THE MECHANICAL POWER OUTPUT OF A TETTIGONIID WING MUSCLE DURING SINGING AND FLIGHT

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SUMMARY

1. The mesothoracic wings of tettigoniid insects are used in song production and flight; the metathoracic wings in flight only. In *Neoconocephalus triops* the wing stroke frequency during flight is about 25 Hz; the frequency during singing about 100 Hz.

2. The twitch duration of mesothoracic, first tergocoxal (Tcx1) wing muscles is only about one-half the duration of the upstroke or downstroke portion of the wing cycle. During tethered flight the Tcx1 muscles are activated on each cycle with short bursts of action potentials, each burst typically containing four action potentials. Activating the muscles with brief, tetanizing bursts increases the duration of muscle activity and the mechanical power output per wing cycle above that obtainable with single twitch contractions of the muscle.

3. The mechanical power output was determined for mesothoracic Tcx1 muscles undergoing sinusoidal length change and stimulated phasically in the length cycle. At 25 Hz, the power at optimum muscle strain and optimum stimulus phase was 5 W kg^{-1} at 30 °C for muscles activated with a single stimulus per cycle and about 33 W kg^{-1} for muscles activated with bursts of stimuli in the normal pattern of flight.

4. The maximum power output at 100 Hz, the singing frequency, was 18 W kg^{-1}. This was achieved with a single stimulus per wing cycle.

5. From published values of oxygen consumption by tettigoniids during singing, it is concluded that the efficiency of conversion of metabolic to mechanical power during singing is about 3 %.

INTRODUCTION

Adult, male tettigoniids and crickets attract mates by rubbing their forewings together to produce a calling song. The wing muscles used in sound production are, with a few possible exceptions, the same muscles used in flight. Some wing muscles of insects have been termed bifunctional because they participate in both walking and flight (Wilson, 1962). The forewing muscles of male tettigoniids and crickets are

multifunctional in that they participate in sound production, and flight, and for many of the muscles in leg movements as well.

The forewing muscles of some tettigoniids are remarkable for the high contraction frequencies achieved during song production: 100 Hz in *Neoconocephalus triops* (Josephson, 1984), 150 Hz in *Euconocephalus nasutus* (Josephson, 1973) and up to 200 Hz or more in *N. robustus* (Josephson & Halverson, 1971). The operating frequency of these same muscles during flight is 19–25 Hz (Josephson, 1973, 1984; Ready, 1983). Although their operating frequency can be very high, the forewing muscles of tettigoniids are synchronous muscles with an action potential or burst of action potentials for each contraction (Josephson & Halverson, 1971). The high contraction frequencies of the forewing muscles are achieved in part because of muscle modifications leading to very short twitch duration. These modifications include hypertrophy of the sarcoplasmic reticulum of the muscle fibres (Elder, 1971, 1975; Ready, 1983). In each of the three species of tettigoniids mentioned above, the isometric twitch duration is about one-half as long in the mesothoracic muscles, which move the forewings, as in the metathoracic homologues, which drive the hindwings (onset to 90 % relaxation at 30 °C is 10–14 ms for mesothoracic muscles, 20–30 ms for metathoracic ones; Josephson, 1973, 1984).

One of the questions to be considered below is the relationship between twitch duration and muscle effectiveness during flight. Ideally a muscle should be fully active over the half-cycle during which it shortens, so that it may deliver maximum power to the wing upstroke or to the downstroke depending on muscle type, and fully inactive during the half-cycle during which the antagonists are active, so that little work is required to re-extend the shortened muscle. With muscles which are activated once per cycle to give twitch-like contractions, as happens sometimes in metathoracic muscles of the tettigoniid *N. triops* (Josephson, 1985) and frequently in flight muscles of the locust *Schistocerca gregaria* (Wilson & Weis-Fogh, 1962), the twitch duration should match the half-cycle duration for maximum muscle effectiveness. This is indeed the case in metathoracic muscles of the tettigoniids mentioned above in which the half-cycle duration (20–25 ms for wing stroke frequency of 20–25 Hz) is quite similar to the total twitch duration (20–30 ms to 90 % relaxation). With mesothoracic muscles, however, the twitch duration is only about half the half-cycle duration, so a twitch contraction of a mesothoracic muscle could deliver power to the wings for only a fraction of the relevant half-cycle. One therefore anticipates that either the mesothoracic muscles, with their short twitch duration, are relatively ineffective contributors to flight, or that the activation pattern per cycle is different in mesothoracic and metathoracic muscles. It will be shown that the latter is the case.

The second matter to be considered is the mechanical power output of muscles operating at the high contraction frequencies of singing. Information on this would help to resolve some uncertainties about the efficiency of converting muscle work to sound energy by insects (see Bennet-Clark, 1970; Counter, 1977; MacNally & Young, 1981). In addition, some recent models of work output by cyclically-contracting muscle have suggested that mechanical power should increase monotonically with normal operating frequency (Weis-Fogh & Alexander, 1977; Pennycuick & Rezende, 1984). The high-frequency, forewing muscles of tettigoniids offer an opportunity to examine this suggestion.

MATERIALS AND METHODS

The muscles to be considered are mesothoracic, first tergocoxal (Tcx1) muscles from adult males of the tettigoniid *Neoconocephalus triops*. Animals were captured while they were singing in the early evening in fields and urban areas near the university campus in Irvine, California. Animals were given fresh grass and water in the laboratory and were used within a day or two of capture.

Action potentials were recorded from wing muscles of animals during tethered flight with silver wires, 50 μm in diameter and insulated to the tip, which were inserted into the selected muscle through small holes in the dorsal exoskeleton. The electrodes were held in place with cyanoacrylate cement. Action potential recordings were made at ambient temperatures of about 25 °C.

Mechanical work output from Tcx1 muscles was measured using an approach described in detail elsewhere (Josephson, 1985). Basically, the muscle is subject to periodic length change of an appropriate wave form, amplitude and frequency, and the muscle is stimulated at a selected phase of the length cycle. The work output per cycle is determined from the area of the loop formed by plotting muscle force against length over a full cycle. The parameters affecting work output are the amplitude, frequency and trajectory of the imposed length cycle; the number and pattern of stimuli given to the muscle; the phase of stimulation; and the muscle temperature. In the experiments to be described, the muscle was subjected to sinusoidal length change at 25 Hz, which is the wing stroke frequency during flight, and 100 Hz, which is the wing stroke frequency during stridulation (Josephson, 1984). Muscles were stimulated with silver wire electrodes (50 μm diameter) which were implanted through the dorsal exoskeleton so as to bracket the origin of the muscle. The stimuli were 0·5-ms shocks at twice the intensity required to activate the three motor units of the muscle (Josephson, 1984). All work measurements were made at a muscle temperature of 30 °C.

An experimental trial consisted of a set of five or six consecutive cycles of muscle length change and stimuli. Short bursts of activity were used in order to minimize fatigue and the possibility that work output was limited by the oxygen supply rather than inherent properties of the contractile apparatus. One cycle, usually the fourth or fifth, was analysed for each trial.

The amplitude of the imposed sinusoidal length change (= muscle strain) and the phase of stimulation in the length cycle were systematically varied to find optimum values for maximizing work output. Initially, an optimum strain was estimated and the stimulus phase varied in steps of about 3 % of cycle duration until the optimum phase was found. Using this phase, the strain was then systematically varied in steps of about 0·4 % of muscle rest length to determine the optimum strain. If this strain varied by more than one or two amplitude steps from the initially estimated optimum value, the optimum phase was redetermined using the new value for optimum strain.

For metathoracic Tcx1 muscles, the work output per cycle has been found to decline with decreasing inter-trial interval (Josephson, 1985). In contrast, with mesothoracic muscles the work output per cycle increased with decreasing inter-trial intervals. For the results presented below, the inter-trial interval was held at 5 s, an interval sufficiently long to allow changing parameters between trials but sufficiently

short to have significant facilitation of work output. After the optimum phase and strain for a given set of conditions had been determined, the preparation was allowed to rest for 1 or 2 min and then subjected to a set of trials at the optimum stimulus phase and muscle strain. The work output per cycle gradually increased over the first 5–10 trials until it reached a steady rate. The values for work output reported here are the average of those from five adjacent trials at steady state for each preparation.

RESULTS

Firing patterns during activity

Muscle action potentials from mesothoracic Tcx1 muscles during tethered flight occur as short bursts of 4–6 spikes on each wing stroke (Fig. 1). The spike frequency within a burst is often quite regular. This firing pattern contrasts with that of
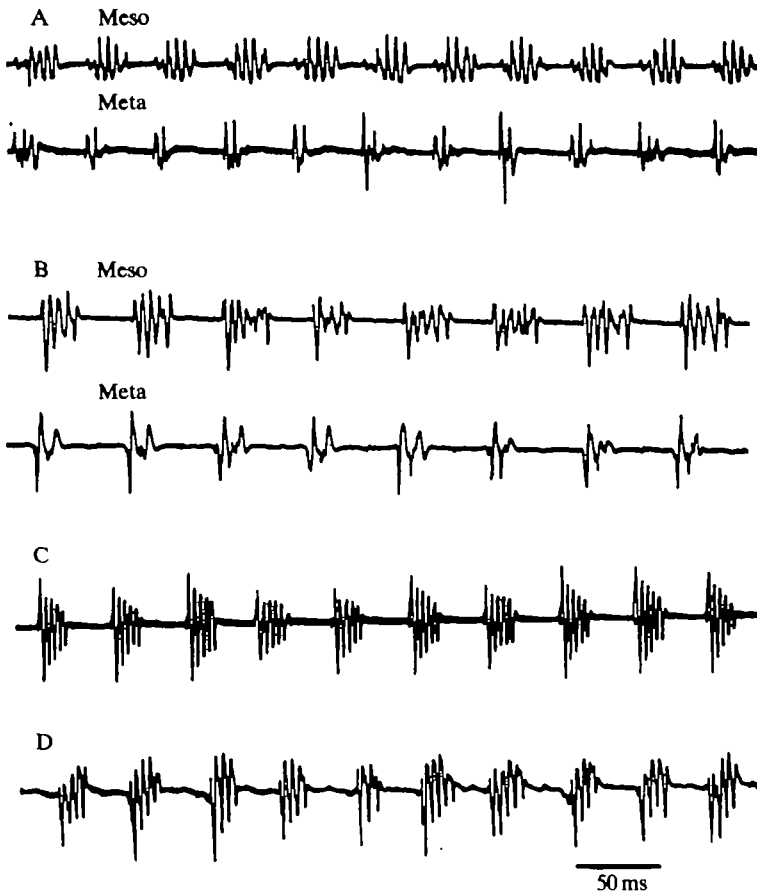

Fig. 1 Muscle action potentials from first tergocoxal muscles during tethered flight. (A) and (B) are simultaneous recordings from mesothoracic and metathoracic muscles, (C) and (D) from mesothoracic muscles alone. Each trace or pair of traces is from a different animal.
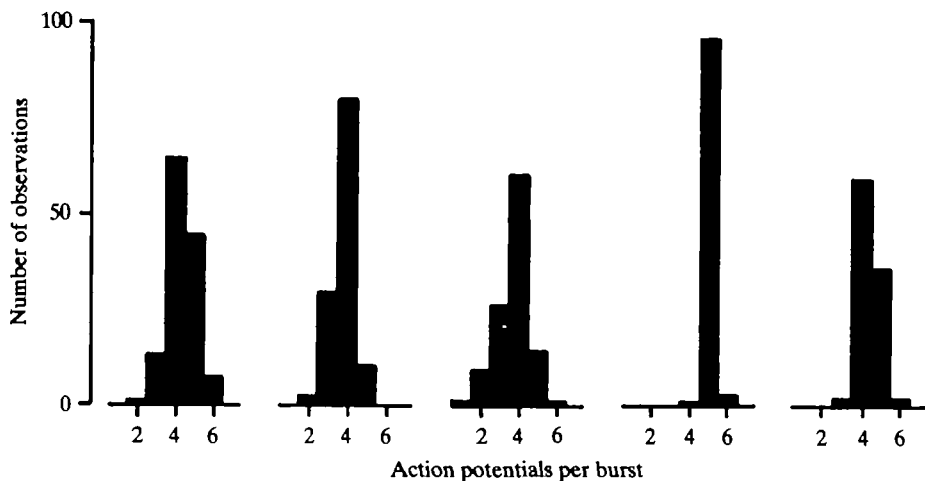
Fig. 2. Distribution of the number of action potentials per wing stroke cycle. Each histogram is from a different animal and each plots the number of spikes per burst in 100–130 sequential wing cycles. The next to last distribution is from the same animal as Fig. 1C.

metathoracic Tcx1 muscles, in which there are single action potentials or short bursts of 2–3 action potentials per wing stroke (Fig. 1; see also Josephson, 1985).

Recordings from five animals in which individual action potentials were sufficiently distinct that they could be counted with little ambiguity were selected for analysis. In four of the five animals the modal number of spikes per burst was 4; in the fifth animal there were, almost without exception, 5 spikes per burst (Fig. 2). In the animals which produced bursts principally with 4 spikes, the burst duration in those cycles with 4 spikes, measured from the peak of the first spike to the peak of the fourth, ranged from 11 to 19 ms with a grand mean of 15·8 ms. Thus a burst of 4 spikes per wing stroke with an interspike interval of about 5·3 ms is a typical activation pattern during flight for mesothoracic Tcx1 muscles of male *N. triops*. This pattern is used below in measurements of work output. Because of the repetitive firing, the mesothoracic muscle must be strongly activated throughout most of the half-cycle of the wing stroke during which it is functional, despite the short twitch duration of the muscles.

One animal sang while there were electrodes in its mesothoracic Tcx1 muscle. The pattern of action potentials during stridulation was very much like that described earlier for the tettigoniid *N. robustus*, with one action potential per sound pulse and wing stroke (Josephson & Halverson, 1971).

Mechanical power output

Power output at optimum strain and stimulus phase was determined for a set of 10 preparations under the following conditions: 25 Hz, 1 stimulus per cycle (common operating conditions for metathoracic wing muscles during flight); 25 Hz, 4 stimuli per cycle, interstimulus interval of 5·3 ms (common operating conditions for mesothoracic wing muscles during flight); and 100 Hz, 1 stimulus per cycle (the probable operating conditions during stridulation). Power output under these conditions is summarized in Table 1 and examples of force-position loops are shown in Fig. 3.

Table 1. *Mechanical power output and optimum length change per cycle*

Cycle frequency (Hz)	25	25	100
Stimuli per cycle	1	4	1
		Mesothoracic Tcx1 ($N = 10$)	
Power (W kg^{-1})	5·2 (0·8)	32·5 (1·7)	17·9 (1·0)
Optimum strain (% rest length)	4·3 (0·3)	6·1 (0·20)	2·3 (0·1)
		Metathoracic Tcx1	
Power (W kg^{-1})	38·0 (2·0)	61·0 (5·0)	

The values for metathoracic muscles are from Josephson (1985), with the four stimuli at 4-ms intervals. Mean ± s.e.

The twitch duration is shorter and the twitch tension lower in mesothoracic Tcx1 muscles than in metathoracic counterparts (Josephson, 1984). As a consequence, the power output of the mesothoracic muscles operating at 25 Hz and with a single twitch contraction per cycle is much lower than that from the metathoracic muscles under similar conditions. When mesothoracic muscles are activated with brief, tetanizing bursts of stimuli per cycle, as they are during normal flight, the power output is greatly increased over that from single, twitch-like contractions and approaches the power normally delivered by the metathoracic muscles. At the stridulation frequency of 100 Hz there is partial fusion of adjacent twitches (Fig. 3), and the work per cycle (0·18 J kg^{-1}) is less than that with single twitch contractions at 25 Hz (0·21 J kg^{-1}). However, because of the greater operating frequency, the power output at 100 Hz and 1 stimulus per cycle is about three times greater than at 25 Hz with 1 stimulus per cycle.

Giving multiple stimuli per cycle, which increases the duration of the muscle activation, reduces rather than increases power output at the high repetition frequency of singing. In several preparations examined, the maximum power output at 100 Hz with paired shocks separated by 2 ms was one-fifth to one-half of that obtainable with a single stimulus per cycle.

The optimum strain (6·1 %) for the mesothoracic Tcx1 muscle at flight frequency and multiple stimuli per cycle is essentially the same as that found earlier for the metathoracic Tcx1 muscle (Josephson, 1985). The optimum strain (2·3 %) for mesothoracic muscle at singing frequency is much smaller than that at flight frequency.

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

Much of the earlier research on tettigoniid wing muscles was with *N. robustus* rather than *N. triops* which was used in the investigation being considered here. The Tcx1 muscles of *N. robustus* and of *N. triops* are of similar dimensions and have almost identical isometric contraction kinetics and force-velocity relationships (Josephson, 1984). Further, the calling songs of the two species are similar, as is the temperature gradient between thorax and surroundings during singing. Because of the demonstrated similarities in muscles of the two species, it will be assumed in the following
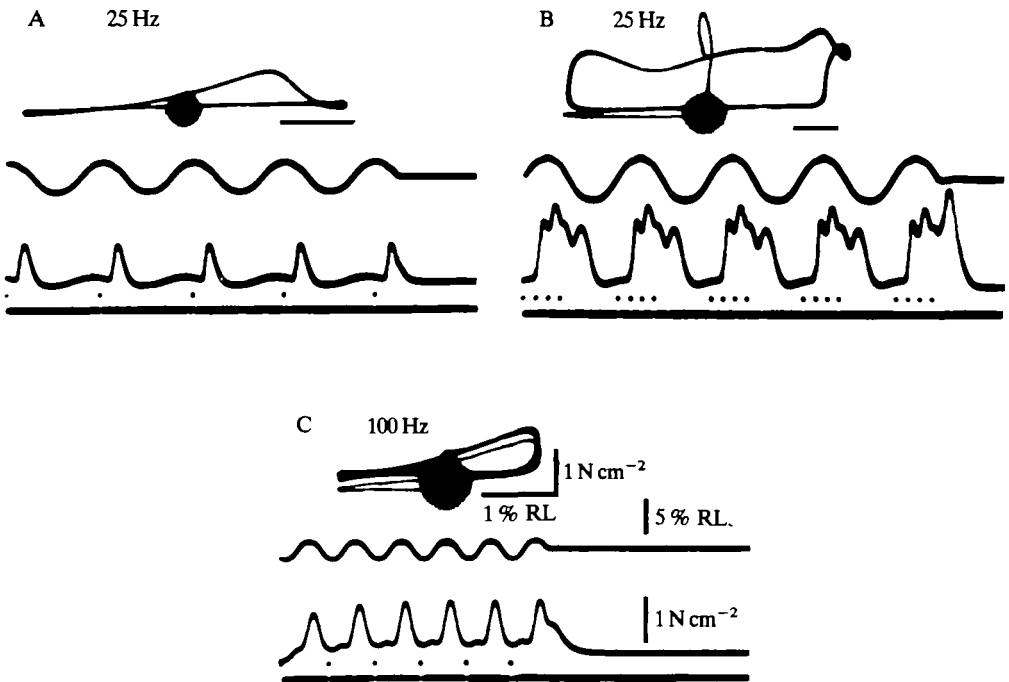
Fig. 3. Muscle length, muscle tension and work loops (tension against length) at 30 °C. The three sets of traces are from the same animal and each is taken at optimum strain and stimulus phase for work output. The lowest trace in each set marks stimuli. The steady-state work output per cycle for each example was: (A) 25 Hz, 1 stimulus per cycle, 0.22 J kg^{-1}; (B) 25 Hz, 4 stimuli per cycle, 1.51 J kg^{-1}; (C) 100 Hz, 1 stimulus per cycle, 0.22 J kg^{-1}. RL, resting length.

discussion that information about muscle structure, ultrastructure and oxygen consumption obtained from *N. robustus* is also applicable to *N. triops*.

Mesothoracic muscles as flight muscles

Because of their short twitch duration, the mechanical power output from mesothoracic Tcx1 muscles at flight frequency and with 1 stimulus per cycle is quite low, about one-sixth the mass specific power output of metathoracic muscles under similar conditions. In normal flight the insect cleverly compensates for the brief twitch duration by activating the mesothoracic muscles with short, nearly-tetanizing bursts of action potentials, in this way increasing the duration of muscle activity per cycle and greatly increasing the power output. Modifications of the central motor programme of flight, which at least partially maintain muscle effectiveness during flight, have accompanied the modifications in contraction kinetics of the mesothoracic muscles which allow the high-frequency contractions of singing. But even with repetitive activation in a normal pattern (4 action potentials at 5·3-ms intervals per cycle), the specific power output of the mesothoracic Tcx1 muscles (33 W kg^{-1}) is still less than that obtainable from metathoracic Tcx1 muscles (38 W kg^{-1} with 1 stimulus per cycle, up to 76 W kg^{-1} with multiple stimuli; Josephson, 1985).

The low power output of mesothoracic muscles is not due entirely to a short twitch duration, at least not directly so. Part of the difference between mesothoracic and

metathoracic performance is a result of different amounts of contractile material in muscles of the two segments. In *N. robustus*, myofibrils make up about 44 % of the muscle fibre volume in mesothoracic muscles and about 57 % in metathoracic muscles (Ready, 1983). The remaining volume in each case is largely mitochondria, sarcoplasmic reticulum and T-tubules. Thus the myofibril volume, that fraction of muscle which contributes directly to mechanical power output, is about 23 % less per kg muscle in mesothoracic muscles than in their metathoracic counterparts. The reduced relative volume of myofibrils in mesothoracic muscle fibres is due in part to an increased relative volume of sarcoplasmic reticulum, so the reduced myofibril volume is a consequence of the muscle modifications which allow short twitches and therefore the potential for high contraction frequency.

The mass specific power at flight frequency is less for mesothoracic than metathoracic wing muscles. However, the total mass of mesothoracic muscle in adult males is greater than that of metathoracic muscle, so the total power available to drive the wings is similar in the two segments. Total weights of mesothoracic and metathoracic wing muscles were determined in *N. robustus*. Animals which had been starved for 12 h were weighed and fixed in 70 % ethanol. Some days later the wing muscles were dissected free, rehydrated in insect saline, and weighed. Muscle weights were corrected for the 12 % weight loss expected with ethanol fixation (Ready, 1983). In these animals the mean animal weight was 815 mg (s.D. = 105 mg), the mean total weight of all mesothoracic wing muscles was 98 mg (s.D. = 21 mg) and the mean total weight of all metathoracic wing muscles was 56 mg (s.D. = 10 mg). Assuming that the mass specific power output of mesothoracic and metathoracic muscles is the same in *N. robustus* as in *N. triops*, the total mechanical power which might be delivered to the wings during flight is 3·2 mW for mesothoracic muscles (at 4 action potentials per cycle) and 2·1–4·3 mW for metathoracic muscles depending on whether the muscle is activated by single action potentials or by bursts of action potentials at optimum number and frequency.

Operating frequency and power output

Two recent theoretical accounts have examined the sustained mechanical power output which might be available from muscle (Weis-Fogh & Alexander, 1977; Pennycuick & Rezende, 1984). Both models predict that the power output should rise monotonically with operating frequency. In neither model is there a decline in power output with increasing operating frequency, which was the result found here in comparisons of expected power output during flight and singing in *N. triops*. It is of interest, therefore, to consider the two theoretical models and possible deficiencies in them that could lead to failure to predict real muscle behaviour.

In the Weis-Fogh & Alexander model the muscle is treated as being composed of two compartments; a myofibril volume which produces the mechanical power, and a volume (largely filled with mitochondria) involved in ATP production. The myofibrils are assumed to have an isometric stress-strain curve adequately described as one-half cycle of a cosine curve, and a stress-shortening velocity relationship given by Hill's characteristic equation (1938). Muscle shortening and lengthening are each assumed to occupy one-half cycle, and during each half-cycle the shortening velocity or lengthening velocity is constant.

The Pennycuick & Rezende model is in several ways similar to the previous model. The muscle is again treated as consisting of two components, mitochondria and myofibrils. The muscle is assumed to operate at a characteristic frequency which varies from species to species and which, presumably, is inversely related to animal size for homologous muscles. When operating at its characteristic frequency, a muscle is assumed to shorten at constant velocity on each cycle to a constant fraction of its rest length, a fraction which is assumed to be the same for all homologous muscles. The stress during shortening is assumed to be constant and positive, and the stress during lengthening is assumed to be zero. With these assumptions, the work per cycle per unit mass of myofibril is independent of frequency, and therefore the power output per unit mass of myofibril is directly proportional to frequency.

Two features, common to both models, account for much of the failure to predict declining power output at very high frequency. First, both models neglect the fraction of muscle volume which is involved in calcium regulation and the control of myofibril activation, i.e. the sarcoplasmic reticulum (SR) and the T-tubules. The fraction of muscle volume occupied by SR and T-tubules is directly related to twitch brevity. In muscles with very brief twitches, the volume density of SR and T-tubules can be one-fifth to three-quarters of the fibre volume (Rosenbluth, 1969; Elder, 1971, 1975; R. K. Josephson & D. Young, in preparation). To operate at high frequencies requires brief twitches, which in turn requires hypertrophy of the SR and T-tubules. Hypertrophy of the SR and T-tubules, in turn, reduces the fractional volume of muscle which is myofibrils and therefore reduces the power output per unit mass of muscle. Second, both models assume that activation of the myofibrils is instantaneous at the onset of the shortening half-cycle and so is inactivation at the onset of the lengthening half-cycle. In fact, at high operating frequencies the time course of muscle activation and inactivation is likely to be appreciable relative to cycle length. Through some or much of the shortening phase of the cycle the muscle may be only partially activated, and the muscle may remain partially activated into the lengthening phase. Incomplete activation during shortening would reduce the potential work output during shortening; partial activation into the lengthening phase would require that work be done on the muscle to re-stretch it and this would reduce the net work output per cycle. In *N. triops* the twitch duration is longer than the half-cycle duration for stridulation. Therefore the muscle must be partially contracted during lengthening, which must reduce the net work output. Power losses associated with muscle activation and inactivation time must become relatively more important the higher the operating frequency and must at least partially limit power output at high frequencies.

As mentioned above, in the Pennycuick & Rezende model it is assumed that homologous muscles, operating at their characteristic frequencies, shorten by a constant fraction of their rest length per cycle. For the strain to be constant and independent of operating frequency, the strain rate must be directly proportional to operating frequency. However, there are reasons to suspect that muscle strain rate has an upper limit, and so the proposal that strain rate should increase indefinitely with operating frequency is unrealistic. Maximum strain rate often varies directly with twitch brevity in different muscles (Close, 1965), but in very fast muscles strain rate reaches a maximum and is no longer correlated with twitch time course. For example, inferior rectus muscles of the rat or mouse produce much shorter twitches than do extensor

digitorum longus muscles of the same animals, yet the stress *vs* strain rate curves for the two muscle types are almost identical (Close & Luff, 1974; Luff, 1981). Again, although the maximum operating frequency *in vivo* of mesothoracic wing muscles in *N. triops* is about four times higher than that of metathoracic wing muscles, and twitches of mesothoracic muscles are much shorter than those of metathoracic muscles, the maximum strain rates for wing muscles of the two segments are almost identical (Josephson, 1984). As pointed out by Weis-Fogh & Alexander (1977), if the strain rate is fixed, the optimum strain per cycle for maximizing work output should become smaller with increasing cycle frequency. This is indeed seen in the mesothoracic wing muscles of *N. triops* for which the optimum strain when operating at 100 Hz is considerably less than that when operating at 25 Hz (Table 1).

The efficiency of stridulation

The metabolic input to the singing muscles of *N. robustus* during stridulation has been estimated from muscle temperature measurements during singing and subsequent cooling, and from the animal's oxygen consumption during singing (Heath & Josephson, 1970; Stevens & Josephson, 1977). For reasons discussed in Stevens & Josephson (1977), metabolic rates based on muscle temperature during singing and the cooling rate at the cessation of activity are probably underestimates. Therefore the metabolic rate based on oxygen consumption will be used here.

During stridulation, the metabolic rate in *N. robustus* rises from about $1 \cdot 7$ ml O_2 h^{-1} animal^{-1} for active, non-singing animals to about $14 \cdot 1$ ml O_2 h^{-1} animal^{-1} during singing; thus there is an increase during singing of about $12 \cdot 4$ ml O_2 h^{-1} animal^{-1}. Using as a conversion factor $19 \cdot 8$ J per ml O_2 (e.g. MacNally & Young, 1981) gives an increased metabolic input associated with singing of $68 \cdot 2$ mW per animal. From the value given above for the mass of the mesothoracic wing muscle per animal (98 mg), and the anticipated mechanical power output ($17 \cdot 9$ W kg^{-1} muscle), the expected mechanical power output is $1 \cdot 75$ mW per animal. The efficiency, defined as the ratio of work output to metabolic input, is thus $2 \cdot 6$ %. A. Mizisin (personal communication) has calculated the efficiency of locust wing muscle during flight to be 7–10 %, using published values for oxygen consumption during flight and mechanical power output determined essentially as was done here for tettigoniid muscles. These values of efficiency are consistent with recent suggestions by Ellington (1984, 1985) that the efficiency of insect wing muscle during flight is 10 % or less rather than the 20–30 % hitherto commonly assumed.

The value for efficiency calculated above is based on the mechanical power output of a muscle undergoing sinusoidal length change. It is possible that there is a click mechanism in the wing articulation which results in more rapid development of shortening and lengthening velocity at the top and bottom of the wing stroke than would be true for a sinusoidal cycle. If so, the measured power output with sinusoidal strain may somewhat underestimate the power output and efficiency of the muscle during its normal operation (for discussion see Pringle, 1981).

Counter (1977) reports that the power output as sound from a singing *N. robustus* is $12 \cdot 5$ mW. MacNally & Young (1981) question this value as being too high. These authors, using other data provided by Counter, estimate the sound power from *N. robustus* to be $1 \cdot 8$ mW. Even this value is disconcertingly large, for it requires that the

mechanical power output (1·75 mW) be converted to sound energy with an efficiency of about 100 %. Bennet-Clark (1970), using a generous estimate of muscle mechanical power output (70 W kg^{-1}), has calculated that the efficiency of conversion of muscular to sound power is 35 % in the mole cricket *Gryllotalpa vineae*. If the muscle power is lower than the estimated value, the conversion efficiency would have to be even higher to account for the intensity of the sound output. Thus there is some precedent for high efficiencies in converting mechanical power to sound in insects. But 100 % efficiency is clearly unreasonable. Either the estimates of mechanical power output by wing muscles during singing are too low, or estimates of power output as sound are too high, or both are true. Which of these possibilities is correct cannot be determined without additional information.

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