EFFECTS OF SPEED AND EXTENT OF STRETCHING ON THE ELASTIC PROPERTIES OF ACTIVE FROG MUSCLE*

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SUMMARY

The work done during fast recoil of active striated muscle (as in a jump) was measured at 2 and 12 °C by making tetanized frog sartorii shorten from about 2 mm above slack length, l_0, at high speed (6–9 $l_0 . s^{-1}$) (1) during a state of isometric contraction and (2) after stretching the muscle, while active, at different speeds and by different amounts. The work done increases with the force developed by the muscle according to a sigmoidal curve, having a point of inflexion that is displaced to greater values of force at 12 °C than at 2 °C. Previous stretching leads to an upward shift of this curve, i.e. to an iso-force gain of energy. This gain increases towards a maximum as the speed and extent of stretching are increased, attaining 60–80% of the total work done from a state of isometric contraction; this fraction decreases when stretching begins from lengths smaller than l_0. The apparent elastic behaviour of muscle is thus described by a set of curves rather than by a single curve. Active muscle behaves as a more rigid structure when it transmits the generated force to an external load (as in an isometric contraction) and as a more compliant structure when, stretched by an external force, it has the opportunity to store external mechanical energy.

INTRODUCTION

Muscles must satisfy two contradictory requirements. Their contractile machinery needs to be connected to the external load by a link sufficiently rigid to transmit the generated force quickly and effectively. On the other hand, in some exercises (e.g. running) the contracted muscles behave mainly as elastic bodies and require a compliant structure capable of storing a large amount of energy during stretching without attaining excessively high and dangerous force values. The solution of this dilemma could be that the contracted muscle, when it is stretched and released, behaves as a more compliant structure than when it develops force and is subsequently released

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during a state of isometric contraction. In fact, Cavagna & Citterio (1974) found that the elastic behaviour of contracted muscle was modified in this way as a result of previous stretching. As a consequence of this modification, a greater amount of 'elastic' energy is released by a muscle which has been stretched, even when this energy is measured for the same reduction of force at the muscle extremities. In this paper we have investigated the effect of the speed and amount of stretching, temperature and average muscle length on this iso-force gain of energy, which may represent 60–80% of the 'elastic' energy released from a state of isometric contraction. The results provide a possible explanation of the finding that the role of 'elastic' storage and recovery becomes relatively more important with the increase of running speed both in man (Cavagna & Kaneko, 1977) and in some animals (Dawson & Taylor, 1973; Alexander & Vernon, 1975; Cavagna, Heglund & Taylor, 1977).

METHODS

The experiments were carried out on sartorii of *Rana esculenta* (resting muscle length, l_0, 2.96 ± 0.30 cm, M, 0.088 ± 0.025 g, mean and S.D., $n = 21$). The muscles were bathed in oxygenated Ringer solution kept at 2 °C or 12 °C. In order to rule out the possible interference of neuromuscular transmission, in some experiments curare was added at a concentration of $7.5 \cdot 10^{-5}$ g.ml^{-1}: the results were not affected by this procedure.

Stimulation

Two platinum electrodes (3.1 cm.0.5 cm) were placed 0.9 cm apart on either side of the muscle. Supramaximal stimuli were given by means of condenser discharges alternating in polarity: the maximum voltage of each shock, measured across the electrodes in saline was about 19 V, declining according to a time constant of $1–1.5$ ms. The frequency of the impulses was the smallest serving to produce a fused tetanus: 12 and 38 Hz respectively at 2 and 12 °C.

Measurement of the force developed by the muscle

A strain-gauge force transducer was fixed at the bottom of the muscle chamber and was protected from the surrounding saline by means of a rubber shield. The transducer has a compliance (measured at the level of muscle attachment) of 9 μm.N^{-1}; its natural frequency is 3150 Hz in air and 2500 Hz in Ringer. The error due to the dynamic response of the transducer was calculated according to Ford, Huxley & Simmons (1977, appendix F) and found to be always less than 3%: it was therefore ignored.

Muscle attachment

A piece of the pelvic bone was slid under a narrow slit in the plexiglas cover of the transducer; the yielding structures at this extremity of muscle were therefore the tendon and the transducer. The attachment of the distal muscle extremity was made as follows: a thread was wound and knotted four times round the tendon as near as possible to the muscle (the length of the tendon between the knot and the muscle

res was less than 1 mm) and the knot was slid above a thick iron loop at one end of a rigid bar connecting this extremity of the muscle to a Levin and Wyman ergo-meter. The compliance at this extremity was therefore that of the tendon below the knot and that due to the compression of the knot against the iron loop. The overall stray compliance of the apparatus and of the connexions was negligible; in fact the recoil of the elastic elements of frog sartorius, measured by means of this apparatus, was on the average about equal to that reported by Jewell & Wilkie (1958) and Hill (1970) after correction for the stray compliance of their apparatus.

Length changes

Stretches (0·2–4 mm) were imposed on the muscle by means of a Levin and Wyman ergometer driven by compressed air. The extent of shortening imposed (2–4 mm) was always such that the force developed by the muscle fell to zero. In order to avoid large vibrational disturbances a gradual acceleration of the lever was allowed, with the consequence that the speed of shortening was increasing during most of the fall of the force (Fig. 1). An average speed of shortening was therefore calculated from the distance shortened and the time taken for the muscle force to fall to zero. This speed was 180 mm.s^{-1} during shortening from a state of isometric con-traction, 210 mm.s^{-1} after slow stretching and 285 mm.s^{-1} after fast stretching. These values could be reduced appreciably before steady cycling of bridges increased the measured length change. The time necessary for the force to fall to zero was 4–5 ms. The speed of stretching was often affected by some oscillation: the values given in the results indicate average speeds.

Experimental records

The displacement signal from the Levin and Wyman ergometer was fed to the X plates of an oscilloscope, and the output of the force transducer to the Y plates, in order to obtain dynamic force–length diagrams. At the same time force and length were also recorded as a function of time on another oscilloscope (Fig. 1). An adequate number of points on the force–shortening tracing (differing according to the details of the curve) was fed into a microcomputer to calculate and plot average stress–strain and work–stress curves (Figs. 2 and 3).

Experimental procedure

The contracted muscle was stretched from a length (l_0) at which it still exerted the maximal isometric force (P_0), but above which the isometric force declined. In the study of the effect of the speed of stretching, the lengthening of muscle was on average 6·8% of l_0 (about 2 mm), whereas in the study of the effect of the extent of stretching it ranged from 0·5 to 14% of l_0 and was applied at speeds greater than 0·5 l_0.s^{-1}. At the length attained during stretching, l_{mx}, the isometric force was only slightly smaller than at l_0 and the force exerted by the parallel elastic elements was still a negligible fraction of that developed by the active muscle. The experiments used to construct the average curves in Fig. 2 comprised six tetani, organized in mirror pairs: in one pair (at the beginning and at the end of the experiment) the muscle was released from l_{mx} during a state of isometric contraction, in the second pair (tetani 2 and 5) the
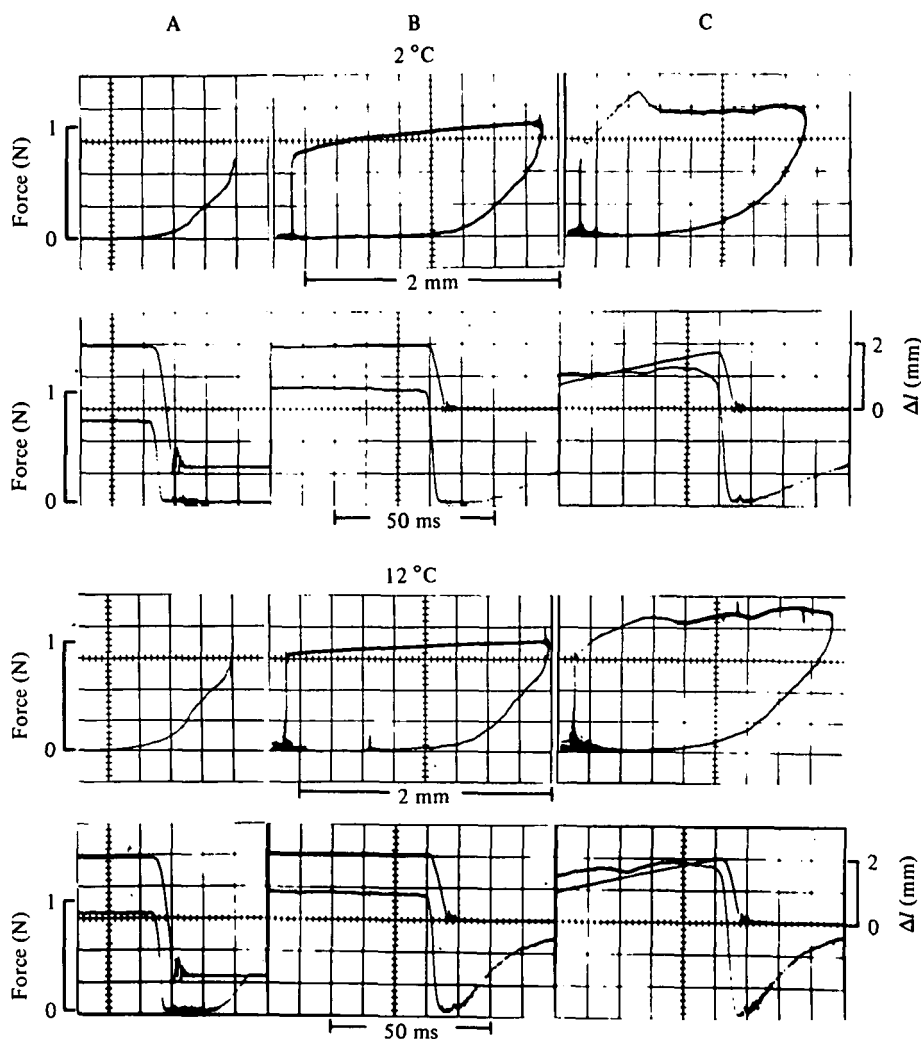
Fig. 1. Dynamic force–length diagrams determined on a frog sartorius (l_0 = 3·05 cm, M = 0·088 g) tetanically stimulated at 2 °C (1st row) and 12 °C (third row): (A) during shortening from a state of isometric contraction at a length 2 mm above l_0; (B) during stretching at low speed (0·033 $l_0.s^{-1}$) from a length equal to l_0, followed immediately by shortening; (C) as in (B) but with a greater speed of stretching (0·72 $l_0.s^{-1}$). The corresponding force–time (lower) and length–time (upper) tracings (recorded immediately before, during and after shortening) are shown in the second and fourth row. The average speed of shortening was 191–251 mm.s^{-1} (6·3–8·2 $l_0.s^{-1}$).

muscles were released from l_{mx} after having been stretched slowly (1·1 mm.s^{-1}) by about 2 mm in excess of l_0; in the third pair (tetani 3 and 4) the muscles were released from l_{mx} after having been stretched rapidly (22·9 mm.s$_0^{-1}$) by about 2 mm in excess of l_0.
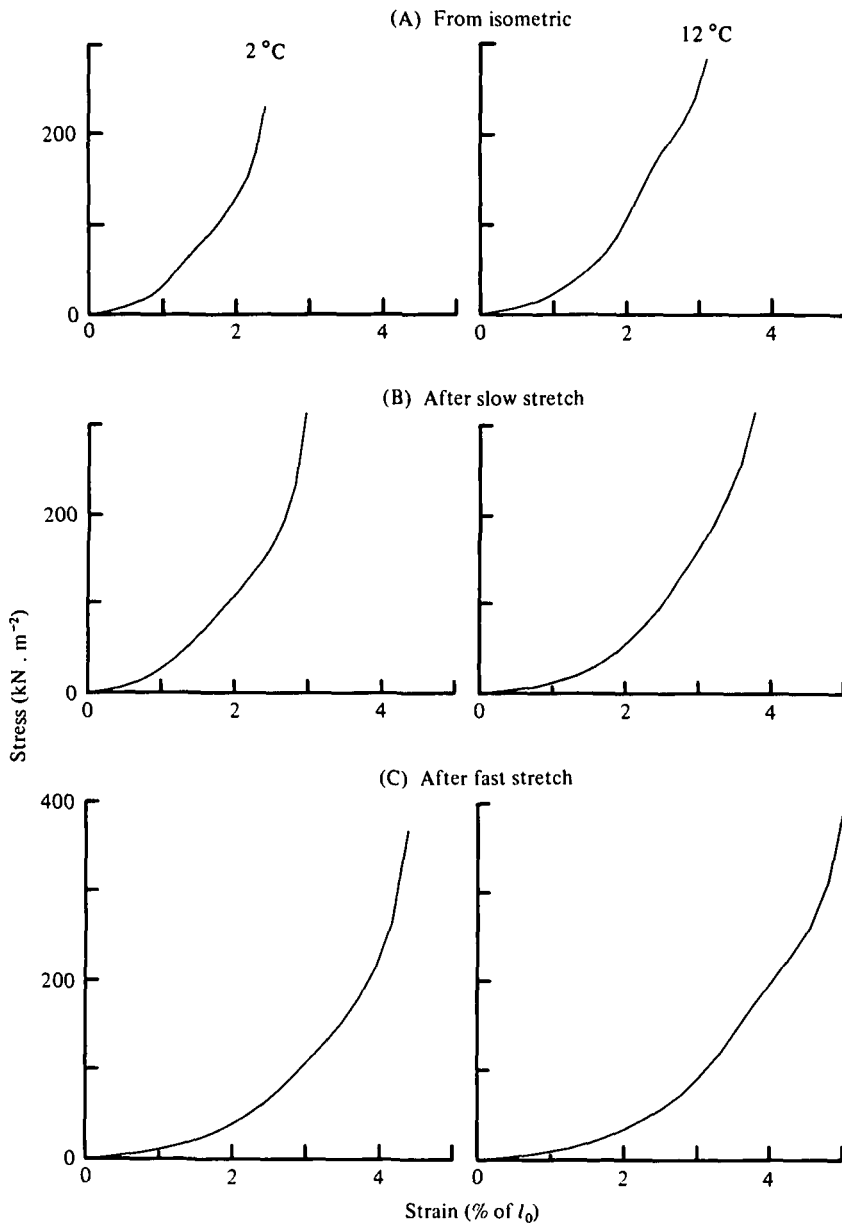
Fig. 2. Average stress–strain curves (stress $P\rho l_0 . M^{-1}$, where ρ is the muscle density, which was taken to be the same as that of water, strain $\Delta l . 100 . l_0^{-1}$) determined during release of frog sartorii tetanically stimulated at 2 and 12 °C. The curves (from top to bottom) refer to shortening at $6-9.5\ l_0 . s^{-1}$: (A) from a state of isometric contraction at a length 2 mm above l_0; (B) immediately after stretching from l_0 to $(l_0 + 2$ mm) at low speed ($0.035\ l_0 . s^{-1}$); (C) as in (B) but after stretching the muscle at greater speed ($0.75\ l_0 . s^{-1}$). The average curves were calculated and plotted by means of a microcomputer: standard deviation of stress values decreases progressively from about 20 %, below 30 $kN . m^{-2}$, to 7 % at peak stress values ($n = 20$ for the curves at 2 °C (10 muscles) and $n = 8$ at 12 °C (4 muscles), except for slow stretch where $n = 6$ (3 muscles)).
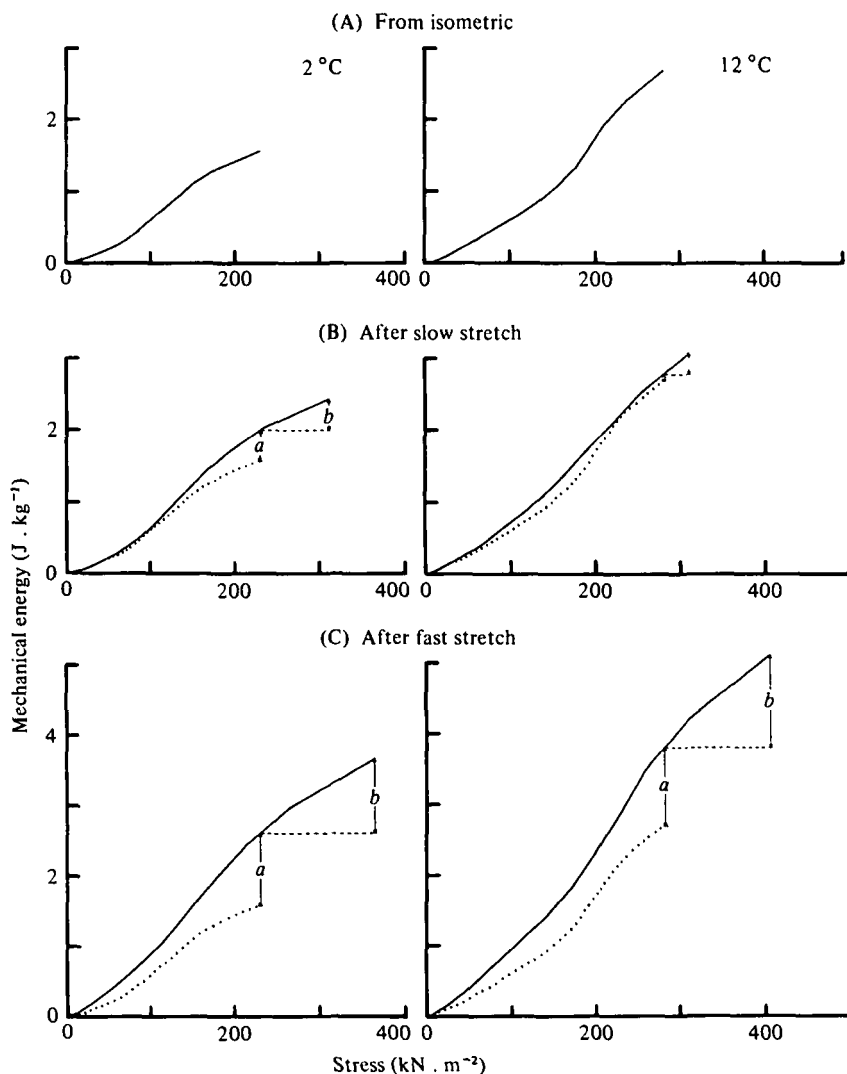
Fig. 3. The work done during release (calculated from the area below the curves in Fig. 2) is plotted as a function of the stress. The amount of additional work done after stretching is given as the sum of (*a*) the work done during the decrease of the force from the isometric value, P_0, to zero; and (*b*) the work done during the decrease of the force from its maximal value to P_0.

RESULTS

Release from a state of isometric contraction

Average stress–strain curves obtained during recoil of frog sartorius from an isometric tetanus at 2 °C (left) and 12 °C (right) are given in the upper tracings, A, of Fig. 2. The mechanical energy has been calculated from the area below the curves and plotted as a function of the stress in Fig. 3. This figure shows for each stress the strain–energy which is released in the subsequent shortening. Average values of stress, strain and energy are given in Table 1. The experimental tracings in Fig. 1 and the

Table 1. Average values of maximum developed stress before shortening and mechanical energy delivered by frog sartorius in controlled releases at 2 and 12 °C

(Average values of maximum developed stress ($P\rho l_0.M^{-1}$, where ρ is the muscle density, which was taken to be the same as that of water) before shortening from a length 2 mm above, l_0, maximum length change during recoil (strain $= \Delta l.100.l_0^{-1}$) and mechanical energy ($SP\rho l.M^{-1}$) delivered by frog sartorius in controlled releases at 2 and 12 °C. Muscle shortened from a state of isometric contraction (top) and immediately after stretching at low (middle) and high speed (bottom). The data refer to the curves in Figs. 2 and 3.)

	Temperature (°C)	Maximum stress (kN.m⁻²)	Maximum strain (% of l_0)	Mechanical energy (J.kg⁻¹)			
				Total	From F_{mx} to $F = P_0$ (b in Fig. 3)	From $F = P_0$ to zero	From $F = P_0$ to zero in excess of isometric (a in Fig. 3)
From isometric contraction	2	230·5±18·6	2·42±0·26	1·57±0·21	—	—	—
	12	283·4±14·7	3·11±0·40	2·69±0·27	—	—	—
After slow stretch	2	312·8±23·5	2·97±0·26	2·44±0·23	0·42±0·15	2·02±0·16	0·45±0·12
	12	313·8±19·6	3·77±0·41	3·06±0·15	0·18±0·12	2·88±0·13	0·06±0·21
After fast stretch	2	365·8±27·5	4·39±0·37	3·61±0·38	0·97±0·24	2·64±0·24	1·06±0·25
	12	409·0±17·7	5·06±0·60	5·04±0·25	1·20±0·34	3·84±0·33	1·15±0·33

Values are given as mean ± S.D.; $n = 20$ for the data at 2 °C (10 muscles); at 12 °C $n = 8$ (4 muscles), except for slow stretch where $n = 6$ (3 muscles). Average muscle length, l_0, is 3·11 ± 0·15 cm (mean ± S.D., $n = 10$) at 2 °C and 2·98 ± 0·12 cm ($n = 4$) at 12 °C; average muscle mass is 0·096 ± 0·024 g at 2 °C and 0·83 ± 0·003 g at 12 °C. Average speed of slow stretching is 1·1 mm.s⁻¹; average speed of fast stretching is 22·9 mm.s⁻¹. Extent of stretching is about 2 mm.

average curves in Fig. 2 reveal a 'shoulder' which is more evident and occurs soon after release (i.e. at higher values of stress) at 12 °C than at 2 °C. As a consequence of this 'shoulder' the energy–stress curve is sigmoidal in shape and displays a point of inflexion; this point of inflexion occurs at higher stress values at 12 °C than at 2 °C (Fig. 3).

Release after a given amount of stretching at different speeds

The middle and lower curves in Fig. 2 were obtained by releasing the contracted muscle about 50 ms after stretching it at low speed, B, and about 2 ms after stretching it at high speed, C. The stress–strain curves obtained after stretching are more compliant than those relating to release from a state of isometric contraction, indicating a modification of the apparent elastic properties of muscle as a result of previous stretching (Cavagna & Citterio, 1974). The present results show that this modification increases with increasing speed of stretching. The effect of previous stretching is better shown by the curves describing the mechanical energy released as a function of the stress. Like those relating to recoil from a state of isometric contraction, these curves are sigmoidal in shape and display a point of inflexion which occurs at higher values of stress when the temperature is increased from 2 °C to 12 °C. As expected, the mechanical energy released after stretching is greater than that released when shortening begins from an isometric tetanus. The difference can be divided into two parts of about the same order of magnitude, a and b in Fig. 3: b is the mechanical energy released because, after stretching, the force starts falling from a value greater than P_0; a, on the contrary, is the additional mechanical energy released after stretching for the same fall of force (from P_0 to zero). Since the fall of force is the same, the additional mechanical energy a must be due entirely to the modification of the mechanical properties of muscle induced by previous stretching; a was therefore taken as an index of this modification. It increases with the speed of stretching to a maximum, attained at about $0 \cdot 5 \, l_0 . \mathrm{s}^{-1}$, which seems to be slightly greater at 12 °C than at 2 °C (Table 1). However, if a is expressed as a percentage of the mechanical energy released when shortening begins from a state of isometric contraction, the relative increase due to stretching is greater at 2 °C than at 12 °C.

Effect of the extent of stretching

In Fig. 4 a is plotted as a function of the extent of stretching. In order to rule out the effect of the speed of stretching, we plotted only the data obtained when the speed of stretching exceeded $0 \cdot 5 \, l_0 . \mathrm{s}^{-1}$. In spite of the large scatter of the experimental data, it appears that a critical length change of about 5–6% of l_0 is required in order to attain the maximum iso-force gain of energy. This represents a substantial fraction of the total energy released during fast recoil of the muscle. After fast and large stretches at 2 °C, a amounts to 80% of the energy released from a state of isometric contraction, W_0. At 12 °C this percentage is reduced to about 60%, mainly due to the increase with temperature of P_0 and consequently of W_0.
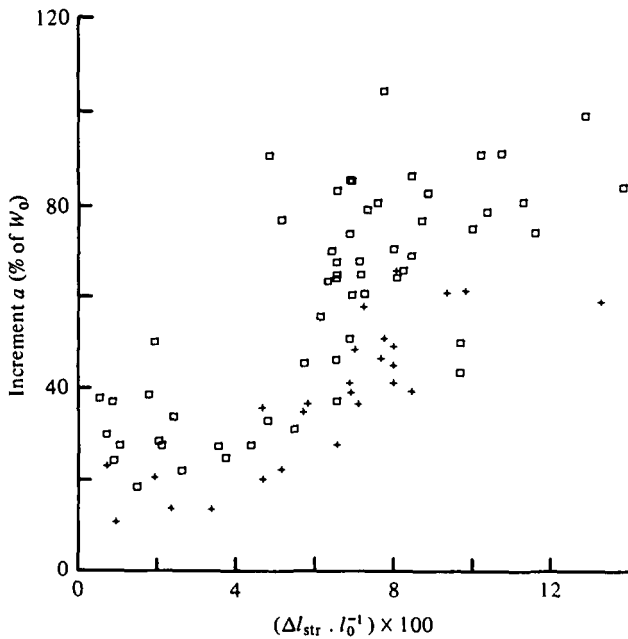
Fig. 4. The increment a in Fig. 3 (given as a percentage of the mechanical energy delivered from a state of isometric contraction, W_0) is plotted as a function of the extent of stretching of the contracted muscle (Δl_{str}, given as a percentage of l_0). The data are from 18 frog sartorii at 2 °C (squares) and 10 frog sartorii at 12 °C (plus sign). The speed of stretching was always greater than $0.5 \, l_0.s^{-1}$.
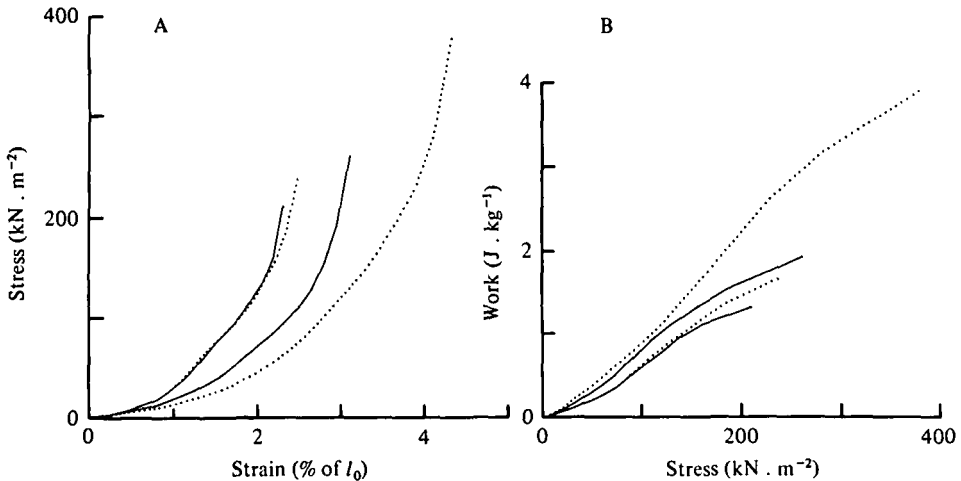

Fig. 5. Average stress–strain (A) and work–stress (B) curves of 4 frog sartorii ($l_0 = 3.1$ cm, $M = 0.089$ g, 2 °C) relating to release from 2 mm above l_0 (dotted lines, $n = 8$) and 5 mm below l_0 (continuous lines, $n = 4$), from a state of isometric contraction and immediately after stretching (2 mm at $0.73 \, l_0.s^{-1}$). The curves reaching the greater values of stress were obtained after stretching. The curves relating to the state of isometric contraction do not differ appreciably at the two lengths; the effect of previous stretching is much more pronounced at the greater length. Standard deviation of stress values decreases progressively from about 20 %, below 30 kN.m^{-2}, to 13 % at peak stress values.

Effect of average muscle length

All the results reported above were obtained by stretching the muscle from its optimal length, l_0. Stretching the tetanized muscle from lengths smaller than l_0 always reduced the enhancement due to previous stretching. The work–stress curves given in Fig. 5 are an average of those obtained in four experiments performed by releasing the muscle from the usual length (2 mm above l_0) and from a length 5 mm less than l_0. It can be seen that the upward shift of the work–stress curve, induced by previous stretching, is much smaller at the smaller length. But when shortening begins from a state of isometric contraction, there is little difference between the work–stress curves at the two lengths.

<div align="center">DISCUSSION</div>

Muscle 'elastic' elements: stiff or compliant?

Fig. 2 shows that the average stiffness of the muscle elastic elements is much greater, in the range from P_0 to zero, during recoil from a state of isometric contraction, A, than after fast stretching, C. The upper curves in Fig. 2 were obtained when the force was decreasing during shortening of the muscle. The greater stiffness revealed by these curves implies that, even during development of tension, the force can be transmitted more rapidly to the external load. If the stiffness were as low as that revealed by the lower curves in Fig. 2, a greater extension of the connecting structures, and consequently a greater delay of force transmission, would be necessary.

On the other hand the greater compliance (reduced stiffness) exhibited when shortening follows fast stretching (Fig. 2, C) means that the force is maintained for a longer shortening distance, i.e. a greater amount of positive work is done for a given reduction of force. This is shown by the upward shift of the energy–stress curves in Fig. 3 in the after-stretch condition: this shift indicates a substantial iso-force gain of energy induced by previous stretching. Without this modification of the elastic behaviour, the release of the same amount of mechanical energy would require the extrapolation of the top curves in Fig. 3, A, to force values unattainable by the contractile component. contractile component.

Thus, instead of compromising by adopting connecting structures of intermediate stiffness to meet the two contrasting requirements of fast force generation and appreciable storage of external mechanical energy, the striated muscle changes its mechanical characteristics according to need and behaves as a more rigid structure when the force is developed internally and as a more compliant structure when shortening immediately after being stretched by an external force.

Effect of the speed of movement

Experiments on animal locomotion have suggested that the elastic storage and recovery which takes place at each step becomes more efficient as the speed of movements increases (Dawson & Taylor, 1973; Alexander & Vernon, 1975). The present data suggest that this greater efficiency is due at least in part to the increase of the iso-force gain of energy resulting from the increase of the speed of stretching (Fig. 3). The mechanical energy stored in the tendons must also be taken into account, parı

ularly in the case of those muscles having long tendons and short fibres (Alexander & Bennet-Clark, 1977; Cavagna, Citterio & Jacini, 1979).

Shape of the force-length curve

The 'shoulder' in the curves of Fig. 2 and, as a consequence, the sigmoidal shape of the work–stress curves in Fig. 3, are probably due to the release of energy by the rotation of the heads of the myosin over the actin (Huxley & Simmons, 1971; cf. also fig. 29 of Ford *et al.* 1977). The present results show that: (1) this energy output occurs sooner after release at higher temperature (shift to the right of the inflexion point of the curves in Fig. 3); and (2) the inflexion of the work–stress curves is more pronounced after fast stretching than after slow stretching.

Recoil of tendons and sarcomeres

According to the findings of Ford *et al.* (1977), the sarcomeres can shorten about $1\cdot33\%$ of their initial length (i.e. 14 nm.half sarcomere^{-1}) within 2–5 ms after release from a state of isometric contraction at 0–3 °C (before steady cycling of bridges begins). In the present experiments the average recoil from a state of isometric contraction at 2 °C is $2\cdot42\%$ of l_0 and occurs in 4·4 ms. The total shortening of tendons (t) plus sarcomeres (x) over the recoil of sarcomeres will then be $(t+x)/x = 2\cdot42/1\cdot33$, and consequently $t = 0\cdot82\,x$.

This confirms the conclusion of Jewell & Wilkie (1958) who found that the total recoil of frog sartorius from a state of isometric contraction consisted almost equally of the recoil of tendons and that of sarcomeres.

The force attained at the end of stretching is greater than the isometric force; as a consequence the recoil of the tendons will be greater when shortening follows stretching than when it takes place from a state of isometric contraction. However, the force–length curves obtained during shortening in the two different conditions can be compared over the same range of forces, e.g. from the isometric value (P_0) to zero. Fig. 2 shows that the length change taking place after fast stretching when the force falls from P_0 to zero is 1·67 times greater (at 2 °C) than the length change taking place after release from a state of isometric contraction. Assuming that when the force falls from P_0 to zero the recoil of tendons (t) is the same in both conditions: $(t+z)/(t+x) = 1\cdot67$, where z is the shortening of the sarcomeres occurring after stretching for the same fall of the force. Since $t = 0\cdot82\,x$, $z = 2\cdot22\,x$. Since $x = 14$ nm. half sarcomere^{-1} (Ford *et al.* 1977), $z = 31$ nm.half sarcomere^{-1} (this value is close to those given by Rack & Westbury, 1974). It must be emphasized that z is the recoil of the most strained bridges and that a fraction of them could shorten less than that. The additional shortening of the most strained bridges is therefore $31-14 = 17$ nm.half sarcomere^{-1}. The additional energy simultaneously released is 1·06 J.kg^{-1} or about 1 mJ.m^{-2}.half sarcomere^{-1} (increment a in Table 1: this is an underestimated value when referred to a most-strained half sarcomere because some sarcomeres within the muscle may be less strained). This figure compares closely with the potential energy difference between two 'preferred' cross-bridge states calculated by Flitney & Hirst (1978*b*). According to these authors this energy difference is absorbed by the cross-bridges during stretching with the consequence that their energy level at the end of stretching

is greater than the isometric energy level. The present results suggest that th[...] additional amount of energy is given back, in some conditions, during subsequent shortening (increment a).

Effect of speed, extent of stretching and average muscle length

The effect of the speed of stretching can be understood if one considers that during the time in which the bridges remain attached to the actin, the elastic elements within the bridges stretch more when stretching takes place at high speed. As mentioned above, a greater extension of the bridges leads to a greater recoil of the whole muscle (Fig. 2). A small extent of stretching, even if imposed at high speed, does not lead to the maximum iso-force gain of energy (Fig. 4). According to Flitney & Hirst (1978a) the amount of stretching required to induce sarcomere 'give' is an index of the range of movement over which a cross-bridge can remain attached to actin during a stretch (about 1.2% of the sarcomere length). At the end of this displacement the heads of the myosin would have been rotated backwards (fig. 7 of Flitney & Hirst, 1978b); they could therefore reverse their movement, releasing mechanical energy during sub-sequent shortening over the distance of about 30 nm calculated above. The present experiments, however, show that if after stretching the muscle is released just before or after the 'give' point (i.e. after a length change of about 1.7% of l_0 in Fig. 1) the gain of energy (increment a) is much smaller than when the extent of stretching is increased to over 6% of l_0 (Fig. 4). In other words, the extent of stretching necessary to cause muscle 'give' is appreciably smaller than that required to obtain the maximum iso-force gain of energy.

Previous stretching of the active muscle not only leads to the described modification of its 'elastic' properties, but also to a shift towards higher force values of the force-velocity curve (Cavagna & Citterio, 1974; Edman, Elzinga & Noble, 1978). Further-more, it has been reported by Edman, Elzinga & Noble (1978) that the shift of the force–velocity relation is particularly evident when stretching occurs at the greater muscle lengths; the present findings show that this is also true with regard to the modification of the elastic properties of muscle.

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