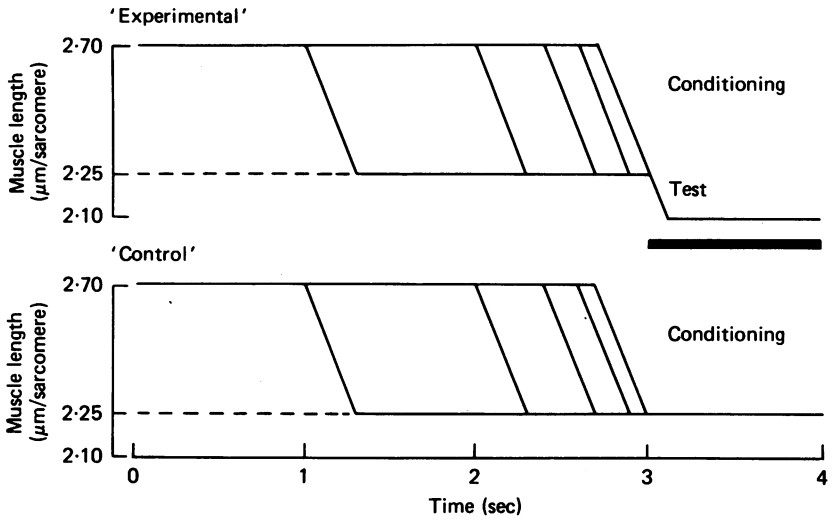

Fig. 1. Experimental design. All tetani were of 4 sec duration and heat production was measured between 3 and 4 sec (horizontal bar). In 'experimental' tetani (upper panel) both a conditioning and a test shortening were imposed, in the length ranges 2·70–2·25 and 2·25–2·10 μm/sarcomere respectively. (Sarcomere lengths were measured in resting muscles). Each shortening occurred at a constant velocity of 1·5 μm/sec per sarcomere. The test shortening always began at 3 sec and was of 0·1 sec duration; the interval between shortenings varied between 0 and 1·7 sec. In 'control' tetani (lower panel) only the conditioning shortening occurred, at the same time as in the corresponding 'experimental' tetanus. In an additional pair of tetani (dashed lines), one with and one without the test shortening, there was *no* conditioning shortening.

After dissection the muscles were left to recover for at least 2 hr at 0 °C. Maximal stimulus parameters were determined, then the timing cycle used throughout the rest of the experiment was begun. This consisted of a period of 15 min with the muscles in Ringer solution alternating with a period of 8 min in air. In the latter period three 4 sec tetani were given, each of which was preceded 90 sec earlier by adjustment to the desired muscle length followed by a twitch to ensure shortening of the muscle to this length. The first of these tetani occurred 2 min after draining the Ringer solution; no measurements were made on this tetanus. The remaining two tetani followed at 3 min intervals. Typically four complete cycles were given to attain steady-state conditions; then the experiment was carried out with a series-and-return design, with each type of tetanus occurring twice. The mean tension developed in the second occurrence was 94% of that in the first.

RESULTS

Experimental design

The experimental design is shown in Fig. 1. In the 'experimental' series (upper panel) a conditioning period of shortening was imposed at various times in the tetanus and was followed after a variable interval by a smaller test shortening, which always started at the same time in the tetanus. In a 'control' series of observations (lower panel) the test shortening did not take place.

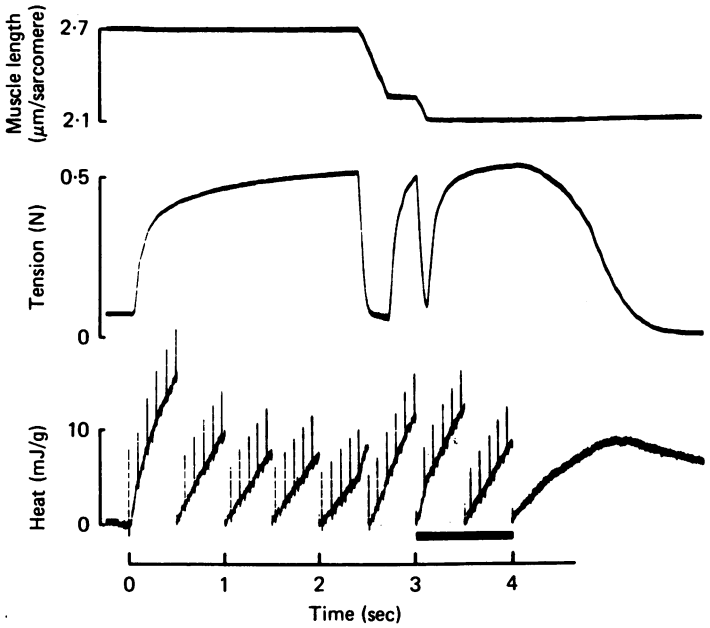

Fig. 2. Muscle length, tension and heat production in a 4 sec tetanus. For the first 2·4 sec the muscles were held at length 2·70 μm/sarcomere. They then shortened at constant velocity to 2·25 μm/sarcomere and were held at this length for 0·3 sec before shortening once more at the same velocity to a final length 2·10 μm/sarcomere. The heat record has been automatically returned to baseline at 0·5 sec intervals; the spikes are artifacts due to the stimuli. The bar denotes the interval over which heat production was measured. Blotted weight of muscle pair was 73·1 mg; muscle length was 26·0 mm at sarcomere length 2·25 μm.

All shortenings occurred at a constant velocity of 1·5 μm . sec^{-1} per sarcomere, which is about half of the maximum shortening velocity. The test shortening took place in the range of muscle length from 2·25 to 2·10 μm/sarcomere, where both isometric tension (Gordon, Huxley & Julian, 1966) and shortening heat (Lebacq, 1972) have their maximum values.

Records of muscle length, tension and heat production during a tetanus containing two periods of shortening separated by a 0·3 sec interval are shown in Fig. 2. At the start of each period of shortening the rate of heat production increased sharply. The total heat production was measured over a 1 sec period beginning with the start of the test shortening (bar in Figs. 1, 2), although the duration of the test shortening itself was only 0·1 sec.

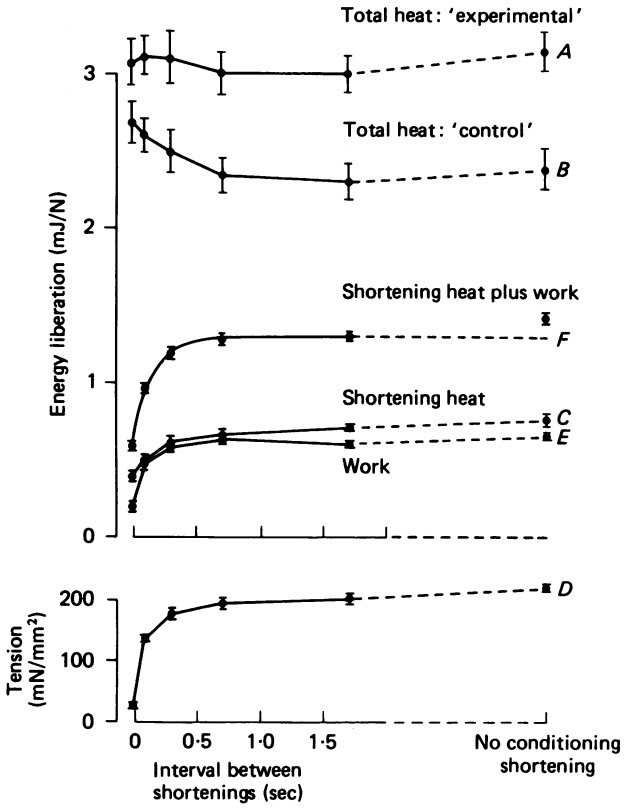

Fig. 3. Energy liberation and tension production as a function of the interval between conditioning and test shortenings (if no test shortening occurs, the abscissa represents the interval between the end of the conditioning shortening and the start of the heat measurement period (see Fig. 1)). The case with no conditioning shortening in the tetanus is represented at the right-hand side; in all other cases a conditioning shortening occurred. *A*, total heat production in the measurement period in 'experimental' tetani (containing a test shortening). *B*, total heat production in the measurement period in 'control' tetani (no test shortening). *C*, shortening heat associated with the test shortening, from paired differences in heat production between 'experimental' and 'control' tetani with the same conditioning (*A*–*B*). *D*, tension immediately preceding the test shortening. *E*, work production (excluding series elastic work) associated with the test shortening. *F*, total extra energy liberation due to the test shortening (*C*+*E*). The continuous curve through points *F* is the line 1·30–0·68 exp(−6·5*t*) mJ/N (*t* is in sec). All points are means ± S.E. of mean from six muscle pairs except those at 0·3 and 0·7 sec, which are from five. Batch parameters for muscle pairs, means (and range): blotted weight, 118·2 (73·1–164·4) mg; isometric tension at length 2·25 μm/sarcomere, 214·9 (188·2–245·8) mN/mm²; total muscle length at 2·25 μm/sarcomere, 27·8 (24·8–32·0) mm; extent of test shortening, 1·95 (1·93–1·97) mm.

Thermal effects of the conditioning shortening

Heat production in the measurement period for 'experimental' tetani in which the test shortening occurred is shown in Fig. 3, line *A*, for various intervals between conditioning and test shortenings. In this case the heat production shows no clear dependence on the inter-shortening interval. However in 'control' tetani (line *B*) heat

production clearly declines with increasing interval between the end of the conditioning shortening and the start of the measurement period. Evidently some extra heat production associated with the conditioning shortening is recorded up to 0·7 sec after its completion. This probably reflects a genuine delay between shortening and the extra heat production associated with it, but other possible mechanisms, such as a lag in heat conduction between muscles and thermopile, have not been excluded.

The extra heat production (shortening heat) associated with the *test* shortening was obtained by pairwise subtraction of 'experimental' and 'control' observations with the same conditioning protocol. The shortening heat associated with the test shortening is shown in Fig. 3, line *C* as a function of the interval between conditioning and test shortenings. With no interval the shortening heat (normalized by isometric tension at 2·25 μm/sarcomere) was reduced to $0{\cdot}397 \pm 0{\cdot}028$ mJ/N (mean $\pm$ S.E. of mean, $n = 6$), about half of its value without the conditioning shortening: $0{\cdot}766 \pm 0{\cdot}034$ mJ/N. It showed a clear monotonic recovery with increasing interval between shortenings, and this recovery was more than half-complete with an interval of 0·3 sec. A small deficit, $0{\cdot}058 \pm 0{\cdot}021$ mJ/N (paired differences, $n = 6$) remained with the largest interval studied, 1·7 sec.

Because the measurement period for these observations (1 sec) is long compared to the duration of the test shortening (0·1 sec), the lag between the shortening and the recording of the associated thermal response cannot affect the shortening heat associated with the test shortening. In addition, components of heat production due to thermoelastic effects (Hill, 1953; Woledge, 1961; Gilbert & Matsumoto, 1976) and length changes in compliant structures in series with the sarcomeres will also have a negligible contribution to the shortening heat determined in this way. This is because tension redevelopment is almost complete at the end of the measurement period (Fig. 2), so the net tension change in this period (for a given conditioning protocol) is almost the same in tetani with and without the test shortening.

In tetani containing the test shortening the muscle length was 2·10 μm/sarcomere for most of the measurement period; when there was no test shortening the muscles remained at 2·25 μm/sarcomere. The difference in heat production, the shortening heat, therefore contains a systematic error due to the length dependence of the isometric heat rate. However the isometric heat production in the measurement period at the two lengths involved was $2{\cdot}38 \pm 0{\cdot}13$ mJ/N (mean $\pm$ S.E. of mean, $n = 6$) and $2{\cdot}42 \pm 0{\cdot}10$ mJ/N respectively, so the difference is negligible compared to the shortening heat (typically 0·6 mJ/N).

Tension and work production

The tension immediately preceding the test shortening is shown in Fig. 3, line *D* for the various intervals between conditioning and test shortenings. For small intervals, the tension had not fully redeveloped from its value at the end of the conditioning shortening, which was 13 % of the isometric tension at the same length. Redevelopment of tension was more than half complete in 0·1 sec, but was still less than the isometric value 1·7 sec after the end of the conditioning shortening. The deficit at this time was $6{\cdot}8 \pm 1{\cdot}9$ % (mean $\pm$ S.E. of mean, $n = 6$, paired differences). The time course of tension redevelopment (Fig. 3, line *D*) was similar to that of the shortening heat recovery (Fig. 3, line *C*), but the proportional change was greater for the former.

The work production associated with the test shortening was calculated by numerical integration of the tension during shortening (see Methods). Small corrections were made to allow for work done *by* series elastic elements during the tension fall at the start of shortening and work done by the muscle *on* series elastic elements during tension redevelopment. The latter component also occurs, with a maximum value of about 0·3 mJ/N, in 'control' observations in which there is no test shortening in the measurement period. Net work production was calculated as the difference in the measurement period between 'experimental' and 'control' tetani, so that the results would be directly comparable with those for shortening heat production.

The work associated with the test shortening is shown in Fig. 3, line *E* as a function of interval between conditioning and test shortenings. With no interval, the work was reduced to 30 % of its value without the conditioning shortening, but a large recovery took place for even a small (0·1 sec) interval between shortenings. However the work production associated with the test shortening was still less than its value without the conditioning shortening, by $9{\cdot}9 \pm 3{\cdot}3$ % (mean ± S.E. of mean, $n = 6$), in the case of the largest interval studied (1·7 sec). As expected, work production is closely related to the tension at the start of the test shortening (Fig. 3, line *D*). In addition, the two components of the extra energy liberation due to shortening – the work and the shortening heat (Fig. 3, line *C*) – show a similar dependence on the interval between shortenings.

Total extra energy liberation due to shortening

The total extra energy production associated with the test shortening, the sum of the shortening heat and the work, is shown as a function of the interval between shortenings in Fig. 3, line *F*. The experimental points for intervals up to 1·7 sec are well fitted by an exponential curve with rate constant 6·5 sec^{-1}, but this curve does not account for the difference between the value at 1·7 sec and that obtained with no conditioning shortening. The recovery of the extra energy liberation associated with the test shortening is dominated by a rapid component with exponential dependence on inter-shortening interval, but there is a small component of slow or incomplete recovery from the effects of the conditioning shortening.

DISCUSSION

The experiments described above have shown that a conditioning period of shortening leads to a reduction in the shortening heat and work produced in a subsequent test shortening. As the interval between shortenings was increased there was a large rapid recovery of the shortening heat and work, but a small reduction remained with the largest interval studied (1·7 sec).

The small long-term reduction in shortening heat and work which occurs as a result of the conditioning shortening is accompanied by a deficit in the tension developed by the muscle under these conditions. The deficits (relative to the corresponding value in a tetanus without the conditioning shortening) in the tension, shortening heat and work were $6{\cdot}8 \pm 1{\cdot}9$ (mean ± S.E. of mean, $n = 6$), $7{\cdot}6 \pm 2{\cdot}7$ and $9{\cdot}9 \pm 3{\cdot}3$ %, respectively, 1·7 sec after the conditioning shortening. Heat production in the isometric state from 1·7 to 2·7 sec after the conditioning shortening was also less than in the corresponding period in a tetanus without the conditioning shortening, by $3{\cdot}5 \pm 1{\cdot}1$ % (mean ± S.E.

of mean, $n = 6$, paired differences) (Fig. 3, line B). The results are therefore consistent with the idea that about 5% of the cross-bridges become unavailable for contractile interaction as a result of the conditioning shortening.

The phenomenon of incomplete tension redevelopment after shortening in tetanic contraction has been investigated in frog sartorius muscles (Maréchal & Plaghki, 1979) and single muscle fibres (Julian & Morgan, 1979). Julian & Morgan showed that most of the sarcomere shortening occurs at the ends of the fibres in releases at low or moderate speeds. The sarcomere length in the centre of the fibre is consequently larger after the release than in an isometric tetanus at the same total fibre length, and this could be responsible for the observed tension deficit. This mechanism would be expected to produce a smaller effect in the case of rapid shortening, and may not operate in whole muscle. Observations of markers on sartorius muscles during rapid shortening indicated that the fractional shortening of a central segment was within 5% of that of the ends of the muscle (Irving, 1979 and unpublished observations). This degree of non-uniformity in a release of 0·45 μm/sarcomere seems too small to account for the magnitude of the tension deficit observed in the present experiments, and it seems likely that some other explanation is required.

The main effect of the conditioning shortening is the large decrease in subsequent shortening heat and work production seen for small intervals between shortenings. The time course of the recovery of these components of the energy liberation is similar to that of tension redevelopment, so it might be possible to interpret the results as a tension-dependence of the shortening heat and work production. Such an effect has in fact been reported for shortening heat production in isotonic releases (Hill, 1964). The shortening heat per unit shortening (α), normalized by the isometric tension (P_0), was found to be related to the steady tension during shortening (P) by the equation

$$\alpha/P_0 = 0{\cdot}16 + 0{\cdot}18\,P/P_0.$$

There is no evidence that this relationship would apply from moment to moment during isovelocity releases, but if it did it would predict a reduction in the shortening heat in the second of two periods of shortening, when the interval between them was sufficiently small to cause a reduction in mean tension in the second shortening. In the present experiments the mean value of P/P_0 for the test shortening was 0·128 with no interval between shortenings and 0·397 when there was no conditioning shortening. The equation above predicts that this would produce a shortening heat reduction of 21% in the case of no interval between shortenings, compared with the observed reduction of 48%. The load dependence of the shortening heat observed in isotonic releases is therefore too small to account for the results of the present experiments. Thus shortening heat is not solely an instantaneous function of muscle tension.

The correspondence between work production in the second of two shortenings and tension redevelopment after the first shortening is expected; in terms of cyclical models of muscle contraction (Huxley, 1957) both of these quantities reflect net re-attachment of cross-bridges after shortening. The parallel behaviour of the shortening heat suggests that its production is also related to cross-bridge cycling. The observation that shortening heat and isometric tension have a similar dependence on sarcomere length (Lebacq, 1972; Irving, Homsher & Lebacq, 1980) supports this view. Shortening heat production is not accompanied by simultaneous extra ATP

hydrolysis; rather it seems that extra ATP is hydrolyzed *after* shortening (Rall *et al.* 1976; Homsher *et al.* 1981). It therefore would be wrong to interpret shortening heat as an increase in the number of complete cross-bridge cycles with each cycle involving the hydrolysis of one ATP molecule. The results of Rall *et al.* imply that rapid shortening is accompanied by a net exothermic transition between cross-bridge states. After shortening, the original distribution of cross-bridge states would then be restored by a pathway involving ATP hydrolysis. The results of the present experiments fit neatly with this hypothesis; until the original cross-bridge states are repopulated after the first shortening, the net transition responsible for extra energy liberation cannot occur to its full extent in a subsequent period of shortening. The time course of the recovery of the extra energy liberation (Fig. 3, line *F*) suggests that the net transition between cross-bridge states after shortening occurs with a rate constant of 6·5 sec^{-1}.

M.I. was an M.R.C. Research Scholar.

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