The Journal of Experimental Biology **199**, 593–601 (1996)
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JEB0095

POWER AT THE EXPENSE OF EFFICIENCY IN CONTRACTION OF WHITE MUSCLE FIBRES FROM DOGFISH *SCYLIORHINUS CANICULA*

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Accepted 26 October 1995

Summary

Work and heat production of white myotomal muscle fibres from dogfish were measured during sinusoidal movement (0.71–5.0 Hz) at 12 ˚C. Stimulus phase (stimulus timing relative to movement) and duty cycle (stimulus duration as a fraction of movement cycle duration) were varied to determine the parameters optimal for power output and for efficiency (work/total energy output). Movements of 0.067 and 0.120L_0 were used, where L_0 is the muscle fibre length giving maximum force in an isometric tetanus. At each frequency of movement and duty cycle, the stimulus phase giving the highest power was the same as that giving the highest efficiency. In contrast, at each frequency and optimal stimulus phase, the dependence of power on duty cycle was very different from the dependence of efficiency on duty cycle. Power generally increased with increasing duty cycle, whereas efficiency decreased. Thus, high power can be achieved at the expense of efficiency by adjusting stimulus duty cycle. When stimulus phase and duty cycle were optimized, efficiency was always higher for the larger distance of movement. The efficiency of energy conversion can be maintained at a high level as the frequency of movement increases from 1.25 to 5.0 Hz.

Key words: muscle contraction, energetics, efficiency, power, work, heat production, dogfish, *Scyliorhinus canicula.*

Introduction

Power output and efficiency are two aspects of muscle energetics that are particularly relevant to determining the locomotory potential of an animal. Investigation of power output requires only measurement of force and length change; power has been the subject of considerable investigation (Josephson, 1993). From these studies, we know the conditions of stimulation and movement that give the highest power output. Efficiency, the ratio of work done to energy used, has been investigated rather less. Measurements of energy output as heat or measurements of chemical change are required to obtain values for efficiency.

We have measured efficiency and power output of dogfish muscle under a range of conditions similar to those that probably occur during swimming. Muscle shortening during swimming is approximately sinusoidal and, during each cycle of length change, the muscle is active for a period considerably shorter than the cycle time (for example, see Bone, 1966; Mos *et al.* 1990). The timing of the beginning of the activity with respect to the shortening (stimulus phase) is an important determinant of the work and energy output during the cycle; it has been investigated previously in dogfish muscle (Curtin and Woledge, 1993*a*,*b*) and mouse muscle (Barclay, 1994). The duration of stimulation (expressed as a proportion of the mechanical cycle time, the duty cycle) is clearly also likely to have a crucial influence on the energetics of the cycle, but it has been investigated relatively little (Curtin and Woledge, 1993*a*,*b*; Barclay, 1994). Few measurements have been made of the amplitude of movement *in vivo*, but it is known to influence the power output (Altringham and Johnston, 1990), and so an investigation of whether this factor also influences efficiency is necessary. Thus, the following four independent parameters, stimulus duty cycle and phase, movement amplitude and duration, are required to specify the conditions which the muscle experiences during a swim-like cycle of sinusoidal movement. We have varied these parameters to find the conditions that are best for the efficiency of energy conversion and those best for power output.

From comparisons of different muscle fibre types, it seems that fibres designed for high power usually have low efficiency (Woledge *et al.* 1985; Barclay, 1994). So for one fibre type,

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choosing conditions that give maximal power output might be expected to compromise efficiency. The experiments in this study were designed to see whether this is the case.

Materials and methods

Dogfish, *Scyliorhinus canicula* (L.), from 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 70 to 75 cm and mass from 1.123 to 1.272 kg were used. 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, 292.0; KCl, 3.2; $CaCl_2$, 5.0; $MgSO_4$, 1.0; Na_2SO_4, 1.6; $NaHCO_3$, 5.9; urea, 483; 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 1.1, Ling Dynamic Systems Ltd, Royston, UK) and length transducer (variable transformer DFg2.5, RS646-460). To measure muscle temperature, 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).

The preparation was electrically stimulated end-to-end using 0.2 or 0.5 ms pulses. In each experiment, the relationship between stimulus voltage and twitch tension was investigated to establish supramaximal stimulus strength. The number of live fibres in the preparation was taken to be equal to the number of steps in the relationship between stimulus strength and force response. Stimulus frequency was adjusted to give a fused tetanus and was about 20 Hz.

The relationship between fibre length and tension was also investigated, so that appropriate initial and final lengths, near the plateau of the length–tension relationship, could be chosen for the experiments using tetani with sinusoidal movement. L_0 was defined as the fibre length at which force in an isometric tetanus was greatest.

Two cycles of movement and stimulation were performed while stimulation, motor position, force and temperature of the preparation were controlled and recorded by a ViewDac (Keithley, UK) sequence with a data acquisition board (LabMaster DMA). There was a 3 min recovery period between trials. The stimulus phase and duty cycle (defined below), and the frequency and amplitude of the sinusoidal movement, were varied (four frequencies were used between 0.71 and 5.0 Hz and two peak-to-peak amplitudes, 0.50 and 0.75 mm). The stimulus phase was varied in steps of 5 % of the cycle time. Values for the stimulus duty cycle and the amplitudes and frequencies of movement are given in the Results. Records were also made of the force and temperature changes during isometric tetani at the long, middle (L_0) and short lengths.

Stimulus phase designates the timing of the stimulus relative to the movement and is 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. Duty cycle is the duration of tetanic stimulation expressed as a fraction of the duration of the mechanical cycle. A single stimulus (twitch) is referred to as having a duty cycle of zero.

Measurements of energy output

A record of force production during sinusoidal movement of the unstimulated muscle was subtracted from each record of force produced by the stimulated muscle to give a record of the active force production. Work output 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 the period being considered. For a complete cycle of movement, the net power was 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 the thermopile. Each thermocouple produced 89.3 μV °C^{-1}. There were four thermocouples per millimetre along the length of the thermopile, and in eight of the experiments we recorded from a 3 mm length of thermopile; in the other three experiments we recorded from a length of 4 mm.

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 for a known time. This produced a known quantity of heat due to the Peltier effect. An exponential function 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 preparation.

The observed heat values were corrected for heat due to the stimulus current. The stimulus heat was measured in control observations at the end of each experiment. A drop of saline containing procaine (18 mmol l^{-1}) was placed on the preparation, which made it inexcitable. After removing excess saline, stimuli were applied and the heat signal was recorded. Observations were made for a range of stimulus voltages and pulse durations covering that used in the experiments on living fibres. The stimulus heat per stimulus (μJ) observed in this way amounted to $0.03735V^2t$, where V is the stimulus strength (in volts) and t is the pulse duration (in milliseconds).

Values of work, power, heat and efficiency reported here are from the first complete mechanical cycle (the cycle starts when shortening starts, see example in Fig. 1). Results were obtained from 11 preparations. Of these, one preparation was used for both amplitudes of movement (peak-to-peak, 0.50 and 0.75 mm).

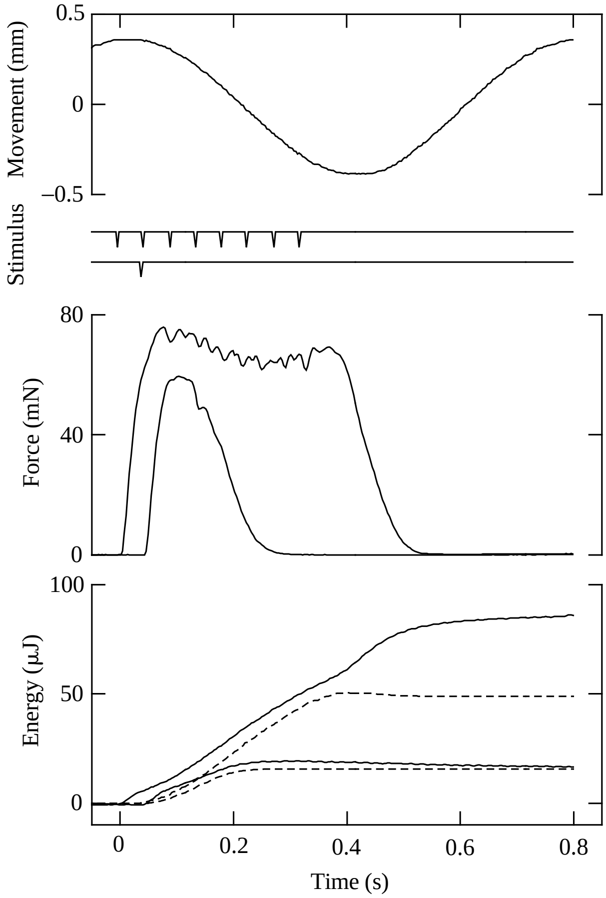

Fig. 1. Sample records of movement, stimulus pulses, force and energy during movement at 1.25 Hz. Each panel shows superimposed records for a single stimulus defined as duty cycle = 0 (stimulus phase = +5 %) and for a tetanus at a duty cycle of 0.4 (stimulus phase = 0 %). The lower of the two force records and the lower pair of energy records are for the single stimulus. Work is shown as broken lines and total energy (heat + work) as solid lines in the energy panel. For this muscle preparation and frequency of movement (1.25 Hz), maximum power was produced with a duty cycle of 0.4, and maximum efficiency with a single stimulus.

Fibre size

At the end of each experiment, the length of the preparation was measured under a stereomicroscope and the fibre bundle was removed from the thermopile. The preparation was pinned at the measured length in a Sylgard-containing dish and fixed in ethanol. After fixation, the myosepta were carefully removed and the fibre length measured (L_0=7.02±0.34 mm; mean ± s.e.m., *N*=11). The fibres were dried at room temperature after rinsing with distilled water. Dried fibre bundles were weighed on a Cahn electrobalance. The dry mass and length of the fibres, and information about the number of live fibres and the total number of fibres, were used to normalize the measured values of force and energy for fibre bundle size. Dry mass of live fibres was 0.2339±0.037 mg (mean ± s.e.m., *N*=11). In a separate series of observations, the ratio of wet to dry muscle mass was measured and found to be 4.90 ±0.05 (mean ± s.e.m., *N*=10).

Where stated, values are given as means ± s.e.m.

Results

Dependence of efficiency and power on stimulation phase

For each stimulus duty cycle (duration of stimulation/cycle duration), the stimulus phase (timing of the start of stimulation relative to the start of shortening) was varied to find the stimulus phase that gave the highest efficiency. Fig. 2 shows these stimulation patterns in relation to the sinusoidal movement. Each horizontal bar shows, for one preparation, the period of stimulation in the position giving the highest efficiency. Results for different duty cycles are shown; the stimulus bars are arranged with the larger duty cycles at the top in each graph. The experiments were made with peak-to-peak amplitudes of 0.5 mm (0.067L_0, solid stimulus bars) and 0.75 mm (0.120L_0, broken stimulus bars). The stimulus phases for maximum efficiency were similar for the two amplitudes of movement.

A main feature of Fig. 2 is that, for each frequency of movement, the stimulation started earlier as duty cycle was increased, but the period of stimulation remained centred around the same time. Table 1 summarizes the timing of these midpoints of stimulation. The timing of the midpoint of stimulation varied with the frequency of movement, occurring earlier as the frequency of movement increased, and corresponding to the start of shortening at the fastest frequency of movement. At the lowest frequency, 0.71 Hz, the midpoint of stimulation was at about 0.226 s after the start of shortening (16.2 % of the cycle time) for both distances of movement; by this time, the fibre preparation had shortened by about 25 % of the total shortening distance (Table 1).

The muscle is active (producing force) for somewhat longer than the period of stimulation. This is because although the force increases very rapidly when stimulation starts, force does not decline as rapidly at the end of stimulation (see Fig. 1). The time required for relaxation can be a significant fraction of the cycle time, especially at high frequencies of movement. For this reason, the midpoint of the period of muscle activity is always somewhat later than that of the period of stimulation. We quantified this by measuring the time required to produce half of the mechanical impulse (integral of tension and time). These values (Table 1) show that, for all frequencies of movement, this index of the midpoint of muscle activity is approximately in the centre of the period of shortening, corresponding to the time at which the velocity is highest. It is probably the need to keep the period of muscle activity centred on the period of shortening that causes the optimal time for starting stimulation to be earlier for short cycles than for long cycles.

The stimulus phases optimal for power output were determined, as well as those optimal for efficiency. As shown in Fig. 3, there was no consistent difference between them. Evidently, the muscle cannot make compromises between power and efficiency by altering the timing of a period of stimulation of given duration (duty cycle).

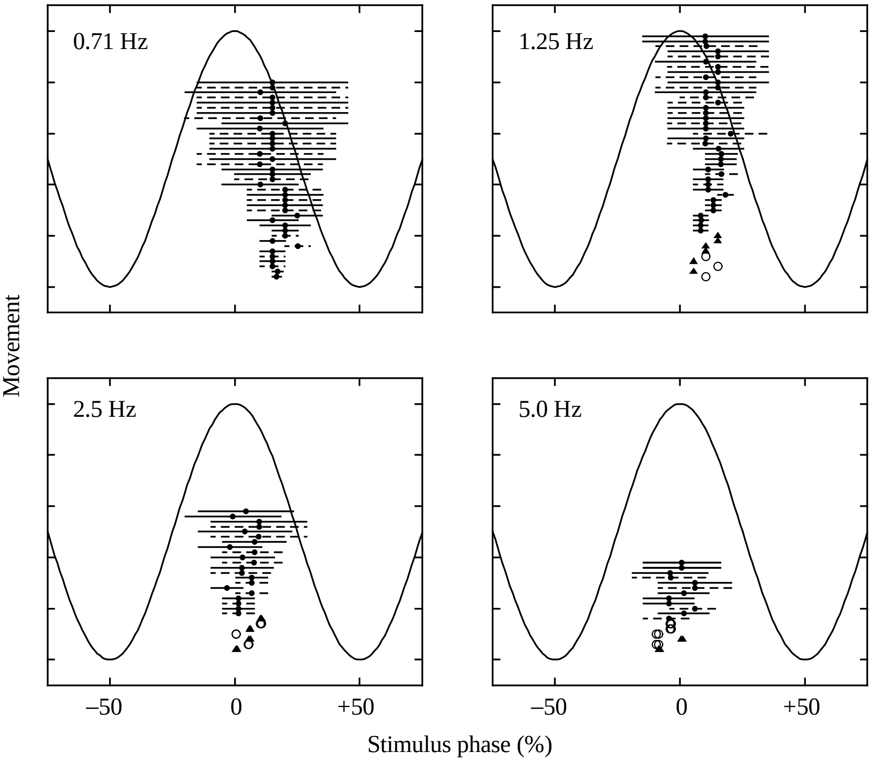

Fig. 2. Sinusoidal movement and a summary of the stimulation patterns giving maximum efficiency. Results are shown separately for movement at 0.71, 1.25, 2.5 and 5.0 Hz. Horizontal lines show the timing of tetanic stimulation relative to the movement. Results are shown for all the duty cycles that were tested; long duty cycles are at the top of each figure. Twitch results are shown at the bottom [open circles are for 0.5 mm peak-to-peak movement ($0.067L_0$), filled triangles are for 0.75 mm peak-to-peak movement ($0.120L_0$)]. The solid lines are for tetanic stimulation with a movement of 0.5 mm, and the broken lines are for 0.75 mm. The filled circles mark the midpoint of each period of tetanic stimulation. The scale for the stimulus phase is shown, where 0 % corresponds to the start of muscle fibre shortening. The results are from 11 muscle fibre preparations.

Table 1. *Tetanus parameters with stimulus phase optimum for power and efficiency*

	Frequency of movement (Hz)			
	0.71	1.25	2.50	5.00
A 0.50 mm peak-to-peak amplitude of movement				
Stimulus midpoint				
(% cycle time)	16.2±0.7 (23)	12.2±0.6 (24)	3.05±1.0 (14)	–2.3±1.3 (12)
(s)	0.226	0.098	0.12	–0.005
Distance shortened at stimulus midpoint				
(% total)	24.6	14.0	0.9	–0.5
(mm)	0.12	0.07	0.005	–0.003
Midpoint of tension–time integral				
(% cycle time)	24.3±0.5 (22)	23.9±0.4 (25)	23.4±0.5 (15)	24.7±1.0 (12)
(s)	0.342	0.191	0.093	0.049
B 0.75 mm peak-to-peak amplitude of movement				
Stimulus midpoint				
(% cycle time)	16.1±1.1 (16)	12.1±0.8 (24)	6.0±0.9 (13)	–0.6±2.4 (6)
(s)	0.225	0.096	0.024	–0.001
Distance shortened at stimulus midpoint				
(% total)	23.4	13.7	3.5	–0.04
(mm)	0.18	0.10	0.026	–0.001
Midpoint of tension–time integral				
(% cycle time)	23.3±0.6 (17)	23.3±0.4 (24)	21.8±0.3 (13)	21.3±0.5 (6)
(s)	0.326	0.186	0.087	0.043

See text and Fig. 2.
Values are means ± S.E.M. (*N*).

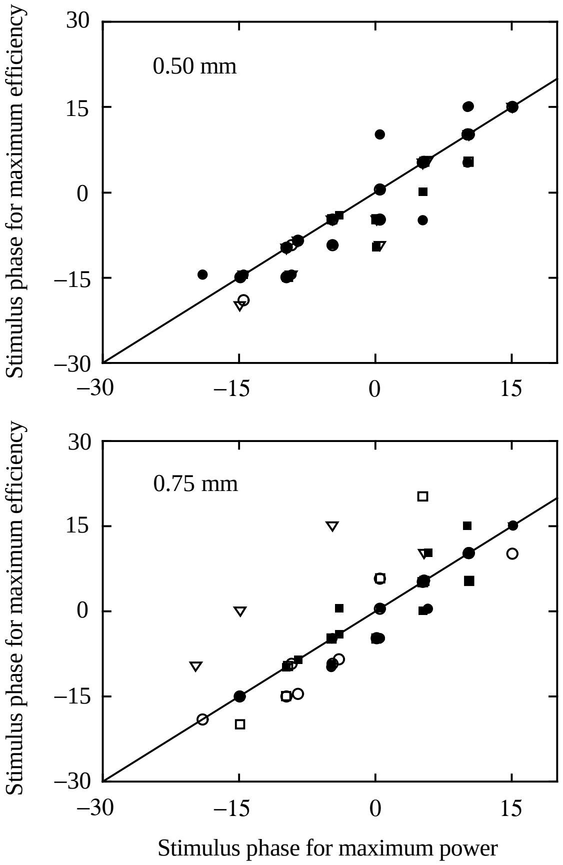

Fig. 3. Stimulus phase giving maximum power plotted against stimulus phase giving maximum efficiency. Stimulus phase (as a percentage of cycle time) is the time of the start of stimulation relative to the start of shortening; it was varied in 5 % steps. Results for movements of 0.50 mm (0.067L_0) and 0.75 mm (0.120L_0) are shown in separate graphs. Values are shown for all the frequencies of movement and all stimulus duty cycles that were tested; each point is for a particular frequency of movement and stimulus duty cycle. Results for 11 muscle fibre preparations; different preparations are shown by different symbols. Identity is shown by the solid line.

Dependence of efficiency and power on duty cycle

Fig. 4 shows the dependence of efficiency and of power on stimulus duty cycle for movements of 0.5 and 0.75 mm at the four frequencies of movement. The efficiency and power are those produced at the optimal stimulus phase. The values are for a complete cycle of movement, shortening followed by stretch back to the original length.

In Fig. 4, efficiency generally decreases as duty cycle increases; brief stimulation favours high efficiency. In contrast, power generally increases with increasing duty cycle over the range used here; longer stimulation favours high power output. Thus, it is clear that different patterns of stimulation must be used for maximum efficiency and for maximum power.

Efficiency

Some insight into why whole-cycle efficiency decreases as duty cycle increases can be gained by considering the energy changes in the two halves of the cycle separately, as shown in Fig. 5.

Considering shortening first (first column Fig. 5A,B), increasing the duty cycle increased both work and heat. There was a roughly proportional increase in work and in total energy turnover (heat + work) so that efficiency during shortening changed little with duty cycle (filled circles, last column, Fig. 5A,B).

Therefore, the reason for the decrease in efficiency for a whole cycle of movement as duty cycle increased must be found during the stretch half of the cycle. Two possible effects during stretch could reduce the overall efficiency: additional heat production and negative work (that is the work done on the muscle by the motor as the muscle is lengthened). The results presented in the middle columns of Fig. 5A,B show that, as duty cycle increased, both heat and negative work increased, but in all cases the increase in heat was the dominant factor for the range of duty cycles used here. Therefore, the total energy turnover increased almost as much as the heat output did. Thus, efficiency for the whole cycle decreased with increasing duty cycle because, with extra stimulation, energy turnover continued into the stretch part of the cycle. This effect was quantitatively more important than the small amounts of negative work.

Power

As discussed above, increasing the duty cycle usually resulted in an increase in power output for the whole cycle of movement (see Fig. 4). Movement of 0.5 mm at the highest frequency was an exception; overall power increased to a peak and then decreased as duty cycle increased. This occurred because the increase in negative work during stretch was much greater than the increase in positive work during shortening as duty cycle increased (Fig. 5A, last row). When the duty cycle is long enough, this same effect will presumably occur at all frequencies of movement. The beginning of this can be seen, for example, in the 0.71 Hz results for duty cycle values greater than 0.5.

Dependence of efficiency on frequency and amplitude of movement

Fig. 6 shows how efficiency depended on cycle frequency and distance moved when both stimulus phase and duty cycle were optimised. For each distance moved, the efficiency shows a broad plateau with respect to cycle frequency. At the lowest frequency, efficiency is less than the plateau value. The results also show that the efficiency is higher for the larger amplitude of movement, by an amount that is independent of the cycle frequency.

Discussion

Is a ‘trade-off’ possible between efficiency and power?

Can an animal use the same muscle in different ways: to produce a reduced power at the highest efficiency and to produce a higher power but at a lower efficiency? We have

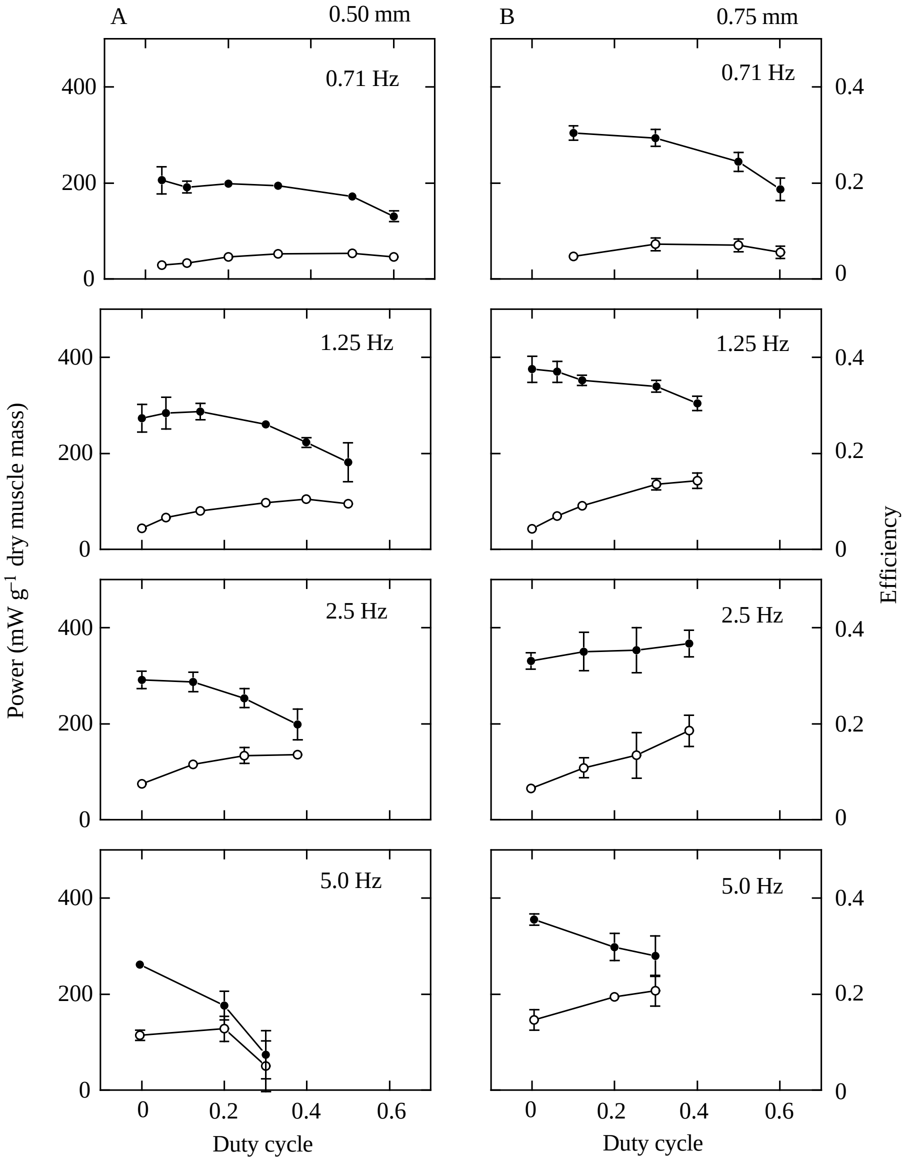

Fig. 4. The dependence of power (open circles) and of efficiency (filled circles) on stimulus duty cycle at optimal stimulus phase. (A) Results for a peak-to-peak movement of 0.50 mm ($0.067L_0$) at four frequencies of movement as indicated on each graph, N=6 muscle fibre preparations. (B) Results for a movement of 0.75 mm ($0.120L_0$), N=6 muscle fibre preparations. Each symbol is the mean of between two and seven values. Error bars indicate ± 1 S.E.M.

investigated two ways that this might be achieved: by varying the stimulus phase (the timing of stimulation with respect to shortening) and by varying the duty cycle. The first of these did not have the effect in question, but the second did. At all the frequencies of movement that we studied, the efficiency was greatest with a smaller duty cycle than that giving the highest power. The differences are quite appreciable; for example, with a movement of 0.5 mm at 2.5 Hz, changing from the stimulus duty cycle which is optimal for efficiency (single stimulus, duty cycle 0) to that optimal for power (duty cycle 0.38) raises the power by 82 % but at the price of lowering the efficiency by 32 %.

Why does efficiency depend on stimulus duty cycle?

The results show that efficiency decreases as the stimulus duty cycle increases. As explained in the Results, this is not due to a reduction in efficiency during the shortening; it *is* due predominantly to heat production during stretch. It might have been expected that negative work would be a major reason for the reduction in efficiency. However, the negative work is small because the force only lasts for a short time and the muscle only moves a small distance during this time because it is at the start of stretch when the velocity of movement is slow.

It is interesting to consider possible sources of heat production during stretch. We have looked at the time course of heat production during stretch for the two experiments which included the most complete set of movement frequencies and stimulus patterns and found that, during stretch, most of the heat (75 %) was produced before force had relaxed to 10 % of its initial value. This suggests a relationship between force and heat production. Two possible sources of heat production during stretch are (1) degradation of internal work, and (2) ATP splitting due to continuing crossbridge cycles.

The work being considered here is ‘internal work’ done by

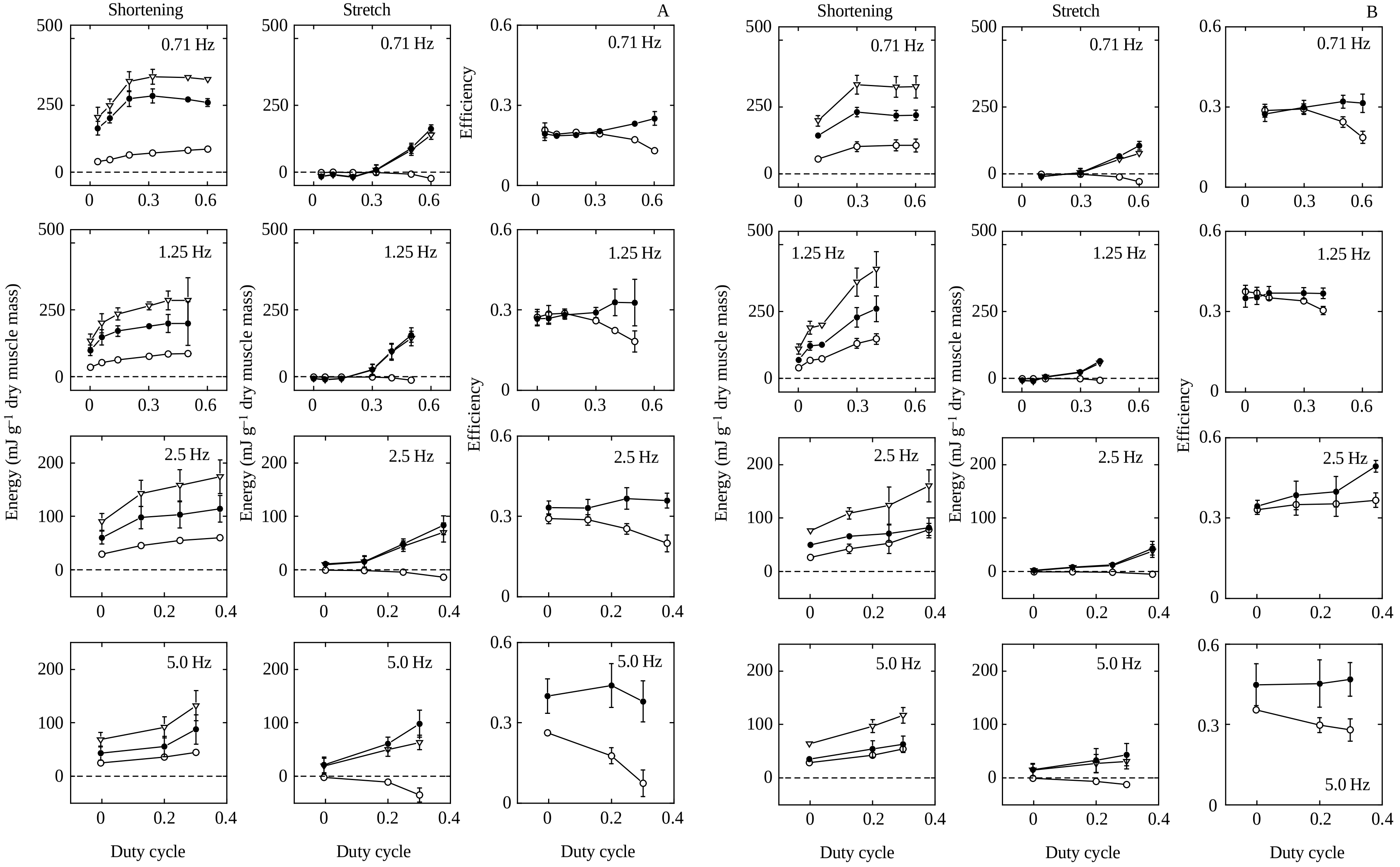

Fig. 5. The dependence of energy changes on stimulus duty cycle during sinusoidal movement. Results for peak-to-peak movement of (A) 0.50 mm (0.067L_0) and (B) 0.75 mm (0.120L_0). Each row of graphs shows results for one frequency of movement. The first column in A and B shows the work (open circles), heat (filled circles) and work + heat (open triangles) during shortening. The second column shows the corresponding energy changes during stretch. The third column shows the efficiency during the shortening half of the cycle of movement (filled circles) and the efficiency for the whole cycle (open circles). Results are means ± 1 S.E.M. for stimulus phases giving maximum efficiency. A and B each include results for six muscle fibre preparations. Each symbol is the mean of between two and seven values.

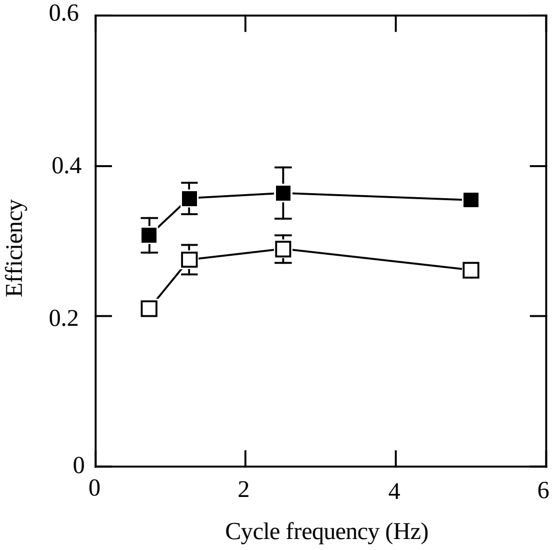

Fig. 6. Dependence of efficiency on frequency of sinusoidal movement with stimulus phase and duty cycle giving maximum efficiency. Open symbols show results for a peak-to-peak movement of 0.50 mm ($0.067L_0$), results for six muscle preparations. Filled symbols are for 0.75 mm ($0.120L_0$), results for six muscle fibre preparations. Values are means ± 1 S.E.M. of between two and six values.

the muscle fibres shortening against the series elasticity while force is increasing earlier in the cycle. This 'internal work' is temporarily stored in the system until force falls. It is degraded to heat when force declines during relaxation and the series elasticity shortens against the relaxing muscle fibres. Could this source be quantitatively important? The observation that the heat output is high during force relaxation, particularly when the force change is large, suggests that it might be quantitatively important (see the record for the large duty cycle in Fig. 1).

We have considered how much heat could come from this source. The 'internal work' degraded into heat while force relaxes during stretch is $F^2 \times SC$, where F is force and SC is series compliance. For F, we used the average force during this time, taken to be half the force at the start of stretch, and for SC we used values measured in 'step-and-ramp' experiments on other preparations of white muscle fibres from dogfish (see Jewell and Wilkie, 1958, for the rationale of this method). The heat from degradation of the 'internal work' estimated in this way was not negligible. However, it was not sufficient to account for all of the observed heat production; the extra heat presumably comes from the ATP used during continuing crossbridge cycles during relaxation. Two ATP molecules split per myosin head during relaxation would be sufficient to account for the observed heat.

Efficiency and frequency of movement

The results in Fig. 6 show that even when both phase and duty cycle are optimised, the efficiency for a whole movement cycle declines from the plateau value as the frequency of movement is reduced. This may be related to the fact that the 'instantaneous' value of efficiency (the ratio of work rate to rate of energy output) is a function of velocity in fully active muscle during shortening at a constant velocity. This was first shown by Hill (1939) for frog sartorius muscle. In Hill's experiments, the instantaneous efficiency reached a maximum value at shortening speeds between $0.13V_{\max}$ and $0.2V_{\max}$ and it was clearly less than optimal at speeds below $0.1V_{\max}$ (where $V_{\max}$ is the maximum velocity of shortening). Curtin and Woledge (1991), using dogfish white myotomal muscle fibres, found a relationship between velocity and instantaneous efficiency similar to Hill's, but velocities less than $0.1V_{\max}$ were not tested. In the present study of sinusoidal movement, the average shortening velocities for the lowest frequency of movement (0.71 Hz) were $0.026V_{\max}$ (0.5 mm shortening) and $0.045V_{\max}$ (0.75 mm shortening). Even the peak velocities reached (0.039 and $0.070V_{\max}$, respectively) are thus likely to have been well below the velocity required to achieve optimal instantaneous efficiency. The failure to achieve a high efficiency at the low frequencies can thus plausibly be explained. However, we do not know the extent to which the instantaneous relationship between efficiency during constant-velocity shortening of a fully active, tetanised muscle applies within a whole cycle of sinusoidal movement (velocity continuously changing) in which the muscle receives only one or a few stimuli.

The highest frequency of movement that we used (5 Hz) is not very far from the maximum at which appreciable net power can be produced by this muscle at 12 °C. At higher frequencies, the time required for relaxation of force becomes an appreciable fraction of the total cycle time. Consequently, the muscles cannot relax quickly enough to avoid absorbing work during the stretch part of the cycle. Thus, although in this series of experiments, we have not found the upper frequency limit of the efficiency plateau, it cannot be much beyond the highest frequency we used.

Efficiency and the amplitude of movement

Only two amplitudes of movement were used in this study. Nevertheless, it is clear that the maximum efficiency attainable does depend on the distance shortened when stimulus phase, duty cycle and cycle frequency are optimised. This is consistent with our earlier preliminary study (Curtin and Woledge, 1994) in which a wider range of amplitudes was used. The earlier study suggested that the optimal amplitude for efficiency varies with the frequency of movement. The nature of this dependence needs further investigation.

We thank the staff of the Marine Biological Association UK, Plymouth, for their help during these experiments and the Science and Engineering Research Council, UK, and The Royal Society for financial support.

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