

MUSCLE ACTION DURING LOCOMOTION: A COMPARATIVE PERSPECTIVE

By IAN A. JOHNSTON

*Gatty Marine Laboratory, Department of Biology and Preclinical Medicine,
University of St Andrews, Fife, Scotland, KY16 8LB, UK*

Summary

This essay explores how the properties of striated muscles are matched to the tasks they perform during running, swimming and flying. During exercise the major locomotory muscles undergo alternate cycles of lengthening and shortening. Force development is greatly influenced by the timing of stimulation in relation to the length-change cycle and by the nature of elastic structures connecting the muscle fibres to the skeleton. The storage and recovery of elastic strain energy by the tendons (apodema in insects) results in a considerable saving of metabolic energy. Strain is independent of locomotory frequency, body size and muscle temperature. In contrast, the frequency of cycles, and hence strain rate, generally increases with speed and is inversely proportional to body size. The maximum isometric stress (P_0) striated muscles can exert is rather similar. During steady running or hopping in mammals the peak muscle stress is around one-third of P_0 . Behaviours such as vertical jumping impose higher stresses requiring disproportionately larger muscles and tendons, which may limit the storage of elastic strain energy. Muscles of small animals consume significantly more energy per gram than do those of large ones. This may be because they need to activate and deactivate their muscles at a higher rate to move at an equivalent speed. When differences in force production are normalised, by multiplying the energy consumed per stride by stride frequency, similar values for the mass-specific cost of locomotion are found in animals with different leg architectures, numbers of legs, skeletal type, body sizes and muscle temperatures.

The power output of isolated muscle fibres can be measured by imposing cyclical strain fluctuations and stimulating briefly during each cycle to approximate normal operating conditions *in vivo*. This approach yields values for maximum power output of 76–130 W kg⁻¹ for synchronous insect flight muscles at temperatures and wingbeat frequencies appropriate for flight. Frog sartorius muscle produces 20 W kg⁻¹ at the hopping frequency used during escapes at 20°C. The strain rates and deactivation rates of muscle fibres are optimised to produce maximum power over a particular range of locomotory frequencies. In vertebrates this necessitates the sequential recruitment of muscle fibre types with faster maximum strain rates and shorter contraction times as speed increases. Estimates of overall muscle efficiency during locomotion in insects, fish and small mammals are mostly in the range 6–20 %.

Key words: exercise, locomotion, skeletal muscle, muscle mechanics, muscle energetics.

Introduction

The ability of striated muscles to shorten and produce force is dependent on overlapping arrays of actin and myosin filaments, arranged in serially repeated sarcomeres. Although the mechanism underlying the conversion of chemical energy to mechanical energy is the same in all animals, numerous aspects of sarcomere structure and organisation can be varied to produce muscles with a diversity of mechanical properties (see Hill, 1950; Huxley, 1985; Squire *et al.* 1990). The action of muscles in locomotion is further modified by their anatomical arrangement, the lengths and properties of tendons, and by the operation of lever systems formed with the skeleton or cytoskeleton.

Whole-animal studies of muscle function

Terrestrial locomotion

During running or hopping, the major muscle groups are alternately stretched and then shortened during each stride (see Alexander, 1977). Inverted pendulum-like mechanisms operate at walking speeds in a wide range of legged animals (Full, 1989), but are most effective in bipeds (Cavagna *et al.* 1977). The common principle is that kinetic energy and gravitational potential energy are exchanged, and therefore saved, as the centre of mass of the animal rises and falls during each stride. Above certain speeds, pendulum mechanisms become ineffective and running or bouncing gaits are used. Animals running at constant speed over level ground do relatively little net work against the environment. The work done by the muscles and tendons serves to lift and accelerate the body and limbs, with positive work only just exceeding negative work. Prior to active shortening, the limb extensor muscles are stretched by the momentum of the animal. A proportion of the work done on the muscles is stored as elastic strain energy, which can be recovered during subsequent shortening of tendons and muscles (Cavagna *et al.* 1977). Thus, the muscles and tendons serve as springs which alternately store and release strain energy as the animal moves along, resulting in a considerable saving of metabolic energy (Cavagna *et al.* 1977).

Energy storage in the series elastic components is divided between the tendon and the muscle fibres, and depends on tendon length and compliance and the number of sarcomeres in series in the muscle fibres. Griffiths (1989) estimated that in the wallaby (*Thylogale billardierii*) up to 39% of the work done on the gastrocnemius (MG) muscle during hopping was stored as elastic strain energy, mostly in the tendon. Since the tendon is essentially elastic, most of this energy is recovered during the propulsive phase of the stride (Griffiths, 1989). Humans achieve even greater savings during running, with more than half of the energy supplied to lift and reaccelerate the centre of mass during each stride being obtained from elastic energy storage mechanisms (Cavagna *et al.* 1964).

Terrestrial mammals have 'preferred speeds' within each gait which are associated with minimal energy costs. Taylor (1985) has proposed that these preferred speeds and stride frequencies are those required to maximize the storage and

recovery of elastic strain energy and to minimise the cost of generating force. The peak stress in the ankle extensor muscles of white rats galloping at their 'preferred speed' was found to be around one-third of the peak isometric stress measured *in situ* (Perry *et al.* 1988). This is similar to that reported for kangaroo rats hopping at their 'preferred speed' (Biewener and Blickhan, 1988), and it may be a common feature of running and bouncing gaits.

Specialized runners, such as ungulates, have short muscles with long tendons in the lower parts of their legs that are slender in proportion to the forces they have to transmit. This increases the effectiveness of elastic energy storage. An extreme example of this is provided by the plantaris muscle of the camel, in which the tendon runs almost the whole length between the femur and insertions on the phalanges, and the muscle fibres are reduced to 1–3 mm (Alexander *et al.* 1982). In contrast, in the kangaroo rat (*Dipodomys spectabilis*), much less strain energy is stored in the ankle extensor tendons and muscles, with only 14 % of the work done on the muscles being recovered (Biewener *et al.* 1981). Biewener and Blickhan (1988) have proposed that these animals have disproportionately large muscles and tendons for their body mass, limiting energy savings by elastic storage and recovery. They propose that well-developed hindlimb muscles, tendons and bones are needed in kangaroo rats to match the large stresses involved in the high vertical jumps used to avoid predators (Biewener and Blickhan, 1988). Stresses developed in the plantaris and MG muscles were found to increase from 33–110 kN m⁻² during hopping at a steady speed (0.6–2.1 ms⁻¹) to 350 kN m⁻² for 50 cm jumps (Fig. 1). These large jumps characteristically followed landing from a previous jump, providing the means for stretching the active ankle extensor muscles to give up to 1.75 times the maximum isometric force measured *in situ* (Fig. 1). During maximum jumps the force exerted on the ground was three times that exerted at the fastest steady hopping speed. The maximum stresses produced in the ankle extensor muscles are matched to the strengths of tendons and bones, providing a consistent safety factor to failure of 1.5–2.0 for the hindlimb as a whole (Fig. 1). It would seem that the muscles and skeletal structures of different animals have similar safety factors for the avoidance of injury. Thus, there may be a compromise in evolution between the design features needed for rapid acceleration/deceleration and maximum elastic energy storage and recovery.

Relatively few studies have recorded changes in the activity, length and force of muscles during normal locomotion. One elegant study, which illustrates a number of general principles, was recently carried out on freely hopping wallabies (Griffiths, 1989). Telemetry was used to record electromyograms (EMG) from the medial head of the gastrocnemius (MG) muscle, and force was measured simultaneously with a surgically implanted force transducer mounted on the tendon. In order to calculate joint angles and muscle length, five dots were placed on the shaved right leg of the wallaby and filmed with a high-speed ciné camera synchronized to the EMG and force records. For constant-speed hopping the EMG was found to start about 30–40 ms prior to foot contact, which begins with the toenail of the large fourth digit digging into the ground to prevent slippage. A

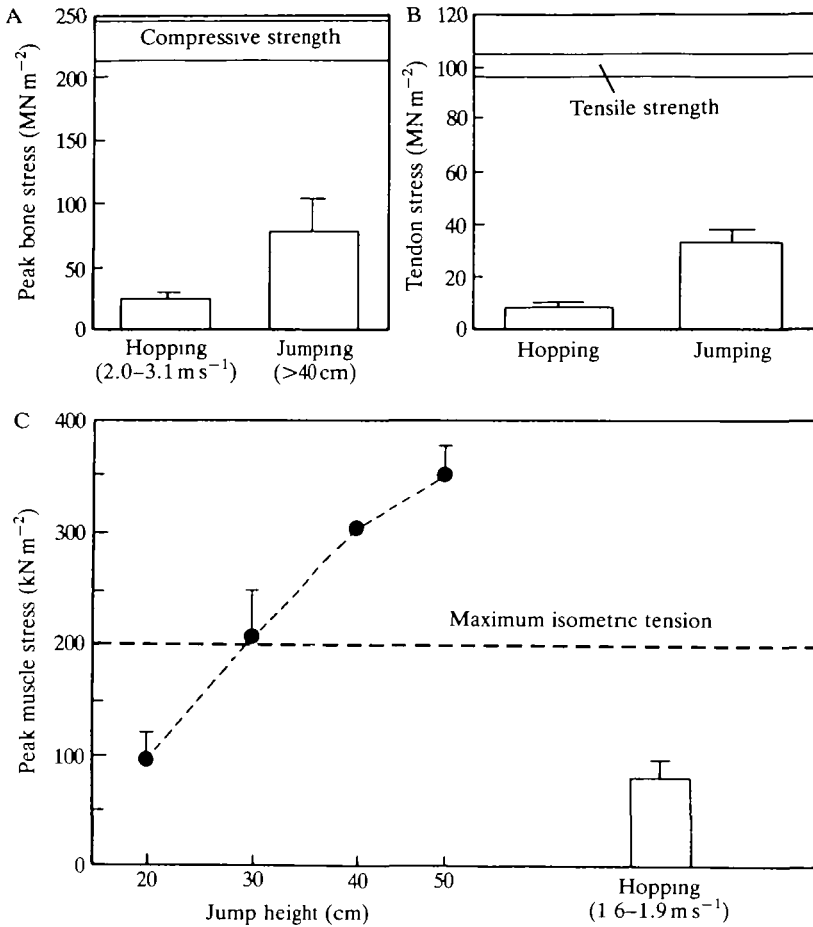


Fig. 1. Peak stresses in the bone (A), tendon (B) and plantaris muscle (C) of the kangaroo rat (*Dipodomys spectabilis*) during hopping and jumping. (Adapted from Biewener and Blickhan, 1988.)

few milliseconds later the ankle extensor muscles are rapidly stretched prior to shortening, as the pad under the phalanges makes contact (Fig. 2). The momentum of the wallaby results in the tendon being stretched, which further stretches the muscle fibres. This produces a rapid rise in force, peaking at the end of the stretch (Griffiths, 1989). The external stretch of the muscle reduces the series elastic compliance, providing a much more rapid increase in force (Hill, 1951). Initial rates of stretch at high hopping speeds are around $5\text{--}6$ muscle lengths s^{-1} , producing a rate of force development which is 10 times that during an isometric contraction (Griffiths, 1989). The muscle was found to resist the stretch with a constant impedance that was independent of hopping speed. Increases in hopping speed caused the MG muscle to be stretched by larger amounts, producing higher forces, which suggests negligible muscle viscosity (Fig. 2). Both positive and negative work by the muscle increased for speeds up to 18 km h^{-1} . At high

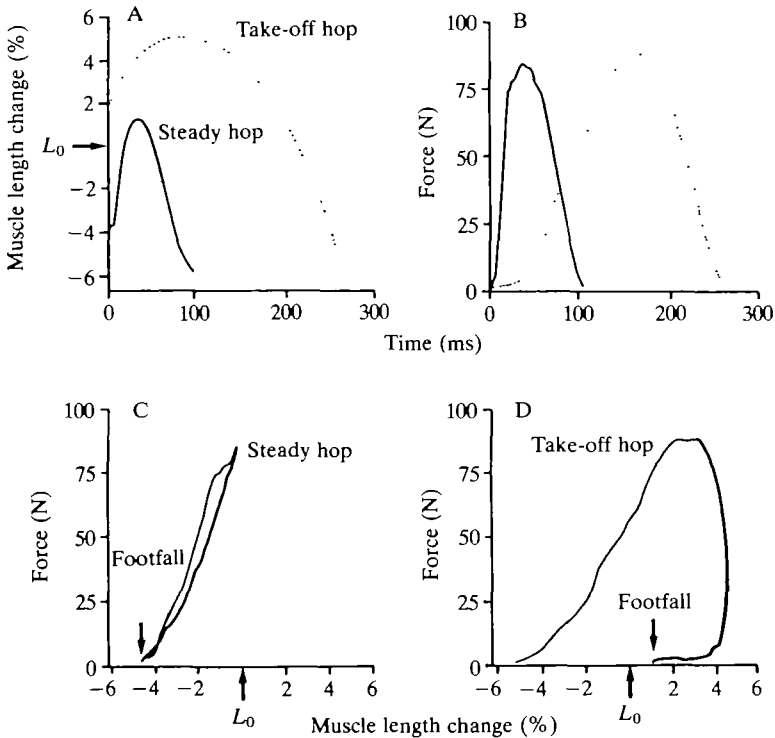


Fig. 2. Muscle action during unrestrained locomotion in the wallaby (*Thylogale billiardierii*). Changes in length (A) and force (B) in the gastrocnemius (MG) muscle during a single stride for constant-speed hopping at 11 km h^{-1} and for a bipedal take-off hop. (C,D) The corresponding force-position or work loops. The body mass of the wallaby was 7 kg and resting MG length (L_0) was 197–198 mm. (Adapted from Griffiths, 1989.)

speeds, stride length stabilised and hop frequency increased so that muscle force and work per hop remained constant.

The leg muscles in the wallaby function differently during steady hopping and take-off hops from rest. During bipedal take-off hops, the MG muscle was stretched by a more modest amount before generating force in a near-isometric contraction (Fig. 2). This resulted in a slower development of force than during constant-speed hopping (Fig. 2). As a result, the work done by the muscle was around two times higher for bipedal take-offs than for constant-speed hopping of similar speed (Fig. 2). Take-off hops are energetically more expensive because the MG muscle has to stretch the long compliant tendon actively.

Scaling studies

It might be expected that muscle stresses would be proportional to (body mass) $^{0.33}$, since for geometrically similar animals the force required to support the body is proportional to body mass, whereas the cross-sectional area of muscles is proportional to body mass $^{0.67}$. However, mean stresses exerted by the leg muscles

are about the same in mammals of all sizes (Biewener, 1989). This can be explained by differences in the mechanical advantage of leg muscles in different species achieved mainly by changes in limb posture, with larger animals running on more upright limbs (Biewener, 1989).

The muscles of small mammals consume significantly more energy per gram during running than do the muscles of large ones (Taylor *et al.* 1970). Taylor (1985) has suggested that this is because small mammals must turn their muscles on and off at a higher rate to generate the forces needed to move at an 'equivalent' speed. Normalizing for differences in force production, by multiplying the cost per stride by stride period, produces values for the mass-specific cost of locomotion per stride that are similar over four orders of magnitude of body mass (Heglund and Taylor, 1988; Kram and Taylor, 1990). Surprisingly, body mass also accounts for around 85 % of the variation in the mass-specific costs of terrestrial locomotion in animals with different leg architectures, numbers of legs, skeletal type and body temperature (Full *et al.* 1990). To a first approximation, 0.9 J kg^{-1} is required to move the centre of mass 1 km (Full and Tu, 1990). The fact that six- and eight-legged invertebrates produce similar force patterns to those of mammals suggests a comparable whole-body stiffness. Thus, animals may function as tuned mechanical spring systems with similar characteristics due to the basic material properties of muscles, connective tissue and skeletal structures (Full and Tu, 1990).

Swimming

Most fish swim by the sequential activation of myotomes on alternate sides of the body. This produces a wave of lateral bending from the head to the tail, developing a reactive thrust from the water. In order to bend a complete transection of the body, several myotomes need to shorten. Individual myotomes are bounded by sheets of connective tissue (myosepta) into which the muscle fibres are inserted *via* short tendons. Most superficial muscle fibres run parallel to the longitudinal axis of the body, whereas deeper fibres make angles of up to 40° (Alexander, 1969). The shape of the myotomes is complex and changes along the length of the body, with the muscle fibres making more acute angles with the myosepta towards the tail (Videler, 1985). The 'helical trajectories' of the deeper muscle fibres in bony fishes may allow fibres at different distances from the medial plane to contract by a similar amount as the body bends (Fig. 3). In addition, the arrangement of myotomes and muscle fibres is thought to provide a significant mechanical advantage during flexion of the body, helping to generate large forces with a small percentage shortening of muscle blocks. During continuous swimming, the EMG travels faster than the mechanical wave of bending (Williams *et al.* 1989; Van Leeuwen *et al.* 1990). This results in systematic phase differences in force and length cycles along the body, implying that muscle fibres are active at different strain rates (Hess and Videler, 1984). Synchronized electromyography and high-speed cinematography have been used to measure recruitment patterns and body movements in the common carp (*Cyprinus carpio* L.), allowing the strain fluctuations of the superficial slow muscle fibres to be calculated (Rome *et al.* 1988).

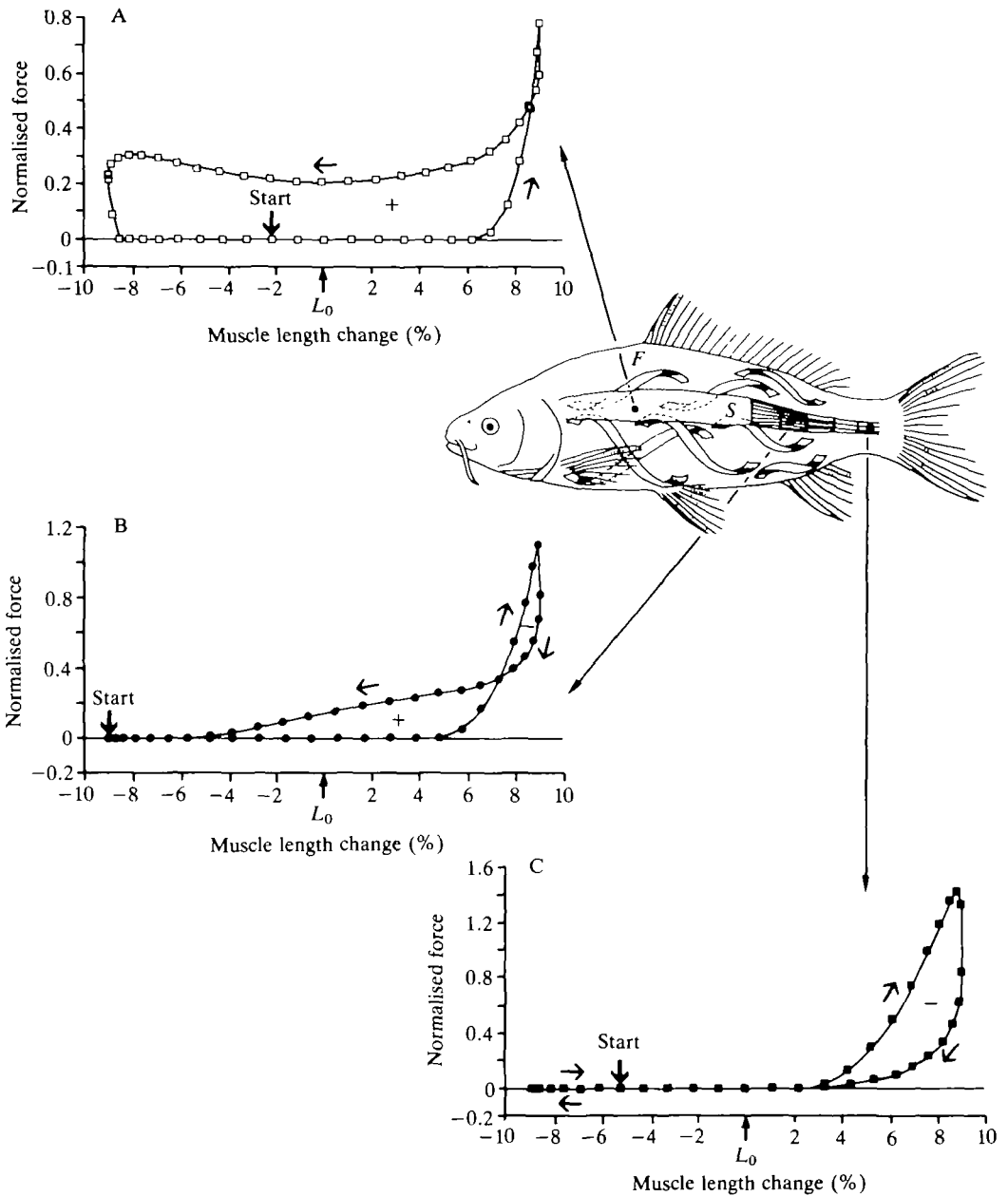


Fig. 3. Normalised force-position loops calculated for slow muscle fibres from the common carp (*Cyprinus carpio*) during steady swimming. Three loops are shown (A–C) from myotomes at different points along the length of the fish. (Adapted from Van Leeuwen *et al.*, 1990.) The arrangement of the superficial slow muscle fibres (S) and deeper fast muscles (F) in the fish is illustrated. (Adapted from Rome *et al.* 1988.) +, positive work; –, negative work; L_0 , resting fibre length.

Van Leeuwen *et al.* 1990). For continuous swimming, the amplitude of strain fluctuations is similar along the trunk, except for the most anterior myotomes. Therefore, it would appear that there is a strict relationship between the minimum radius of curvature of the body and the initial position, and angle, of the muscle fibres with respect to the longitudinal axis of the fish. Van Leeuwen *et al.* (1990) recorded EMGs from eight points along the body. They were able to model normalised muscle power output from these measurements from a knowledge of the lengths of the actin and myosin filaments and by making certain assumptions about the properties of the muscle fibres. Their analysis showed that, except for a short initial period, the muscle fibres in anterior myotomes are active during shortening, producing net positive work over the entire tailbeat cycle (Fig. 3A). Towards the anus muscle, fibres are active during both shortening and lengthening, such that the amounts of positive and negative work almost cancel each other out (Fig. 3B). In contrast, muscle fibres near the tail develop force mainly while being stretched, resulting in the production of net negative work (Fig. 3C.). Thus, most of the positive work is done by muscle fibres in the anterior myotomes, resulting in the stretching of muscle and collagen fibres in the region of the tail blade.

During startle responses (C-starts) muscle fibres in the carp shorten by a larger amount than during continuous swimming. Rome *et al.* (1988) calculated that, because of their special geometry, the fast fibres would only need to contract at one-quarter of the speed of the superficial slow fibres. Allowing for this, the maximum strain rate of the fast fibres would occur at around $0.3V_{\max}$. This corresponds to the shortening speed required for maximum power output. In contrast, during fast starts the slow fibres shorten at around four times their V_{\max} , producing no positive work.

Insect flight

There are two types of insect flight muscle, synchronous and asynchronous. In synchronous flight muscles there is direct nervous stimulation of each contraction, limiting wingbeat frequencies to a maximum of 100 Hz. Much higher wingbeat frequencies are achieved by insects with asynchronous flight muscles, in which nervous stimulation and contraction cycles of the muscles are uncoupled. The sarcoplasmic reticulum in asynchronous muscles is greatly reduced and relatively ineffective in releasing and sequestering Ca^{2+} . Instead, contraction is under mechanical control and is maintained by an oscillatory mechanism. Strain fluctuations of the muscles distort the thorax, inducing movement of the wings by means of a specialized articulation between the wings and thorax. The stiffness in asynchronous flight muscles is higher than in synchronous insect flight muscles, which exceeds that for vertebrate skeletal muscle (Pringle, 1977). It is likely that both types of insect flight muscle can store a very high proportion of the inertial energy of the oscillating wings as elastic energy, even with the small strain amplitudes needed for flight ($< 5\%$) (Ellington, 1984). Machin and Pringle (1959) discovered that for oscillatory operation the asynchronous flight muscle of the

Conut beetle (*Oryctes rhinoceros*) needed to be under static tension and to be dynamically stretched by an inertial load before it would contract. A special feature of asynchronous insect muscle is that it shows a marked strain activation (a small stretch increases force after a short delay), which may result from a mismatching of the actin and myosin filament arrays with changing sarcomere length (Squire *et al.* 1990). Estimates of the mechanical power requirements for free hovering flight have been obtained both from measurements of metabolic rate and from aerodynamic theory (Ellington, 1984; Casey and Ellington, 1989). Ellington and co-workers have carried out a comprehensive study on the kinematics, aerodynamics and metabolism of flight in euglossine bees, which vary in body mass by more than an order of magnitude. They found that, for hovering flight, mass-specific power input and wing-stroke frequency were inversely related to body mass (Casey and Ellington, 1989). However, the mass-specific energy expenditure per wing stroke was not correlated with body mass. They calculated that the mass-specific muscle power output required for the bees to fly was 100 W kg^{-1} , assuming perfect elastic storage, and 200 W kg^{-1} , assuming zero elastic storage (Casey and Ellington, 1989). The aerobic performance of insects during hovering flight exceeds that of the mass-specific V_{O_2} of vertebrates (Bartholomew, 1981). Both the fraction of the fibres occupied by mitochondria and the oxygen consumption rate per unit volume of mitochondria are higher for insect flight muscle than for vertebrate striated muscle (Casey and Ellington, 1989). For 1 g bees, mitochondria constitute around 43 % and myofibrils constitute 54 % of the muscle fibre volume. Thus, the mechanical power output of the myofibrils estimated for small bees is extremely high, in the range $206\text{--}440 \text{ W kg}^{-1}$, depending on the assumptions made about the storage of elastic strain energy (Casey and Ellington, 1989).

Studies with isolated muscles

Measurements of oscillatory work

The vast majority of studies on the mechanical properties of isolated muscles have been designed to answer questions concerning the mechanisms of muscle contraction. These studies have mostly involved contractions at constant length (isometric) or shortening under constant load (isotonic). This contrasts with the cyclical contractions that muscles perform during locomotion at constant speed. *In vivo* muscle stress and strain rates vary in a complex manner throughout the strain cycle (Figs 2, 3). The work done by the muscle is critically dependent on the timing of stimulation relative to the start of the length-change cycle and can be dramatically altered by the nature of previous strain cycles. Muscles that develop force during shortening and relax completely during subsequent extension produce net positive work during each contraction cycle. In contrast, if force is developed whilst the muscle is being stretched, then the net work output per cycle is negative, and work is done on the muscle by other components of the locomotory system.

In some cases, including insect flight muscle and fish myotomal muscle, the length trajectories of fibres are approximately sinusoidal for steady movements. Machin and Pringle (1960) used sinusoidal length changes to measure the power output of isolated asynchronous beetle flight muscle fibres performing oscillatory work. Josephson (1985) developed this technique to measure the power output of a synchronous insect flight muscle in a way that mimicked normal operating conditions. Muscle fibres were subjected to imposed sinusoidal length changes, at a frequency and amplitude appropriate to flight, and given single or multiple stimuli at selected phases in the strain cycle. Work output per cycle was calculated from the area of the loop formed by plotting force against length over a full cycle. The area of the loop represents the difference between the work required to stretch the muscle and the work done by the muscle during subsequent shortening. An example of this method of measuring work output is shown in Fig. 4. Anti-clockwise components of the force-position loops indicate positive work, clockwise components negative work (Josephson, 1985). The power output of the muscle is net work per cycle multiplied by frequency.

Parameters that influence the net work done by the muscle include the amplitude and frequency of muscle length changes, and the number, pattern and timing of stimuli relative to the length-change cycle. Josephson (1985) found that for tettigoniid (*Neoconocephalus triops*) flight muscle maximum positive work was done when the stimulus was timed to produce maximum force near the middle of the shortening portion of the cycle. In contrast, maximum net negative work was produced when peak force occurred near the middle of the lengthening portion of the cycle. At intermediate stimulus phases the work loops became complex, with both positive and negative components (Josephson, 1985). For fish, measurements of changes in body curvature enable strain fluctuations to be calculated during swimming and synchronised with the EMG wave (Van Leeuwen *et al.* 1990). For anterior myotomes, modelling studies predict that force is maximal as the fibres shorten through their resting lengths, producing net positive work throughout most of the tailbeat cycle (Hess and Videler, 1984) (see also Fig. 3). Altringham and Johnston (1990a) systematically varied the parameters affecting the work output of muscle fibres in the teleost *Myoxocephalus scorpius* in order to mimic the likely operating conditions of the anterior myotomes. They found that the net work per cycle was maximal over a narrow range of phase shifts. Maximum power output was produced when the stimulus was retarded relative to the start of the length-change cycle by around 30° (full cycle=360°) (Fig. 5B). Under these conditions, the negative work done in stretching the active muscle was less than the extra positive work obtained by virtue of the higher force during shortening. The peak force at the optimal stimulus phase-shift exceeded that during an isometric contraction by 15–30% (Altringham and Johnston, 1990b). It is also possible to reproduce the shape of force-position loops predicted for more posterior myotomes by further delaying the stimulus with respect to the start of the length-change cycle (Johnson and Johnston, 1991). Maximum negative work (clockwise loops) occurs with a stimulus phase-shift of 210°, and exceeds

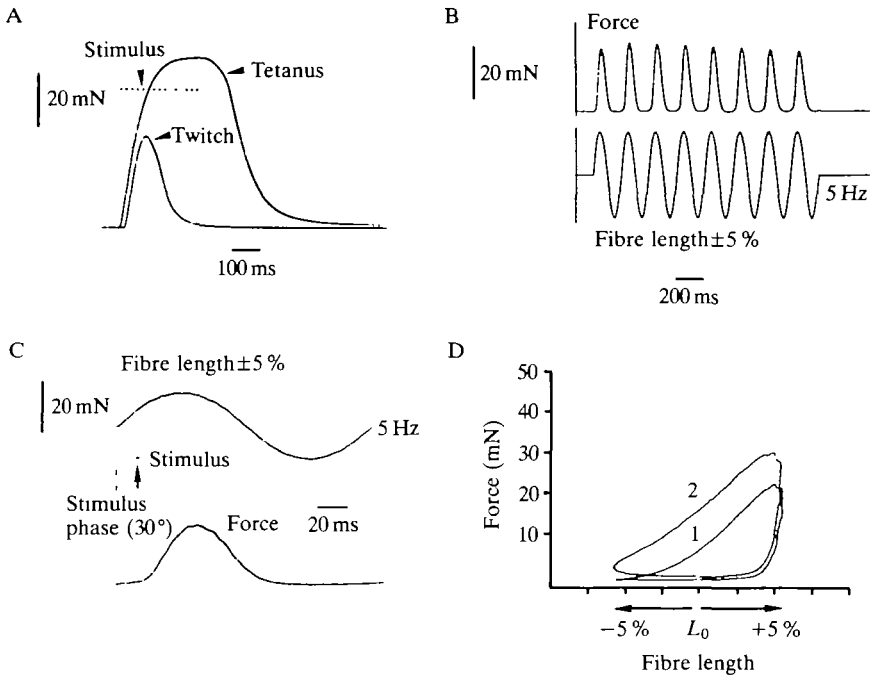


Fig. 4. Record illustrating the 'work loop' technique for measuring the power output of isolated muscle fibres undergoing cyclical contractions. These recordings are from unpublished experiments with fast myotomal muscle fibres from the cold-water marine teleost *Myoxocephalus scorpius*. All recordings were made at 4°C . (A) Isometric twitch and tetanus. Note that the twitch has been delayed relative to the start of the tetanus. (B, C) The measurement of oscillatory work with sinusoidal strain fluctuations and a single stimulus per cycle. Values of strain, cycle frequency and stimulus phase (full cycle= 360°) were chosen to maximise net positive work. (D) Loop 1, the force-position loop for the second cycle shown in B; loop 2, the increase in work obtained with a second stimulus and an inter-stimulus period of 20 ms. The peak stress is around 34% of that during an isometric tetanus under conditions for maximum positive work ($\pm 5\%$ strain, 5 Hz cycle frequency, 30° stimulus phase and 2 stimuli cycle $^{-1}$ at 50 Hz). L_0 , resting fibre length.

maximum positive work at 30° phase-shift by 20–30% (Johnson and Johnston, 1991).

The work output of muscle fibres is also strongly dependent on the amplitude of the sinusoidal length changes (strain). Josephson (1985) found that the area of negative work loops increased continuously with increasing strain. In contrast, at the optimum stimulus phase for net positive work, the work output increased with increasing strain values until it reached a maximum and then declined (see also Fig. 5A). Similar results have been obtained for muscles from other insects (Mizisin and Josephson, 1987; Stevenson and Josephson, 1990), a crab (Stokes and Josephson, 1988), a frog (Stevens, 1988) and several fish species (Altringham and Johnston, 1990a,b). Stevens (1988) showed that the optimal strain amplitude for

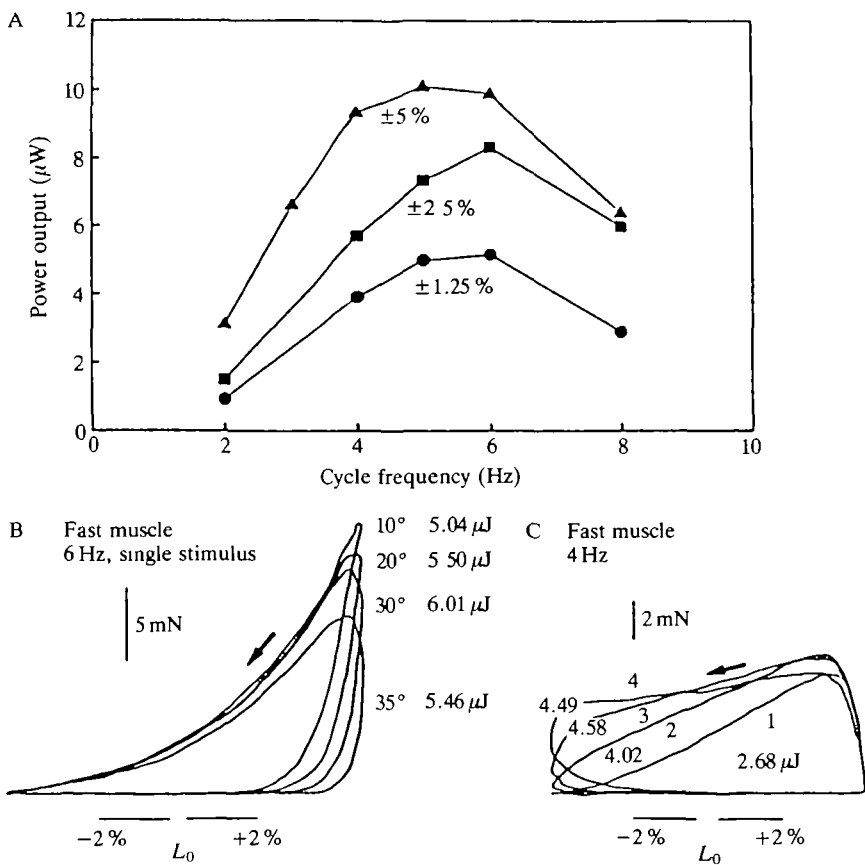


Fig. 5. The measurement of oscillatory work in bundles of fast muscle fibres from the teleost *Myoxocephalus scorpius*. (A) Effects of varying strain at a range of cycle frequencies; 1 stimulus cycle⁻¹ and a stimulus phase of 30°. (B) Effects of varying stimulus phase at 6 Hz cycle frequency and optimal strain. (C) Superimposed work loops at 4 Hz with 1–4 stimuli cycle⁻¹ (marked on the loops), an inter-stimulus interval of 20 ms and a stimulus phase of 30°. Net work was maximal with three stimuli. The optimum number of stimuli depends on stimulus phase, inter-stimulus interval and the cycle frequency. From Altringham and Johnston (1990a).

frog sartorius muscle *in vitro* ($\pm 6\%$ resting muscle length) corresponded to the actual range of sarcomere excursions found *in vivo*, measured from the changing angle of each joint as the leg extends in jumping (Calow and Alexander, 1973). The effects of strain on work output are a complex function of passive compliance, the length–tension curve, the force–velocity relationship, shortening deactivation and length-dependent changes in twitch duration (Josephson and Stokes, 1989).

For muscles stimulated with a single shock there is an optimal stimulus phase and optimal strain required to maximize positive net work at any particular cycle, frequency or temperature (Altringham and Johnston, 1990a,b; Stevenson and Josephson, 1990). The effect of multiple stimuli per cycle on work output varies

With cycle frequency. Measured at the normal wing-stroke frequency (25 Hz) and operating temperature (30°C) for flight, the tettigoniid muscle produces its maximum power output (76 W kg⁻¹) with three stimuli per cycle at 4 ms intervals (Josephson, 1985). In order to maximise net work per cycle, the force–time integral during the shortening phase of each cycle (minus any negative work performed during stretch) must be maximised. For fast myotomal muscle fibres from the teleost *Myoxocephalus scorpius* at 3°C, and under optimal conditions of strain and stimulus phase, only a single stimulus is required at high cycle frequencies, but as frequency decreases more stimuli are needed owing to the longer duration of the shortening phase (Fig. 5C). If too many stimuli are given at a given cycle frequency then force levels remain high during the stretch part of the cycle, resulting in an increase in the negative work component. Negative work is performed by the servo system *in vitro*, and by the antagonistic muscles in a swimming fish. Grillner and Kashin (1976) have shown that the duration of EMGs remains a constant proportion of the tailbeat cycle, except at very high speeds. Thus, the number of stimuli delivered to a fibre in each cycle is likely to decrease with increasing tailbeat frequency, maximising the net work output.

Strain, stimulus phase, inter-stimulus interval and the number of stimuli per cycle can be optimised at each cycle frequency, and muscle power output determined over the range of frequencies found during locomotion. For all muscles investigated, work output increases with cycle frequency to some maximum value, and then decreases (Josephson, 1985; Stevenson and Josephson, 1990; Altringham and Johnston, 1990a). Maximum power output is produced at a higher cycle frequency than that required to produce the maximum net work per cycle (Stevenson and Josephson, 1990). Estimates of the maximum power output of synchronous insect flight muscles measured at the temperatures and wingbeat frequencies appropriate for flight range from 50 to 90 W kg⁻¹ (Stevenson and Josephson, 1990) and are within the range predicted by current aerodynamic theory (Ellington, 1984). Frog sartorius muscle has a maximum power output of 20 W kg⁻¹ at the hopping frequency used during escapes at 20°C (Stevens, 1988). These values of power output take into account the work required to restretch the muscle after shortening and the fact that the muscle is only active for a fraction of each cycle. They are, therefore, considerably lower than those obtained from traditional force–velocity curves, which measure the instantaneous power output of fully activated muscles during linear shortening.

Muscle fibre types

Fish myotomes contain anatomically discrete layers of different muscle types (Fig. 3). Slow sustained speeds are entirely supported by a relatively small volume (5–7 % body mass) of aerobic slow twitch muscle (Bone, 1966; Johnston, 1981). As speed increases there is a sequential recruitment of faster-contracting fibre types which are dependent on anaerobic pathways for their energy supply (Johnston *et al.* 1977). Altringham and Johnston (1990a) used the work loop technique to measure the power output of fast and slow muscle fibres in

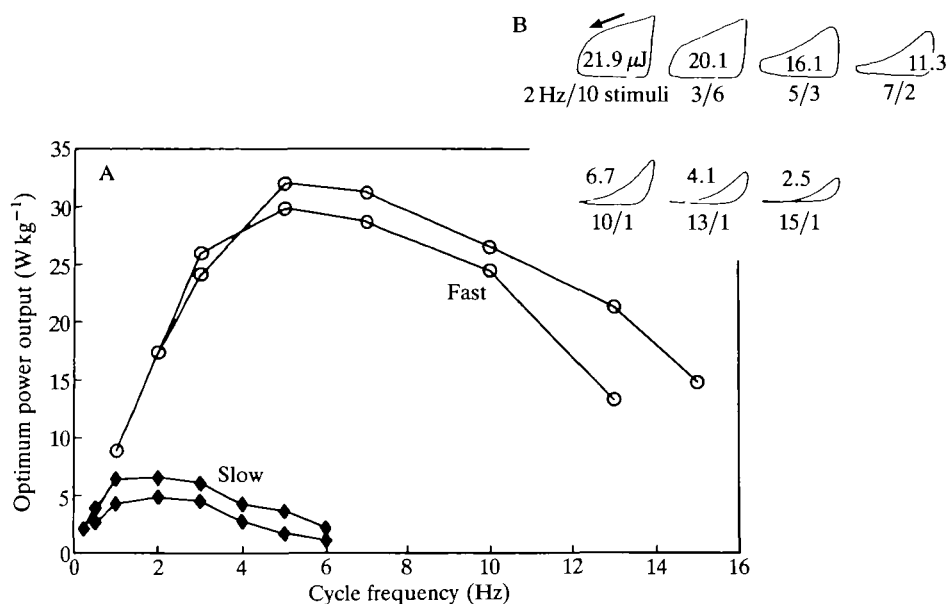


Fig. 6. (A) Maximum power output of fast (open symbols) and slow (closed symbols) myotomal muscle fibres from the teleost *Myoxocephalus scorpius*. (B) Optimum work loops for each point on the upper fast fibre curve in A. Cycle frequency, number of stimuli and net work are given for each. The optimum 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). Experiments were at 3°C. (From Altringham and Johnston, 1990a.)

M. scorpius, at 3°C, over the full range of frequencies used during swimming. The various parameters influencing work were adjusted to optimise positive work at a range of cycle frequencies, simulating the behaviour of the anterior myotomes. Slow fibres were found to develop their maximum power output of 5–8 W kg⁻¹ at 2 Hz, whereas fast fibres produced around five times more power at 5–8 Hz (25–35 W kg⁻¹) (Fig. 6). The power output of the slow fibres was negligible relative to that of fast fibres at high cycle/tailbeat frequencies. Indeed, above 8 Hz the twitch kinetics and maximum strain rate of the slow fibres were too slow to generate positive work. Maximum strain rates at the optimal cycle frequencies were around 0.3 muscle lengths s⁻¹ for slow fibres and 1.1–1.3 muscle lengths s⁻¹ for fast muscle fibres. Thus, in order to produce maximum net positive work, fast muscle fibres shorten at around 0.23–0.29 V_{\max} , the speeds predicted by the force–velocity relationship for maximum power and efficiency (Altringham and Johnston, 1988). Rome and co-workers have suggested, from a study of sarcomere excursions during swimming, that fast fibres in the common carp are recruited when V/V_{\max} for slow fibres exceeds 0.17–0.36 (Rome *et al.* 1988, 1990a). Thus, in order to produce maximum positive work, the deactivation rate and strain rate of muscle fibres must be matched to the frequency of locomotory movements (see

so Marsh, 1990). This provides an explanation of why different fibre types are necessary for locomotion over a wide range of speeds.

Temperature and muscle power requirements

Thoracic temperatures of the tobacco hawkmoth (*Manduca sexta*) during hovering flight are 36–42°C, and wingbeat frequencies range from 26 to 32 Hz (Heinrich, 1971). At lower ambient temperatures a warm-up period is needed prior to take-off, involving low-amplitude wingbeats to generate heat. Stevenson and Josephson (1990) used the work loop technique to measure the maximum power output of an indirect synchronous flight muscle in *Manduca* at different temperatures. They found that the cycle frequency that produced maximum power output increased from around 13 Hz at 20°C (20 W kg⁻¹) to 28 Hz at 40°C (90 W kg⁻¹). Thus, the *in vitro* experiments support the hypothesis that *Manduca* needs a muscle temperature of at least 30°C to produce the necessary wingbeat frequency and power levels for flight.

Temperature is also a major factor determining the swimming performance of fish. The maximum tailbeat frequency and speed increase with temperature, whereas maximum tailbeat amplitude does not. For submaximal speeds the same tailbeat frequency and amplitude are used at all temperatures (Rome *et al.* 1990a). This implies that strain is independent of temperature, whereas shortening speed and the frequency required for maximum power output should both increase with temperature. Johnson and Johnston (1991) investigated the effects of temperature on the properties of fast muscle fibres from the short-horned sculpin, a cold-water fish widely distributed around the coasts of northern Europe. They found that the strain for maximum power output ($\pm 5\%$) was similar at 4 and 15°C, whereas the cycle frequency required for maximum work increased from 5–7 Hz at 4°C to 9–13 Hz at 15°C. Under optimal conditions muscle fibres developed twice the maximum stress at 15°C in summer-acclimatized compared to values in winter-acclimatized fish. The maximum muscle power output at this temperature was 9 W kg⁻¹ in winter-caught fish and 30 W kg⁻¹ in summer-caught fish. At a typical winter temperature of 4°C, the power output of fast muscles from both groups of fish was 20–25 W kg⁻¹ (Johnson and Johnston, 1991). The mechanical properties of muscle fibres in some freshwater fish, such as common carp, also show phenotypic plasticity in response to seasonal temperature change. However, in this case the major adjustments in contractile properties occur with cold-acclimation. Following several weeks below 10°C, V_{\max} and isometric tension increase at low temperatures whereas twitch duration decreases (Johnston *et al.* 1990).

Scaling studies

The maximum force per unit cross-sectional area and maximal relative shortening are governed by the dimensions of a muscle's contractile filaments and are independent of body size. The amount of work done per contraction cycle is therefore a scale-independent variable, and power output is proportional to

contraction frequency. Maximum tailbeat frequencies range from 40–60 Hz in 1 cm fish to 5–8 Hz in 1 m fish (Wardle, 1975). Altringham and Johnston (1990b) investigated the effects of cycle frequency on work output in fast fibres from the Atlantic cod (*Gadus morhua*). They found that the cycle frequency for maximum power output (f_{opt}) decreased from 12.5 Hz in 13 cm fish to 5 Hz in 67 cm fish ($f_{\text{opt}} = 46.8 \cdot l^{-0.52}$). Thus, the strain rate of fibres required to produce maximum positive work decreases from 2.2 muscle lengths s^{-1} in 10 cm cod to around 0.7 muscle lengths s^{-1} in 100 cm cod. However, other experiments with fast muscle fibres from the dogfish suggest that both V_{max} and the curvature of the force–velocity relationship are essentially independent of body length (Curtin and Woledge, 1988). For mammals, comparisons of V_{max} over a 1200-fold range of body mass suggest that slow muscle fibres scale to $(\text{body mass})^{-0.18}$ and fast twitch fibres to $(\text{body mass})^{-0.07}$ (Rome *et al.* 1990b). These results would seem to imply that muscle fibres operate at different values of V/V_{max} in small and large animals, which is puzzling.

Muscle efficiency

There are several ways of defining muscle efficiency (Woledge, 1989). An overall measure of efficiency appropriate to locomotion would be the ratio of the work done by the muscle to the total free energy dissipated. Provided there are no hidden or delayed metabolic costs, the overall efficiency can be obtained from oxygen consumption measurements or from the observed output of work and heat. Heglund and Cavagna (1987) measured the work done by isolated frog and rat muscles during repeated stretch–shortening cycles and the subsequent oxygen consumption during recovery. For the highest shortening speeds studied, a prestretch was found to increase muscle efficiency significantly over that measured during shortening from an isometric contraction, particularly in the rat extensor digitorum longus (EDL) muscle. This is consistent with the *in vivo* observation that overall efficiency increases up to the highest running and hopping speeds attained. The highest values of efficiency for isolated muscles were obtained when stimulation began during stretching and continued during the first part of shortening. This yielded values of 35 % in frog sartorius, 50 % in rat EDL and 40 % in rat soleus muscle (Heglund and Cavagna, 1987). Measurements of muscle efficiency during running and hopping which take into account energy storage and recovery during the negative work phase of contraction cycles yield values that range from 6.5 % in small animals to 41 % in large ones (Heglund and Cavagna, 1985). This is because mass-specific metabolic power input increases with decreasing body size, whereas mass-specific mechanical power output is independent of body size. Muscle efficiency during hovering flight also increases with body mass. For the extreme assumptions of zero and perfect elastic energy storage, values of muscle efficiency calculated for bees (0.1–1 g) range from 8 to 34 %, and from 4 to 16 %, respectively (Casey and Ellington, 1989). Stevenson and Josephson (1990) obtained direct measurements of the mechanical power output of a synchronous flight muscle in the tobacco hawkmoth using the work loop

Technique. Comparison with published values of energy expenditure during hovering flight suggested a muscle efficiency of around 10 %.

Moon *et al.* (1991) used the work loop technique to measure phosphocreatine (PCr) splitting by cod fast myotomal muscle fibres under conditions producing maximum positive work. In these experiments, the fibres were poisoned with iodoacetate and nitrogen to block the resynthesis of ATP. Muscle economy (work/PCr breakdown) increased over the first 8–10 cycles, reaching a value of around $12 \text{ mJ } \mu\text{mol}^{-1} \text{ PCr}$ at 4°C . Using a value for Gibbs free energy change for PCr hydrolysis *in vivo* of 55 kJ mol^{-1} (Woledge, 1989), this yields efficiency values ranging from 12 to 21 % (Moon *et al.* 1991).

I am grateful to F. W. Flitney for useful comments on the manuscript and to the Science and Engineering Research Council of the UK for grant support. I also thank Drs R. I. Griffiths, A. A. Biewener and J. L. Van Leeuwen for permission to use their figures and for numerous helpful comments.

References

- ALEXANDER, R. McN. (1969). Orientation of muscle fibres in the myomeres of fishes. *J. mar. biol. Ass. U.K.* **49**, 263–290.
- ALEXANDER, R. McN. (1977). Terrestrial locomotion. In *Mechanics and Energetics of Animal Locomotion* (ed. R. McN. Alexander and G. Goldspink). pp. 168–203. Chapman and Hall, London.
- ALEXANDER, R. McN, MALOIJ, G. M. O., KER, R. F., JAYES, A. S. AND WARUI, C. N. (1982). The role of tendon elasticity in the locomotion of the camel (*Camelus dromedarius*). *J. Zool., Lond.* **198**, 293–313.
- ALTRINGHAM, J. D. AND JOHNSTON, I. A. (1988). The mechanical properties of polyneuronally innervated, myotomal muscle fibres isolated from a teleost fish (*Myoxocephalus scorpius*). *Pflügers Arch.* **412**, 524–529.
- ALTRINGHAM, J. D. AND JOHNSTON, I. A. (1990a). Modelling muscle power output in a swimming fish. *J. exp. Biol.* **148**, 395–402.
- ALTRINGHAM, J. D. AND JOHNSTON, I. A. (1990b). Scaling effects on muscle function: power output of isolated fish muscle fibres performing oscillatory work. *J. exp. Biol.* **151**, 453–467.
- BARTHOLOMEW, G. A. (1981). A matter of size: An examination of endothermy in insects and terrestrial vertebrates. In *Insect Thermoregulation* (ed. B. Heinrich), pp. 45–78. New York: Wiley.
- BIEWENER, A. A. (1989). Scaling support in mammals: limb posture and muscle mechanics. *Science* **245**, 45–48.
- BIEWENER, A. A., ALEXANDER, R. McN. AND HEGLUND, N. C. (1981). Elastic energy storage in the hopping of kangaroo rats (*Dipodomys spectabilis*). *J. Zool., Lond.* **195**, 369–383.
- BIEWENER, A. A. AND BLICKHAN, R. (1988). Kangaroo rat locomotion: design for elastic energy storage or acceleration? *J. exp. Biol.* **140**, 243–255.
- BONE, Q. (1966). On the function of the two types of myotomal muscle fibre in elasmobranch fish. *J. mar. biol. Ass. U.K.* **46**, 321–349.
- CALOW, L. J. AND ALEXANDER, R. McN. (1973). A mechanical analysis of a hind leg of a frog (*Rana temporaria*). *J. Zool. Lond.*, **171**, 293–321.
- CASEY, T. M. AND ELLINGTON, C. P. (1989). Energetics of insect flight. In *Energy Transformations in Cells and Organisms* (ed. W. Wieser and E. Gnaiger), pp. 200–210. Stuttgart, New York: Georg Thieme Verlag.
- CAVAGNA, G. A., HEGLUND, N. C. AND TAYLOR, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243–R261.

- CAVAGNA, G. A., SAIBENE, F. P. AND MARGARIA, R. (1964). Mechanical work in running. *J. appl. Physiol.* **19**, 249–256.
- CURTIN, N. A. AND WOLEDGE, R. C. (1988). Power output and force–velocity relationship of live fibres from white myotomal muscle of the dogfish, *Scyliorhinus canicula*. *J. exp. Biol.* **140**, 187–197.
- ELLINGTON, C. P. (1984). The aerodynamics of hovering insect flight. VI. Lift and power requirements. *Phil. Trans. R. Soc. ser. B* **305**, 145–181.
- FULL, R. J. (1989). Mechanics and energetics of terrestrial locomotion: Bipeds to polypeds. In *Energy Transformations in Cells and Organisms* (ed. W. Wieser and E. Gnaiger), pp. 175–182. Stuttgart, New York: Georg Thieme Verlag.
- FULL, R. J. AND TU, M. S. (1990). Mechanics of six-legged runners. *J. exp. Biol.* **148**, 129–146.
- FULL, R. J., ZUCCARELLO, D. A. AND TULLIS, A. (1990). Effect of variation in form on the cost of terrestrial locomotion. *J. exp. Biol.* **150**, 233–246.
- GRIFFITHS, R. I. (1989). The mechanics of the medial gastrocnemius muscle in the freely hopping wallaby (*Thylogale billardierii*). *J. exp. Biol.* **147**, 439–456.
- GRILLNER, S. AND KASHIN, S. (1976). On the generation and performance of swimming in fish. In *Neural Control of Locomotion* (ed. R. M. Herman, S. Grillner, P. S. G. Stein and D. G. Stuart), pp. 181–201. New York: Plenum Press.
- HEGLUND, N. C. AND CAVAGNA, G. A. (1985). Efficiency of vertebrate locomotory muscles. *J. exp. Biol.* **115**, 283–292.
- HEGLUND, N. C. AND CAVAGNA, G. A. (1987). Mechanical work, oxygen consumption, and efficiency in isolated frog and rat muscle. *Am. J. Physiol.* **253**, C22–C29.
- HEGLUND, N. C. AND TAYLOR, C. R. (1988). Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *J. exp. Biol.* **138**, 301–318.
- HEINRICH, B. (1971). Temperature regulation of the sphinx moth, *Manduca sexta*. I. Flight energetics and body temperature during free and tethered flight. *J. exp. Biol.* **43**, 141–152.
- HESS, F. AND VIDELER, J. J. (1984). Fast continuous swimming of saithe (*Pollachius virens*): a dynamic analysis of bending moments and muscle power. *J. exp. Biol.* **109**, 229–251.
- HILL, A. V. (1950). The dimensions of animals and their muscular dynamics. *Proc. R. Instn* **34**, 450–473.
- HILL, A. V. (1951). The effect of series compliance on the tension developed in a muscle twitch. *Proc. R. Soc. B* **138**, 325–329.
- HUXLEY, H. E. (1985). The crossbridge mechanism of muscular contraction and its implications. *J. exp. Biol.* **115**, 17–30.
- JOHNSON, T. P. AND JOHNSTON, I. A. (1991). Power output of fish muscle fibres performing oscillatory work: Effects of acute and seasonal temperature change. *J. exp. Biol.* **157**, 409–423.
- JOHNSTON, I. A. (1981). Structure and function of fish muscles. *Symp. zool. Soc. Lond.* **48**, 71–113.
- JOHNSTON, I. A., DAVISON, W. AND GOLDSPIK, G. (1977). Energy metabolism of carp swimming muscles. *J. comp. Physiol.* **114**, 203–216.
- JOHNSTON, I. A., FLEMING, J. D. AND CROCKFORD, T. (1990). Thermal acclimation and muscle contractile properties in cyprinid fish. *Am. J. Physiol.* **259**, R231–R236.
- JOSEPHSON, R. K. (1985). Mechanical power output from striated muscle during cyclical contraction. *J. exp. Biol.* **114**, 493–512.
- JOSEPHSON, R. K. AND STOKES, D. R. (1989). Strain, muscle length and work output in a crab muscle. *J. exp. Biol.* **145**, 45–61.
- KRAM, R. AND TAYLOR, C. R. (1990). Energetics of running: a new perspective. *Nature* **346**, 265–267.
- MACHIN, K. E. AND PRINGLE, J. W. S. (1959). The physiology of insect fibrillar muscle. II. Mechanical properties of a beetle flight muscle. *Proc. R. Soc. Lond. B* **151**, 204–225.
- MACHIN, K. E. AND PRINGLE, J. W. S. (1960). The physiology of insect fibrillar muscle. III. The effects of sinusoidal changes in length on a beetle flight muscle. *Proc. R. Soc. Lond. B* **152**, 311–330.
- MARSH, R. L. (1990). Deactivation rate and shortening velocity as determinants of contractile frequency. *Am. J. Physiol.* **259**, R223–R230.

- IZISIN, A. P. AND JOSEPHSON, R. K. (1987). Mechanical power output of locust flight muscle. *J. comp. Physiol. A* **160**, 413–419.
- MOON, T. W., ALTRINGHAM, J. D. AND JOHNSTON, I. A. (1991). Muscle energetics and power output of isolated fish fast muscle fibres performing oscillatory work. *J. exp. Biol.* (in press).
- PERRY, A. K., BLICKHAM, R., BIEWENER, A. A., HEGLUND, N. C. AND TAYLOR, C. R. (1988). Preferred speeds in terrestrial vertebrates: are they equivalent? *J. exp. Biol.* **137**, 207–219.
- PRINGLE, J. W. S. (1977). The mechanical characteristics of insect fibrillar muscle. In *Insect Flight Muscle*, (ed. R. T. Tregear), pp. 221–268. Amsterdam: North Holland.
- ROME, L. C., FUNKE, R. P. AND ALEXANDER, R. MCN. (1990a). The influence of temperature on muscle velocity and sustained swimming performance in carp. *J. exp. Biol.* **154**, 163–178.
- ROME, L. C., FUNKE, R. P., ALEXANDER, R. MCN., LUTZ, G., ALDRIDGE, H. D. J. N., SCOTT, F. AND FREADMAN, M. (1988). Why animals have different muscle fibre types. *Nature* **355**, 824–827.
- ROME, L. C., SOSNICKI, A. A. AND GOBLE, D. O. (1990b). Maximum velocity of shortening of three fibre types from horse soleus muscle: implications for scaling with body size. *J. Physiol., Lond.* **431**, 173–185.
- SQUIRE, J. M., LUTHER, K. P. AND MORRIS, E. P. (1990). Organisation and properties of the striated muscle sarcomere. In *Molecular Mechanisms in Muscular Contraction* (ed. J. M. Squire), pp. 1–29. London: Macmillan Press.
- STEVENS, E. D. (1988). Effect of pH and stimulus phase on work done by isolated frog sartorius muscle during cyclical contraction. *J. Muscle Res. Cell Motil.* **9**, 329–333.
- STEVENSON, R. D. AND JOSEPHSON, R. K. (1990). Effects of operating frequency and temperature on mechanical power output from moth flight muscle. *J. exp. Biol.* **149**, 61–78.
- STOKES, D. R. AND JOSEPHSON, R. K. (1988). The mechanical power output of a crab respiratory muscle. *J. exp. Biol.* **140**, 287–299.
- TAYLOR, C. R. (1985). Force development during sustained locomotion. *J. exp. Biol.* **115**, 253–262.
- TAYLOR, C. R., SCHMIDT-NIELSEN, K. AND RAAB, J. L. (1970). Scaling of energetic costs of running to body size in mammals. *Am. J. Physiol.* **219**, 1104–1107.
- VAN LEEUWEN, J. L., LANKHEET, M. J. M., AKSTER, H. A. AND OSSE, J. W. M. (1990). Function of red axial muscles of carp (*Cyprinus carpio*): recruitment and normalized power output during swimming in different modes. *J. Zool., Lond.* **220**, 123–145.
- VIDELER, J. J. (1985). Fish swimming movements: A study of one element of behaviour. *Neth. J. Zool.* **35**, 170–185.
- WARDLE, C. M. (1975). Limit of fish swimming speed. *Nature* **255**, 725–727.
- WILLIAMS, T. L., GRILLNER, S., SMOLJANINOV, V. V., WALLÉN, P., KASHIN, S. AND ROSSIGNOL, S. (1989). Locomotion in lamprey and trout: the relative timing of activation and movement. *J. exp. Biol.* **143**, 559–566.
- WOLEDGE, R. C. (1989). Energy transformations in living muscle. In *Energy Transformations in Cells and Organisms* (ed. W. Wieser and E. Gnaiger), pp. 36–45. Stuttgart, New York: Georg Thieme Verlag.

