

MODELLING MUSCLE POWER OUTPUT IN A SWIMMING FISH

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Summary

Intact, electrically excitable fibre bundles were isolated from the fast and slow myotomal muscle of the bullrout (*Myoxocephalus scorpius* L.). Power output was measured under conditions simulating their activity in a fish swimming at different speeds. Preparations were subjected to sinusoidal length changes of $\pm 5\%$ of resting length, and stimulated briefly during each cycle. The number and timing of stimuli were adjusted at each cycle frequency to maximise power output. Maximum power was produced at 5–7 Hz for fast fibres ($25\text{--}35\text{ W kg}^{-1}$) and 2 Hz for slow fibres ($5\text{--}8\text{ W kg}^{-1}$). Under these conditions, pre-stretch of active muscle provides an important mechanism for storing potential energy for release during the shortening part of the cycle.

Introduction

The power output of muscle fibres is normally measured under isotonic conditions. However, the results from such experiments are not directly relevant to locomotion (Johnston and Altringham, 1988) during which muscles are subject to cyclical length changes. Under these conditions power output is a complex function of the dynamic effects of muscle lengthening and shortening, and the fraction of each locomotory cycle during which the muscle is active. Josephson (1985) pioneered an approach more applicable to locomotion, by measuring power output of synchronous insect flight muscle under conditions simulating a wingbeat frequency of 25 Hz. Fish swimming provides a particularly favourable model for studying how muscles operate during locomotion. The anatomical separation of fibre types in myotomes facilitates the analysis of recruitment patterns in relation to swimming speed (Johnston *et al.* 1977; Bone *et al.* 1978) and the relationship between muscle activity and muscle length change has also been studied (Grillner and Kashin, 1976; Hess and Videler, 1984). Using a similar approach, we have measured the power output of live muscle fibres from a teleost fish, over the full

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range of tailbeat frequencies used during swimming. Both fast and slow fibres were studied, to gain insights into the workings of a motor system which operates over a wide range of speed and power requirements.

Materials and methods

Bullrout, *Myoxocephalus scorpius* L., were caught in the Firth of Forth in February and March, 1989, and kept in the laboratory in flow-through aquaria at 5°C for up to 2 weeks before use. This species is locally abundant, and yielded a robust preparation for these studies. All experiments were carried out at $3 \pm 0.1^\circ\text{C}$, on fish 23–29 cm in length. Fish were killed by a blow to the head and pithed. After total length and weight had been recorded, the muscle fibres were removed. Fast fibre preparations consisted of 1–10 fibres, 7.5–14 mm in length; slow fibre preparations contained 20–50 fibres, 3–4 mm in length. Fast fibres were dissected from abdominal myotomes, slow fibres from the wall of the lateral line canal, as previously described (Altringham and Johnston, 1988). The myotomes sampled were located 0.5–0.6 body lengths from the head. The preparation was immersed in a flow-through chamber, and the composition of the Ringer's solution was (in mmol l^{-1}): NaCl, 132.2; sodium pyruvate, 10; KCl, 2.6; MgCl_2 , 1; CaCl_2 , 2.7; NaHCO_3 , 18.5; NaH_2PO_4 , 3.2; pH 7.4 at 5°C. One end of the preparation was attached to a servo motor, the other to an isometric force transducer (AME 801, AME, Horten, Norway). The fibres were stimulated directly, by means of two parallel platinum wire electrodes, with a stimulus duration of 2 ms. Cross-sectional areas were determined at the end of each experiment by freezing the preparation, cutting 10 μm frozen sections, and digitising fibre outlines after histochemical staining for myosin ATPase and succinic dehydrogenase (Johnston *et al.* 1974).

Kinematic analysis of swimming fish (Hess and Videler, 1984) shows that length changes of myotomal fibres during steady swimming describe a near perfect sine wave. Preparations were therefore subjected to sinusoidal length changes, symmetrical about *in situ* rest length, and stimulated at selected phases in each cycle. Up to eight cycles were given, until the net work performed per cycle reached a steady state (Fig. 1A,C). By plotting force against muscle length for each cycle a loop is generated (Fig. 1B,D), the area of which is the work performed (see Josephson, 1985, for details). Power output is net work per cycle multiplied by frequency. Under optimum conditions, net work per cycle reached a steady or near-steady state by the fourth cycle. Power output measurements were therefore based on the fourth cycle. The experiments were controlled through a microcomputer (IBM 'clone'), and the data collected and analysed on-line, using in-house software.

Results

Our aim was to construct curves of maximum power output against tailbeat frequency. This involved an analysis of the effects of several parameters on power

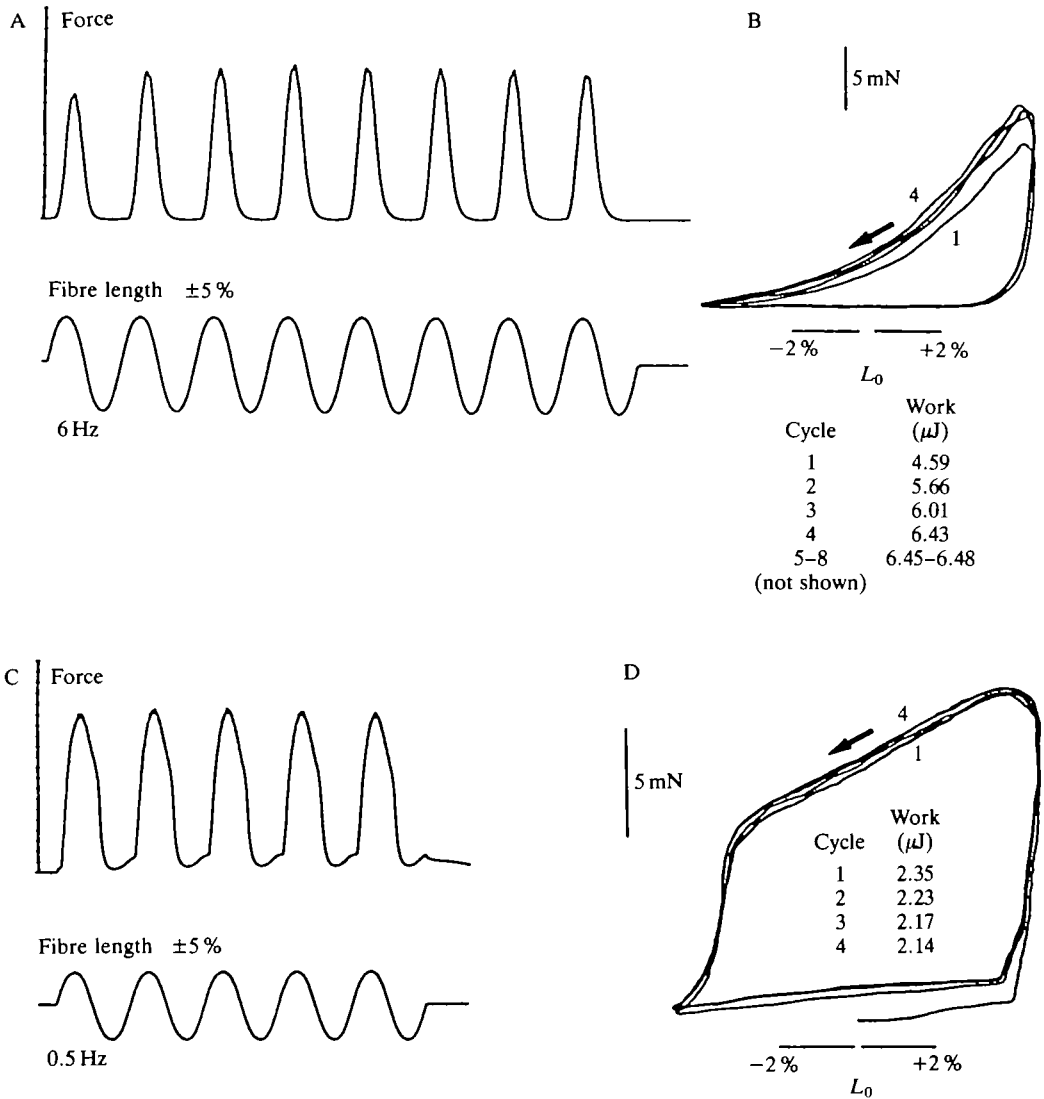


Fig. 1. The measurement of oscillatory work in muscle fibre bundles from *Myoxocephalus scorpius* L. (A,B) Fast muscle fibre preparation subjected to eight sinusoidal length change cycles of $\pm 5\%$ of resting fibre length (FL) at 6 Hz. A single supramaximal stimulus was given 20° after the start of each cycle from rest length. In A, force and muscle length have been plotted against time, in B force has been plotted against muscle length to produce a loop for each cycle. (C,D) Results from a slow fibre preparation, subjected to 15 stimuli at 15 Hz, in each of five length change cycles at 0.5 Hz ($\pm 5\% FL$). The first stimulus was given at 20° . Force calibrations in A and C are 20 mN full scale. L_0 , resting fibre length in a fish lying flat on the bench, corresponding to a sarcomere length of $2.3\text{--}2.4\ \mu\text{m}$ (measured by laser diffraction).

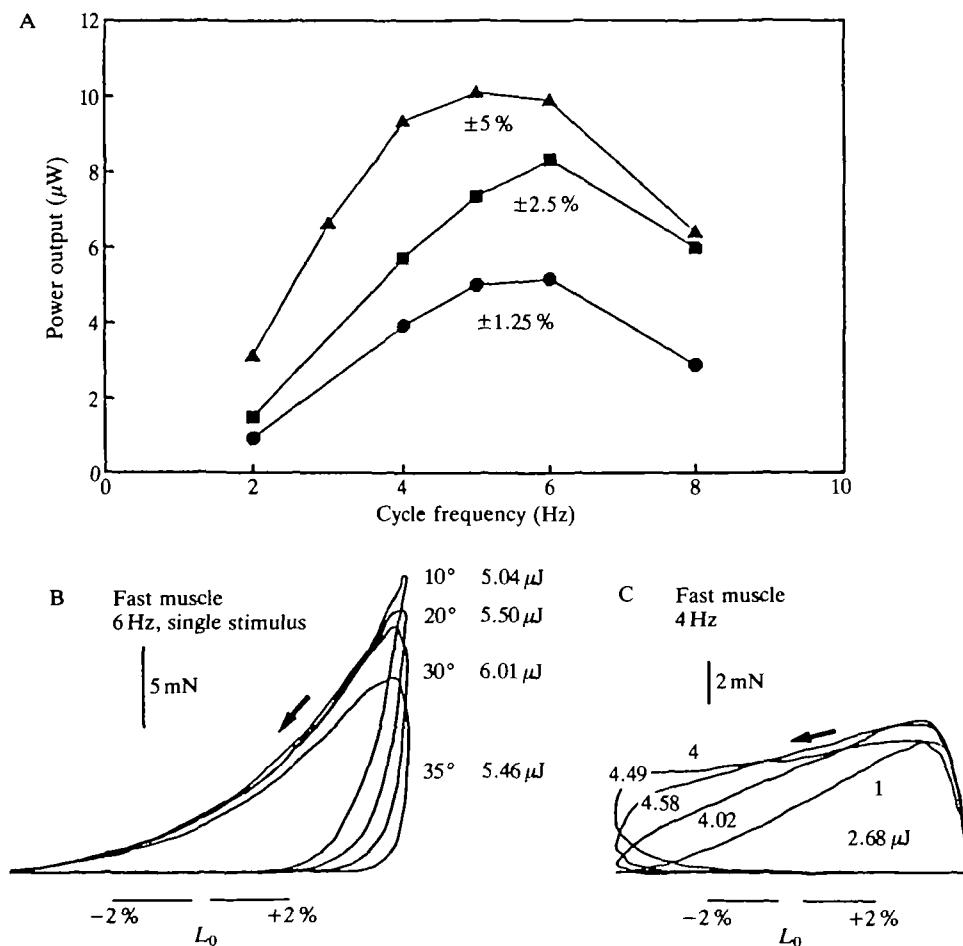


Fig. 2. (A) Effect of length change amplitude on power output at different cycle frequencies for a fast fibre preparation. A single stimulus was given in each cycle; phase shift was optimised for 6 Hz. (B) Effect of changing the phase shift between the stimulus and the start of the length change cycle. Superimposed work loops from the fourth of eight cycles, obtained from a fast fibre preparation stimulated once during each 6 Hz cycle ($\pm 5\%$ FL). Maximum net work per cycle was obtained when peak tension lagged behind maximum length by 30° . (C) Effect of increasing the number of stimuli per cycle. Superimposed work loops at 4 Hz, with 1–4 stimuli. Net work was maximal with three stimuli. The optimum number of stimuli depends upon the phase shift.

output, and their interactions. In Fig. 2A, the effect of changing the sine wave amplitude on power output is summarised. Similar results were obtained for slow fibres. Power output was maximal at $\pm 5\%$ of resting fibre length (FL), and declined at amplitudes greater than $\pm 6\%$ (results not shown). Since our aim was to determine power output under optimum conditions, a length change of $\pm 5\%$ FL was used to construct power–frequency curves.

Power output also depended upon the timing of stimulation. An example is shown in Fig. 2B, where the stimulus was progressively retarded relative to the start of stretch from resting length. The phase shift is defined as the delay between peak force and maximum length. Power output was maximal over a narrow phase shift range, over which the active muscle was given a small stretch prior to shortening. Under optimum conditions the mechanical cost of stretching active muscle was less than the extra positive work obtained by virtue of the higher force during shortening.

To maximise power output, the force . time integral during the shortening phase of each cycle (minus any negative work performed during stretch) must be maximised. This required only a single twitch at high cycle frequencies, but as frequency decreased more stimuli were needed owing to the longer duration of the shortening phase. Too many stimuli at a given cycle or tailbeat frequency prevented the muscle from relaxing before the onset of stretch, resulting in an increase in the negative work component (performed by antagonistic muscles in a swimming fish, and by the servo system in our experiments). The effect on net work per cycle of increasing the number of stimuli is illustrated in Fig. 2C. There is also some interaction between the number of stimuli and the phase shift, shown in Fig. 3. At each cycle/tailbeat frequency there was an optimal phase shift angle, and this was greatest at 5–7 Hz, i.e. the frequency for maximum power output. The optimum phase shift was also determined for single stimuli (lower curve, Fig. 3), and again showed a systematic dependence on tailbeat frequency.

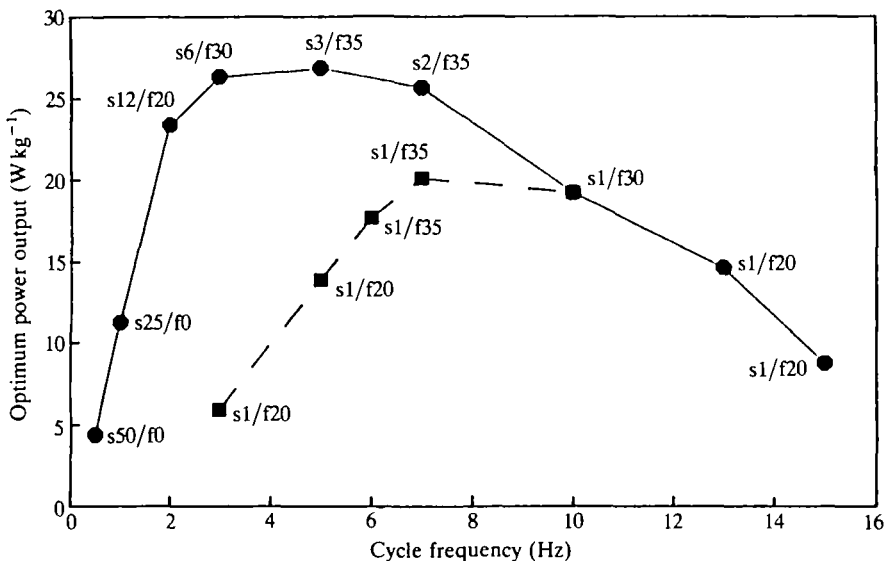


Fig. 3. Optimum power output at different cycle/tailbeat frequencies for a fast fibre preparation. Solid line, all parameters optimised (amplitude, phase shift and number of stimuli). Dotted line, optimum curve with a single stimulus. s_x/f_y , number of stimuli/phase shift between peak force and maximum length (in degrees, complete cycle = 360°).

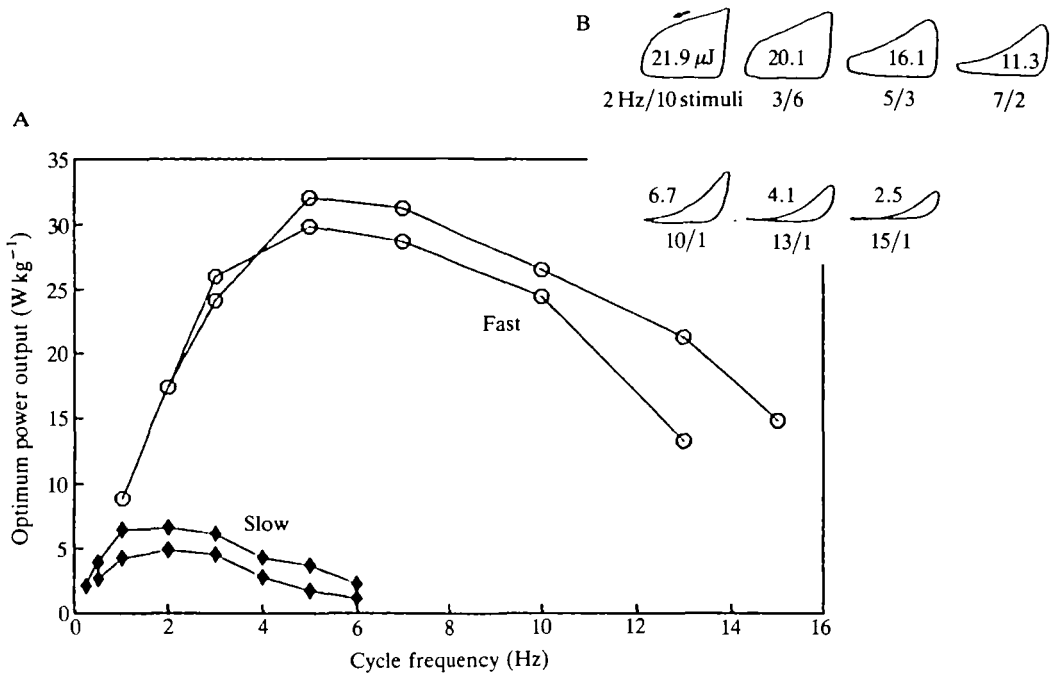


Fig. 4. (A) Optimum power output plotted against cycle/tailbeat frequency for two representative preparations of fast fibres (open symbols) and slow fibres (closed symbols). The lower fast curve is from a single fibre. (B) Optimum work loops for each point on the upper fast fibre curve of A. Cycle frequency, number of stimuli and net work are given for each. The optimum frequency of the stimulus train within each cycle was that which gave a fused isometric tetanus (50 and 15 Hz in fast and slow fibres, respectively).

We determined the maximum power output of fast and slow fibres at different cycle frequencies by optimising all parameters. Representative results are shown in Fig. 4. Slow fibres develop maximum power output at around 2 Hz. Fast fibres produce around five times more power than slow fibres, at an optimal frequency of 5–7 Hz.

Discussion

The amplitude of muscle length changes *in vivo* are determined by tailbeat amplitude, which is almost independent of swimming speed (Webb *et al.* 1984) and the location of the muscle fibres in the body (Hess and Videler, 1984). The observed amplitude for optimum power output is comparable to estimates of muscle length changes from kinematic (Hess and Videler, 1984) and theoretical (Alexander, 1969) studies. Similar results have been reported for frog muscle by Stevens (1988), but Josephson (1985) observed optimum power output at an amplitude of 6% peak-to-peak in synchronous insect flight muscle.

Kinematic analysis (Hess and Videler, 1984) also provides information on the

phase relationship between the muscle length changes and the tension transient. The wave of body deformation runs from head to tail, but the bending moment is a standing wave, resulting in a systematic phase difference between force and length cycles. The constraints on the muscle at different points along the body can, in theory, be modelled, and thus a complete picture of the swimming fish built up. At around 0.65 body lengths from the head (from which position our preparations were taken) force is maximal during shortening, and power output is positive throughout most of the cycle. We have approximated these conditions by timing stimulation to give optimum power output. The value for fast muscle is comparable to that of 34.5 W kg^{-1} reported by Stevens (1988), for frog sartorius muscle, performing oscillatory work at 2 Hz and 20°C.

The forces measured under optimum conditions, when the active fibres are given a small stretch before the onset of shortening, are considerably higher than under isometric conditions. Thus force-enhancement by stretch appears to be an important mechanism for storing potential energy in the muscle, for release during the working part of the cycle.

The power required for swimming increases as a power function of speed, with an exponent between 2 and 3. Since the distance moved during one tailbeat is an approximately constant proportion of body length (Webb *et al.* 1984), tailbeat frequency is a major determinant of swimming speed. The low power demand of low-speed swimming is met by a small volume of slow muscle fibres (Johnston *et al.* 1977; Bone *et al.* 1978). Slow fibres develop maximum power output at around 2 Hz, a tailbeat frequency which can be sustained for long periods. The low power output and aerobic metabolism of the slow fibres make them ideally suited to driving slow swimming. At high swimming speeds more power is required, and this is obtained by the recruitment of fast fibres (Johnston *et al.* 1977; Bone *et al.* 1978). These produce around five times more power at an optimal frequency of 5–7 Hz, and constitute over 90 % of the myotomal muscle mass. The power output of slow fibres is negligible relative to that of fast fibres at high tailbeat frequencies. In fact, the twitch kinetics of slow fibres are too slow to generate positive work above 8 Hz: this provides one explanation of why different fibre types are needed for locomotion. Grillner and Kashin (1976) have shown that the duration of electromyographical activity remains a constant proportion of the tailbeat cycle. Thus, the number of stimuli delivered to a fibre in each cycle is likely to decrease with increasing tailbeat frequency. This parallels our own observation that the number of stimuli required to give maximum power output decreases with increasing cycle frequency. At intermediate cycle/tailbeat frequencies, fast fibres receiving a single stimulus per cycle can generate power outputs comparable to those of slow fibres (Figs 3, 4). Although electrical activity has been recorded in teleost fast muscle at intermediate swimming speeds (Johnston *et al.* 1977; Bone *et al.* 1978), the conditions under which they are operating are unknown. It is possible that the motor programme is sufficiently flexible to allow fast muscle fibres to operate with fewer than the optimum number of stimuli at intermediate speeds. At intermediate speeds, fibres with contraction kinetics between those of

fast and slow are also recruited (Johnston *et al.* 1977). Cod myotomal muscle can be differentiated into seven fibre types on histochemical grounds alone (Korneliusson *et al.* 1978). In conclusion, the wide range of power requirements needed for swimming may be met both by the recruitment of different numbers and types of fibres, and by changing the conditions under which they operate.

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