J. exp. Biol. **140**, 287–299 (1988)
Printed in Great Britain

THE MECHANICAL POWER OUTPUT OF A CRAB RESPIRATORY MUSCLE

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Accepted 17 June 1988

Summary

The mechanical power output was measured from scaphognathite (SG = gill bailer) muscle L2B of the crab *Carcinus maenas* (L.). The work was determined from the area of the loop formed by plotting muscle length against force when the muscle was subjected to sinusoidal length change (strain) and phasic stimulation in the length cycle. The stimulation pattern (10 stimuli per burst, burst length = 20 % of cycle length) mimicked that which has been recorded from muscle L2B in intact animals. Work output was measured at cycle frequencies ranging from 0·5 to 5 Hz. The work output at optimum strain and stimulus phase increased with increasing cycle frequency to a maximum at 2–3 Hz and declined thereafter. The maximum work per cycle was 2·7 J kg^{-1} (15 °C). The power output reached a maximum (8·8 W kg^{-1}) at 4 Hz. Both optimum strain and optimum stimulus phase were relatively constant over the range of burst frequencies examined.

Based on the fraction of the total SG musculature represented by muscle L2B (18 %) and literature values for the oxygen consumption associated with ventilation in *C. maenas* and for the hydraulic power output from an SG, we estimate that at a beat frequency of 2 Hz the SG muscle is about 10 % efficient in converting metabolic energy to muscle power, and about 19 % efficient in converting muscle power to hydraulic power.

Introduction

Water is drawn across the gills of decapod crustaceans by a bilateral pair of pumps which lie in the exhalant canals anterior to the branchial chambers. The moving component of each pump is a flattened, blade-like appendage, the scaphognathite (SG), whose up-and-down sculling movements propel the water. The rate of water pumping by an SG increases with the SG beat frequency which ranges from about 0·7 to 4–5 Hz (e.g. Hughes *et al.* 1969; Mercier & Wilkens, 1984*a*; Wilkens *et al.* 1984). Each scaphognathite is powered by a set of about 10 levator and depressor muscles (Young, 1975). The SG muscles are activated on each beat by bursts of motoneurone action potentials (e.g. Young, 1975; Mercier &

Key words: muscle, power, work, scaphognathite, *Carcinus maenas*.

Wilkens, 1984*b*). Those SG muscles that have been examined have strong requirements for neuromuscular facilitation, and only bursts of action potentials evoke significant muscle contraction (Mercier & Wilkens, 1984*b*; Josephson & Stokes, 1987).

In the green crab, *Carcinus maenas*, the mechanical power output of the SG pump has been determined from the hydraulic pressure difference developed across the pump and the volume of fluid propelled by the pump (Mercier & Wilkens, 1984*a*). The power output increases monotonically with beat frequency. The overall efficiency of the ventilatory pump has been estimated to be about 3 %, determined from the ratio of the hydraulic work output and the portion of the resting metabolism attributable to ventilatory activity (Wilkens *et al.* 1984).

The following is a study of the mechanical power output of an SG muscle from *C. maenas* under conditions mimicking those during normal ventilation. These measurements, together with the results from earlier examinations of ventilatory performance mentioned above, allow determination of the efficiency of the SG muscle in converting metabolic power input into mechanical power, and determination of the efficiency of the SG system in converting muscle power to hydraulic power. The mechanical power output of the SG muscle was measured using an approach originally developed with insect wing muscles (Josephson, 1985*a*,*b*; Mizisin & Josephson, 1987). Insect wing muscles operate over a rather narrow frequency range during flight. The SG muscles of *C. maenas*, in contrast, operate over a wide frequency range. With the SG muscle it was possible to examine the effects of operating frequency on power output, using a muscle for which operating frequency is an important parameter.

Materials and methods

The muscle studied was scaphognathite levator L2B from the crab *C. maenas*. The crabs were obtained at the Marine Biological Laboratory, Woods Hole, MA, and ranged from 42 to 107 g. An earlier paper (Josephson & Stokes, 1987) gives details on dissecting and mounting the muscle and on the saline used. The distal end of the isolated muscle was attached to an ergometer (Cambridge model 300H, Cambridge Technology, Cambridge, MA 02140) by a hooked rod made from a fine insect pin. The ergometer was used both to measure the force generated by the muscle and to impose length changes on the muscle. The muscle was activated by stimulating its motor nerve with a suction electrode. The stimuli were 0·5 ms current pulses whose intensity was 1·5–2 times that needed to evoke a maximum contraction in response to a burst of stimuli. The saline surrounding the preparation was continuously aerated and maintained at about 15 °C (range = 14·6–15·4 °C).

Power output was measured as the SG muscle was subjected to cyclic length changes at frequencies comparable to those *in vivo* and stimulated phasically in the length cycle. If the cyclic muscle responses were in steady state, a plot of the muscle force against muscle length over a full cycle formed a closed loop (Fig. 1).

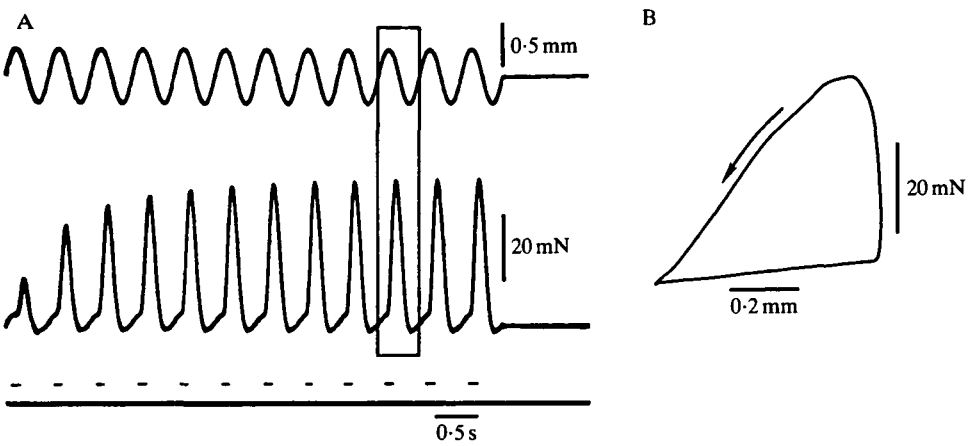

Fig. 1. (A) Muscle force (middle trace) during imposed sinusoidal length change (upper trace) and stimulation (lower trace) which was phase-locked to the length cycle. The muscle was scaphognathite levator L2B from *Carcinus maenas*. The stimuli were a burst of 10 shocks in 100 ms. (B) The work loop (= muscle force against muscle length over a full cycle) for the tenth cycle of the series in A, that cycle enclosed in the box. The area of the loop is the work done on or by the muscle. Here the loop was traversed in an anticlockwise direction, indicating that work was done by the muscle on the apparatus. The work for this cycle was 15·6 μJ (= 2·93 J per kg muscle mass).

The area of this loop is the mechanical *work output* for that cycle. This area times the cycle frequency is the average *power output*.

Many parameters affect the power output of a muscle preparation. These include the frequency, pattern and amplitude of the imposed, cyclic length change; the timing in the length cycle of the muscle stimulation; the pattern of the phasic stimulation, i.e. the number and intensity of the individual stimuli in a burst and the pattern of the intervals between the stimuli; the cycle of a series chosen for analysis; and the muscle temperature. We did not explore the whole of this large parameter space. Rather we used activation patterns which mimicked the neural activation patterns during normal ventilation, and sought values for average muscle length, imposed change in length, and stimulus phase which maximized work output for the given stimulus conditions.

The cyclic length change imposed upon the muscle was sinusoidal. The trajectory of the SG blade during beating is actually rather complicated, and is different at different positions across the blade (Young, 1975, fig. 12). Muscle L2B inserts near what has been called the hinge region of the blade (Young, 1975), and the blade movement at the hinge is approximately sinusoidal but with several jerky components. The sinusoidal length change imposed on the muscle thus may be an inexact approximation of the muscle trajectory *in vivo*. The peak-to-peak amplitude of the length change, measured in millimetres or as a percentage of the muscle length, will be termed *strain*.

The *phase* of muscle stimulation in the length cycle is defined by the relationship

between the time of the expected tension peak, based on isometric measurements, and the time of maximum muscle length. Specifically: phase (%) = $100[(A+B-C)/D]$, where A is the delay from cycle onset to the onset of stimulation, B is the isometric tension rise time measured from the start of stimulation, C is the delay from cycle onset to peak length, and D is the cycle duration. A phase of 0 indicates that the time of expected maximum tension coincides with the time of maximum length; a positive phase indicates that the time of expected maximum tension occurs during muscle shortening, and a negative phase that the time of expected maximum tension occurs during muscle lengthening.

In each experimental trial the muscle was subjected to 12 consecutive cycles of length change and associated stimulation. By the tenth cycle of the set the muscle responses were nearly in steady state (Fig. 1), and the tenth cycle was selected for work measurement. Force and position values for the tenth cycle were sampled with an analog to digital converter (12 bit resolution, one force or position sample each 200 μs) and analysed with an on-line digital computer. Trials were repeated regularly at 2-min intervals.

During the initial dissection, after the muscle had been exposed, the SG was pushed into a fully depressed position and the length of muscle L2B was measured with an ocular micrometer (see Josephson & Stokes, 1987). This length, which is the longest length reached by the muscle *in vivo*, will be termed the *reference length*. The reference length in the muscles examined ranged from 8·7 to 11·3 mm. At the end of an experiment the muscle length was set at what had been determined to be the *optimum length* for work output (see below) and the muscle was fixed, without detaching it from the ergometer, in 70 % ethanol. After 10–30 min in ethanol, the muscle was removed from the apparatus and stored in 70 % ethanol. The following day the muscle was dissected free from its attachments and its fixed length measured with an ocular micrometer. The muscle was then stored for several days to several weeks in ethanol, rehydrated overnight in saline, and weighed. The mass of the muscle was multiplied by 1·36 to correct for the expected mass loss associated with alcohol fixation and storage (Josephson & Stokes, 1987). The corrected mass of muscles used in experiments ranged from 3·2 to 12·9 mg.

The total mass of SG muscles was determined from whole animals fixed in 70 % ethanol. The SG on one side was exposed and all the muscles which move it were removed, rehydrated in saline, and weighed.

Muscle activation patterns

Muscle activation patterns were selected to mimic those *in vivo* based on motor nerve recordings and EMG recordings from beating scaphognathites of *C. maenas* obtained by Young (1975) and by Mercier & Wilkens (1984*b*).

Mercier & Wilkens found that the muscle L2B is activated by bursts of motoneurone potentials on each cycle, and that the frequency of action potentials within the bursts is proportional to the cycle frequency. They further noted that

the number of pulses per burst is typically independent of burst frequency, and can be nearly constant over a wide range of burst frequencies (see also Young, 1975). We define *duty cycle* as the ratio between burst duration and burst period, where burst period is the interval from the start of one burst to the start of the next. A consequence of (1) the average interpulse interval within a burst being a constant fraction of the burst period (this follows from the proportionality between pulse frequency and burst frequency), and (2) the number of pulses per burst being independent of frequency, is that (3) the duty cycle is independent of cycle frequency. For the preparation of Mercier & Wilkens from which the largest number of observations was obtained, the interpulse interval was about 2·6 % of the burst period and the number of pulses per burst was, with a few exceptions, 8 or 9 (the range in all preparations was 4–29 pulses per burst). For this relative pulse interval and pulse number the predicted duty cycle is 18–21 %. Young (1975) earlier found the duty cycle of muscle L2B to be about 20 %. We have chosen 10 pulses per burst and a duty cycle of 20 % as being representative of a normal activation pattern.

Experimental protocol

There is an optimum muscle length for work output and, for a given set of stimulus conditions, an optimum strain and an optimum stimulus phase (Figs 2, 3, 4; see also Josephson, 1985*a*; Mizisin & Josephson, 1987). The following sequence was used to determine the work output as a function of burst frequency at optimum muscle length, strain and stimulus phase.

(1) *Determination of the tension rise time.* The muscle was held at a fixed length and stimulated at a burst frequency of 2 Hz (10 shocks per burst, 20 % duty cycle). The isometric tension rise time for the tenth response of the set was measured and used in phase calculations.

(2) *Determination of optimum length* (Fig. 2). Using an estimated value for optimum phase (typically about 20 %) and an estimated value for the optimum strain (typically 0·75 mm, about 7·5 % of muscle length), work output was determined in a series of trials at different lengths to find the optimum length. The initial trial of the series was at a length well below the anticipated optimum, and the muscle length was increased in steps of 0·25 mm (about 2·5 %) between each trial.

(3) *Determination of optimum phase* (Fig. 3). The stimulation phase for maximum work output was determined at the determined optimum length and with the estimated optimum strain, beginning with a phase well below the optimum and increasing the stimulus phase in steps of approximately 5 % between trials.

(4) *Determination of optimum strain* (Fig. 4). At the determined values for optimum length and optimum phase, the optimum strain was found in a series of trials, beginning with a strain below the expected optimum and increasing the strain by 0·125 mm between each trial. If the measured value for optimum strain was appreciably different from that estimated in step 3, step 3 was then repeated

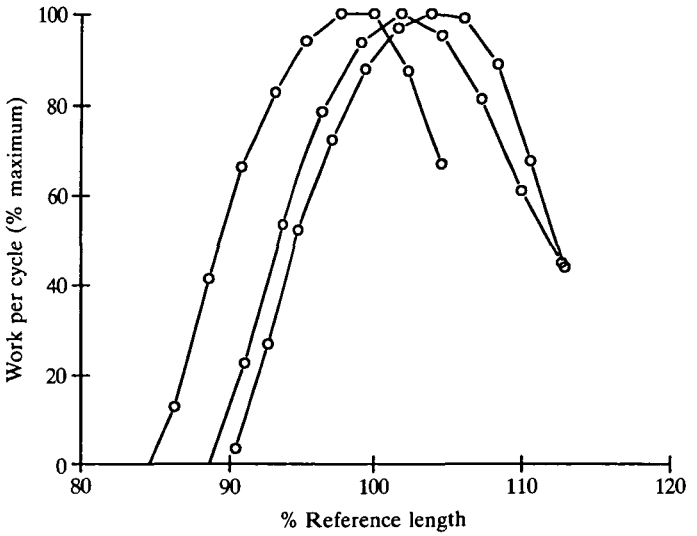

Fig. 2. Work output and muscle length. Work output was measured at a burst frequency of 2 Hz and with estimated values for optimum muscle strain and stimulus phase. Each of the curves is from a separate preparation. Together the curves represent three of the six preparations used in Fig. 5. The preparations selected were that with the lowest value of optimum length, that with the highest value of optimum length, and one whose optimum length was close to the average value.

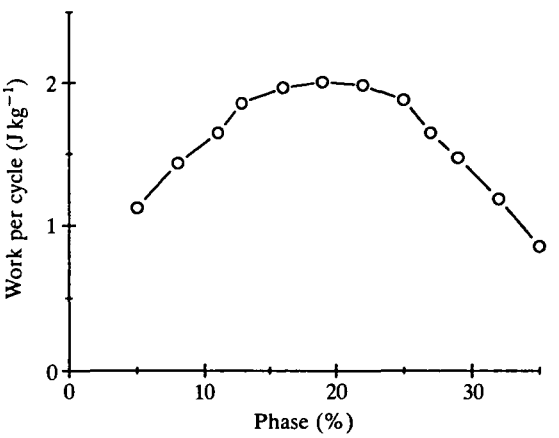

Fig. 3. Work output and stimulus phase. The burst frequency was 2 Hz, the resting muscle length was at the optimum length for work output, and the strain for the imposed length change was 1·0 mm (= 9 %, length excursion from 95·5 % resting length to 104·5 % resting length). The data points are from a single muscle and are the average of a determination at each test phase during an ascending series and a determination at each phase in a descending series immediately following.

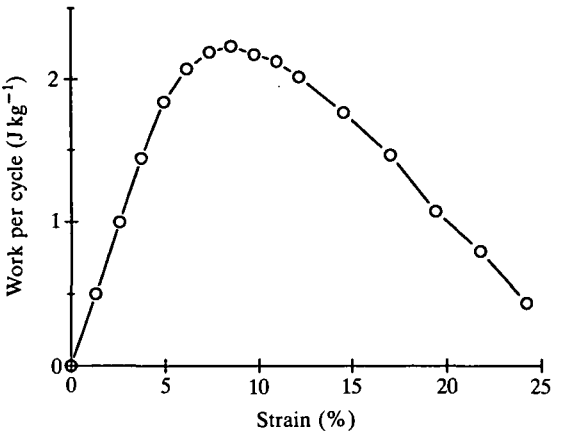

Fig. 4. Work output and strain. The burst frequency was 2 Hz, the stimulation phase 25 %, and the average muscle length that at which work was maximal. The individual points are averages from an ascending and a descending series. This muscle is different from the one of Fig. 3.

using the new value for optimum strain. The work output at 2 Hz, at optimum length, phase and strain, was taken as the maximum work measured at this time during the experimental series.

(5) *Determination of maximum work per cycle at a new frequency.* A new burst frequency was selected randomly from the series 0·5, 1, 1·5, 3, 4, 5 Hz and the stimulus parameters were adjusted appropriately. The tension rise time was determined as in step 1 but with the new stimulation parameters. Steps 3 and 4 were repeated to determine the maximum work output per cycle at the new frequency.

(6) *Redetermination of maximum work at 2 Hz.* The burst frequency was returned to 2 Hz. The phase and strain were set at the values determined initially in steps 2 and 3. Five trials were given. Values from the fifth trial were used as the work output at 2 Hz at this stage in the experiment.

(7) *Steps 5 and 6 were repeated.* New values for burst frequency were selected randomly from those remaining in the series until all values had been used.

With this protocol, each measurement with a new burst frequency was immediately preceded and immediately followed by a determination at 2 Hz. This procedure allowed us to express work values relative to those at 2 Hz, and thus to compensate for progressive changes in the condition of the preparation which sometimes occurred during these rather lengthy measurements.

In analysing our data, the first dozen or so experiments, in which performance was somewhat variable, have been discarded. The results reported are from six preparations made after the quality of performance from experiment to experiment seemed to have reached a plateau.

Results

Frequency, work and power

The mechanical work output per cycle increased with burst frequency to a maximum at 2–3 Hz beyond which it decreased with frequency (Fig. 5). The mechanical power output, which is the product of work per cycle and cycle frequency, reached a maximum at an average repetition frequency of 4 Hz (range = 3–5 Hz). The absolute values for work output at 2 and 3 Hz were 2·7 and 2·5 J kg^{-1}, respectively (S.D. = 0·9 J kg^{-1} for each, $N = 6$, values for 2 Hz are based on the mean value for all the series at 2 Hz with each preparation). The power output at 4 Hz averaged 8·8 W kg^{-1} (S.D. = 3·3 W kg^{-1}, $N = 6$).

The values for work and power in Fig. 5 are expressed as relative values, defined as the work or power at a given burst frequency divided by the average work or power for the trials at 2 Hz immediately preceding and following the trial at the test frequency. In each of the six preparations used in Fig. 5 there was a decline in muscle performance over the period required to collect the data, but the decline was only moderate. The fractional reduction in work output between the first series at 2 Hz and the last series at 2 Hz, which came almost 3 h and some 50 trials later, averaged only 27 % (S.D. = 14 %) for the six preparations.

Optimum length, phase and strain

The relationship between average muscle length and work output is a steeply rising and falling curve with a narrow optimum (Fig. 2). In 36 preparations used in this study and in related studies the optimum length for work output, measured as in Fig. 2, averaged 101·1 % of the muscle reference length (S.E. = 1·2 %).

To minimize the number of times a muscle was stimulated, the steps used in

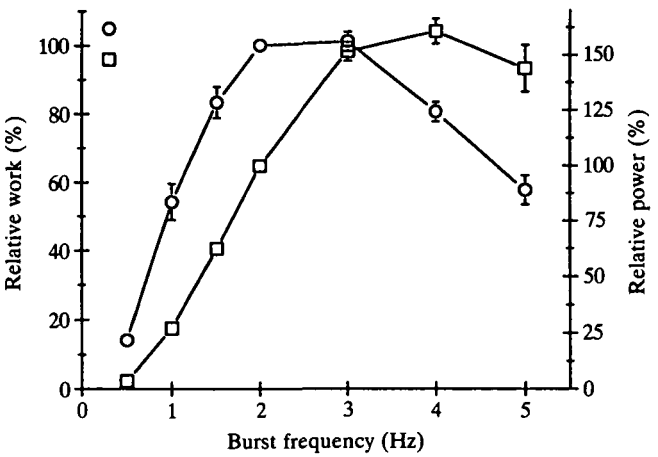

Fig. 5. Work (○) and power (□) as a function of burst frequency. Relative work or power is the value at a given burst frequency divided by the average of the work or power for the trials at 2 Hz immediately before and immediately after that at the test frequency. Vertical bars (shown only where larger than the symbol) are standard errors ($N = 6$).

determining the optimum phase and strain in the work measurements above were rather coarse, 5 % for phase and 0·125 mm (about 1·25 %) for strain. With muscle L2B the curves relating work output with strain and with phase have rather broad peaks (Figs 3, 4) so there cannot have been much error in estimates of maximum work caused by failure to locate accurately the exact phase or strain optimum.

With the stimulus patterns used, the optimum phase was independent of burst frequency (Fig. 6). The optimum strain, however, did vary somewhat with frequency; rising with increasing frequency to a peak at 1·5 Hz and falling thereafter (Fig. 7). During ventilatory beating the SG blade sweeps across the entire chamber in which it is housed, and its movement is limited by the roof and the floor of the cavity (Pilkington & Simmers, 1973; Young, 1975; Mercier & Wilkens, 1984*a*). Thus the amplitude of the SG stroke is constant and so,

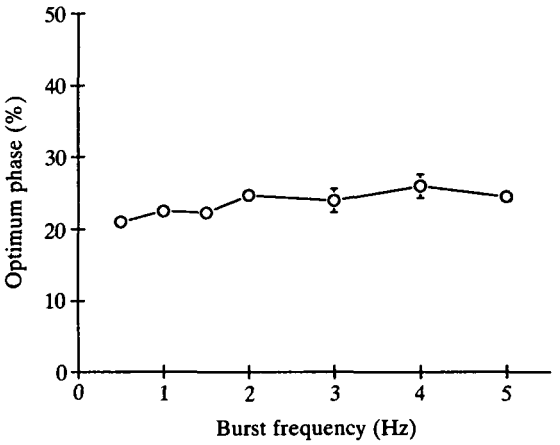

Fig. 6. The optimum phase for work output for the trials of Fig. 5 as a function of burst frequency. Vertical bars are standard errors.

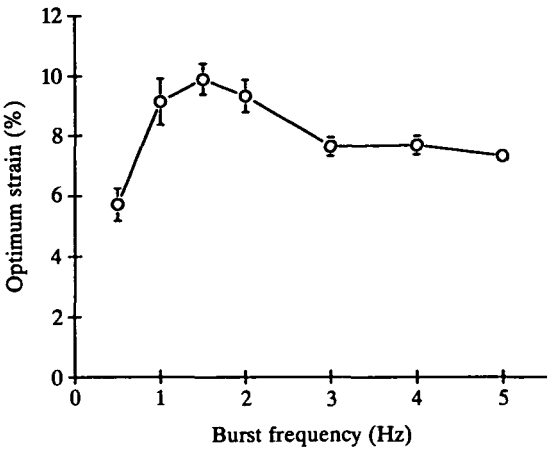

Fig. 7. Optimum strain for work output, again for the trials of Fig. 5. Vertical bars are standard errors.

presumably, is the strain for muscle L2B. A corollary of frequency-dependent optimum strain and frequency-independent operating strain is that muscle L2B cannot operate at optimum strain at all frequencies. Because the curve relating work and strain has a relatively broad peak, the work output of L2B should not be greatly depressed when the muscle operates near to but not exactly at the optimum strain.

Discussion

Work and power

With stimulus patterns that mimic those *in vivo*, the mechanical work available from SG muscle L2B is maximal at beat frequencies of 2–3 Hz, which is near the middle of the normal operating range (0·7 to 4–5 Hz; Hughes *et al.* 1969; Wilkens *et al.* 1984; Mercier & Wilkens, 1984*a*,*b*). The work per cycle does not drop off rapidly at frequencies above the optimum (Fig. 5), and the mechanical power available from the muscle increases to a maximum near to or at the maximal operating frequency. Over most or all of the normal operating range the muscle power available to drive the SG pump increases with beat frequency.

The maximum power output measured from the SG muscle ($8{\cdot}8\,W\,kg^{-1}$) is less than that measured from insect wing muscles using similar methods. The maximum power output of ordinary flight muscles from two species of locust and one tettigoniid was found to be $73–76\,W\,kg^{-1}$ (20, 25 Hz, 30°C; Mizisin & Josephson, 1987; Josephson, 1985*a*,*b*), that of a tettigoniid wing muscle used in both singing and flight was $33\,W\,kg^{-1}$ (25 Hz, 30°C, Josephson, 1985*b*). The lower mechanical power output from the crab muscle is in part a result of the lower temperature used in the crab measurements. If the Q_{10} for power output were 2, warming the crab muscle to 30°C, the temperature at which the insect measurements were made, would be expected to increase the power output of the crab muscle to $25\,W\,kg^{-1}$. In addition, the power output from muscle L2B was measured using stimulus patterns similar to the muscle activation patterns during normal beating, and these patterns are not necessarily those which maximize power output. In the measurements of work output described above there were 10 stimuli per burst. In several preliminary experiments, using a burst frequency of 2 Hz, we have found that doubling the number of stimuli per burst from 10 to 20, without changing the interstimulus interval, increased the power output by 30–70%. The activation parameters during normal beating may have been evolutionarily selected to maximize efficiency, or to maximize the ability to grade power, or to optimize some other performance characteristic, and not to maximize power output.

The average muscle length which was optimal for work output was about 1% greater than the reference length (S.E. = 1·2%). This is a bit surprising, for it indicates that the average muscle length *in vivo* is less than the optimum length for work output. The length of levator muscle L2B is greatest when the SG is fully depressed, and this is the length which we have measured as the reference length.

The average length of muscle L2B *in vivo* must be less than the reference length, how much less depends on the actual muscle strain per cycle. If the muscle strain *in situ* were 9 %, which is the optimum strain measured for the isolated muscle at 2 Hz (Fig. 7), the muscle would shorten to 91 % and lengthen to 100 % of the reference length on each cycle, and the average muscle length would be 95·5 % of the reference length. The curve relating work output to muscle length falls steeply on either side of an optimal length (Fig. 2). We estimate the expected work output at 95·5 % of the reference length to be about 70 % of that at the optimum muscle length. It is certainly possible that there are unknown, systematic errors in our length measurements, and that we have underestimated the maximum muscle length *in vivo* or overestimated the optimum length for work output. If there are no errors in our length measurements, the work output of the muscle *in vivo* must be less than the maximum values which we measured, since these maximum values were determined from isolated muscles at longer and more favourable lengths than those at which the muscle normally operates. Because the standard error in the ratio of optimum length to reference length is rather large, making it difficult to evaluate accurately the actual relationship between the two measures (and also suggesting inaccuracies in the length measurements), we have not corrected for operating length in our estimates of the mechanical power available *in vivo*. We have assumed that the muscle power available to the crab is the maximum power which we can obtain from its isolated muscle under appropriate patterns of stimulation.

Efficiency

The hydraulic power output of the SG pump in *C. maenas* has been estimated from the hydraulic pressure developed across the pump and the rate of fluid movement by the pump against this pressure gradient (Mercier & Wilkens, 1984*a*). The power output, determined for a single SG during periods of unilateral beating, increased exponentially with beat frequency (Fig. 8).

In a set of *C. maenas* of varying size, we found that muscle L2B made up 18 % of the total power musculature of an SG (S.E. = 1 %, $N = 7$). Assuming that the properties of the other SG muscles are like those of L2B, the combined work and power from all the muscles of an SG is estimated by multiplying the values for L2B by 5·56 (= the reciprocal of 0·18). The calculated power available from the SG musculature is comfortably greater than that expended by the SG pump for frequencies up to about 4·7 Hz, which may be higher than beat frequencies actually reached in intact animals (Fig. 8).

One measure of the efficiency of the SG pump is the ratio of the muscle power input to the hydraulic power output. For the data in Fig. 8, the efficiency has a minimum of 13 % at 1 Hz, rising to 19 % at 2 Hz and 36 % at 3 Hz. The efficiency would be 64 % at 4 Hz if the hydraulic power output continued to rise with frequency as predicted in Fig. 8.

The efficiency of the SG muscles in converting metabolic energy into mechanical work can be estimated from the metabolic cost of ventilation. Wilkens *et al.* (1984)

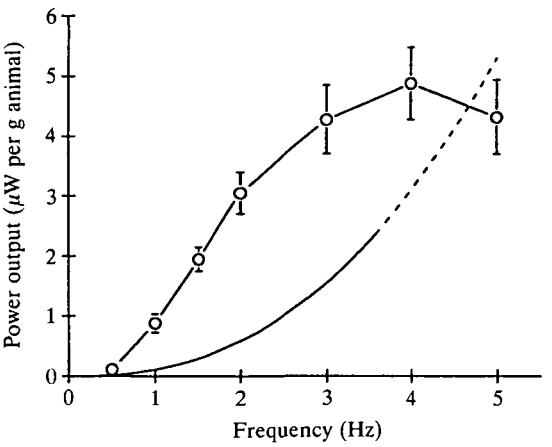

Fig. 8. The mechanical power available for the muscles of a single scaphognathite, estimated from the mechanical power output of muscle L2B and the fraction of the total SG musculature represented by L2B. Vertical bars are standard errors, $N = 6$. The curve below is the hydraulic power output of a single SG determined by Mercier & Wilkens (1984*a*). The solid portion of the curve is the power function best fitting the data points in fig. 2D of Mercier & Wilkens; specifically: $P = 0{\cdot}11F^{2{\cdot}4}$ where P is the hydraulic power (μW per g animal) and F is the beat frequency (Hz). The dotted portion of the curve is the extension of the function to beat frequencies above those from which data were collected.

measured the metabolic cost of ventilation by comparing oxygen consumption before and after SG ablation. The gills of the experimental animals were externally perfused after SG amputation so as to maintain blood oxygen and lactate concentrations at normal levels, and to ensure that the reduced oxygen consumption was a consequence of removing respiring tissue and not a general reduction because of reduced blood oxygenation. At a water flow rate corresponding to a total SG beat frequency (right plus left) of 3·9 Hz, the metabolic cost of ventilation was 55 μW per g animal (calculated from oxygen consumption values assuming 1 mmol O_2 is equivalent to 450 J; Dejours, 1975). If the combined beat frequency were a result of right and left SGs each beating at about 2 Hz (power output per SG = 3·1 μW per g animal, Fig. 8), the total muscle mechanical power output (right plus left) would be $2 \times 3{\cdot}1 = 6{\cdot}2$ μW per g animal, and the efficiency of converting metabolic power to muscle power would be $6{\cdot}2/55 = 11\%$. If the combined beat frequency were due to one SG beating at 4 Hz while the other was quiescent, the efficiency would be about 9 %. Thus about 10 % of the metabolic power input is available as mechanical power by the muscles, and of the latter about one-third becomes hydraulic power output by the pump. The estimated value of muscle efficiency (10 %) is less than the commonly accepted value of 25–30 % for vertebrate muscles (e.g. Margaria, 1976; Woledge *et al.* 1985); but it is similar to estimates of the efficiency of muscles in flying insects (Ellington, 1985) and of the muscles used in locomotion by small mammals (Heglund *et al.* 1982).

Supported by NSF grant DCB-8416277. We thank R. Shockley for skilled assistance throughout the course of this study.

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