*J. exp. Biol.* ***183****, 137–147 (1993)*
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# EFFICIENCY OF ENERGY CONVERSION DURING SINUSOIDAL MOVEMENT OF WHITE MUSCLE FIBRES FROM THE DOGFISH *SCYLIORHINUS CANICULA*

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*Accepted 21 June 1993*

## Summary

Net work output and heat production of white myotomal muscle fibres from the dogfish were measured during complete cycles of sinusoidal movement at 12°C. The peak-to-peak movement was about 9% of the muscle fibre length; three stimuli at 32ms intervals were given in each mechanical cycle. The frequency of movement and the timing of the stimulation were varied for each preparation to find the optimal conditions for power output and those optimal for efficiency (the ratio of net work output to total energy output as heat+work). To achieve either maximum power or maximum efficiency, the tetanus must start while the muscle fibres are being stretched, before the beginning of the shortening part of the mechanical cycle. The highest power output, averaged over one cycle, was 0.23±0.014 $W g^{-1}$ drymass (±S.E.M., $N$=9, 46.9±2.8mW $g^{-1}$ wetmass) and was produced during movement at 3.5Hz. The highest efficiency, 0.41±0.02 (±S.E.M., $N$=13), occurred during movements at 2.0–2.5Hz. This value is higher than the efficiency previously measured during isovelocity shortening of these fibres. The implications of the high efficiency for crossbridge models of muscle contraction are discussed.

## Introduction

Efficiency of muscle contraction can be defined as the net work output for each ATP molecule used. This quantity is of vital importance to an animal because it determines the distance the animal can travel on a given supply of metabolic fuel and the speed of travel when the rate of energy expenditure is limited, for example, when it is matched to the rate of oxygen supply.

Although muscle efficiency has been investigated in relatively few species, it clearly varies among species. In many studies, efficiency was measured for muscles undergoing shortening at a steady velocity or under a fixed load (Kushmerick and Davies, 1969, frog; Hill, 1964, frog; Aubert, 1956, frog; Heglund and Cavagna, 1987, frog, rat; Woledge,

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Key words: muscle, fish, dogfish, efficiency, mechanical power, heat, *Scyliorhinus canicula.*

1968, tortoise; Curtin and Woledge, 1991, dogfish). In other studies of efficiency, the muscle was subjected to oscillatory length changes like those that occur *in vivo* (Josephson and Stevenson, 1991, locust; Moon *et al*. 1991, cod). Here we report experiments on dogfish muscle in which we used sinusoidal length changes and a stimulus regime estimated to be like that during swimming. The maximum efficiency was greater than that found in an earlier study of efficiency during shortening at uniform velocity (Curtin and Woledge, 1991). The relatively high value of efficiency can be accommodated by some models of the crossbridge cycle, but not by others.

## Materials and methods

Dogfish, *Scyliorhinus canicula* (L.) from the holding tanks at the Citadel Hill site of the Plymouth Marine Laboratory were killed by decapitation followed by pithing. Large fish, ranging in length from 570–660mm, were selected. Bundles of 2–14 fibres were dissected under saline from thin slices of the white myotomal muscle taken from the immediate post-anal region. A piece of myoseptum at each end of the bundle was held in a platinum foil clip. The saline solution contained ($mmol\,l^{-1}$): NaCl, 292; KCl, 3.2; $CaCl_2$, 1.8; $MgCl_2$, 2.2; $Na_2SO_4$, 3.5; $NaHCO_3$, 5.9; urea, 483; and tubocurarine, $1.5 mg\,l^{-1}$. The composition is based on the standard Plymouth elasmobranch saline.

The experiments were carried out at 12°C with the fibre bundle mounted horizontally between a force transducer (Cambridge Technology, Inc. model 401) and a combined motor (vibration generator, model 101 Ling Dynamic Systems Ltd, Royston, UK) and length transducer (variable transformer DFg2.5, RS646-460). Motor position was controlled by the sine wave output of a function generator gated by a Digitimer. The bundle was in contact with a thermopile, made by deposition of antimony and bismuth on a mica substrate as described by Mulieri *et al.* (1977), that measured fibre temperature.

The preparation was electrically stimulated end-to-end with 0.2ms pulses. In each experiment the stimulus voltage–twitch tension relationship was investigated to establish supra-maximal stimulus strength.

The fibre length–tension relationship was also investigated so that appropriate initial and final lengths, near the plateau of the length–tension relationship, could be chosen for the tetani with sinusoidal movement.

Small values were chosen for stimulus duration and frequency for the experiments with sinusoidal movement, in an effort to minimize the number of stimuli applied to the preparation because a wide range of stimulus phases and mechanical frequencies were to be tested in each preparation. During each mechanical cycle, three stimulus pulses were given with 32ms between pulses. This pattern of stimulation gave close to the maximum isometric force and was expected to give maximum power. The timing was designated as the ‘stimulus phase’ which we defined as the time from the beginning of muscle shortening to the beginning of stimulation expressed as a percentage of the duration of the mechanical cycle. Thus, when stimulation started before shortening, the stimulus phase was negative.

Two cycles of movement and stimulation were performed while stimulation, motor position, force and temperature of the preparation were recorded. There was a 3min

recovery period between each trial. The stimulus phase and the frequency of sinusoidal movement were varied. The number of stimuli, stimulus frequency and distance of the movement were kept constant. The peak-to-peak movement was 9.3±0.3% (±S.E.M., $N$=13), expressed as a percentage of the fibre middle length during movement.

Records were also made of the force and temperature change during isometric tetani at the long, middle and short lengths.

### *Measurements of energy output*

A record of force during sinusoidal movement of the unstimulated muscle was subtracted from the record of force produced by the stimulated muscle to give a record of active force. The work done was calculated by integrating the product of the active force record and the differentiated record of length change. The mechanical power output during a cycle of movement was found by dividing work by the cycle duration. Note that this gives the average mechanical power during one complete cycle of movement, and that this is the net power calculated from the work done by the muscle fibres and any work that may have been done on them during the part of the mechanical cycle when they were stretched.

Heat output was determined from temperature changes detected by a thermopile. Each thermocouple produced 83.2 $\mu V\,^{\circ}C^{-1}$ temperature difference. There were four thermocouples per millimetre along the length of the thermopile, and we usually recorded the output from a 2mm length of thermopile.

Temperature records were converted to values of heat production and corrected for heat loss using characteristics determined for each fibre preparation by passing a known current through the whole thermopile. This produces a known quantity of heat due to the Peltier effect. The sum of two exponential functions was fitted to the time course of heat loss following a period of Peltier heating to give values for the heat loss characteristics and the heat capacity of the fibres.

The observed heat value was corrected for the heat due to the stimulus current. The stimulus heat was measured in a control experiment in which stimuli were applied to a fibre preparation which did not produce force in response to stimulation, having spontaneously become inactive. Observations were made for a range of stimulus voltages covering that used in the experiments on living fibres. The stimulus heat (μJ) observed in this way amounted to $0.0115V^2$, where $V$ is the stimulus voltage.

Values of net work, average mechanical power, heat and efficiency reported here are from the first complete mechanical cycle (the cycle starts when shortening starts, see example in Fig. 1).

### *Fibre size*

At the end of each experiment, the length of the fibres was measured under a stereomicroscope and the bundle was removed from the thermopile. Myosepta and any other non-fibre material were carefully removed, and the fibres were dried at room temperature. Dried fibre bundles were weighed on a Cahn electrobalance. The dry mass and length of the fibres were used to normalize the measured values of force, heat and mechanical power for fibre bundle size. In a separate series of observations, the wet to dry

mass ratio was measured and found to be 4.90±0.05 (±S.E.M., $N$=10). Where stated, errors are expressed as standard error of the mean (S.E.M.).

## Results

Fig. 1 shows a set of example records of length, stimulation, force, work and heat for one fibre bundle for movement at 3.33Hz. The stimulus phase was −15%; in other words, stimulation started 0.045s (=0.15/3.33Hz) before shortening started. These are the conditions that gave the maximum mechanical power for this fibre bundle.

The force record shows that force fell after stimulation ended as the muscle shortened;

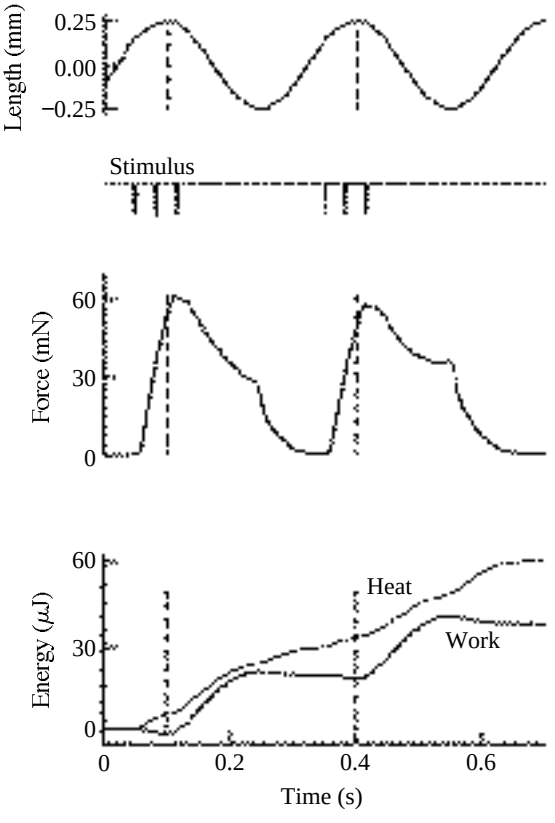


Fig. 1. Sample records of length, stimulus and force during sinusoidal movement at 3.33Hz with a brief tetanus during each cycle of movement. The vertical dashed lines mark the beginning and end of the mechanical cycle for which values are reported. On the length record, a positive slope indicates muscle lengthening, a negative slope muscle shortening. The peak-to-peak amplitude of movement was 9.8% of the fibre middle length. In this example, the stimulus phase was −15%, that is the time when stimulation started was 15% of the mechanical cycle time before shortening started. Active force is shown. Force produced during sinusoidal movement of the resting fibres was small and has been subtracted. In the bottom panel, the broken line shows the heat produced. The solid line is the work calculated as described in the Materials and methods section.

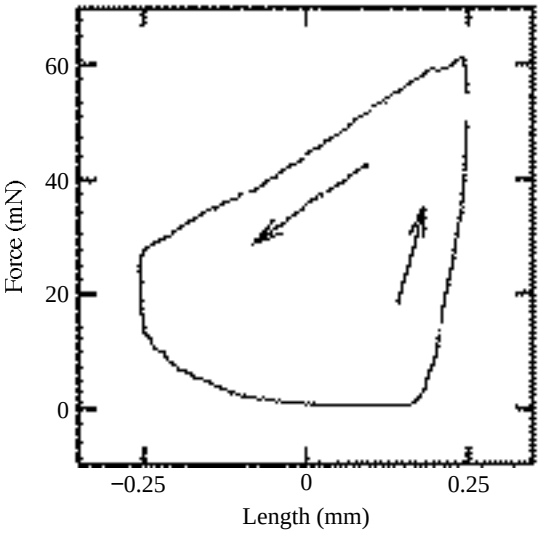


Fig. 2. Work loop formed by plotting force against length for the records between the two dashed vertical lines shown in Fig. 1. The arrows show the direction of progress around the loop. The net work for the cycle is the area enclosed by the loop.

by the end of shortening, it had fallen to about 40% of its peak value. Force fell even more rapidly as the stretch part of the mechanical cycle started and reached zero before stimulation started again.

A work loop for this cycle is shown in Fig. 2. The net work is the area enclosed by this loop. The work output as a function of time, which was calculated from the length and force records as described in the Materials and methods section, is shown in Fig. 1. Note that the work decreases when the muscle is stretched while it is producing force. The values of work, power and efficiency were measured for the period (one mechanical cycle) between the vertical dashed lines in Fig. 1. The mechanical power in the cycle was found by multiplying the net work in the cycle by the frequency of movement; thus, the value of mechanical power that we report is the average power during one complete cycle.

The heat production is shown along with work in Fig. 1. The total energy produced by the muscle fibres in one mechanical cycle is the sum of the work and heat production. The work output during the cycle shown in Fig. 1 is less than half of the total energy produced by the muscle fibres.

In each experiment we varied the mechanical cycle frequency and the stimulation phase, while keeping stimulus duration and frequency and amplitude of movement constant. Fig. 3 summarizes the values of work, mechanical power and efficiency measured on the fibre bundle that gave the records in Figs 1 and 2. For each frequency of movement, the range of stimulus phases was sufficient to encompass the values of stimulus phase optimal for work, for power and for efficiency. When the stimulation starts earlier or later in the cycle there is less work or power or lower efficiency. The ‘optimal stimulus phases’ varied with the mechanical cycle frequency; to be optimal, the stimulation had to start earlier in the mechanical cycle as the mechanical frequency

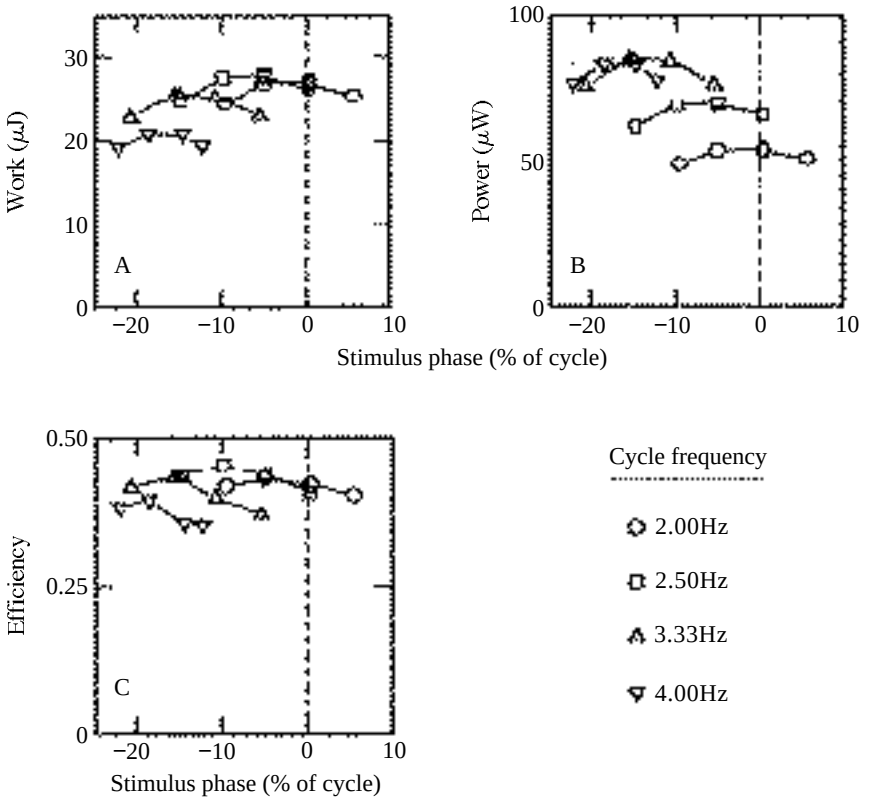


Fig. 3. Values of work (A), power (B) and efficiency (C) for one fibre bundle during sinusoidal movement with various phases of stimulation. Results for four frequencies of movement are shown. The vertical dashed line marks zero stimulus phase, the phase at which stimulation and shortening start at the same time.

increased. It is also noteworthy that the optimal stimulus phases are all negative: stimulation had to start during the stretch part of the cycle to give maximum work and maximum power as has been reported previously (Josephson, 1985; Altringham and Johnston, 1990). This is also true for maximum efficiency.

### *Peak power*

The mean of the peak power output by each fibre bundle was 0.227± 0.014 $W g^{-1}$ drymass ($N$=9). In four of the 13 bundles investigated, we did not investigate a wide enough range of mechanical frequencies to identify the peak power, so only nine values were included. The rate of energy output (heat rate+power), efficiency [power/(heat rate+power)] and the mechanical frequency values for the conditions giving peak power are given in Table 1.

### *Efficiency*

The efficiency data were summarized by selecting, for each muscle bundle, the maximum efficiency found when the stimulus phase was varied at each frequency of

Table 1. *Mechanical properties of dogfish white muscle fibres*

| | |
|---|---|
| $P_0$ ($N\,mg^{-1}$ drymass) | 0.876±0.114 (13) |
| Peak mechanical power ($W\,g^{-1}$ drymass) | 0.227±0.014 (9) |
| Velocity at maximum mechanical power (fibrelengths $s^{-1}$) | 0.63* |
| Frequency of sinusoidal movement (Hz) | 3.48±0.10 (9) |
| Total rate of energy production at maximum mechanical power ($W\,g^{-1}$ drymass) | 0.573±0.037 (9) |
| Mechanical power/total rate of energy production at maximum mechanical power | 0.379±0.022 (9) |

Values are means ± S.E.M. with the sample size in parentheses.

$P_0$ is the peak isometric force at the middle of the length range used for sinusoidal movement.

*This is the average velocity during the sinusoidal movement (peak-to-peak amplitude divided by half the cycle time).

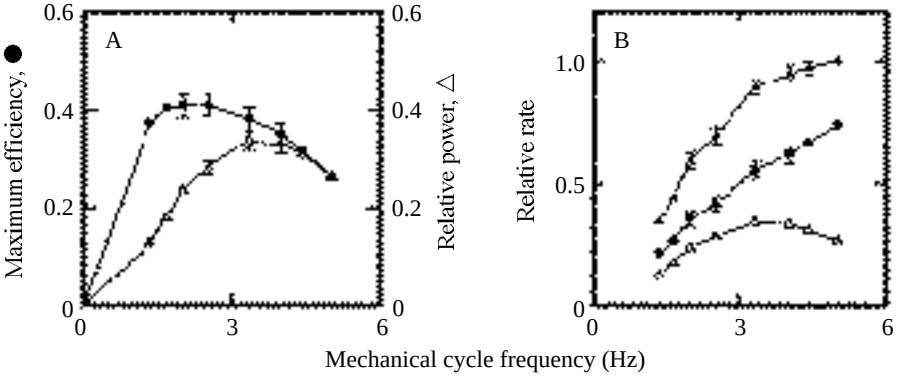


Fig. 4. (A) Variation of efficiency (filled circles) and relative power (open triangles) with frequency of sinusoidal movement. Each point is the mean (±1S.E.M.) for all fibre bundles of the maximum efficiency found by varying stimulus phase. The number of values included in the means are, from left to right, 1, 2, 10, 13, 11, 9, 1, 1. (B) Mean rate of total energy output (power+heat rate, filled triangles), mean heat rate (filled circles) and mean power output (open triangles) for conditions giving the maximum efficiencies shown in A. Values for each fibre bundle were normalized by the highest rate of total energy output by that fibre bundle. This normalization procedure removes variation due to differences in the amount of active, contractile material in the bundles.

movement. Fig. 4A shows the means for all the fibre bundles of the maximum efficiencies for each frequency of movement. The power, heat rate and rate of energy output under conditions giving maximum efficiency are shown in Fig. 4B. Movement at 2.0 and 2.5Hz are the most efficient, with power amounting to 0.409 and 0.408, respectively, of the total rate of energy output. At higher frequencies of movement, the efficiency is lower. For 3.33 and 4.0Hz, the power has increased, but the total rate of energy output has increased even more. For frequencies of movement above 4.0Hz, power output falls while the rate of total energy output continues increasing. The highest rate of energy output was found at the highest frequency used (5Hz).

The mean value of the highest efficiency for each fibre bundle, regardless of stimulus phase and frequency of movement, was 0.412±0.021 ($N$=13). In these tetani, the force at the start of shortening was 105.2±3.7% ($N$=11) of the force under isometric conditions after the same period of stimulation.

## Discussion

We have used measurements of work output and of heat production to assess energy utilisation by muscle fibres during a single cycle of sinusoidal movement. Under conditions giving maximum power, the amount of ATP used is about $1\,\mu mol\,g^{-1}$ wetmass or 3–4% of the phosphocreatine (PCr) in the muscle (calculated as described below from the results in Table 1). This quantity is small and would be at the limits of resolution of alternative techniques such as $^{31}P$ nuclear magnetic resonance spectroscopy, direct chemical analysis or measurement of oxygen consumption. Our experiments give measurements, in the same units, of work output and of heat output by the muscles. These can readily be expressed as a measure of efficiency: the ratio of work to the total energy output (heat+work).

### *Efficiency and the work done per molecule of ATP*

The efficiency results can be used to give a value for the work output per molecule of ATP split. To make this calculation, it is assumed that all of the energy comes from the splitting of ATP and the simultaneous resynthesis of ATP by the creatine kinase reaction, so that the net reaction is PCr splitting. The molar enthalpy of this reaction under the conditions inside the muscle is $34\,kJmol^{-1}$ (Woledge and Reilly, 1988). Thus, the efficiency multiplied by $-34\,kJmol^{-1}$ gives the amount of work done by the muscle for each mole of ATP split. Division by Avogadro's number gives the amount of work per molecule of ATP split. For the maximum efficiency we observed, 0.41, the result is $23\times10^{-21}$ J of work done for each molecule of ATP split.

How does this compare with the amount of work that can be done by one crossbridge cycle in Huxley and Simmons (1971) model, in which the work is done as the attached crossbridge goes through a series of mechanical transitions? The work is the integral of the relationship between force and shortening for an attached bridge (area under the $T_2$ curve, Fig. 19 in Ford *et al.* 1977). Taking 1.99pN as the isometric force for one crossbridge (that is, one myosin head), the work predicted by the model is $17.8\times10^{-21}$ J per crossbridge.

The following information is used to calculate the isometric force per myosin head. Isometric force produced by an intact white fibre from dogfish is $241\,mNmm^{-2}$ cross section of fibre (Curtin and Woledge, 1988). There is one thick filament in each $2.48\times10^{-9}\,mm^2$ of cross section; this is based on the filament spacings in fin muscle from plaice, *Pleuronectes platessa* (Harford and Squire, 1986) and a myofibrillar volume density of 0.778 in white fibres from dogfish (Bone *et al.* 1986). The two halves of the thick filament operate in series, so each half produces the whole of the isometric force. There are about 150 myosin molecules in each half of the thick filament (Squire, 1981, p. 284) and two heads per myosin.

The work actually obtained from contracting muscle per molecule of ATP split is thus

more than can be explained by this interpretation of the Huxley and Simmons' (1971) mechanical experiments. So it seems that work performance by muscle cannot be explained by crossbridges performing the Huxley and Simmons cycle and splitting one ATP molecule per cycle. A way of getting more work per ATP molecule has been suggested by Lombardi *et al.* (1992). They give evidence from mechanical experiments suggesting that there are additional mechanical transitions ('power strokes') of the crossbridge for each ATP molecule that is split. Our evidence from observations of muscle efficiency supports this view.

*Comparison of efficiency during sinusoidal movement and during ramp shortening*

The maximum efficiency found in this series of experiments using sinusoidal movements and optimally phased stimulation was 0.41±0.02 (mean of maximum value for each bundle of fibres). This can be compared with the value of 0.33±0.01 that we have previously reported for the same type of muscle shortening at uniform speed during continuous tetanic stimulation (Curtin and Woledge, 1991). The fact that the efficiency is higher for the sinusoidal movement is surprising because the velocity of movement is continually changing and thus cannot always be close to that optimal for efficient energy conversion. The following three factors may contribute to making the efficiency greater in the sinusoidal experiments.

(1) Fewer stimuli were used in the sinusoidal experiment and, therefore, less energy was used by the ATP-driven $Ca^{2+}$ pump. We can estimate the size of this effect from values of energy use by the $Ca^{2+}$ pump in other types of muscle (there are no reports of measurements of energy for $Ca^{2+}$ pumping in dogfish muscle). Results from amphibian muscle show that the $Ca^{2+}$ pump accounts for 25% of total ATP turnover in an isometric tetanus at full filament overlap (Woledge *et al.* 1985, p. 200). The corresponding value is 12% for ramp shortening at maximum efficiency. This value is calculated by assuming that the rate of the $Ca^{2+}$ pump is unaffected by shortening and by using the observed ratio of 2.1:1 for the rate of total energy output at peak efficiency:rate of total energy output under isometric conditions (Curtin and Woledge, 1991, Fig. 3). Deducting this quantity from the total energy cost we measured during shortening at uniform velocity gives the myofibrillar use of ATP and a value of 0.38 for the myofibrillar efficiency. This value is still less than 0.41 found in the sinusoidal experiment, which would also be somewhat increased by correction for the ATP used in $Ca^{2+}$ pumping. Thus, although this explanation probably contributes, it does not seem to be enough to explain the entire difference. We must be somewhat tentative about this conclusion; it may be incorrect if an unexpectedly large proportion of the energy in dogfish muscle is used by the $Ca^{2+}$ pump.

(2) It is noteworthy that in the isovelocity experiments shortening was preceded by an *isometric* period, whereas in the sinusoidal experiments the highest efficiency was achieved when the muscle was being stimulated while being *stretched* before shortening. However, the distance the fibres were stretched while being stimulated was quite small, 0.82±0.19% of fibre length ($N$=13). As noted in the Results, the force at the end of stretch (start of shortening) was not significantly greater than the isometric force for the same period of stimulation.

Heglund and Cavagna (1987) used a fundamentally different concept of efficiency from that used here. They define efficiency as the ratio of positive work done to energy used (energy determined from oxygen consumption in their experiments). This 'efficiency' is based only on work during shortening, and thus it is enhanced by work storage during stretch and subsequent release during shortening. Therefore, we emphasise that efficiency as we define and measure it here is not affected by energy storage. The reason is that the work value used in calculating efficiency was the net or total work for the entire cycle; that is, the work done by the muscle during shortening minus the work done on the muscle during stretching. Thus, any work done on the muscle and 'absorbed' by it during stretching and subsequently 'delivered' during shortening has no effect on the net work. We use this definition of efficiency because it is the thermodynamically correct one and, in locomotion, any work done on a muscle is ultimately derived from work done by other muscles in the body.

Because energy storage cannot be responsible for high efficiency, there must be some other explanation. If the preceding stretch is responsible, it seems that stretch would have to make subsequent energy conversion by the crossbridge more efficient. We have no suggestion for the mechanism of such an effect, but it is a possibility worthy of further exploration.

(3) During much of the shortening phase of sinusoidal movement the muscle is not being stimulated and force is declining. This contrasts with the situation during the isovelocity shortening when the muscle is continuously tetanised (Curtin and Woledge, 1991). Perhaps muscle is a more efficient energy convertor after the end of stimulation, when it is less than fully active. A suggestion can be made as to why this might be the case. As we have seen above, each crossbridge has to go through two or more power strokes to deliver the amount of work that is obtained per ATP molecule split. We suggest that there might be some competition between crossbridges as they undergo the reorganisation necessary to deliver the second and subsequent power strokes. For example, the crossbridge might have to move to another actin between power strokes, and could not do so if that site were occupied by another bridge. This would mean that each crossbridge could perform more power strokes per ATP molecule split when it faced less competition, and therefore be more efficient as an energy converter. After the end of stimulation, the number of active crossbridges diminishes, so competition would also diminish.

Although quite speculative, these ideas suggest additional experiments that could be carried out to establish why we found a higher efficiency during sinusoidal movement than during constant-velocity shortening.

### *A link between low power and high efficiency*

We note that the idea of competition between crossbridges could also explain why very efficient muscle has a relatively low power output. For example, tortoise muscle has an efficiency of about 0.72 and power output of $0.038\,W\,g^{-1}$ drymass (see Curtin and Woledge, 1991, Table 1). At a given speed of filament sliding, the rate of energy output of tortoise muscle is substantially less than that reported here for dogfish muscle. This must be due to a lower probability in tortoise muscle than in dogfish muscle of a myosin

reacting with an actin site as it passes by. Consequently, fewer crossbridges would be attached in shortening tortoise muscle and there would be less of the hypothetical competition process between them. As explained above, less competition would lead to higher efficiency.

We thank Dr J. V. Howarth, Dr Q. Bone and the staff of the Marine Biological Association, Plymouth, for their help and advice. We also thank the Browne Research Fund of the Royal Society and the SERC for financial support for this work.

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